

Ambiguities in visual perception  
The aperture problem and the role of eye movements in perceptual  
bistability

Loes C.J. van Dam

Helmholtz  Instituut

School for Autonomous Systems Research

# Veur mien Pap en Mam

The cover illustration is a stereogram that can be viewed with red-green glasses to obtain a depth impression. Make sure that the red filter is in front of the left eye and the green filter is in front of the right eye. For information on this stereogram see the contents of this thesis.

De kaft is één groot stereogram dat bekeken kan worden met een rood-groen brilletje om een diepte-indruk te krijgen. Zorg ervoor dat het rode filter links zit en het groene rechts. Lees de inhoud van dit proefschrift voor meer informatie over dit stereogram.

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**Ambiguities in visual perception**  
**The aperture problem and the role of eye movements**  
**in perceptual bistability**

Ambigüiteiten in visuele perceptie  
Het apertuurprobleem en de rol van oogbewegingen in bistabiele  
waarneming

(met een samenvatting in het Nederlands)

**Proefschrift**

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**Loes Catharina Jacobus van Dam**

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**Promotor:** Prof.Dr. Casper J. Erkelens

**Co-promotor:** Dr. Raymond van Ee

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# Contents

<b>1</b>	<b>General introduction</b>	<b>7</b>
1.1	The matching problem . . . . .	7
1.2	Perceptual bistability . . . . .	9
1.3	Perceptual bistability: the role of voluntary control . . . . .	11
1.4	Perceptual rivalry versus binocular rivalry: One mechanism? . . . . .	12
1.5	The outline of this thesis . . . . .	13
<b>2</b>	<b>Stereoscopic matching and the aperture problem</b>	<b>15</b>
2.1	Introduction . . . . .	16
2.2	General Methods . . . . .	20
2.3	Experiment 1: Vertical Aperture . . . . .	24
2.4	Experiment 2: Various aperture orientations . . . . .	27
2.5	Control Experiment: Aperture imposed matching direction . . . . .	32
2.6	Discussion . . . . .	35
<b>3</b>	<b>The role of (micro)saccades and blinks in perceptual bi-stability from slant rivalry</b>	<b>37</b>
3.1	Introduction . . . . .	38
3.2	Experiment 1: Slant estimates . . . . .	40
3.3	Experiment 2: Gaze positions . . . . .	44
3.4	Experiment 3: Correlation between (micro)saccades, blinks and perceptual flips . . . . .	49
3.5	Experiment 4: The role of button presses . . . . .	57
3.6	Discussion . . . . .	60
<b>4</b>	<b>The role of saccades in exerting voluntary control in perceptual and binocular rivalry</b>	<b>65</b>
4.1	Introduction . . . . .	66
4.2	General Methods . . . . .	67
4.3	Experiment 1: Natural Viewing Condition . . . . .	73
4.4	Experiment 2: the Role of Voluntary Control . . . . .	77
4.5	Discussion . . . . .	83
<b>5</b>	<b>Local retinal image changes, rather than saccades per se, trigger perceptual alternations in grating rivalry</b>	<b>85</b>
5.1	Introduction . . . . .	86

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5.2	Experiment 1: comparison of monocular and binocular rivalry . . . . .	87
5.3	Experiment 2: binocular rivalry and fixation . . . . .	93
5.4	Experiment 3: retinal image changes without saccades . . . . .	95
5.5	Discussion . . . . .	97
<b>6</b>	<b>Summary and conclusions</b>	<b>101</b>
<b>7</b>	<b>Samenvatting en conclusies</b>	<b>103</b>
	<b>References</b>	<b>107</b>
	<b>Publications</b>	<b>115</b>
	<b>Dankwoord</b>	<b>117</b>
	<b>Curriculum Vitae</b>	<b>119</b>

# Chapter 1

## General introduction

As human beings we continuously interact with the 3-dimensional world that surrounds us. Our senses are the window through which we perceive this 3D world, and one of the senses we mostly rely on is vision. Vision enables us to detect light which is scattered by objects in our visual field. The light coming from the 3D environment is projected on the retina of the eye which results in a essentially 2D image. A large portion of our brain is continuously engaged to reconstruct a 3D interpretation of these 2D retinal images. One source of information to reconstruct the third dimension of depth is binocular disparity. Binocular disparities are slight differences between the two retinal images, due to the slightly different viewpoints of our two eyes (see for instance figures 1.1, 1.2 and 1.4). The ability to retrieve depth information from these binocular disparities is called stereo-vision or stereopsis. Other cues that can be used are linear perspective, motion parallax, occlusion etc. For most of these cues the processing is based on assumptions or priors about the world around us and these priors allow us to pick a most likely 3D-interpretation of the multitude of theoretically possible 3D-interpretations to the same 2D retinal images. However, the priors are not always correct, leading to visual illusions, and sometimes the visual ambiguity is not completely resolved and the resulting percept will alternate between different interpretations to the same visual input (multi-stable perception). By studying such visual ambiguities we can learn more about the visual system and perhaps visual awareness. Visual ambiguities therefore, play a large role in the scientific field of visual perception.

### 1.1 The matching problem

One example of a visual ambiguity which is usually resolved into one percept is the matching problem. Consider the figure 1.1. The left image shows the image for the left eye and the middle image shows the image for the right eye. In order to obtain depth information from these two images, the features (for the purpose of this example let us assume the small squares or dots) in the left image have to be *matched* to similar features in the right image. Disregarding any further information, for instance about the position of the two eyes, there would theoretically be a multitude of possible matches between these two images, since each dot in one image can be matched to any of the dots in the other image. Even taking information about the horizontal alignment of the two eyes

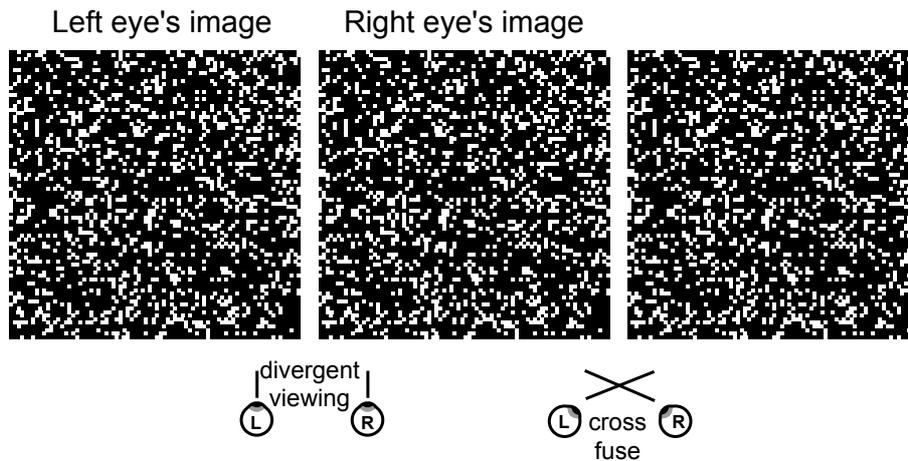


Figure 1.1: *Random dot stereogram, an example of visual ambiguity that is usually resolved. Divergent viewers should fuse the left two images. Crossfusers should fuse the right two images. In theory, every dot in the left image (the image for the left eye) could be matched to any dot in the middle image (the image for the right eye) which leads to a multitude of possible solutions to combine these two images and calculate the disparities. However, readers who are able to fuse these images will have no problem detecting the two concentric circles which are hidden in this stereogram.*

into account, and thus choosing a horizontal matching direction, there is still more than one solution to this problem. However, if we project these image on the two retinae we perceive one single stable percept instead of a vague mix of multiple interpretations. How does our visual system do this? What information is used and what assumptions are being made by the system? As noted above, the matching direction between the two eyes retinal images is part of the solution to the matching problem. A horizontal matching direction seems logic, since our eyes are horizontally aligned but, there is evidence that matches can occur in other directions as well (e.g. Stevenson & Schor, 1997; van Ee & Schor, 2000). For instance van Ee & Schor (2000) investigated the assigned disparity for an ‘infinitely’ long line and found a ‘default’ matching direction which had a vertical component. It is also known that visible end points of lines can be used by the visual system for determining the assigned disparity (Mitchison & McKee, 1987; van Ee & Schor, 2000). This indicates that the visual system uses different solutions with different amounts of available visual information in order to resolve the ambiguity of the matching problem. This leads to an interesting question: what happens when the ‘infinitely’ long line of van Ee & Schor (2000) is occluded at the flanks, resulting in visible ‘termination’-points of the line where the line intersects with the occluders. Does the visual system use these intersection points to obtain a match between the two line half-images, or does the visual system recognize the situation as an occlusion of a longer line and therefore use the default match, as determined by van Ee & Schor (2000)? Some studies concerning the role of intersection points in the binocular matching problem concluded that intersections do not play a role for determining the matching direction, but that components of the half-images that are left unpaired by using a fixed matching direction (meaning that part of the image in one eye is not matched to any part of the image in the other eye) signal to the brain

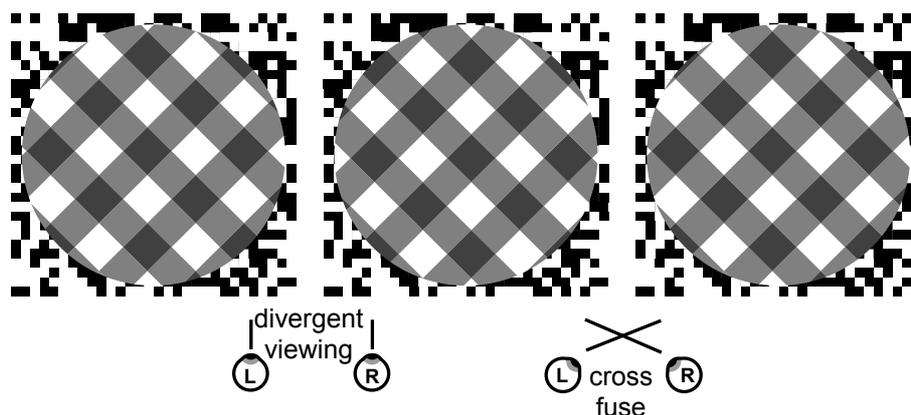


Figure 1.2: *Stereoplaid*. Divergent viewers should fuse the left two images. Crossfusers should fuse the right two images. Farell (1998) showed that for short stimulus presentations the two independent gratings are seen as one plaid for which the intersections determine the perceived depth. With prolonged viewing either of two interpretations can be perceived alternately (bistable perception): two gratings which are segregated in depth or one plaid on a single depth plane.

that there must be an occlusion (Anderson, 1994; Anderson & Nakayama, 1994; Malik, Anderson & Charowhas, 1999; Nakayama & Shimojo, 1990). In these studies unambiguous features of the partially occluded objects disambiguated the matching direction. For more ambiguous situations there is evidence that intersections *can* play a very important role for determining the assigned disparities (Farell, 1998).

Consider for instance figure 1.2 which shows a stereo-pair of two independent orthogonal gratings, each with its own disparity. If the matching direction is always a default direction, then the visual system should have no problem segregating the two gratings at their separate depth planes. However, the intersection points of the two gratings could also be the determinant features for obtaining a matching direction and this would lead to the percept of one single plaid instead of two independent gratings. By using similar ‘stereoplaid’, Farell (1998) showed that for short stimulus durations the two gratings are primarily perceived as one single plaid and that it is indeed the intersections between the two gratings that determined the perceived depth of this plaid. With prolonged viewing however, both interpretations appear alternately over time, which leads us to the subject of perceptual bistability.

## 1.2 Perceptual bistability

Perceptual bistability occurs when two possible interpretations of the same stimulus ‘compete’ or ‘rival’ for perceptual dominance and the percept alternates between these two interpretations. A well-known example is the Necker Cube shown in figure 1.3 (Necker, 1832). The top panel of figure 1.3 represents the original cube and in the bottom panel the two possible interpretations are shown. Scientific studies of such phenomena start appearing in the 19th century and several of these studies suggested that eye movements were responsible for the perceptual alternations by shifting the image on the retina and thereby changing the retinal input (Necker, 1832; Wundt, 1898). Other studies suggested

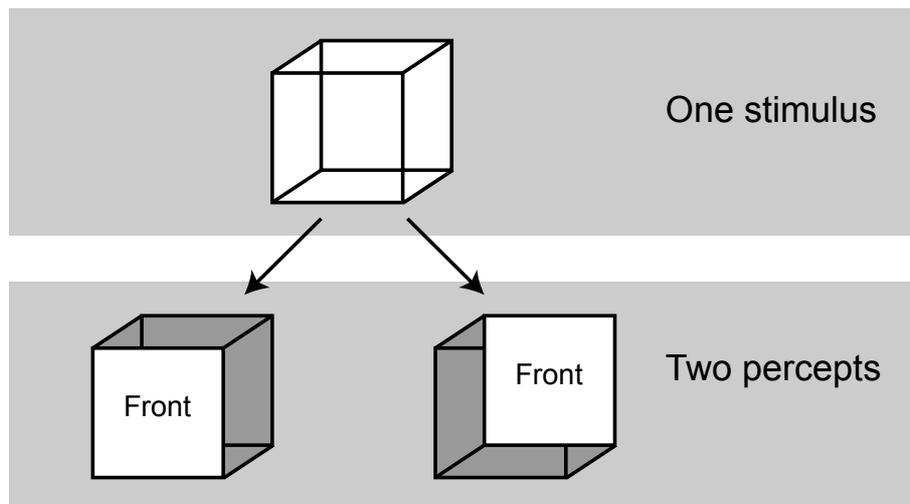


Figure 1.3: *Top panel: the Necker Cube, which is an example of a stimulus which has two possible perceptual interpretations. Bottom panel: The two possible interpretations of the Necker Cube. Over time the percept of the original Necker cube changes from one to the other interpretation and vice versa. These percept changes are called perceptual alternations, flips, reversals or switches.*

that the alternation between the two percepts, represents some cognitive process occurring in the brain, and that the alternation process can be influenced by focussing our attention on a specific interpretation or aspect of the stimulus (Becher, 1910; von Helmholtz, 1910; McDougall, 1903). Since several authors showed that perceptual alternations are possible with stimuli that are more or less stabilized on the retina it has been implicitly agreed that perceptual bistability is instigated by a central process in our brain for which eye movements at least are not necessary (Blake, Fox & McIntyre, 1971; Lack, 1971; McDougall, 1903; Pritchard, 1958; Scotto, Oliva & Tuccio, 1990). Therefore, by studying perceptual bistability we might gain knowledge about the central processes that are involved in visual awareness. But, in order to interpret the results from such studies correctly, it *is* necessary to take eye movements into account, since there is also evidence that there is at least some interaction between eye movements and perceptual alternations when eye movements are allowed (e.g. Becher, 1910; Einhäuser, Martin & König, 2004; Glen, 1940; Ito, Nikolaev, Luman, Aukes, Nakatani & van Leeuwen, 2003; Necker, 1832; Pheiffer, Eure & Hamilton, 1956; Wundt, 1898). Whether it is the eye movement that facilitates a perceptual alternation or the alternation that facilitates an eye movement is still a matter of much debate.

To study perceptual bistability there are many stimuli to choose from. A few years ago an interesting bistability paradigm called slant rivalry was re-introduced (van Ee, van Dam & Erkelens, 2002; Wheatstone, 1852). An example of the slant rivalry stimulus is shown in figure 1.4. The stimulus consists of a planar grid which is rotated about a vertical axis. Linear perspective indicates that the right side is farther away than the left side. However, when the stereogram half-images are properly fused and attention is focussed on binocular disparity it can be seen that it is the the left side that is farther away than the right side. With prolonged viewing the percept will alternate between a perspective-dominated percept and a disparity-dominated percept and the alternation

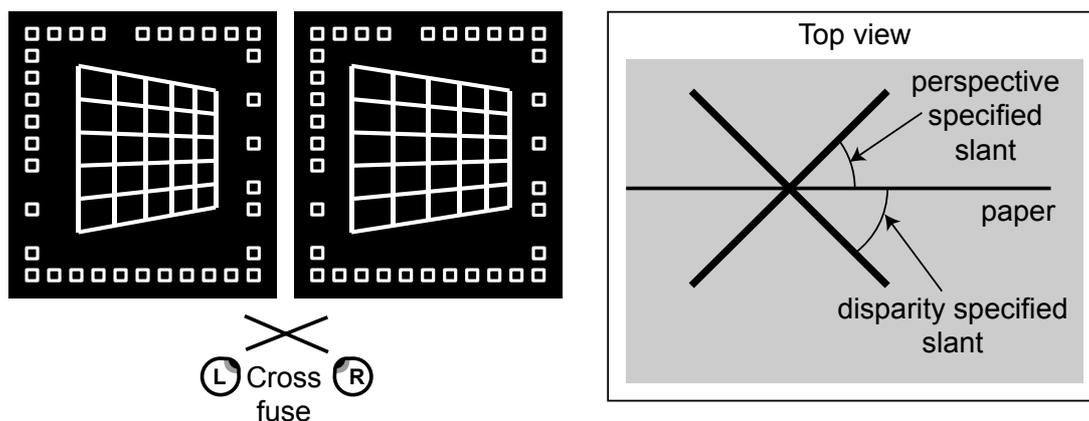


Figure 1.4: *Slant rivalry*. *Linear perspective specifies a slant from left side near to right side far. When the images are properly fused, the binocular disparities will specify a slant from left side far to right side near. With prolonged viewing the percept will alternate between a perspective-dominated percept and a disparity-dominated percept.*

process is a result of the conflict between the two depth cues. Slant rivalry presents us with an interesting form of perceptual bistability, since for this stimulus the conflict between the two percepts can be changed parametrically by manipulating the independent depth cues in the stimulus. When the conflict is very small (disparity and perspective specifying similar slants), the depth cues are combined in order to form one single percept and no rivalry occurs. Thus slant rivalry also provides us with information about the integration of the two different depth cues. Since, slant rivalry has only recently been introduced as a perceptual bistability paradigm, many aspects of the paradigm need to be investigated. One of the important aspects is the role of eye movements for perceptual alternations to occur in order to establish whether the alternation process for this particular paradigm is central.

### 1.3 Perceptual bistability: the role of voluntary control

Since perceptual bistability is considered to be a central process it is of interest to examine to what extent we are able to consciously influence what we see when we view such ambiguous figures. This issue has been addressed by several authors by studying percept durations and perceptual alternation rates in different voluntary control conditions, like trying to hold a specific percept or to speed up/slow down the alternation rate (for recent studies see for instance Hol, Koene & van Ee, 2003; Meng & Tong, 2004; Toppino, 2003; van Ee, van Dam & Brouwer, 2005). The results from such studies indicate that we do have some influence on what we perceive, but different ambiguous figures allow for different amounts of voluntary control (Meng & Tong, 2004; van Ee, van Dam & Brouwer, 2005). One question that remains relatively unaddressed however, is the extent to which eye movements are responsible for the exertion of voluntary control in perceptual bistability. If, for instance, there is a positive correlation between eye movements and perceptual

alternations, observers might be able to influence the percept by (consciously or unconsciously) applying a specific eye movement strategy, meaning that there does not have to be any other, more central mechanism to influence the percept (e.g. top-down attentional processes). Thus, in order to examine to what extent central top-down processes are responsible for voluntary control in perceptual bistability, it is necessary to take eye movements into account. Hitherto, the combination of voluntary control and the role of eye movements has not been investigated thoroughly, but for instance for the example of the Necker cube Toppino (2003) studied perceptual alternations 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 did 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) and found that there was a positive correlation between perceptual alternation frequency and eye movement frequency. Although, these studies provide some insights into the role of eye movements in exerting voluntary control, they are not very specific about the precise interaction between the two.

## 1.4 Perceptual rivalry versus binocular rivalry: One mechanism?

As noted above there are many stimuli that instigate perceptual bistability. One important type that so far has not yet been introduced in this thesis is binocular rivalry. In binocular rivalry each eye is presented with a different stimulus and the two retinal images are not fused to form one percept but instead compete for perceptual dominance. Usually the stimuli for the two individual eyes are gratings that differ in orientation by 90 degrees (see figure 1.5 left panel) but binocular rivalry occurs for any combination of stimuli provided that the images for the two eyes are sufficiently dissimilar, for instance when one eye is presented with the image of a house and the other eye with the image of a face (Tong, Nakayama, Vaughan & Kanwisher, 1998, see figure 1.5 right panel). By some researchers binocular rivalry is seen as something different from other types of rivalry. They argue that for binocular rivalry it appears to be the retinal image of one eye that rivals with the retinal image of the other eye, whereas for other stimuli, e.g. the Necker cube, it appears to be one possible interpretation or percept of a stimulus that rivals with another interpretation / percept (hence leading to the name perceptual rivalry). Other researchers argue that binocular rivalry and perceptual rivalry are just different manifestations of the same or similar alternation mechanisms (for reviews on this controversy see for instance Blake, 2001; Blake & Logothetis, 2002; Leopold & Logothetis, 1999; Tong, 2003). If the latter is true, then both perceptual and binocular rivalry should similarly depend on for instance attention or voluntary control. Therefore, in order to resolve the question whether binocular and perceptual rivalry are due to the same rivalry mechanism, it might be useful to investigate such aspects for both types of rivalry in the same study and compare the results as has been done by Meng & Tong (2004); van Ee, van Dam & Brouwer (2005).

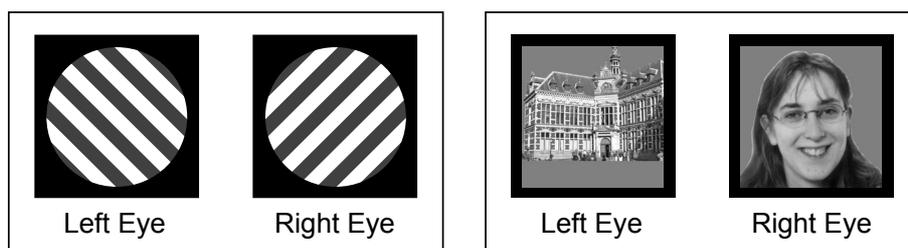


Figure 1.5: *Left panel: the left and right eye are presented with gratings that differ in orientation by 90 degrees. The image seen by the left eye and the image seen by the right will be perceived alternately. Right panel: another example of binocular rivalry where one eye views the image of a house and the other eye views the image of a face.*

Also the role of eye movements or differences therein for perceptual and binocular rivalry might provide useful insights to this question.

## 1.5 The outline of this thesis

The research reported in this thesis is devoted to visual ambiguities and the bistable percepts in which they can result. As noted above, for some ambiguities our visual system picks one possibility of a multitude of possible perceptual interpretations and this leads to one single and stable percept. An example of such an ambiguity is the aperture problem for stereopsis, for which our matching system usually picks one of a theoretically infinite number of solutions. In the **second chapter** we investigated this aperture problem by examining the disparity that is assigned to an ‘infinitely’ long test line seen through an aperture. We determined the assigned disparity for the test line for different contextual situations. This second chapter only concerns binocular disparity information (stereovision).

In the **third chapter** we investigated the perception of a slanted plane when the depth cues of binocular disparities (stereo-information) and linear perspective (which essentially is a monocular cue) were manipulated independently. When these cues specify similar slants our visual system combines these cues to provide one single percept. However, when the conflict between these two sources of depth information is large, then the percept alternates between a perspective-dominated percept and a disparity-dominated percept (slant rivalry). Thus, large perspective versus disparity conflicts lead to perceptual bistability of one single stable stimulus. We studied the perceived slants for the perspective and disparity-dominated percepts for different perspective versus disparity conflicts and in order to determine whether the alternation between the two possible percepts is a central process (occurring within our brain) we investigated the role of eye movements for this specific bistability paradigm.

In the **fourth chapter** we further investigated the role of eye movements in perceptual bistability for several bistability paradigms and compared results for perceptual rivalry (Necker cube rivalry and slant rivalry) and binocular rivalry (grating and house-face stimuli). We investigated whether there was an interaction between voluntary control in percept dominance and eye movements schemes for three different paradigms (slant rivalry,

Necker cube rivalry and house-face rivalry). One of the interesting findings in this chapter is that for binocular rivalry there is a high positive correlation between eye movements and perceptual alternations. In the **fifth chapter** we investigated whether this correlation represented an intrinsic link between eye movements and perceptual alternations or if this correlation is due to the retinal changes due to the eye movements.

In **chapter six** we offer a summary of the results.

## Chapter 2

# Stereoscopic matching and the aperture problem

### Abstract

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In order to perceive stereoscopic depth, the visual system must define binocular disparities. Consider an oblique line seen through an aperture formed by flanking occluders. Because the line is perceived behind the aperture the line must have disparity relative to the aperture. What is the assigned disparity of the line in this aperture problem? To answer this question five observers adjusted the horizontal disparity of a probe until it was perceived at the same depth as the disparate line behind the aperture. The results show that, when both the horizontal and the vertical disparities of the occluders are well defined, the probe must have the same horizontal disparity as the horizontal separation between the line half-images in order to be perceived at the same depth. However, when the horizontal and vertical disparities of the occluders are ill-defined, the intersections of the line and the occluder borders can determine the assigned horizontal disparity for the test line. In the latter case the matching direction varies with the aperture orientation and there is considerable variability across observers.

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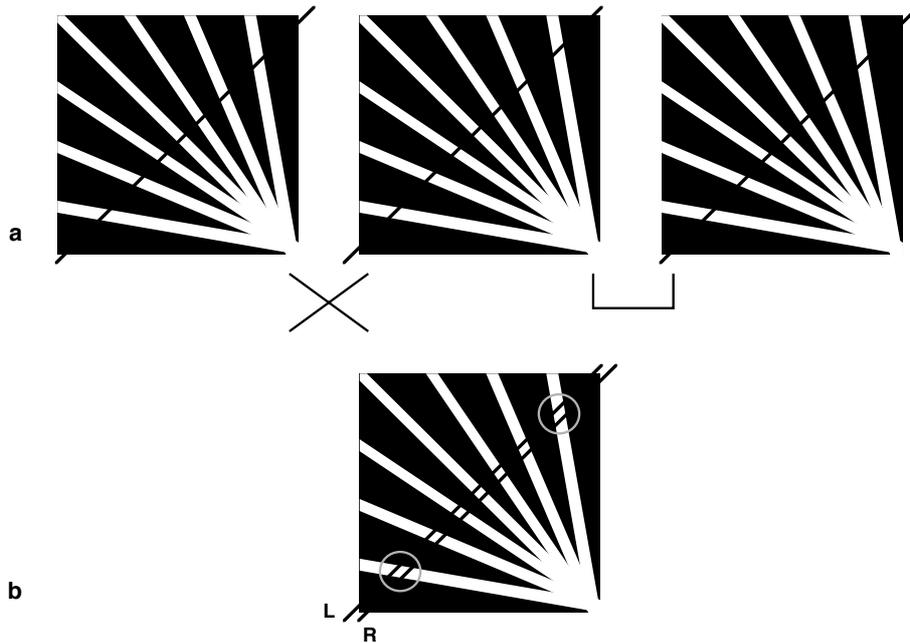


Figure 2.1: a) *Demonstration of the aperture problem for stereopsis. Crossfusers should fuse the left two images. Divergers should fuse the right two images.* b) *Superposition of the half-images of the stereogram. The shift of the half-images of the line changes with aperture orientation from nearly horizontal (grey circle bottom left) to nearly vertical (grey circle top right).*

## 2.1 Introduction

The stereogram in figure 2.1 shows a horizontally shifted line and a zero disparity occluder.<sup>1</sup> When the two stereogram half-images are being fused, the line clearly appears behind the occluder and all parts of the line have the same depth. In figure 2.1b the two half-images are superimposed, showing that the horizontal shift of the line results in shifts in several directions across the straight apertures.

Is the line in figure 2.1 binocularly matched according to these aperture induced shifts or is there a single matching direction for all these line parts? More generally, what is the assigned disparity of a line that is observed through an aperture? To investigate this problem it is useful to concentrate on conditions in which matching is unconstrained.<sup>2</sup> Note that in figure 2.1 the end points of the test line are visible and these points might constrain the match for the whole line by interpolation (Mitchison & McKee, 1987; van Ee & Schor, 2000). Figure 2.2 shows a stereogram similar to that of figure 2.1, but now the end points of the test line are no longer visible. The line has a well defined non-zero horizontal shift relative to the occluders. When the half-images are being fused the test line will appear behind the occluders. Considering that the test line could theoretically have

<sup>1</sup>For consistency disparity is specified in screen coordinates and not in retinal coordinates.

<sup>2</sup>The horizontal and vertical tolerance to disparity for binocular fusion was described by Tyler (1975) and their dynamics by Schor & Tyler (1981). These studies were primarily interested in disparity limits for fusion and used constrained matching features. We are primarily interested in the stimulus locations that become matched from the multitude of possible locations that can be fused in *unconstrained* matching stimuli.

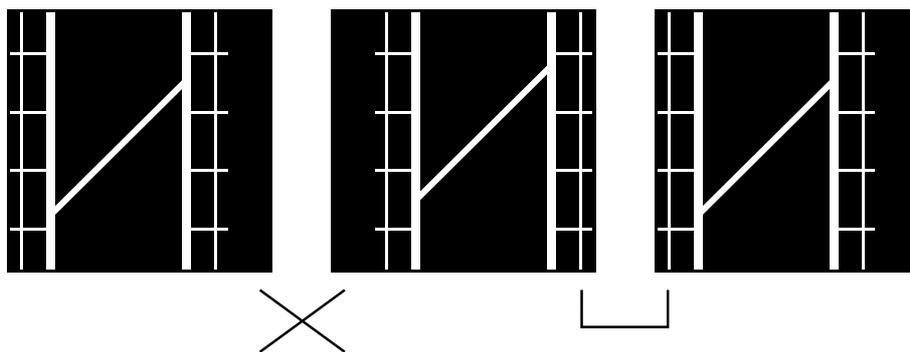


Figure 2.2: *Stereogram depicting an oblique line seen through a vertical aperture formed by flanking occluders.*

its end points everywhere behind the occluder, matching of the line is highly ambiguous. This means that a point on one half-image of the line could theoretically be matched with every point of the other eye's half-image.

Although there are many studies on the aperture problem for stereopsis and also many binocular matching studies, none of them quantitatively investigated binocular matching for partially occluded objects.<sup>3</sup> For such an aperture problem there is a continuum of matching solutions. The literature provides at least four plausible hypotheses, of which the predictions are indicated in figure 2.3. This figure shows the superposition of the half-images for the stereogram of figure 2.2. The four matching predictions are labeled the horizontal match (arrow 1), the perpendicular match (arrow 2), the intersection match (arrow 3) and the aperture direction match (arrow 4). These predictions will be described below.

## Horizontal Match

The *horizontal match* refers to a match in the horizontal direction (arrow 1 in figure 2.3). Since the eyes are separated horizontally, and since non-horizontal directions do not match corresponding portions of objects from an epipolar geometrical point of view (Anderson, 1999a), horizontal matching theories have dominated the studies on binocular vision. However there is also undebated experimental evidence that matches can occur in other directions (e.g. Stevenson & Schor, 1997; van Ee & Schor, 2000). In a study that resembles the current study van Ee & Schor (2000) found that, for a long line (unconstrained matching), matching occurs according to a default match, which has a vertical component as well as a horizontal component.<sup>4</sup> Even though this default match is not strictly horizontal it is very close to horizontal and in many studies horizontal matching models apply very well. Especially in computer vision, matching computations are immensely

<sup>3</sup>Existing studies on stereoscopic matching of gratings or similar structures using apertures and occlusions (Morgan & Castet, 1997; Tyler, 1980; van Ee & Anderson, 2001; van Ee, Anderson & Farid, 2001), used stimuli that are fundamentally different from ours.

<sup>4</sup>This vertical range is approximately 1/6 of the horizontal disparity range that can be used to process static stereoscopic depth (Schor, Wood & Ogawa, 1984) and 1/24 of the horizontal disparity range for dynamic stereoscopic depth (Richards & Kaye, 1974).

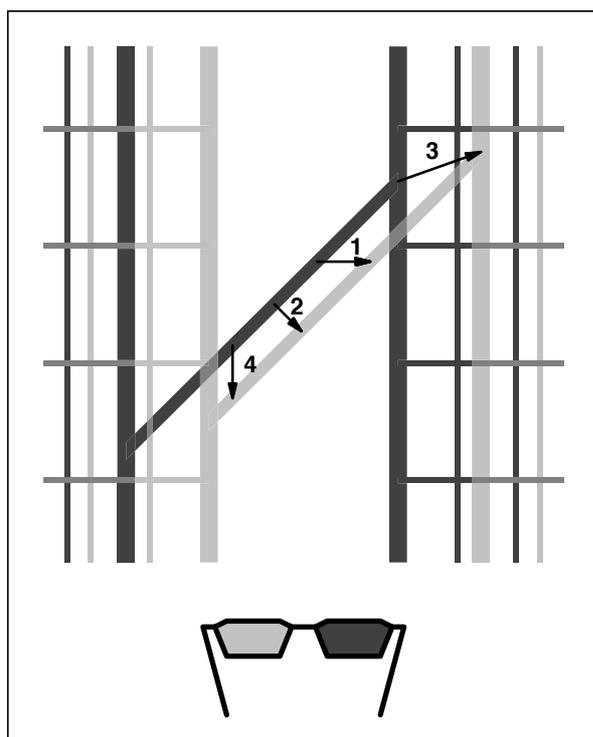


Figure 2.3: *Superposition of the stereogram half-images of figure 2.2. There are at least four theoretically plausible matching directions. (1) depicts a horizontal match. (2) depicts a match perpendicular to the orientation of the test line. (3) depicts the match according to the visible termination points of the test line. We call it the intersection match. (4) depicts the aperture direction match.*

simplified by assuming a horizontal matching direction (epipolar geometry).

Several studies have suggested that horizontal matching of the half-images occurs and that components of the half-images that are left unpaired signal to the brain that there must be an occlusion (Nakayama & Shimojo, 1990; Anderson, 1994; Anderson & Nakayama, 1994; Malik, Anderson & Charowhas, 1999).

## Perpendicular Match

The *perpendicular match* refers to a match perpendicular to the orientation of the test line as indicated by arrow 2 in figure 2.3. Note that the perpendicular matching direction is equivalent to nearest neighbour matching.

Farell (1998) studied the perceived depth evoked by stereoplaid (figure 2.4). To create the plaids he superimposed two sinusoidal gratings with different orientations and different horizontal shifts between the two half-images. He reasoned that these different shifts ought to result in different perceived depths for the two gratings. However he observed that these two superimposed gratings are perceived in one single depth plane and not in two depth planes. See figure 2.4c for a demonstration of his effect. Note that Farell presented his stimuli for short observation periods. With prolonged viewing the reader might (just like some of our observers did) perceive both one single plaid and distinct depth of the component gratings, alternately. Farell used an adaptation method and suggested that, although 2D features (intersections) seem to determine the perceived depth polarity (see intersection match prediction below), the 1D components (gratings) serve as primitives for perpendicular matching on the mechanistic (disparity detector) level.

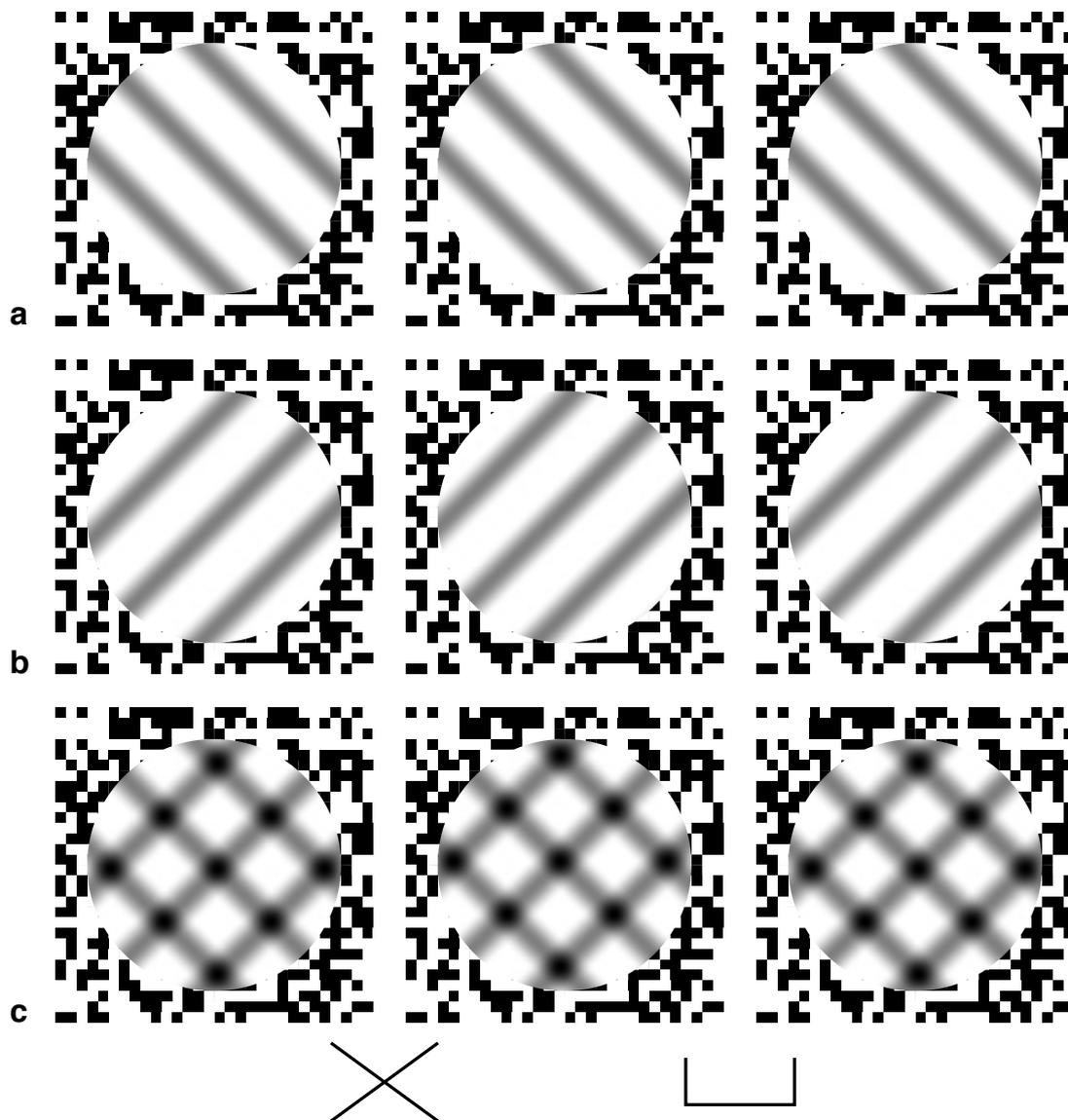


Figure 2.4: *Example of partly occluded stereoplaid composed of sinusoidal gratings. Crossfusers should fuse the left two images and divergers the right two images. The random dot pattern constitutes a zero disparity background. a) shows a grating with an orientation of 45 degrees compared to vertical. There is no horizontal shift between the two half-images, so that the grating is perceived at the same depth as the random dot pattern. b) shows a grating with an orientation of -45 degrees compared to vertical. The half-images have uncrossed disparity and the grating is perceived behind the random dot pattern. In c) the stereograms of a) and b) are superimposed. When fused the two gratings can be perceived at the same depth to form one single stereoplaid. In other words, in accordance with Farell (1998), one does not necessarily perceive the individual components at their distinct depths as given in panels a) and b).*

## Intersection Match

We refer to the *intersection match* as the match for which the visible termination points of the test line are being matched (arrow 3 in figure 2.3). These termination points reside in the half-images where the test line ‘intersects’ the border of the occluder.

Stereoplaids are examples in which such intersection points seem to determine the perceived depth polarity (see figure 2.4c). Farell (1998) stated “*It is clear that relative depth is not predictable from component disparities alone.*” And he continued, “*What does predict the depth judgements,*” of these plaids, “*is the horizontal component of the disparity of the plaids’ 2D features.*” According to this hypothesis the perceived depth polarity of the plaid (the superimposed gratings) corresponds to the sign of the horizontal disparity of the intersections of the two gratings.

Another possible argument for the intersection match is that the visual system can interpret the test line within the aperture as an object which is completely visible and not as a longer line of which only a part can be seen. In this case the visible end points (i.e. the intersection points of the test line and the occluder) would determine the matching direction so that every visible point of the test line in one half-image is matched with a visible point in the other eye’s half-image (leaving no unpaired regions).

## Aperture Direction Match

In our stimulus of figure 2.2 and figure 2.3 the main axis of the aperture is oriented vertically. The *aperture direction match* (arrow 4 in figure 2.3) implies that the test line half-images are matched in the direction of the main axis of the aperture (i.e. vertical in our example). This would mean that the matching direction is determined by the aperture orientation. The aperture direction prediction has a well-known analogue in the aperture problem for motion, namely the barber-pole effect. In the barber-pole effect a line is moving behind an aperture. If the motion of the line has a component perpendicular to the line orientation, the line will appear to be moving along the main axis of the aperture, regardless of the true motion of the line. There are many similarities between the aperture problem for motion and the aperture problem for stereopsis. For instance subjective occluding contours (subjective meaning that the occluding contours were not explicitly defined in the stimulus, e.g. by contrast) have been reported for both the aperture problem for stereopsis (Anderson, 1994) and the aperture problem for motion (Anderson & Sinha, 1997) for similar stimulus conditions. It might be the case that the aperture direction influences binocular matching in a similar manner as it influences matching the images of separate moments in time for the aperture problem for motion.

## 2.2 General Methods

To examine the assigned disparity (the matching direction) of a line that is observed through an aperture we use a depth probe method (Richards, 1971; Mitchison & McKee, 1987; van Ee & Schor, 2000). In this method a probe is shown besides the test line as in figure 2.5. The test line half-images, the dark grey and light grey lines in figure 2.5, have a certain disparity and the line is thus perceived in a certain depth plane. The right

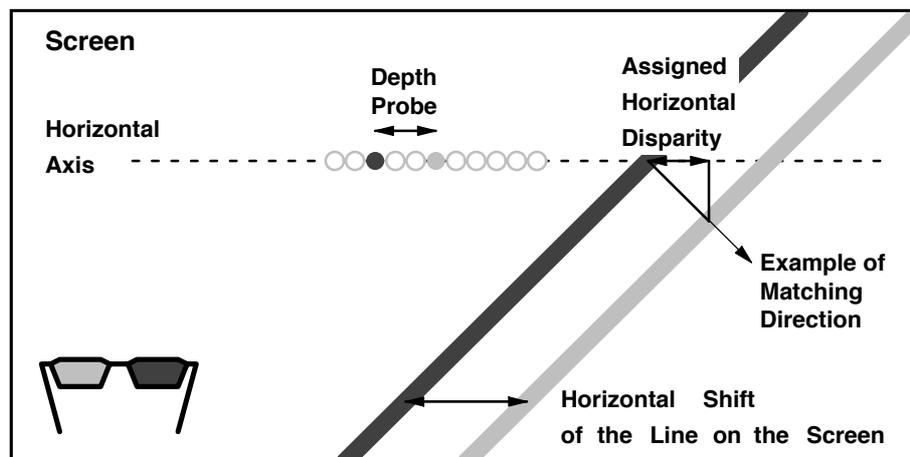


Figure 2.5: *The depth probe method. The dark grey line and dot are seen by the right eye and the light grey line and dot are seen by the left eye (crossed disparities). The horizontal disparity of the probe is varied. By asking the subjects whether they see the probe in front or behind the test line, the assigned horizontal disparity of the test line can be obtained. In this figure the geometrically assigned horizontal disparity corresponds to a matching direction which is perpendicular to the test line.*

eye's half-image of the probe has a fixed position on the screen, but the position of the left eye's half-image of the probe can be varied along a horizontal line. In this way the horizontal disparity, and thus the perceived depth of the probe is varied (van Ee & Schor, 2000). When the probe and the line are perceived at the same depth, the geometrically assigned horizontal disparity for the probe and the line ought to be the same.<sup>5</sup> Since the horizontal disparity for the probe is unambiguous, the assigned horizontal disparity of the line (i.e. the horizontal disparity component of the match) can be measured in this way.<sup>6</sup>

## Apparatus

The anaglyphic stimuli were projected onto a large screen (240 by 190 cm) in an otherwise dark room with black walls, ceiling and floor. The intensities of the red and green stereogram half-images were adjusted until they appeared equally bright when viewed through the red and green filters, respectively. There was no visible crosstalk between the half-images. One pixel subtended 3 by 3 arcmin and lines were anti-aliased. The image on

<sup>5</sup>van Ee & Schor (2000) tested this assumption by using short test lines and adding vertical disparities to the probe. We replicated their results in our setup, before conducting the experiments described in this paper.

<sup>6</sup>While the depth probe analysis is correct from a geometrical point of view, it is not necessarily a measure for the matching direction on disparity detector level. The depth probe analysis reveals the matching direction for the assigned horizontal disparity (see also footnote 5). Farell (1998, 1999, 2003) refers to matching in terms of the underlying disparity detectors, meaning that there can be a difference between the horizontal disparity that is assigned (high-level) to the stimulus and the mechanistic (low-level) matching direction. Concerning this issue it is relevant to cite a recent debate in the literature between Farell and Anderson (Anderson, 1999a; Farell, 1998, 1999) on the definition of disparity. According to Anderson (1999a), whose work concerns the high-level disparity assignment, matching is horizontal since non-horizontal directions do not match corresponding portions of objects.

the screen was refreshed every 14 msec. To obtain a fixed head position and orientation a chin rest was used. This chin rest was positioned at 200 cm from the screen.

## Stimuli

Several different stimulus patterns were used in the experiments (see figures 2.6, 2.7 and 2.8). A fixation cross (0.9 by 0.9 degrees) was presented in the center of the screen.

Two types of occluder conditions were examined in this study (see figure 2.8). For the first type, the occluders consisted of grids on either side of an aperture. The occluders were placed so that the fixation cross was in the middle of the aperture. The size of a rectangle in the grids was 1.3 by 4.3 degrees and the size of the entire stimulus was 44 by 40 degrees. 5% of the rectangles in the occluders were filled to prevent subjects from fusing the grid in the wrong depth plane (the wall-paper effect). The width of the lines within the grid was 0.26 degrees. At the borders of the aperture thicker lines were drawn with a width of 0.4 degrees. The horizontal disparity of the occluders was 26 arcmin relative to the fixation cross. For consistency we will refer to these occluders as surface occluders throughout this chapter.

For the second type of occluder conditions, the occluders consisted of single lines specifying only the borders of the occluder. The length of these lines was 40 degrees and the width was 0.4 degrees. This line occluder condition is interesting because it provides a stimulus in which there is no clear vertical disparity information for the visual system as opposed to the surface occluder condition for which global vertical disparity is well defined. It could be that, when there is no clear matching information for the occluder itself, the intersections of the test line with the occluder borders become more important.

The orientation of the test line within the aperture was 45 degrees compared to horizontal. The width of the test line was 0.5 degrees and the length of the test line was 3 degrees. This length was chosen such that the test line fitted the width of the aperture. The horizontal separation between the test line half-images was 17 arcmin.

The depth probe was always presented simultaneously with the test line. The diameter of the depth probe was 0.5 degrees. The depth probe was presented slightly above the position of the fixation cross and the test line was presented slightly below. The distance between the fixation cross and both the depth probe and the test line was 1.5 degrees.

## Task and Procedure

At the beginning of every session both the stereoscopic surface occluders and the fixation cross were presented for 11.5 sec. The grid structure of the surface occluders helped to stabilize vertical and cyclotorsional eye alignment (van Ee & Schor, 2000; van Ee & van Dam, 2003). At the start of each trial, the surface occluder and fixation cross were visible for 1.5 sec (see figure 2.6). Subsequently the fixation cross disappeared for 98 msec to prevent masking effects. In this period the surface occluders remained on the screen for trials in which the surface occluders were present (figure 2.6a). For other trials the screen was completely black (figure 2.6b). Then the oblique test line and the depth probe were

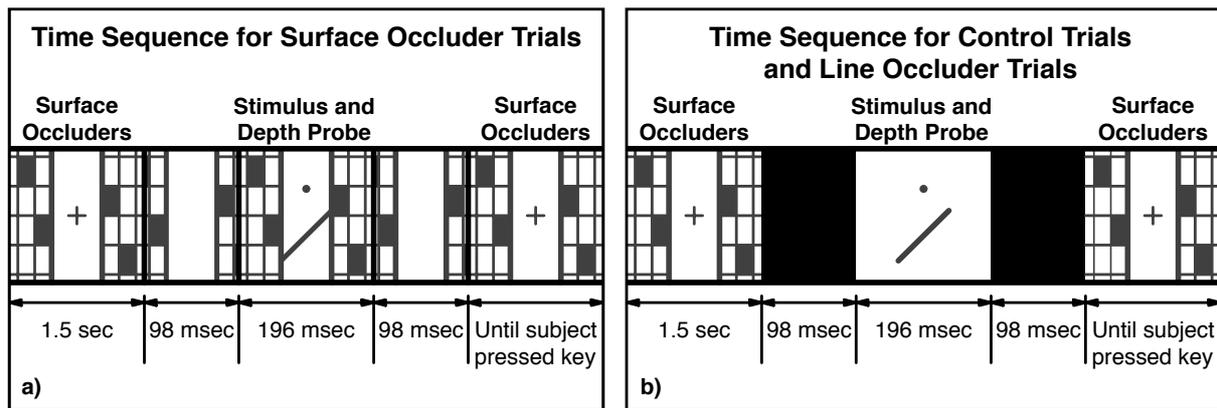


Figure 2.6: *a) Procedure for surface occluder trials. b) Procedure for line occluder trials and control trials. For the line occluder condition (not shown) only the borders of the occluders were defined by single lines. In the control trials (shown) no occluders were present.*

flashed within the aperture for 196 msec.<sup>7</sup> Afterwards either the grid was shown or the screen became black for 98 msec, depending on the condition, until the fixation cross (and surface occluders if the screen was black) appeared again.<sup>8</sup> Subjects then pressed a button to indicate, whether they had perceived the depth probe in front or behind the test line. After the subject had responded the surface occluders and fixation cross remained visible on the screen for 1.5 sec before the next trial started.

A 1-up/1-down staircase method was used to determine at which horizontal disparity subjects perceived the depth probe at the same depth as the test line. For the different conditions the staircases were interleaved. Step size was initially 2 pixels (6.0 arcmin), but was reduced to 1 pixel (3.0 arcmin) after the second reversal and to 0.5 pixel (1.5 arcmin) after the fourth reversal. This subpixel step size of the probe could be obtained using conventional anti-aliasing techniques. The result from a single staircase measurement was obtained from the last 12 reversal points. For every condition there were two such staircase measurements.

In order to determine biases in the responses of the subjects, there was a control condition, in every experimental session. For this condition no occluder was present and the length of the test line was 0.5 degrees. This line length was chosen such that the test line had about the same size as the depth probe. In this condition the test line half-images were shifted horizontally by 17 arcmin. Because of its short length, matching of this test line is unambiguous and the results for this condition can be used as a measure for the bias in the depth probe settings (van Ee & Schor, 2000). Results for other conditions were corrected afterwards for this bias.

Five subjects participated in the experiments. All subjects had normal or corrected-to-

<sup>7</sup>Note that this time is sufficiently short to prevent eye movements. Saccades can be planned and started but not completed, and should therefore not interfere.

<sup>8</sup>Before conducting the experiments we piloted with different exposure times (0 and 50 ms blank time between fixation and stimulus and stimulus presentations of 126 and 154 ms). We found that exposure time did not significantly affect the results. However with shorter presentation and blank times the task became increasingly more difficult to perform and staircases did frequently not converge within 60 stimulus presentations.

normal vision and all were able to distinguish disparities of different signs and magnitudes within a range of -1 to 1 degree in a stereo-anomaly test (van Ee & Richards, 2002).

## 2.3 Experiment 1: Vertical Aperture

In the first experiment we used vertical apertures. The width of this aperture was 2.1 degrees so that the length of the oblique test line within the aperture was 3 degrees. We examined both the surface occluder condition and the line occluder condition. For the intersection match the test line ought to have the same assigned horizontal disparity component as the vertical occluder (26 arcmin). For the horizontal match the assigned horizontal disparity ought to be the same as the horizontal separation of the test line half-images (17 arcmin). For the perpendicular match the assigned horizontal disparity ought to be half the horizontal separation (8.5 arcmin), since the orientation of the test line was 45 degrees compared to horizontal. For the aperture direction match (in this case vertical) the assigned horizontal disparity ought to be 0 arcmin.

There were three control conditions in this experiment. In these conditions, the test line had the same length (3 degrees) and position as the test lines in the occluder conditions, but there was no occluder present in the stimulus (see also figure 2.6). The test line half-images could be shifted either horizontally, vertically or in a way as if an occluder would have been present ('gapwise shift'). For the gapwise shift condition, the end points in the half-images of the test line were at the same positions as the intersections for the occluder condition would have been. The horizontal separation between the half-images of the test line was always 17 arcmin.

Van Ee & Schor (2000) showed that with increasing line length the visual system matches the test line more and more according to a default match, which is nearly horizontal. This means that if the test line continues into the periphery, the default match is predicted, whether or not the occluders are actually there. Thus, to study the matching direction of the occluded test line, the length of the test line (and therefore, the width of the aperture) is limited. To check whether the test line length of 3 degrees exceeds this limit, we first checked whether the test line can still be matched according to end point matching (when occluders are absent). If so, then the results for the gapwise shift condition should be near the prediction for the intersection match; the results for the horizontal shift condition should be near the prediction for the horizontal match and the results for the vertical shift condition should be near the aperture direction match prediction.

We estimated horizontal and vertical fixation disparity using a nonius line procedure described in van Ee, Banks & Backus (1999). The staircases for the nonius condition were intermixed with the stimuli staircases. In this way the fixation disparity could be directly related to the outcomes of the stimulus staircases.

## Results

We first present the results for the control conditions, since these also justify the setup for this experiment (figure 2.7). The results for the gapwise shift condition are presented in figure 2.7a, the results for the horizontal shift condition are presented in figure 2.7b and the results for the vertical shift condition are presented in figure 2.7c. Each of the

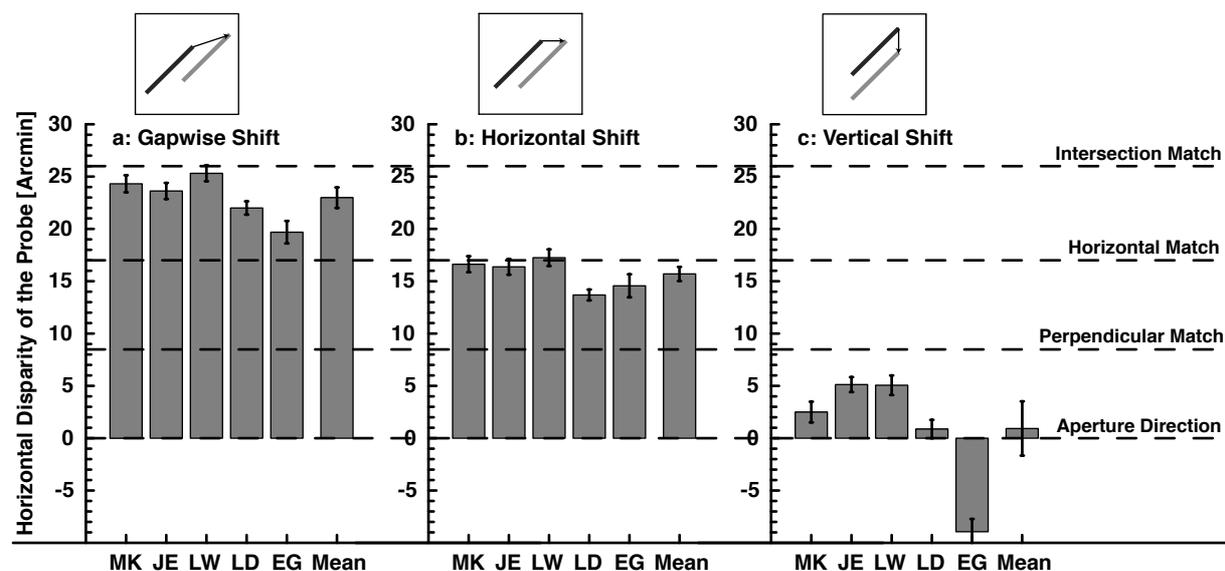


Figure 2.7: Results for the control conditions in experiment 1 for which the stimulus did not contain occluders. The horizontal disparity of the probe, for which the probe and the test line are perceived at the same depth, is plotted for every subject. Dashed lines indicate the four theoretical predictions as described for the occluder conditions (see figure 2.3). a) the results for the gapwise shift. For this condition the end points of the test line had a horizontal disparity component of 26 arcmin (which corresponds to the intersection match prediction). b) the results for the horizontal shift. For this condition the end points of the test line had a horizontal disparity of 17 arcmin (which corresponds to the horizontal match prediction). c) results for the vertical shift. For this condition the end points of the test line had a horizontal disparity component of 0 arcmin (which corresponds to the aperture direction prediction). Error bars represent standard errors. The results indicate that the end points of the test line were being matched.

panels of figure 2.7 depicts the horizontal disparity of the probe, for which the probe was perceived in the same depth plane as the test line. The mean across all five subjects is presented by the sixth bar in each panel. The error bars represent standard errors.

The results for the control conditions show that the end points of the test line were being matched as predicted. The results for the gapwise shift are close to the prediction for the intersection match. The results for the horizontal shift are close to the horizontal match prediction. The results for the vertical shift condition are somewhat diverse but overall they are close to the aperture direction (vertical) prediction. This also means that the intersections of the test line with the occluder borders are not located too far in the periphery to be used for matching. This in turn justifies the choice of the test line length of 3 degrees for the occluder conditions.

For the occluder conditions the horizontal disparity of the probe, for which the probe was perceived at the same depth as the test line, is presented in figure 2.8a for the surface occluder condition and in figure 2.8b for the line occluder condition. The mean across all subjects is again presented by the sixth bar in the figure for each condition. The dashed lines indicate the predictions for the four matching hypotheses. Error bars represent standard errors. The mean for the surface occluder as well as the mean for the

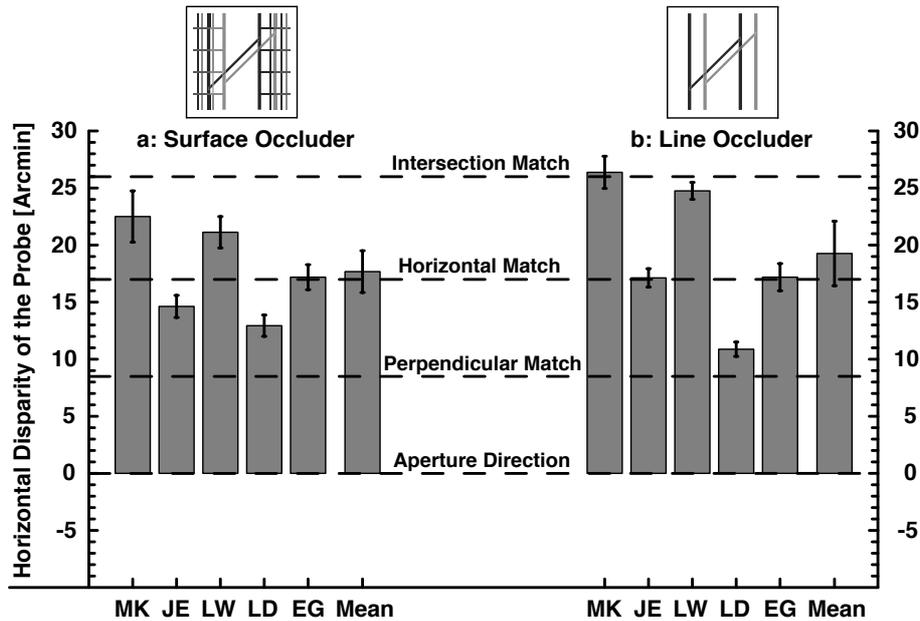


Figure 2.8: Results for the occluder conditions in experiment 1. The horizontal disparity of the probe for which the probe and the test line are perceived at the same depth is presented for every subject. The dashed lines indicate the theoretical predictions. For the intersection match the test line ought to have the same horizontal disparity component as the occluder (26 arcmin). For the horizontal match the horizontal disparity ought to be the same as the horizontal separation of the test line half-images (17 arcmin). For the perpendicular match the horizontal disparity ought to be 8.5 arcmin (half the horizontal separation of the test line half-images). For the aperture direction match (in this case vertical) the horizontal disparity ought to be 0 arcmin. a) the results for the surface occluder and b) the results for the line occluder. Error bars represent standard errors. For the surface occluder the results indicate that matching took place roughly in the horizontal direction. For the line occluder condition the matching direction is subject dependent.

line occluder condition indicate that the test line in these conditions was matched in the horizontal direction.

For the surface occluder condition the results for individual subjects are centered more or less around the horizontal match prediction, although the result for subject MK is closer to the intersection match prediction and the result for subject LD is inbetween the horizontal match and the perpendicular match predictions. Although there are relatively large differences between the subjects, it is clear that none of the subjects matched the test line half-images in the aperture direction. The results of figure 2.8 differ significantly from both the aperture direction prediction and the results for the vertical shift control condition (figure 2.7c).

For the more ambiguous line occluder condition, there are strong differences in matching directions between the subjects. The results for subjects MK and LW indicate that they matched the intersection points of the test line; subjects JE and EG matched the test line in the horizontal direction and the result for subject LD corresponds more or less to the perpendicular match prediction (although this could be due to underestimation which is also present in the results for the control conditions for this subject (figure 2.7a

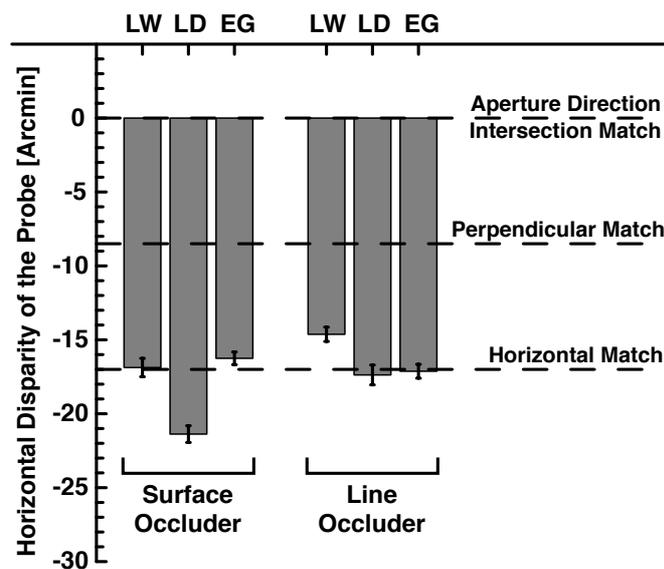


Figure 2.9: Results for the occluder conditions when the aperture disparity was zero relative to the fixation cross. The horizontal disparity of the probe for which the probe and the test line are perceived at the same depth is presented for subject LW, LD and EG. The black dashed lines indicate the theoretical predictions. Error bars represent standard errors. The results show that matching occurred in a roughly horizontal direction.

and b)).

## Fixation disparity

We used a large (crossed) disparity of the surface occluders relative to the fixation cross, because some subjects had difficulties in matching uncrossed test line disparities within the short stimulus presentation durations that were used. Such a large disparity might have evoked fixation disparity. Horizontal fixation disparity does not have an effect for the horizontal match or the intersection match, but it affects both the perpendicular match and the aperture direction match. As noted, during the experiment we estimated horizontal and vertical fixation disparity. We did not find significant vertical fixation errors. And the pattern of horizontal fixation disparity was completely unrelated to the pattern of results in figure 2.8.

For those subjects who did not have difficulties in matching uncrossed test line disparities we repeated experiment 1 but now the *uncrossed* disparity for the test line was 17 arcmin and the occluders had zero disparity relative to the fixation cross. The procedure and task were the same as in experiment 1 and the session also contained nonius trials to measure fixation disparity. Figure 2.9 shows the results along with the theoretical predictions. The results are similar to those in experiment 1 and support our suggestion that the test line was matched horizontally. Again the fixation errors of the subjects were unrelated to their matching results.

## 2.4 Experiment 2: Various aperture orientations

The results of experiment 1 show that the matching direction for our occluded test line is mainly horizontal, as would be predicted from the horizontal separation between the two eyes. However, the results for two of our subjects show that they matched the test line according to the intersection match (figure 2.8b) at least for the specific circumstances

that were used in experiment 1. Therefore, we conducted a second experiment in which we manipulated the aperture orientation and specifically focussed on the horizontal and intersection match predictions. The aperture orientation affects the above-mentioned matching predictions in fundamentally different ways. Using the aperture orientation as a variable enables us to examine to what extent the theoretical predictions are valid.<sup>9</sup> It also enables us to examine the puzzling differences in matching results across subjects that we found in experiment 1.

## Stimuli and Procedure

For this experiment the setup was the same as in the first experiment except that the main axis of the aperture could now have various orientations of -70, -20, 0, 20, 45, 70 or 90 degrees compared to vertical (positive angles meaning anti-clockwise variation from vertical). The orientation of the test line was always 45 degrees compared to the horizontal (which is -45 degrees compared to the vertical). In order to maintain a fixed line length of 3 degrees, the width of the aperture varied with aperture orientation.<sup>10</sup>

In this experiment the occluders consisted again of either the surface occluders or the single lines defining the borders (line occluders). For the different orientations of the aperture the horizontal and vertical lines of which the surface occluders consisted did not change orientation (see also figure 2.10). The only lines that changed their orientation were the lines defining the border of the surface occluders. The horizontal shift of the occluders was again 26 arcmin in all aperture orientation conditions. To prevent masking effects the pattern that was on the screen between trials (fixation cross and surface occluders) contained the aperture orientation for the next trial.

As a control the ‘gapwise shift’ condition was examined for the various aperture orientations. For this condition there was no occluder present in the stimulus, but the end points of the test line were located at the same positions as the intersection points in the occluder conditions would have been. In this case the visible end points of the test line ought to be matched (van Ee & Schor, 2000, see also figure 2.7). Thus if for the occluder conditions, subjects match the intersections points when viewing the stimulus, the results for these conditions ought to be the same as those for the gapwise shift condition.

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<sup>9</sup>There are fundamental reasons why we chose to manipulate aperture orientation in stead of test line orientation. For instance, when the test line is more horizontal, one would expect a horizontal match to become more noisy (van Ee & Schor, 2000) due to increasing ambiguity for that match. Similarly for a more vertical test line, one would expect less ambiguity for a horizontal match but the predictions for the intersection match and the horizontal match would be closer to each other (most of the variation being in the vertical component of the intersection match), making it only harder to distinguish between the two predictions.

<sup>10</sup>For the vertical aperture condition we conducted pilot experiments for several aperture widths (test line length thus changing accordingly). We did this for the occluder conditions as well as the gapwise shift condition. For the vertical occluder condition the results did not change significantly with aperture width. However, with increasing width the results for the gapwise shift converged to a more or less horizontal matching direction (van Ee & Schor, 2000) indicating that the end points in this case, and thus possibly the intersection points in the occluder conditions, were too far in the periphery to be of any use for the binocular matching system.

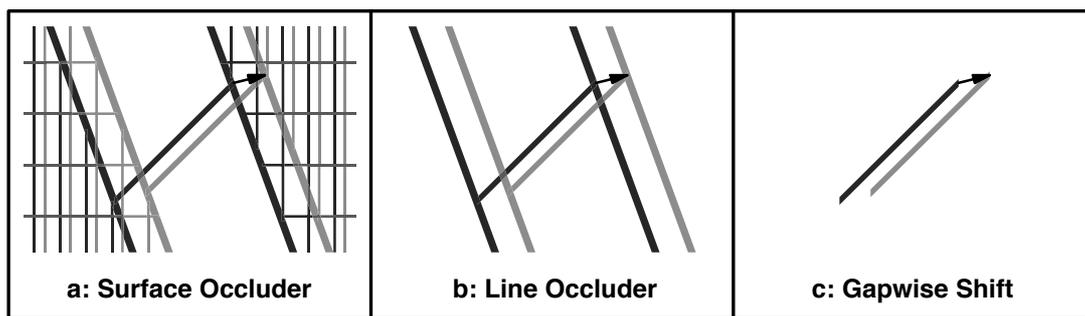


Figure 2.10: *Stimuli in experiment 2 in which we measured the assigned horizontal disparity of the test line with varying aperture orientations. Dark grey lines are seen by the right eye, light grey lines by the left eye. a) The surface occluder condition. b) For the line occluder condition only the borders of the occluders are specified. c) For the gapwise shift condition the test line was shifted the same way as for the occluder conditions (as indicated by the arrows), but there was no occluder present in the stimulus. For the gapwise shift condition these visible end points of the test line half-images ought to be matched so that the results for this condition ought to correspond to the intersection match prediction.*

## Predictions

If the test line is matched horizontally then the aperture orientation should have no influence on the assigned horizontal disparity of the line. Accordingly, when the probe is perceived at the same depth as the test line, the disparity of the probe should be close to the horizontal separation of the test line half-images on the screen (17 arcmin). However if the test line is matched using the intersections with the occluder, then the assigned horizontal disparity should vary with aperture orientation. How this horizontal disparity varies with aperture orientation is derived below (see also figure 2.11).

Let the intersection of the test line and the occluder border for the right eye be the origin  $(0,0)$ . Then if  $\alpha$  is the angle of the test line compared to horizontal and  $dl$  is the horizontal separation of the test line half-images, the test line in the left eye can be described as follows.

$$\text{Test line left eye} = \begin{pmatrix} dl \\ 0 \end{pmatrix} + \lambda \begin{pmatrix} 1 \\ \tan \alpha \end{pmatrix} \quad (2.1)$$

In this equation  $\lambda$  is a variable. If  $\beta$  is the angle of the aperture compared to vertical and  $da$  is the horizontal disparity of the occluder, then the occluder border in the left eye can be described as:

$$\text{Occluder border left eye} = \begin{pmatrix} da \\ 0 \end{pmatrix} + \gamma \begin{pmatrix} -\tan \beta \\ 1 \end{pmatrix} \quad (2.2)$$

Here  $\gamma$  is a variable. When these lines intersect it follows from these equations that  $\gamma = \lambda \tan \alpha$  and  $\lambda = \frac{da - dl}{1 + \tan \alpha \tan \beta}$ . The horizontal component  $\delta$  of this intersection point is then given by:

$$\delta = dl + \frac{da - dl}{1 + \tan \alpha \tan \beta} \quad (2.3)$$

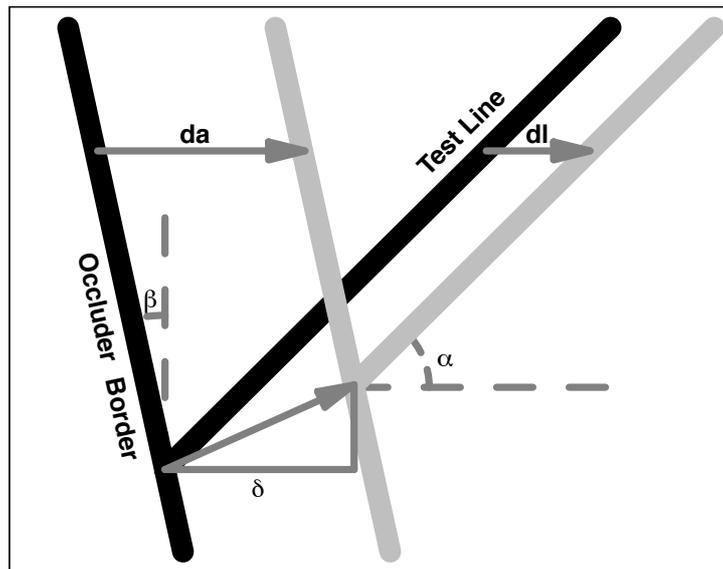


Figure 2.11: Schematic picture indicating the parameters that play a role in the derivation of the horizontal disparity component for the intersection match. Dark grey lines are seen by the right eye, light grey lines by the left eye.  $dl$  is the horizontal separation between the test line half-images on the screen.  $da$  is the horizontal disparity of the occluders (on the screen).  $\alpha$  is the angle of the test line compared to horizontal.  $\beta$  is the orientation of the aperture compared to vertical.  $\delta$  is the assigned horizontal disparity component in the case of the intersection match.

This is also the horizontal component of the disparity between the intersection point in the right and left eye, and thus the horizontal disparity of the intersection match.

## Results

The results of experiment 2 are shown in figure 2.12. The filled circles represent the results for the surface occluder condition. The open circles represent the results for the line occluder condition and the squares represent the results for the gapwise shift condition. The black dashed lines show the prediction for the horizontal match. The grey dashed lines represent the prediction for the intersection match. The error bars represent standard errors. The singularity in the prediction for the intersection match (at -45 degrees) arises because the aperture has the same orientation as the test line and thus they never intersect. The significance within subjects was tested pairwise for each combination of data points, using a two-sided mean difference test with a normal distribution as the underlying distribution.

The main result of this experiment is that, when subjects viewed the surface occluder (black discs in figure 2.12), they mainly matched the line horizontally. The results for the surface occluder condition are close to the horizontal match prediction, although some subjects show an overall overestimation and some others show an overall underestimation compared to this prediction.

The results for the gapwise shift condition (white squares in figure 2.12) are close to the intersection match prediction for all subjects. (For a number of subjects (e.g. LD)

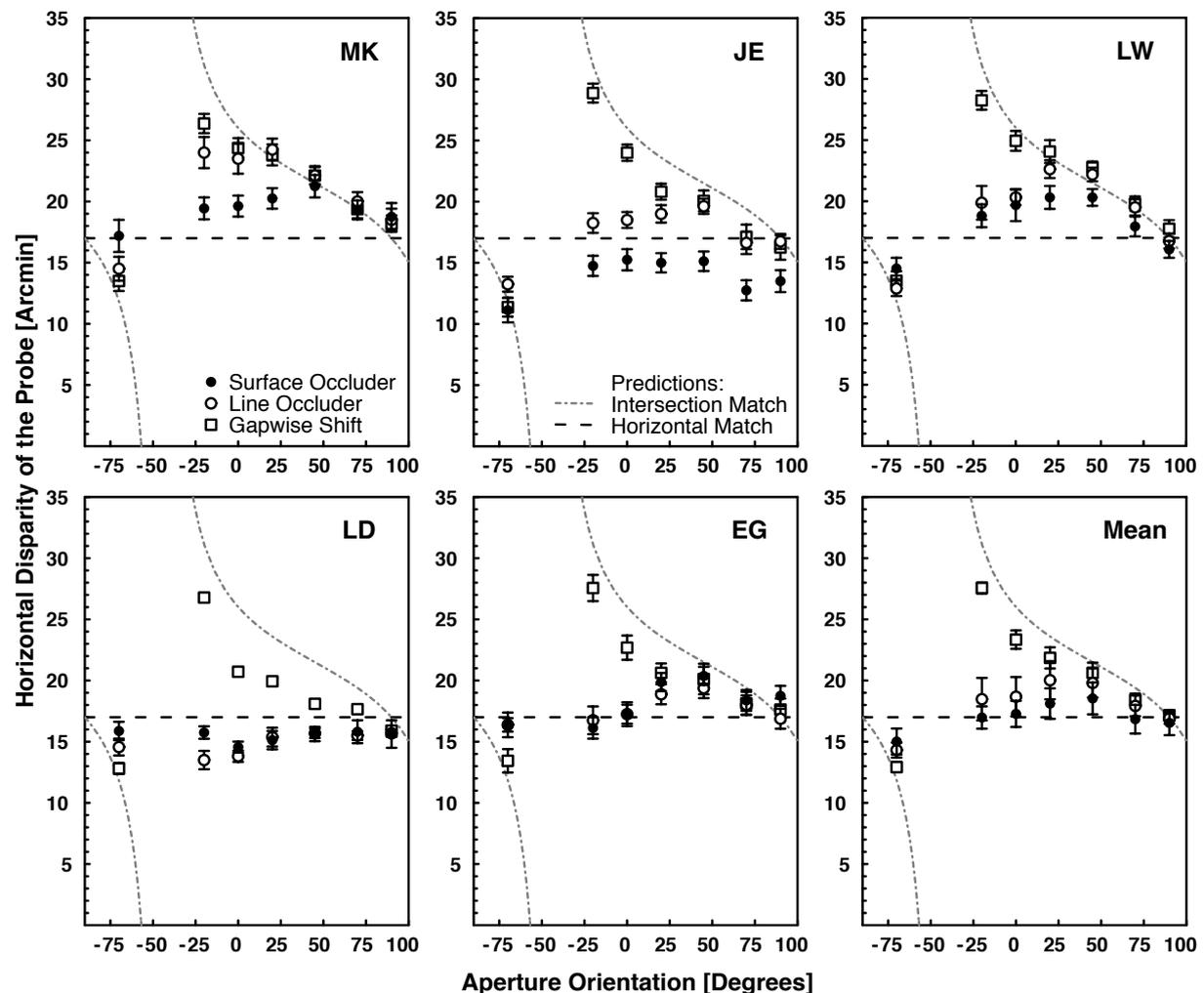


Figure 2.12: Results of experiment 2. The horizontal disparity of the probe for which the probe and the test line are perceived at the same depth is plotted versus the aperture orientation ( $\beta$  in figure 2.11). Zero indicates a vertical aperture. Positive angles indicate that the aperture orientation is rotated anti-clockwise from vertical. The black dashed lines show the prediction for the horizontal match and the grey dashed lines show the prediction for the intersection match. The singularity in the intersection match prediction at an aperture orientation of -45 degrees arises because in this case the aperture and the test line have the same orientation and thus they never intersect.  $\bullet$  and  $\circ$  represent the results for the surface occluder and the line occluder conditions, respectively.  $\square$  represent the results for the gapwise shift. Error bars represent standard errors. For the surface occluder matching occurred in a horizontal direction. For the line occluder the results are subject dependent (some subjects match horizontally and others according to the intersection match). The gapwise shift results correspond quite well to the intersection match prediction.

there is however an overall underestimation. This underestimation was also present in experiment 1.) This means that for the gapwise shift condition the visible end points of the test line were being matched, as predicted. These visible end points were located at the same positions in the stimulus where otherwise, had it been an occluder condition, the intersections between the test line and the occluder borders would have been. Thus, if indeed these intersection points in the stimuli for the surface occluder condition were being matched, then the results for the surface occluder condition and the gapwise shift condition ought to be the same for all aperture orientations. However the results for these two conditions are significantly different for a number of aperture orientations. This supports the conclusion that for the surface occluder condition matching occurred in the horizontal direction.

The results for the line occluder condition (open circles in figure 2.12) differ across subjects. For subjects LW, LD and EG these results are the same as the results for the surface occluder. They basically match the partially occluded test line in the horizontal direction (although for subject LW there seems to be an influence of the intersection points on the resulting match for aperture orientations of 20 and 45 degrees). For subject JE the results for the line occluder condition appear to be shifted to a larger horizontal probe disparity for all aperture orientations compared to the results for surface occluder condition. The cause of this shift is not clear. Subject MK is inclined to match the intersection points. Although there are some significant differences between the results for the line occluder condition and the intersection match prediction, none of these results for the line occluder condition are significantly different from the results for the gapwise shift condition.

In sum, for the surface occluder condition (in which the horizontal and vertical disparities of the occluders are well defined) matching of the test line occurs in the horizontal direction. For the line occluder condition (in which matching of the occluders is ambiguous) the matching direction is subject dependent and the intersections of the test line with the occluder borders play a role in binocular matching.

## 2.5 Control Experiment: Aperture imposed matching direction

We reasoned that a well defined surface occluder on both sides of the aperture might have imposed a matching direction on our test line. Our surface occluders had clear features that the visual system could use for matching. The disparity of the occluders indicated a horizontal match (the half-images of the occluders were shifted horizontally on the screen). Also the occluders covered a relatively large area of the visual field (44 by 40 degrees). If the horizontal matching direction for the occluders would be imposed on our ambiguous test line then it is not surprising that we found a horizontal match in our results. We conducted a control experiment in which the surface occluders are again presented on both sides of the aperture, but they no longer occlude the test line (either the test line is shorter or the width of the aperture is larger compared to the occluder conditions in the previous experiments). This allows us to examine whether the test line is matched according to the shift of the visible end points of the test line, or according to a horizontal

match imposed by the surface occluders on either side of the aperture.

## Stimuli

In this control experiment the setup was the same as in experiment 1. The surface occluders were presented on both sides of a vertical aperture and always had a horizontal disparity on the screen of 26 arcmin. There were two aperture conditions. In the first aperture condition the test line had the same length as in experiment 1 and 2 (namely 3 degrees). In this case the aperture had a width of 5.8 degrees. Note that this means that there were gaps between the surface occluders and the test line and thus the test line was no longer occluded. In the second aperture condition the width of the aperture was the same as in experiment 1 (2.1 degrees), but the test line length was decreased to 0.5 degrees. In this second aperture condition there were also no occlusions.

In each of these two aperture conditions there were four test line shift conditions. In each condition the test line was shifted in a different way but the horizontal separation between the test line half-images remained the same (17 arcmin). In one condition the test line half-images were shifted according to the gapwise shift, already described in experiments 1 and 2. In this condition the end points of the test line were, where the intersection points would have been, had it been an occluding condition (thus the end points of the test line have a horizontal disparity component of 26 arcmin on the screen). In the second condition the test line half-images were shifted horizontally (the end points have a horizontal disparity of 17 arcmin). In the third they were shifted perpendicularly to the orientation of the test line. In this case the end points of the test line have a horizontal disparity component of 8.5 arcmin (half the half-images separation). In the last condition the test line half-images were shifted vertically, so the end points have a horizontal disparity component of 0 arcmin.

For every condition there were two staircase measurements and the bias condition was also included, so in sum there were 18 interleaved staircases. In this control experiment only one subject participated (subject LD).

## Predictions

What is the effect of the surface occluders with well defined disparities on the matching direction for the test line? van Ee & Schor (2000) showed, in a similar experiment in which the stimuli only contained the test line and the depth probe (thus without the occluders), that the assigned horizontal disparity of the test line corresponds to the horizontal disparity component of the end points of the test line provided the test line is sufficiently short (see also the control conditions in experiments 1 and 2 in this paper).

One of the fundamental features of the conditions described above is that the end points of the test line are visible. If these local end points of the test line determine the match for the line, independent of the horizontal disparity of the surface occluders, then the probe settings would vary linearly with the horizontal disparity component of the end points.

If however the surface occluders impose a matching direction onto the test line then in all conditions the test line should be matched horizontally and the probe disparity

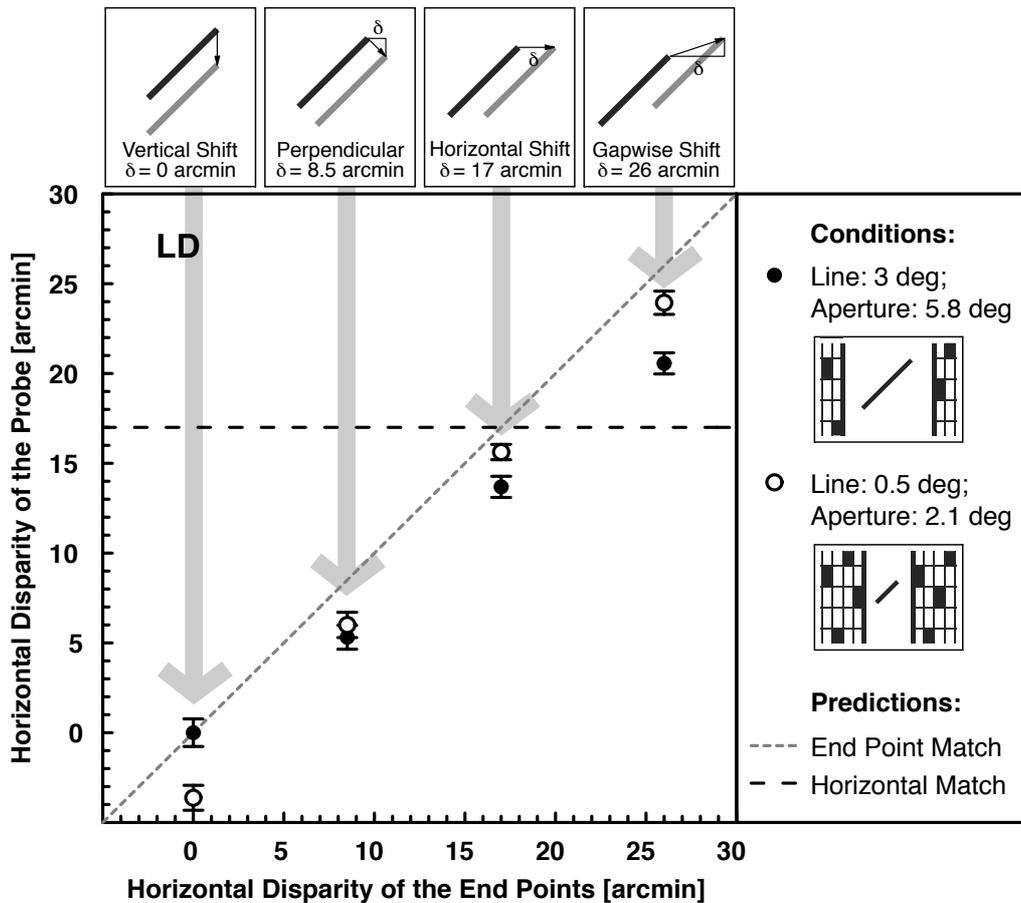


Figure 2.13: *The results of the control experiment in which we measured matching directions of test lines with visible end points. Surface occluders with well defined disparities were presented on both sides of the aperture. The horizontal disparity of the probe for which the probe is perceived at the same depth as the test line is shown versus the horizontal disparity of the end points of the test line. (The test line shifts are indicated in the boxes at the top). The black dashed line shows the prediction for an imposed horizontal match. The grey dashed line shows the prediction for the end point match. ● shows the results for the condition in which the aperture width was 5.8 degrees and the test line length was 3 degrees. ○ shows the results for the condition in which the aperture width was 2.1 degrees and the test line length was 0.5 degrees. Error bars represent standard errors. The results show that the test line was matched according to the shift of the end points.*

would always be set close to 17 arcmin (i.e. the horizontal separation between the test line half-images).

## Results

The results of the control experiment are presented in figure 2.13. The horizontal disparity of the probe for which the probe is perceived at the same depth as the test line is shown versus the horizontal disparity of the end points of the test line for each condition. The

test line shifts are indicated in the boxes at the top of the figure. The black dashed line shows the prediction for the horizontal match. The grey dashed line shows the prediction for the end point match. The filled circles represent the results for the condition in which the aperture width was 5.8 degrees and the test line length was 3 degrees. The open circles represent the results for the condition in which the aperture width was 2.1 degrees and the test line length was 0.5 degrees. The error bars represent standard errors.

These results show that the local end points determine the matching direction for the test line. All the results are close to the prediction for the end point match, implying that the horizontal disparities of our surface occluders do not necessarily impose a horizontal match on the test line. We conclude that the results we found in experiments 1 and 2 are not simply imposed by the horizontal matching features of the surface occluders and that local matching of the test line can have matching directions that differ from the more global matching of these surface occluders.

## 2.6 Discussion

We have quantitatively examined binocular matching for a partially occluded test line. We have done so using a depth probe method (Mitchison & McKee, 1987; van Ee & Schor, 2000) which means that we have analysed binocular matching at a geometrical level (as opposed to a mechanistic neural level). We summarised four possible matching hypotheses. The first one implied that binocular matching of partially occluded objects occurs in the horizontal direction. Our results show that indeed the matching direction is horizontal when the horizontal and vertical disparities of the occluders are well defined. The horizontal match is supported by the work of Anderson (Anderson, 1994, 1999b; Anderson & Nakayama, 1994; Anderson & Sinha, 1997). He investigated the perception of subjective occluding contours (subjective meaning that the occluder was not explicitly defined in the stimulus, i.e. by contrast etc.). He explained his findings by assuming that matching occurs in the horizontal direction. He reported that, in order to perceive the subjective occluding contours, reference points on the occluded object as well as in the surround are needed. When these reference points are absent then the subjective occluding contours are no longer perceived. This dependence on the presence of reference points is rather similar to the dependence on well defined disparities of the occluders in our study. When the disparities of the occluders are ill-defined the partially occluded line is not necessarily matched in the horizontal direction. In this case the intersections of the test line and the occluder borders play a role as shown by our experiment 2.

Consider again the oblique line behind an aperture (figure 2.1). Farell (1998) suggested that the half-images of the line (figure 2.1b) may be matched in a variety of directions. He stated: *“in naturalistic, ‘layered’ scenes of occluding and transparent surfaces, stereo correspondence becomes a two-dimensional (2D) matching problem in which horizontal disparity is not a reliable cue to depth.”* In his stereoplaid the intersections of its component gratings, rather than the horizontal disparities of the gratings, could be responsible for the perceived depth. For, if the visual system would prefer to compute the perceived depth from the horizontal shifts of the 1D components (the gratings) only, it would have decomposed the stereoplaid in two separate gratings, both having different horizontal disparities, rather than fusing the gratings to form one stereoplaid in one depth plane.

For our aperture problem such a mechanism would suggest that the perceived depth of the line is related to the shift of the intersections of the line with the occluder (so according to our intersection match hypothesis). Our results show that indeed the intersection points can determine the matching direction for the test line, but only when the matching direction for the occluders is ambiguous. This is consistent with the reported observations of Farell's study (see figure 2.4 for a demonstration of his effects), since for his stereoplaids, too, matching was ambiguous for both gratings (i.e. for the occluding as well as for the occluded lines). In addition, it is worth noting that for Farell's stimulus (figure 2.4c) we found considerable variance across observers, just as for our ambiguous stimuli, and with prolonged viewing some observers are able to perceive both a depth percept based upon intersection matches and a percept based upon horizontal matches.

According to the aperture direction match, the test line half-images would be matched in the direction of the main axis of the aperture as might be predicted from the similarities between the aperture problem for motion (barber-pole effect) and the aperture problem for stereopsis (Anderson, 1994; Anderson & Sinha, 1997). These similarities would suggest that matching two images at separate moments in time is rather similar to matching the images of the two separate eyes. However our results indicate that binocular matching does not occur along the main axis of the aperture as is the case for the aperture problem for motion. It has been reported that the barber-pole effect for motion is not present when the barber-pole lines have uncrossed disparity relative to the occluders (Anderson, 1999b; Shimojo, Silverman & Nakayama, 1989). In this case the lines appear to be moving perpendicular to their own orientation. For the aperture problem for stereopsis, the reasoning that matching for motion detection and matching for stereopsis are similar, could therefore, also lead to a perpendicular match prediction for our test line. The fact that the horizontal match was observed instead, indicates that the analogy between matching for motion detection and matching for stereopsis is limited.

## Conclusion

So far, no studies exist in the literature that quantitatively reveal the disparity that is assigned to a partially occluded line in the aperture problem. Our results show that from a geometrical point of view matching of partially occluded objects is horizontal when the occluders are well defined in terms of horizontal and vertical disparity (conform Anderson, 1994). However if the visual input lacks this information, then the matching direction for the occluders becomes ambiguous and the intersections of the test line and the occluder borders play a role in the determination of the perceived depth of the test line (conform Farell, 1998). In the latter case the matching direction of the test line varies with aperture orientation and there is a relatively large variability across subjects.

## Chapter 3

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

### Abstract

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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.

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## 3.1 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 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 (Lack, 1971; McDougall, 1903). 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 & 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 & van Leeuwen, 2003; Peckham, 1936; Pheiffer, Eure & Hamilton, 1956; Ruggieri & Fernandez, 1994; Sabrin & Kertesz, 1980). Ruggieri & Fernandez (1994) reported for several different ambiguous figures that eye movements

caused perceptual flips, whereas Pheiffer, Eure & Hamilton (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 & 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 figure 3.1. The slant rivalry stimulus consists of a planar grid for which perspective and disparity specify different slants. When the half-images of figure 3.1 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 to 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, 2005).<sup>1</sup> 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, van Dam & Brouwer, 2005).

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

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<sup>1</sup>The relatively long percept durations have also been employed to study the neural correlates of stereoscopic depth perception in the visual cortex (Brouwer, van Ee & Schwarzbach, & van Ee, 2005).

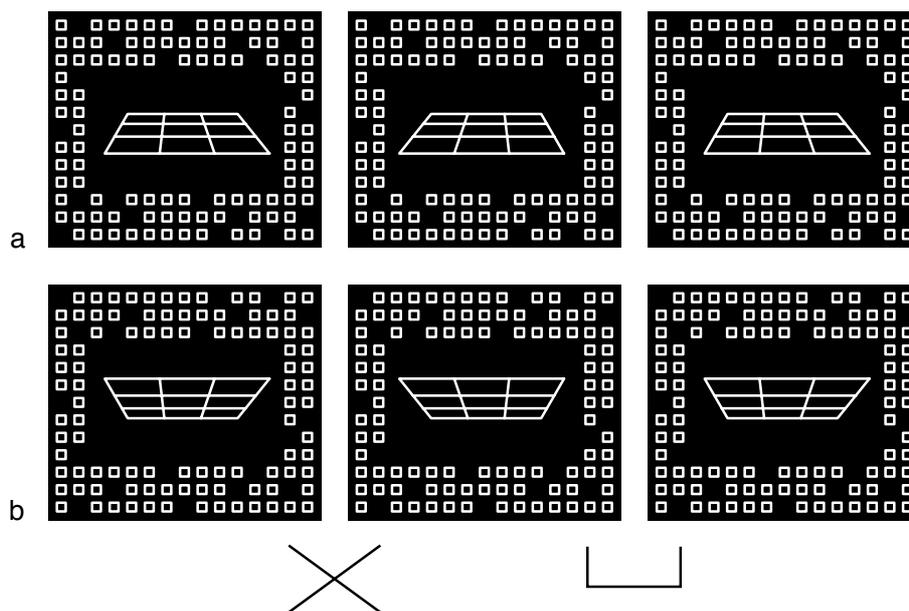


Figure 3.1: *Demonstration of bi-stable slant perception (slant rivalry) for slants about a horizontal axis. Crossfusers should fuse the left two images. Divergers should fuse the right two images. a) perspective indicates a negative (floor) slant and disparity a positive (ceiling) slant. b) perspective indicates a positive (ceiling) slant and disparity a negative (floor) slant.*

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

## 3.2 Experiment 1: Slant estimates

### Methods

#### 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 by 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 by 1200 pixels and lines were anti-aliased. The images on the monitor were refreshed every 13 msec. 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

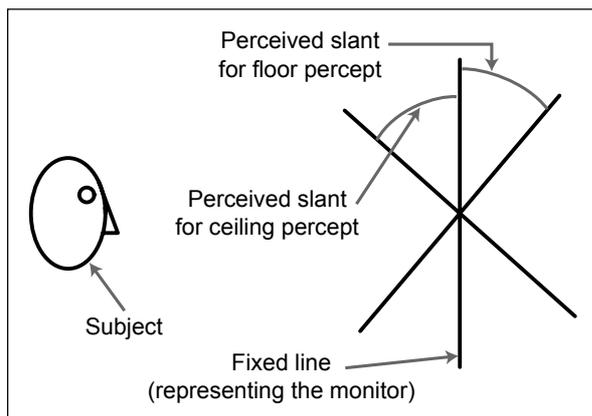


Figure 3.2: *The subjects were instructed to match the angles between a fixed vertical line (representing a side view of the monitor) and two rotatable lines to the slants they had perceived in the stimulus. When the subject failed to experience bi-stability, both lines were matched to the single slant that was perceived.*

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.

### 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 (figure 3.1) subtending 4.0 by 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 by 17.7 deg and the size of a square in the background was 0.5 by 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 by 8.5 deg) in which the planar grid was displayed.

We varied both the perspective-specified slants ( $-70$  to  $70$  deg in 6 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 sec. 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 the subjects' head and three frontoparallel lines were shown (see figure 3.2). 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 stereoacuties were lower than 10 arcsec, and they were able to distinguish disparities of different signs and magnitudes within a range of  $-1$  to  $1$  degree in a stereoanomaly test (van Ee & Richards, 2002).

## Results

The slant estimates are presented in figure 3.3. 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, Krumina, Pont & van der Ven, 2005; van Ee, van Dam & Erkelens, 2002). 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, Adams & Mamassian, 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.

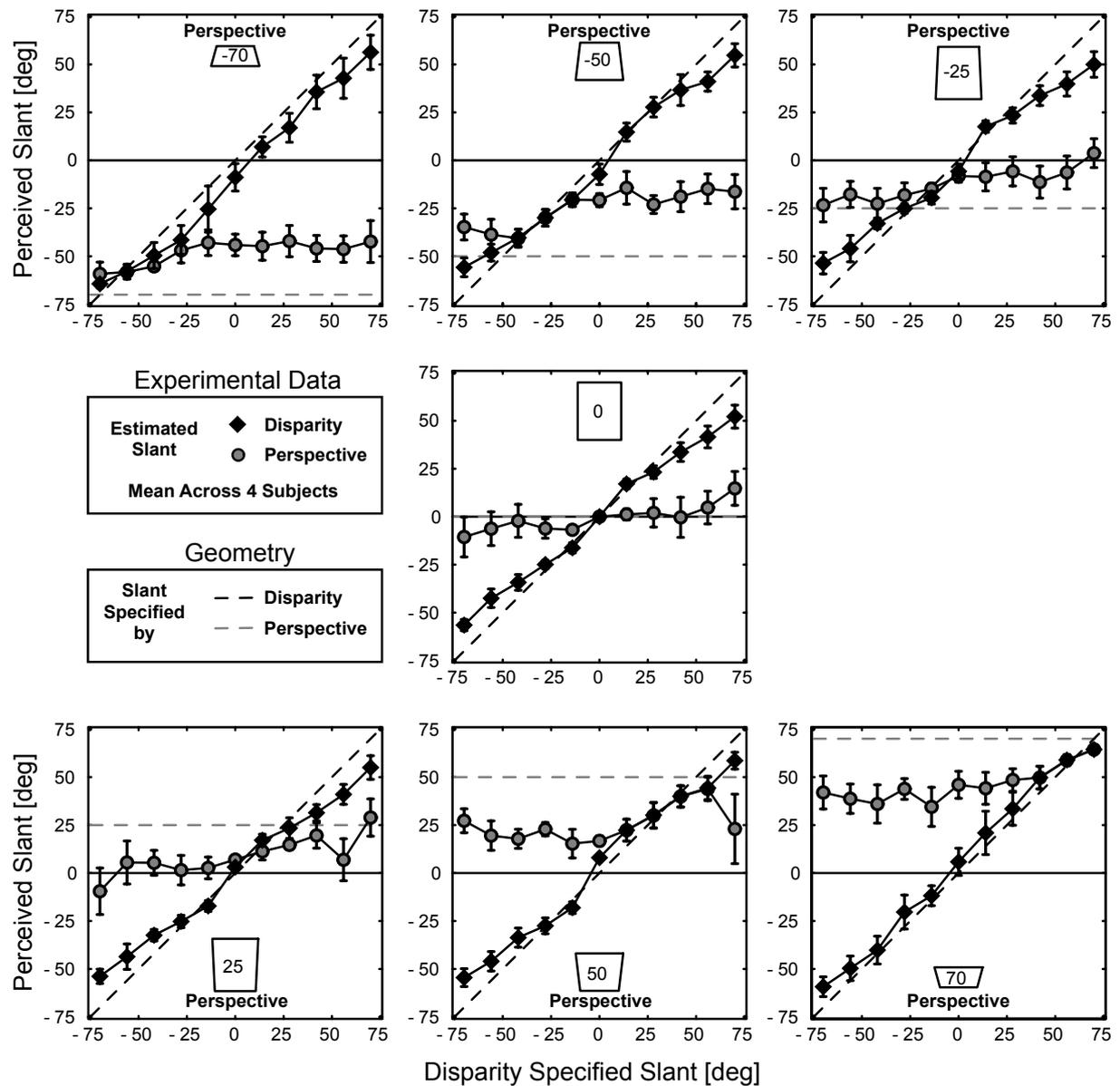


Figure 3.3: Results of experiment 1 showing the mean perceived slants as a function of the disparity-specified slant across four observers. The trapezoidal icons in each panel represent the perspective-specified slant. Black diamonds and grey disks represent the results for the disparity-dominated percept and the perspective-dominated percept, respectively. The error bars represent the standard error across the four observers.

### 3.3 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 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.

#### Stimuli and Procedure

The size of the trapezoidal figure on the monitor was 5.7 by 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 minutes. The subjects were instructed to press one of two buttons to indicate their current percept. A fixation dot (7 arcmin), 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 9 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:

$$\vec{v}_n = \frac{\vec{x}_{n+2} + \vec{x}_{n+1} - \vec{x}_{n-1} - \vec{x}_{n-2}}{6\Delta t}, \quad (3.1)$$

where  $\vec{v}_n$  represents the  $n^{\text{th}}$  velocity sample,  $\vec{x}_i$  represents the  $i^{\text{th}}$  version angle sample and  $\Delta t$  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 were set at the last sample before the absolute speed signal exceeded a threshold of 18 deg/sec. 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.

## Results

Figure 3.4a 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 sec to 100 sec 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 figures 3.4b and c. Figures 3.4b and c show the horizontal (left) and vertical (middle) version and the horizontal vergence (right) of a time interval starting 2.0 sec before until 0.5 sec 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, figures 3.4b and c (on top of figure 3.4a), 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 direction. 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 msec before the moment of the button press until 1000 msec after the moment of the button press. Blinks (including 4 samples prior to each blink and 4 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 msec 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 msec prior to the moment of the

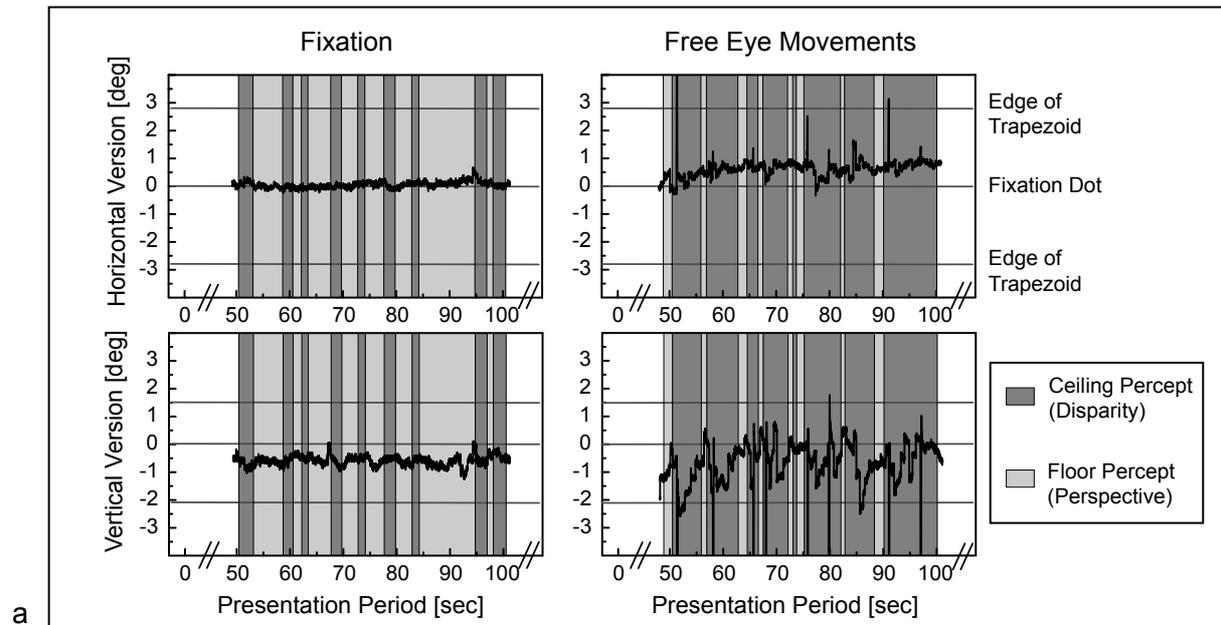
button press (during this interval there were no large changes in average gaze positions for all subjects). The average gaze positions were then obtained by averaging across the corresponding flips.

Figure 3.5 shows the average gaze positions during 1000 msec 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 figure 3.5 show the gaze positions for the same data as already used for the right two panels of figure 3.4a. 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 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 average 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.

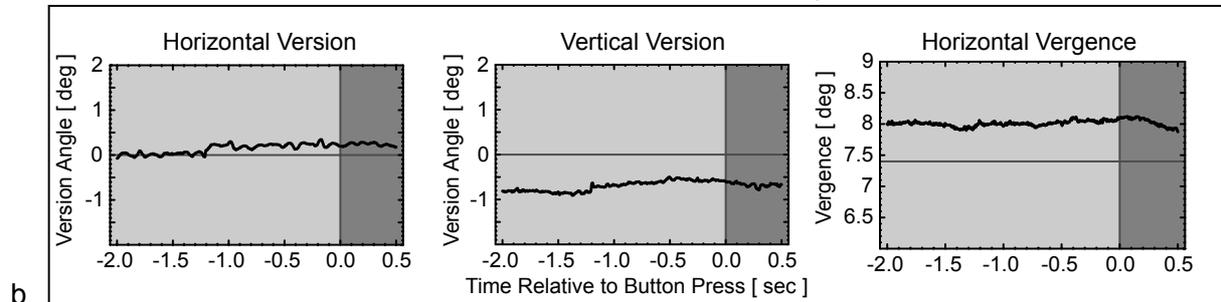
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Figure 3.4 (on the next page): *Results of experiment 2. a) shows examples of horizontal (top) and vertical version (bottom) versus elapsed stimulus presentation time for two different conditions. The left two panels show the version angles when the 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) and c) show the horizontal version (left), vertical version (middle) and horizontal vergence (right) during a period of 2.0 sec before to 0.5 sec 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.*



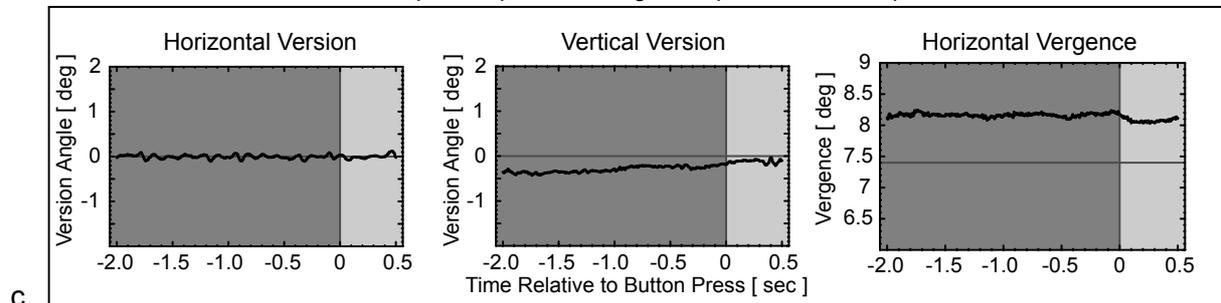
a

Perceptual Flip from Floor Percept to Ceiling Percept



b

Perceptual Flip from Ceiling Percept to Floor Percept



c

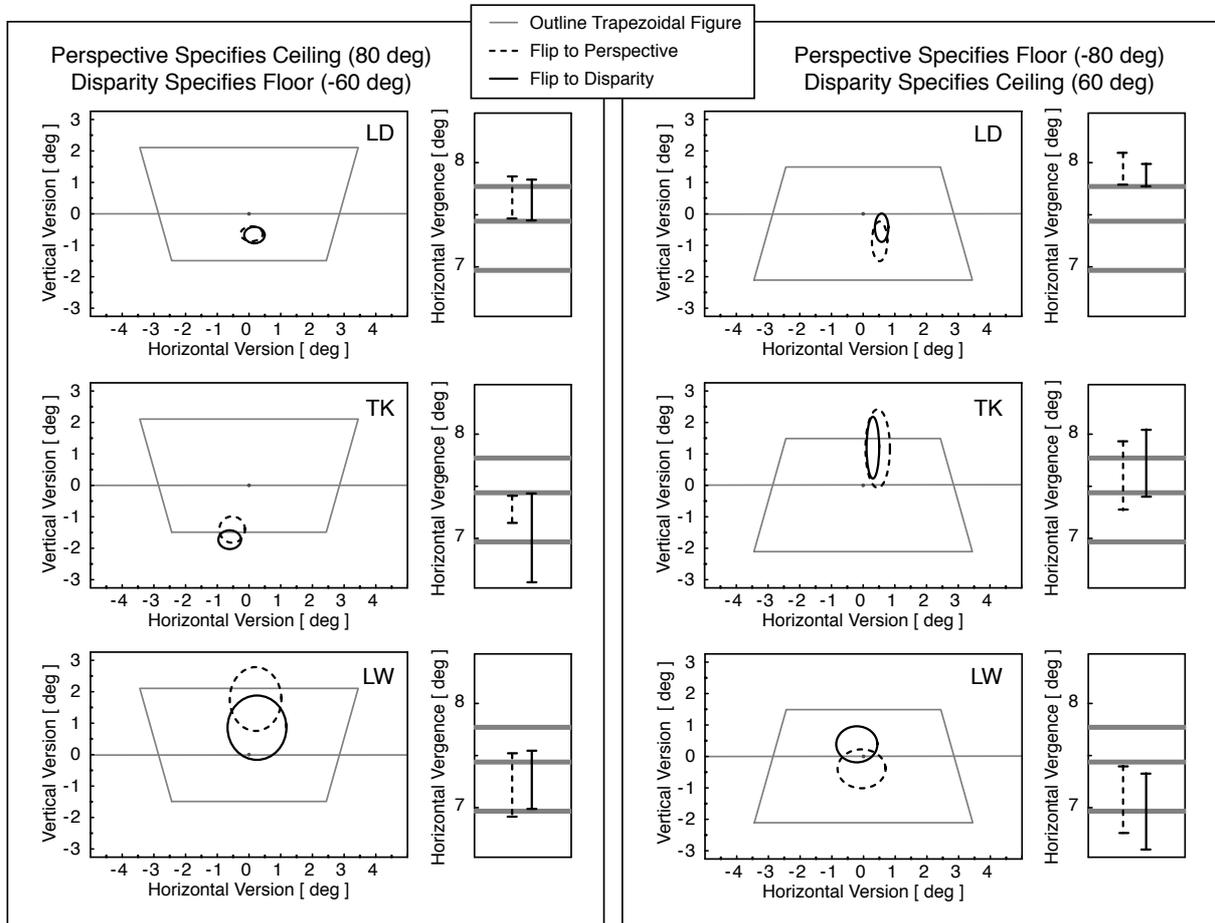


Figure 3.5: *The average gaze position (vertical versus horizontal version) and horizontal vergence during 1000 msec prior to the moments of the button presses (thus at about the moment of the perceptual flip) when eye movements were allowed. The left panel shows the results when perspective specified 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.*

### 3.4 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 correlation between flips and both saccades and blinks. We also take microsaccades into account.

#### 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 by 6.0 deg. The chin rest was positioned at 55 cm from the screen.

#### Task and Procedure

Subjects initiated the stimulus onset, after which the stimulus was shown for 5 minutes. 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 sec). These physical polarity changes in the stimulus will be called '*stimulus flips*' throughout this thesis. 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: 4 perceptual flip conditions (2 for which the perspective-specified slant was positive and 2 for which the perspective-specified slant was negative) and 2 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.

## Eye movement analysis

We measured gaze positions using the previously described SMI-eyelink system and setup. Formula 3.1 was used to calculate the velocities for each eye separately (thus, in this case  $\vec{x}_i$  represents the  $i^{\text{th}}$  gaze position sample expressed in Fick-angles). Saccades were detected by first removing all the blinks from the data (including 4 samples prior to each blink and 4 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 & 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.

$$\sigma_{x,y}^2 = \langle v_{x,y}^2 \rangle - \langle v_{x,y} \rangle^2, \quad (3.2)$$

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 6 times the variance in the x and y direction, respectively (we adopted the number used by Engbert & Kliegl (2003)). 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 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 4 samples (12 msec) to further reduce noise. Since saccades, including microsaccades (Martinez-Conde, Macknik & Hubel, 2004), are conjugate in nature we only included binocular saccades.

## 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 sec before the moment of a button press (i.e. at  $-10.0$  sec) to 10.0 sec after the moment of a button press (at  $+10.0$  sec), using a bin-width of 100 msec. The intervals  $-10.0$  to  $-5.0$  sec and  $+5.0$  to  $+10.0$  sec were used to calculate the mean and the standard deviation of the bin height (as a reference level). The interval  $-5.0$  to  $+5.0$  sec 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  $+5.0$  sec 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 autocorrelation 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.

## Results

Figure 3.6 displays the results of experiment 3 in which we investigated the correlation between eye movements (saccades 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 msec) 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  $-5.0$  sec and  $5.0$  to  $10.0$  sec, as explained in the data analysis section. The black vertical line at zero sec 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.

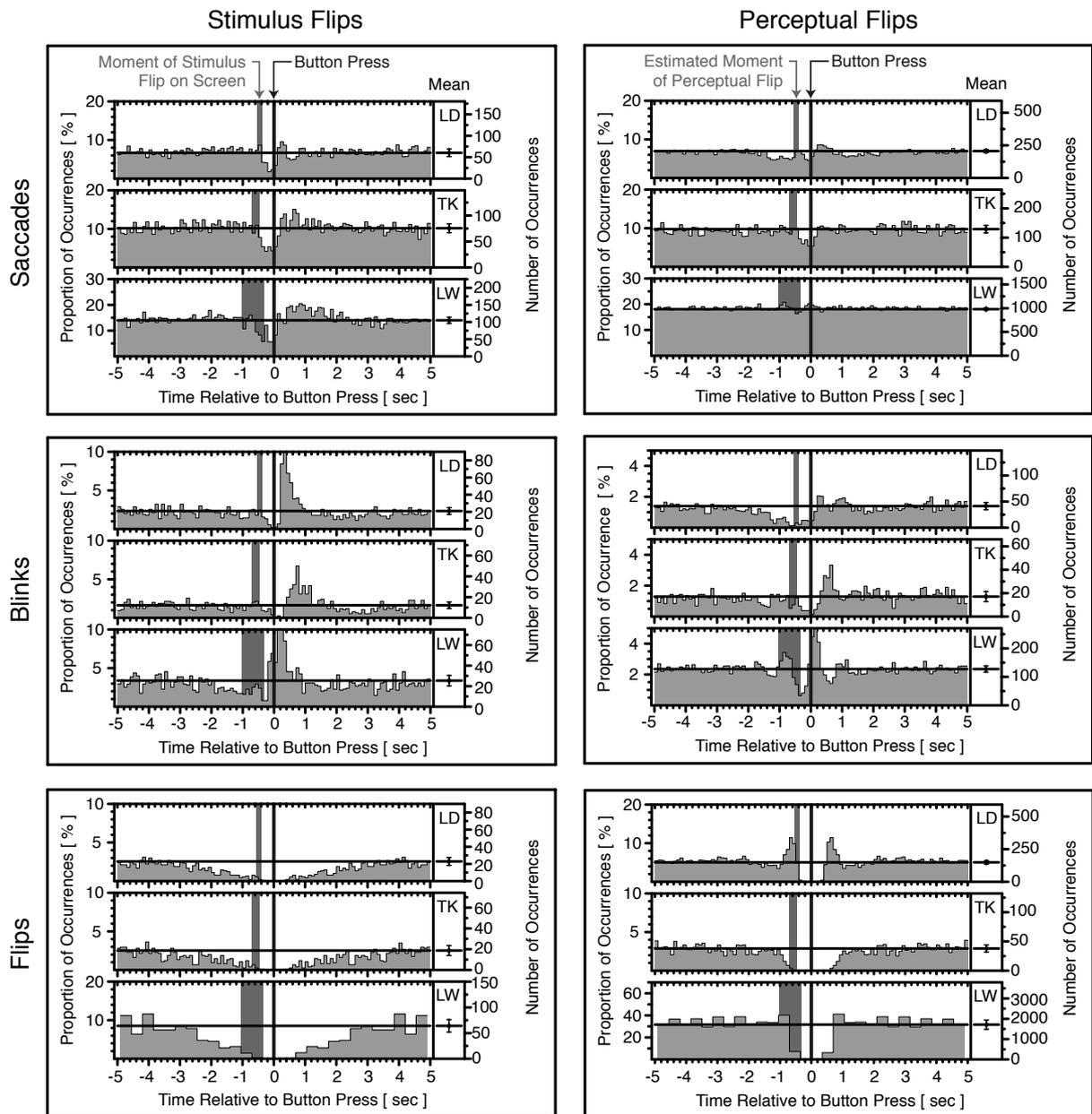
For the perceptual flip condition there is also a reduced probability of both saccades and blinks between the moment of the flip and the moment of the button press, although for saccades for subject LW it is hardly visible and for subject LD it appears to start earlier than for the stimulus flip condition 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 figure 3.7 where the flips are divided in flips to the disparity-dominated percept and flips to the perspective-dominated percept).<sup>2</sup> 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 sec). 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

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<sup>2</sup>Due to a computer timing error the button presses for subject LW could only be recorded at about 350 msec intervals. For this subject the bin-size for the flip occurrence histograms is, therefore, 350 msec. Since a bin of 350 msec 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 msec 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.

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Figure 3.6 (on the next page): *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 msec) 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  $-5.0$  sec, and  $5.0$  to  $10.0$  sec (in those periods no correlation is expected). The black vertical line at zero sec 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 chapter. 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.*



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). Figure 3.7 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 (figure 3.4) and this is also consistent with the average percept durations reported by van Ee, van Dam & Brouwer (2005). For subjects LD and LW the dominance of disparity is very clear. Due to the high autocorrelation of perceptual flips for subjects 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 sec). 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 button press corresponding to a flip to the disparity-dominated percept, but not after the moment of a button press corresponding to 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 percept and increased probabilities of both saccades and blinks are due to flips to the disparity-dominated percept) are consistent

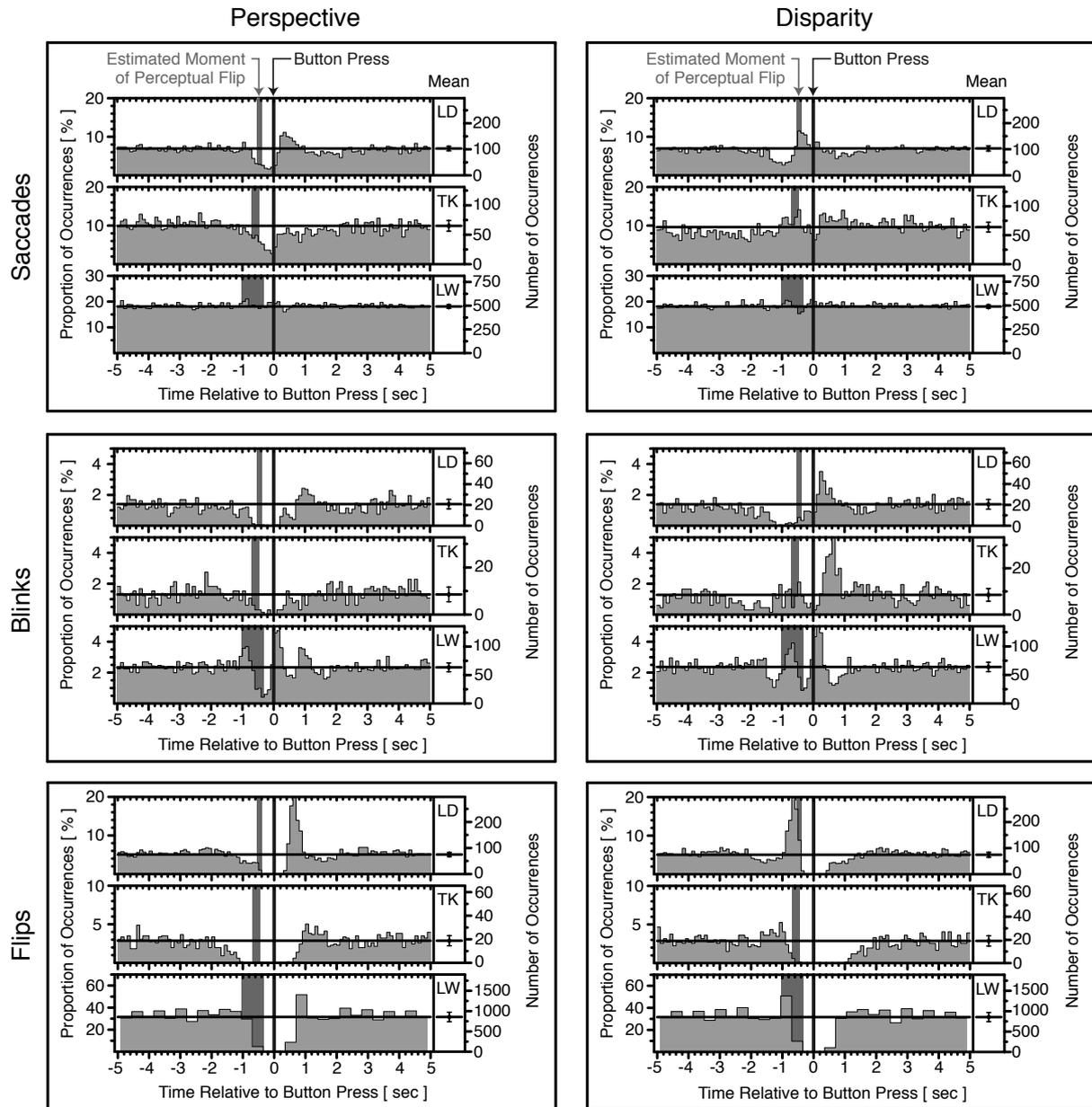


Figure 3.7: Similar to figure 3.6 but for perceptual flips, divided into flips to the perspective-dominated percept (left panels) and flips to the disparity-dominated percept (right panels). There appear to be differences between flips to the perspective-dominated percept and flips to the disparity-dominated 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.

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.

### Microsaccades

It is important to examine to what extent very small saccades, usually referred to as microsaccades (for a review see Martinez-Conde, Macknik & Hubel, 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 figures 3.6 and 3.7 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  $5.0$  to  $10.0$  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 arcmin. For subject LD the amplitude threshold was 15 arcmin and for TK it was 18 arcmin. For subject LW the decrease in the probability of saccades is relatively small (figure 3.6 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 figure 3.8.

The left panel of figure 3.8 shows the occurrences of microsaccades (smaller than 15 arcmin for LD and smaller than 18 arcmin for TK). For a fair comparison, the right panel shows the occurrences for a similar amount of larger saccades: larger than 72 arcmin for LD and between 54 and 63 arcmin 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).<sup>3</sup> 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 figure 3.8 right panel).

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

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<sup>3</sup>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 arcmin), 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.

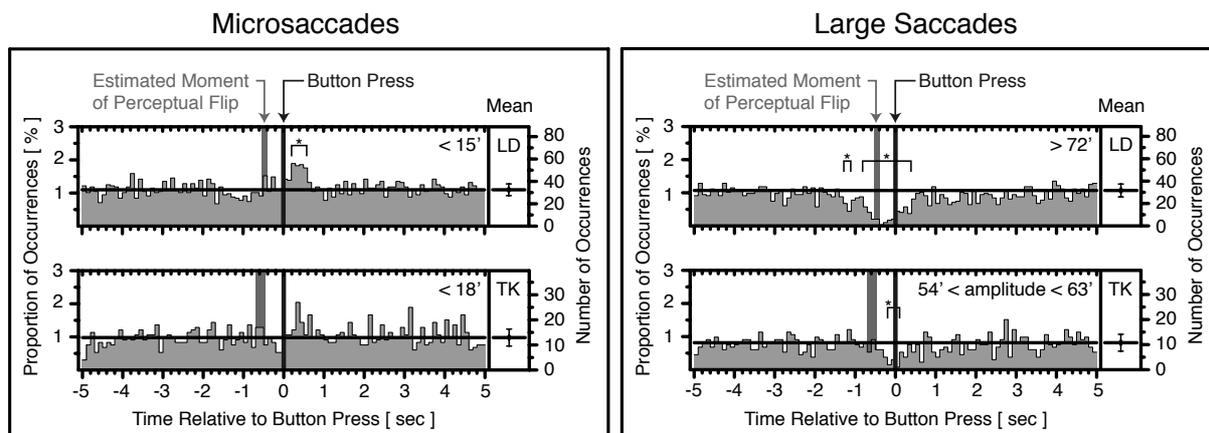


Figure 3.8: *Similar to figure 3.6 but here we compared the role of microsaccades (left panel) with the role of larger saccades (right panel) for perceptual flips for subjects LD and TK. To obtain a sufficient amount of saccades (such that the mean bin height differed significantly from zero) we considered saccades with amplitudes smaller than 15 arcmin for subject LD and smaller than 18 arcmin 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  $\star$  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.*

### 3.5 Experiment 4: The role of button presses

The results of experiment 3 show that the occurrence probability of both saccades and blinks are reduced after the moment that a flip occurred for both perceptual flips and the physically induced stimulus flips (see figure 3.6). Furthermore there is a peak in the histograms for blinks just after the moment of the button press (figure 3.6 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.

#### 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 sec). 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 by 1.9 degrees 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 sec. 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 figure 3.6), 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 the occurrence probabilities of saccades and blinks.

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

## Results

Figure 3.9 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. Figure 3.9a 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 figure 3.6).

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Figure 3.9 (on the next page): *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 (figure 3.9a, b and d) or physical flips (c) for two subjects (LD and LW). a) shows 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) through 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.*

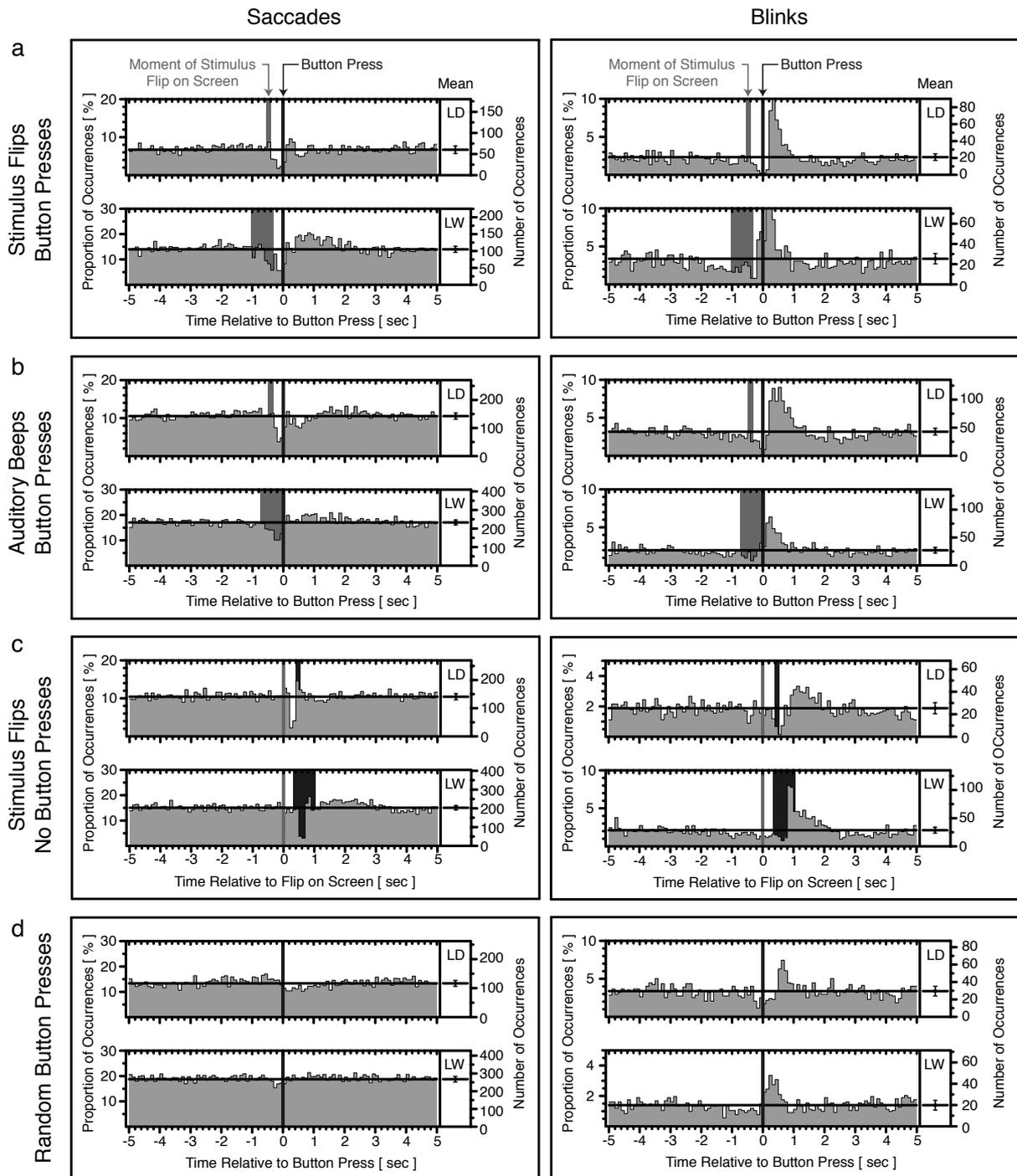


Figure 3.9b shows the results for the condition for which subject responded to auditory beeps by pressing buttons. Figure 3.9c shows the results for the condition for which subject counted the visual stimulus flips without pressing any buttons. Figure 3.9d shows the results when subjects pressed buttons 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 msec) 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 figure 3.9c 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  $-5.0$  sec and  $5.0$  to  $10.0$  sec. The black vertical line in figures 3.9a, b and d represents the moment of the button press. The black vertical bar in figure 3.9c 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 figures 3.9a 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 figure 3.9c 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 (figure 3.9a and c) or auditory beeps (figure 3.9b). The reduced probability even occurred when the subjects did not have to press buttons (figure 3.9c), whereas it was absent for saccades, and less pronounced for blinks, when subjects were pressing buttons at random (figure 3.9d).<sup>4</sup>

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.

## 3.6 Discussion

We have examined the role of eye movements for perceptual flips when subjects viewed the slant rivalry 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, Adams & Mamassian, 2003; van Ee,

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<sup>4</sup>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  $-0.15$  sec) that individually is significantly different ( $P < 0.01$ ) from the mean bin height.

Krumina, Pont & van der Ven, 2005; van Ee, van Dam & Erkelens, 2002). 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.

## 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 figure 3.9c), whereas the decrease in probability was absent when subjects pressed buttons at random (figure 3.9d). 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 & Stark (1978) 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 (Deubel & Schneider, 1996; Hoffman & Subramaniam, 1995; Kowler, Anderson, Doshier & 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; Sato & Schall, 2003). 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).<sup>5</sup> 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 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.

### **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 (figure 3.7 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 (figure 3.7 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 figure 3.4).

### **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

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<sup>5</sup>Reaction times of saccades as a response to stimulus onset, can be as fast as 175 msec 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 msec). However, saccade latencies after stimulus onset are known to depend on stimulus complexity and task. Longer saccade latencies of about 400 msec or more have been reported for various tasks (Hooge, Beintema & van den Berg, 1999; Kowler, Anderson, Doshier & Blaser, 1994; van Loon, Hooge & van den Berg, 2002; Zelinsky & Sheinberg, 1997).

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 Engbert & Kliegl (2003); Hafed & Clark (2002) and Steinman, Cunitz, Timberlake & Herman (1967) 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; Martinez-Conde, Macknik, Troncoso & Dyar, 2006). 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.

## 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 (figure 3.9d). 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).<sup>6</sup> 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.

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<sup>6</sup>Note also that Ito, Nikolaev, Luman, Aukes, Nakatani & van Leeuwen (2003) reported, for a version of Attneave's (1968) triangles, a decrease and increase in blink frequency, similar to the results reported here.

## 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 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.

# Chapter 4

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

### Abstract

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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.

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## 4.1 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, Nikolaev, Luman, Aukes, Nakatani & van Leeuwen, 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 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, van Dam & Brouwer, 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, van Dam & Brouwer, 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.

## 4.2 General Methods

### Apparatus

We used red-green anaglyph stimuli that were displayed on a computer monitor (40 by 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 by 1200 pixels and lines were anti-aliased. The images on the monitor were refreshed every 13 msec. A

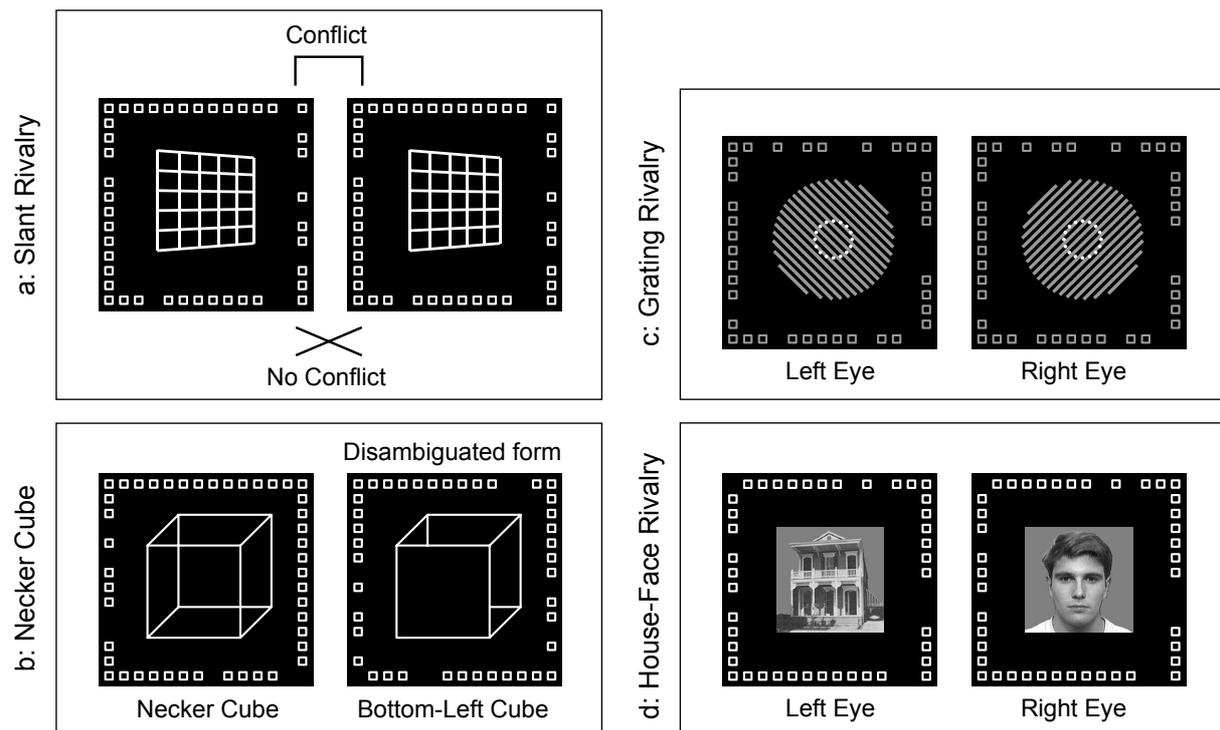


Figure 4.1: *Demonstration of the stimuli. a) slant rivalry stimulus for slants about a vertical axis. When the images are divergently fused an ambiguous stimulus is obtained for which either a disparity-dominated slant or a perspective-dominated slant will be perceived. When the images are cross-fused 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).*

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 stereoacuties 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).

## 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 figure 4.1). The size of the reference background was  $40.0$  by  $30.5$  deg and the size of a square in the background was  $0.5$  by  $0.5$  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 by 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 chapter.

### **Slant Rivalry**

For the slant rivalry paradigm (van Ee, van Dam & Erkelens, 2002), we used stimuli that consisted of a planar grid (figure 4.1) subtending 10.0 by 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.

### **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 by 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 (figure 4.1b right side). Stimulus flips were created by switching the front opaque plane between the two frontoparallel cube sides.

### **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 in order to distinguish them from the rivalry stimulus.

### **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 by 6.2 deg. The center of the image of the house contains high contrast elements relative to the center 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 in order 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.

## **Data analysis**

### **Eye movement analysis**

Binocular eye movements were monitored using a SMI-eyelink system which sampled the gaze position every 4 msec (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 equation 3.1 (see previous chapter). 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/sec. 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 4 samples prior to each blink and 4 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 & Kliegl (2003) with a few modifications (see also the previous chapter). 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 (see equation 3.2). 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 6 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 4 samples (12 msec) to further reduce noise. Since saccades are conjugate in nature we only included binocular saccades.

### 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 figure 4.2) 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 sec before a button press (i.e. at  $-10.0$  sec) to 10.0 sec after a button press (at  $+10.0$  sec), using a bin-width of 100 msec. The intervals  $-10.0$  to  $-5.0$  sec and  $+5.0$  to  $+10.0$  sec were used to calculate the mean and the standard deviation of the bin height (as a reference level). The interval  $-5.0$  to  $+5.0$  sec was the period for which we investigated the correlation between saccades and flips. We considered a peak or trough in the interval  $-5.0$  to  $+5.0$  sec 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 gray-scale representation of the occurrence histograms described above. As shown in figure 4.2, these gray-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 gray-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 (gray lines). The gray straight horizontal line represents zero deviation from the baseline. The gray vertical line at zero sec 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 chapter.

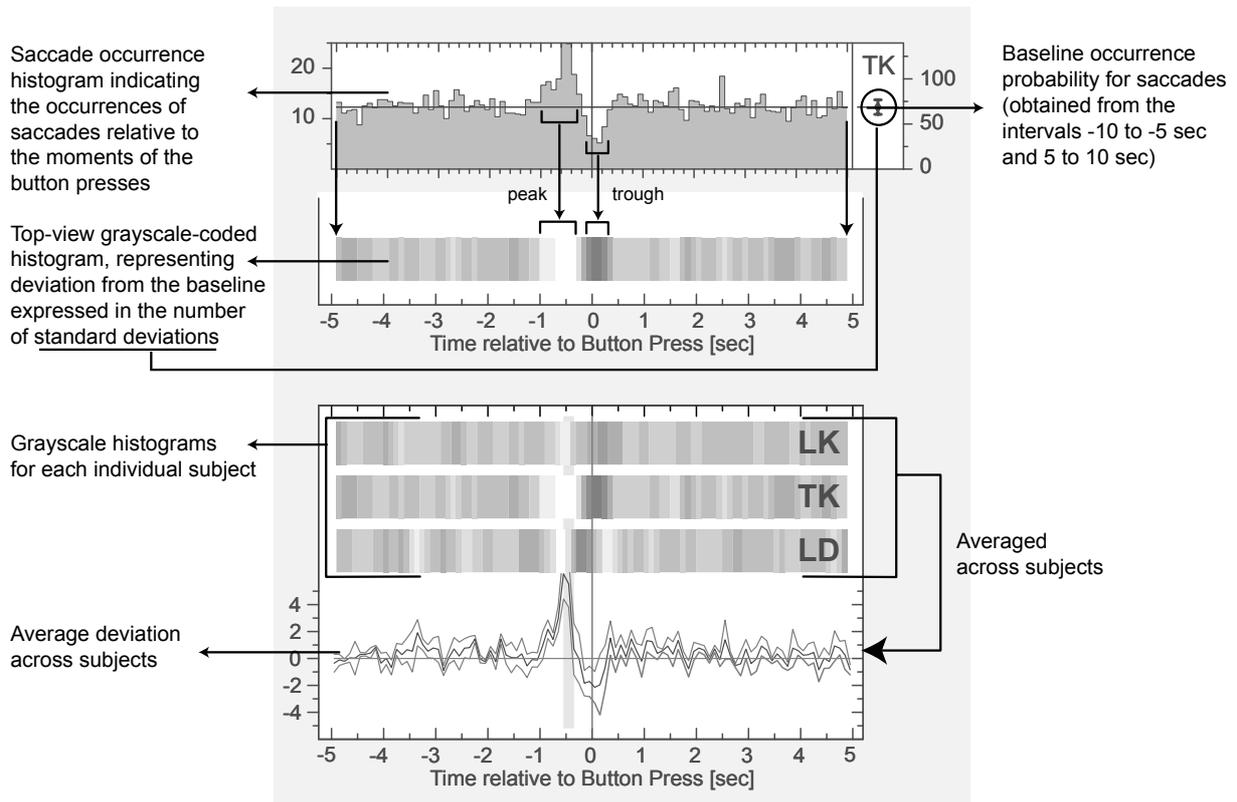


Figure 4.2: Conversion from raw saccade occurrence histogram representation to gray-scale-coded histograms. The top graph shows an example of an occurrence histogram containing the raw saccade occurrences as described in the data analysis. The histogram gets transformed into a gray-scale representation 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 gray lines represent the average deviation plus or minus one standard error across the subjects.

### 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 to 340 msec 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 positions for which the standard deviation in the version angles during the -540 to -340 msec 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 experiment 1 and 2) with Mann-Whitney post-hoc testing.

## 4.3 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 seconds. 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.

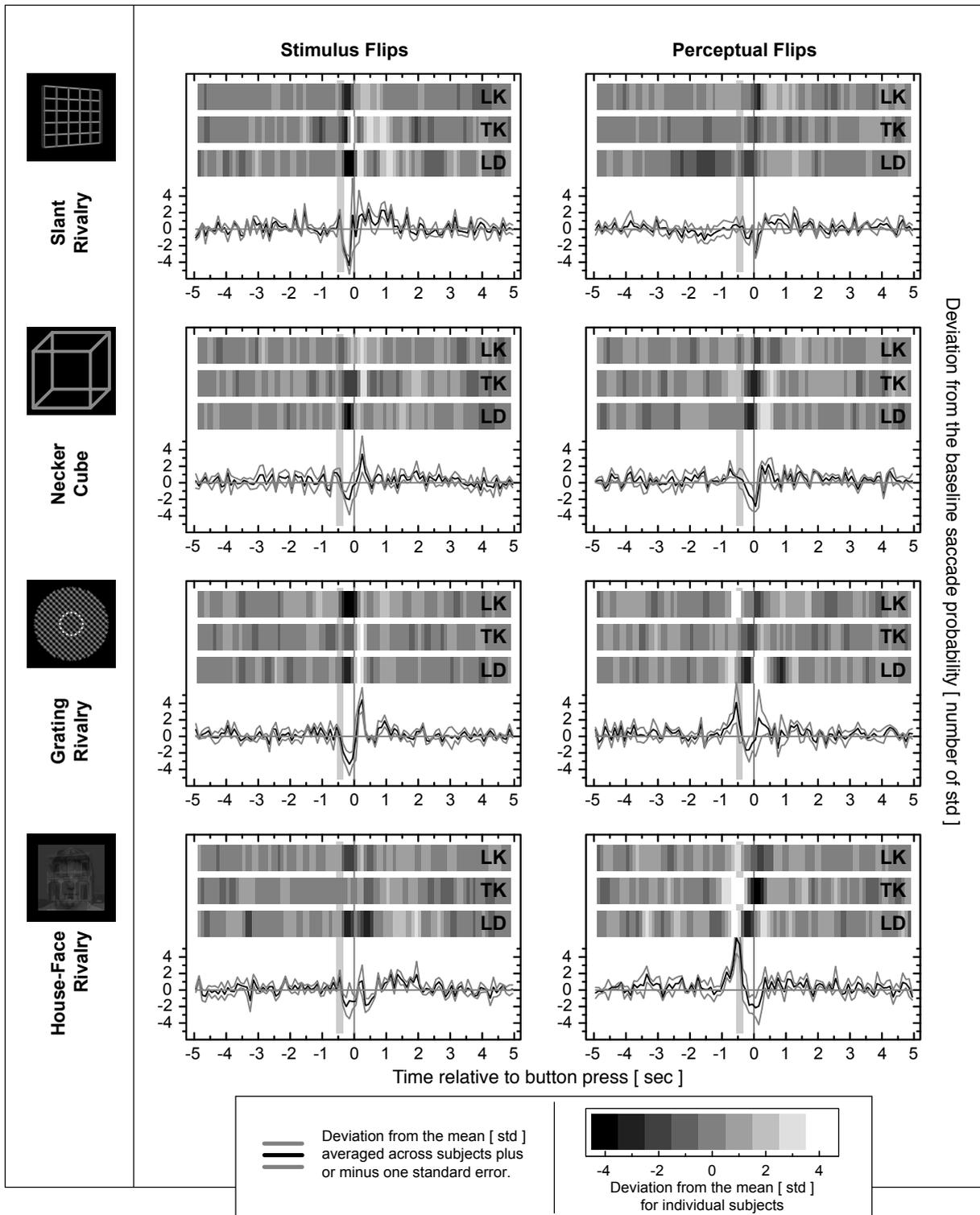
## Results experiment 1

Figure 4.3 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, the Necker cube, grating rivalry, and house-face rivalry. Within each panel three gray-scale representations of the occurrence histograms are shown, one for each subject (see also figure 4.2). The gray-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 (gray lines) are shown. The gray straight horizontal line represents zero deviation from the baseline. The gray vertical line at zero sec 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

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Figure 4.3 (on the next page): *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 conditions. Within each panel three gray-scale representations of the occurrence histograms are shown, one for each subject. The gray-scale in these plots represents the deviation within a bin (100 msec) from the mean bin height (obtained from the bins in the intervals  $-10.0$  to  $-5.0$  sec, and  $5.0$  to  $10.0$  sec, 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 (gray lines). The gray straight horizontal line represents zero deviation from the baseline saccade probability. The gray vertical line at zero sec 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.*



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 in order to make strong correlations (like the peak before the flip for binocular rivalry) completely disappear (taking into account the bin size of 100 msec 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 can not be due to the mere act of pressing buttons (van Dam & van Ee, 2005). Considering that in each of the perceptual flip histograms in figure 4.3 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 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 the section 4.2.

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.

## 4.4 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, van Dam & Brouwer, 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.<sup>1</sup> 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, van Dam & Brouwer, 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 trial (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).

## Results experiment 2

The results of experiment 2 are shown in figure 4.4a,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 sec and 0 to 2 sec.

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<sup>1</sup>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).

## Slant Rivalry

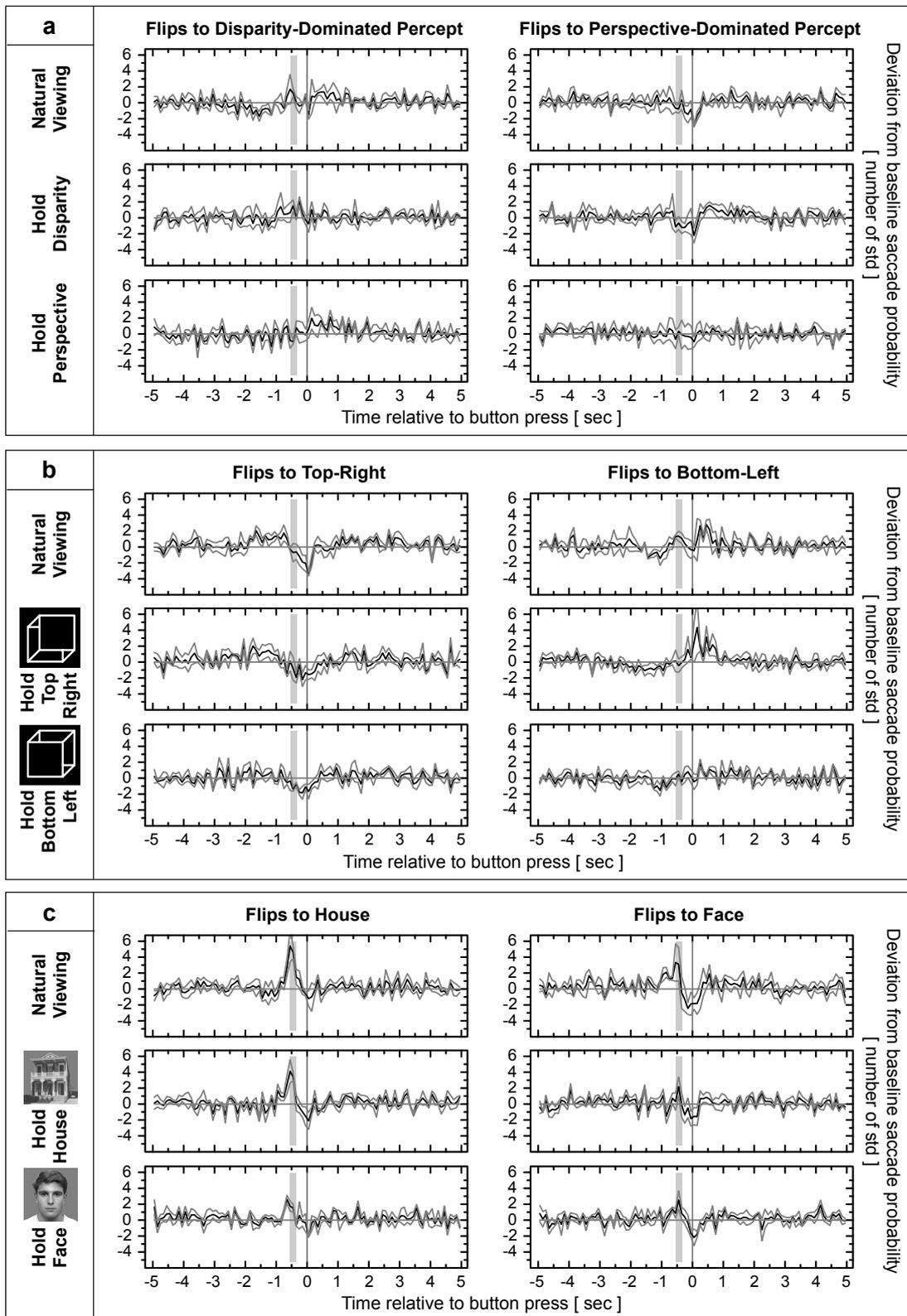
For the slant rivalry stimulus the instruction was either to hold the left side in front or to hold the right side in front. For each separate trial the experimenter is able to associate the perceived slant polarities with the disparity-dominated percept or the perspective-dominated percept. We expect the results for the left side in front and 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 figure 4.4a 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.

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

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Figure 4.4 (on the next page): *Similar to figure 4.3 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.*



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 result in a slight smearing of the effects in the histograms and thus would result in a slight decrease in the amount of correlation.

## Necker Cube

Figure 4.4b 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 durations 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.

## House-Face Rivalry

Figure 4.4c 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.

## Fixation Positions

The median fixation positions at the moments of perceptual flips are displayed in figure 4.5. 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, 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 figure 4.5 represent the two different hold percept conditions. Open symbols depict the results for the hold 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 ( $P < 0.01$ ).<sup>2</sup> 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.

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<sup>2</sup>Although, in some cases, this difference is evident only for individual sessions.

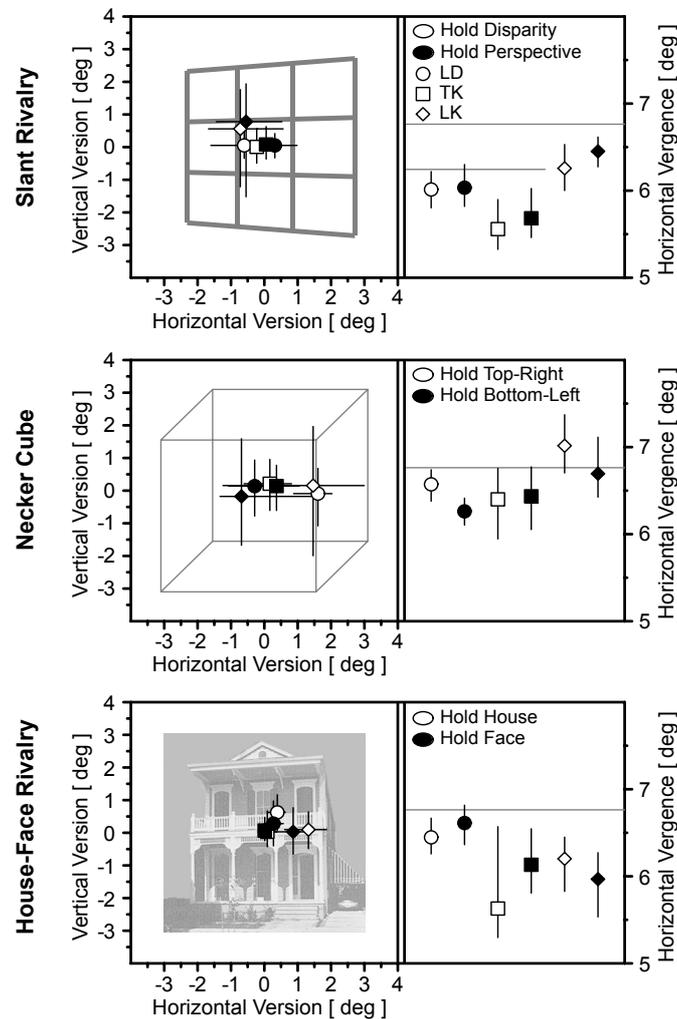


Figure 4.5: The median fixation positions at about the moments of perceptual flips for the two different hold percept conditions for the slant rivalry (top), Necker cube (middle) and house-face rivalry (bottom). Since, within each hold percept condition for each stimulus no significant differences were 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, 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.

## 4.5 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 figure 4.3). 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, see also chapter 3).

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 (figure 4.4). 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 flip in figures 4.3 and 4.4b). 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 (Einhäuser, Martin & König, 2004; Pheiffer, Eure & Hamilton, 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 (figure 4.5) 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).

## 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.

## 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, Nikolaev, Luman, Aukes, Nakatani & van Leeuwen, 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).

## 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 in order 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.

## Chapter 5

# Local retinal image changes, rather than saccades per se, trigger perceptual alternations in grating rivalry

### Abstract

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We have investigated the role of local retinal image changes for the correlation between saccades and perceptual alternations. Subjects viewed  $\pm 45$  deg grating stimuli and were asked to report perceptual alternations while we recorded saccades. By using grating stimuli, which by definition are repetitive in space, we distinguished saccades that did produce foveal image changes from saccades that did not. Our results reveal a strong correlation between foveal retinal image changes and percept dominance. We conclude that retinal image changes are crucial for the correlation between saccades and perceptual alternations and that (micro)saccades and, more specifically, their resulting retinal image shifts are at least in part responsible for determining percept dominance.

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### In preparation as:

van Dam, L.C.J. & van Ee, R. (in preparation). *Not saccades per se, but the resulting retinal image shifts can cause perceptual alternations in binocular rivalry.*

## 5.1 Introduction

In binocular rivalry each eye is presented with a different stimulus resulting in a competition for perceptual dominance. Perhaps as old as the interest in this phenomenon is the question whether eye movements play an important role in the alternation process, for eye movements cause the retinal images, and therefore the sensory input, to change. To test whether eye movements are necessary for perceptual alternations to occur, several studies used after-images (Blake, Fox & McIntyre, 1971; Lack, 1971; McDougall, 1903) and showed that perceptual alternations occurred even though the stimulus (the after-images) did not shift on the retina. However, the difference in alternation rates between after-image rivalry and real-image rivalry does suggest a role for eye movements in binocular rivalry alternations (Wade, 1974, 1975a). Furthermore, Kaufman (1963) showed that there might be a coupling between eye movements and the spread of suppression in binocular rivalry. For saccades (van Dam & van Ee, 2006) as well as for microsaccades (Sabrin & Kertesz, 1980, 1983) it has been shown that there is a positive correlation between the saccades and perceptual alternations. Does this correlation between saccades and perceptual alternations represent an intrinsic link or is it the retinal image change resulting from the saccade that is crucial for saccades to trigger perceptual alternations?

For a related perceptual bi-stability paradigm, in which two perceptually alternating orthogonal gratings are both presented to the same eye (monocular rivalry), a number of studies have reported that the retinal image changes determine the dominant percept (Bradley & Schor, 1988; Georgeson, 1984; Georgeson & Philips, 1980). This led to a discussion whether retinal after-images together with eye movements could fully explain the phenomenon of monocular rivalry (Bradley & Schor, 1988; Crassini & Broerse, 1982; Georgeson, 1984; Georgeson & Philips, 1980; Mapperson, Bowling & Lovegrove, 1982) which resulted in the notion that, although most of the experimental results support an after-image and eye movement explanation for monocular rivalry (Bradley & Schor, 1988; Georgeson, 1984; Georgeson & Philips, 1980), it is not sufficient to explain all of the phenomenology (Bradley & Schor, 1988). Since monocular and binocular rivalry have much in common, potentially retinal image changes play a similar role for both. In the first experiment we tested this hypothesis and compared results for binocular rivalry to the results for monocular rivalry. We used a conventional orthogonal grating paradigm for both monocular rivalry and binocular rivalry. The advantage of using gratings, which by definition are repetitive in space, is that not all eye movements lead to foveal image changes as is shown in figure 5.1 for a left-oblique grating. The left panel of figure 5.1 shows two examples of saccades, one from point A to point B and one from point A to point C. Both these saccades are roughly in the same direction. For the saccade from A to B, the local retinal image has not changed after the arrival at point B (figure 5.1 right top panel), since the grating phase shift across the saccade is a whole number of cycles of the grating. However, for the saccade from A to C the local retinal image is entirely reversed in luminance after the arrival at point C, since the saccade results in a half-cycle phase shift of the grating (figure 5.1 right bottom panel). This example demonstrates that the direction of a saccade alone does not provide sufficient information on the local retinal change across that saccade and one must take the retinal phase shift of the gratings into account. By tracking eye movements while subjects viewed the rivalrous stimuli we were

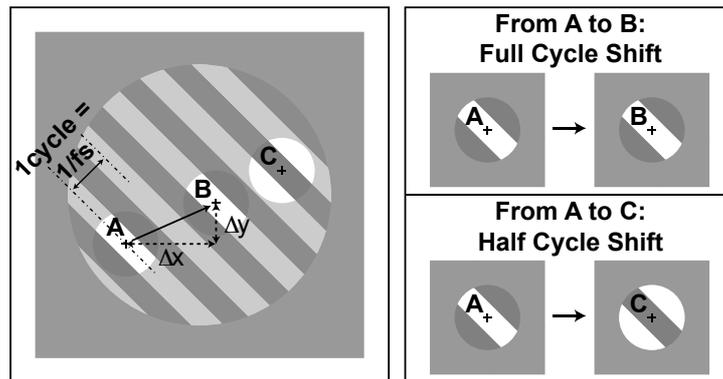


Figure 5.1: *Example of a retinal image shift across a saccade for the left-oblique grating. A saccade from A to B shifts the whole image on the retina, but locally, and more specifically in the fovea, the image has not changed (see also the right top panel). For a saccade from A to C, which is in the same direction as a saccade from A to B, the local foveal image does change (see right bottom panel).*

able to determine the correlation between eye movements and perceptual alternations.

Recently, in a study that concerned perceptual fading due to steady fixation (the Troxler effect (Troxler, 1804)), it was found that microsaccade probability was increased just before transitions to visibility and that just before a fading period the microsaccade probability was decreased (Martinez-Conde, Macknik, Troncoso & Dyar, 2006), implying a strong correlation between microsaccade production and target visibility during fixation. In experiment 2 we investigated whether microsaccades affect grating visibility in binocular rivalry in a similar manner and again we examined whether retinal image shifts are crucial for microsaccades to trigger perceptual alternations. In experiment 3 we examined whether retinal image changes without eye movements (by manipulating the stimulus), were sufficient to determine the percept.

## 5.2 Experiment 1: comparison of monocular and binocular rivalry

As mentioned above, for monocular rivalry it is known that retinal image changes of the gratings play a cardinal role in determining the percept (Bradley & Schor, 1988; Georgeson, 1984; Georgeson & Philips, 1980). To examine whether saccades and the saccadic retinal image changes play a similar role in binocular rivalry we conducted an experiment in which monocular and binocular rivalry were compared.

### Apparatus

For the binocular rivalry condition in experiment 1 we used red-green anaglyph stimuli that were displayed on a computer monitor (40 by 30 cm) in an otherwise dark room. The intensities of the red and green half-images were adjusted until they appeared equi-luminant 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 by 1200 pixels and lines were anti-aliased. The images on the monitor were refreshed every 13 msec. 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 experiment 1 (two were naive with respect to the purpose of this experiment; the third was one of the authors). All subjects had normal or corrected-to-normal visual acuity and excellent stereo-vision.

## Stimuli

We used  $\pm 45$  deg sinusoidal gratings (a left-oblique grating with lines from top left to bottom right and a right-oblique grating with lines from top right to bottom left) with a spatial frequency of 0.75 cycles / deg. This spatial frequency enables to distinguish saccades that result in a retinal change in only one of the gratings from saccades that do not. Also the perceptual alternation rate for both monocular and binocular rivalry is relatively low for this spatial frequency (Kitterle, Kaye & Nixon, 1974; Wade, 1975b). Low alternation rates help to resolve the correlation between saccades and perceptual alternations. The gratings were presented in a circular region with a diameter of 6.5 deg. The monocular rivalry gratings were viewed binocularly without the red-green glasses.

To obtain a reaction time for a response after a perceptual flip we constructed a non-rivalrous stimulus condition for which only one grating was presented binocularly. The orientation of this grating was changed by 90 deg at random moments. These physical stimulus changes will be called stimulus flips throughout this chapter and also served to check whether the subjects adhered to the instructions.

For each of the above described conditions (monocular rivalry, binocular rivalry and stimulus flip condition) the actual stimulus was displayed within a reference background which consisted of small squares. The size of the reference background was 40.0 by 30.5 deg and the size of a square in the background was 0.4 by 0.4 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 (9.2 by 10.0 deg) in which the stimulus was displayed.

## Task and procedure

Subjects initiated stimulus onset, after which the stimulus was shown for 120 seconds. The subjects' task was to press one of two buttons to indicate their perceptual alternations. For binocular rivalry this means that subjects indicated which grating perceptually covered the centre of the 6.5 deg diameter display region as patchwise rivalrous images occurred. For monocular rivalry subjects indicated which grating appeared more distinct, since for monocular rivalry complete disappearances of one of the two gratings seldom occur (Wade,

1975b). Subjects were free to make eye movements. The different stimuli (monocular and binocular rivalry) were presented in separate sessions. Each session contained eight perceptual alternation trials, which were presented in random order. For four trials the left-oblique grating was presented to the left eye and the right-oblique grating to the right eye. For the four other trials the gratings were switched. The stimulus flip trials described above were distributed across the separate sessions. Depending on the flip and saccade frequency there were two or more sessions per stimulus per subject until a sufficient amount of perceptual flips were made for our statistical analysis.

## Data analysis

### Eye movement analysis

Binocular eye movements were monitored using a SMI-eyelink system which sampled the gaze position every 4 msec (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. A detailed description of how saccade begin and end marks were filtered from the gaze position data can be found elsewhere (van Dam & van Ee, 2006, see also chapters 3 and 4). Note, that the filtering of the saccade begin and end marks included the detection of microsaccades. As noted above, it is best to take the phase shifts of the gratings on the retina as a measure of retinal image change. For each saccade we calculated the resulting retinal phase shifts of the gratings in the rivalry stimuli (on a scale from 0 to 1 cycle) from the begin and end marks:

$$\begin{aligned} p_{lo} &= \sqrt{\frac{1}{2}}(\Delta x + \Delta y)f_s \pmod{1} \\ p_{ro} &= \sqrt{\frac{1}{2}}(\Delta x - \Delta y)f_s \pmod{1}, \end{aligned} \tag{5.1}$$

where  $p_{lo}$  and  $p_{ro}$  are the phase shifts with respect to the left-oblique and right-oblique gratings, respectively;  $\Delta x$  and  $\Delta y$  are the differences in the horizontal and vertical gaze positions between the end and begin marks of the saccades (see figure 5.1);  $f_s$  is the spatial frequency of the gratings. The saccades were then subdivided into three different groups according to their phase shifts. If  $p_{lo}$  was close to a half-cycle (between 0.25 and 0.75) and  $p_{ro}$  was close to whole-cycle ( $< 0.25$  or  $> 0.75$ ), the saccade was categorised as leading to a retinal change for the left-oblique grating only (change-LO saccades), since the left-oblique grating was shifted retinally, whereas the right-oblique grating did not change on the retina. Alternatively, if  $p_{lo}$  was close to a whole-cycle and  $p_{ro}$  was close to a half-cycle the saccade was categorised as leading to a retinal change for the right-oblique grating only (change-RO saccades). For saccades for which  $p_{lo}$  and  $p_{ro}$  were similar (both close to a half-cycle or both close to a whole-cycle) it was hard to differentiate which of the gratings had changed the most on the retina and therefore these saccades were not used in the further analysis.

### 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 the button press response to a flip for

each subject. This reaction time served as an estimate for when an perceptual alternation 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 perceptual alternations we made occurrence histograms (similar to correlation histograms generally used in spike-train analysis (Perkel, Gerstein & Moore, 1967; van Dam & van Ee, 2005, 2006)). In these occurrence histograms 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 sec before a button press (i.e. at  $-10.0$  sec) to 10.0 sec after a button press (at  $+10.0$  sec), using a bin-width of 100 msec. The intervals  $-10.0$  to  $-5.0$  sec and  $+5.0$  to  $+10.0$  sec were used to calculate the mean and the standard deviation of the bin height (as a reference level). The interval  $-5.0$  to  $+5.0$  sec was the period for which we investigated the correlation between saccades and flips. We considered a peak or trough in the interval  $-5.0$  to  $+5.0$  sec 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; van Dam & van Ee, 2005, 2006).

The results of this analysis for each individual subject will be presented as a gray-scale representation of the occurrence histograms described above. The gray-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 gray-scale of each bin thus represents the deviation from the mean bin height expressed in the number of standard deviations (for a more detailed description of the histograms see: van Dam & van Ee, 2006, and chapter 4).

A measure for the differences between the histograms was obtained by applying the Kolmogorov-Smirnov test in a pairwise manner on the raw saccade perceptual alternation intervals within the ranges  $-2$  to  $0$  sec and  $0$  to  $2$  sec.

### **Correlation between saccades and the dominant percept**

To examine the role of saccadic retinal image changes during percept dominance intervals, we subtracted 750 msec from the end of each percept interval (as measured from button press to button press). These 750 msec correspond to the reaction time for the succeeding percept plus the temporal width of the previously found peak of saccades that is correlated to perceptual alternations (van Dam & van Ee, 2006). Note that the reaction time corresponding to the investigated percept duration is also excluded. For each of the thus obtained percept durations we determined the number of change-LO saccades and the number of change-RO saccades during the percept interval. Then, for all the left-oblique percept durations combined we obtained the proportion of change-LO saccades versus the change-RO saccades during that specific percept (ignoring saccades that led to similar retinal changes for both gratings), and similarly for the right-oblique grating percept. For each individual subject, the proportions of change-LO saccades for both the perceptual states were compared to 0.5 (chance level) using the exact test.

## Results experiment 1

Figures 5.2 and 5.3 display the results of experiment 1 in which we investigated the correlation between saccades and perceptual alternations for both monocular rivalry (figure 5.2) and binocular rivalry (figure 5.3). Below we will discuss the results for each paradigm separately.

### Monocular rivalry

Figure 5.2 displays the results for monocular rivalry. The panels show the deviation from the baseline saccade probability versus the time relative to the moment of the button press for flips to the left-oblique grating (left column) and flips to the right-oblique grating (right column). The top panels show the histograms for saccades that resulted in a retinal change for the left-oblique grating, but not for the right-oblique grating (change-LO saccades). The bottom panels show the histograms for saccades that resulted in a retinal change for the right-oblique, but not for the left-oblique grating (change-RO saccades). Within each panel three gray-scale representations of the occurrence histograms are shown, one for each subject. The gray-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 (gray lines) are shown. The gray straight horizontal line represents zero deviation from the baseline. The gray vertical line at zero sec 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).

If we consider the top row of results (the change-LO saccades) we see that there is a clear positive correlation between the change-LO saccades and perceptual flips to the left-oblique grating at about the moment of the perceptual flips (left panel). For flips to the right-oblique grating this positive correlation is absent (right panel). This indicates that saccades that result in a retinal image change for the left-oblique grating only, can result in an perceptual alternation toward to left-oblique grating but is not very likely to result in a flip toward the right-oblique grating. Similarly, the bottom row of panels of figure 5.2 shows that there is a clear positive correlation at about the moment of the flip between the change-RO saccades and the perceptual alternations toward the right-oblique grating (right side), but hardly between the change-RO saccades and perceptual alternations toward the left-oblique grating (left side). These results indicate that its not the saccade itself that correlates strongly with the perceptual alternation, but rather its the local retinal image change. If local retinal image changes were not important we would expect all the histograms of figure 5.2 to appear very similar.

During the left-oblique percept intervals (determined as described in the data analysis section) the proportion of change-LO saccades was significantly higher ( $P < 0.01$ ) than chance for two out of three subjects (on average the proportion was 57%). During the right-oblique percept intervals the proportion of change-LO was significantly lower than chance (on average 36%;  $P < 0.01$ ) for all subjects. The difference in the proportion of change-LO saccades during the two different perceptual states indicates that there is also a correlation between the saccadic retinal image changes and the dominant percept.

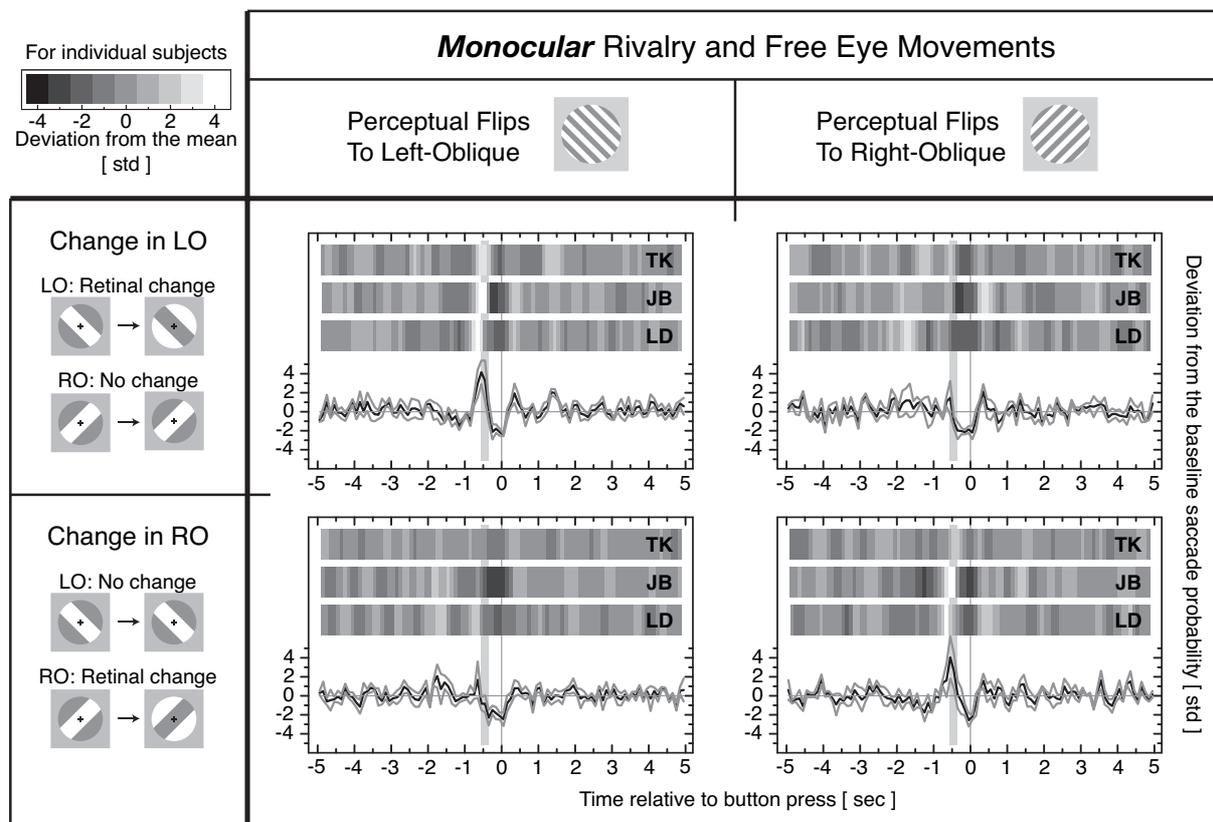


Figure 5.2: The correlation between saccades and perceptual flips for monocular rivalry. The panels show the deviation from the baseline saccade probability versus the time relative to the button press for flips to the left-oblique grating (left column) and flips to the right-oblique grating (right column). The top panels show the histograms for saccades that resulted in a retinal change for the left-oblique grating, but not for the right-oblique grating (change in LO). The bottom panels show the histograms for saccades that resulted in a retinal change for the right-oblique grating, but not for the left-oblique grating (change in RO). Within each panel three gray-scale representations of the occurrence histograms are shown, one for each subject. The gray-scale in these plots represents the deviation within a bin (100 msec) from the mean bin height (obtained from the bins in the intervals  $-10.0$  to  $-5.0$  sec, and  $5.0$  to  $10.0$  sec, 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 (gray lines). The gray straight horizontal line represents zero deviation from the baseline saccade probability. The gray vertical line at zero sec 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 button press (a reaction time obtained from the stimulus flip condition). The top-left and the bottom-right panels show a clear positive correlation between saccades and perceptual alternations at about the moment of the perceptual alternations. In the top-right and bottom-left panels this correlation is absent. This indicates that retinal image changes due to saccades are systematically correlated with the perceptual alternations.

This suggests that, apart from triggering perceptual alternations, saccades can help to maintain a specific percept, by inducing retinal changes for the dominant grating only. Note, that the histograms in figures 5.2 do not show any well-defined peaks after the moment of the button press (even when taking into account that percept durations after the button presses are of varying length). This indicates that the saccadic retinal image changes during a percept dominance period are not subject to specific timing with respect to the onset of the dominance period.

Note, that the results confirm those of Georgeson (1984) and Bradley & Schor (1988) who showed that the phase shifts in the gratings due to saccades are systematically correlated with perceptual alternations in monocular rivalry.

### Binocular rivalry

Figure 5.3 displays the results for binocular rivalry. For binocular rivalry too, we see that the change-LO saccades are strongly correlated with perceptual alternations toward the left-oblique grating and hardly with perceptual alternations to the right-oblique grating. The change-RO saccades are strongly correlated with perceptual alternations to the right-oblique grating, rather than alternations to the left-oblique grating. These results indicate that local retinal image changes across saccades are strongly correlated with perceptual alternations in binocular rivalry.<sup>1</sup> Note, that all histograms show the decrease in saccade probability between the moment of the perceptual flip and the moment of the button press that we found previously (van Dam & van Ee, 2006).

The proportion of change-LO saccades was significantly higher than chance during left-oblique percept intervals (on average 63%;  $p < 0.01$  for all individual subjects) and significantly lower than chance during right-oblique percept intervals (on average 30%;  $P < 0.01$  for all individual subjects). These results indicate that there is also a correlation between the saccadic retinal image change during percept intervals and the prevailing dominant percept.

In sum, the results for both monocular and binocular rivalry indicate that retinal image changes are crucial for the correlation between saccades and perceptual alternations and that retinal image changes can aid in maintaining perceptual states.

## 5.3 Experiment 2: binocular rivalry and fixation

In experiment 1 we found a strong correlation between the saccadic retinal image changes of the gratings and perceptual alternations for both the monocular and binocular rivalry paradigms. In experiment 1 the subjects were free to make eye movements. Recently, Martinez-Conde, Macknik, Troncoso & Dyar (2006) showed that microsaccade probabil-

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<sup>1</sup>Sinusoidal gratings of 0.75 cycles / deg strongly induce monocular rivalry (Atkinson, Campbell, Fiorentini & Maffei, 1973) and perceptual fading of the gratings (Tulunay-Keesey, 1982). Such ‘monocular rivalry’ alternations might play a role in our binocular rivalry paradigm. Therefore we repeated the experiment for two subjects, using square-wave gratings, for which the number of monocular rivalry alternations and the amount of perceptual fading should be reduced (Atkinson, Campbell, Fiorentini & Maffei, 1973; Campbell & Howell, 1972; Tulunay-Keesey, 1982). The results for the square-wave gratings were very similar to the results described here for the sinusoidal gratings.

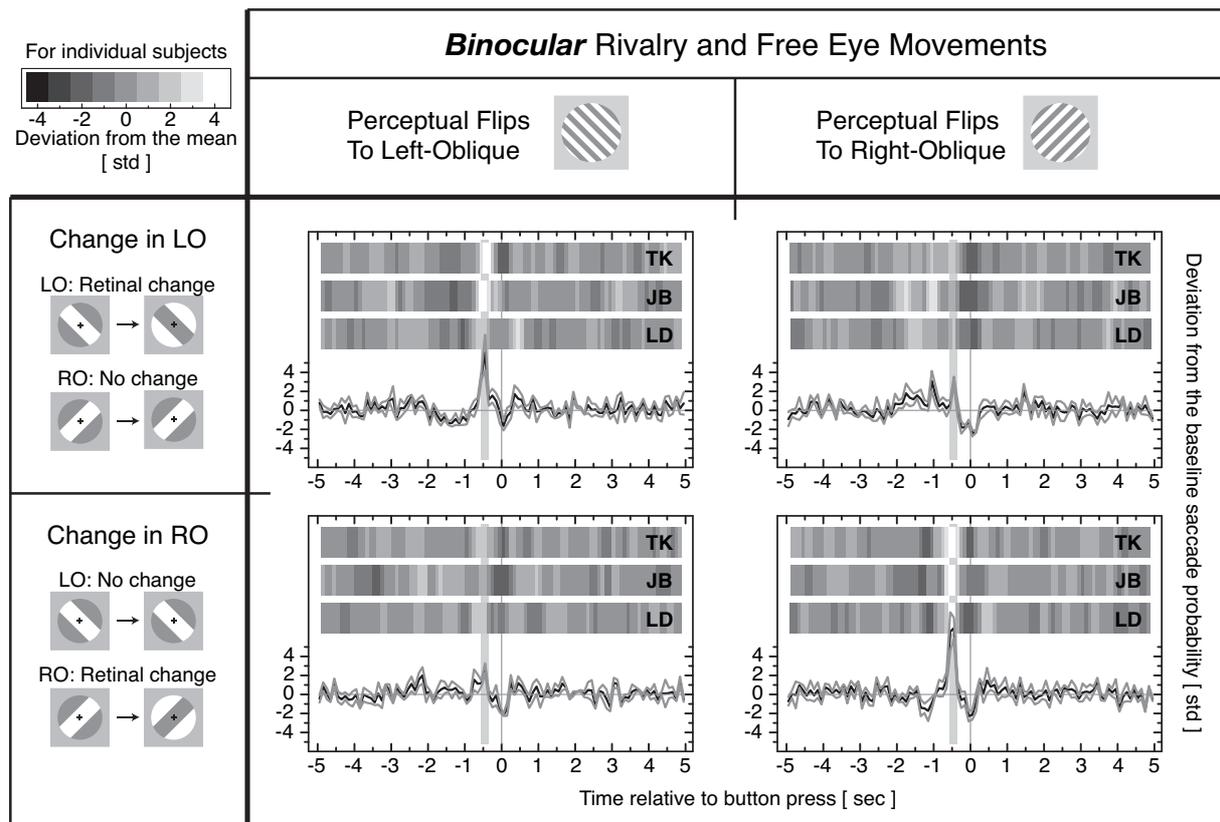


Figure 5.3: Similar to figure 5.2 but now for binocular rivalry. For binocular rivalry too, there is a strong positive correlation between change-LO saccades and perceptual alternations to the left-oblique grating, and similarly, between change-RO saccades and perceptual alternations to the right-oblique grating. In the top-right and bottom-left panels this positive correlation is absent. This indicates that for binocular rivalry too, the retinal image changes produced by saccades are systematically correlated with perceptual alternations.

ity is strongly correlated with target visibility for the Troxler effect (perceptual fading). To investigate the correlation between microsaccades and perceptual alternations in grating rivalry, we repeated experiment 1, but now with strict fixation and we investigated whether retinal image shifts are crucial for microsaccades to trigger perceptual alternations. Since, for monocular rivalry, the role of retinal image shifts has already been investigated extensively (Georgeson & Philips, 1980; Georgeson, 1984; Bradley & Schor, 1988, the results of which we replicated in our experiment 1) we concentrated on binocular rivalry.

## Stimuli, task and procedure

The stimulus was very similar to the one used in experiment 1. The circular region in which the stimulus was displayed was reduced to 4.5 deg in diameter to reduce patchiness (the black window in the reference background was reduced accordingly to 7.6 by 6.8 deg) and a fixation dot of 0.2 deg in diameter was added in the centre of the circular region. The task and procedure were the same as for experiment 1 and the same three subjects

participated.

## Results experiment 2

The saccades were again divided in the change-LO and the change-RO groups. We combined the occurrence histograms of the change-LO saccades for perceptual alternations to the left-oblique grating with the histograms of the change-RO saccades for alternations to the right-oblique grating. Together, these histograms provide the correlation between the perceptual alternations and saccades that produce a retinal change in the grating that becomes dominant, but not in the grating that gets suppressed. The histograms for these “change to dominant” saccades are shown in the top panel of figure 5.4. Similarly, the histograms of the change-LO saccades for alternations to the right-oblique grating and of the change-RO saccades for alternations to the left-oblique grating can be combined to form the histograms for the “change to suppressed” saccades, which are shown in the bottom panel of figure 5.4.

The results again demonstrate a strong correlation between the retinal image changes and the grating that becomes dominant (there does appear to be a small peak in the change-in-suppressed saccades for subject JB, but, even for this subject the difference between the two histograms is significant ( $P < 0.05$  with a Kolmogorov-Smirnov test within the interval  $-2.0$  to  $0.0$  sec)).

The proportion of change-to-dominant saccades during the percept intervals was again significantly higher than chance-level (on average 59% with  $P < 0.01$  for two subjects and  $P < 0.05$  for the third subject), indicating that microsaccades can help to maintain a percept even when the subjects are instructed to fixate.

## 5.4 Experiment 3: retinal image changes without saccades

The results of experiment 1 and 2 strongly suggest that the retinal image changes due to saccades, rather than the saccades per se, cause perceptual alternations for both the monocular and binocular rivalry conditions. This suggestion predicts that local retinal image shifts without co-occurring eye movements should be sufficient to trigger perceptual alternations.

### Stimuli, task and procedure

To test this prediction we used a stimulus similar to the one used in experiment 1, but now in de center of the stimulus there was a black disk (1.6 deg) and a fixation cross (0.4 deg) (see figure 5.5a).

Subjects initiated stimulus onset. We then presented alternately the stimulus described above (0.5 sec intervals), and a blank stimulus in which only the background and the fixation cross were included (53 msec intervals). After the second blank, one out of four possible stimulus manipulations occurred (for an example see figure 5.5b): the left-oblique grating could be counterphased relative to the first two stimulus presentations;

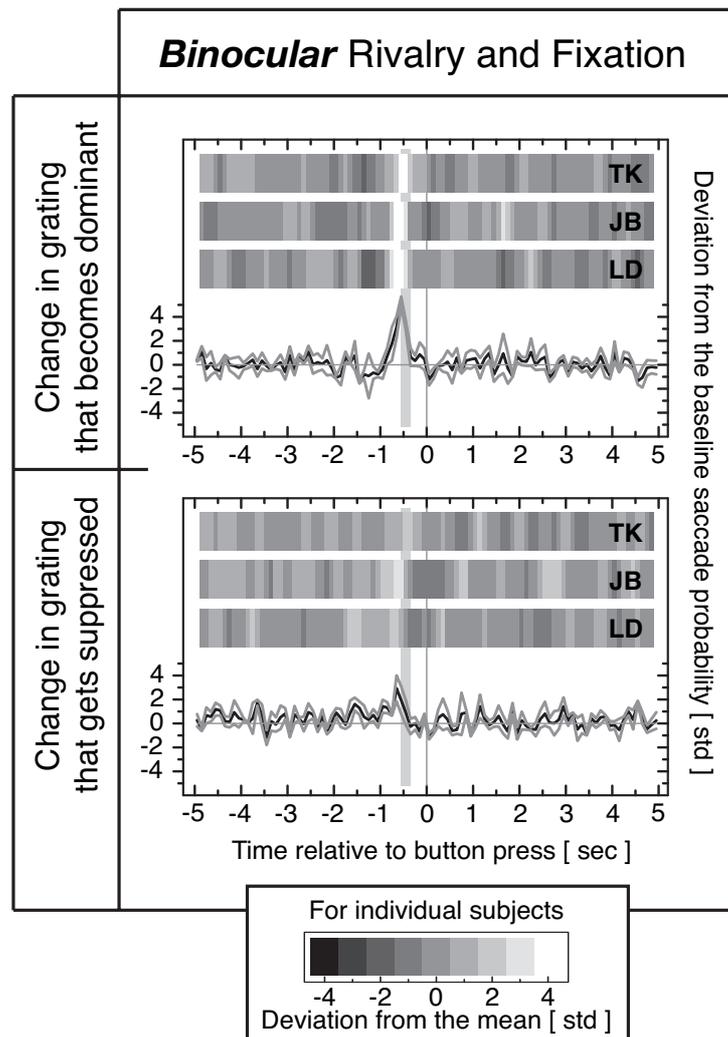


Figure 5.4: Results for experiment 2 in which we investigated the correlation between fixational saccades and perceptual alternations for binocular rivalry. Respectively, the top and bottom panels show the histograms for change-to-dominance saccades and change-to-suppressed saccades. In each panel three gray-scale representations of the occurrence histograms are shown, one for each subject and, as before, the average deviation across the three subjects is shown in the bottom graph of each panel. There is a strong positive correlation between the change-to-dominant saccades and the perceptual alternations (peak at the moment of the perceptual alternations). For the change-to-suppressed saccades this positive correlation is either absent or much reduced. These results reveal a high correlation between microsaccadic retinal image changes and perceptual alternations for binocular rivalry.

the right-oblique could be counterphased; both the left-oblique and right-oblique could be counterphased or the stimulus remained unaltered. After the manipulation the stimulus was removed at varying intervals (0.25, 0.5, 0.75, 1.0, 1.25, 1.50, 1.75 and 2.0 sec relative to the moment of the start of the blank period after which the manipulated stimulus appears) and substituted by a mask of dynamic random dots (density was 9.8 dots/deg<sup>2</sup>). The mask had the same diameter as the stimulus (6.5 deg) and a dot in the random dot pattern was

0.4 deg in diameter (thus, there was a large overlap between dots). The subjects' task was to report the percept they had the instant before the stimulus was substituted by the mask. Three subjects participated, two of whom had also been subjects in experiments 1 and 2.

### Results experiment 3

Trials in which subjects either blinked or made saccades that resulted in more than a 0.25 cycle phase shift for one or both gratings (see also data analysis for experiment 1) after the first 500 msec were excluded from the analyses. For each time interval, for each stimulus manipulation condition, the proportion left-oblique grating dominant was calculated. The results are shown in figure 5.5c. The average left-oblique dominant proportion is shown versus time relative to the moment of stimulus manipulation. The dark gray filled circles represent the results for the condition in which only the left-oblique grating was counterphased; the light gray filled squares represent the results for the counterphased right-oblique grating condition; open dark gray circles represent results for the counterphase both gratings condition and open light gray squares represent the results for the condition in which the stimulus was not manipulated. Error bars represent standard errors across subjects.

The results show very clearly that the left-oblique grating either becomes, or remains, dominant when only the left-oblique grating is counterphased and similarly the right-oblique grating either becomes, or remains, dominant when the right-oblique grating is counterphased. When either both or none of the gratings are counterphased, subjects do not show a preference for either the left-oblique or right-oblique grating. In sum, we conclude that retinal changes without saccades are strongly correlated to percept dominance.

Another interesting aspect in figure 5.5 is that after about 1 sec of percept dominance in the counterphase left-oblique and counterphase right-oblique conditions, the proportions left-oblique grating perceived start returning to 0.5 indicating that perceptual alternations occur. These alternations can not be due to large retinal changes caused by saccades, since trials in which such saccades occurred were removed from the analysis (even if we remove all trials in which saccades were detected regardless of their amplitudes and directions, this result still persists). The fact that alternations occur without saccades or further stimulus manipulations indicates that abrupt retinal image changes are not essential for perceptual alternations to occur.

## 5.5 Discussion

We have examined whether retinal image changes are crucial for saccades to determine percept dominance in binocular grating rivalry. We found that for both a free eye movement condition (experiment 1) and a fixation condition (experiment 2) retinal changes are crucial for the interaction between saccades and perceptual alternations, and that retinal image changes without saccades are indeed sufficient to trigger a perceptual alternation (experiment 3). This means that there does not have to be an intrinsic link between the saccades and perceptual alternations, unless that link contains the full information about

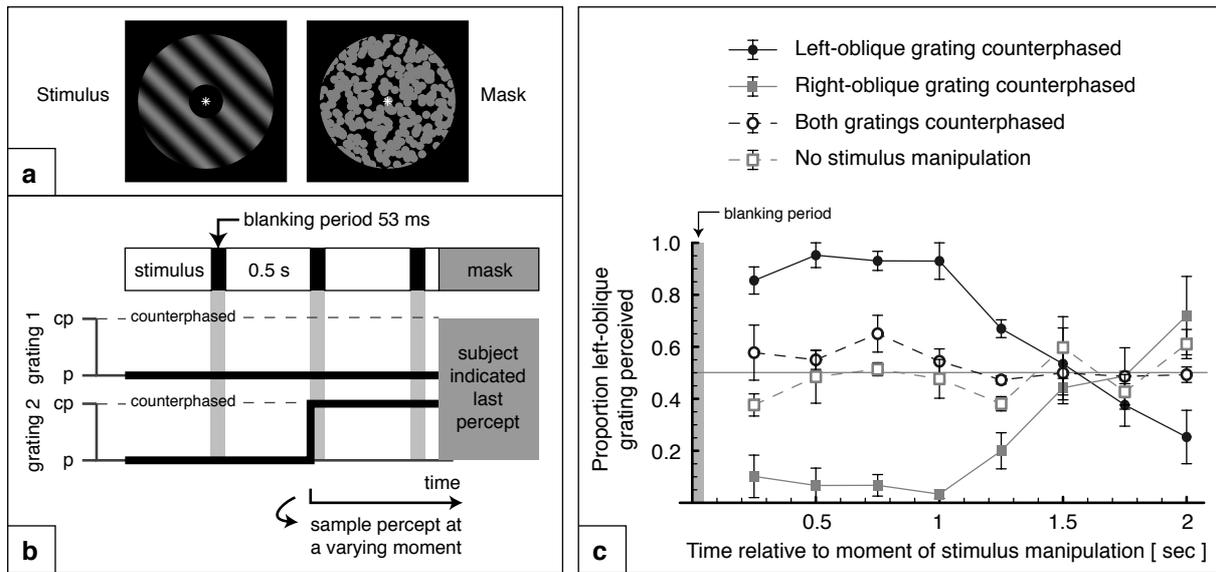


Figure 5.5: *a)* and *b)* show the setup of experiment 3 in which we investigated by using physical stimulus shifts, whether retinal shifts without saccades were sufficient to trigger perceptual alternations. *a)* shows examples of the stimulus (left-oblique grating only) and the mask. *b)* shows the temporal sequence for a single trial. The grating stimulus (0.5 sec) and a blank stimulus (53 msec) were presented alternately. In the second blank either none, only one, or both gratings were counterphased. At various but distinct moments after the stimulus manipulation the stimulus was substituted by a mask and subjects had to indicate their last percept. *c)* shows the average proportions (across subjects) of left-oblique grating perceived versus the time relative to the moment of stimulus manipulation. Filled symbols represent the results for the conditions in which only one grating was counterphased. Open symbols represents the results for the conditions in which either both gratings or none of the gratings were counterphased. Error bars represent standard errors across subjects. The results demonstrate that if one grating alone is counterphased, that grating becomes dominant, thus, retinal image changes without saccades are sufficient to manipulate the percept.

saccade begin and end points relative to the stimulus. The latter seems very unlikely given the relatively large saccadic errors when saccades are made to well-defined targets (van Opstal & van Gisbergen, 1989). The fact that retinal image changes are crucial for saccades to trigger perceptual alternations suggests that the correlation between the saccadic retinal shifts and perceptual alternations is a true causal relationship, thus that there is no other confounding variable that causes both the saccade and the perceptual alternation.

Apart from the strong correlation between saccadic retinal changes and the perceptual alternations, we found that there was a significant correlation between the retinal changes and the currently dominant percept, indicating that the saccadic retinal changes are also important for maintaining a specific percept in binocular rivalry.

Our results reveal that retinal changes play a similar role for both monocular and binocular rivalry (see figures 5.2 and 5.3). It has been suggested that negative retinal after-images are responsible for *monocular* rivalry to occur (Georgeson, 1984; Georgeson

& Philips, 1980). The negative afterimage of a grating, which appears as an inverted copy of the real image, will cause the perceived contrast of the grating to decrease with increased time of steady fixation. If, after such a period of steady fixation, one of the rivaling gratings is shifted on the retina by a half-cycle due to a saccade (see for instance the saccade from A to C in figure 5.1), the negative afterimage will temporarily cease to cancel the real image of that grating and, thus, that grating will temporarily appear to have gained a higher contrast relative to the other grating and may therefore appear more dominant. For monocular rivalry the disappearances are seldom complete (Wade, 1975b), but most often appear as contrast decreases of one grating relative to the other, which is consistent with an important role for after-images in monocular rivalry.

According to our results for *binocular* rivalry, it appears very likely that temporary contrast increases due to after-image and image superposition, or possibly just the retinal change by itself of one grating relative to the other, can trigger a perceptual alternation. Several studies have shown that abrupt changes in the stimulus of one eye relative to the other (i.e. either phase or frequency changes of a grating (Walker & Powell, 1979), transient contrast changes (Blake, Westendorf & Fox, 1990; Walker & Powell, 1979; Wilson, Blake & Lee, 2001) or a delay in the onset of the image of one eye (Wolfe, 1984)), can determine percept dominance. As our results show, saccades can be responsible for a large number of perceptual alternations by producing abrupt retinal image shifts, and thus they have a large influence on the percept duration distributions and the perceptual alternation rates (although we would like to stress that eye movements do not explain the phenomenon of binocular rivalry, since, for instance, they can not account for the perceptual disappearance of one eye's image as the other image becomes dominant).

For more complicated binocular rivalry stimuli saccades are also strongly correlated with perceptual alternations, as we have shown in a previous study for the house-face stimulus, in which one eye is presented with the image of a house and the other eye with the image of a face (van Dam & van Ee, 2006). Even for afterimage rivalry, a role of eye movements can not be completely ruled out, since the perception of after-images is known to depend on eye movements. For instance, afterimages tend to disappear (e.g. Kennard, Hartmann, Kraft & Boshes, 1970) and reappear after the execution of a saccade (e.g. Ditchburn, 1973; McDougall, 1903). For stabilized image rivalry by controlling for occurring eye movements, the stabilisation of the image on the retina is usually not perfect, otherwise the images would perceptually completely disappear (Ditchburn & Ginsborg, 1952; Riggs, Ratliff, Cornsweet & Cornsweet, 1953). Thus, it remains to be verified whether or not perceptual alternations during stabilized image rivalry are influenced by eye movements, as is the case for normal real-image rivalry as we have shown here.

What does the fact that saccades can trigger perceptual alternations imply for existing and future binocular rivalry studies? In most studies subjects are instructed to fixate in order to minimize the amount of eye movements. However, eye movements (saccades as well as microsaccades) are known to depend on the specific task (Steinman, Cunitz, Timberlake & Herman, 1967; Winterson & Collewijn, 1976; Yarbus, 1967). Furthermore, Engbert & Kliegl (2003); Hafed & Clark (2002) and Laubrock, Engbert & Kliegl (2005) demonstrated that spatial attention shifts are often accompanied by microsaccades in the direction of the attention shift even during periods for which subjects are instructed to fixate. The retinal shift resulting from microsaccades can in turn trigger perceptual

alternations (see experiment 2). Therefore, our results underscore the importance of either controlling or correcting for eye movements when studying binocular rivalry, especially when comparing different attentional or task conditions.

# Chapter 6

## Summary and conclusions

The research reported in this thesis is devoted to visual ambiguities and the resulting bistable percepts. In the **second chapter** we investigated the aperture problem for stereopsis, an ambiguity for which our matching system usually picks one of a theoretically infinite number of solutions. More specifically we investigated the assigned disparity corresponding to the perceived depth of a line which was occluded at the flanks and thus seen through an aperture. We showed that from a geometrical point of view, matching of the partially occluded line occurred in the horizontal direction when the occluders were well defined in terms of horizontal and vertical disparity. However, when matching of the occluders was ambiguous as well, the intersections between the occluded test line and the occluders played a role in the determination of the assigned horizontal disparity of the test line and the assigned horizontal disparity can vary with aperture orientation.

The second chapter only concerned binocular disparity information. In the **third chapter** we investigated the perception of a slanted plane when the depth cues of binocular disparity (stereo-information) and linear perspective (which essentially is a monocular cue) were manipulated independently. When these cues specify similar slants our visual systems combines these cues to provide one single percept. However, when the conflict between these two sources of depth information is large, then the percept alternates between a perspective-dominated percept and a disparity-dominated percept (slant rivalry). Thus, large perspective versus disparity conflicts lead to perceptual bistability of one single stable stimulus. We studied the perceived slants for the perspective and disparity-dominated percepts for different perspective-disparity conflicts and in order to determine whether the alternation between the two possible percepts is a central process (occurring within our brain) we investigated the role of eye movements for this specific stimulus. We found that eye movements (saccades, microsaccades, vergence eye movements and blinks) are not essential for perceptual alternations to occur and that on average there is no positive correlation between perceptual flips and both saccades and blinks that occurred prior to a perceptual flip. However, when eye movements are allowed they can help to obtain a disparity-dominated percept. After the moment of the 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.

In the **fourth chapter** we further investigated the role of eye movements in perceptual bistability for several bistability paradigms. We compared results for perceptual rivalry (in our study Necker cube rivalry and slant rivalry) and binocular rivalry (binocular grating rivalry and house-face rivalry). We found that, at the moments of perceptual alternations, there is high positive correlation between saccades and perceptual alternations for binocular rivalry, rather than for perceptual rivalry, indicating that saccades play an active role in alternating the percept for binocular rivalry. For perceptual rivalry in a natural viewing condition (meaning that subjects were instructed not to influence the perceptual alternation rate) we found small differences in fixation positions at the moment of perceptual flips to the two different percepts. It appeared that changes in the fixation position during perceptual rivalry occurred after the perceptual alternation, rather than before. We also investigated whether there was an interaction between voluntary control in percept dominance and eye movements schemes for three different paradigms (slant rivalry, necker cube rivalry and house-face rivalry). In separate experimental trials subjects were instructed to either view the stimulus in a natural way (thus, without trying to influence the reversal rate) or to try to hold one specific percept. We found that the pattern of temporal correlation did not change with these different voluntary control conditions, indicating that subjects did not use different eye movement schemes in order to exert voluntary control (although the amount of correlation could be different for different voluntary control conditions). However, we did find differences in fixation positions at the moments of perceptual alternations between the two different hold-percept conditions for each paradigm (but not between the two different percepts within each hold-percept condition). This indicates that, although fixation position within the stimulus does not by itself determine the percept, subjects prefer to look at different positions for different hold percept conditions.

In the fourth chapter we found that for binocular rivalry there is a high correlation between saccades and perceptual alternations. In the **fifth chapter** we investigated whether this correlation represented an intrinsic link between saccades and perceptual alternations or if this correlation is due to the retinal changes caused by the saccades. By using grating stimuli, which by definition are repetitive in space, we distinguished saccades that did produce local retinal image changes (of the gratings) from saccades that did not. We found that there is a strong (causal) correlation between specific local retinal image changes and percept dominance, indicating that retinal image changes are crucial for the correlation between saccades and perceptual alternations. Furthermore, we found that this correlation even emerged for fixational saccades (thus when subjects were instructed to fixate). Therefore, the fifth chapter underscores the importance of either controlling or correcting for eye movements when studying binocular rivalry (although eye movements alone can not be responsible for the phenomenon binocular rivalry).

# Chapter 7

## Samenvatting en conclusies

Het onderzoek dat in dit proefschrift beschreven staat is gewijd aan visuele ambiguïteiten en de bistabiele waarneming waarin zij kunnen resulteren. In het **tweede hoofdstuk** hebben we een voorbeeld van visuele ambiguïteit onderzocht, waarvoor onze hersenen één enkele oplossing kiezen uit een theoretisch oneindige hoeveelheid mogelijke oplossingen. De gekozen enkele oplossing resulteert dus in één enkel percept. Het onderzochte voorbeeld is het zogenaamde apertuurprobleem. Het apertuurprobleem behandelt de vraag hoe de ‘matching’ (het vinden van overeenstemmingen in de retinale beelden van de beide ogen) en het diepte percept tot stand komen, voor objecten die bekeken worden door een apertuur en dus maar gedeeltelijk zichtbaar zijn. Om precies te zijn, hebben we onderzocht wat het diepte percept en de toegekende dispariteiten zijn voor een ‘oneindig’ lange lijn die bekeken wordt door een apertuur. We hebben aangetoond dat vanuit geometrisch oogpunt het matchen van de slechts gedeeltelijk zichtbare lijn in de horizontale richting gebeurt, als de apertuur en alles wat daarbij hoort goed gedefiniëerd is in termen van horizontale en verticale dispariteiten. Maar, als het matchen van de apertuur zelf ook ambigu is, dan spelen de snijpunten van de apertuur en de testlijn een rol in het bepalen van de toegekende dispariteit van de lijn. In dat laatste geval kan de toegekende dispariteit zelfs variëren met de oriëntatie van de apertuur.

In het **derde hoofdstuk** hebben we onderzocht wat de waarneming is van een gedraaid vlak waarvoor binoculaire dispariteit (dus de stereo-informatie zoals in hoofdstuk twee) en lineair perspectief (wat hoofdzakelijk een monoculaire cue is) onafhankelijk van elkaar worden gemanipuleerd. We vonden dat, als dispariteit en perspectief gelijke draaihoeken specificeren, dat dan ons visuele systeem deze twee cues combineert om zo tot één percept te komen. Maar als het conflict in draaihoek tussen deze twee cues groot wordt (bijvoorbeeld als perspectief specificeert dat de ene kant van het gedraaide vlak naar voren komt en dispariteit specificeert dat de andere kant naar voren komt), dan alterneert het resulterende percept tussen een perspectief-gedomineerde percept en een dispariteit-gedomineerde percept. Dus grote perspectief-dispariteit conflicten leiden tot de bistabiele waarneming van een enkele stabiele stimulus. In hoofdstuk drie hebben we o.a. de verschillende waargenomen draaihoeken van het gedraaide vlak voor de verschillende perspectief-dispariteit conflicten in kaart gebracht.

Om te onderzoeken of de alternatie tussen de perspectief-gedomineerde en dispariteit-gedomineerde percepten daadwerkelijk een centraal proces is dat in ons hoofd gebeurt,

hebben we bekeken wat de rol van oogbewegingen is voor deze specifieke stimulus. Immers als oogbewegingen volledig verantwoordelijk zouden zijn voor de percept alternaties dan hoeven daar geen neuronen in ons hoofd mee bezig te zijn. We vonden dat saccades (snelle oogbewegingen), microsaccades, vergentie oogbewegingen (veranderingen in fixatie-diepte) en oogknipperingen niet essentieel zijn voor perceptuele alternaties tussen de twee percepten. Er was geen positieve correlatie tussen perceptuele alternaties en zowel saccades als oogknipperingen die voor een perceptuele alternatie plaatsvonden. Wel vonden we, dat wanneer proefpersonen vrij waren om oogbewegingen te maken, oogbewegingen konden helpen om het dispariteit-gedomineerde percept te verkrijgen. Ook vonden we dat na een perceptuele alternatie de kans op een oogbeweging (zowel saccades als oogknipperingen) tijdelijk was gereduceerd. De reductie in saccade-waarschijnlijkheid trad hoofdzakelijk op voor de grotere vrijwillige saccades in plaats van de meer onvrijwillige microsaccades en deze reductie zou als een reset van de saccade planning geïnterpreteerd kunnen worden.

In het **vierde hoofdstuk** hebben we de rol van oogbewegingen in de bistabiele waarneming verder onderzocht en nu ook voor verschillende bistabiliteitsparadigma's. We hebben de resultaten voor perceptuele rivaliteit (in onze studie, de draaihoek bistabiliteit (slant rivalry) uit hoofdstuk drie en de Necker kubus) en binoculaire rivaliteit (binoculaire raster rivaliteit en huis-gezicht rivaliteit) met elkaar vergeleken. We vonden dat op het moment van een perceptuele alternatie er een grote positieve correlatie is tussen saccades en perceptuele alternaties voor binoculaire rivaliteit. Voor perceptuele rivaliteit was deze positieve correlatie niet of nauwelijks aantoonbaar. Dit toont aan dat saccades een grotere rol spelen in het alternatie proces voor binoculaire rivaliteit dan voor perceptuele rivaliteit. Voor perceptuele rivaliteit vonden we dat er kleine verschillen waren in fixatieposities op het moment van perceptuele alternaties naar de twee verschillende percepten. Het lijkt erop dat de veranderingen in fixatiepositie na de perceptuele alternatie plaats vond in plaats van ervoor.

In hoofdstuk vier hebben we ook onderzocht of er een interactie bestaat tussen de vrijwillige percept beïnvloeding en saccades voor drie verschillende bistabiliteitsparadigma's (slant rivalry, Necker kubus en huis-gezicht rivaliteit). In aparte trials werden de proefpersonen gevraagd om óf de stimulus op een natuurlijk manier te bekijken (dus zonder de percept-dominantie te beïnvloeden), óf om te proberen om een specifiek percept te houden. We vonden dat het patroon van de temporele correlatie tussen saccades and percept alternaties voor elk van de onderzochte paradigma's niet veranderde met de beïnvloedingstaak (de grootte van de correlatie kon wel veranderen met de vrijwillige beïnvloedingstaak). Dit betekent dat de proefpersonen geen verschillende oogbewegingspatronen gebruiken om zo de vrijwillige beïnvloeding tot stand te brengen. Wel vonden we verschillen in fixatie posities op het moment van de percept-alternaties voor de twee verschillende houd-percept condities voor elk paradigma (maar niet tussen de twee verschillende percepten in elke houd-percept conditie). Dit wijst erop, dat proefpersonen graag naar verschillende posities in de stimulus kijken voor de verschillende houd-percept condities, al kan fixatiepositie alleen niet verantwoordelijk zijn voor het resulterende percept.

In hoofdstuk vier vonden we dat voor binoculaire rivaliteit er een grote correlatie bestaat tussen saccades en perceptuele alternaties. In het **vijfde hoofdstuk** hebben we onderzocht of hier een intrinsieke koppeling tussen saccades en perceptuele alternaties aan

ten grondslag ligt of dat deze correlatie indirect tot stand komt doordat oogbewegingen in veranderingen van het retinale beeld resulteren. Door raster stimuli te gebruiken, die per definitie periodiek zijn in de ruimte, konden we onderscheid maken tussen saccades die lokaal in een verandering van het retinale beeld resulteerde en saccades waarbij dat niet zo was. We vonden dat er sterke correlatie was tussen specifieke retinale beeld veranderingen en het dominante percept, wat erop wijst dat retinale beeldveranderingen cruciaal zijn voor de correlatie tussen oogbewegingen en percept alternaties in binoculaire rivaliteit. Ook vonden we dat deze correlatie zelfs optrad wanneer de proefpersonen was opgedragen om op een fixatiepunt te fixeren, dus voor fixationele saccades (microsaccades). Het vijfde hoofdstuk onderschrijft daarom het belang om voor oogbewegingen te controleren of te corrigeren als men binoculaire rivaliteit wil onderzoeken (alhoewel in gedachten moet worden gehouden dat oogbewegingen an sich geen verklaring kunnen zijn van het fenomeen binoculaire rivaliteit).



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- van Dam, L.C.J. & van Ee, R. (2004). *Stereoscopic matching and the aperture problem*, Perception, **33**, 769–787.
- 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.
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## Refereed Abstracts

- van Dam, L.C.J. & van Ee R. (2001). *The Matching Problem: Head-centric or Retina-centric*, NVP conference in Egmond aan Zee.
- van Dam, L.C.J. & van Ee, R. (2002). *Stereoscopic matching and the aperture problem*, Perception, Suppl. page 159 (ECPV 2002).
- van Dam, L.C.J. & van Ee, R. (2003). *Bistability in stereoscopically perceived slant about a horizontal axis*, Journal of Vision, 3(9), 467a (VSS 2003).
- van Dam, L.C.J. & van Ee, R. (2005). *The role of eye movements in bistability from perceptual and binocular rivalry and the role of voluntary control*, Journal of Vision, 5(8), 704a (VSS 2005).

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  - van Dam, L.C.J. & van Ee, R. (submitted). *Saccadic retinal shifts correlate with perceptual alternations in binocular rivalry*, Perception (ECPV 2006).
  - van Ee, R., Brascamp, J.W., Brouwer G.J. & van Dam L.C.J. (2006). *Endogenous control over either of the two percepts that compete for visual awareness in perceptual rivalry*, Association for the scientific study of consciousness, 10 (ASSC 2006).
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  - van Ee, R., van Dam, L.C.J. & Brouwer, G.J. (2003). *Attention-driven conscious bi-stable stereoscopic depth perception*, Society for NeuroScience, 339.1.
  - van Ee, R., van Dam, L.C.J., Brouwer, G.J. & Korsten, N.J.H. (2003). *Bistable stereoscopic 3D percepts: Will-power, flip frequency, eye movements and blinks*, Journal of Vision, 3(9), 160a, (VSS 2003).

# Recept proefschrift

In dit proefschrift staat het onderzoek beschreven, dat ik tijdens mijn AIO-schap gedaan heb. Bij het bereiden van een proefschrift komt echter heel wat kijken en goed onderzoek doen is dan ook moeilijk zonder de juiste ingrediënten. Bij deze het recept voor mijn proefschrift.

## **Benodigheden proefschrift:** (voor 1 persoon)

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- 1 dagelijks begeleider (c.q. co-promotor)
- 1 promotor
- 2 flinke scheppen technische ondersteuning
- ca 3000 kg collega's
- handjevol proefpersonen
- 2 paranimfen
- flinke dosis diverse ondersteuning uit verschillende hoeken
- papier
- inkt
- 1 Unix-computer
- 4 Macs (1 bureau-doos, 1 laptop, 2 mac-meetcomputers)
- 1 windoos
- 1 set infrarood-camera's
- 1 glazen hoofd (in stukjes)

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## **Bereidingswijze:** (bereidingstijd: ca 4 jaar)

Zet de proefpersonen in het donker (met behulp van de technische ondersteuning). Eventueel is een kleine hoeveelheid licht toegestaan (bij voorkeur (infra)rood en/of groen licht). Denk eraan dat de proefpersonen een van de belangrijkste ingrediënten zijn, want zonder hen behaal je zeker geen resultaat. Verzorg ze dus goed! Beweging is ook goed voor ze, dus laat ze af en toe ook eens een knopje indrukken (zeer belangrijk). Als de proefpersonen gaar zijn, verplaats dan de info die de proefpersonen achter hebben gelaten van de ene naar de andere computer en gebruik de diverse computers voor de verdere bereiding van de info. Neem het papier en de inkt en gebruik dit om de resultaten op te schrijven. Laat dit bij je begeleider en promotor bij-garen (bij voorkeur in diverse tussenstadia) en bediscussieer de resultaten met je collega's. Voeg naar smaak de ondersteuning vanuit de verschillende hoeken en van de paranimfen toe (zeker als je even in de dip zit). Neem het papier en de inkt wat over is, doe daar wat leuks mee en klaar is je proefschrift.

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# Curriculum Vitae

Loes van Dam was born in Grubbenvorst, the Netherlands on June 2nd, 1977. After attending primary school in Grubbenvorst and VWO (pre-university education) at the Blariacum College in Blerick, Venlo, she came to Utrecht University to study physics. During the years of her study she became actively involved in the student association A-Eskwadraat and became a full-time member of the board of A-Eskwadraat (secretary) in the academic year 1999 – 2000. She did her research internships at the physical computer science group of the faculty of physics and astronomy and at the Helmholtz Institute for autonomous systems research. After obtaining her masters degree she continued her research in the perceptual motor integration group of the Helmholtz Institute as a PhD-student. She was active in the PhD student union of Utrecht (BAU/PrOUt) as a representative for the PhD students of the faculty of Physics and Astronomy for a period of one and half years.