The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry

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Abstract

We exposed the visual system to an ambiguous 3D slant rivalry stimulus consisting of a grid for which monocular (perspective) and binocular (disparity) cues independently specified a slant about a horizontal axis. When those cues specified similar slants, observers perceived a single slant. When the difference between the specified slants was large, observers alternatively perceived a perspective- or a disparity-dominated slant. Eye movement measurements revealed that there was no positive correlation between a perceptual flip and both saccades (microsaccades as well as larger saccades) and blinks that occurred prior to a perceptual flip. We also found that changes in horizontal vergence were not responsible for perceptual flips. Thus, eye movements were not essential to flip from one percept to the other. After the moment of a perceptual flip the occurrence probabilities of both saccades and blinks were reduced. The reduced probability of saccades mainly occurred for larger voluntary saccades, rather than for involuntary microsaccades. We suggest that the reduced probability of voluntary saccades reflects a reset of saccade planning.

1. Introduction

We are frequently able to influence visual perception. For instance, we are able to perceive the well known Necker cube as if viewed from above or as if viewed from below. There have been numerous studies that used stimuli of which the perception was bi-stable, like the Necker cube, to study conscious vision, including the influence of voluntary control, drugs, accommodation etc. (for reviews see for example: Blake, 2001; Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Logothetis, 1998; Rees, Kreiman, & Koch, 2002; Tong, 2003). Many of these studies assumed that the alternation between percepts is a cognitive process and that each percept is brought about by different neural states which process the same unchanging retinal image. However, during the visual inspection of a stimulus eye movements cause the retinal image to change continuously. In order to verify that perceptual bi-stability is indeed a cognitive process it is necessary to show that eye movements are not essential to flip from one percept to the other.

There is a longstanding and still ongoing debate whether eye movements (and therefore changes in the retinal image) play a key-role in determining the percept. Many studies on the role of eye movements during bi-stable perception investigated whether different fixation positions necessarily led to different percepts, either by instructing subjects to fixate at certain positions within the stimulus (e.g. Becher, 1910; Toppino, 2003; Wundt, 1898), or by measuring the fixation positions (e.g. Ellis & Stark, 1978; Gale & Findlay, 1983; Kawabata, Yamagami, & Noaki, 1978). As early as 1898, Wundt reported that he perceived the different representations of

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reversible perspective figures (e.g. the Necker cube and the Schröder staircase) by looking at different specific aspects of the stimuli. He concluded that the perceptual flips were caused by eye movements and not by any cognitive process. In contrast, Becher (1910) reported that he was able to perceive both representations of a reversible perspective figure when keeping fixation on a single aspect of the stimulus, meaning that eye movements are not needed to flip from one percept to the other. Recently, Toppino (2003) reported for the Necker cube that fixation position can bias the percept to one of the two representations (conform Wundt), but that fixation position within the stimulus does not by itself determine the percept (conform Becher), especially when trying to hold either of the two percepts. Several other studies reported that bi-stability occurred when the images on the retina were stabilized, either by compensating for occurring eye movements (Pritchard, 1958; Scotto, Oliva, & Tuccio, 1990) or by using afterimages (McDougall, 1903; Lack, 1971). This led to the conclusion that eye movements are not necessary for perceptual bi-stability. Another approach to study the role of eye movements for perceptual bi-stability is the one used by Ross and Ma-Wyatt (2004) who instructed subjects to make saccades at specified moments to study the effect on the perceptual flip rate. They found that the flip rate was larger when subjects made saccades than when subjects kept fixation, and thus, they concluded that eye movements and perceptual flips are correlated. Several studies have recorded the occurrences of eye movements as well as the occurrences of perceptual flips and tried to determine whether or not an eye movement occurred before or after each perceptual flip (Glen, 1940; Ito, Nikolaev, Luman, Aukes, & Nakatani, 2003; Peckham, 1936; Pheiffer, Eure, & Hamilton, 1956; Ruggieri & Fernandez, 1994; Sabrin & Kertesz, 1980). Ruggieri and Fernandez (1994) reported for several different ambiguous figures that eye movements caused perceptual flips, whereas Pheiffer et al. (1956) claimed that it was the perceptual flip that caused the eye movement. Peckham (1936) reported, however, that there was no temporal relationship between perceptual flips and eye movements. Sabrin and Kertesz (1980) investigated the role of microsaccades for the binocular rivalry paradigm and found that microsaccades occurred more often during rivalry than during normal viewing. Furthermore, these authors reported that microsaccadic activity decreased during percept intervals and suggested that microsaccades play a role in determining the moment of a perceptual flip.

Thus, the precise nature of the correlation between perceptual flips and eye movements is yet unclear. Very little is known on the role of microsaccades. Furthermore, most studies only investigated whether or not an eye movement occurred before or after a perceptual flip, but did not investigate *when* exactly the eye movement

occurred relative to the flip or whether there was any variability in the intervals between the different events.

In the current study we investigated the role of eye movements, including microsaccades, for perceptual bi-stability. We used the recently developed slant rivalry paradigm (van Ee, 2005; van Ee, van Dam, & Erkelens, 2002). An example of the stimulus is portrayed in Fig. 1. The slant rivalry stimulus consists of a planar grid for which perspective and disparity specify different slants. When the half-images of Fig. 1 are being fused, a perspective-dominated slant and a disparity-dominated slant can be perceived alternatively. A benefit of the slant rivalry stimulus over classical rivalry stimuli for studying the role of eye movements is that the perceptual flip rate is relatively slow. The rate of perceptual alternations for classical stimuli typically lies in the range of 0.3–1 alternations per second. The slant rivalry stimulus generally causes slower alternations, averaging in the order of 0.2 per second (van Ee, 2005; van Ee, van Dam, & Brouwer, 2005a).[1] Slow alternation rates help to resolve the temporal correlation between eye movements and perceptual flips. Furthermore, to gain insight in the correlation between eye movements and perceptual flips we instructed subjects to attempt to flip as fast as possible. For this (speed-up) instruction this correlation is likely to be enhanced. Note that for the already short percept durations of the classic bi-stability paradigms the instruction to flip as fast as possible could further hamper the determination of the correlation between eye movements and perceptual flips. It is of interest here to note that we have analyzed the stability over time of the speed-up alternation process for slant rivalry on the basis of a large number of perceptual alternations, finding that it is reasonably stable across both sequential small data chunks and experimental repetitions (van Ee et al., 2005a).

For the existing slant bi-stability studies the planar grid of the stimulus has been rotated about a vertical axis, meaning that both a horizontal disparity gradient and foreshortening occurred along the horizontal axis. Thus, we assumed a subject would most likely make horizontal eye movements while viewing the stimulus. Such a preference for horizontal eye movements might hamper the disentangling of eye movements that change the monocular 2D-fixation position from horizontal eye movements that change binocular 3D-fixation depth (horizontal vergence). Therefore, here we rotated the planar grid about a horizontal axis. We first examined, in experiment 1, the perceived slants as a function of perspective- and disparity-specified slants. In experiments 2, 3 and 4 we continued with examining the role of eye movements for perceptual flips caused by the

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[1] The relatively long percept durations have also been employed to study the neural correlates of stereoscopic depth perception in the visual cortex (Brouwer, Tong, Schwarzbach, & van Ee, 2004).
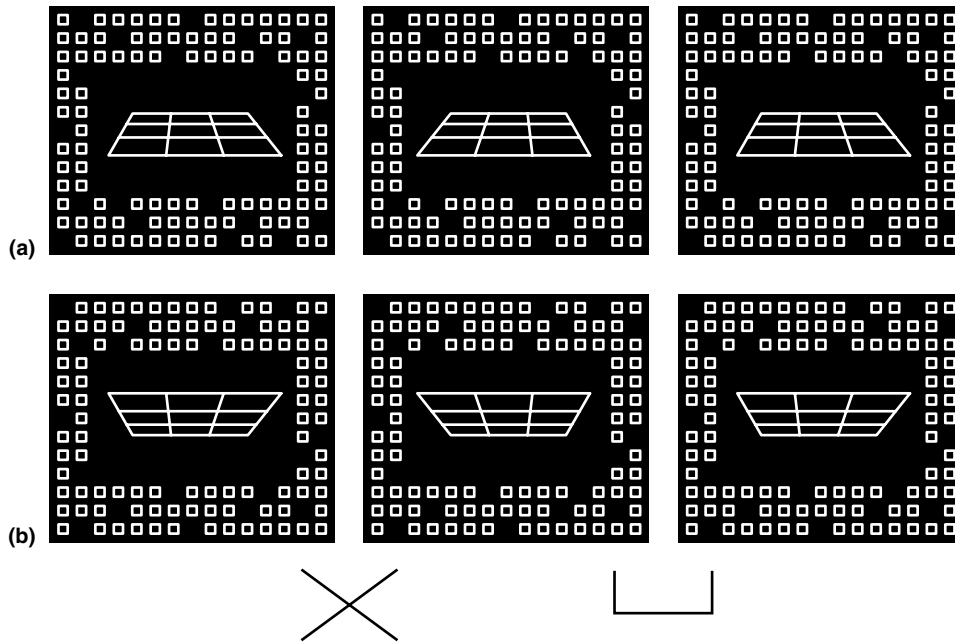
Fig. 1. Demonstration of bi-stable slant perception (slant rivalry) for slants about a horizontal axis. Crossfusers should fuse the left two images. Divergers should fuse the right two images: (a) perspective indicates a negative (floor) slant and disparity a positive (ceiling) slant and (b) perspective indicates a positive (ceiling) slant and disparity a negative (floor) slant.

slant rivalry stimulus. We specifically included the role of microsaccades in our analyses.

2. Experiment 1: Slant estimates

2.1. Methods

2.1.1. General apparatus

To obtain stimuli that carried both perspective and disparity information, we used red–green anaglyph stimuli that were displayed on a computer monitor (40×30 cm) in an otherwise dark room. The intensities of the red and green half-images were adjusted until they appeared equiluminant when viewed through the red and green filters. The red and green filters were custom-made (using transmission filters provided by Bernell, Belgium) so that their transmission spectra matched the emission spectra of the monitor as well as reasonably possible. Photometric measurements showed that minute amounts of the green and the red light leaked through the red (0.4%) and the green (0.2%) filter, respectively. The stimuli were generated using OpenGL libraries. The resolution of the monitor was 1600×1200 pixels and lines were anti-aliased. The images on the monitor were refreshed every 13 ms. A chin rest restricted the head movements of the subject. This chin rest was positioned at 50 cm from the monitor for both experiment 1 and 2 in which we measured slant estimates and gaze positions, respectively. The distance was 55 cm for the eye movement (saccades and blinks)

recording experiments (experiments 3 and 4). Gaze positions were measured using a SMI-Eyelink system with a sample frequency of 250 Hz.

2.1.2. Stimuli and procedure

To study the perceived slant about the horizontal axis when perspective and disparity provide conflicting information, we used stimuli that consisted of a planar grid (Fig. 1) subtending 4.0×5.7 deg (in unslanted conditions). The grid was surrounded by a reference background which consisted of small squares. The size of the reference background was 27.5×17.7 deg and the size of a square in the background was 0.5×0.5 deg. Only 80% of the squares in the reference background were shown to prevent subjects from experiencing the wallpaper effect. In the centre of the background there was a black window (8.5×8.5 deg) in which the planar grid was displayed.

We varied both the perspective-specified slants (-70 to 70 deg in six steps) and the disparity-specified slants (-70 to 70 deg in 10 steps). Positive slants were defined as bottom side away (ceiling). There were three trials for every condition. The subjects' task was to estimate the perceived slant(s) of the grid. They were instructed that both ambiguous (flip) and non-ambiguous (non-flip) stimuli would be presented. The subject pressed a mouse button to initiate a trial, after which the stimulus was shown for 12 s. After the presentation of the stimulus subjects indicated the slants that were perceived during the stimulus presentation using a visual slant estimation method (van Ee & Erkelens, 1996). A figure symbolizing
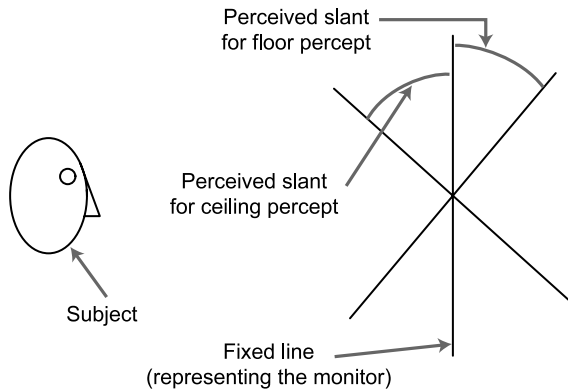
Fig. 2. The subjects were instructed to match the angles between a fixed vertical line (representing a side view of the monitor) and two rotatable lines to the slants they had perceived in the stimulus. When the subject failed to experience bi-stability, both lines were matched to the single slant that was perceived.

the subjects' head and three frontoparallel lines were shown (see Fig. 2). One of these lines was fixed and vertical, representing the side-view of the monitor. The two remaining frontoparallel lines could be rotated about their centre. Either of the two lines represented the side-view of the perceived grid, one for the perspective-dominated percept and one for the disparity-dominated percept. Subjects were instructed to match the angles between the rotatable lines and the fixed vertical line to the perceived slant(s) of the grid. When the subject failed to experience bi-stability (i.e. only one surface slant was perceived), then the two lines were set on top of each other to match the single slant the subject had perceived. Because the lines and the head-figure were displayed in the plane of the screen they also served as a zero-slant reference between successive trials. The subjects were free to move their eyes during the course of the experimental session.

Four observers participated in experiment 1, all of whom had excellent stereovision. Their stereoacuities were lower than 10″, and they were able to distinguish disparities of different signs and magnitudes within a range of −1 to 1 deg in a stereoanomaly test (van Ee & Richards, 2002).

2.2. Results

The slant estimates are presented in Fig. 3. Each individual graph depicts the perceived slant as a function of disparity-specified slant. The perspective-specified slant for each graph is depicted by the trapezoid-shaped icons. The black diamonds represent the results for the disparity-dominated percept and grey disks represent the results for the perspective-dominated percept. Error bars represent standard errors across four observers.

When the perspective-specified slant and the disparity-specified slant are very similar only one slant is perceived, implying that the two cues are reconciled to form one percept. When the perspective-specified slant and the disparity-specified slants are quite different the subjects experience bi-stability and are able to select either of the two perceived slants. The perceived slants for the disparity-dominated percept are only a little smaller than the disparity-specified slant. The results for the perspective-dominated percept are proportional to the perspective-specified slant, but there is clear attenuation for all conditions.

Whether the cues specify a ceiling or a floor does not appear to influence the perceived slant angle. This can be seen when, for instance, the top left panel is compared to the bottom right panel. The data in these and other panels are mirror symmetric (using the R^2-measure, we found that the mirrored results of the bottom three panels and the right half of the middle panel account for 98% of the variance of the data of the top three panels and the left half of the middle panel).

The perceived slants about the horizontal axis are similar to those found previously for slants about the vertical axis (van Ee, Adams, & Mamassian, 2003; van Ee et al., 2002; van Ee, Krumina, Pont, & van der Ven, 2005b). In other words the perceived slants can be understood in a Bayesian frame work that describes the quantitative aspects of perceived slant on the basis of the likelihoods of both perspective and disparity slant information combined with prior assumptions about the shape and orientation of objects in the scene (van Ee et al., 2003). As noted above, for slant about the horizontal axis vergence eye movements are perpendicular to the direction in which the disparity changes. Assuming that subjects will most likely make eye movements along the disparity gradient and in the direction in which foreshortening occurs, the usage of slant about the horizontal axis might help to disentangle eye movements that change the 2D-fixation position (horizontal and vertical version) from eye movements that change 3D-fixation depth (horizontal vergence). Slant about the horizontal axis does therefore provide useful circumstances to examine the role of eye movements in perceptual bi-stability. In the following experiments we use our stimulus to study the role of eye movements.

3. Experiment 2: Gaze positions

The results of experiment 1 show that conflicting information provided by two different cues (in our case perspective and disparity) can result in two different percepts. Subjects reported seeing the two percepts alternatively (i.e. they experienced bi-stability). The phenomenon of perceptual bi-stability is one instance in vision where a given unchanging retinal image produces a changing representation of that image in awareness. In order to examine whether the alternations in the
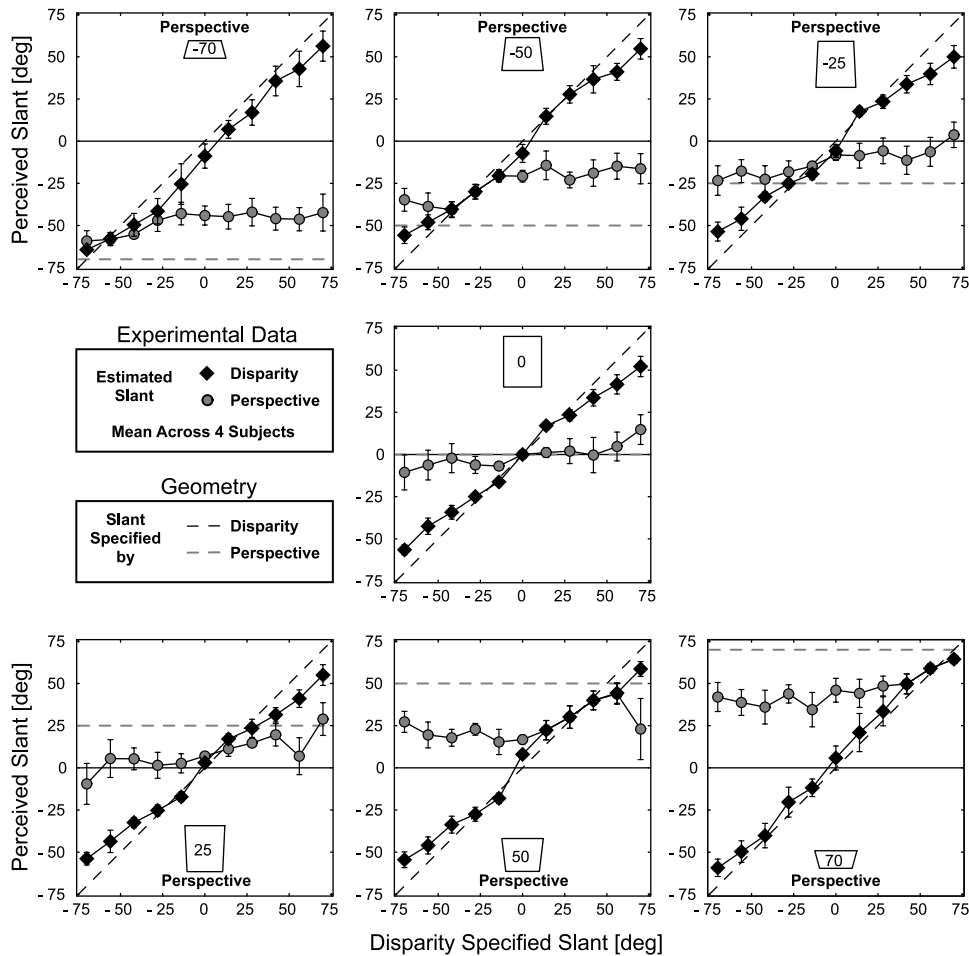
Fig. 3. Results of experiment 1 showing the mean perceived slants as a function of the disparity-specified slant across four observers. The trapezoidal icons in each panel represent the perspective-specified slant. Black diamonds and grey disks represent the results for the disparity-dominated percept and the perspective-dominated percept, respectively. The error bars represent the standard error across the four observers.

perception of the stimulus are indeed cognitively induced it is necessary to investigate whether eye movements are essential to flip from one percept to the other. We therefore conducted the following experiment in which subjects were instructed to either fixate a dot or to freely look around while viewing our ambiguous stimulus.

3.1. Stimuli and procedure

The size of the trapezoidal figure on the monitor was 5.7×3.5 deg and the specified slant angles were either plus or minus 80 deg for the perspective-specified slant and minus or plus 60 deg, respectively, for the disparity-specified slant. In this way we created a large cue conflict and thus obtained a stimulus whose bi-stable percepts could be alternated frequently. Prior to every trial the subject was instructed by a message on the monitor to either maintain fixation on a fixation dot or to freely make eye movements. Then the stimulus was

shown for 2 min. The subjects were instructed to press one of two buttons to indicate their current percept. A fixation dot (7′), which was displayed only in trials for which the instruction was to fixate, was positioned in the centre of the monitor (also the grid's centre).

Binocular gaze positions were measured using a SMI-eyelink system which sampled at 250 Hz. The eyelink system used infrared cameras to monitor the eyes and gaze positions were obtained by detecting the pupil in the images that the cameras provided. The raw gaze position data were median filtered (the window width was nine samples), converted to Fick-angles and finally transformed to version and vergence angles. Velocities (to detect blinks) were calculated from the version angles using a five-point sliding window:

$$\vec{v}_n = \frac{\vec{x}_{n+2} + \vec{x}_{n+1} - \vec{x}_{n-1} - \vec{x}_{n-2}}{6 \Delta t} \qquad (1)$$

where $\vec{v}_n$ represents the nth velocity sample, $\vec{x}_i$ represents the ith version angle sample and Δt represents the time interval between two samples.

Blinks were selected by searching for intervals in which the pupil was absent in the images or by selecting large back and forth vertical eye movements for which the pupil-area signal contained a clear decrease and increase. Begin marks of the blinks where set at the last sample before the absolute speed signal exceeded a threshold of 18 deg/s. End marks were set at the sample where the absolute speed signal first dropped below this threshold. Three subjects participated in this experiment, two of whom also participated in experiment 1.

3.2. Results

Fig. 4a shows examples of the horizontal and vertical version relative to the centre of the monitor, for one subject. The version angles in the period starting at 50–100 s from stimulus onset are shown. This period is representative for the whole trial. For both trials the perspective-specified slant was −80 deg (indicating a floor) and the disparity-specified slant was 60 deg (indicating a ceiling). The gaze position data for the reverse condition (perspective specifying 80 deg and disparity −60 deg) as well as for other subjects are similar. The data in the left two panels show the version angles for the fixation condition and the right two panels show the version angles for the free eye movements condition. The grey horizontal lines indicate the edges of the trapezoidal figure and the position of the fixation dot. The dark grey vertical regions indicate the periods that the subject perceived a ceiling (disparity-dominated percept) and the light grey regions indicate the periods that the subject perceived a floor (perspective-dominated percept). For the fixation condition, examples of the gaze positions at about the moment of a flip are shown in Fig. 4b and c. Fig. 4b and c show the horizontal (left) and vertical (middle) version and the horizontal vergence (right) of a time interval starting 2.0 s before until 0.5 s after the moment of the button press corresponding to a flip from a floor to a ceiling percept and to a flip from a ceiling to a floor percept, respectively. The grey horizontal line in each of these graphs represents the position of the fixation dot (i.e. at the depth of the monitor for the horizontal vergence graphs).

In the fixation condition perspective appears to be dominant in determining the perceived slant, indicated by the dominance of the wide light grey regions. Whereas in the free eye movement condition disparity appears to be dominant. This suggests that in order to keep a certain percept it helps to modify the number of eye movements. None the less, Fig. 4b and c (on top of Fig. 4a), show clearly that both types of flips can occur when the subject adheres to the fixation instruction.

Most of the variation of the version angles for the free eye movements condition is in the vertical direc-

tion. This is also the direction in which there is a disparity gradient and foreshortening due to perspective. To examine whether the subjects instigated perceptual flips by alternately fixating different details of the stimulus when they were allowed to make eye movements, we calculated the average gaze positions and average vergence angle as a function of the time relative to the moments of the button presses for the interval 2000 ms before the moment of the button press until 1000 ms after the moment of the button press. Blinks (including four samples prior to each blink and four samples after each blink) were removed from the data for this analysis. The average gaze positions and vergence angle were calculated separately for flips toward the two separate percepts. We did not discover abrupt changes in the average gaze positions and vergence angles in the 2000 ms interval prior to the moment of the button press (only for subject LW did we find changes in the investigated interval but always after the moment of the button press). To summarize the results for the average gaze positions and average vergence angle we calculated the average gaze positions at the moment of the flip for the two individual percepts. Because we did not know exactly when the actual perceptual flips occurred relative to the moments of the button presses, we estimated the gaze position for each individual flip by averaging the gaze samples during 1000 ms prior to the moment of the button press (during this interval there were no large changes in average gaze positions for all subjects). The average gaze positions were then obtained by averaging across the corresponding flips.

Fig. 5 shows the average gaze positions during 1000 ms prior to the moment of the button presses for the two different conflict conditions. The left panel shows the result when perspective specified a ceiling (80 deg) and disparity specified a floor (−60 deg). The right panel shows the result when perspective specified a floor (−80 deg) and disparity specified a ceiling (60 deg). In each panel the results for the individual subjects are shown in separate graphs. The left graphs in each panel show the average vertical version angle and standard deviation versus the average horizontal version and standard deviation. The right graphs in each panel show the average horizontal vergence and standard deviation. The grey lines depict the outlines of the trapezoidal figure and the rotation axis. The black dashed lines and ellipses represent the average gaze for flips to the perspective-dominated percept and the black continuous lines represent the average gaze for flips to the disparity-dominated percept. The top graphs in the right panel of Fig. 5 show the gaze positions for the same data as already used for the right two panels of Fig. 4a. Only subject LW shows a tendency to direct the gaze towards that part of the stimulus that he will perceive in front after the flip. However, for each conflict condition the
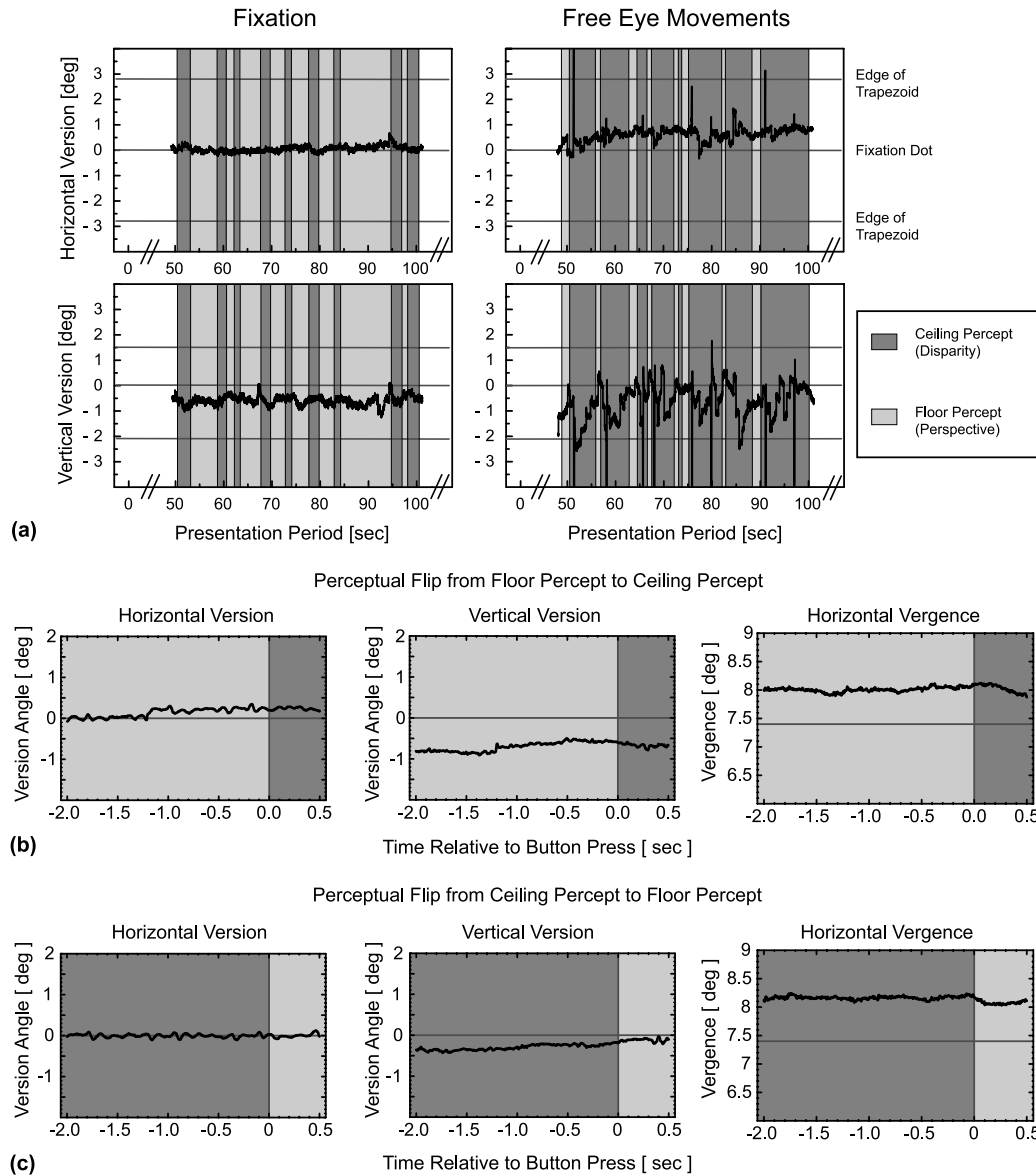
Fig. 4. Results of experiment 2. (a) Examples of horizontal (top) and vertical version (bottom) versus elapsed stimulus presentation time for two different conditions. The left two panels show the version angles when the subject was instructed to fixate. The right two panels show the version angles when the subject was allowed to make eye movements. The version angles are specified relative to the position of the fixation dot. In both cases the perspective-specified slant was −80 deg (floor) and the disparity-specified slant was 60 deg (ceiling). Light grey regions correspond to a floor percept and dark grey regions correspond to a ceiling percept, indicating that disparity is more dominant when making eye movements, and that perspective is more dominant during fixation. (b, c) The horizontal version (left), vertical version (middle) and horizontal vergence (right) during a period of 2.0 s before to 0.5 s after the moment of the button press corresponding to a perceptual flip from (b) a floor to a ceiling percept, and (c) a ceiling to a floor percept. These flips occurred in the fixation condition. The grey horizontal line in each graph represents the position of the fixation dot (i.e. at the depth of the monitor for the horizontal vergence graphs). These examples show that perceptual flips can occur without previously making an eye movement.

average gaze position for flips to the perspective-dominated percept and flips to the disparity-dominated percept were not significantly different ($P > 0.05$). Subject TK tends to look at that part of the trapezoid that has the smallest width. There is, however, no difference for flips to the disparity-dominated percept with respect to flips to the perspective-dominated percept. The aver-

age horizontal vergence for each subject is similar for both flips to the perspective-dominated percept and flips to the disparity-dominated percept.

In sum, these results indicate that the perceptual flips are not necessarily instigated by either directing the gaze to certain details in the stimulus or systematically changing the vergence angle.
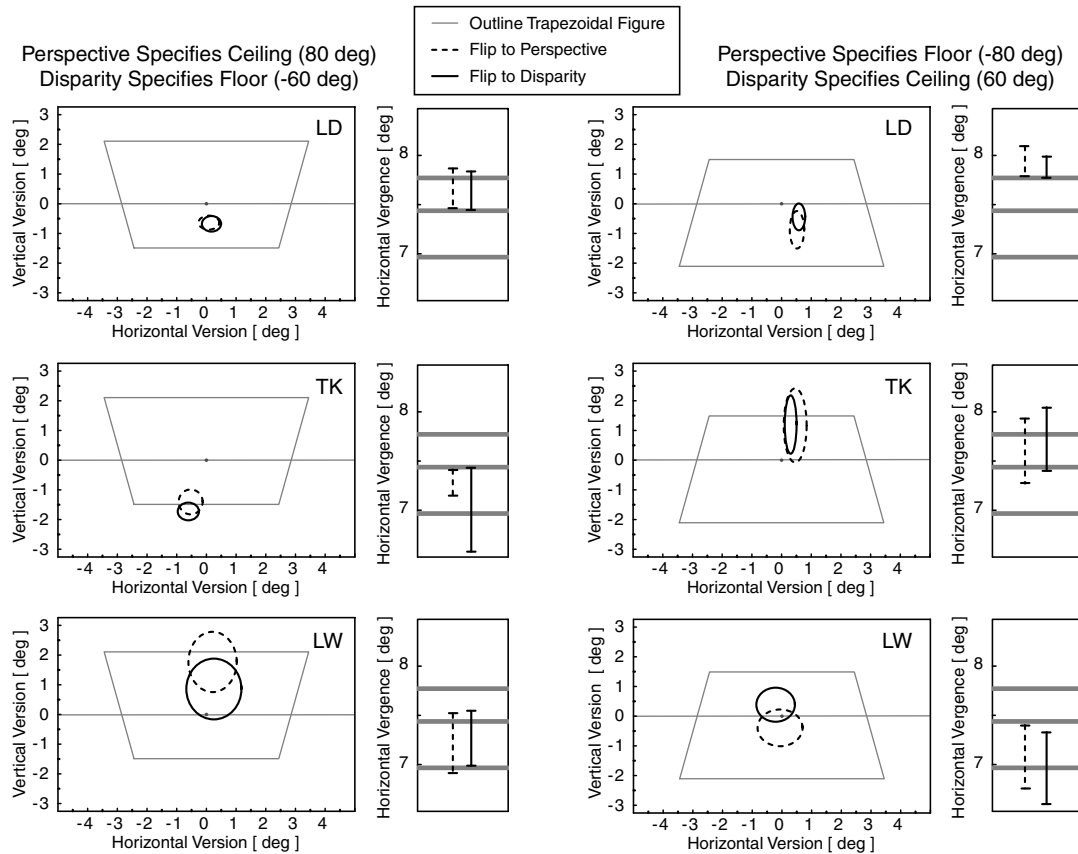
Fig. 5. The average gaze position (vertical versus horizontal version) and horizontal vergence during 1000 ms prior to the moments of the button presses (thus at about the moment of the perceptual flip) when eye movements were allowed. The left panel shows the results when perspective specified a slant of 80 deg and disparity specified a slant of −60 deg. The right panel shows the results when perspective specified a slant of −80 deg and disparity specified a slant of 60 deg. The grey lines indicate the outline of the trapezoidal figure and the rotation axis. The black dashed ellipses (for version angles) and lines (for horizontal vergence) indicate the average gaze position and standard deviation for flips to the perspective-dominated percept. The black continuous ellipses and lines show the same but for flips to the disparity-dominated percept. The results indicate that subjects LW directs the gaze to different areas in the stimulus in order to flip from one percept to the other. For subjects LD and TK the results indicate that perceptual alternations are caused neither by systematically changing the gaze position toward certain stimulus details, nor by systematically changing the vergence angle.

4. Experiment 3: Correlation between (micro)saccades, blinks and perceptual flips

The above described results of experiment 2 show that perceptual flips are possible without first having to make an eye movement. However eye movements did regularly occur for the free eye movement condition and in experiment 2 we did not specifically examine microsaccades (which also regularly occurred during the fixation condition). For the individual perceptual flips it appears rather random whether or not an eye movement occurred within a specific time interval prior to the flip. But this does not necessarily mean that there is no temporal correlation whatsoever between eye movements and perceptual flips. For instance an eye movement could increase the chance that a flip might occur instead of definitely causing a flip. Therefore, in experiment 3 we investigate whether there is any correla-

tion between flips and both saccades and blinks. We also take microsaccades into account.

4.1. Stimulus

The disparity-specified slant was either plus or minus 60 deg and the perspective-specified slant was either plus or minus 85 deg. The width of the trapezoidal figure was 5.2 deg for the far away side (as specified by perspective) and 7.8 deg for the near side. The height of the trapezoidal figure was 1.9 deg. The window in the centre of the reference background was 9.5×6.0 deg. The chin rest was positioned at 55 cm from the screen.

4.2. Task and procedure

Subjects initiated the stimulus onset, after which the stimulus was shown for 5 min. The stimulus could

either be a conflict stimulus (perspective- and disparity-specified slants having opposite signs), which causes perceptual flips, or a no-conflict stimulus (perspective- and disparity-specified slants having the same sign). In the latter case the polarity of the slant specified in the stimulus was changed at random moments (with an average interval of 5.0 s). These physical polarity changes in the stimulus will be called "*stimulus flips*" throughout this paper. For the stimulus flip condition we monitored the occurrences of the stimulus flips as well as the responses of the subjects to the flips. It is of interest to note that the subjects were instructed to indicate the percept after a flip by pressing buttons. Thus, the subjects also responded to a stimulus flip when they missed the stimulus flip itself due to a co-occurring saccade or blink. The stimulus flip condition served as a control for the perceptual flip condition for which the actual occurrences of the flips are unknown and can only be monitored by recording the responses of the subjects. One session contained six trials which were presented in random order: four perceptual flip conditions (two for which the perspective-specified slant was positive and two for which the perspective-specified slant was negative) and two stimulus flip conditions. There were five or more sessions per subject, depending on the flip, saccade and blink frequency of the subject.

The task of the subject was to attempt to maximize the perceptual flip rate and to press keys to indicate when he or she perceived the 'ceiling'-percept and the 'floor'-percept. The "flip as fast as possible" instruction was applied to elucidate the temporal correlation between eye movements and perceptual flips optimally, since for this condition any correlation will most likely be enhanced. The subjects were free to move their eyes. The three subjects who participated in experiment 2 also participated in this experiment.

4.3. Eye movement analysis

We measured gaze positions using the previously described SMI-eyelink system and setup. Formula 1 was used to calculate the velocities for each eye separately (thus, in this case $\vec{x}_i$ represents the ith gaze position sample expressed in Fick-angles). Saccades were detected by first removing all the blinks from the data (including four samples prior to each blink and four samples after each blink in order to prevent that any left over speed signal of the blink is detected as a saccade). Then we applied the method of Engbert and Kliegl (2003) with a few modifications. For each eye separately we calculated velocity thresholds for detecting saccades by calculating the variance in the velocity signals for the x and y direction separately (using medians) within a sliding window of 751 samples.

$$\sigma_{x,y}^2 = \langle v_{x,y}^2 \rangle - \langle v_{x,y} \rangle^2$$

where $\langle \cdot \rangle$ denotes the median estimator. Note that the sliding window does not represent a constant absolute time interval, since the time intervals corresponding to blinks were excluded from this analysis. The separate velocity thresholds for the x and y direction for the middle 51 samples (to reduce the number of computations) within the sliding window were then set at six times the variance in the x and y direction, respectively (we adopted the number used by Engbert and Kliegl (2003)). In this way differences across sessions in the set-up of the eyelink cameras are taken into account and, due to the sliding window, noise which results from small body movements can be omitted. Begin marks of the saccades were set at the last sample before the velocity signal exceeded the velocity thresholds. End marks were set at the sample where the velocity signal first dropped below the thresholds. Furthermore, we assumed a minimal saccade duration of four samples (12 ms) to further reduce noise. Since saccades, including microsaccades (Martinez-Conde, Macknik, & Hubel, 2004), are conjugate in nature we only included binocular saccades.

4.4. Data analysis

From the stimulus flip condition (in which the stimulus physically changed) we obtained the mean reaction time for each subject (and the standard deviation) for a response after a flip had occurred. This reaction time served as an estimate for when a flip occurred prior to the moment of the button press for the perceptual flip conditions. Note however that response latencies for stimulus flips and perceptual flips need not be the same, since perceptual flips usually do not appear to be as abrupt as real physical changes in the stimulus.

To examine the correlation between saccades or blinks with either perceptual flips or stimulus flips we made occurrence histograms (similar to correlation histograms generally used in spike-train analysis (Perkel, Gerstein, & Moore, 1967)). In these occurrence histograms we plotted the occurrences of saccades or blinks relative to the moments of the button presses. We calculated these occurrence histograms for a time interval starting 10.0 s before the moment of a button press (i.e. at −10.0 s) to 10.0 s after the moment of a button press (at +10.0 s), using a bin-width of 100 ms. The intervals −10.0 to −5.0 s and +5.0 to +10.0 s were used to calculate the mean and the standard deviation of the bin height (as a reference level). The interval −5.0 to +5.0 s was the period for which we investigated the correlation between eye movements and flips.

We considered a peak or trough in the interval −5.0 to +5.0 s to be significant when two or more neighbouring bins within the peak or the trough differed more than two standard deviations from the mean (Davis & Voigt, 1997).

For a correct interpretation of the eye movements occurrence histograms it was necessary to take the auto-correlation of flips into account. For instance, if there would be a strong correlation between perceptual flips, any effect that we would find for saccades or blinks

could be caused by several flips instead of just the one at zero sec. Therefore we made similar occurrence histograms for button presses relative to the moments of other button presses and applied the above described analysis.

4.5. Results

Fig. 6 displays the results of experiment 3 in which we investigated the correlation between eye movements (sac-
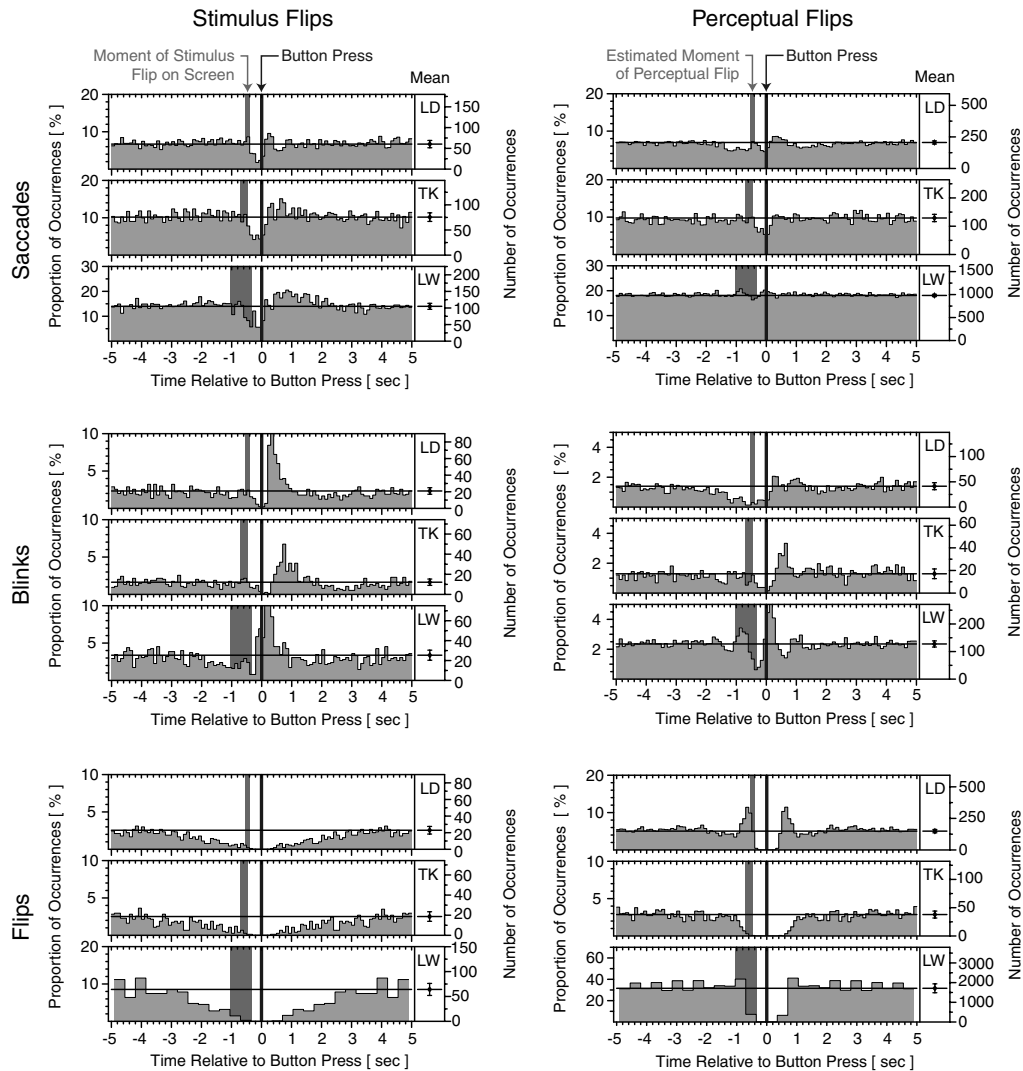

Fig. 6. Results for experiment 3 in which we investigated the correlation between eye movements (saccades and blinks) and perceptual or stimulus flips. From top to bottom the panels show the occurrences of saccades, blinks and flips versus the time relative to the moment of the button press. The left panels show the results for the stimulus flip condition (where the stimulus physically flipped). The right panels show the results for the perceptual flip condition. Within each panel three histograms are shown, one for each subject. For each histogram the scale on the left side represents the percentage of occurrences within the bin (100 ms) relative to the total amount of flips that contribute. The scale on the right side represents the absolute number of occurrences. The black horizontal line and the error bar on the right side of each histogram represent the mean bin height and standard deviation of bins in the intervals −10.0 to −5.0 s, and 5.0–10.0 s (in those periods no correlation is expected). The black vertical line at 0 s represents the moment of the button press. The dark grey vertical bar represents an estimate of the moment of the actual flip relative to the moment of the button press (a reaction time obtained from the stimulus flip condition). This format for the histograms will be used throughout this paper. For the stimulus flip condition there is a decrease in the occurrence probabilities of both saccades and blinks just after the moment of a stimulus flip until the moment of the button press (reaction period). Blinks occur more frequently after the moments of the button presses. For the perceptual flip condition the decrease in blink probability starts before the flip and the peak of blinks after the moments of the button presses is smaller.

cades and blinks) and both stimulus flips and perceptual flips. From top to bottom the panels show the occurrences of saccades, blinks and other button presses relative to moments of the button presses. The left panels show the results for the stimulus flip condition and the right panels show the results for the perceptual flip condition. Within each panel three histograms are shown, one for each subject. For each histogram, the scale on the left side represents the percentage of occurrences within the bin (100 ms) relative to the total amount of flips that contribute to the histogram. In this way the bin heights can be seen as probabilities of events occurring in the time interval of the bin relative to the moment of the flip or button press. The scale on the right side represent the absolute number of occurrences within a bin. The *x*-axis represents time relative to the moment of the button press. The black horizontal line and the error bar on the right side of each histogram represent the mean bin height and standard deviation of bins in the intervals −10.0 to −5.0 s and 5.0–10.0 s, as explained in the data analysis section. The black vertical line at 0 s represents the moment of the button press. The dark grey vertical bar represents our estimate of when the actual flip occurred relative to the moment of the button press (obtained from the stimulus flip condition).

As mentioned in the data analysis section, we considered a peak or a trough in the data to be significant when two or more neighbouring bins differed more than two standard deviations from the mean (in the same direction). The effects that are mentioned in this results section are all significant according to this criterion unless otherwise stated. For the stimulus flip condition (left panels) the occurrence probabilities of both saccades and blinks are reduced during the interval between the moment of the flip and the moment of the corresponding button press (for blinks the occurrence probability is reduced even before the moment of the flip for subjects LD and LW). Just after the moment of the button press the occurrence probabilities of saccades and blinks are increased, resulting in a significant peak for blinks and a significant shallower but wide peak for saccades.

For the perceptual flip condition there is also a reduced probability of both saccades and blinks between the moment of the flip and the moment of the button press, although for saccades for subject LW it is hardly visible and for subject LD it appears to start earlier than for the stimulus flip condition and there is an interruption in the reduced probability (at the moment of the flip the bin height temporarily returns to the reference level). There is an increased probability of blinks after the moment of a button press for all subjects (this increase in blink probability also occurred for the stimulus flip condition). For subject LW there is an extra peak of blinks at about the moment of the flip. Note that for subjects LD and LW the percept alternates relatively frequently and for these two subjects there is a relatively

high correlation between flips (bottom right panel; for subject LW this is shown more clearly in Fig. 7 where the flips are divided in flips to the disparity-dominated percept and flips to the perspective-dominated percept).[2] This could be the cause of the extra peak for blinks for subject LW and the earlier start of the reduced probability for subject LD. For subject TK there was no significant correlation between flips in the perceptual flip condition other than that there is a minimum time between flips (0.5 s). For this subject the results for the perceptual flip condition are rather similar to the results for the stimulus flip condition, except that there is no increase in saccades just after the moment of the button press. The similarity in the results for subject TK for both stimulus flips and perceptual flips indicate that, as far as eye movements are concerned, the processing of a perceptual flip is rather similar to the processing of a change in the stimulus.

In contrast to other bi-stable stimuli (e.g. Necker cube, binocular rivalry), the two percepts in our stimulus are instigated by two different variable cues, namely perspective and disparity. To examine whether there are differences in eye movement behaviour between flips to a perspective-dominated percept and flips to a disparity-dominated percept we divided the flips into these two categories and determined the correlations in the above described manner and applied the same significance criterion (see data analysis section). Fig. 7 shows the correlations for flips to the perspective-dominated percept (left) and flips to the disparity-dominated percept (right). The bottom panels (occurrences of button presses) clearly show that for all three subjects disparity is a rather dominant cue. There is an increased chance of flipping (towards the disparity-dominated percept) after a flip to the perspective-dominated percept. For flips to the disparity-dominated percept there is no increased flip probability after the moment of the button press, but instead an increased flip probability appears prior to the moment of the button press. This means that the perspective-dominated percept is relatively short lived compared to the disparity-dominated percept. This is consistent with the results for free eye movements of experiment 2 (Fig. 4) and this is also consistent with the average percept durations reported by van Ee et al. (2005a). For subjects LD and LW the dominance of disparity is very clear. Due to the high autocorrelation of perceptual flips for subjects

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[2] Due to a computer timing error the button presses for subject LW could only be recorded at about 350 ms intervals. For this subject the bin-size for the flip occurrence histograms is, therefore, 350 ms. Since a bin of 350 ms can contain a whole effect, we already considered one bin that differed more than two standard deviations from the mean bin height as a significant peak or trough in these flip occurrence histograms for subject LW. This timing error of 350 ms also explains the relatively large standard deviation for the reaction time of subject LW and this will also have caused some aliasing in the saccade and blink occurrences histograms.
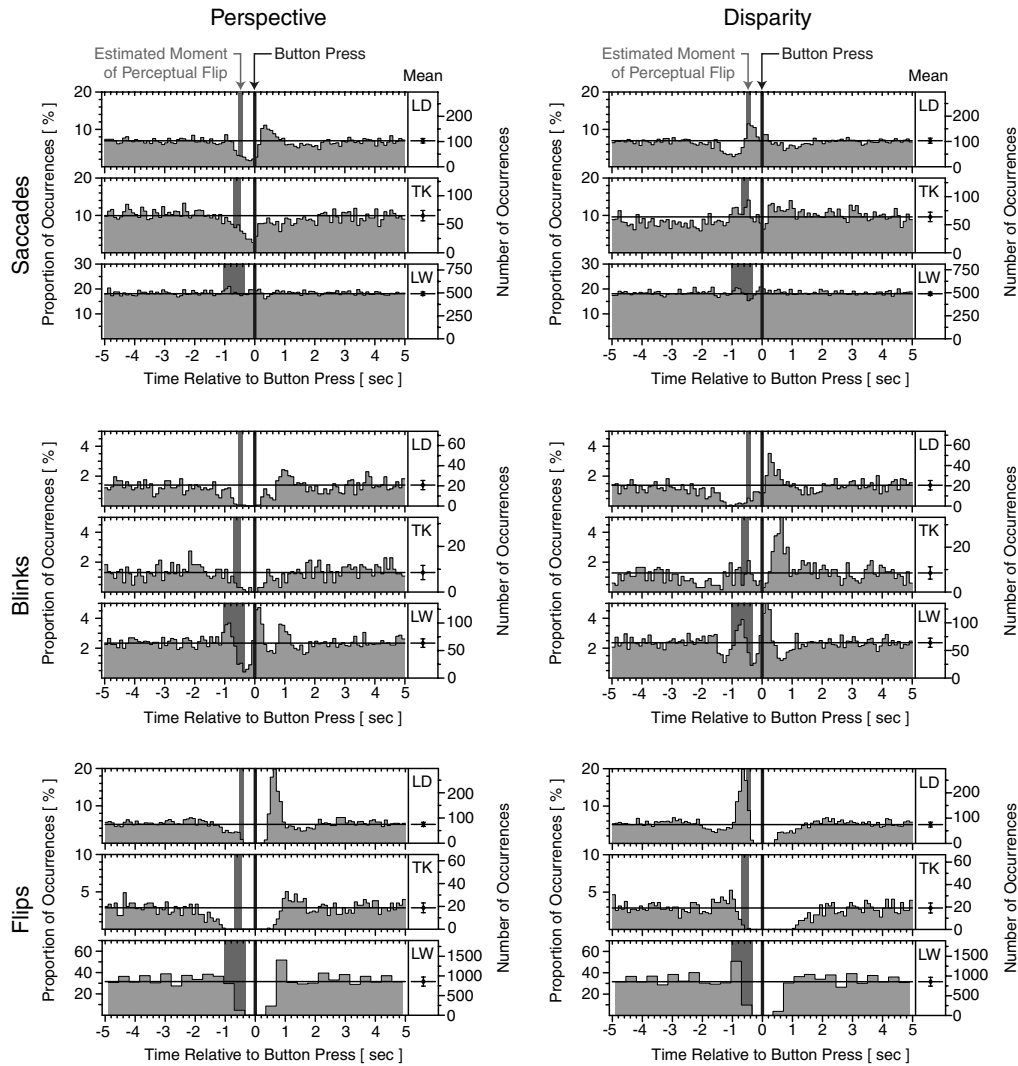
Fig. 7. Similar to Fig. 6 but for perceptual flips, divided into flips to the perspective-dominated percept (left panels) and flips to the disparity-dominated percept (right panels). There appear to be differences between flips to the perspective-dominated percept and flips to the disparity-dominated percept: for subject TK the reduced probability of saccades occurs mainly for flips to the perspective-dominated percept and the increase in blink probability after the moment of the button press occurs only for flips to the disparity-dominated percept.

LD and LW it is hard to interpret their results for saccades and blinks in terms of causality. For instance for subject LD the two histograms for saccades (for flips to the perspective-dominated percept and flips to the disparity-dominated percept) are rather similar, except for a shift in time that corresponds to the time interval between the peak of button presses and zero in the flips histograms (0.6 s). Therefore, any effect that the histograms show could be caused either by the flip to the disparity-dominated percept or by the flip to a preceding perspective-dominated percept. For subject TK the correlation between flips to the perspective-dominated percept and flips to the disparity dominated percept is much less and for this subject the histograms for saccades and blinks for flips to the perspective-dominated percept and flips to the disparity-dominated percept do not appear as copies shifted over time. From the results for this

subject it is clear that the reduced occurrence probability of saccades mainly occurs for flips to the perspective-dominated percept. For flips to the disparity-dominated percept there is a slight increase in saccade probability at about the moment of the flip, indicating that saccades can help to flip to the disparity-dominated percept. This increase mostly concerns saccades for which the vertical component is larger than the horizontal component (vertical saccades along the disparity gradient). This suggests that a conflict between perceived slant and required vergence change during a saccade can bias the percept toward the disparity-dominated percept. The probability of blinks increases after the moment of a flip to the disparity-dominated percept, but not after the moment of a flip to the perspective-dominated percept. These conclusions for the data of subject TK (that the reduced probability of saccades is due to a flip to the perspective-dominated
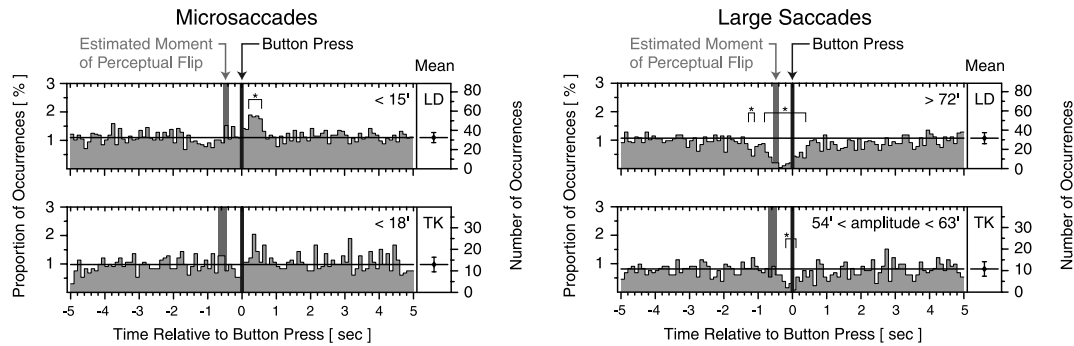
Fig. 8. Similar to Fig. 6 but here we compared the role of microsaccades (left panel) with the role of larger saccades (right panel) for perceptual flips for subjects LD and TK. To obtain a sufficient amount of saccades (such that the mean bin height differed significantly from zero) we considered saccades with amplitudes smaller than 15′ for subject LD and smaller than 18′ for subject TK. In order to perform a fair comparison we took similar sized portions of small and large saccades: for LD 644 and 657 saccades, respectively, and for TK 503 and 521 saccades, respectively. The time intervals indicated by the ★ contain a significant peak or trough (see data analysis section). The main point of these graphs is that microsaccade probability is not decreased at or after the moment of the flip but the probability of larger saccades is.

percept and increased probabilities of both saccades and blinks are due to flips to the disparity-dominated percept) are consistent with the results for subjects LD and LW.

In our experiment the bi-stable figure could be perceived as either a floor or a ceiling. We examined whether the perceived slant polarity results in differences in eye movement behaviour between flips to a floor percept and flips to a ceiling percept, but no differences of interest were found.

4.5.1. Microsaccades

It is important to examine to what extend very small saccades, usually referred to as microsaccades (for a review see Martinez-Conde et al., 2004), correlate with perceptual flips. These microsaccades are particularly interesting because during such a microsaccade the visual world shifts on the retina, yet subjects are usually unaware of this, since a large portion of the foveal information remains on the fovea during the saccade. Microsaccades occur frequently during fixation (microsaccades are sometimes also referred to as fixational saccades). For each subject we set a saccade amplitude threshold below which there was a sufficient amount of saccades to make a similar histogram as in Figs. 6 and 7 for the perceptual flips condition. We concluded to have a sufficient amount of microsaccades when the mean bin height in the intervals −10.0 to −5.0 and 5.0–10.0 differed significantly ($P < 0.001$) from zero. Note however that the current setup is not suitable to detect all microsaccades especially when the amplitudes are smaller than 5′. For subject LD the amplitude threshold was 15′ and for TK it was 18′. For subject LW the decrease in the probability of saccades is relatively small (Fig. 6, top panel). We examined several saccade amplitude intervals for this subject, but none of the histograms for these saccade amplitude intervals showed a significant saccade-probability decrement or any other effect. Therefore we excluded the data for subject LW

from the analysis. The resulting histograms for subject LD and TK are shown in Fig. 8.

The left panel of Fig. 8 shows the occurrences of microsaccades (smaller than 15′ for LD and smaller than 18′ for TK). For a fair comparison, the right panel shows the occurrences for a similar amount of larger saccades: larger than 72′ for LD and between 54′ and 63′ for TK. These saccade amplitude ranges for the larger saccades are different for the two subjects since they did not make similar amounts of saccades within the same saccade amplitude intervals. There does not appear to be a significant decrease in the probability of microsaccades at or after the moment of the flip (left panel).[3] For subject LD there is a significant increase in microsaccade probability just after the moment of the button press, suggesting that some microsaccades might have been caused by the flips. The above reported decrease in saccade probability that occurred prior to the moment of the button press mainly occurred for larger saccades (see Fig. 8, right panel).

We conclude that prior to the perceptual flip there is no interaction between microsaccades and the perceptual flip.

5. Experiment 4: The role of button presses

The results of experiment 3 show that the occurrence probability of both saccades and blinks are reduced

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[3] For subject TK there are two bins near zero that appear as a small probability decrease, but they are not significantly different from the mean ($P > 0.05$). However if we would have included more microsaccades (by allowing saccades slightly larger than 18′), then these bins would become significantly different from the mean. This decrease in saccade probability becomes more pronounced for larger saccade amplitude intervals implying that the decrease in saccade probability mainly occurs for larger saccades.

after the moment that a flip occurred for both perceptual flips and the physically induced stimulus flips (see Fig. 6). Furthermore there is a peak in the histograms for blinks just after the moment of the button press (Fig. 6 middle panels). In experiment 4 we examined whether both the reduced probability of saccades and blinks, and the peak of blinks are induced by either the perceptual flip or changes in the stimulus, or if they are side effects of having to press buttons.

5.1. Stimuli and procedure

In this experiment four different conditions were compared. The first, base line condition, was the stimulus flip condition of experiment 3. In this condition there was no conflict between perspective and disparity but the slant polarity was switched at random intervals (the average interval was 5 s). The subject pressed buttons to indicate whether he or she perceived a ceiling or a floor.

For the second condition both perspective and disparity indicated a slant of zero degrees (frontoparallel). The size of the planar grid was 6.2×1.9 deg to match the size of the slanted plane of the first condition. The stimulus on the screen did not change in the course of a trial but auditory beeps were presented at random intervals. Again the average interval was 5 s. The beep could have either a high or a low frequency which were easy to distinguish and the subjects were acquainted with the two sounds before starting a session. By pressing buttons the subject indicated whether he or she had heard a high or a low beep. The results for this condition will reveal whether a decrease in the probability of saccades and blinks occurs (as shown in the top panels of Fig. 6), when attending to events other than changes in the visual stimulus.

For the third condition the stimulus was the same as for the first condition. Perspective- and disparity-specified similar slants (no conflict) and the slant polarity was switched at random intervals. The subjects were instructed to count the number of flips, in order to make sure that they attended to the stimulus, but they neither pressed buttons nor did they make any other response to a stimulus flip. At the end of each trial the subjects had to report the number of flips they had counted. For this condition only changes in the stimulus will play a role, since the subjects were instructed not to press buttons. Therefore, if the effects we found in experiment 3 (reduced probability of saccades and blinks and the peak of blinks) are absent for this condition, then it can be concluded that the effects were mainly caused by the act of pressing buttons. If the results are the same as for the first condition (stimulus flip condition with button presses) then it can be concluded that the effects are mainly induced by the changing stimulus or changing percept.

For the fourth condition the stimulus was the same as for the second condition (perspective- and disparity-specified zero slant). The subjects were instructed to press buttons at will, but as randomly as possible. This condition will provide information about any effect the motor task of pressing buttons will have on saccades and blinks.

The data analyses and significance test were the same as for experiment 3. Subjects LD and LW participated.

5.2. Results

Fig. 9 portrays the results of experiment 4, showing the role of button presses. The left panels show the histograms for saccades and the right panels show the histograms for blinks for the four conditions described above. Fig. 9a shows the results for the condition for which there were physically induced stimulus flips and the subjects had to indicate the new percept by pressing buttons (see also the left panels of Fig. 6). Fig. 9b shows the results for the condition for which subject responded to auditory beeps by pressing buttons. Fig. 9c shows the results for the condition for which subject counted the visual stimulus flips without pressing any buttons. Fig. 9d shows the results when subjects pressed buttons at random. Within each panel two histograms are shown, one for each subject. The scale of the y-axis on the left side of each histogram represents the percentage of occurrences within the bin (100 ms) relative to the total amount of flips, beeps or button presses that contribute to the histogram. The scale on the right side represent the absolute number of occurrences within a bin. The x-axis represents time relative to the moment of the button press, except for Fig. 9c where the x-axis represents the time relative to the moment of the stimulus flip on the screen. The black horizontal line and the error bar on the right side of each histogram represent the mean bin height and standard deviation of bins in the intervals −10.0 to −5.0 s and 5.0–10.0 s. The black vertical line in Fig. 9a, b and d represents the moment of the button press. The black vertical bar in Fig. 9c represents the estimate of when a button press would have occurred if the subjects would have pressed buttons for this condition. The dark grey vertical bar in Fig. 9a and b represents an estimate (mean reaction time and standard deviation) of when the actual flip occurred relative to the moment of the button press. The dark grey vertical line in Fig. 9c represents the actual moment of the stimulus flip on the screen.

The decrease in the occurrence probabilities of both saccades and blinks has been caused by changes in the stimulus rather than by merely pressing buttons. It occurred when the subjects were paying attention to either changes in the visual stimulus (Fig. 9a and c) or auditory beeps (Fig. 9b). The reduced probability even occurred when the subjects did not have to press buttons
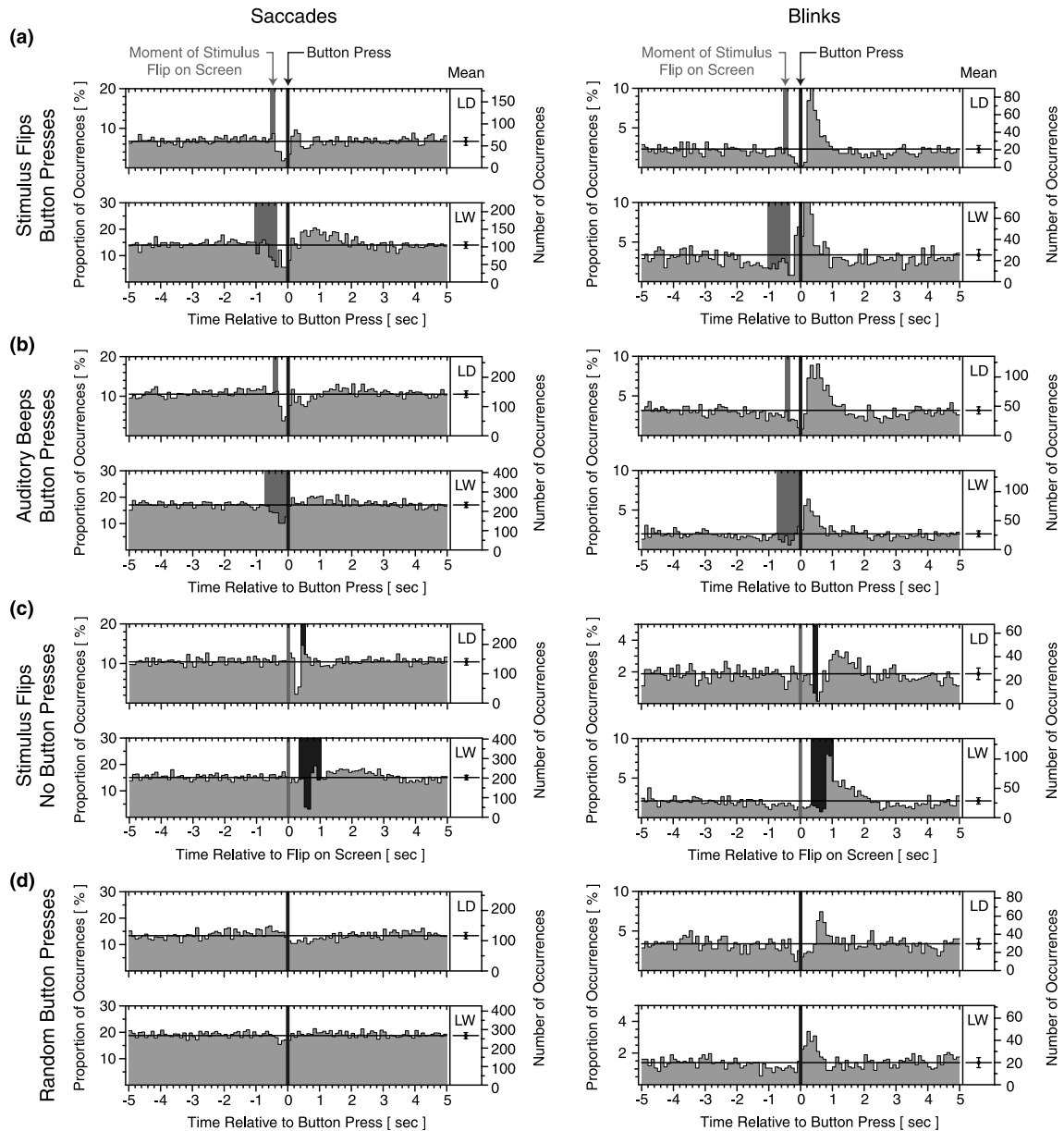
Fig. 9. Results of experiment 4 in which we investigate the role of button presses. The left panels show the occurrences of saccades, and the right panels show the occurrences of blinks versus the time relative to the moments of the button presses (a, b and d) or physical flips (c) for two subjects (LD and LW). (a) The results for the physical induced stimulus flip condition, (b) for the auditory beeps condition, (c) for stimulus flips when no buttons were pressed, and (d) for the condition for which the subject pressed buttons at random. In the latter case there is no significant decrease in saccade probability, implying that the reduced probability of saccades between the moment of the flip and the moment of the button press in panels (a)–(c) is an effect induced by the changing stimulus. The reduced probability of blinks and the increase of blinks after the button press are effects of both the changes in the stimulus and button presses, since they appear in all graphs.

(Fig. 9c), whereas it was absent for saccades, and less pronounced for blinks, when subjects were pressing buttons at random (Fig. 9d).[4]

The increase in blink probability just after the moment of the button press appears in all graphs. Thus

one can conclude that this increase is caused by changes in the stimulus as well as by a possible interaction between the motor task of pressing buttons and the motor act of blinking.

6. Discussion

We have examined the role of eye movements for perceptual flips when subjects viewed the slant rivalry

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[4] For subject LD the trough in the histogram for blinks at the moment of the button press is not significant (according to our above described criterion). There is only one bin (at −0.15 s) that individually is significantly different ($P < 0.01$) from the mean bin height.

stimulus. The perceptual flips were instigated by a conflict between perspective-specified slant and disparity-specified slant. We first examined, in experiment 1, the perceived slants as a function of perspective-specified slant and disparity-specified slant. We found that one slant was perceived when perspective- and disparity-specified similar slants. Moreover, two alternating slants were perceived when perspective- and disparity-specified quite different slants. Our results are similar to those reported previously for slants about a vertical axis (van Ee et al., 2003; van Ee et al., 2002; van Ee et al., 2005b). In experiment 2 we investigated gaze positions while subjects viewed the stimulus and found that eye movements were not essential for the instigation of a perceptual flip, which means that perceptual flips were governed by a cognitive process. When subjects were allowed to make eye movements the average gaze positions (in version as well as vergence angles) were similar for both flips to the perspective-dominated percept, and flips to the disparity-dominated percept. In experiments 3 and 4 we have used the occurrence histogram (most commonly used in spike train analysis) to investigate the temporal correlation of perceptual flips with both saccades and blinks. This method turned out to be an excellent tool, because it provides information about all eye movements relative to the occurrence of a flip, rather than just the eye movement occurring closest in time as examined by previous studies. We did not find a positive (causal) correlation of both saccades and blinks that occurred prior to perceptual flips. After the moment of a perceptual flip the occurrence probabilities of both saccades and blinks were reduced (for blinks the decrease in the occurrence probability could even start before the moment of a perceptual flip). This reduced probability was not caused by the button press response. For microsaccades there was neither a positive correlation prior to perceptual flips, nor was there a reduced probability around the moment of the flip. There was a slight increase in microsaccade probability just after the moments of the button press responses. For blinks, too, we found an increase in occurrence probability just after the moment of the button press.

6.1. Reset of saccade planning

An interesting question is: what causes the found reduced probability of saccades after the moment of a perceptual flip? This reduced probability was present when the physical slant polarity changed at random moments (physical stimulus flip condition) and no buttons were pressed (see Fig. 9c), whereas the decrease in probability was absent when subjects pressed buttons at random (Fig. 9d). Thus, the reduced probability of saccades is not an effect of the preparation for a button press, but has to be linked to a perceptual change (both for perceptual flips and physical stimulus flips). Note that especially for stimulus flips the reduced probability of saccades occurs in its entirety after the moment of the flip. For perceptual flips at least the major part of the period for which the saccade-occurrence probability is reduced lies after the moment of the flip (although in this case the moment of the flip is of course less clear), and for both stimulus flips and perceptual flips the period in which the reduced probability of saccades occurs is much longer than the duration of the saccades themselves (even taking the variance in reaction time into account). Therefore, it seems very likely that the reduced probability of saccades is caused by the flip, rather than that flips occur due to a temporary absence of saccades. The reduced probability of saccades is consistent with a longer fixation duration at the moment of a flip as reported previously for the Necker cube (Ellis & Stark, 1978). Ellis and Stark proposed that the longer fixation duration at the moment of a flip represents the time needed to construct a new three-dimensional representation of the cube. Following their line of thought one could state that on a cognitive level each perceptual flip is considered as the onset of a new stimulus. The "new stimulus" would first have to obtain a spatial representation within the brain before a new saccade can be planned. Furthermore, a new stimulus presentation would arouse attention and it is known that a shift in spatial visual attention precedes the execution of a saccade (Hoffman & Subramaniam, 1995; Kowler, Anderson, Dosher, & Blaser, 1994), and that spatial visual attention and saccades are processed in overlapping areas in the brain (Corbetta, 1998; Corbetta & Shulman, 2002; Kustov & Robinson, 1996; Nobre, Gitelman, Dias, & Mesulam, 2000; Schall, 2004). The reset of saccade planning due to a perceptual flip can explain both the decrease in saccade probability after the moment of the flip and the smaller increase in saccade probability after the moment of the button press (when saccades occur more or less synchronized with respect to the flip).[5] Furthermore, the interpretation of a perceptual flip as the onset of a new stimulus explains the similarities of the results for both perceptual flips and the physically induced stimulus flips (the latter are, in fact, presentations of a new stimulus). The interpretation of a perceptual flip as the onset of a new stimulus could also explain that our results for the responses to auditory beeps appear to be similar to the results for both

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[5] Reaction times of saccades as a response to stimulus onset, can be as fast as 175 ms when there is no uncertainty as to when, or where, to move the eyes (for a review see Rayner, 1998). This lower limit of saccade latency is much shorter than the period for which we found a reduced saccade probability after a perceptual flip (about 500 ms). However, saccade latencies after stimulus onset are known to depend on stimulus complexity and task. Longer saccade latencies of about 400 ms or more have been reported for various tasks (Hooge, Beintema, & van den Berg, 1999; Kowler et al., 1994; van Loon, Hooge, & van den Berg, 2002; Zelinsky & Sheinberg, 1997).

perceptual and stimulus flips. The auditory beeps, like the stimulus flips, are presentations of a new stimulus, albeit not a visual stimulus. In this respect it is of interest to note that spatial attention has a supramodal component (Doyle & Snowden, 2001; Eimer, 1998, 2001; Schubotz, Cramon, & Lohmann, 2003) and that auditory stimulation can affect the execution of saccades (Frens & van Opstal, 1998; Harrington & Peck, 1998). It can be suggested that auditory beeps arouse visual attention in the same manner as does a new visual stimulus.

6.2. Role of slant cues: Perspective versus disparity

We found differences in eye movement behaviour for flips to a perspective-dominated percept and flips to a disparity-dominated percept. The reduced probability of saccades mainly occurred for flips to the perspective-dominated percept (Fig. 7, top-left panel). For flips to the disparity-dominated percept we found a small but significant increase of saccades along the disparity gradient at about the moment of the flip (Fig. 7, top-right panel). This suggests that, although eye movements are not essential, a conflict between perceived slant and required vergence change during a saccade can bias the percept toward the disparity-dominated percept. Our results suggest that making eye movements at short intervals helps to maintain the disparity-dominated percept. This idea is consistent with disparity being the dominant cue for slant when subjects are making eye movements and perspective being dominant when subjects are fixating (see Fig. 4).

6.3. Microsaccades

Since microsaccades do not change the main feature that is foveated microsaccades are not particularly useful to inspect a large visual scene in detail. In this view microsaccade planning, contrary to the planning of larger saccades, might be less affected by the onset of a new stimulus that requires a new inspection of the visual world (although Steinman, Cunitz, Timberlake, and Herman (1967), Engbert and Kliegl (2003), and Hafed and Clark (2002) have reported that microsaccades are influenced by attention that, in turn, can be triggered by changes in the visual field). As we have proposed a perceptual flip might be interpreted as the onset of a new stimulus, and therefore it would affect the planning of large saccades more than the planning of microsaccades. That a perceptual flip would affect larger saccades more than microsaccades is consistent with our results, since our results show that the decrease in saccade probability occurs mainly for the larger saccades and that there is no significant decrease in the occurrence probability of microsaccades. Furthermore, voluntary control has more influence on larger saccades than on microsaccades, which are regarded as involuntary fixational eye movements that serve to counteract retinal adaptation and perceptual fading (Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). It seems to be the case that perceptual flips affect only the larger, more voluntary saccades and do not disrupt the timing of the more automatic, involuntary microsaccades.

6.4. Blinks

In addition to a reduced occurrence probability of saccades we also found a decreased probability of blinks at the moment of the flip. Further, we found an increase in blink probability just after the moment of a button press, which even occurred when the subjects' task was to press buttons at more or less random intervals (Fig. 9d). This indicates that there is an interaction between the motor tasks of pressing buttons and blinking. The interaction between these motor tasks does not have to be a direct interaction, but can be mediated through attention or effort. Pressing buttons at random intervals requires at least some effort and it is known that blink frequency drops with increasing difficulty in task or increasing amount of relevant information within the visual field (Veltman & Gaillard, 1998; Zangemeister, Sherman, & Stark, 1995). Our results suggest furthermore that blinks become synchronized with task relevant events (i.e. in this study perceptual or stimulus flips, beeps or button presses).[6] If the mechanism that is responsible for blinks somehow assumes that one task relevant event does not immediately follow another event, then to blink just after such an event decreases the likelihood that the event occurs during a blink (and relevant information would be missed). Blinks might be delayed till just after a task relevant event, waiting for the event to happen first. Such a delay of blinks would naturally mean that less blinks occur at the moment of the event itself and even before the event (which can also be seen in some of the graphs), thereby also explaining the decrease in blink probability at, and sometimes before, the moment of a stimulus flip or a perceptual flip.

7. Conclusion

We have investigated the role of eye movements for perceptual bi-stability instigated by the slant rivalry stimulus. We have first established that perceived slants about the horizontal axis are similar to those found about the vertical axis implying that perceived slants can be understood in a Bayesian frame work that describes the quantitative aspects of perceived slant on

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[6] Note also that Ito et al. (2003) reported, for a version of Attneave's (1968) triangles, a decrease and increase in blink frequency, similar to the results reported here.

the basis of the likelihoods of both perspective and disparity slant information combined with prior assumptions about the shape and orientation of objects in the scene. Our eye movement analyses revealed that there was no positive correlation between a perceptual flip and both saccades (microsaccades as well as larger saccades) and blinks that occurred prior to a perceptual flip. We also found that changes in horizontal vergence were not responsible for perceptual flips. Thus, eye movements were not essential to flip from one percept to the other. After the moment of a perceptual flip the occurrence probabilities of both saccades and blinks were reduced. This reduced probability mainly occurred for larger voluntary saccades, rather than for involuntary microsaccades. We suggest that this reduced probability of voluntary saccades reflects a reset of saccade planning.

Acknowledgments

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