ELSEVIER

The role of saccades in exerting voluntary control in perceptual and binocular rivalry

Loes C.J. van Dam, Raymond van Ee *

Helmholtz Institute, Utrecht University, PrincetonPlein 5, 3584 CC, Utrecht, The Netherlands

Abstract

We have investigated the role of saccades and fixation positions in two perceptual rivalry paradigms (slant rivalry and Necker cube) and in two binocular rivalry paradigms (grating and house–face rivalry), and we compared results obtained from two different voluntary control conditions (natural viewing and hold percept). We found that for binocular rivalry, rather than for perceptual rivalry, there is a marked positive temporal correlation between saccades and perceptual flips at about the moment of the flip. Across different voluntary control conditions the pattern of temporal correlation did not change (although the amount of correlation did frequently, but not always, change), indicating that subjects do not use different temporal eye movement schemes to exert voluntary control. Analysis of the fixation positions at about the moment of the flips indicates that the fixation position by itself does not determine the percept but that subjects prefer to fixate at different positions when asked to hold either of the different percepts.
© 2005 Elsevier Ltd. All rights reserved.

Keywords: Perceptual rivalry; Binocular rivalry; Voluntary perceptual control; Saccades

1. Introduction

Visual rivalry is an interesting and much studied phenomenon, because there is more than one possible interpretation of one and the same sensory input. Therefore, knowledge on visual rivalry can provide valuable insights on visual awareness. One specific aspect of interest is the role of voluntary control on the perceptual alternation rate (e.g., Lack, 1978; Meng & Tong, 2004; van Ee, van Dam, & Brouwer, 2005). Here it is of importance to know the extent to which eye movements are responsible for the exertion of voluntary control.

Commonly, researchers assume that the sensory input remains the same across the period of time for which they investigate perceptual alternations, and that eye movements do not play an important role. Indeed several studies have shown by either compensating for occurring eye movements (Pritchard, 1958; Scotto, Oliva, & Tuccio,

1990) or using afterimages (Blake, Fox, & McIntyre, 1971; Lack, 1971; McDougall, 1903) that eye movements are not necessary for perceptual alternations to occur. This indicates that there is a cognitive process that by itself can be sufficient for bi-stability to occur. There is however also a huge body of evidence showing that when eye movements are allowed there is at least some interaction between eye movements and perceptual alternations (e.g., Becher, 1910; Einhäuser, Martin, & König, 2004; Glen, 1940; Ito et al., 2003; Necker, 1832; Pheiffer, Eure, & Hamilton, 1956; van Dam & van Ee, 2005; Wundt, 1898), but whether it is the eye movement that facilitates a perceptual alternation or the alternation that facilitates an eye movement is still of much debate. By investigating the correlation between eye movements and perceptual alternations in several voluntary control conditions we attempt to gain a clearer insight on the interaction between eye movements and perceptual alternations.

Hitherto, the combination of voluntary control and the role of eye movements has not been investigated thoroughly, but for instance Toppino (2003) studied perceptual

---

* Corresponding author.
  E-mail address: R.vanEe@phys.uu.nl (R. van Ee).

alternations for the Necker cube for different voluntary control conditions (natural viewing and hold percept) when subjects were also instructed to fixate specific aspects within the stimulus. He reported that for each fixation position it was possible to exert voluntary control although fixation position does have a small influence on the percept dominance percentages. Glen (1940) examined the frequency of eye movements and perceptual alternations for the Necker cube in three different viewing conditions (natural viewing, speed up alternation rate, and slow down alternation rate). For the speed-up condition he reported that subjects were indeed able to increase the number of perceptual alternations, but also the number of eye movements was increased relative to the number of eye movements in the natural viewing condition (and vice versa for the slow-down condition). He, therefore, concluded that there is some interdependence between eye movements and the voluntary control of perceptual alternations, but he was unable to determine the precise interaction between the two. Lack (1971) studied the role of accommodation in exerting voluntary control. He reported that voluntary control in binocular rivalry was possible with artificial small pupils and also when the ciliary muscles were paralyzed, and thus he concluded that accommodation is not necessary to exert voluntary control.

In the current study, we investigated the role of saccades in exerting voluntary control in three different stimuli: slant rivalry, Necker cube rivalry, and house–face rivalry. Two of these paradigms can be classified as perceptual rivalry (slant rivalry and Necker cube rivalry) for which there is a clear role of voluntary control, and house–face rivalry can be classified as binocular rivalry, for which voluntary control plays a role but has less influence than for perceptual rivalry (Meng & Tong, 2004; van Ee et al., 2005). We used two different control exertion instructions: the natural viewing instruction (for which subjects are instructed not to influence the percept or the alternation rate) and the hold percept instruction (for which subjects are instructed to hold one of the two possible percepts for as long as possible). If the results reveal different patterns of correlation between saccades and perceptual flips for the different voluntary control conditions this would mean that voluntary control can at least in part be exerted by changing the eye movement scheme.

In addition to the three different stimuli mentioned above (slant rivalry, Necker cube rivalry, and house–face rivalry) we also investigated the interaction between saccades and perceptual alternations in the natural viewing condition for a fourth stimulus, namely binocular grating rivalry. Binocular grating rivalry is one of the stimuli that has been studied most frequently and therefore it is of importance to know the interaction between saccades and perceptual alternations for this stimulus. It has been found that voluntary control in grating rivalry has little influence on the percept or the perceptual alternation rate (Meng & Tong, 2004; van Ee et al., 2005) and therefore we only studied the interaction between saccades and perceptual alternations for the natural viewing condition for this stimulus.

The reason to study several rivalry paradigms instead of only one is that it is rather unclear whether results that are found for one specific stimulus can be generalized to all rivalry paradigms. Part of the discussion on the interaction between eye movements and perceptual alternations could be due to the fact that different authors studied different stimuli. In the current study, we used the same tools for each of the studied rivalrous stimuli, and compared the role of saccades for the four different paradigms. The results from the different paradigms can shed light on whether there is only one rivalry mechanism as far as eye movements are concerned or whether each stimulus has its own interaction between eye movements and the perceptual alternations.

2. General methods

2.1. Apparatus

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 red-green glasses were used for all stimuli, even though the half-images for both eyes could be the same (e.g., in the case of the Necker cube). 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. The chin rest was positioned at 55 cm from the monitor. Gaze positions were measured using a SMI-Eyelink system with a sample frequency of 250 Hz.

Three subjects participated in all experiments. All subjects had excellent stereovision. Their stereoacuities were lower than 10 arcsec, 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. Stimuli

To study the role of saccades for bi-stable perception we examined perceptual rivalry (slant rivalry and Necker cube rivalry) and binocular rivalry (grating rivalry and house–face rivalry). For each of these paradigms the stimulus was displayed within a reference background which consisted of small squares (see Fig. 1). The size of the reference
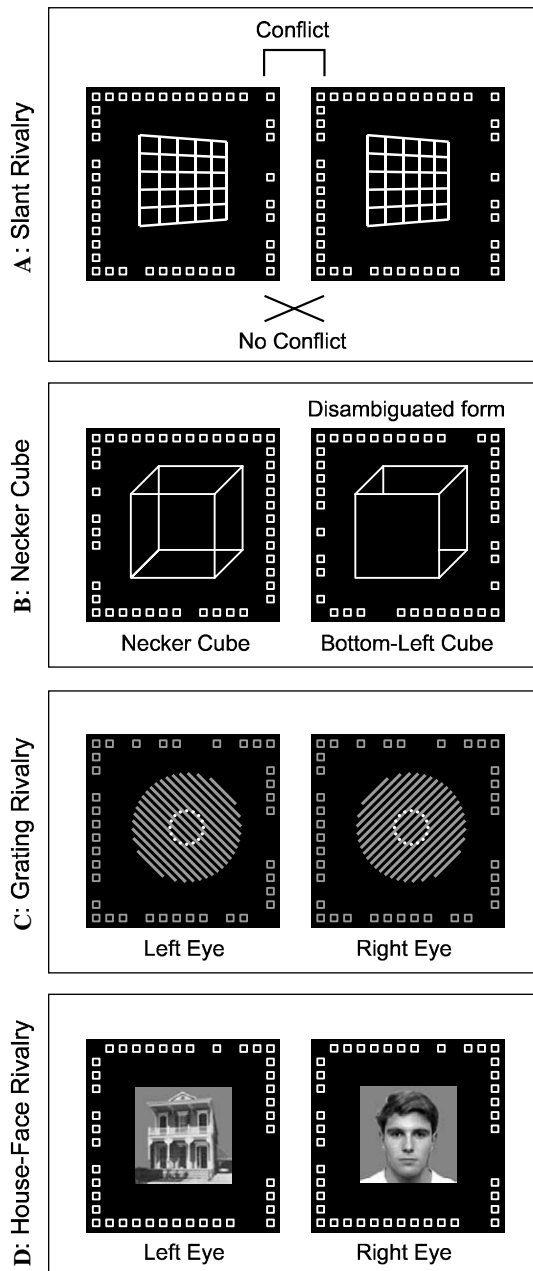
Fig. 1. Demonstration of the stimuli. (A) Slant rivalry stimulus for slants about a vertical axis. When the images are divergently fused an ambiguous stimulus is obtained for which either a disparity-dominated slant or a perspective-dominated slant will be perceived. When the images are cross-fused a stable slant percept will be obtained. (B) Left side: the Necker cube. The right side shows one of the two unambiguous representations. (C) Binocular rivalry of square-wave gratings. To obtain an unambiguous stimulus the same grating (either plus or minus 45 deg) was presented to both eyes (not shown). (D) Stimulus for house–face rivalry. To obtain an unambiguous stimulus either the house or the face was presented to both eyes (not shown).

background was 40.0×30.5 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 (8.8×9.4 deg) in which the stimulus was displayed.

To obtain a reaction time for a response after a perceptual flip we constructed for each bi-stability paradigm a non-ambiguous stimulus, which will be described below separately for each paradigm. When the non-ambiguous stimulus was shown, the stimulus was changed at random moments between the two possible representations. These physical stimulus changes will be called stimulus flips throughout this paper.

2.2.1. Slant rivalry

For the slant rivalry paradigm (van Ee, van Dam, & Erkelens, 2002), we used stimuli that consisted of a planar grid (Fig. 1) subtending 10.0×5.0 deg (in unslanted conditions). Perspective and disparity cues specified different slants about a vertical axis. The perspective-specified slant was either plus or minus 60 deg (positive angles were defined as left side near). The disparity-specified slant was either plus or minus 30 deg. For two of our subjects (LD and TK) disparity was a rather dominant cue. For these subjects we added an uncrossed standing disparity of 0.5 deg to the stimulus (so that the stimulus appeared behind the background) to increase the dominance times for the perspective-dominant percept.

The slant rivalry stimulus could either be an ambiguous conflict stimulus (perspective and disparity-specified slants having opposite signs), causing perceptual flips, or it could be a non-ambiguous no-conflict stimulus (perspective and disparity-specified slants having the same sign) in which case perspective and disparity cues were reconciled and only a single stable slant was perceived. In the non-ambiguous no-conflict condition the slant polarity specified in the stimulus was changed at random moments to create the stimulus flips.

2.2.2. Necker cube rivalry

The second stimulus that we used was the well-known Necker cube. The size of the image of the cube was 6.2×6.2 deg.

We obtained the non-ambiguous stimulus by making one of the two frontoparallel cube sides opaque, determining it as the front plane (Fig. 1B, right side). Stimulus flips were created by switching the front opaque plane between the two frontoparallel cube sides.

2.2.3. Grating rivalry

For binocular grating rivalry we used square-wave gratings with a spatial frequency of 2.9 cycles/deg. The square-wave gratings were presented in a circular region with a diameter of 6.2 deg. The orientation of the gratings could either be plus or minus 45 deg from vertical. For the conflict stimulus the two individual eyes were presented with gratings that differed in orientation by 90 deg. For the non-ambiguous stimulus both eyes were presented with gratings that had the same orientation. This orientation was changed by 90 deg at random moments to create the stimulus flips.

A binocular rivalry stimulus of 6.2 deg can result in patchiness of the percept (containing different grating orientations at different locations). A circle of 16 dots, which were presented binocularly, indicated a region for which subjects were instructed to make their response in those cases. This circle of dots was placed in the centre of the binocular rivalry stimulus. The diameter of the circle was 2.0 deg and the diameter of each dot was 0.2 deg. The brightness of the dots was 2.9 times as high as the brightness for the gratings to distinguish them from the rivalry stimulus.

2.2.4. House–face rivalry

For house–face rivalry one of the eyes viewed an image of a house and the other eye viewed an image of a face, resulting in the perception of alternatively a house or a face (Meng & Tong, 2004; Tong, Nakayama, Vaughan, & Kanwisher, 1998; van Ee, 2005). The size of the images was 6.2 × 6.2 deg. The centre of the image of the house contains high contrast elements relative to the centre of the image of the face. Dominance times in binocular rivalry are known to depend on contrast and luminance differences between the images (e.g., Alexander, 1951; Breese, 1899; Levelt, 1966). We decreased the contrast of the house image to 60% compared to the contrast of the face image to balance the dominance durations of the house and face percepts for natural viewing conditions.

The non-ambiguous house–face stimulus contained a binocular image of either a house or a face. At random moments the images were changed from house to face or vice versa to create the stimulus flips.

2.3. Data analysis

2.3.1. Eye movement analysis

Binocular eye movements were monitored using a SMI-eyelink system which sampled the gaze position every 4 ms (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 9 samples) and converted to Fick-angles. Velocities were calculated using a five-point sliding window

$$\overrightarrow{v}_n = \frac{\overrightarrow{x}_{n+2} + \overrightarrow{x}_{n+1} - \overrightarrow{x}_{n-1} - \overrightarrow{x}_{n-2}}{6\Delta t},$$

where $\overrightarrow{v}_n$ represents the nth velocity sample, $\overrightarrow{x}_i$ represents the ith gaze position sample, and Δt represents the time interval between two samples (see also Engbert & Kliegl, 2003).

Blinks were detected by selecting intervals in which the pupil was absent in the images and 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 were set at the last sample before the absolute version speed signal exceeded a threshold of 12 deg/s. End marks were set at the sample where the absolute speed signal first dropped below this threshold.

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 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

$$\sigma^2_{x,y} = \langle v^2_{x,y} \rangle - \langle v_{x,y} \rangle^2,$$

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). In this way differences across sessions in the setup of the eyelink cameras are taken into account and, due to the sliding window, noise which results from small body movements can be excluded. 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 are conjugate in nature we only included binocular saccades.

2.3.2. Temporal correlation between saccades and flips

We used the stimulus flip condition (in which the stimulus physically changed) to obtain a mean reaction time (and standard deviation) for each subject for a response after a flip had occurred. This reaction time served as an estimate for when a flip occurred prior to 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 and 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 (see Fig. 2) we plotted the occurrences of saccades relative to the moments of the button presses. We calculated these occurrence histograms for a time interval starting 10.0 s before a button press (i.e., at −10.0 s) to 10.0 s after 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 saccades and flips.
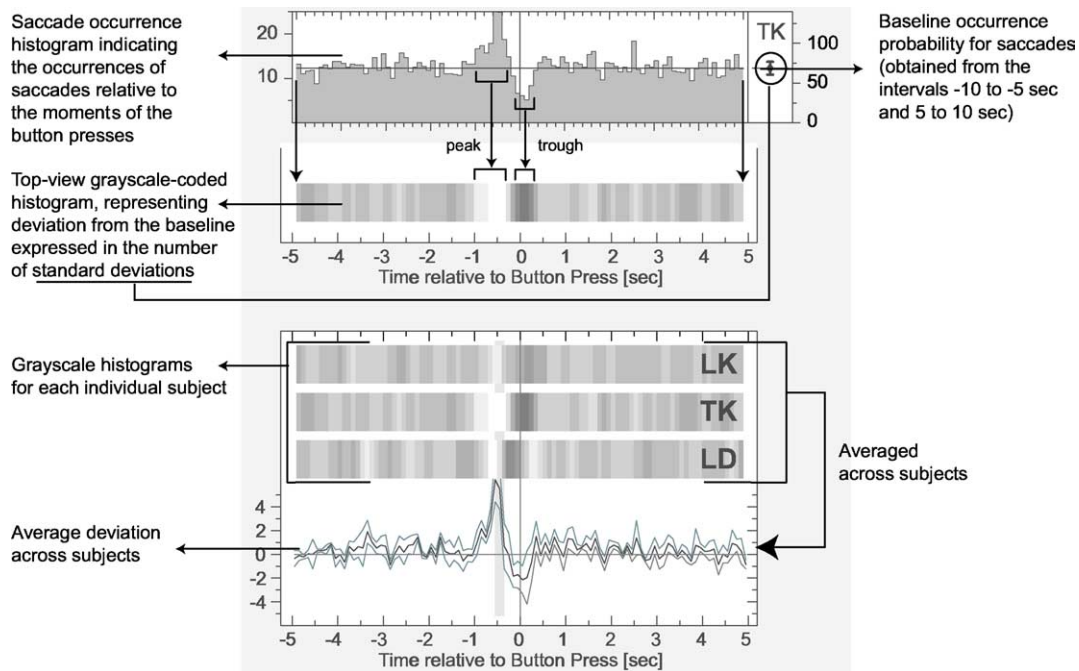
Fig. 2. Conversion from raw saccade occurrence histogram representation to grey-scale-coded histograms. The top graph shows an example of an occurrence histogram containing the raw saccade occurrences as described in Section 2.3. The histogram gets transformed into a grey-scale representation by coding the deviation from the baseline probability (expressed in the number of baseline standard deviations). If a bin is coloured light (a peak) this means that within this bin the saccade occurrence probability is larger than on average and a dark coloured bin (a trough) means that within the bin the saccade probability was smaller than on average. To obtain a group effect, the deviations from the baseline were averaged across subjects as shown in the bottom graph. The black line in the bottom graph represents the average deviation across the subjects and the two flanking grey lines represent the average deviation plus or minus one standard error across the subjects.

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).

The results of this analysis for each individual subject will be presented as a grey-scale representation of the occurrence histograms described above. As shown in Fig. 2, these grey-scale histograms were obtained by subtracting the mean bin height from the original occurrence histograms and then dividing each bin by the standard deviation. The grey-scale of each bin thus represents the deviation from the mean bin height expressed in the number of standard deviations. The plotted lines depict the average deviations across the three subjects (black line) plus or minus one standard error across the subjects (grey lines). The grey straight horizontal line represents zero deviation from the baseline. The grey vertical line at 0 s represents the moment of the button press. The thick grey vertical bar represents an estimate of when the actual flip occurred relative to the moment of the button press (a reaction time obtained from the stimulus flip condition). This format for the results will be used throughout this paper.

2.3.3. Fixation positions at the moment of a flip

To investigate the gaze position at the moments of the perceptual flips, we averaged the version and vergence gaze samples during the interval 540–340 ms prior to the moment of the button press (this interval represents an estimate of when the perceptual flip occurred relative to the moment of the button press). We determined whether there was more than one distinct fixation position across all the corresponding flips and we also determined whether there was a distinct fixation location within the background of the stimulus. If this was not the case, the median gaze positions were obtained by taking the median across all the corresponding flips (for the slant rivalry stimulus mirror-symmetric situations were combined). Fixations lying outside the range of the stimulus by more than 1 deg in version angles (incidental fixation in the background) or by more than 1.5 deg in vergence angle (stimulus not properly fused) were discarded. We also discarded the positions for which the standard deviation in the version angles during the −540 to −340 ms was more than 0.5 deg (meaning that a large eye movement occurred during that interval for which it could not be determined whether it occurred before or after the flip). For each individual stimulus we determined whether there were significant differences for the fixation positions between the different percepts and different conditions, using the Kruskal–Wallis test (including the results of both Experiments 1 and 2) with Mann–Whitney post hoc testing.

3. Experiment 1: Natural viewing condition

We first examined the role of saccades for the natural viewing condition for which the subjects were instructed to view the stimulus in a natural way, thus, without trying to influence the reversal rate. Subjects initiated stimulus onset, after which the stimulus was shown for 180 s. The subjects task was to press one of two buttons to indicate their current percept. No fixation restrictions were imposed upon the subjects, thus, the subjects were free to make eye movements. The different stimuli (slant rivalry, Necker cube, binocular grating rivalry, and house–face rivalry stimuli) were presented in separate sessions. Each session contained six trials, which were presented in random order. Two trials within each session were stimulus flip trials and four were perceptual flip trials.

For the slant rivalry stimulus, the four perceptual flip trials within each session consisted of two trials for which perspective specified a negative slant and disparity specified a positive slant. For the other two perceptual flip trials within each session, perspective specified a positive slant and disparity specified a negative slant. For the binocular grating rivalry stimulus, the four perceptual flip trials within each session consisted of two trials for which the left eye viewed the left-oblique grating (with lines from top-left to bottom-right) and the right eye viewed the right-oblique gratings (lines from top-right to bottom-left) and two trials for which the gratings were reversed. Similarly, a session for house–face rivalry contained two trials for which the left eye viewed the image of a house and the right eye viewed the image of a face, and two trials for which the left eye viewed the image of a face and the right eye viewed the image of a house. Depending on the flip and saccade frequency there were two or more sessions per stimulus per subject. Note that for the slant rivalry, Necker cube, and house–face rivalry paradigms, the natural viewing and stimulus flip trials of Experiment 2 were also included in the analysis for Experiment 1.

3.1. Results of Experiment 1

Fig. 3 displays the results of Experiment 1 in which we investigated the correlation between saccades and both stimulus flips (left column) and perceptual flips (right column) for the four perceptual bi-stability paradigms. From top to bottom the panels show the deviation from baseline-saccade probability for slant rivalry, Necker cube rivalry, grating rivalry and house–face rivalry. Within each panel three grey-scale representations of the occurrence histograms are shown, one for each subject (see also Fig. 2). The grey-scale of each bin represents the deviation from the mean bin height expressed in the number of standard deviations. At the bottom of each panel the average deviations across the three subjects (black line) and the average deviation plus or minus one standard error across the subjects (grey lines) are shown. The grey straight horizontal line represents zero deviation from the baseline. The grey

vertical line at 0 s represents the moment of the button press. The thick grey vertical bar represents an estimate of when the actual flip occurred relative to the moment of the button press (a reaction time obtained from the stimulus flip condition).

As noted before we considered a peak or trough in the individual histograms to be significant when two or more neighbouring bins within the peak or the trough differed more than two standard deviations from the mean. The significance of the effects that are mentioned concerning individual conditions has been evaluated according to this criterion. For the stimulus flip condition (left panels), there is, on average, a significant decrease in saccade probability during the interval between the flip and the corresponding button press, for all stimuli. Just after the moment of the button press the occurrence probability of saccades is increased for all but the house–face stimulus.

For the perceptual flip condition there is also a decrease in saccade probability between the moment of the flip and the moment of the button press, for all stimuli. More interestingly, for the binocular rivalry stimuli (grating and house–face) there is an increased saccade probability just before or at the moment of the perceptual flip, indicating that for these stimuli saccades can help to alter the percept. Note that the results for the slant rivalry stimulus (top panels) are consistent with the previously reported results for the speed-up condition for this stimulus (van Dam & van Ee, 2005).

It could be proposed that the difference between the binocular and the perceptual rivalry paradigms is due to a difference in the variance of the button press response times for the different paradigms. However, the variance in the button press response would have to be considerably large to make strong correlations (like the peak before the flip for binocular rivalry) completely disappear (taking into account the bin size of 100 ms in the histograms). Furthermore, a difference in the variance of the button press response would affect peaks and troughs in the histograms alike, since the found patterns of correlation cannot be due to the mere act of pressing buttons (van Dam & van Ee, 2005). Considering that in each of the perceptual flip histograms in Fig. 3 there are clearly correlation patterns visible, we think it very unlikely that such differences in the variance of the response times between the different paradigms, if indeed they exist, can be responsible for the huge differences between the histograms for the perceptual and the binocular rivalry paradigms.

To investigate the role of eye movements in bi-stable perception, it is not only of interest to look at the temporal relationship between saccades and perceptual flips, but also the gaze positions at the moments of perceptual flips should be taken into account. For instance, since the house–face stimulus can be considered as a binocular rivalry stimulus where contrasts differ locally, it is of interest to know whether the saccades that contribute to the peak at the moment of the perceptual flip were directed to a specific stimulus detail. Also for perceptual rivalry stimuli, like the
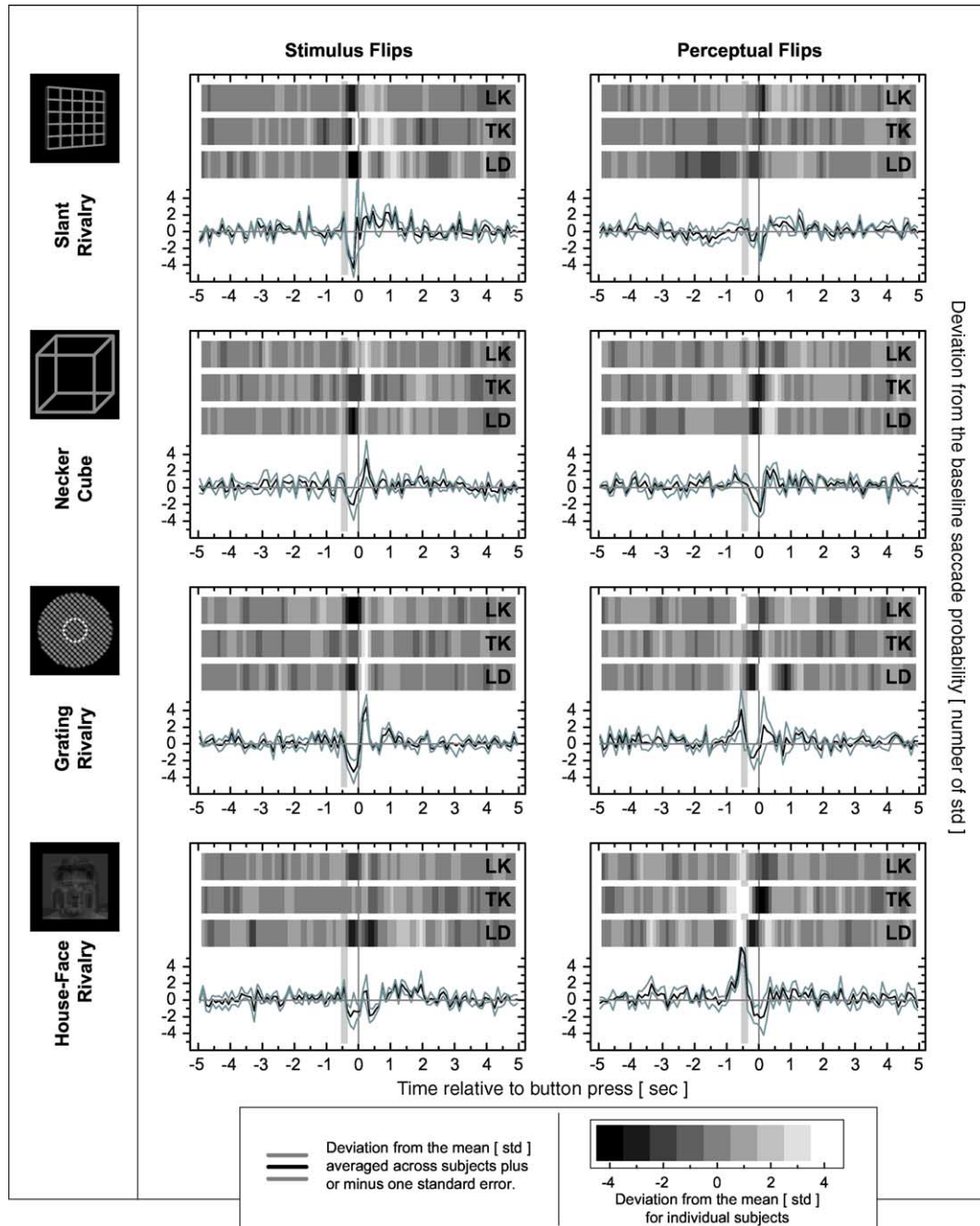
Fig. 3. Results for Experiment 1 in which we investigated the correlation between saccades and perceptual as well as stimulus flips in the natural viewing condition. From top to bottom, the panels show the deviation from the baseline saccade probability versus the time relative to the moment of the button press, for the slant rivalry stimulus, the Necker cube, binocular grating rivalry, and binocular house–face rivalry, respectively. The left panels show the results for the stimulus flip conditions (where the stimulus physically changed). The right panels show the results for the perceptual flip condition. Within each panel three grey-scale representations of the occurrence histograms are shown, one for each subject. The grey-scale in these plots represents the deviation within a bin (100 ms) from the mean bin height (obtained from the bins in the intervals −10.0 to −5.0 s, and 5.0 to 10.0 s, when no correlation is expected), expressed in the number of standard deviations. The graph at the bottom of each panel depicts the average deviations across the three subjects (black line) and the average deviation plus or minus one standard error across the subjects (grey lines). The grey straight horizontal line represents zero deviation from the baseline saccade probability. The grey vertical line at 0 s represents the moment of the button press. The thick grey vertical bar represents an estimate of the moment that the actual flip occurred relative to the moment of the button press (a reaction time obtained from the stimulus flip condition). There is a reduced saccade probability just after the moment of a flip until the moment of the button press for the stimulus flip conditions as well as for the perceptual flip conditions. Note that for the binocular rivalry stimuli (the two lower right panels), there is an increased saccade probability just before or at the moment of a perceptual flip indicating that saccades can help to alter the percept for these stimuli. There is no such increase for the perceptual rivalry stimuli.

Necker cube it has often been reported that fixation position within the stimulus influences the percept and although we did not find a strong positive correlation between saccades and perceptual flips for this stimulus, it could be that the fixation position influence is not time-locked with saccades towards that position. We analyzed the fixation positions at the moment of the perceptual flips as described in Section 2.3.

Examination of the fixation positions at the moment of perceptual flips revealed significant differences ($P < 0.01$) in version angles between the two different percepts for slant rivalry and for the Necker cube. For the two binocular rivalry paradigms (grating and house–face rivalry) no significant differences in fixation positions were found. This indicates that fixation position within the stimulus plays a larger role for perceptual than for binocular rivalry and that the increase in saccade probability at the moment of a perceptual flip for the binocular rivalry paradigms is purely a temporal correlation and thus that the perceptual flips are not locked to saccades towards a specific position in the stimulus. Note that we did not find any difference between the horizontal vergence angles at the moment of the flips to the two different percepts for each stimulus. This indicates that for all stimuli subjects do not alternate the percept by adjusting the fixation depth.

4. Experiment 2: The role of voluntary control

In Experiment 1, we investigated the role of saccades for perceptual alternations in natural viewing conditions, thus when the subjects were instructed not to exert voluntary control over the percept. Several studies have shown that it is possible to influence the perceptual alternation rate by attempting either to hold a percept or to speed up the perceptual flip rate (e.g., Lack, 1978; Meng & Tong, 2004; van Ee et al., 2005). The role of eye movements in the exertion of voluntary control has not been thoroughly investigated. One of the primary goals of the current study is to examine whether subjects use different eye movement schemes, when they attempt to hold a percept, compared to the natural viewing condition.[1] In this experiment the binocular grating stimulus will not be used, since it has been shown that voluntary control has little influence on the percept durations for this stimulus (Meng & Tong, 2004; van Ee et al., 2005).

The stimuli, procedure, and subjects were the same as for Experiment 1. At the start of each trial the subjects were instructed to hold one specific percept during that tri-

al (either left in front or right in front for the slant rivalry stimulus; either bottom-left or top-right cube for the Necker cube; either the house or the face for house–face rivalry). Each session contained six trials of which four were hold percept trials and the remaining two were either stimulus flip trials or natural viewing trials (the data of the stimulus flip trials and the natural viewing trials were included in the analysis for Experiment 1 and the natural viewing trials of Experiment 1 were included in the analysis for Experiment 2).

4.1. Results of Experiment 2

The results of Experiment 2 are shown in Figs. 4A, B, and C for slant rivalry, the Necker cube, and for house–face rivalry, respectively. As noted before, we considered a peak or trough in the individual occurrence histograms to be significant when two or more neighbouring bins within the peak or the trough differed more than two standard deviations from the mean. For each subject, we checked for differences between the histograms for the different viewing conditions by applying the Kolmogorov–Smirnov test in a pairwise manner, using the raw saccade perceptual flip interval data within the ranges −2 to 0 s and 0 to 2 s.

4.1.1. Slant rivalry

For the slant rivalry stimulus the instruction was either to hold the left side in front or to hold the right side in front. For each separate trial the experimenter is able to associate the perceived slant polarities with the disparity-dominated percept or the perspective-dominated percept. We expect the results for the left side in front and the right side in front percepts to be symmetric, but that results can be different between flips to the perspective-dominated percept and flips to the disparity-dominated percept (van Dam & van Ee, 2005). Therefore, we divided the perceptual flips into flips to the disparity-dominated percept and flips to a perspective-dominated percept for each control exertion instruction.

The left and right columns of Fig. 4A show the saccade occurrence histograms for flips to the disparity-dominated percept and for flips to the perspective-dominated percept, respectively. From top to bottom the graphs show the results for the natural viewing condition (of Experiment 1), the hold disparity-dominated percept condition and the hold perspective-dominated percept condition. Each graph represents the average deviations across the three subjects. Inspection of the dominance durations and dominance percentages for the different voluntary control conditions revealed that all subjects were able to adhere to the voluntary control instructions. On average the dominance percentages for the disparity-dominated percept changed significantly from 65% in the natural viewing condition to 78% in the hold disparity-dominated percept condition and to 39% in the hold perspective-dominated percept condition.

---

[1] We did not investigate the role of saccades when subjects were instructed to speed up the alternation rate (speed-up condition), since for some stimuli the alternation rate was already relatively high in the natural viewing condition of Experiment 1. For high alternation rates it becomes hard to resolve the temporal correlation between saccades and perceptual flips. Note also that for the slant rivalry stimulus the temporal correlation between saccades, blinks, and perceptual flips in the 'speed-up' condition has been investigated in an earlier study (van Dam & van Ee, 2005).
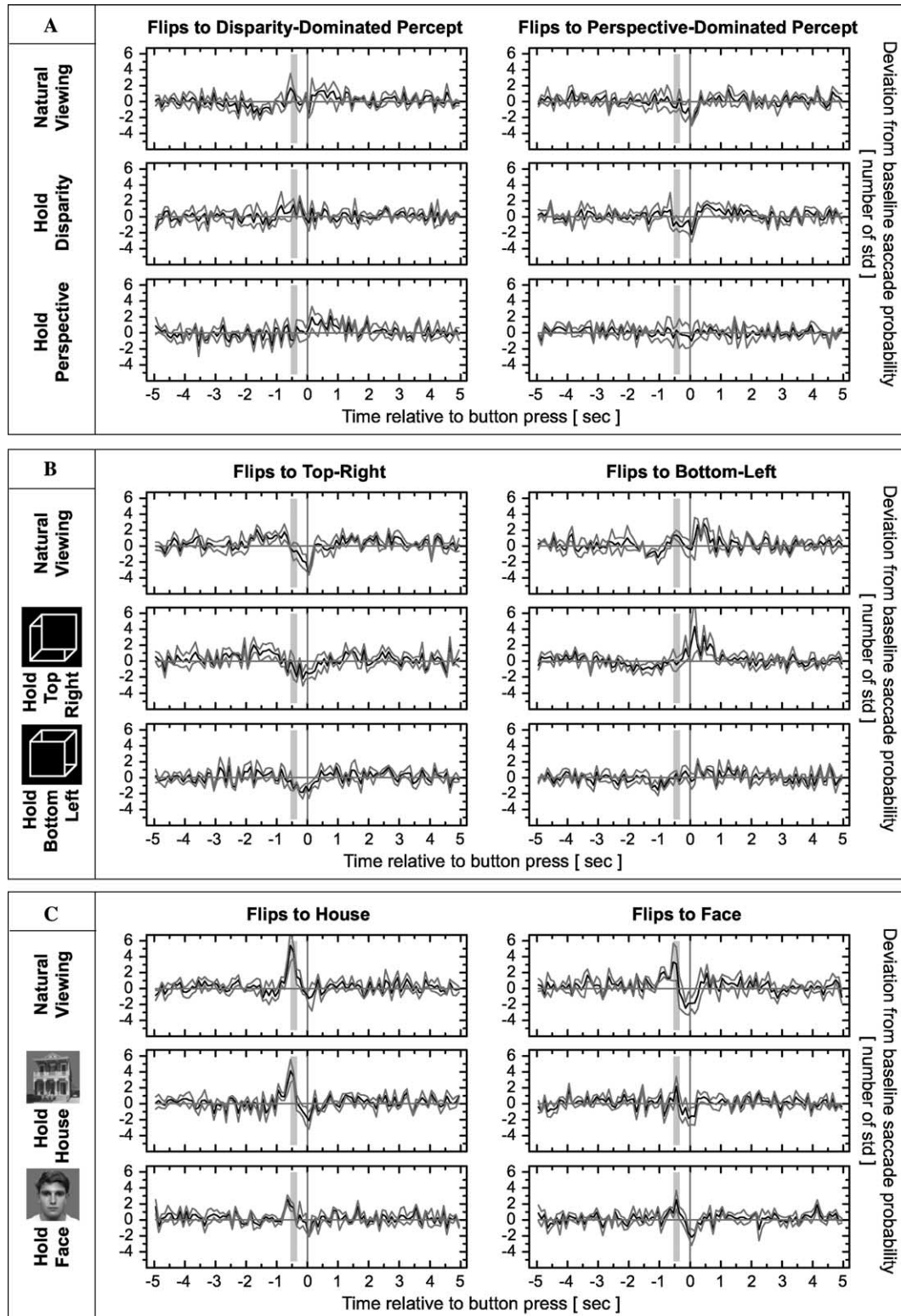
Fig. 4. Similar to Fig. 3 but now only the average deviations across the three subjects are shown for (A), slant rivalry; (B), the Necker cube; and (C) house–face rivalry, for three different control exertion instructions. The top graphs in each panel display the results for the natural viewing instruction of Experiment 1; the middle graphs for the hold disparity-dominated percept, the hold top-right cube, and hold house instructions, respectively; the bottom graphs for the hold perspective-dominated percept, hold bottom-left cube, and hold face instructions, respectively. The left column shows the results for flips to the disparity-dominated percept (A), flips to the top-right cube (B), and flips to the house (C), respectively and the right column for flips to the perspective-dominated percept (A), flips to the bottom-left cube (B), and flips to the face (C), respectively. Within each panel, from top to bottom the correlations appear to be very similar to one another in nature but the amount of correlation in the hold conditions are sometimes different from the amount of correlation in the natural viewing condition. These results indicate that the viewing condition (natural viewing or hold percept) does not influence the nature of the correlation between saccades and perceptual flips.

For flips to the perspective-dominated percept, a decrease in saccade probability occurred, as previously reported (van Dam & van Ee, 2005). For flips to the disparity-dominated percept saccades can occur just before or at the moment of a flip. For the hold conditions the correlation between saccades and perceptual flips is rather similar to the correlation in the natural viewing condition (i.e., for all voluntary control conditions peaks and troughs in the saccade occurrence histograms occur in the same interval relative to the moment of the button press). However, specifically for the hold perspective-dominated percept condition it appears that the amount of correlation is slightly different ($P < 0.05$) compared to the amount of correlation in the natural viewing condition. This difference becomes more evident when subjects' data are analysed separately.

These results indicate that different voluntary control instructions do not lead to different patterns of correlation (different eye movement schemes) but can result in a different amount of correlation. This slight difference in the amount of correlation could be due to a change in the variance of the button press response times with different voluntary control conditions. A relatively higher variance in the button press response times would results in a slight smearing of the effects in the histograms and thus would result in a slight decrease in the amount of correlation.

4.1.2. Necker cube

Fig. 4B portrays the results for the Necker cube. The left and right columns show the occurrence histograms for flips to the top-right percept and for flips to the bottom-left percept, respectively. From top to bottom the graphs show the results for the natural viewing condition (of Experiment 1), the hold top-right percept condition, and the hold bottom-left percept condition. All subjects were able to adhere to the voluntary control instructions. On average the dominance percentages for the top-right cube percept changed significantly from 41% in the natural viewing condition to 56% in the hold top-right cube condition and to 23% in the hold bottom-left cube condition.

Since the two percepts for the Necker cube are physically symmetric, it might be expected that the results for flips to the top-right percept would be similar to the results for flips to the bottom-left percept. However, when the left column is compared with the right column there are differences in the patterns of the histograms ($P < 0.01$). For flips to the top-right percept the saccade probability is decreased at about the moment of the flip until the moment of the button press. For flips to the bottom-left percept there is an increase of saccade probability just after the moment of the button press. Thus, one could conclude that perceptually the two percepts are not symmetric, supporting the frequently reported bias for the two Necker cube percepts. In general, there is a preference to view objects as if viewed from above (e.g., Mamassian & Landy, 1998) and tops of objects appear to be more salient than bottoms (Chambers, McBeath, Schiano, & Metz, 1999). Indeed for the natural viewing condition the average and median percept dura-

tions for the bottom-left percept are longer than the average and median percept durations for the top-right percept (the Kolmogorov–Smirnov statistics indicated a significant difference between the distributions of the durations of the two percepts, for each subject ($P < 0.01$)).

The patterns in the graphs for the two hold conditions are similar to those for the natural viewing condition, but again the amount of correlation can be different for the different voluntary control conditions specifically for flips to the bottom-left percept ($P < 0.01$). Note that this difference in the amount of correlation in the hold conditions relative to the natural viewing condition was also observed for the slant rivalry stimulus.

4.1.3. House–face rivalry

Fig. 4C portrays the results for the house–face stimulus. The left and right columns show the occurrence histograms for flips to the house percept and for flips to the face percept, respectively. From top to bottom the graphs show the results for the natural viewing condition (of Experiment 1), the hold house percept condition, and the hold face percept condition. Subjects were able to adhere to the voluntary control instruction. On average the dominance percentages for the house percept changed significantly from 50% in the natural viewing condition to 60% in the hold house condition and to 37% in the hold face condition.

There are no marked differences between the graphs for flips to the house percept and the graphs for flips to the face percept, although the peak at the moment of the flip appears to be larger for flips to the house percept than for flips to the face percept ($P < 0.01$). For the hold percept conditions the amount of correlation between saccades and perceptual flips appears to be less than for the natural viewing condition ($P < 0.05$). Again this indicates that different voluntary control instructions do not lead to different temporal eye movements schemes, but they can influence the amount of correlation between saccades and perceptual flips.

4.1.4. Fixation positions

The median fixation positions at the moments of perceptual flips are displayed in Fig. 5. Within each panel, the left graph shows for each individual subject the median fixation position in horizontal and vertical version angles, the right graph shows the median horizontal vergence angles. The horizontal line in the right graph represents the depth of the monitor and for subjects LD and TK also the depth of the slant rivalry stimulus is represented. The results for each subject are depicted with a separate symbol (LD: circle, TK: square, and LK: diamond). We did not find any significant differences in average fixation position between the two percepts within each single hold percept condition for each stimulus. Therefore, we grouped the data for the different percepts together. The two different symbol fill types in Fig. 5 represent the two different hold percept conditions. Open symbols depict the results for the hold
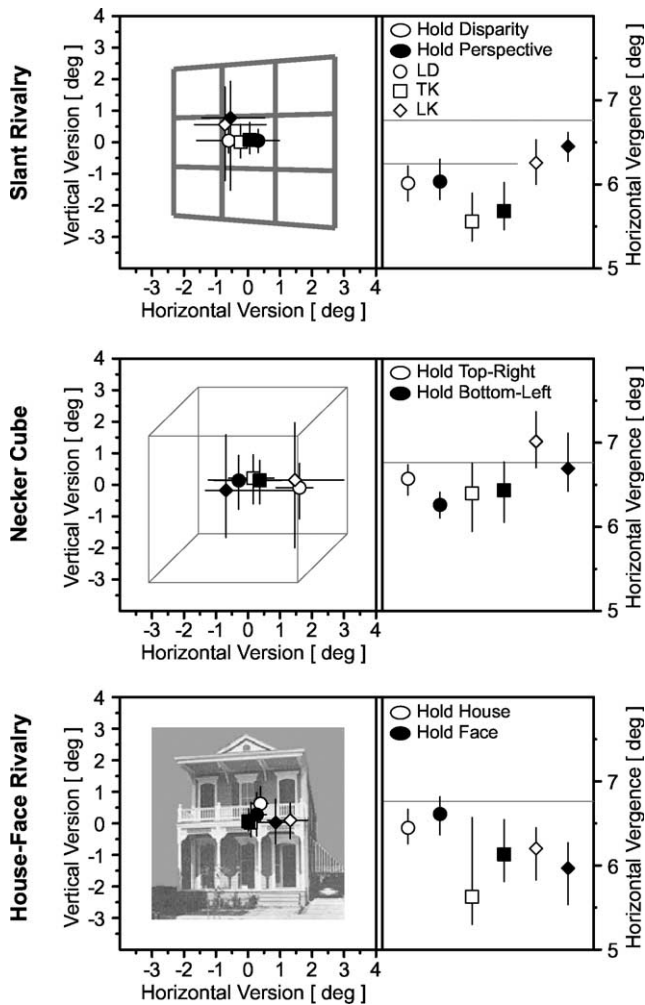
Fig. 5. The median fixation positions at about the moments of perceptual flips for the two different hold percept conditions for the slant rivalry (top), Necker cube (middle), and house–face rivalry (bottom). Since, within each hold percept condition for each stimulus no significant differences were found between the fixation positions at the moment of the flips to the different percepts, we combined the data for all the flips in each condition and compared the two hold percept conditions for each paradigm. Within each panel, the left graph shows the median fixation position in horizontal and vertical version angles, the right graph shows the median horizontal vergence angle for each subject. The horizontal lines in the right graph represents the depth of the monitor (and for the slant rivalry stimulus (top panel) also the depth of the stimulus for subjects LD and TK is portrayed). The results for each subject are depicted with a separate symbol (LD: circle, TK: square, and LK: diamond). The two different fill types represent the two different hold conditions for each rivalry paradigm. The error bars depict the 25% and the 75% quartiles. Between the hold percept conditions for each individual paradigm we found significant differences in fixation position, indicating that fixation positions can be used to bias the percept.

disparity-dominated percept condition (slant rivalry), the hold top-right cube condition (Necker cube), and the hold house percept condition (house–face rivalry). Closed symbols show the results for the other hold percept conditions. The error bars depict the 25% and the 75% quartiles.

For the two different hold conditions for each stimulus there were different preferred fixation positions in version

angles and sometimes even vergence angles ($P < 0.01$).[2] Note, however, that the different hold conditions were measured in separate trials within the same sessions. It is possible that this might have influenced the difference in fixation positions between the two conditions. The results indicate that subjects prefer to look at different aspects of the stimulus when asked to hold either of the different percepts, but that the fixation position by itself does not determine the percept since flips to both percepts for each paradigm occurred when the subject fixated the same location.

5. Discussion

We have examined the role of saccades and fixation positions for perceptual flips in four different bi-stability paradigms: slant rivalry, Necker cube rivalry, grating rivalry, and house–face rivalry. We found that for binocular rivalry (grating rivalry and house–face rivalry) there is a relatively strong positive correlation between saccades and perceptual flips at about the moment of the flip. This indicates that for the binocular rivalry paradigms saccades can play an active role in altering the percept. Analysis of the fixation positions at the moment of the perceptual flips revealed that this positive correlation between saccades and perceptual flips does not have a fixed absolute spatial component (perceptual flips are not locked to saccades towards a specific position in the stimulus). For the perceptual rivalry paradigms (slant rivalry and Necker cube) the positive correlation at the moment of perceptual flips was either absent or very weak (see Fig. 3). For all stimuli the saccade occurrence probability was decreased in the period between a perceptual flip and the corresponding button press as has been previously reported for the slant rivalry stimulus (van Dam & van Ee, 2005).

Another interesting finding is that for all stimuli the pattern of correlation between saccades and perceptual flips did not change with different voluntary control conditions (i.e., increases and decreases in saccade probability occurred at the same temporal interval from the button presses in the different voluntary control conditions). The amount of correlation frequently, but not always, changed when subjects were instructed to hold a percept, compared to when they were instructed not to attempt to influence the percept (Fig. 4). This indicates that subjects do not use different eye movement schemes for perceptual alternations to occur in different voluntary control conditions.

For the perceptual rivalry paradigms (slant rivalry and Necker cube) the fixation position at the moment of a perceptual flip in the natural viewing condition was slightly different for the two possible percepts. It appears that changes in the fixation positions occur after the flip and not before (see also the peak of saccades after a perceptual

---

[2] Although, in some cases, this difference is evident only for individual sessions.

flip in Figs. 3 and 4B). This would suggest that it is the percept that results in a certain fixation position and not the other way around. That perceptual flips can cause shifts in fixation position has been previously reported for the Schroeder staircase and the Necker cube (Einhauser et al., 2004; Pheiffer et al., 1956). The median fixation positions at the moment of a perceptual flip did not differ significantly for the two possible percepts for each paradigm within single hold percept conditions. However, fixation positions did differ between the two hold percept conditions (Fig. 5) for the slant rivalry, the Necker cube, and for the house–face paradigms (although for the latter paradigm the differences were very small). This indicates that fixation position within a rivalrous stimulus by itself does not determine the resulting percept but rather that subjects prefer to look at different aspects of the stimulus when asked to hold either of the two percepts. Several authors reported that fixation position has an influence on the dominance times of the percepts (e.g., Becher, 1910; Ellis & Stark, 1978; Gale & Findlay, 1983; Kawabata, Yamagami, & Noaki, 1978; Necker, 1832; Peterson & Hochberg, 1983; Toppino, 2003; Wundt, 1898).

5.1. Microsaccades

Although the focus of this study was to determine the correlation between any kind of saccade and perceptual flips, our data also enables us to determine the correlation between microsaccades and perceptual flips for each bi-stability paradigm, when we group the data of all the viewing conditions for each individual paradigm together. Investigation of the microsaccades confirmed for all stimuli what was already found in a previous study (van Dam & van Ee, 2005), part of which was focussed on microsaccades, that microsaccades are not likely to be actively involved in alternating the percept but that perceptual alternations can cause microsaccades.

5.2. Blinks

We did not specifically focus on the role of blinks for perceptual alternations, but the blinks we did collect can give us an indication of the role of blinks in perceptual and binocular rivalry. As has been reported before (Ito et al., 2003; van Dam & van Ee, 2005), we observed that for the perceptual rivalry stimuli (slant rivalry and Necker cube rivalry) a decrease in blink probability occurred between the moment of the flip until the moment of the corresponding button press. After the moment of the button press we observed an increase in blink probability. For the binocular rivalry stimuli (grating and house–face) we furthermore observed an increase in the blink probability just before or at the moment of the perceptual alternation. This indicates that, like saccades, blinks can also play an active role in inducing a perceptual alternation for binocular rivalry. It can be suggested that blinks as well as saccades influence the visual processing at early stages (which

play a large role in binocular rivalry) but not necessarily at the later levels of spatial representations (which are necessary for the interpretation of the Necker cube and the slant rivalry stimulus).

6. Conclusion

Our main conclusion is that for binocular rivalry (grating and house–face rivalry), rather than for perceptual rivalry (slant and Necker cube rivalry), there is a marked positive correlation between saccades and perceptual flips at about the moment of the perceptual flip, indicating that for these paradigms, saccades are likely to play an active role in altering the percept. The pattern of temporal correlation did not change with different voluntary control conditions, indicating that subjects do not use different temporal eye movement schemes to exert voluntary control.

For the perceptual rivalry paradigms, but not for the binocular rivalry paradigms, we found small differences in fixation positions for flips to the two different percepts in the natural viewing condition. Between the two hold percept conditions we found significant differences in fixation positions at the moments of perceptual flips. This indicates that, although fixation position within a stimulus does not by itself determine the percept, subjects prefer to look at different positions for different hold percept conditions.

References

Alexander, L. T. (1951). The influence of figure–ground relationships in binocular rivalry. *Journal of Experimental Psychology, 41*, 376–381.

Becher, E. (1910). Über umkehrbare Zeichnungen. *Archiv für die gesamte Psychologie, 16*, 397–417.

Blake, R. R., Fox, R., & McIntyre, C. (1971). Stochastic properties of stabilized image binocular rivalry alternations. *Journal of Experimental Psychology, 88*, 327–332.

Breese, B. B. (1899). On inhibition. *Psychological Monographs, 3*, 1–65.

Chambers, K. W., McBeath, M. K., Schiano, D. J., & Metz, E. G. (1999). Tops are more salient than bottoms. *Perception & Psychophysics, 61*, 625–635.

Davis, K. A., & Voigt, H. F. (1997). Evidence of stimulus-dependent correlated activity in the dorsal cochlear nucleus of decerebrate gerbils. *Journal of Neurophysiology, 78*, 229–247.

Einhäuser, W., Martin, K. A. C., & König, P. (2004). Are switches in perception of the Necker cube related to eye position? *European Journal of Neuroscience, 20*, 2811–2818.

Ellis, S. R., & Stark, L. (1978). Eye movements during the viewing of Necker Cubes. *Perception, 7*, 575–581.

Engbert, R., & Kliegl, R. (2003). Microsaccades uncover the orientation of covert attention. *Vision Research, 43*, 1035–1045.

Gale, A. G., & Findlay, J. M. (1983). Eye movement patterns in viewing ambiguous figures. In R. Groner, C. Menz, D. F. Fisher, & R. A. Monty (Eds.), *Eye movements and psychological functions: international*

views (pp. 145–169). Hillsdale, New Jersey: Lawrence Erlbaum Associates.

Glen, J. S. (1940). Ocular movements in reversibility of perspective. *The Journal of General Psychology, 23*, 243–281.

Ito, J., Nikolaev, A. R., Luman, M., Aukes, M. F., Nakatani, C., & van Leeuwen, C. (2003). Perceptual switching, eye movements, and the bus paradox. *Perception, 32*, 681–698.

Kawabata, N., Yamagami, K., & Noaki, M. (1978). Visual fixation points and depth perception. *Vision Research, 18*, 853–854.

Lack, L. C. (1971). The role of accommodation in the control of binocular rivalry. *Perception & Psychophysics, 10*, 38–42.

Lack, L. C. (1978). *Selective attention and the control of binocular rivalry.* The Netherlands, Mouton: The Hague.

Levelt, W. J. M. (1966). The alternation process in binocular rivalry. *British Journal of Psychology, 57*(3 and 4), 225–238.

Mamassian, P., & Landy, M. S. (1998). Observer biases in the 3D interpretation of line drawings. *Vision Research, 38*, 2817–2832.

McDougall, W. (1903). The physiological factors of the attention-process III. *Mind, 12*, 473–488.

Meng, M., & Tong, F. (2004). Can attention selectively bias bistable perception? Differences between binocular rivalry and ambiguous figures. *Journal of Vision, 4*, 539–551.

Necker, L. A. (1832). Observations on some remarkable optical phenomena seen in Switzerland; and on an optical phenomenon which occurs on viewing a figure of a crystal of geometrical solid. *London and Edinburgh Philosophical Magazine and Journal of Science, 1*, 329–337.

Perkel, D. H., Gerstein, G. L., & Moore, G. P. (1967). Neuronal spike trains and stochastic point processes II. Simultaneous spike trains. *Biophysical Journal, 7*, 419–440.

Peterson, M. A., & Hochberg, J. (1983). Opposed-set measurement procedure: A quantitative analysis of the role of local cues and intention in form perception. *Journal of Experimental Psychology: Human Perception and Performance, 9*, 183–193.

Pheiffer, C. H., Eure, S. B., & Hamilton, C. B. (1956). Reversible figures and eye-movements. *American Journal of Psychology, 62*, 452–455.

Pritchard, R. M. (1958). Visual illusions viewed as stabilized retinal images. *Quaterly journal of experimental psychology, 10*, 77–81.

Scotto, M. A., Oliva, G. A., & Tuccio, M. T. (1990). Eye movements and reversal rates of ambiguous patterns. *Perceptual and Motor Skills, 70*, 1059–1073.

Tong, F., Nakayama, K., Vaughan, J. T., & Kanwisher, N. (1998). Binocular rivalry and visual awareness in human extrastriate cortex. *Neuron, 21*, 753–759.

Toppino, T. C. (2003). Reversible-figure perception: Mechanisms of intentional control. *Perception & Psychophysics, 65*, 1285–1295.

van Dam, L. C. J., & van Ee, R. (2005). The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry. *Vision Research, 45*, 2417–2435.

van Ee, R. (2005). Dynamics of perceptual bi-stability for stereoscopic slant rivalry and a comparison with grating, house-face, and Necker cube rivalry. *Vision Research, 45*, 29–40.

van Ee, R., & Richards, W. (2002). A planar and a volumetric test for stereoanomaly. *Perception, 31*, 51–64.

van Ee, R., van Dam, L. C. J., & Brouwer, G. J. (2005). Voluntary control and the dynamics of perceptual bi-stability. *Vision Research, 45*, 41–55.

van Ee, R., van Dam, L. C. J., & Erkelens, C. J. (2002). Bi-stability in perceived slant when binocular disparity and monocular perspective specify different slants. *Journal of Vision, 2*, 597–607.

Wundt, W. (1898). Die geometrisch-optischen Täuschungen. *Abhandlungen der mathematisch-physischen Classe der Königlich Sächsischen Gesellschaft der Wissenschaften, 24*, 55–83.