

Perceived visual direction at the edge between two surfaces at different stereoscopic depths

Author:

Marlow, Phillip James

Publication Date:

2010

DOI:

<https://doi.org/10.26190/unsworks/23285>

License:

<https://creativecommons.org/licenses/by-nc-nd/3.0/au/>

Link to license to see what you are allowed to do with this resource.

Downloaded from <http://hdl.handle.net/1959.4/45633> in <https://unsworks.unsw.edu.au> on 2024-05-06

Perceived visual direction at the edge between two surfaces at different stereoscopic depths

Phillip Marlow

University of New South Wales

**Thesis submitted in partial completion of the requirements of the
degree of Doctor of Philosophy 2010**

**School of Psychology
University of New South Wales
Kensington
Australia**

Supervisor: Prof. Barbara Gillam

Acknowledgements

I am extremely grateful for the encouragement, guidance and support of my supervisor, Prof. Barbara Gillam.

I thank my co-advisor Prof. Bart Anderson his contributions to my understanding of the research problem and its context.

The funding provided in joint by Prof. Barbara Gillam and the School of Psychology at the University of New South Wales is greatly appreciated.

I thank all who gave up their time to participate in these experiments, especially Elia Vecellio, James Townsend, Joel Roast, Luke Vu and Judit O'Vari for participating in many pilot experiments.

I appreciate the helpful comments on written expression provided by Derek Loh.

I am indebted to my wife and family for their understanding and support throughout the duration of my studies.

Phillip Marlow

Abstract

The perceived relative direction of a pair of features can be intermediate between their relative direction in the two eyes. It is known that the perceived relative direction of the features can be altered by making their disparity gradient steep. Features at the edge between two surfaces at different depths form steep disparity gradients. These features are typically next to features on the same surface with the same disparity. These additional features were found to mitigate the effect of steep disparity gradients on perceived direction. The effect of the additional features was found to vary with their contrast, their contrast polarity and their separation relative to the features that define a steep disparity gradient. Hence, these stimulus properties determine whether disparity gradients affect the perceived direction of features at surface edges.

That the perceived relative direction of a pair of features can be an average of the angles that they subtend at each eye supports the theory that perceived visual directions are referred to a point midway between the eyes (cyclopean eye). However, from this reference point, an occluding surface would hide features on the background that are visible to the left eye next to its left edge or visible to the right eye next to its right edge. Ono et. al. (2002) proposed that the perceived direction of these features is shifted laterally from their true direction when the occluder is fixated and the occluder is shifted in the opposite direction when the background is fixated. Erkelens et. al. (1996) proposed that the perceived direction of features is referred to the eye that views the monocular region instead of a cyclopean eye so that both surfaces may be perceived in their true direction. In the present study, two occluders were arranged so that a left side

edge was physically aligned with a right side edge. The monocularly visible background texture next to these edges was also physically aligned. Consistent with the first proposal, the monocular regions or the edges of the occluders were found to appear laterally offset from one another indicating that their perceived direction was incorrect. Erkelens et. al. (1996) found that the perceived direction of the left and right edges of an occluding surface relative to a line on the background was found to be more strongly influenced by their position in the eye that views the monocular region of the background next to the edge than by their position in the other eye. In the present study, this Erkelens-bias was found with fixation on the background surface, but was not found with fixation on the occluder, which is also consistent with the first proposal. The Erkelens-bias decreased with the lateral separation of a target line on the occluder from its edge. The Erkelens-bias was found even when all texture on the surfaces was eliminated except for the outline of a foreground surface and a single line on the background surface. This indicates that the Erkelens-bias does not require the presence of either steep disparity gradients or monocular texture. The Erkelens-bias was eliminated by presenting the outline as the farthest feature in the stimulus, which is incompatible with it specifying the edges of a foreground surface.

Contents

Acknowledgements.....	ii
Abstract.....	iii
List of figures.....	viii
1 Introduction	1
1.1 Horizontal binocular disparity.....	4
1.1.1 Relative horizontal disparity	5
1.1.2 Absolute horizontal disparity	7
1.1.3 Vergence eye movements	9
1.1.4 Stereopsis	10
1.1.5 Random dot stereogram	12
1.2 Monocular regions	14
1.2.1 The stereoscopic depth of monocular features.....	16
1.2.2 Binocular rivalry of features in monocular regions.....	24
1.3 The fusion limit	29
1.3.1 The fusion limit as a function of spatial frequency	30
1.3.2 The fusion limit of surfaces.....	32
1.3.3 Fusional hysteresis.....	33
1.3.4 The disparity gradient constraint on fusion.....	34
1.4 Perceived visual direction	36
1.4.1 The perceived direction of monocularly visible features: The cyclopean illusion 38	
1.4.2 The perceived direction of features that are seen double.....	44
1.4.3 The perceived direction of fused binocular features	46
1.5 Perceived direction at the left and right edges of occluding surfaces	51
1.5.1 Hering's laws of visual direction applied to the left and right edges of occluding edges.....	51
1.5.2 Measurements of the perceived direction of features within a monocular region.....	57
1.5.3 The perceived direction of the left and right edges of an occluding surface.....	61
1.5.4 Competing theories of the perceived direction of features in the vicinity of the left and right edges of an occluding surface.	66
2 Aims of the present study.....	72
2.1 General Method.....	74

2.1.1	Display	74
3	Perceived direction at the horizontal edges of occluding surfaces	75
3.1	Experiment 1: The influence of the disparity gradient on the perceived direction of features at surface edges.	75
3.1.1	Method	82
3.1.2	Results.....	84
3.1.3	Discussion	87
3.2	Experiment 2: The nature of the benefit of support features.	90
3.2.1	Method	92
3.2.2	Results.....	94
3.2.3	Discussion	97
3.3	Experiment 3: The effect of the support features when their luminance differs from the target features.....	99
3.3.1	Method	101
3.3.2	Results.....	103
3.3.3	Discussion	105
3.4	General Discussion	107
3.4.1	The receptive field size explanation of the disparity gradient constraint on fusion	108
3.4.2	Nature of the benefit of the support squares	111
4	Perceived direction at the left and right edges of a surface	114
4.1	Experiment 4: Mapping the region affected by the Erkelens-bias	114
4.1.1	Method	118
4.1.2	Results.....	121
4.1.3	Discussion	125
4.2	Experiment 5: Perceived direction of the left and right edges of a surface and features abutting those edges.	127
4.2.1	Method	131
4.2.2	Results.....	133
4.2.3	Discussion	136
4.3	Experiment 6: The stimulus conditions for the Erkelens-bias	138
4.3.1	Method	141
4.3.2	Results.....	143
4.3.3	Discussion	149
4.4	Experiment 7: Bias magnitude in the Erkelens et al. (1996) study.	154
4.4.1	Method	158

4.4.2	Results.....	161
4.4.3	Discussion	164
4.5	Experiment 8: Magnitude of the Erkelens-bias with fixation at the depth of the occluder or the background.	165
4.5.1	Results.....	168
4.5.2	Discussion	171
4.6	Experiment 9: Is perceived direction at occlusions veridical?	174
4.6.1	Method.....	181
4.6.2	Results.....	184
4.6.3	Discussion	184
4.7	Experiment 10: A lateral bias of the perceived direction of the edges of an occluding surface from their physical direction.....	187
4.7.1	Method.....	190
4.7.2	Results and Discussion	193
4.8	General Discussion of Experiments 4-10	196
4.9	Summary of recommendations for future experiments	209
5	References	213

List of figures

Figure 1. Relative horizontal disparity of two features.....	5
Figure 2. Relative horizontal disparity of a pair of features along the median plane.....	6
Figure 3. Veith-Müller circle.....	7
Figure 4. Wheatstone stereoscope.	10
Figure 5. Stereogram of a cube.....	11
Figure 6. A random dot stereogram.	12
Figure 7. Monocular regions.	14
Figure 8. Minimum depth constraint.	17
Figure 9. Stimuli used by Nakayama and Shimojo (1990).	18
Figure 10. Stereogram of Panum's limiting case.	19
Figure 11. Stimulus used by Cook and Gillam (2004).	20
Figure 12. Monocular feature separated from the edge of the surface.	21
Figure 13. Stimuli used by Anderson (1994).	22
Figure 14. Schematic of the stimuli used by Shimojo and Nakayama (1990).	25
Figure 15. Stimuli used by Forte et. al. (2002).....	27
Figure 16. Stimuli used by Kulikowski (1978).	30
Figure 17. Stimuli used by Kertesz (1981)	32
Figure 18. Stimuli used by Tyler (1975).....	34
Figure 19. Perceived direction of objects situated along the visual axes.....	36
Figure 20. The cyclopean illusion.	38
Figure 21. Individual differences in the location of the cyclopean eye.....	40
Figure 22. Perceived direction of diplopic images according to Hering.	44
Figure 23. Stereogram used by Asher (1953) and Ono et. al. (1977).....	46
Figure 24. Ocular prevalence.	47
Figure 25. Perceived egocentric direction of features with unequal contrast in the two eyes.	50
Figure 26. Perceived direction of the binocular features that border a monocular region.	52
Figure 27. Visual line to the centre of a monocular region with fixation on the background.	53
Figure 28. Perceived direction according to Hering's theory with fixation on the background.	54
Figure 29. Visual line to the centre of a monocular region with fixation on the occluder.	55
Figure 30. Perceived direction according to Hering's theory with fixation on the occluder.....	56
Figure 31. Schematic of stimuli used by Erkelens & van de Grind (1994).	57
Figure 32. Schematic of the stereogram used by Erkelens et. al. (1996).....	61
Figure 33. Stimuli used by Ono et. al. (1977).	66
Figure 34. The portions of the background and occluding surfaces that have the same physical direction relative to a cyclopean eye.....	68
Figure 35. Disparity gradient at the vertical edge of an occluding surface.	76
Figure 36. Schematic of the stimuli used in Experiment 1.	80
Figure 37. Results of Experiment 1.	84
Figure 38. Stereograms of some of stimuli used in Experiment 2.	92
Figure 39. Results of Experiment 2.	94
Figure 40. Results of Experiment 3.	103

Figure 41. Schematic of stimuli for Experiment 4.	116
Figure 42. Results of Experiment 4.	121
Figure 43. Results of the second session of Experiment 4.....	124
Figure 44. Stimuli used in Experiment 5.	131
Figure 45. Results of Experiment 5.	133
Figure 46. Stereograms of the three configurations in Experiment 6.	141
Figure 47. Group data for the textured condition in Experiment 6.	143
Figure 48. Group data for the outline and single edge condition of Experiment 6.	146
Figure 49. Schematic of stimuli used by Erkelens and van Ee (2007).	151
Figure 50. Results of Experiment 7.	161
Figure 51. Results of Experiment 7 for one observer.	162
Figure 52. Group data for Experiment 8.	168
Figure 53. Location of a background line that appears vertically aligned with the edge of an occluder	175
Figure 54. Perceived direction referred to cyclopean eye (A) or to the eye that views the monocular region (B).	176
Figure 55. Stimuli used in Experiment 9.	178
Figure 56. Stereogram of stimuli used in Experiment 10.	190
Figure 57. Results of Experiment 10.	193
Figure 58. The portion of the monocular region of the background that has the same physical direction as the occluding surface relative to a cyclopean eye.	194
Figure 59. The portion of the occluder that lies in the same direction relative to a cyclopean eye as the background visible to one of the eyes.	206

1 Introduction

This thesis describes an investigation of the perceived direction of surfaces and objects in complex scenes. The perceived direction of features is an interesting question because the path along which the image of a feature projects to each eye is different as a result of their horizontal separation. Sections 1.1, 1.1.1, 1.1.2 and 1.1.3 describe the relevant technical aspects of how the positions of features differs between the two eyes. These positional differences can produce a sensation of depth called stereopsis that is described in section 1.1.4.

In complex scenes, some features are only visible to one eye. This is true of parts of the background surface next to the left and right edges of a foreground surface. The experiments in section 4 study the perceived direction of features in the neighbourhood of these monocular regions. The geometry of monocular regions is described in section 1.2. A short review of research on monocular regions showing that they contribute to stereopsis and are rarely suppressed from our experience is provided in section 1.2.1 and section 1.2.2.

It is known that a feature visible to both eyes can either appear to have a single direction or appear in two directions simultaneously. Factors that affect whether a feature has a single perceived direction or is perceived in two different directions simultaneously is described in section 1.3 and its subsections. One of these factors is the disparity gradient defined between a pair of features and this is described in section 1.3.4. Steep disparity gradients are known to cause one member of a pair of dots

presented in empty space to appear in two directions. However, complex scenes are made up of overlapping textured surfaces rather than a few isolated features in empty space. Steep disparity gradients frequently occur in cluttered scenes at the edges of surfaces. Does the disparity gradient have the same effect on the perceived direction of features at surface edges as has been observed for isolated pairs of dots? The experiments described in section 3 addressed this question.

Hering's (1879/1942) theory of how the perceived direction of a feature is related to the posture of the eyes and the retinal locations of a feature is described in section 1.4. Research on the perceived direction of features visible to one eye only is reviewed in section 1.4.1. Sections 1.4.2 and 1.4.3 review research on the perceived direction of a feature that is visible to both eyes and perceived in either two different directions simultaneously (section 1.4.2) or in a single direction (section 1.4.3). The evidence reviewed in these sections largely supports Hering's theory that each feature is perceived along a line that passes through its apparent location and a point midway between the eyes. However, this research generally measured the perceived direction of one or two features presented against empty space. Research studying the perceived direction of features in cluttered scenes that are more typical of natural scenes is reviewed in section 1.5. It has been noted that a paradox is produced when attempting to predict the perceived direction of features in the vicinity of the left and right edges of a surface using Hering's theory (described in section 1.5.1). Measurements of the perceived direction of features in the monocular regions of the background next to the left and right of a foreground surface (see section 1.2) are reviewed in section 1.5.2. Measurements of the perceived direction of the left and right edges of the foreground surface relative to a line on the background surface are reviewed in section 1.5.3. These measurements indicate that Hering's theory does not describe the perceived direction of

features at the left and right edges of a foreground surface. Two competing theories of perceived direction at the left and right edges of a foreground surface have been offered and are reviewed in section 1.5.4. This controversy prompted the experiments described in section 4, the results of which it is argued resolve the controversy (see section 4.8).

1.1 Horizontal binocular disparity

In humans, both eyes face forward so that a portion of the visual scene is visible to both eyes. Within this binocular visual field, differences exist between the perspectives of the two eyes since they view the scene from different vantage points. One way in which the perspectives of the two eyes may differ is *horizontal disparity*. This may be defined as *relative horizontal disparity* (defined 1.1.1) or *absolute horizontal disparity* (defined 1.1.2).

1.1.1 Relative horizontal disparity

Relative horizontal disparity refers to a difference between the eyes of the horizontal angular separation of a pair of binocularly visible features. For example, Figure 1a shows a bird's eye view of the eyes and two features at different depths in front of them. The straight lines that intersect the features, pass through the nodal point of the eyes and intersect the back of the eye are *visual lines*. The angular separation of the visual lines from the left eye to the features is angle α . The angular separation of the visual lines from the right eye to the features is angle β . The relative disparity of the features is the difference between angle α and angle β .

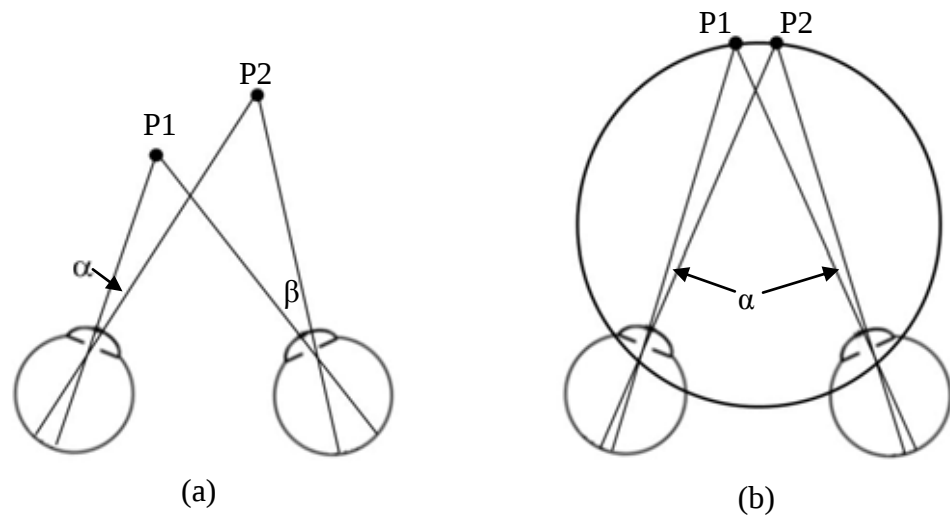


Figure 1. Relative horizontal disparity of two features.

The relative disparity of a pair of features is geometrically related to their relative depth. Features with a relative disparity of zero, such as P1 and P2 in Figure 1b, lie along the perimeter of a circle that passes through the features and the nodal point of each eye. Hence, features with a relative disparity of zero are approximately equidistant from the observer unless one of the features lies in the periphery. For features with a non-zero relative disparity, the eye that views the larger angular separation between the

features is ipsilateral to the farther of the two features. For example, in Figure 1a, the right eye views the larger angular separation between the features and the right rod is more distant than the left rod. If the direction of the horizontal separation of a pair of features is reversed in the two eyes as for the two points in Figure 2, then the closer feature is to the right of the more distant feature for the left eye, but is to the left of the more distant feature for the right eye.

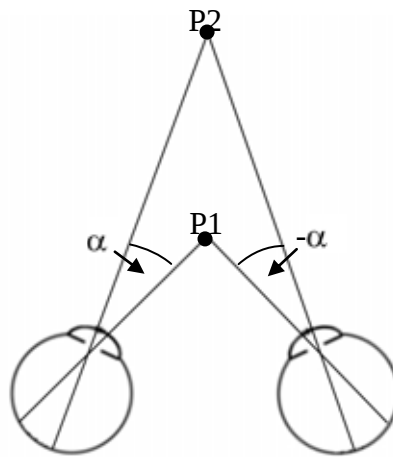


Figure 2. Relative horizontal disparity of a pair of features along the median plane.

1.1.2 Absolute horizontal disparity

The absolute horizontal disparity of a feature refers to its horizontal disparity relative to geometrically corresponding points in the two eyes. The feature that the eyes are converged on, known as the *fixation point*, projects to geometrically corresponding points along the visual axes unless there is *fixation disparity*, in which case the visual axes do not actually converge on the fixation point. Features that subtend the same angle with the fixation point in both eyes project to geometrically corresponding points. For points that are horizontally separated from the fixation point, objects that project to geometrically corresponding points are located on the perimeter of the Veith-Müller

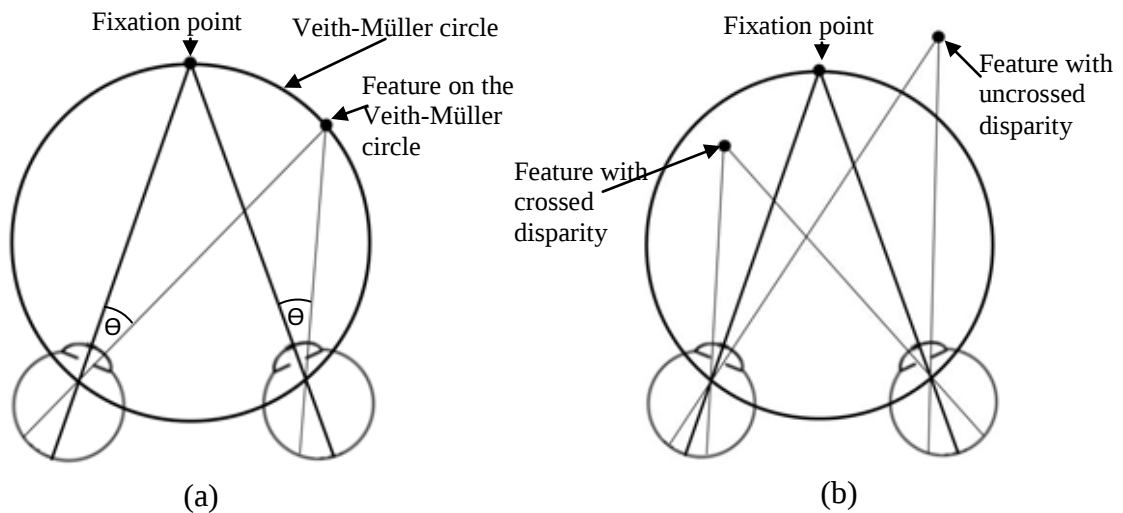


Figure 3. Veith-Müller circle.

circle (Figure 3a), which passes through the nodal points of the eyes and the fixation point (Hering, 1879/1942; Shipley and Rawlings, 1970). A feature located closer or farther than the Veith-Müller circle has an absolute horizontal disparity equal to its horizontal disparity relative to the fixation point. The terms crossed and uncrossed disparity are commonly used to distinguish between absolute horizontal disparities

arising from a feature located closer or farther than the Veith-Müller circle respectively (Figure 3b; Howard, 2002).

1.1.3 Vergence eye movements

When fixation is shifted to a point that is located either closer or farther than the Veith-Müller circle, the rotations of the two eyes differ (Dodge, 1903). Convergence and divergence eye movements shift fixation closer in depth and farther in depth respectively. A convergence or divergence eye movement between two points at different distances along the median plane is accomplished by an equal and opposite direction of rotation of both eyes about the vertical axis. The reaction time of vergence eye movements to a stimulus change is slow compared with other eye movements and requires 140-160 msec (Ginsborg, 1953; Rashbass & Westheimer, 1961). Completion of a vergence eye movement may require an additional 800 msec, but the visual scene is perceived during the eye movement unlike the case for saccadic eye movements (Dodge, 1903; Rashbass & Westheimer, 1961).

1.1.4 Stereopsis

Wheatstone (1838) discovered that the differences between the perspectives of the eyes results in a vivid 3-dimensional depth perception which he called *stereopsis*. Through his invention of the stereoscope, Wheatstone was able to present separate images to the same regions of the left and right eyes. A Wheatstone stereoscope (Figure 4) accomplishes this through the use of a pair of mirrors that are placed in the median plane of the observer. One mirror reflects an image towards the left eye and the other mirror reflects a different image towards the right eye. The pair of images that is

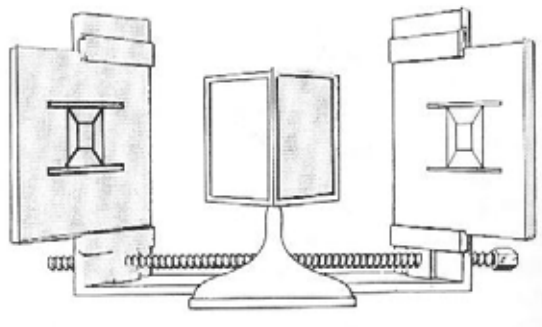


Figure 4. Wheatstone stereoscope. Front view. From Howard and Rogers (2002) after Wheatstone (1838).

presented to the eyes is called a *stereogram*. Wheatstone observed that the stereogram appeared as a single image lying in the median plane beyond the mirrors. When the left and right eyes were presented with identical images (Figure 5a), the fused image appeared flat. However, when the left and right eyes were presented with images of the same object drawn from different perspectives (Figure 5b) the object appeared solid or 3-dimensional. Using skeleton figures like the cube in Figure 5b, Wheatstone (1852) argued that the magnitude of the relative horizontal disparity of the contours determined the magnitude of their perceived relative depth.

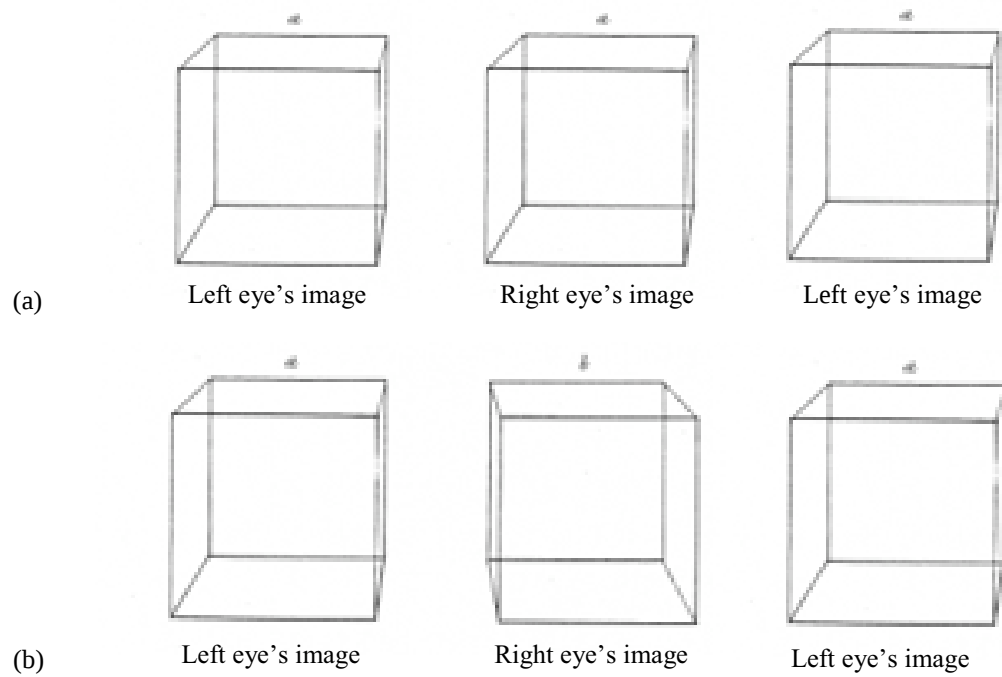


Figure 5. Stereogram of a cube. In (a) the images presented to the eyes are identical, whereas in (b) the images for the left and right eye are of the same cube drawn from slightly different perspectives. After Wheatstone (1838).

1.1.5 Random dot stereogram

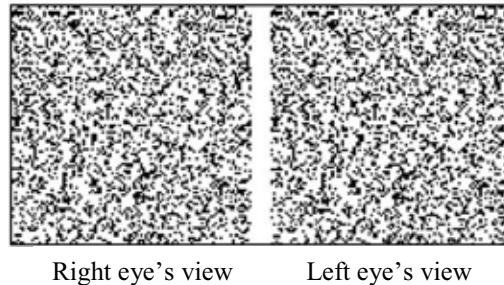


Figure 6. A random dot stereogram.

This section describes random dot stereograms, in order to understand the technical aspects of the experiments described in later sections. A random dot stereogram (Figure 6) is a pair of textured images in which a subregion of the texture is shifted, typically horizontally, in opposite directions in the two images. Julesz (1960; 1964) found that on fusing a random dot stereogram, the shifted region is perceived as a surface in depth with sharply defined edges even though the shifted region is not distinguishable in either monocular image.

Julesz (1960; 1964) described in detail how he constructed these random dot stereograms. First, he generated a texture by dividing an image into small squares and randomly assigning each of those squares to be either black or white. Then he copied the texture, in order to display separate images to each eye. A subregion of the texture was then shifted left in one image and right in the other image. For example, in Figure 6, a subregion of the texture—in the shape of a square—has been shifted to the right in the left eye's view, and to the left in the right eye's view. The shifted region leaves behind a blank region next to the left edge of the shifted region in one image and next to the right edge of the shifted region in other image. These blank regions are then filled with a new random texture in order to camouflage the left and right edges of the shifted

region. Julesz (1960) noted that texture that fills the blank area in each image is only visible to one eye. Julesz (1960) noted that the areas of monocularly visible texture next to the left and right edges of the shifted region, which are the focus of the next section, appear at the depth of the background surface.

1.2 Monocular regions

Opaque surfaces occlude their backgrounds. In binocular vision, a surface may occlude different regions of a background surface from the different vantage points of the left and right eye. Consequently, some background regions are only visible to one eye. These regions are known as *monocular regions* (since they are only visible to one eye) or *half-occlusions* (since they are occluded for only one eye). They are also referred to as *unpaired regions*, since there is no corresponding region in the other eye's view.

When a foreground surface occludes a background, the left eye will view a monocular region of the background next to the left edge of the foreground surface and the right eye will view a monocular region of the background next to the right edge of the foreground surface. This is evident in Figure 7a, which shows a bird's eye view of an occluding surface and the background behind it, and Figure 7b which shows a front view of Figure 7a. The dotted lines that pass by the left and right edges of the foreground surface are the visual lines from the left and right eye to the background surface visible next to the edge in each eye's view. The area of the background surface

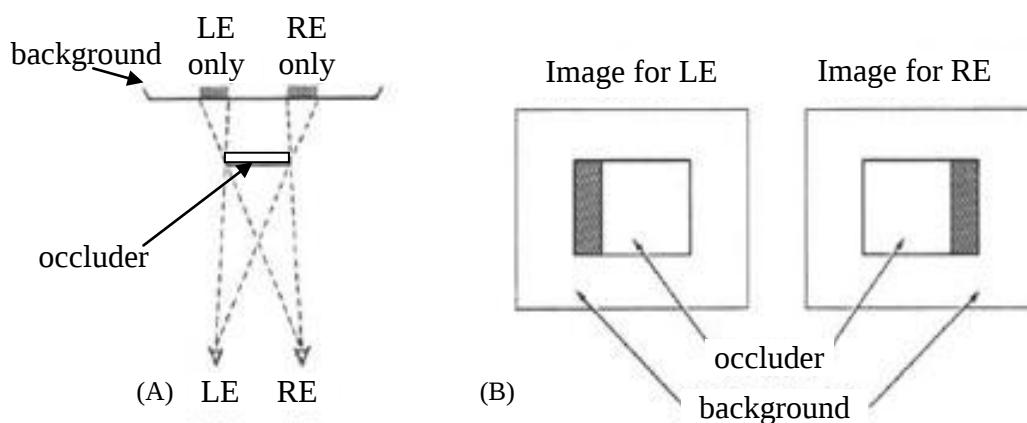


Figure 7. Monocular regions. From a bird's eye view (A) and a front view (B). From Gillam and Borsting (1988) (A), from Nakayama and Shimojo (1990) (B).

between the visual lines to the left edge is a monocular region visible to the left eye and the area of the background surface between the visual lines to the right edge is a monocular region visible to the right eye (shaded areas of Figure 7).

1.2.1 The stereoscopic depth of monocular features

Kaye (1978) found that there is a crude relationship between the retinal location of a monocular feature along the horizontal meridian and its perceived depth. Kaye (1978) presented a large cross or circle for 100ms in the horizontal meridian at retinal eccentricities of 0, 0.5, 1 or 2°. The stimulus was only visible to one eye and hence lacked binocular disparity. Kaye (1978) found that when the monocular stimulus was presented in the nasal portion of either retina (i.e. to the left of fixation in the right eye or to right of fixation in the left eye) it appeared farther in depth than the fixation point. Likewise, when the monocular stimulus was presented on the temporal side of either retina, it appeared closer in depth than the fixation point. Kaye (1978) also found that the magnitude of the monocular feature's perceived depth relative to the fixation point increased with their horizontal separation. This effect was recently replicated by Wilcox, Harris and McKee (2007), also using a short stimulus duration (132ms). Wilcox et. al. (2007) found that the perceived depth of the monocular feature does not vary with retinal eccentricity when observers wore an eye patch over the unstimulated eye. This supports the proposal of Kaye (1978) and Wilcox et. al. (2007) that the perceived depth of the monocular feature is caused by disparity sensitive mechanisms registering a match between the monocular feature and a region in the other eye. Wilcox et. al. (2007) varied the eccentricity of the observers gaze so that the visual axis of the other eye differed from the centroid of the luminance distribution of the display. They found that the perceived depth of the monocular feature was best predicted by the location of the visual axis of the other eye.

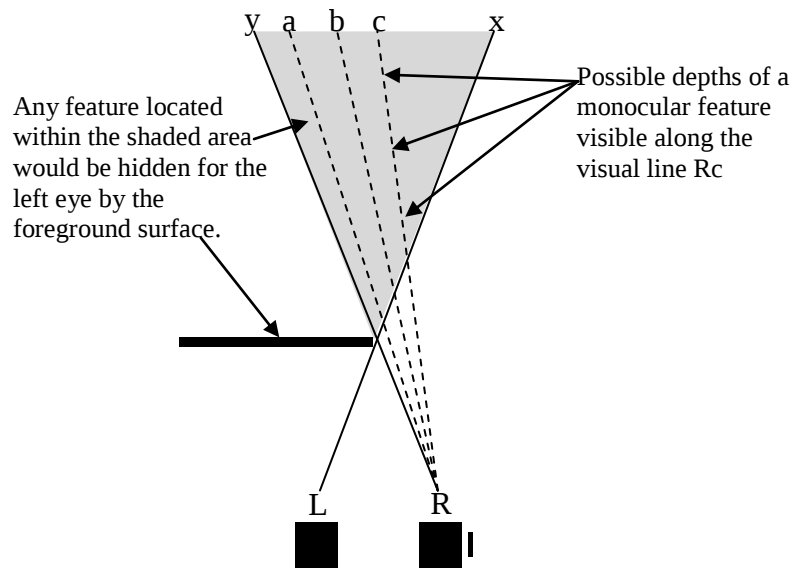


Figure 8. Minimum depth constraint. In order to be occluded in one eye by the surface, monocular features lying along the visual lines R_a , R_b and R_c must be farther in depth than the point where these visual lines intersect the visual line from the other eye to the edge of the foreground surface (L_x). After Nakayama & Shimojo (1990).

Nakayama and Shimojo (1990) proposed that the visual system could locate a monocular feature in depth with a precision comparable to regular disparity based stereopsis when the monocular feature lies to the left or right of a binocularly visible surface. Nakayama and Shimojo (1990) noted that there is a minimum depth for a monocular feature next to a binocular surface that is geometrically compatible with its occlusion in one eye by the surface. For example, in Figure 8, the shaded area represents the area of the visual scene in which an object would be visible to the right eye but hidden for the left eye by the right edge of a foreground surface. It is possible that a monocular object visible along the visual line R_c is located at any of the depths indicated in the Figure. However, an object visible along the visual line R_c would not be hidden from the left eye by the surface if the feature were closer than the shaded area.

Nakayama and Shimojo (1990) noted that the minimum depth of a monocular object increased with its horizontal angular separation from the edge of the surface. For

example, in Figure 8, the occluding edge of the foreground surface is visible to both eyes along the visual lines L_x and R_y . The visual lines R_a , R_b and R_c represent different angular separations of monocularly visible objects from the edge of the surface. Where each of these visual lines intersects the visual line from the other eye to the edge of the surface (L_x) shows the minimum depth for each angular separation. Nakayama and Shimojo (1990) referred to this geometrical relationship between the horizontal separation of a monocular feature from the edge of a surface and the minimum depth compatible with its occlusion by the surface as the *minimum depth constraint*.

Nakayama and Shimojo (1990) proposed that the human visual system uses the minimum depth constraint in order to assign monocular features a depth compatible with their occlusion in one eye. In evidence, Nakayama and Shimojo (1990) found that the perceived depth of a monocular bar was quantitatively related to its lateral separation from a binocular surface to the degree predicted by the minimum depth compatible with occlusion for each separation (Figure 9). Nakayama and Shimojo (1990) referred to the perception of depth based on the minimum depth constraint as *da Vinci stereopsis*.

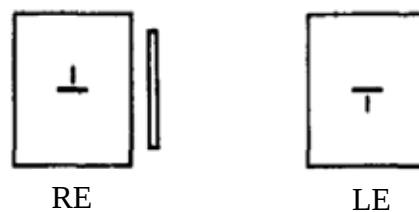


Figure 9. Stimuli used by Nakayama and Shimojo (1990). A large rectangle was binocularly visible and seen against an untextured background surface. A vertical bar was next to the left or right edge and was monocularly visible.

Gillam, Cook and Blackburn (2003) argued that the depth of the monocular bar in the Nakayama and Shimojo (1990) study may be due to conventional horizontal disparity based stereopsis. The basis for this argument is a phenomenon known as Panum's limiting case. In Panum's limiting case, two vertical lines are presented to one eye and a single vertical line is presented to the other eye (Figure 10). On fusing this stimulus, Panum (1858) observed two lines at different depths. Gillam et. al. (2003) noted that the perceived depth in Panum's limiting case is quantitatively related to the angular separation of the lines to the same degree that the minimum depth of a monocular feature is related to its angular separation from the edge of a surface. Therefore, the quantitative depth found by Nakayama and Shimojo (1990) for their stimulus (Figure 9) was expected on the basis of its similarity to Panum's limiting case (Figure 10). Gillam et. al. (1995), McKee, Bravo, Smallman and Legge (1995) and Panum (1858) proposed that the single line presented to one eye in Panum's limiting case is inappropriately matched with both lines presented to the other eye so the depth perceived is due to conventional horizontal disparity based stereopsis. Hence, it is possible that the depth of the monocular feature in the Nakayama and Shimojo (1990) study may be due to conventional disparity based stereopsis instead of da Vinci stereopsis.

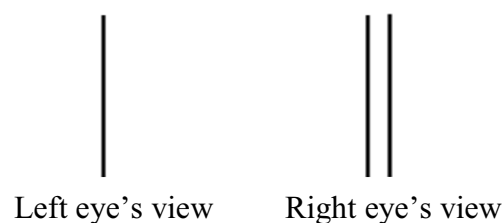


Figure 10. Stereogram of Panum's limiting case.

Evidence for da Vinci stereopsis which cannot be attributed to conventional disparity based stereopsis was provided by Cook and Gillam (2004). They used a stimulus in which the minimum depth constraint specified a different depth to that predicted by conventional disparity based stereopsis. This stimulus is shown in Figure 11. A white rectangle that was visible to only one eye covered part of the left or right side of a black surface, which was visible to both eyes. The edges of the black surface were curved so that the horizontal disparities between the edge of the black surface in one eye and the vertical edge of the monocular rectangle in the other eye was larger in the middle of the edge than at the top and bottom of the edge. Hence, conventional disparity based stereopsis would predict that the perceived depth of the middle of the black surface would differ between the middle and top and bottom sections of the black

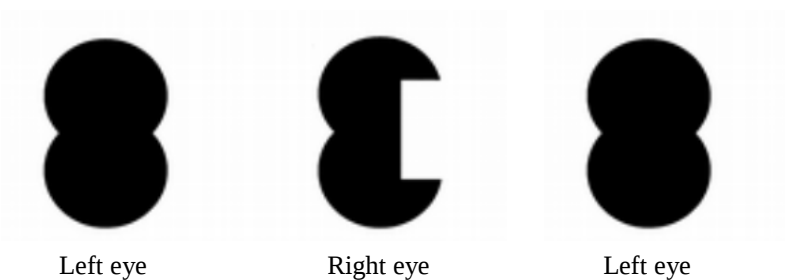


Figure 11. Stimulus used by Cook and Gillam (2004).

surface. The perceived depth of the top middle and bottom regions of the monocular rectangle did not vary relative to each other so the possibility that the depth that is perceived in this stimulus is determined by conventional horizontal disparity based stereopsis can be ruled out (Cook & Gillam, 2004). The prediction for da Vinci stereopsis depended on whether the monocular rectangle covered either the side of the black surface that was ipsilateral or contralateral to the eye that viewed the monocular rectangle. For the ipsilateral configuration (e.g. cross fusion of the middle and right images of Figure 11), it is possible that the rectangle is only visible to one eye because it is camouflaged against the white region of the background for the other eye. For the

contralateral configuration (e.g. cross fusion of the left and middle images of Figure 11), it is possible that the rectangle is only visible to one eye because the black surface is an aperture through which the monocular rectangle is visible to one eye but occluded in the other eye by the white edge of the aperture. In both configurations, the minimum depth consistent with either camouflage or occlusion of the monocular rectangle in one eye is determined by the angular width of the region of the black surface covered by the monocular rectangle. In evidence for da Vinci stereopsis, Cook and Gillam (2004) found that the camouflage and occlusion interpretations could be perceived and that the perceived depth of the monocular rectangle was quantitatively related to its angular width to the degree consistent with either occlusion or camouflage of the monocular rectangle in one eye.

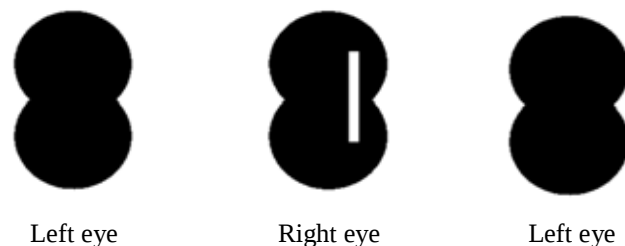


Figure 12. Monocular feature separated from the edge of the surface. From Cook and Gillam (2004)

Cook and Gillam (2004) argued that da Vinci stereopsis does not occur when the monocular feature is separated from the edge of the binocular surface. Cook and Gillam (2004) measured the perceived depth of a monocular bar shown in Figure 12. They found that the monocular bar appeared farther than the surface in the occlusion condition (crossed fusion of the left and middle images of Figure 12) and closer in depth in the camouflage condition (crossed fusion of the middle and left images of Figure 12). However, the perceived depth of the monocularly visible bar (Figure 12) was not

proportional to its separation from the edge of the surface as was the case for the monocular rectangle that was attached to the edge of the surface (Figure 11).

Monocular features that are attached to binocular features can influence the perceived depth of their surroundings. Anderson (1994) paired vertical lines of unequal heights in the two eyes images (Figure 13a). Anderson (1994) noted that the height of a vertical line may differ between the two eyes due to a diagonally shaped occluding

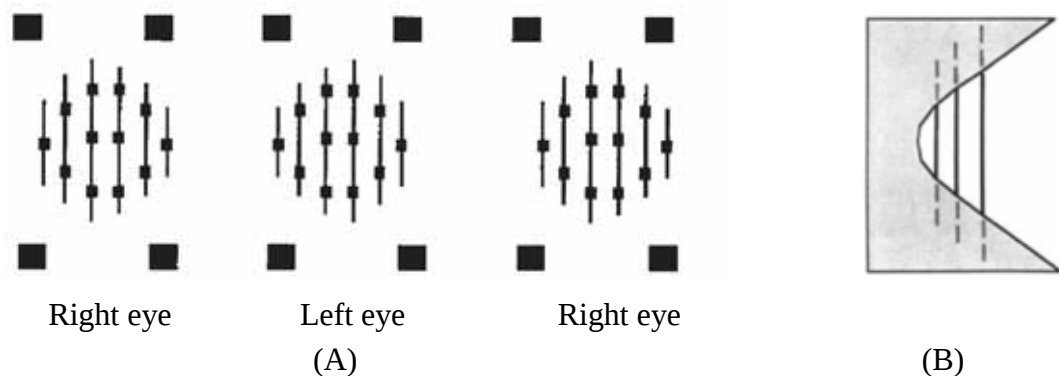


Figure 13. Stimuli used by Anderson (1994).

surface. For example, in Figure 13b, the dashed sections of the three vertical lines represent parts of the lines that would be visible to the right eye but hidden for the left eye by a surface with diagonal edges. Anderson (1994) demonstrated that on fusing the lines of unequal heights in the two eyes shown in Figure 13a, the blank region of the image is perceived as an illusory surface with a diagonally oriented edge as shown in Figure 13b. Gillam and Nakayama (1999) found that a rectangular illusory surface was perceived when the middle section of a vertical line was missing in one eye's view. Gillam and Nakayama (1999) measured the perceived depth of this illusory surface. The perceived depth of the surface increased with the width of the line, although its

perceived depth tended to be greater than that required to hide the missing segment of the line in one eye. Horizontal disparity was lacking in both the Anderson (1994) and Gillam and Nakayama (1999) studies, so they argued that the perception of an illusory surface is only attributable to the presence of the monocularly visible segments of the lines.

1.2.2 Binocular rivalry of features in monocular regions

Different features may project to corresponding points when the images presented to the left and right eye differ. If the images are sufficiently different that they cannot be fused (e.g. a vertical line paired with a horizontal line), then the features in one eye may be perceived while features on corresponding points in the other eye are suppressed. Whether features visible to the left eye are perceived while features visible to the right eye are suppressed or vice versa alternates over time in a phenomenon called *binocular rivalry* (Levelt, 1968).

Shimojo and Nakayama (1990) drew a distinction between *ecologically valid* and *ecologically invalid* monocular features. They argued that a monocular feature is ecologically valid if it is visible to the left eye to the left of a surface or to the right eye to the right of a surface because it is possible that such monocular features lie within a monocular region. A monocular feature is ecologically invalid if it is visible to the right eye to the left of a surface or to the left eye to the right of a surface because monocular regions are not visible to the eye that is contralateral to the edge. Shimojo and Nakayama (1990) proposed that ecologically valid monocular features escape binocular rivalry.

In evidence, Shimojo and Nakayama (1990) measured suppression for ecologically valid and invalid monocular features in a random dot stereogram. In the condition where suppression of valid monocular features was measured, the monocular region of the background was made a different colour from the occluder and the binocularly visible region of the background (Figure 14) so that it could be easily

distinguished. In the condition where suppression of ecologically invalid monocular regions was measured, an invalid monocular region was created by replacing a region of the binocularly visible texture on the background surface with a new random dot texture in one eye. This ecologically invalid monocular region abutted the left or right edge of the occluder in the right and left eye respectively and was the same colour and dimensions as the monocular region in the ecologically valid condition. Shimojo and Nakayama (1990, p. 72) asked observers to indicate if the coloured monocular region appeared to fade “even if momentarily or partially”. Suppression rates of 54-84% were found for invalid monocular regions, whereas the suppression rates for valid monocular regions were 11%-35%. On this basis, Shimojo and Nakayama (1990) concluded that ecologically valid monocular region tend to escape suppression.

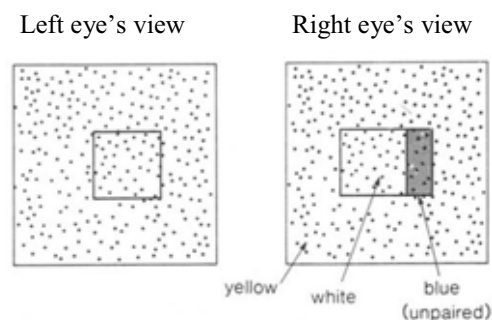


Figure 14. Schematic of the stimuli used by Shimojo and Nakayama (1990). The background surface was yellow, the occluding surface was white and the monocular regions were blue.

Recently, Assee and Qian (2007) challenged the distinction between ecologically valid and invalid monocular regions. Assee and Qian (2007) showed that the ‘ecologically invalid’ monocular region in the Shimojo and Nakayama (1990) study could be produced by a far surface visible through a small aperture in the background surface. Assee and Qian (2007) argued that this stimulus is not is not ecologically invalid since it is possible for a configuration of surfaces in the real world to produce it.

Perhaps Shimojo and Nakayama (1990) found more binocular rivalry was experienced for the ecologically invalid condition because its geometrical interpretation specifies that the monocular regions are seen through an aperture. This possibility is supported by a feature of Cook and Gillam's (2004, reviewed section 1.2.1) results. They found that some observers did not perceive a monocular region in depth when it was visible through an aperture in the background surface.

Assee and Qian (2007) offered a different explanation of Shimojo and Nakayama's (1990) results. Assee and Qian (2007) noted that in the 'ecologically valid' stimulus, one eye views a monocular region while the corresponding location locations in the other eye view a region visible to both eyes. However, corresponding locations in both eyes are presented monocular regions in the 'ecologically invalid' condition. Assee and Qian (2007) argued that higher rates of suppression may have occurred for the invalid than valid conditions because more vigorous suppression occurs when the same region in both eyes is presented texture that has no match in the other eye.

Assee and Qian (2007) neglected to point out that this alternative explanation of Shimojo and Nakayama (1990)'s results was first proposed by Anstis (personal communication cited by Shimojo & Nakayama, 1990) and was tested by Shimojo and Nakayama (1990) in their experiment 2. Shimojo and Nakayama (1990) reasoned that if ecologically valid monocular regions tend to escape suppression because monocularly visible texture is visible to one eye while the texture in the other eye is binocularly visible, then monocular regions that occur as a consequence of vertical disparity should also escape suppression. Shimojo and Nakamaya (1990) found that less suppression occurred for the monocular regions created by horizontal disparity than vertical

disparity and proposed that this was because the monocular regions that occurred as a result of horizontal disparities are ecologically valid, whereas monocular regions created by vertical disparities are not.

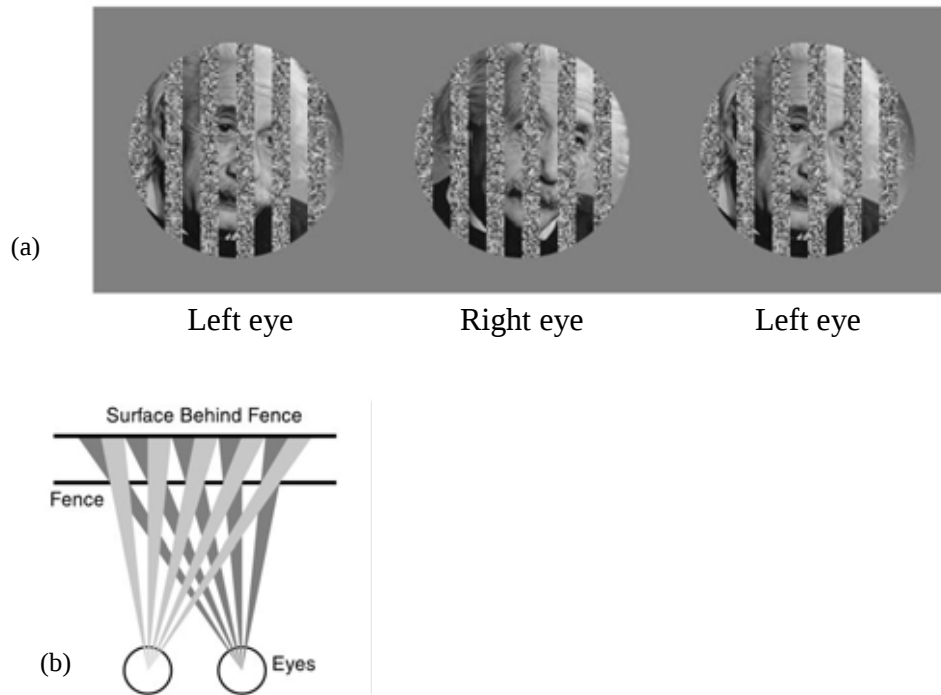


Figure 15. Stimuli used by Forte et. al. (2002). Stereogram in which no part of the background surface is binocularly visible and monocular regions visible to the left and right eye are close together (a). A bird's eye view of the same stimulus

A demonstration created by Forte, Pierce and Lennie (2002) suggests that monocular regions can escape binocular rivalry even when monocularly visible texture is presented to corresponding retinal locations in the two eyes. Figure 15a is a stereogram in which six vertical bars occlude a background surface. Each eye views a monocular region in the space between the bars and no part of the background surface is binocularly visible (Figure 15b). Forte et. al. (2002 p. 1232) reported that the monocular regions were not “generally suppressed” and observers “saw a continuous surface behind bars”, whereas vigorous suppression occurred when the images for the left and right eye were switched. Forte et. al. (2002) noted that the contours on the right side of

each monocular region for the right eye are continued on the left side of the monocular region for the left eye that is visible through the same gap. This continuity is broken in the switched condition for which suppression occurs.

Ono, Lillakas, Grove and Suzuki (2003) observed suppression of texture within monocular regions in their experiment 1. They instructed observers to fixate either a thin vertical rod or a page of text that lay behind the rod. The disparity between the rod and the page of text was very large, whereas Shimojo and Nakayama (1990) used small disparities between the occluder and its background. Consequently, with fixation on the page of text, the absolute disparity of the rod was large and it appeared double. Likewise, with fixation on the rod, the absolute disparity of the background was large and the text appeared diplopic. With fixation at the depth of the background, Ono et. al. (2003) reported that the text in the monocular region suppressed the middle of the rod or in some instances suppressed the rod entirely. Likewise, with fixation at the depth of the rod, the rod tended to suppress parts of the background surface. Ono et. al. (2003) argued that in these cases, suppression is consistent with the finding that features that are in focus tend to suppress features that are blurry (Fahle, 1982), because the accommodation distances of the rod and the text differed in their experiment. Hence, their results are not at odds with those of Shimojo and Nakayama (1990) and Forte et. al. (2002) who found that monocular regions can escape suppression.

1.3 The fusion limit

In binocular vision, an object may sometimes appear *double*, which is to say that the object appears in two directions simultaneously. This phenomenon is known as *double vision* or *diplopia*. Diplopia is most obvious when the coordination of the eyes is disrupted, for example, by pressing gently on one eye or by voluntarily crossing the eyes.

The fusion limit refers to the absolute disparities for which a feature will appear single 50% of the time. The fusion limit was measured by Palmer (1961) and Mitchell (1966) using brief exposures to prevent a vergence eye movement reducing the absolute disparity of the target. Palmer (1961) reported that the fusion limit for a small dot presented in the fovea varied between 30 and 35 minutes of arc across 3 observers and Mitchell (1966) reported that the fusion limit for a vertical line varied between 13.5 minutes of arc - 23 minutes of arc across 11 observers. The fusion limit increases with the eccentricity of the target from the fixation point, such that the fusion limit for a small line at an eccentricity of 5° is approximately 1° (Panum, 1858; Mitchell 1966; Ogle, 1950; Palmer 1961; Schor, Wesson & Robertson, 1986).

1.3.1 The fusion limit as a function of spatial frequency

Kulikowski (1978) found that the fusion limit for sinusoidal variations in luminance (Figure 16a) was larger than the fusion limit for square wave variations in luminance (Figure 16b). Kulikowski (1978) argued that the fusion limit differed between these two stimuli because of the high spatial frequencies present for the square wave but not the sine wave variations in luminance. Using stimuli composed of a narrow range of spatial frequencies, Schor, Wood and Ogawa (1984) measured the fusion limit as a function of spatial frequency. They observed that the fusion limit was approximately 25% of the period of the spatial frequency for spatial frequencies lower than 2.4 cycles per degree. However, for higher spatial frequencies, the fusion limit was approximately 10-14 minutes of arc and did not vary with spatial frequency.

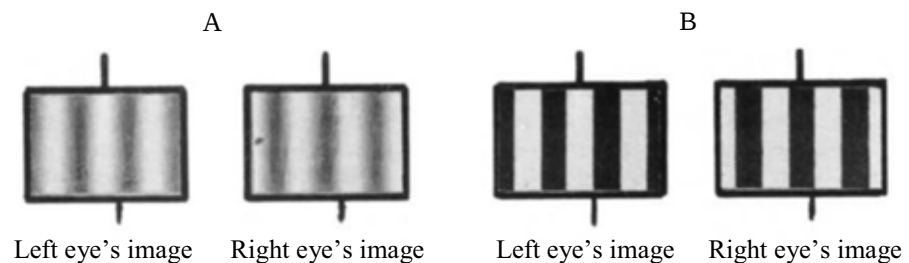


Figure 16. Stimuli used by Kulikowski (1978). The fusion limit for the blurred stereogram (A) is greater than the fusion limit for the sharp stereogram (B). From Kulikowski (1978).

Schor et. al. (1984) proposed that for stimuli composed a broad range of spatial frequencies, the fusion limit is principally limited by the high spatial frequencies. In evidence, Schor et. al. (1984) reported that the fusion limit for a target composed of only high spatial frequencies was the same as the fusion limit for a vertical bar, which also contains medium and low spatial frequencies. However, Rohaly and Wilson (1993) and Roumes, Plantier and Menu (1997) found that the fusion limit for a target composed

of high and low spatial frequencies was intermediate between the fusion limits obtained when the high and low components were presented separately (see also Wilson, Blake & Pokorny, 1988). It is possible that Schor et. al. (1984) observed equivalent fusion limits for a target composed of only high spatial frequencies and a vertical bar because the energy at the low spatial frequencies is much less for a bar than the large targets used by Rohaly and Wilson (1993) and Roumes et. al. (1997).

1.3.2 The fusion limit of surfaces

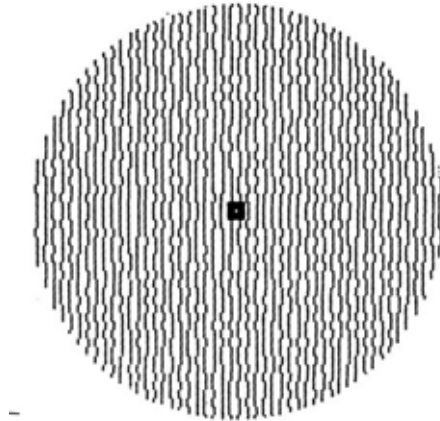


Figure 17. Stimuli used by Kertesz (1981) were surfaces composed of 50 vertical lines that were randomly segmented.

Kertesz (1981) measured the fusion limit as a function of surface size for a surface composed of pseudo-randomly positioned vertical lines (Figure 17). Kertesz found that the fusion limit increased with the size of the surface (Kertesz, 1981; Boman & Kertesz, 1985) and the fusion limit has often reported to exceed 2° for very large stimuli (e.g. Fender & Julesz, 1967; Kertesz, 1981; Boman & Kertesz, 1985; Erkelens, 1988). Kertesz (1981) proposed that more peripheral retinal locations, where the fusion limit is larger (1.3), somehow aid fusion in the fovea via cooperative interactions between adjacent retinal regions. Lee and Dobbins (2006) recently found that the fusion limit of dots comprising an annular surface was the same as the fusion limit for an isolated dot at the same eccentricity as the dots at the outer edge of the annular surface. Although Lee and Dobbins (2006) do not discuss this result with respect to Kertesz' proposal, their results support his theory, which predicts that the presence of eccentric surface regions extends the fusion limit of surface regions at smaller eccentricities, but that the fusion limit of the most eccentric regions of a surface are not increased relative to an isolated feature at the same eccentricity.

1.3.3 Fusional hysteresis

Fender and Julesz (1967) measured the fusion limit for lines and random dot surfaces using the method of limits. They found that the fusion limit was much larger when the disparity of the stimulus was initially small and gradually increased than when disparity was initially large and gradually decreased. Fender and Julesz (1967) proposed that this asymmetry, called *fusional hysteresis*, was due to an extension of the fusion beyond its usual limits when the disparity of the stimulus was gradually increased. However, Erkelens (1988) found that the largest fusible disparity measured by slowly increasing disparity was the same as that measured by presenting the stimulus with a fixed value of disparity. This indicated that fusional hysteresis is due to a reduction of the fusion limit when the stimulus is initially diplopic, rather than an extension of the fusion limit when the stimulus is initially fused and disparity is gradually increased. Erkelens (1988) argued that fusional hysteresis is due to an inhibitory process that prevents fusion occurring when the disparity of the stimulus is initially too large to fuse.

1.3.4 The disparity gradient constraint on fusion



Figure 18. Stimuli used by Tyler (1975).

Tyler (1975) paired a vertical line in one eye with a sinusoidal line in the other eye (Figure 18). The frequency of the sinusoidal line varied vertically and its amplitude varied horizontally. Using this stimulus, Tyler (1975) varied the separation between minimum and maximum values of disparity without affecting the magnitude of the disparity. He found that the fusion limit decreased as the separation between minimum and maximum values of disparity decreased. Braddick (1979) observed that two lines, with a relative disparity of only 6 minute of arc, appeared double when they were narrowly separated, yet appeared single when they were more widely spaced. Burt and Julesz (1980) measured the fusion limit for dot pairs as a function of the visual angle separating the dots for vertical, horizontal and oblique directions of separation. They found that the fusion limit was constrained by a *disparity gradient*, defined as the dot pair's relative disparity divided by their average angular separation in the two eyes. The dots always appeared double when this disparity gradient exceeded a value of 1; which is to say that the dots always appeared double when their relative disparity exceeded their separation. However, Prazdny (1985), Wilson et. al. (1988) and Scharff (1997) demonstrated that the disparity gradient that induces diplopia is not a fixed value of 1. Prazdny (1985) found that disparity gradients as steep as 3 were tolerated without diplopia for dot pairs where one dot was white dot and the other dot was black and

concluded that disparity gradients steeper than 1 are required to induce diplopia for dot pairs of opposite contrast polarity. Wilson et. al. (1988) tested a wider range of disparities than Burt and Julesz (1980) and found that disparity gradients as shallow as 0.5 may induce diplopia. Scharff (1997) found that shallower disparity gradients tend to induce diplopia as the eccentricity of the dot pair from the fovea increases.

1.4 Perceived visual direction

Ptolemy (reviewed by Howard & Wade, 1996), Wells (1792) and Hering (1879) made careful observations of the perceived direction of objects that lay at different distances along the visual axes. Figure 19a shows a bird's eye view of Hering's (1879) version of this situation, which became the most famous. The observer fixates a mark on a window pane so both visual axes intersect the same mark on the window but intersect different landmarks visible through the window.

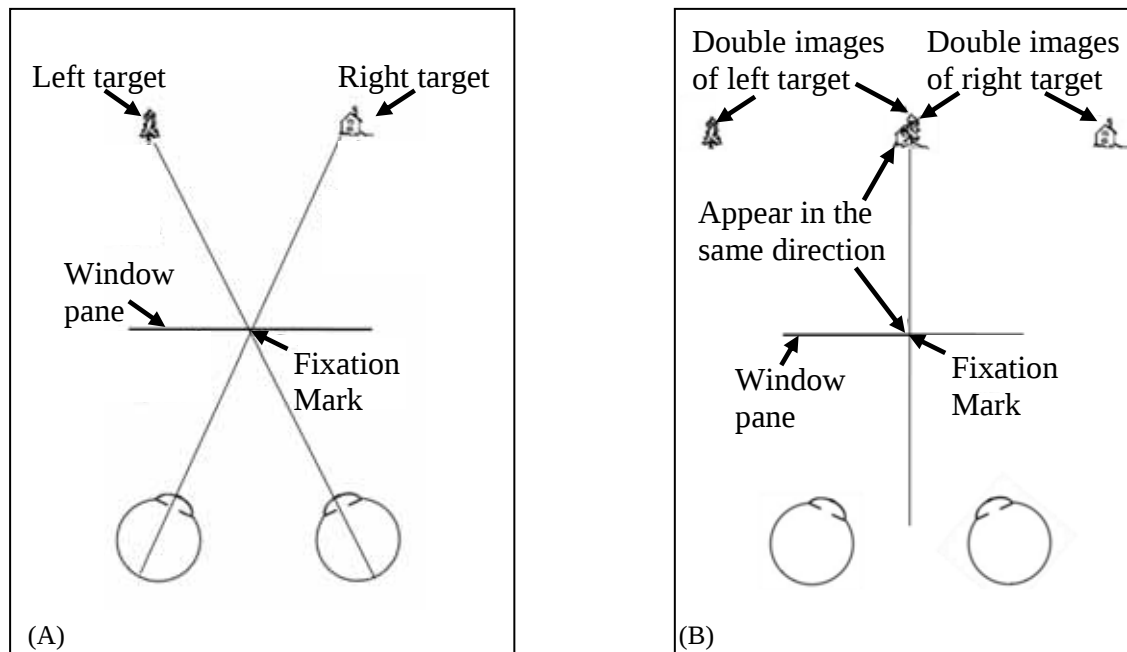


Figure 19. Perceived direction of objects situated along the visual axes. (A) shows the physical locations of the objects and (B) shows their perceived direction. After Hering (1879/1942).

Hering (1879/1942) observed that the mark on the window appeared single but the landmarks visible through the window appeared double (Figure 19b). He observed that one of the double images of each landmark appeared in the same direction as the fixation point. Hering also noted the *perceived egocentric direction* of the features, which refers to the direction of features relative to the observer's body. He observed

that the fixation point and the double images of the landmarks which appeared in the same direction as the fixation mark appeared to lie in the median plane of the head (Figure 19b). Since the physical locations of the landmarks are to the left and right of the median plane, Hering concluded that the perceived egocentric direction of the diplopic images of the landmarks was distorted. Ptolemy (Howard & Wade, 1996) and Wells (1792) reported the same phenomenon with objects also positioned at different distances along the visual axes.

On the basis of these observations, Ptolemy, Wells and Hering made proposals concerning the perceived relative direction and perceived egocentric direction of objects visible along the visual axes. With respect to perceived relative direction, they concluded that objects visible along the visual axis of the left eye are perceived to lie in the same direction as objects visible along the visual axis of the right eye. With respect to perceived egocentric direction, they concluded that objects that lie along the visual axis of either eye are perceived to lie along a line that is the average of the visual axes. This line is called the *common axis* or the *cyclopean axis* and intersects the fixation point and a point midway between the eyes called the *cyclopean eye* (e.g. Hering, 1879/1942; Ono, 1979).

The perceived direction of monocular features that are presented alone are reviewed in the following section 1.4.1. Measurements of the perceived direction of binocular features that appear diplopic are reviewed in section 1.4.2. The perceived direction of binocular features that appear in a single direction is reviewed in section 1.4.3. The perceived direction of monocular features that are proximal to binocular features is reviewed in section 1.5.2.

1.4.1 The perceived direction of monocularly visible features: The cyclopean illusion

On the basis of Hering's (1879/1942) theory (see 1.4; Ono, 1979), it is predicted that the perceived egocentric direction of any monocular feature varies with vergence (e.g. Ono, Wilkinson, Muter & Mitson, 1972). For example, suppose as in Figure 20a, that a target (T) is visible beneath a fixation point (F). There are visible to the left eye but occluded in the right eye by a screen. Ignoring the vertical separation between the target and the fixation point, the target lies along the visual axis of the left eye. Hence, it is predicted that the perceived direction of the target is the cyclopean axis, which is the average of the visual axes as shown in Figure 20b. Now suppose that the fixation point is shifted farther in depth along the visual axis of the left eye so that the right eye rotates clockwise (Figure 20c). Since the cyclopean axis is an average of the visual axes, the cyclopean axis also rotates clockwise, which alters the perceived egocentric direction of the monocular target (Figure 20d).

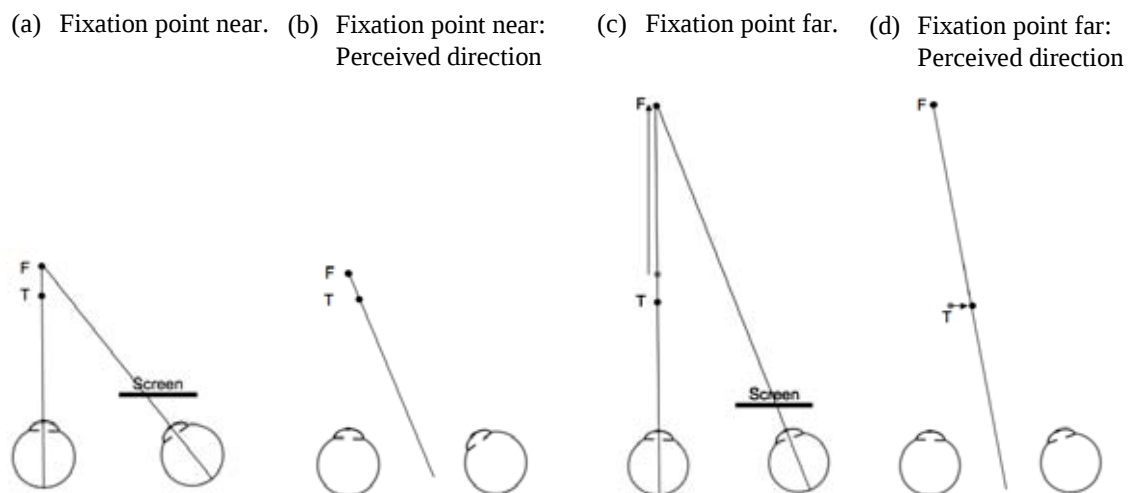


Figure 20. The cyclopean illusion. Shows a monocular target T, which is visible along the visual axis of the left eye. The fixation point, F, recedes in depth as indicated by the vertical arrow in (c), causing the right eye to turn. The perceived direction of the target according to Hering (1879/1942) is the cyclopean axis – the average of the visual axes. Note that in (d) the cyclopean axis and hence the perceived egocentric direction of the monocular target has shifted rightward relative to (c).

The effect of vergence on the perceived egocentric direction of a monocular feature was studied in detail by Ono et. al. (1972). Two points of light were presented at different distances in the dark. These lights were visible to one eye while occluded in the other eye by a screen. The observer indicated the perceived egocentric direction of either the near or the far light by placing a pen beneath the perceived location of the light on the underside of the table. Measurements of the perceived egocentric direction of each light were made while fixating either the near or the far light. Ono et. al. (1972) also measured the apparent lateral movement of the perceived egocentric direction of the lights during the change in fixation from the near to the far light and vice versa. The observer matched the extent of the apparent movement by setting the distance between the collars of a rod. Ono et. al. (1972) found that the perceived egocentric direction of the lights differed between the near and far fixation conditions. Ono et. al. (1972) also found that the perceived egocentric direction of the lights appeared to move during the change in fixation. This shift in the perceived egocentric direction of a monocular feature due to a change in vergence is referred to as the cyclopean illusion (Enright, 1988).

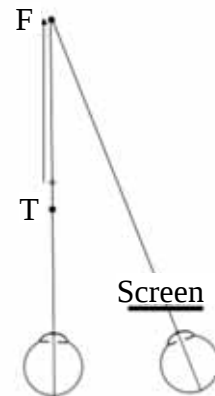
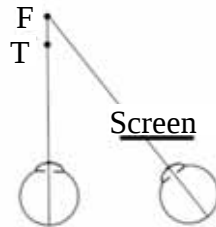
Ono et. al. (1972) found that the magnitude of the cyclopean illusion varied between observers. Ono et. al. (1972) argued that this variability is partly accounted for by individual differences in the extent of the vergence eye movements. In evidence, Ono et. al. (1972) measured phoria and found a correlation of 0.833 between the extent that convergence changed between the near and far fixation conditions and the difference in perceived egocentric direction between these conditions. Similarly, Ono et. al. (1972) found a correlation of 0.771 between the extent convergence changed when the near and far targets were alternately fixated and the extent of the apparent lateral

Left Diagrams: before
rotation of the right eye.

Right Diagrams: after
rotation of the right eye.

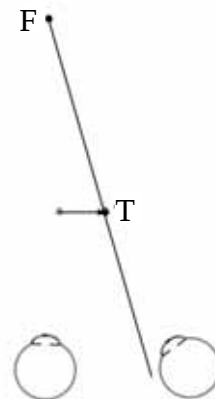
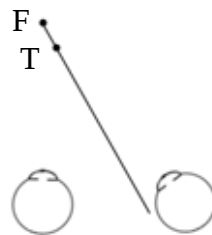
(A)

Physical location of
monocular target and
fixation point



(B)

Perceived direction with
cyclopean eye closer to
the right eye



(C)

Perceived direction
with cyclopean eye
closer to the left eye

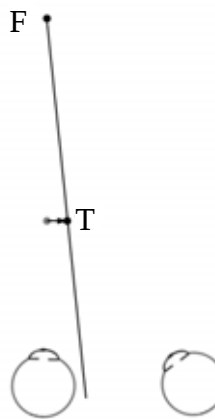
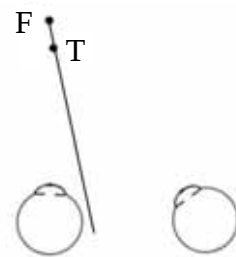


Figure 21. Individual differences in the location of the cyclopean eye. The diagrams in the upper row show two targets, F and T, visible along the visual axis of the left eye. The fixation point is closer in the left diagram than in the right diagram, in which the right eye has rotated clockwise to maintain fixation. The middle and lower row diagrams show the cyclopean axis and the perceived direction of the target. The perceived egocentric direction of the target is distorted least when the cyclopean axis is referred to a cyclopean eye nearer to the left eye than the right eye (lower row) than when the cyclopean axis is referred to a cyclopean eye nearer to the eye that does not view the monocular target (middle row).

movement of the perceived egocentric direction of the lights. Ono and Gonda (1978) presented a single LED in the dark and alternately occluded it in the left and right eye

while observers fixated the LED. They found a correlation of 0.95 between phoria and the LED's apparent movement between the left eye visible state and the right eye visible state.

The cyclopean illusion has been found to be larger when the monocular target is viewed by one eye than the other eye for some observers (Ono et. al. 1972; Barbeito, 1981; Ono & Barbeito, 1982; Barbeito & Simpson, 1991). Ono et. al. (1972) proposed that the point between the eyes where the cyclopean axis is referred, called the cyclopean eye, is closer to one eye than the other in such observers. If the cyclopean eye were closer to the right eye than the left eye, for example in Figure 21b, then a rotation of the right eye (right column of Figure 21 relative to the left column) would influence the orientation of the cyclopean axis more than if the cyclopean eye were closer to the left eye (Figure 21c).

To assess whether individual differences in the location of the cyclopean eye accounts for the interocular difference in the magnitude of cyclopean illusion for some observers, the position of the cyclopean eye must be measured. The method proposed by Howard & Templeton (1966 p.274) has been shown to be the most precise (Mitson, Ono & Barbeito, 1976; Barbeito & Ono, 1979). This method first identifies the physical location of pairs of near and far binocularly visible targets that are judged to point directly at the observer. These pairs are determined for a range of eccentricities from the fixation point. Then straight lines are drawn through the near and far target of each pair. The intersection of these lines defines the location of the cyclopean eye. Using this method, Ono et. al. (1972) did not observe a significant correlation between individual differences in the location of the cyclopean eye and interocular differences in the

magnitude of the cyclopean illusion. However, using a larger number of observers, Barbeito and Ono (1979) found a significant correlation of 0.66.

Ono et. al. (1972) found that the magnitude of the cyclopean illusion was smaller when one eye's view is completely occluded than when the LED that served as the fixation point was visible to both eyes. Ono et. al. (1972) argued that the cyclopean illusion tends to be larger with a binocular fixation point because convergence error is minimised, which increases the difference in vergence between the near and far fixation conditions. Erkelens (2000) proposed an alternative explanation. He argued that the cyclopean illusion tends to be smaller when one eye is completely occluded because then the influence of the direction of the occluded eye on perceived direction is reduced. Erkelens (2000) proposed that the cyclopean illusion is eliminated in day light viewing conditions when one eye's view of the visual scene is completely occluded. In evidence, Erkelens (2000) found that the cyclopean illusion occurred for only a few observers when a near and far LED were presented in the dark to one eye while the other eye's view of the visual scene was completely occluded, either by a screen or by shutting the eye. Of those observers that did experience the cyclopean illusion under these conditions, the cyclopean illusion was eliminated when the far LED was replaced by a large random dot surface.

Ono, Mapp and Howard (2002) argued that it is possible that Erkelens (2000) found a smaller cyclopean illusion when the entire visual field of one eye was occluded because then the vergence eye movement was smaller and slower. This possibility is consistent with the eye movement recordings provided by Erkelens (2000), which show that the change in vergence was smaller and slower when the fixation point was not

binocularly visible. Khokhotva, Ono and Mapp (2005), using LEDs presented in the dark, compared the cyclopean illusion with one eye's view completely occluded and with the fixation point binocularly visible. They observed no phoria in the condition where the fixation point was binocular and predicted a 2cm lateral displacement of the perceived egocentric direction of the target LED. They observed an exophoria in the condition where one eye's view was completely occluded so that the predicted magnitude of the cyclopean illusion was a 2.3cm lateral displacement of the monocular target. Khokhotva, Ono and Mapp (2005) found a lateral displacement of 1.8 cm for both conditions. Khokhotva, Ono and Mapp (2005) argued that their results are inconsistent with the Erkelens (2000) proposal that the influence of the occluded eye is reduced when its view of the visual scene is completely occluded. Khokhotva, Ono and Mapp (2005) argued that the slightly larger cyclopean illusion that was expected for the completely occluded condition due to exophoria was not observed because observers reported the apparent location of the target LED to the nearest centimetre. Mapp, Ono and Khokhotva (2007) found that individual differences in phoria predicted the bias of thrown darts in daylight conditions when one eye was completely occluded. Ono, Mapp and Mizushina (2007) replicated the effect of a large background surface on vergence-induced apparent movement of perceived egocentric direction. However, Ono et. al. (2007, p. 2072) stress that the illusory movement was still observed with a large textured surface and proposed that the apparent movement is reduced because "large backgrounds are interpreted by the visual systems as stationary."

1.4.2 The perceived direction of features that are seen double

In the previous sections on perceived direction, the perceived relative and egocentric directions of features that lie along the visual axis of either eye was considered. Hering (1879/1942) specified the perceived direction of features that do not lie along the visual axes as an angular deviation from the cyclopean axis at the cyclopean eye. Hering placed the cyclopean eye between the eyes on the Veith-Müller circle. The cyclopean axis is the line passing through the cyclopean eye and the fixation point. A visual line, which deviates from the visual axis by a particular angle, is perceived in a direction that forms the same angle with the cyclopean axis at the cyclopean eye. For example, in Figure 22a the visual lines to the far rod differ from their respective visual axis by angle α for the left eye and angle β for the right eye. Figure 22b shows the predicted perceived directions of the far rod, which differ from

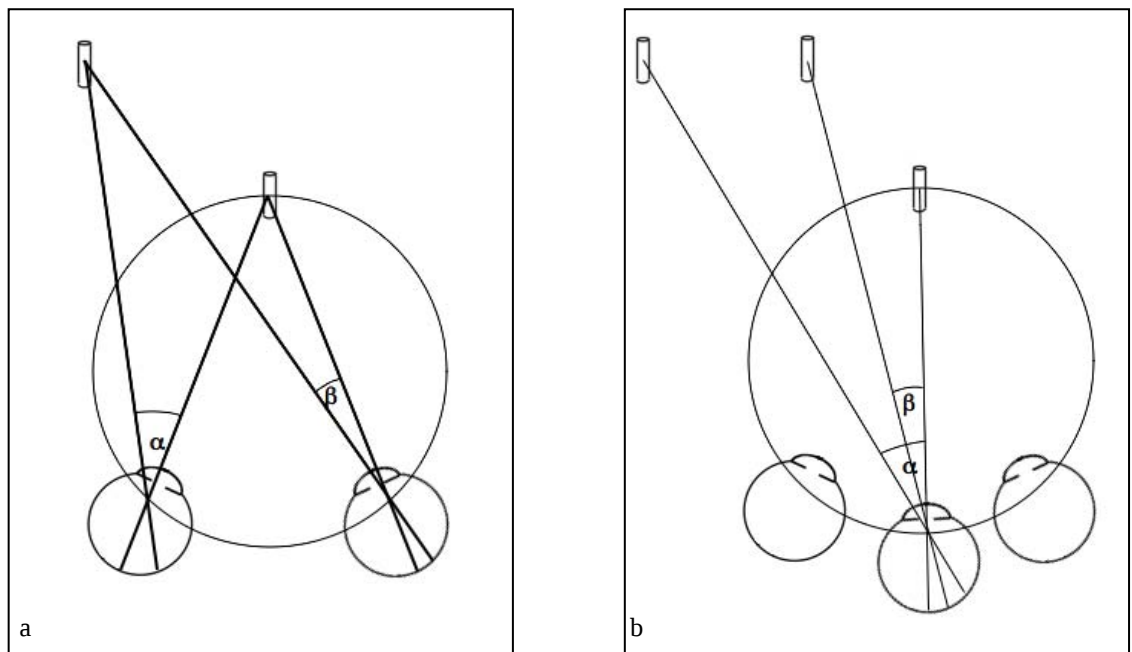


Figure 22. Perceived direction of diplopic images according to Hering. The left Figure (a), shows the physical location of two rods and their angular separation at each eye. The right Figure (b), shows the perceived direction of the rods. The centrally located eye is the cyclopean eye and the vertical line that intersects the near rod is the cyclopean axis.

the cyclopean axis by angles α and β . Note that the correct egocentric direction of the rod lies between the predicted egocentric directions of its diplopic images (Hering, 1879/1942).

Hering's theory predicts that the perceived direction of the double images of a feature differ by an amount equal to the target's absolute disparity, which is the difference between angles α and β in Figure 22. Rose and Blake (1988) measured the apparent separation of diplopic images. They found that for very large disparities, which exceeded the target's fusion limit by 2° or more, the apparent separation of the diplopic images was approximately equal to their absolute disparity as predicted by Hering. However, for disparities that exceeded the fusion limit by less than 1° , the diplopic images appeared up to approximately 30% closer together than Hering predicted.

1.4.3 The perceived direction of fused binocular features

Provided that the disparity of a feature is small, it is usually perceived in a single direction (see section 1.3). Asher (1953) argued that a binocular feature is perceived in a single direction because one of its diplopic directions is suppressed, a view shared by Verhoeff (1935) and Hochberg (1964). In evidence, Asher (1953) referred to the perceived direction of a small black disc in the centre of a ring (Figure 23a). The disc was to the right of centre in one eye's view but to the left of centre in the other eye's view (Figure 23a). Asher (1953) observed that the disc always appeared offset from the centre of the ring, either matching the view of the left or right eye.

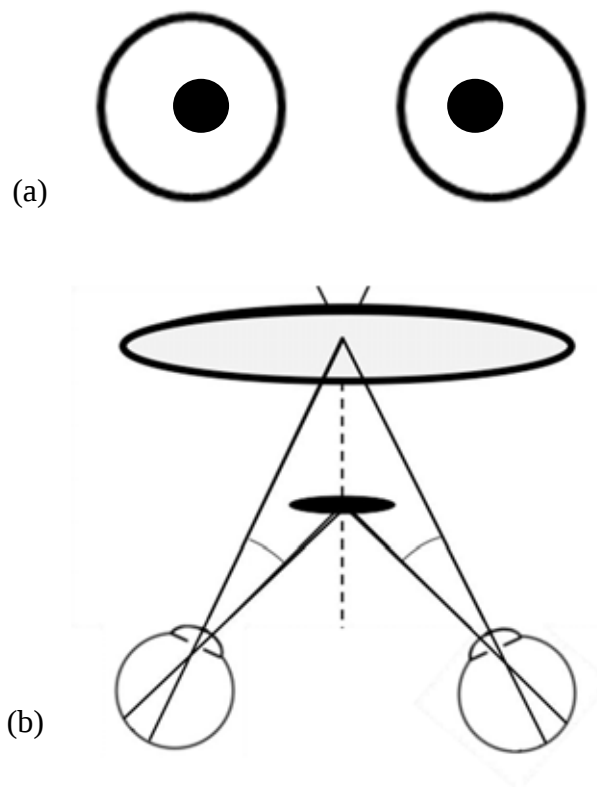


Figure 23. Stereogram used by Asher (1953) and Ono et. al. (1977). (b) shows a bird's eye view of the location of a disc and a ring which would give rise to the two eye's views in (a).

Using the same stimulus, Ono, Angus and Gregor (1977) varied the relative disparity between the disc and the ring. Their observers reported that the disc appeared in the centre of the ring when its disparity was less than 15 minutes of arc and only reported that the disc appeared in a single direction that was offset from the centre of the ring for larger disparities. Using vertical instead of horizontal disparity, Sheedy and Fry (1979) measured the perceived relative direction of two horizontal lines with different values of vertical disparity. Provided that the vertical disparity was smaller than 4-5 minutes of arc, the perceived relative direction of the lines was intermediate between the angle they subtended at each eye.

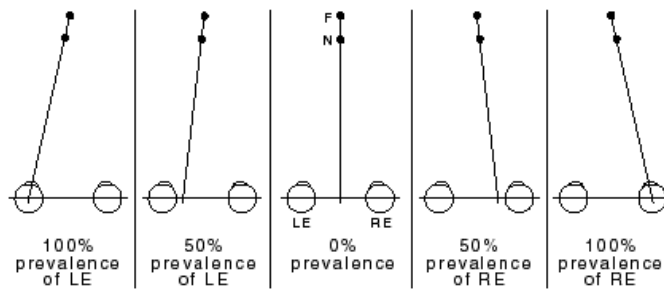


Figure 24. Ocular prevalence. Shows the physical locations of two binocularly visible targets that are judged to appear vertically aligned. An imaginary line passing through these targets is shown to intersect the inter-ocular axis. From Kommerell et. al. (2003).

These results are consistent with Hering's (1879/1942, p.61) proposal that the perceived direction of any binocularly visible feature with a disparity small enough to fuse is an average of its visual lines (see also Ono & Mapp, 1995). For example, Figure 23b shows a bird's eye view of the disc and the ring in Figure 23a. The dashed line is the average of the visual lines to the centre of the ring and is also the average of the visual lines to the centre of the small black disc. Hence, according to Hering's proposal, the centre of the ring and the centre of the disc are perceived to lie in the same direction, as was found by Ono et. al. (1977).

It has often been observed that the perceived relative direction of a pair of binocularly visible features, while intermediate between the angle that they subtend at each eye, is more similar to the angle for one eye than the other (Sheedy & Fry, 1979; Erkelens, Muijs & van Ee, 1996; Kommerell, Schmitt, Kromeier, & Bach, 2003). This can be characterised as a *bias* because the angle subtended by the features at one eye makes a larger contribution to the perceived relative direction of the features than the angle subtended by the features at the other eye. Kommerell et. al. (2003) has referred to such a bias as *ocular prevalence* (Figure 24) and observed that it manifests in individuals with the same acuity for both eyes. Kommerell et. al. (2003) argued that ocular prevalence, which is measured with two fused binocularly visible targets, is distinct from *ocular dominance*, which refers to whether an observer uses their left or their right eye in tests that force observers to sight a target using one eye or the other. Kommerell et. al. (2003) found that ocular prevalence was in the same direction as ocular dominance in 15 of 20 observers.

The perceived relative direction of a pair of binocularly visible features is also biased towards the angle they subtend at one eye when one of the features is brighter or has higher contrast in one eye than the other (Charnwood, 1949; Mansfield & Legge, 1996). In such stimuli, the perceived relative direction of a pair of features more closely resembles the angle subtended at the eye that views the brighter or higher contrast image. Mansfield and Legge (1996) have shown that when the contrast of the images differs between the eyes, the magnitude of the bias increases with the inter-ocular difference in contrast.

In order to account for the effect of interocular differences in contrast on perceived direction, Mansfield and Legge (1996) proposed a model that maximises the precision of the binocular estimate of a feature's direction. The contribution of each eye to the binocular estimate of a feature's direction is weighted according to how precisely it specifies the feature's location. Mansfield and Legge (1996) tested this model by measuring the precision with which monocularly viewed targets were aligned with one another as a function of contrast. When these estimates of precision as a function of contrast were input to their model, Mansfield and Legge (1996) found that their model predicted the magnitude of the bias of the perceived relative direction of the features towards their angular separation in the eye that views the higher contrast image.

It is not known whether the perceived egocentric direction of binocular features with unequal contrast in the two eyes is correct or distorted. For example, Figure 25a shows the location of the mixed contrast target in the Mansfield and Legge (1996) study where it was found to appear vertically aligned with the other (far) target. Mansfield and Legge (1996) proposed that the perceived direction of the targets was referred to a point closer to the eye that viewed the higher contrast image, in which case it is possible that the perceived egocentric directions of both targets was correct (Figure 25b). However Banks, van Ee and Backus (1997) have argued that it is possible that the perceived direction of targets with unequal contrast in the two eyes is referred to the cyclopean eye (Figure 25c), as has been found for features with the same contrast in the two eyes (Mitson et. al. 1976; Barbeito & Ono, 1979). Banks et. al. (1997) argued that if this was the case, then the perceived egocentric locations of both targets would point towards the cyclopean eye (Figure 25c), in which case the perceived egocentric direction of one of the targets must be distorted because they do not actually lie along a line that intersects

the interocular axis midway between the eyes (physical locations of the targets shown in Figure 25a). Mapp and Ono (1999) argued that which of these possibilities is correct can only be resolved by measuring the perceived egocentric direction of a target with unequal contrast in the two eyes, which has yet to be done.

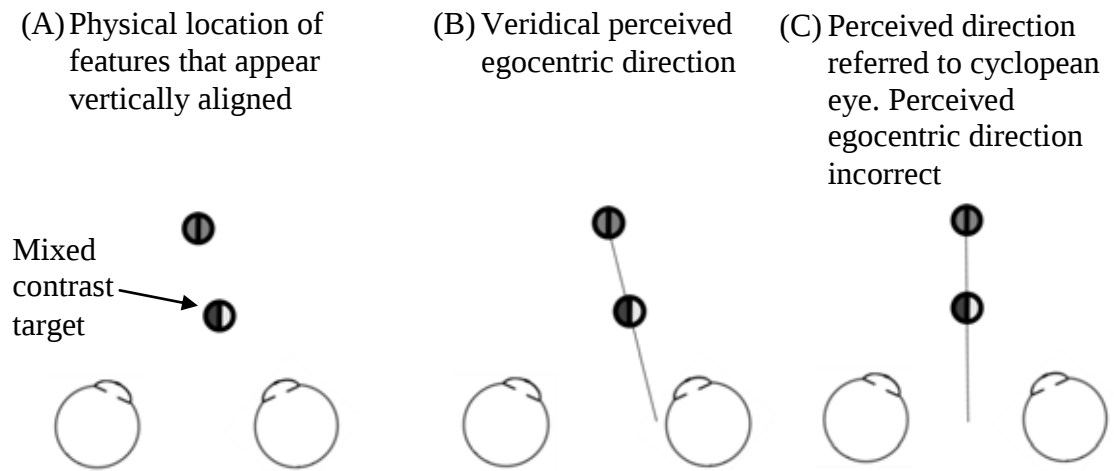


Figure 25. Perceived egocentric direction of features with unequal contrast in the two eyes. (a) shows the physical location of the mixed contrast target (near target) after the observer has vertically aligned it with the far target. (b) and (c) show the perceived direction of the targets according to Mansfield and Legge (1996) (b) and Banks et. al.(1997) (c). In both cases the perceived relative direction of the targets is the same, because both targets are perceived to be aligned as indicated by the straight line passing through the targets in (b) and (c). However, in (b), the perceived egocentric locations of the targets is correct, whereas in (c) the perceived egocentric direction of the mixed contrast target is distorted because its perceived direction is referred to a point midway between the eyes (the cyclopean eye).

1.5 Perceived direction at the left and right edges of occluding surfaces

1.5.1 Hering's laws of visual direction applied to the left and right edges of occluding edges

According to Hering's theory (Hering, 1879/1942; Ono & Mapp, 1995) the perceived direction of any *binocularly* visible feature is an average of its visual lines, provided that its disparity is small (see 1.4.3). According to Hering's theory, the perceived direction of any *monocularly* visible feature forms an angle with the cyclopean axis equal to the angle between the visual line to the feature and the visual axis (see 1.4.2). Erkelens and van de Grind (1994) applied these principles to the left and right edges of occluding surfaces where a monocular region of the background surface occurs between a binocularly visible region of the background surface and the edge of the occluding surface (see 1.2, Figure 26 next page).

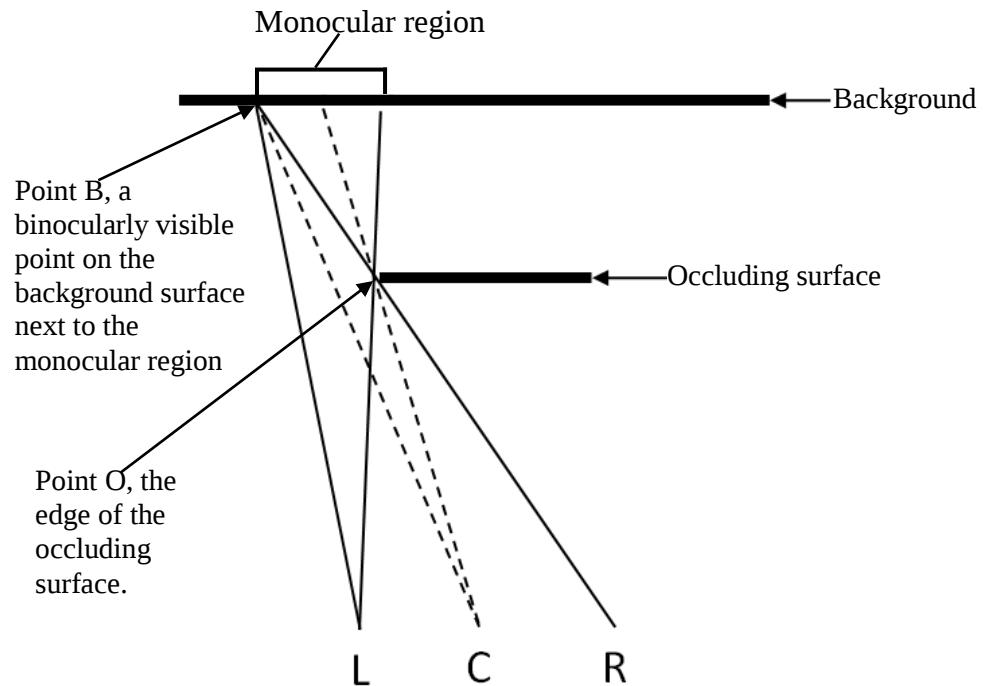


Figure 26. Perceived direction of the binocular features that border a monocular region. L and R indicate the locations of the left and right eye and C is a point midway between the left and right eye (the cyclopean eye). The solid lines from the left and right eye to Point B on the background surface are the visual lines to the binocularly visible feature on the background surface at the edge of the monocular region. The perceived direction of point B and point O according to Hering's theory are the dashed lines.

In Figure 26, the binocularly visible feature on the background surface next to the monocular region is represented by point B. The visual lines of this point are shown in Figure 26 by the solid lines from each eye to point B. The dashed line that intersects point B is the average of these visual lines and hence the perceived direction of point B according to Hering's theory. The binocularly visible feature next to the other edge of the monocular region is the edge of the occluding surface (Point O in Figure 26). The visual lines of the edge of the occluding surface are shown in Figure 26 by the solid lines from each eye to point O. The average of these visual lines is the dashed line that intersects point O and hence the perceived direction of the edge of the occluding surface according to Hering's theory.

The perceived direction that Hering's theory (see 1.4.2) assigns features in the centre of a monocular region is shown below. The perceived direction of a monocular feature is predicted to vary with vergence (see 1.4.1). The perceived direction of a feature in the centre of a monocular region with convergence at the depth of the background surface is shown first and then with convergence at the depth of the occluding surface.

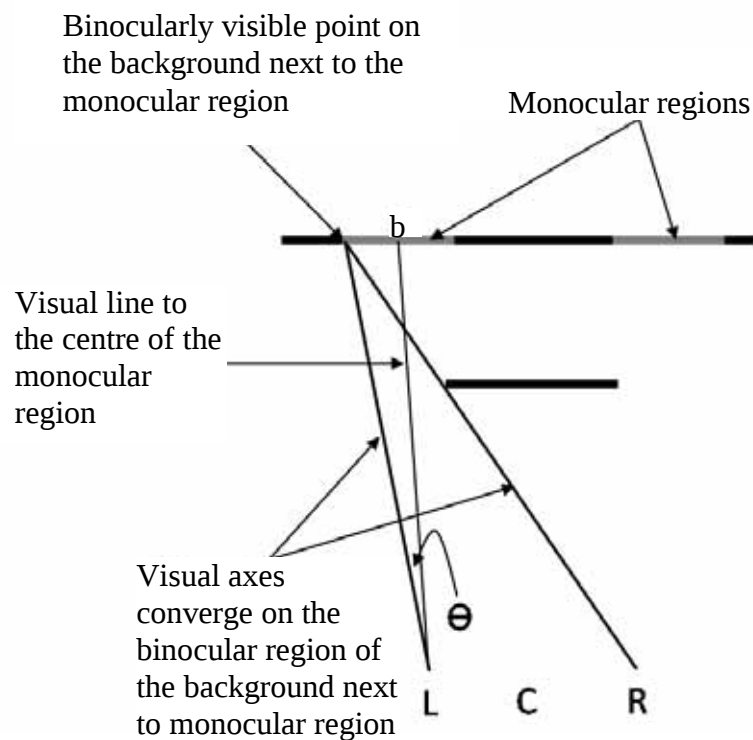


Figure 27. Visual line to the centre of a monocular region with fixation on the background. The grey sections of the background represent monocular regions. The visual axes of the eyes are shown intersecting the binocularly visible region of the background at the edge of the monocular region. The visual line to the centre of the monocular region (b) forms angle Θ with the visual axis of the left eye, which is equal to half the width of the monocular region.

For the situation shown in Figure 27, the fixation point is a binocularly visible point on the background next to the monocular region. The cyclopean axis is the line that intersects this point and the cyclopean eye (Figure 28). Point b in Figure 27 lies in

the centre of the monocular region. Point b forms an angle with the visual axis of the left eye equal to half the angular width of the monocular region (angle Θ in Figure 27). Hence, it is predicted that the perceived direction of point b forms an angle with the cyclopean axis equal to half the angular width of the monocular region (Figure 28). Erkelens and van de Grind (1994) noted that this is the same perceived direction that Hering's theory assigned to the edge of the occluding surface (see Figure 26). Hence, with fixation at the depth of the background surface, Hering's theory assigns the features on the half of the monocular region closest to the occluder the same perceived directions as features on the occluding surface.

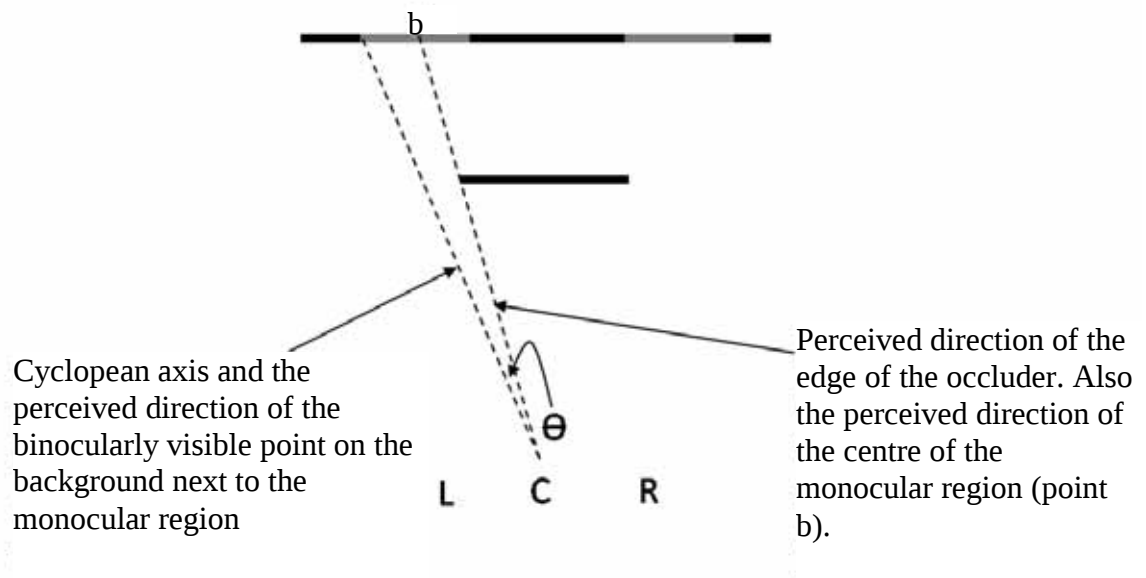


Figure 28. Perceived direction according to Hering's theory with fixation on the background. Point (b) in the centre of the monocular region according to Hering's theory when the visual axes are converged on the background surface as shown in Figure 27. The edge of the occluding surface is predicted by the laws to appear in the same direction as the centre of the monocular region (point b).

Figure 29 shows the same situation as Figure 27 except that the fixation point is the edge of the occluding surface instead of the background next to the monocular region. Under these conditions, the visual line to a feature in the centre of a monocular region visible to the left eye (point b) forms an angle of $-\Theta$ with the visual axis of the

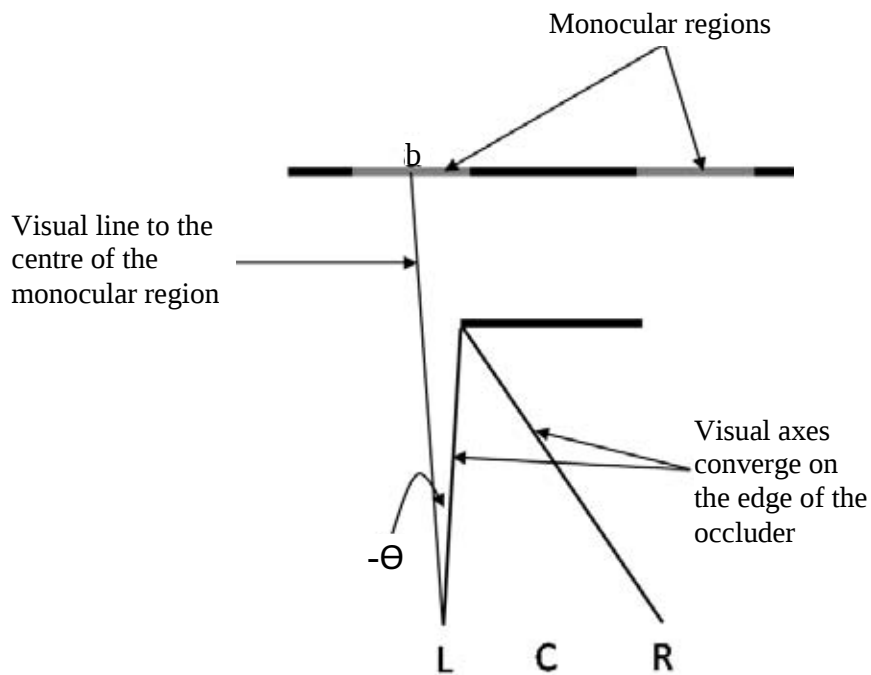


Figure 29. Visual line to the centre of a monocular region with fixation on the occluder. The visual axes of the eyes are shown intersecting the edge of the occluding surface. The visual line to the centre of the monocular region (b) forms angle $-\theta$ with the visual axis of the left eye, which is equal to half the angular width of the monocular region.

left eye. Angle $-\theta$ is approximately equal to half the angular width of the monocular region, since the visual axis of the left eye intersects the occluding edge, which is adjacent to the right edge of the monocular region. The predicted perceived direction of the centre of the monocular region with fixation at the depth of the occluder is shown in Figure 30. The cyclopean axis intersects the left edge of the occluder since that is the fixation point in the situation described in Figure 29. The perceived direction of the centre of the monocular region forms an angle of $-\theta$ with the cyclopean axis (Figure 30). However, this is the same perceived direction that Hering's theory for binocular features assigned the binocular feature on the background surface next to the left side of the monocular region (see Figure 26). Hence, with fixation at the depth of the occluder, Hering's theory for monocular features assigns features in the monocular region on the opposite side of the occluder the same perceived directions that were assigned to features that lie on the binocularly visible region of the background surface next to the

monocular region. Additionally, with fixation at the depth of the occluder, the perceived egocentric directions of the features in the monocular region are predicted to be incorrect. For example, it is predicted that a feature in the centre of a monocular region visible to the left eye (point b in Figure 29) is perceived to lie to the left of its true egocentric direction (Figure 30).

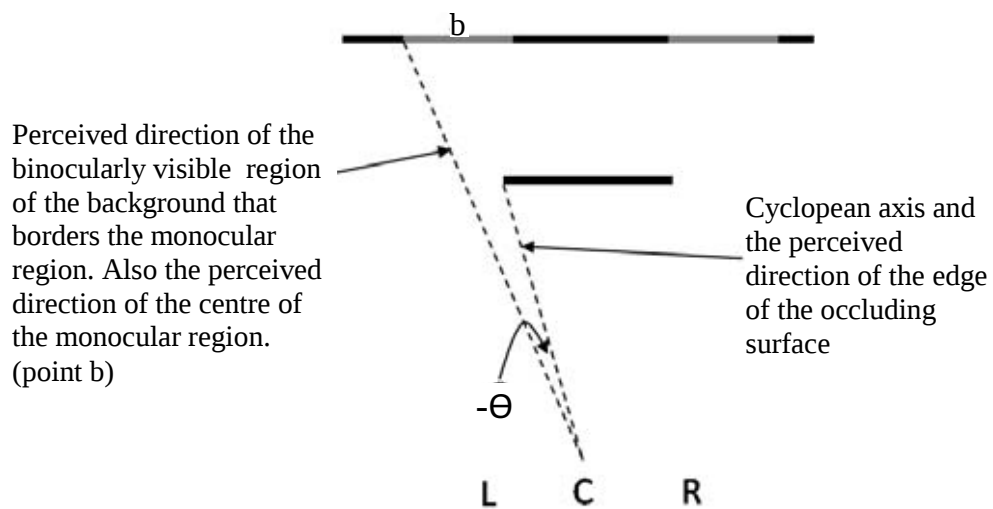


Figure 30. Perceived direction according to Hering's theory with fixation on the occluder. Shows the perceived direction of the edge of the occluder, the binocular region of the background next to the monocular region and a point (b) in the centre of the monocular region according to Hering's theory when the visual axes are converged on the occluding surface (Figure 29).

1.5.2 Measurements of the perceived direction of features within a monocular region

Erkelens and van de Grind (1994) were the first to measure the perceived direction of features lying within a monocular region next to the left and right edges of a surface. Figure 31 shows a schematic of their stimuli. A textured square occluded the central region of a textured background surface. A test line was presented 6 minutes of arc to the right of the centre of the monocular region next to the right edge or 6 minutes of arc to the left of the centre of the monocular region next to the left edge. The perceived direction of the test line was measured using a comparison line that was assigned the same disparity as the background surface and was visible to both eyes above and below the background surface. Observers moved the comparison line horizontally in order to vertically align it with the test line, while fixating a binocular line located in the centre of the occluder.

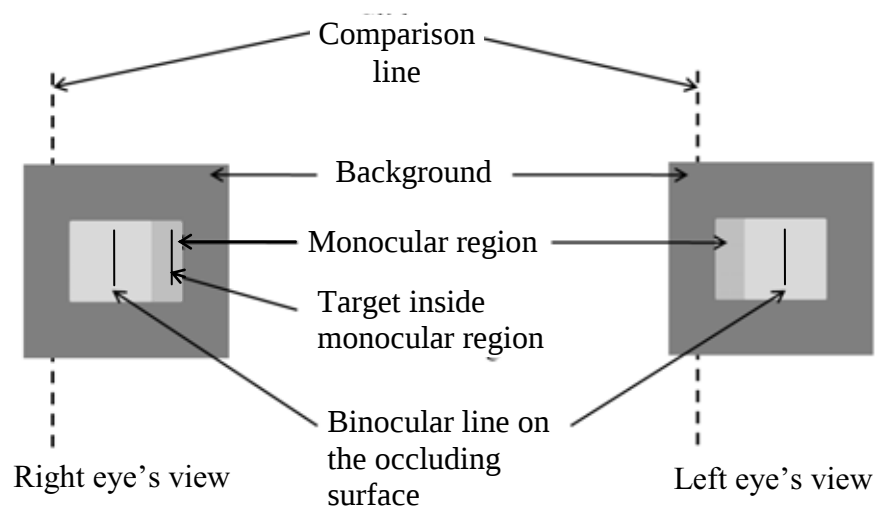


Figure 31. Schematic of stimuli used by Erkelens & van de Grind (1994).

Erkelens and van de Grind (1994) predicted on the basis of Hering's (1879/1942) theory that the perceived direction of the monocularly visible test line would vary with the disparity between the occluder and the background surface. With fixation at the depth of the occluder, it was predicted that the perceived direction of the test line in the monocular region visible to the left eye would shift leftwards by half the increase in disparity and vice versa for the test line in the monocular region visible to the right eye. Hence it was predicted that the comparison line would appear aligned with the monocular test line when the comparison and test lines were offset horizontally by half the disparity difference between the occluder and the background in the image containing the monocular test line. Contrary to Hering's theory, Erkelens and van de Grind (1994) found that the comparison line tended to appear aligned with the test line in the monocular region when the comparison and test lines were actually aligned in the eye viewing the test line.

van Ee, Banks and Backus (1999) have argued that the perceived direction of the test line in the monocular region in the Erkelens and van de Grind (1994) study failed to comply with Hering's theory (1879/1942) because it was proximal to binocularly visible features on the background surface. Erkelens and van Ee (1997a/b) first presented evidence that the perceived direction of a monocular feature does not comply with Hering's theory when the monocular feature is proximal to a binocular feature. In their stimulus, a monocular line was centred in a blank region within a large random dot surface. The stimuli were moved in a randomly determined direction in one eye's view and in the opposite direction in the other eye's view. It was predicted that the binocular surface would appear stationary on the basis that the perceived direction of binocular features is an average of their visual lines (reviewed 1.4.3), while the perceived

direction of the monocular line would vary as a result of the movement of the images. However, Erkelens and van Ee (1997a/b) found that the binocular surface *and* the monocular line appeared stationary. The monocular line only appeared to move when a gap of at least one degree separated the monocular line from the nearest binocular features (Erkelens & van Ee, 1997b; see also Shimono & Wade, 2002; Shimono, Tam, Asakura & Ohmi, 2005). Jaschinski, Jainta and Shürer (2006) later demonstrated that the influence of binocular features on the perceived direction of proximal monocular features is much reduced when the monocular feature is presented for less than 100ms.

Like the Erkelens and van de Grind (1994) study, van Ee, Banks and Backus (1999) and Ono et. al. (2003, experiment 3) measured perceived alignment between a binocular comparison line at the depth of the background and a monocular line presented a few minutes of arc to the left or right of an occluding surface. However, unlike the stimuli used by Erkelens and van de Grind (1994), the background surface did not contain any binocularly visible features except for the comparison line in the van Ee, Banks and Backus (1999) study and two other lines in the Ono et. al. (2003) study at an unspecified horizontal separation from the monocular line. Ono et. al. (2003) found that alignment to the monocular line differed when the comparison line was at the depth of the occluder relative to when the comparison line was at the depth of the background. Ono et. al. (2003) attributed this difference to the depth of the fixation point co-varying with the depth of the comparison line in their study. They argued that according to Hering's theory, the perceived direction of a monocular feature shifts with vergence by an amount equal to half the difference in disparity between the old and the new fixation point, which was 11 minutes of arc in experiment 3 of Ono et. al. (2003). 95% confidence intervals indicate that the obtained shift was 3.1 to 7.2 minutes of arc,

which contains the value of 5.5 minutes of arc predicted by Hering's theory. In the van Ee et. al. (1999) study, when a gap of 30 minutes of arc separated the comparison line from the test line, it was also observed that perceived alignment was consistent with Hering's theory. However, for gaps of a few minutes of arc between the binocular comparison line and the monocular test line, van Ee et. al. (1999) observed that the comparison and test lines appeared aligned when they were aligned in the eye that viewed both lines – consistent with the results of Erkelens and van de Grind (1994). Therefore, van Ee et. al. (1999) argued that the perceived direction of the test line in the monocular region in the Erkelens and van de Grind (1994) study did not comply with Hering's theory because it was influenced by the binocularly visible texture on the background surface. Van Ee et. al. (1999) supported the conclusion drawn by Erkelens and van Ee (1997a/b) that when a monocular feature is proximal to a binocular feature, the perceived direction of the monocular feature is determined as though it were a binocularly visible feature with the same disparity as the proximal binocular feature. Hence, the perceived direction of the monocular feature does not vary with vergence as predicted by Hering's laws. This influence of binocular features on the perceived direction of proximal monocular features is known as *capture of visual direction* (Erkelens & van Ee, 1997a&b).

1.5.3 The perceived direction of the left and right edges of an occluding surface

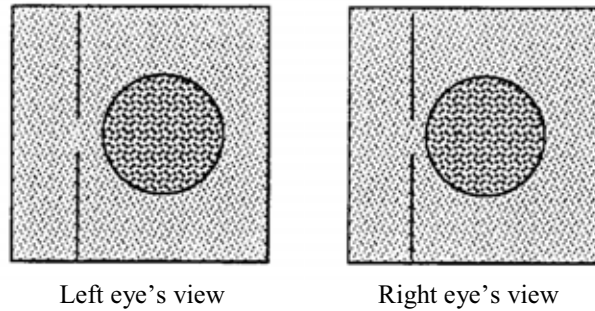


Figure 32. Schematic of the stereogram used by Erkelens et. al. (1996). The vertical line with a small gap in the centre was moved horizontally by observers in order to align it with the left or right edge of the occluding circle. From Erkelens et. al. (1996).

Erkelens, Muijs and van Ee (1996) studied the perceived relative direction of the left and right edges of a circular surface that occluded the central region of a background surface in a random dot stereogram (Figure 32). They instructed observers to change the horizontal location of a vertical line on the background surface so that it appeared vertically aligned with the left or right edge of the occluding surface. According to Hering's theory (Hering 1879/1942; Ono & Mapp, 1995) which was reviewed in section 1.4.3 and applied to features in the vicinity of the left and right of an occluding surface in section 1.5.1, it was predicted that the background line would appear aligned with the edges of the occluder when the average of its visual lines was vertically aligned with the average of the visual lines of the occluding edge. Contrary to this prediction, Erkelens et. al. (1996) found that the background line appeared aligned with the edge when it was aligned with the edge in the eye that viewed the monocular region next to the edge. In other words, the background line appeared aligned with the left edge when it was aligned with the left edge in the left eye and appeared aligned with the right edge when it was aligned with the right edge in the right eye. The term

Erkelens-bias is used to refer to the result that the eye that viewed the monocular region had a stronger influence on perceived alignment of the features than did the other eye.

Ono et. al. (2003) also measured the perceived direction of the left and right edges of an occluding surface relative to a comparison line located at the depth of the background surface. In experiment 2 and 3 of Ono et. al. (2003), the perceived direction of the left and right edges of a rectangular occluder was measured using a binocular comparison line located above the occluder. Observers vertically aligned the comparison line with the edge while fixating on a fixation point that was located above the occluder and at the same depth as the comparison line. The comparison line either lay at the depth of the background or at the depth of the occluder. For the condition in which the comparison line lay at the same depth as the occluder, the relative direction of the comparison line and the occluder was the same in the left and right eye, so perceived alignment in this condition controlled for any response bias. Ono et. al. (2003) reported the difference in perceived alignment between this control condition and the condition in which the comparison line was at the depth of the background. If alignment was based on the average of the visual lines of the edge and the comparison line, then the difference in perceived alignment between these conditions would be zero. If alignment was based solely on the angle that the edge and the comparison line subtended at the eye that viewed the monocular region next to the edge (as was found by Erkelens et. al. 1996), then the difference in perceived alignment would equal 7.5 minutes of arc for experiment 2, since the disparity between the occluder and its background was 15 minutes of arc and would be 5.5 minutes of arc for experiment 3, since the disparity between the occluder and its background was 11 minutes of arc in experiment 3. The observed difference in perceived alignment was 0.81 minutes of arc for experiment 2

and 3.93 minutes of arc for experiment 3. This indicates that the perceived relative direction of the edge and the comparison line was biased towards the angle subtended at the eye that viewed the monocular region (Erkelens-bias), but is a smaller bias than that reported by Erkelens et. al. (1996).

The magnitude of the bias in the two studies may be directly compared by calculating a weighting factor for each eye which indicates its contribution to perceived alignment. A weighting factor of 50% for each eye would indicate that both eyes contributed equally to perceived alignment. When the results of Erkelens et. al. (1996) are expressed in this way, they found that the weighting factor for the eye that viewed the monocular region was 100%. When the results of Ono et. al. (2003) are expressed in this way, they found that the weighting factor for the eye that viewed the monocular region was 55.4% in experiment 2 and 85.7% in experiment 3 (see section 4.2 for the method for calculating these weighting factors).

Ono et. al. (2003) do not refer to the Erkelens et. al. (1996) study and do not discuss what factors may explain the difference in the magnitude of the Erkelens-bias between the studies. The background and occluding surfaces in the Erkelens et. al. (1996) study were densely textured random dot surfaces, whereas the background surface in experiments 2 and 3 of the Ono et. al. (2003) study was blank except for a single vertical line within each monocular region and two additional lines within the binocularly visible region of the background in experiment 3. The disparity gradient between the occluding edge and neighbouring texture on the background surface was twice the disparity gradient limit for fusion for pairs of dots (Burt & Julesz, 1980, reviewed section 1.3.4). Since the background surfaces used by Ono et. al. (2003) were

largely devoid of texture a disparity gradient between the surfaces was lacking. Hence, it is possible that the steep disparity gradient in the Erkelens et. al. (1996) study accounts for why a larger Erkelens-bias was found in that study. This possibility is discussed in greater detail in the introduction for Experiment 1 (see section 3) and in the general discussion of Experiment 4-10 (see section 4.8). Additionally, the influence of a monocular region may propagate more effectively to a distant binocular features when the binocular feature is attached to the monocular region via intervening surface texture. Hence, Erkelens et. al. (1996) may have found a larger Erkelens-bias than Ono et. al. (2003) because the binocular line in the Erkelens et. al. (1996) study was attached to the monocular region via intervening surface texture, whereas the binocular line in the Ono et. al. (2003) study was seen against empty space.

The shape, size and disparity range of the stimuli differed between the Erkelens et. al. (1996) and Ono et. al. (2003) studies. The surfaces that Erkelens et. al. (1996) used were much larger than those in the Ono et. al. (2003) study. The occluding surface used by Erkelens et. al. (1996) subtended 28° , whereas the occluder used by Ono et. al. (2003) subtended $1.5^\circ \times 5.35^\circ$. The large surfaces used by Erkelens supported disparities as large as 2° , whereas the largest disparity used by Ono et. al. (2003) was 15 minutes of arc. The occluding surface in the Erkelens et. al. (1996) study was a circle, whereas it was a rectangle square in the Ono et. al. (2003) study. Additionally, Erkelens et. al. (1996) presented the stimuli as anaglyphs, and consequently, the monocular regions appeared to be a different colour than the binocularly visible regions of the background. This is because the perceived colour of the binocularly visible regions of the stimulus is determined by the colour of that region in both eyes' views, whereas the perceived colour of the monocularly visible region only depends on the colour in one

eye (Erkelens et. al. 1996). Although there is no obvious reason to suspect any of these stimulus variables to affect the magnitude of the Erkelens-bias, it is nevertheless possible that any of these parameters is responsible for the difference in the magnitude of the Erkelens-bias between the Erkelens et. al. (1996) and Ono et. al. (2003) studies. Whether the large Erkelens-biases reported by Erkelens et. al. (1996) are contingent on these parameters was examined in Experiment 7 (see section 4.4).

A procedural difference between the studies was that Ono et. al. (2003) restricted fixation to a single point in the stimulus, whereas the observers in the Erkelens et. al. (1996) study were free to shift fixation between different points in the stimulus. Therefore, the large Erkelens-biases found by Erkelens et al. (1996) could be contingent on observers fixating the stimulus naturally and this possibility was tested in Experiment 8 (see section 4.5).

1.5.4 Competing theories of the perceived direction of features in the vicinity of the left and right edges of an occluding surface.

A pair of fused binocular features can have a perceived relative direction that is equal to the average of the angles that they subtend at the two eyes (e.g. Ono et. al. 1977, Sheedy & Fry 1979; reviewed section 1.4.3). Their perceived relative direction is thus the same as the angle that the features would subtend at a point midway between the eyes, called the cyclopean eye. This correspondence suggests that the features are perceived in their physical direction relative to the cyclopean eye (Ono & Mapp, 1995; reviewed section 1.4.3). For example, Figure 33a shows the two eyes' views of a small

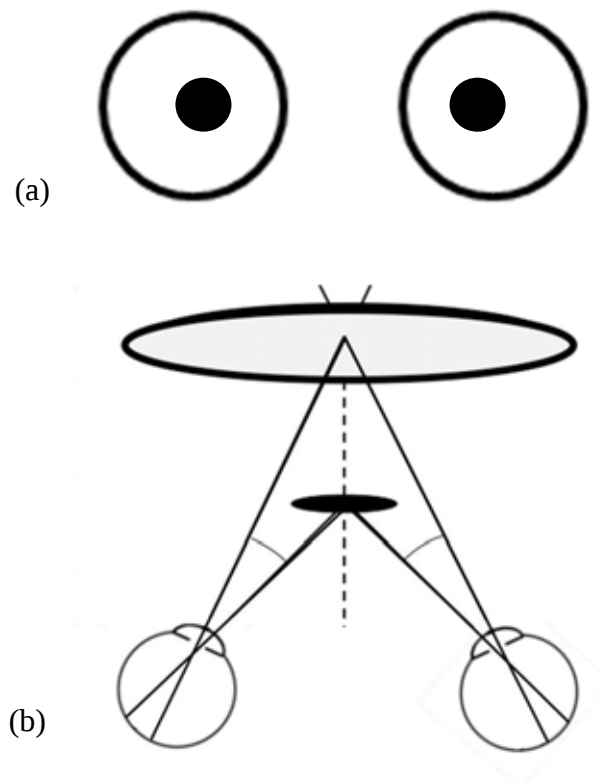


Figure 33. Stimuli used by Ono et. al. (1977).

black disc that lies in front of a large ring and Figure 33b shows a bird's eye view of this situation. The dashed line in Figure 33b shows that the physical direction of the centre of the ring relative to the cyclopean eye is the same as the physical direction of

the centre of the small black disc. If the small black disc was perceived in its physical direction relative to the cyclopean eye (the dashed line in Figure 33), then the small black disc would appear in the centre of the ring, as was found by Ono et. al. (1977) for small disparities.

Erkelens et. al. (1996) and Ono et. al. (2003) measured the perceived direction of the left and right edges of an occluding surface relative to a comparison line on the background surface. They found that the perceived relative direction of the edge and the comparison line was biased towards the angle that the edge and the line subtended at the eye that viewed the monocular region next to the edge (referred to as an Erkelens-bias reviewed in the previous section 1.5.3). On the basis that the perceived relative direction of the edge and the line was not the average of the angles subtended at both eyes, Erkelens et. al. (1996) and Ono et. al. (2003) both concluded that the left and right edges of an occluding surface are not perceived in their physical direction relative to a cyclopean eye.

Erkelens et. al. (1996) and Ono et. al. (2003) argued that the edge of the occluding surface is not perceived in its physical direction relative to a cyclopean eye because it has the same physical direction as the monocular region of the background next to the edge. Erkelens and van Ee (1994) and Anderson and Nakayama (1994) noted that part of a monocular region of the background has the same physical direction relative to a cyclopean eye as the edge of the occluding surface. The left half of a monocular region visible next to the right edge of an occluding surface (Figure 34) has the same physical direction relative to a cyclopean eye as part of the occluding surface, and likewise the

right half of a monocular region visible next to the right edge of an occluding surface has the same physical direction relative to a cyclopean as part of the occluding surface.

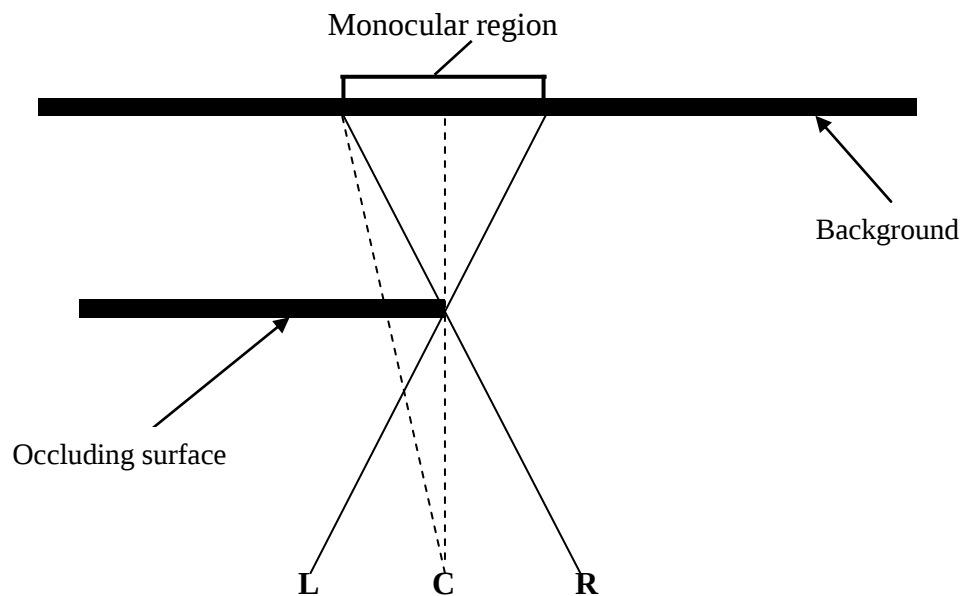


Figure 34. The portions of the background and occluding surfaces that have the same physical direction relative to a cyclopean eye.

Erkelens et. al. (1996) noted that the monocular region of the background does not have the same physical direction as the occluding surface relative to the eye that views the monocular region. For example, in Figure 34, from the perspective of the right eye, none of the features within the monocular region visible to the right eye have the same physical direction as any part of the occluding surface. Erkelens et. al. (1996) proposed that the perceived directions of the monocular region and features within the neighbourhood of the monocular region are the physical direction of those features relative to the eye that views the monocular region. In other words, the perceived direction of a feature in the vicinity of a monocular region matches its visual line to the eye that views the monocular region. Erkelens et. al. (1996) argued that this theory was supported by their measurements of the perceived direction of the edges of the

occluding surface relative to a line on the background surface. If the perceived direction of the edge and the line was their physical direction relative to the eye that views the monocular region, then that eye would be used to align the line with the edge, as Erkelens et. al. (1996) found.

Ono, Wade, and Lillakas (2002) and Ono et. al. (2003) proposed that the perceived direction of the edge of the occluding surface and the monocular region of the background is referred to the cyclopean eye. Ono et. al. (2002; 2003) proposed that the perceived direction of the background surface and the occluding surface differ due to lateral biases of parts of the scene from their physical direction relative to a cyclopean eye. The theory proposes that when the background is fixated, the background surface is perceived in its physical direction relative to a cyclopean eye, while the perceived direction of the edge of the occluding surface is biased laterally away from the monocular region. The theory proposes that when the occluding surface is fixated, the occluding surface is perceived in its physical direction relative to a cyclopean eye, while the perceived direction of the background is biased laterally away from the monocular region. As a result of these lateral biases of perceived direction, it is predicted that a background line will appear vertically aligned with the left edge of an occluding surface when the line and the edge are aligned in the left eye and vice versa for alignment with the right edge of an occluding surface. Ono et. al. (2003) argued that the Erkelens bias (see section 1.5.3 supports this theory. Ono et. al. (2003, p. 261) argued that the Erkelens-bias “clearly indicate that displacement of a binocularly fused stimulus occurs on the surface of the nonfixated plane.” However, a lateral bias of perceived direction is not indicated by the Erkelens-bias found by Ono et. al. (2003), because Erkelens et. al. (1996) argued that the same result supported the proposal that the edge of the occluding

surface is perceived in its physical direction relative to the eye that views the monocular region.

One may expect the occluding surface to appear thinner than veridical if its left and right edges are perceptually displaced as proposed by Ono et. al. (2003). On the other hand, there is no obvious reason to expect a distortion of the perceived aspect ratio of an occluding surface if the perceived direction of its edges is referred to the eye that views the monocular region next to the edge, as proposed by Erkelens et. al. (1996). Van Ee and Erkelens (2000) varied the aspect ratio of a rectangle (5.2°) that occluded the central region of a large background surface (60°) in random dot stereogram. Observers indicated whether the rectangle appeared elongated along its horizontal or vertical axis. Van Ee and Erkelens (2000) varied the disparity of the occluding rectangle in their experiment 1 between 0.5 and 1.5° and varied the stimulus duration from 0.5 to 3.5 seconds in their experiment 1b. In experiment 2, the fixation point was either located at the depth of the background surface or at the depth of the occluding surface or at an intermediate depth. In experiment 3 and 4, van Ee and Erkelens (2000) measured the perceived aspect ratio of the background surface rather than the occluding surface. Van Ee and Erkelens (2000) found that the surfaces were perceived to be about 2% thinner than veridical across all conditions. Hence, although Erkelens et. al. (1996) found perceived direction varied with the disparity of the occluder, van Ee and Erkelens (2000) found perceived aspect ratio did not. Therefore, van Ee and Erkelens (2000) concluded that the Erkelens-bias for the perceived relative direction of the edges was not responsible for the small bias of perceived aspect ratio. This conclusion would have a firmer footing if van Ee and Erkelens (2000) had also measured the perceived direction of the edges of the occluding surface and shown that an Erkelens-bias

occurred under their conditions. Van Ee and Erkelens (2000) attributed the small distortion of perceived aspect ratio in their study to the well known horizontal vertical illusion. Van Ee and Erkelens (2000, p. 920) argued that their results show that “perceived aspect ratio does not follow directly from the comparison of visual directions.” Ono et. al. (2003) proposed that perceived direction and perceived aspect ratio may not interact. Hence, there is currently no decisive evidence in favour of the Erkelens et. al. (1996) or Ono et. al. (2003) theories of the perceived direction of features in the vicinity of the left and right edges of an occluding surface. Experiments 8, 9 and 10 (see sections 4.5, 4.6, 4.7) provide such evidence.

2 Aims of the present study

Natural scenes typically consist of overlapping surfaces, yet most studies of perceived direction have used isolated features. The aim of the experiments in this thesis was to study the perceived direction of features that are part of surfaces. The perceived direction of features in the vicinity of surface edges is of particular interest. Steep disparity gradients (see section 1.3.4) can occur at such edges. The aim of the experiments in section 3 was to determine whether steep disparity gradients have the same effect on the perceived direction of features at surfaces edges as has been demonstrated for pairs of isolated dots.

The experiments in section 4 investigated the perceived direction of features in the vicinity of the left and right edges of a surface. At these edges, a region of the background surface is visible next to the edge for one eye but is hidden by the edge for the other eye (reviewed section 1.2). Erkelens and van de Grind (1994) have noted that Hering's theory of perceived direction (reviewed in sections 1.4.1, 1.4.2, 1.4.3) creates a paradox at the left and right edges of a surface (reviewed in section 1.5.1). Erkelens and van Ee (1996) and Ono et. al. (2003) found that the perceived direction of the edge relative to a line on the background was not the average of their angular separations in both eyes as predicted by Hering's theory. Instead, the perceived direction of the edge relative to the background line was more similar to their angular separation in the eye that viewed the monocular region next to the edge than to their angular separation in the other eye (reviewed 1.5.3). This result is referred to as an Erkelens-bias since Erkelens et. al. (1996) found that the position of the line and the edge in the eye that viewed the

monocular region made a larger contribution to their perceived relative direction than the position of the line and the edge in the other eye. The aim of Experiments 4 and 5 was to measure the region of the visual scene surrounding the edge of the surface wherein the Erkelens-bias occurs. As noted in section 1.5.3, the magnitude of the Erkelens-bias differed between the Erkelens et. al. (1996) and Ono et. al. (2003) studies. The aim of Experiments 6, 7 and 8 was to determine what stimulus differences between these Experiments account for this difference. Experiment 9 and 10 investigated whether the perceived direction of features in the vicinity of monocular regions is veridical and hence provided a critical test of the competing theories of perceived direction at the left and right edges of an occluding surface that were reviewed in section 1.5.4.

2.1 General Method

2.1.1 Display

Stimuli were generated using the Psychtoolbox plugin for Matlab on a PowerPC G4 computer (Brainard, 1997). The stimuli were presented on the screens of two Apple Cinema Displays with a resolution of 1600 x 1200. The screens of the two monitors were set in the frontal plane of the observer at a distance of 145 centimetres. The centre of the left screen was 72.5 centimetres to the left of the median plane of the observer and the centre of the right screen was right of the median plane by the same amount. A mirror was set 120 centimetres in front of each monitor so that their images were reflected towards the median plane of the observer. Two mirrors were set in front of the observer's eyes so that the images were superimposed when the observer was converged at a distance of 200 centimetres, which was the optical distance of the monitors from the eyes. Pixel size was 0.5 minutes of arc. Head position was stabilised with a chin rest. Apertures were set 20 cm from the eyes so that the edges of the screen were not visible and each screen was only visible to one eye. An anglyph display was used in Experiments 7, 8 and 10 and is described in the method section for Experiment 7 (see section 4.4.1).

3 Perceived direction at the horizontal edges of occluding surfaces

3.1 Experiment 1: The influence of the disparity gradient on the perceived direction of features at surface edges.

A disparity gradient is defined as the relative disparity between a pair of features divided by their average angular separation in the two eyes. The disparity gradient constraint on fusion refers to the finding that the fusion limit for a pair of dots or lines is reduced when the disparity gradient between the pair exceeds a critical value (reviewed 1.3.4). The disparity gradient that results in diplopia has been found to vary from 3 for a pair of dots of opposite contrast polarity (Prazdny, 1985) to 0.5 for pairs of dots presented in the periphery (Scharff, 1997).

The impact of the disparity gradient on the perceived direction of features attached to surfaces was studied in the present experiment because natural scenes typically consist of surfaces rather than a pair of features presented alone. For transparent surfaces, it is possible for steep disparity gradients to occur between neighbouring features on the different surfaces. McKee and Verghese (2002) created transparent surfaces in which each dot had the same disparity gradient with its nearest neighbour on the other surface. They were primarily interested in the perceived depth of the dots, which they found was only marginally underestimated as a result of steep disparity gradients. However, they also observed that the dots comprising one of the surfaces appeared double.

Steep disparity gradients also occur at the edges of opaque textured surfaces when features on the occluding surface are directionally adjacent to features on the background surface across the edge. The steepest disparity gradient possible at the edge between two opaque surfaces differs for vertical and horizontal edges. The steepest disparity gradient will occur between the edge of the occluding surface and the point on the background surface that has the smallest angular separation from the occluding edge. At horizontal edges, binocularly visible features on the background surface can abut the edge of the occluding surface so the maximum possible disparity gradient at such edges is theoretically unlimited. Hence, the disparity gradient at a horizontal edge can exceed the value of 1 that Burt and Julesz (1980) found forced pairs of isolated dots to appear diplopic.

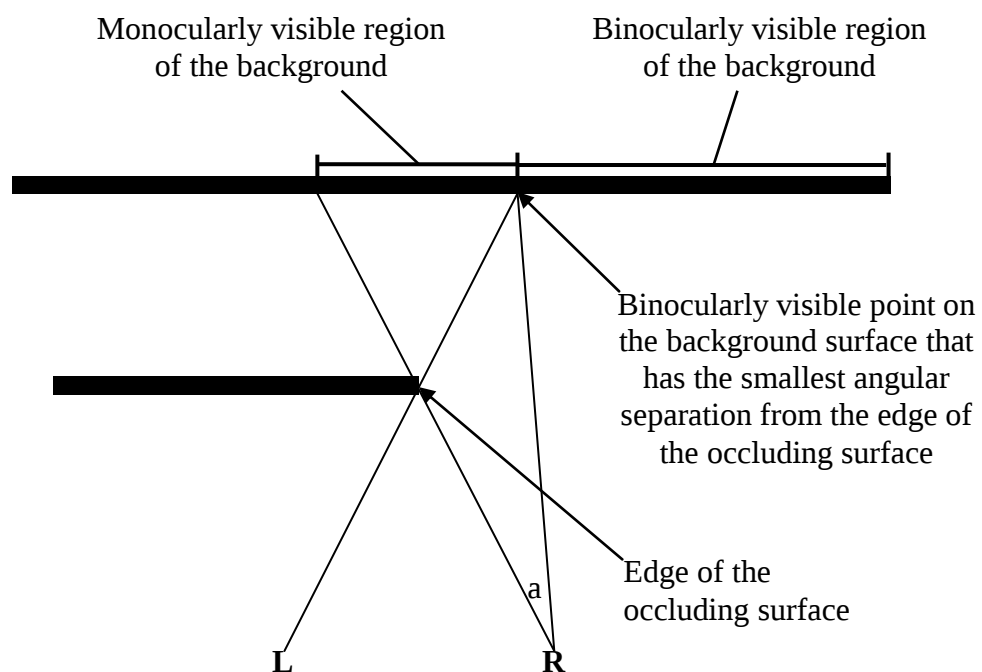


Figure 35. Disparity gradient at the vertical edge of an occluding surface.

Figure 35 shows a bird's eye view of the vertical edge of a surface and the background that it partially occludes. A monocular region of the background (reviewed 1.2) occurs at vertically oriented edges. The monocular region enforces a minimum separation between the binocularly visible features on the background surface and the edge of the occluding surface. Figure 35 shows the point on the background surface that has the smallest angular separation from the vertical edge of the occluder. This point abuts the vertical edge of the occluding surface in the eye that does not view the monocular region, but has an angular separation equal to the angular width of the monocular region in the other eye. Consequently, the average angular separation of this point from the vertical edge of the occluding surface is equal to half the angular width of the monocular region. Since the angular width of the monocular region is equal to the relative disparity of the occluding and background surfaces, the steepest disparity gradient that may occur at a vertical edge between two textured surfaces is equal to 2. Hence, the disparity gradient at a vertical edge can exceed the value of 1 that Burt and Julesz (1980) found forced pairs of isolated dots to appear double. This raises the question of whether fusion is possible at occluding edges in the presence of steep disparity gradients?

Unlike isolated pairs of dots or the transparent surfaces used by McKee and Verghese (2002), the features which define steep disparity gradients at the edges of opaque surfaces are adjacent to other features on the same surface which have the same disparity, which we will call *support features*. Marr and Poggio (1976) proposed that a cooperative interaction between neurons tuned to the same disparity helps to establish correspondence between the two eyes views when features with the same disparity are

next to each other. Therefore, the presence of support features may allow the features at the horizontal edges of surfaces to be fused in the presence of steep disparity gradients.

The perceived relative direction of fused binocular features is an average of the angular separation of the features in each eye, which we refer to as the average prediction (reviewed 1.4.3, e.g. Ono et. al. 1977; Sheedy & Fry, 1979). The monocular prediction refers to the perceived relative direction of a pair of features matching their angular separation in one eye. When one of the features is not fused, the perceived direction of each of its diplopic images relative to the perceived direction of the fused feature is biased towards the monocular prediction away from the average prediction (see section 1.4.2; Rose & Blake, 1988). Therefore, one may evaluate the effect of the disparity gradient on fusion at surfaces edges by either (1) measuring whether the features appear in a single or diplopic direction or (2) by measuring their perceived direction. Duwaer (1983) and McKee and Verghese (2002) have argued that judgments of diplopia are more difficult for features that are part of a surface than for features presented alone. Furthermore, Ono et. al. (1977) observed that it is possible for features with disparities close to the fusion limit to appear in a single direction yet have a perceived relative direction that is more similar to the monocular prediction than the average prediction. It is arguable whether such features should be considered fused because it is possible that single vision in this case is due to the suppression of one of the diplopic images (Verhoeff, 1935; Asher, 1953; Hochberg, 1964). Therefore, determining whether the perceived directions of features is consistent with the average prediction or the monocular prediction is a more reliable method of studying the effect of the disparity gradient on the fusion of features attached to surfaces.

Erkelens et. al. (1996) and Ono et. al. (2003) measured the perceived direction of the vertical edge of an opaque surface relative to a line on the background surface (reviewed 1.5.3). They found that the perceived relative direction of the line and the edge was biased towards their angular separation in the eye that views the monocular region next to the edge, or Erkelens-bias (see section 1.5.3). Erkelens et. al. (1996) and Ono et. al. (2003) attributed the Erkelens-bias to monocular regions that occur next to the vertical edges of an occluder. Erkelens et. al. (1996) argued that the disparity gradient between the background line and the edge of the occluder could not have contributed to the Erkelens-bias because the separation between the line and the edge was sufficiently large that the disparity gradient constraint on fusion was not exceeded. However, the disparity gradient constraint on fusion for surfaces is unknown. Secondly, Erkelens et. al. (1996) did not report the separation between the line and the edge. Thirdly, regardless of the separation between the line and the edge, the disparity gradient between the occluding edge and neighbouring texture on the background surface was twice the disparity gradient limit for fusion for pairs of dots (Burt & Julesz, 1980). The background surface used in experiment 2 of Ono et. al. (2003) was devoid of texture except for a line within the monocular region, so a disparity gradient between the surfaces was lacking. For that experiment, Ono et. al. (2003) found that the eye that viewed the monocular region contributed 55.4% to the perceived direction of the edge. Using a stimulus containing steep disparity gradients, Erkelens et. al. (1996) found that the eye that viewed the monocular region contributed 100% to the perceived direction of the edge. Ono et. al. (2003) found that the eye that viewed the monocular region contributed 85.75% to the perceived direction of the edge in their experiment 3, in which a disparity gradient was defined between the occluding edge and two binocularly visible lines at the depth of the background surface. The size of the disparity gradient in

that experiment is unknown because Ono et. al. (2003) did not specify the horizontal separation of the binocular background lines from the edge of the occluding surface.

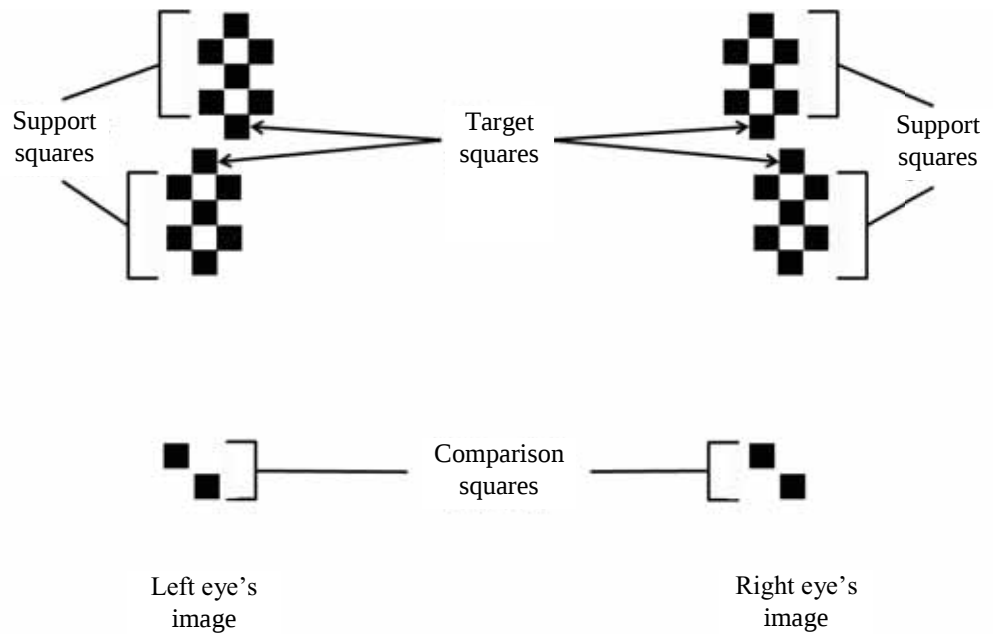


Figure 36. Schematic of the stimuli used in Experiment 1.

The influence of the disparity gradient on perceived direction at surface edges was investigated using the stimulus shown in (Figure 36). Two small surfaces were presented at different depths and had a small vertical separation so that the disparity gradient across the boundary of the surfaces was steep. The border between the surfaces was oriented horizontally so that the additional complexity of the influence of monocular regions on perceived direction was avoided. The closest square on each surface to this boundary were the target squares. The target squares were located so that they would appear vertically aligned when the perceived direction of both squares was an average of their visual lines (average prediction), but would appear horizontally offset from one another if either square appeared in its diplopic directions (monocular prediction). In the second condition, the pair of target squares was presented as in the

first condition but the other squares that comprised the surface (support squares, Figure 36) were eliminated. Comparing the perceived direction of the target squares with and without the support squares would reveal their influence on the disparity gradient constraint on fusion. In the third condition, the target squares were also presented alone but the separation of the target squares was increased so that the disparity gradient was shallow in this condition. This condition would indicate whether a loss of fusion was due to the magnitude of disparity rather than the disparity gradient.

3.1.1 Method

Stimuli

A schematic of the stimuli is shown in Figure 36. Two black squares, which were binocularly visible and subtended 4 minutes of arc, served as the target squares. The luminance of the squares was $<1 \text{ cd/m}^2$ and they were presented against a white background with a luminance of 105 cd/m^2 . The upper target was presented with crossed disparities of 5, 10, 15 or 29 minutes of arc relative to the lower square. The lower of the two target squares was displayed in the centre of the images. In one condition, the upper target square was vertically separated from the lower target square by 21 minutes of arc, measured from the centre of the squares. In the other two conditions, the target squares were vertically separated by 5 minutes of arc. In one of these conditions, six additional squares were arranged in a checkerboard pattern above the upper target square and six were similarly arranged below the lower target square (Figure 36). The disparity of these support squares was the same as the target squares to which they were attached.

Procedure

Each combination of the three stimulus configurations and the four disparities was presented 10 times in a random order to each observer. The perceived relative direction of the target squares was measured by means of a pair of comparison squares. The comparison squares were identical to the target squares except that both comparison squares were assigned the same disparity as the lower target square and were presented 1° beneath the target squares. The upper comparison square could be moved horizontally using the arrow keys.

Prior to the experiment, the experimenter indicated to the observer which squares were the target squares in each of the three stimulus configurations. Observers were instructed to shift the upper comparison square using the arrow keys so that the comparison squares appeared horizontally offset from one another to the same extent as the target squares. The observers were then informed that one of the target squares may sometimes appear in two horizontally separated directions simultaneously, in which case they should match to the perceived direction of the left-most direction of the target square.

Observers

Nine undergraduates studying psychology at the University of New South Wales participated. All were naïve to the purpose of the experiment. Their time was compensated with a small amount of course credit.

3.1.2 Results

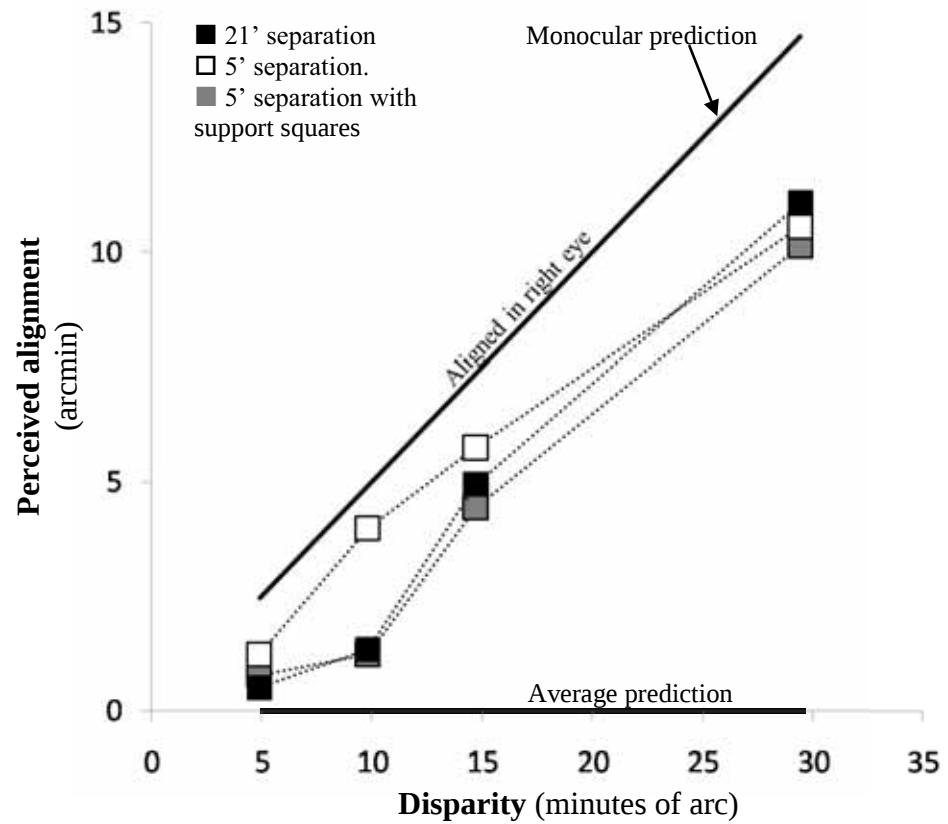


Figure 37. Results of Experiment 1. Group data. N=9.

Group data are shown in Figure 37, which plots the mean offset of the comparison squares against the relative disparity of the target squares. If the perceived relative direction of the target squares matched their angular separation in one eye (monocular prediction), then the alignment settings would fall along the diagonal line. Settings near 0 indicate that the target squares appeared vertically aligned and therefore that the perceived relative direction of the targets was an average of their angular separation in both eyes (average prediction). For the two largest disparities, the alignment settings were closer to the monocular prediction than the average prediction for all configurations. For the 10 minute of arc disparity, when the target squares lacked support squares, alignment for the target squares that were separated by 21 minutes of

arc (■ in Figure 37) was closer to the average prediction than the monocular prediction, but was closer to the monocular prediction than the average prediction when the targets were separated by 5 minutes of arc (□ in Figure 37). This indicates that the disparity gradient limited fusion when the target squares had a relative disparity of 10 minutes of arc and a vertical separation of 5 minutes of arc. For the same combination of relative disparity and vertical separation, the perceived alignment of the target squares was closer to the average prediction when the support squares were present (■ in Figure 37). Differences between the different configurations were small for the 5 minute of arc disparity where the disparity gradient between the target squares was shallowest.

The results were analysed using a multivariate analysis of variance with planned orthogonal contrasts. The Decision-Wise error rate ($\alpha=0.05$) was controlled for each of the contrasts and 95% confidence intervals were calculated using the procedure described by Bird (2004). The conditions with support squares did not differ from the conditions where the target squares were separated by 21 minutes of arc for any of the disparities. However, these conditions differed from the condition in which the target squares were separated by 5 minutes of arc and lacked support squares for the 10 minute of arc disparity ($F_{(1,8)}= 77.7$) and for the 15 minute of arc disparity ($F_{(1,8)}= 9.949$). For the 10 minute of arc disparity, the perceived direction of the target squares that were separated by 5 minutes of arc and lacked support squares, was 2.7 minutes of arc closer to the monocular prediction than the other two configurations. 95% confidence intervals indicate that this difference was 1.99 to 3.4 minutes of arc. For the 15 minute of arc disparity, the perceived direction of the target squares that were separated by 5 minutes of arc and lacked support squares was 1.06 minutes of arc closer to the monocular

prediction than the other two configurations. 95% confidence intervals indicate that this difference was 0.286 to 3.403 minutes of arc.

3.1.3 Discussion

The largest differences between the three stimulus configurations were observed for the 10 minute of arc disparity. The perceived relative direction of the target squares was closer to the average of their angular separations in the two eyes (average prediction) when they were separated by 21 minutes of arc, in which case the disparity gradient was shallow (0.5). Hence, both target squares were fused in this condition. When the target squares were separated by only 5 minutes of arc and the support squares were lacking, the perceived relative direction of the target squares was similar to their angular separation in one eye. This indicates that one of the target squares was not fused, which was expected because the disparity gradient was 2 in this condition, which greatly exceeds the limit of 1 reported by Burt and Julesz (1980). However, despite this steep disparity gradient, the perceived relative direction of the target squares indicates both were fused when they were attached to additional features with common disparity (support squares).

With the additional features, the stimulus was similar to occluding edges that occur in natural scenes, because features that define steep disparity gradients at the edges of surfaces are near features on the same surface with the same disparity. Therefore, the results indicate that the perceived direction of features at occluding edges can be an average of their visual lines in the two eyes despite steep disparity gradients across the edge.

The results also bear on the Erkelens et. al. (1996) and Ono et. al. (2003) studies of perceived direction at the left and right edges of occluding surfaces. These studies

found that the eye that views the monocular region next to the edge has a larger influence on the perceived relative direction of such edges than the other eye (Erkelens-bias see section 1.5.3). It was argued in the introduction that it was possible that the disparity gradient constraint on fusion contributed to the Erkelens-bias because disparity gradients of 2 occurred in the Erkelens et. al. (1996) study, in which the largest Erkelens-bias was found. The results of the present study indicate that fusion is possible at surface edges in the presence of a disparity gradient of 2, which suggests that the disparity gradient constraint on fusion did not contribute to the large Erkelens-bias reported by Erkelens et. al. (1996).

It has been suggested that it is possible that the comparison square settings for the condition where the target squares were attached to the support squares does not reflect the true direction of the target squares. According to this alternative explanation of our results, due to crowding by the support squares, observers did not have a clear experience of the diplopic directions of the target squares and may have matched to the average of the diplopic directions. I believe the similarity between the results for the condition where the target squares had a large separation and the results for the condition where the target squares had a small separation and support squares were present discounts this alternative explanation. Observers were instructed to match to the leftmost diplopic direction in the event that one of the target squares appeared diplopic. Observers clearly understood this instruction because the comparison square settings were consistent with diplopia when the target squares were close together and support squares were lacking. If observers' experience of the diplopic directions was unclear due to crowding when support squares were present, then one would still expect a leftwards bias in the data. However, the comparison square settings for this condition

with support squares was virtually identical to the condition where the support squares were lacking and the target squares had a large vertical separation. Observers reported having a clear sense of the direction of the target squares in the condition with support squares, which is also inconsistent with the crowding explanation.

3.2 Experiment 2: The nature of the benefit of support features.

The disparity gradient constraint on fusion (section 1.3.4) refers to the finding that the fusion limit of a pair of features with different values of disparity is reduced when the angular separation of the features is small. Experiment 1 found that the disparity gradient constraint on fusion was mitigated when a pair of features that defined a steep disparity gradient were each attached to additional features with the same disparity called support features. It is possible that the effect of the support features has the same underlying basis as the disparity gradient constraint on fusion. This was tested in the present experiment by varying the contrast polarity of the support features. Using a pair of squares, Prazdny (1985) found that steeper disparity gradients were required to induce diplopia when the squares were opposite contrast polarity than when they were the same contrast polarity. Would the ability of the support features to mitigate the disparity gradient constraint on fusion show a similar dependency on the support features having the same contrast polarity as the features that define the steep disparity gradient?

The results of Westheimer and Levi (1987) suggest that the effect of the support squares might not depend on their having the same contrast polarity as the features that define the steep disparity gradient. They found that the perceived depth of a line was biased away from the depth of small dots presented approximately 10 minutes of arc from the line. The magnitude of this effect of the dots was found to be the same when the line was white and the dots were black as when the dots were the same colour as the line.

In the present experiment, a disparity of 10 minutes of arc between features separated by 5 minutes of arc was used since Experiment 1 showed that the effect of the support squares was greatest for that disparity. For a disparity of 10 minutes of arc between a pair of dots, Burt and Julesz (1980) observed that separations smaller than 10 minutes of arc between the features reduced the fusion limit. Would the effect of the support squares diminish over a similar range of separations between the support squares and the target squares? If so, then this would also suggest that the effect of the support features has a similar underlying basis to the disparity gradient constraint on fusion. This was evaluated in the present experiment by varying the gap between the support features and the features that define a steep disparity gradient.

3.2.1 Method

Stimuli

The target squares were black and their luminance measured $<1 \text{ cd/m}^2$ as in Experiment 1. Their relative disparity was 10 minutes of arc and they were vertically separated by 5 minutes of arc, as measured from the centre of the squares. The support squares were either black ($<1 \text{ cd/m}^2$, Figure 38a) or white (140 cd/m^2 , Figure 38b). Since the luminance of the background was 70 cd/m^2 , the contrast of the support squares was the same in both conditions. To introduce a gap between the support squares and the target squares, the 6 support squares above the upper target square were shifted up and the 6 support squares below the lower target were shifted down by the same amount. Figure 38c shows the left and right eye's views for the condition where a gap of 4 minutes of arc separates the support squares from the target squares. In a pilot experiment using black target and support squares, gaps of 1, 2, 4, 8, 16 and 24 minutes of arc were tested using a single observer. The results showed that the effect of the

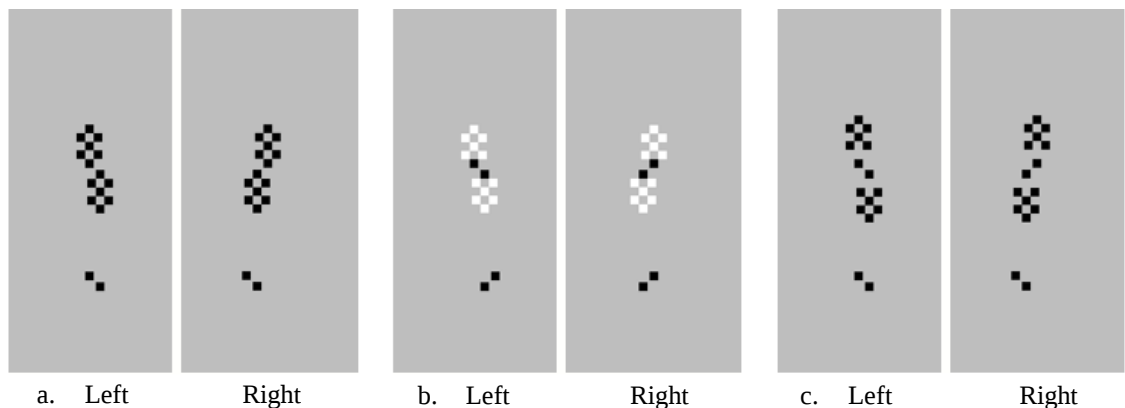


Figure 38. Stereograms of some of stimuli used in Experiment 2. In (a) the support squares are black and about the target squares. In (b) the support squares are white and about the target squares. In (c) the support squares are black and a 4 minute of arc gap separates the support squares from the target squares. The comparison squares are the two squares at the bottom of each image.

support squares was eliminated by a gap of 4 minutes of arc so five small gaps ranging from 0 to 4 minutes of arc were chosen for the main experiment. Only three gap values were chosen for the condition where the support squares were white to reduce the length of the experiment. The target squares were also presented without the support squares in one condition. There was only one no support square condition because target square - support square separation cannot be varied for this condition since support squares are lacking. The stimuli were otherwise identical to that described in Experiment 1.

Procedure

The procedure was the same as for Experiment 1.

Observers

11 undergraduates studying psychology at the University of New South Wales participated. Observers had little or no experience participating in studies of binocular vision. All were naïve to the purpose of the experiment and did not participate in Experiment 1. Their time was compensated with a small amount of course credit.

3.2.2 Results

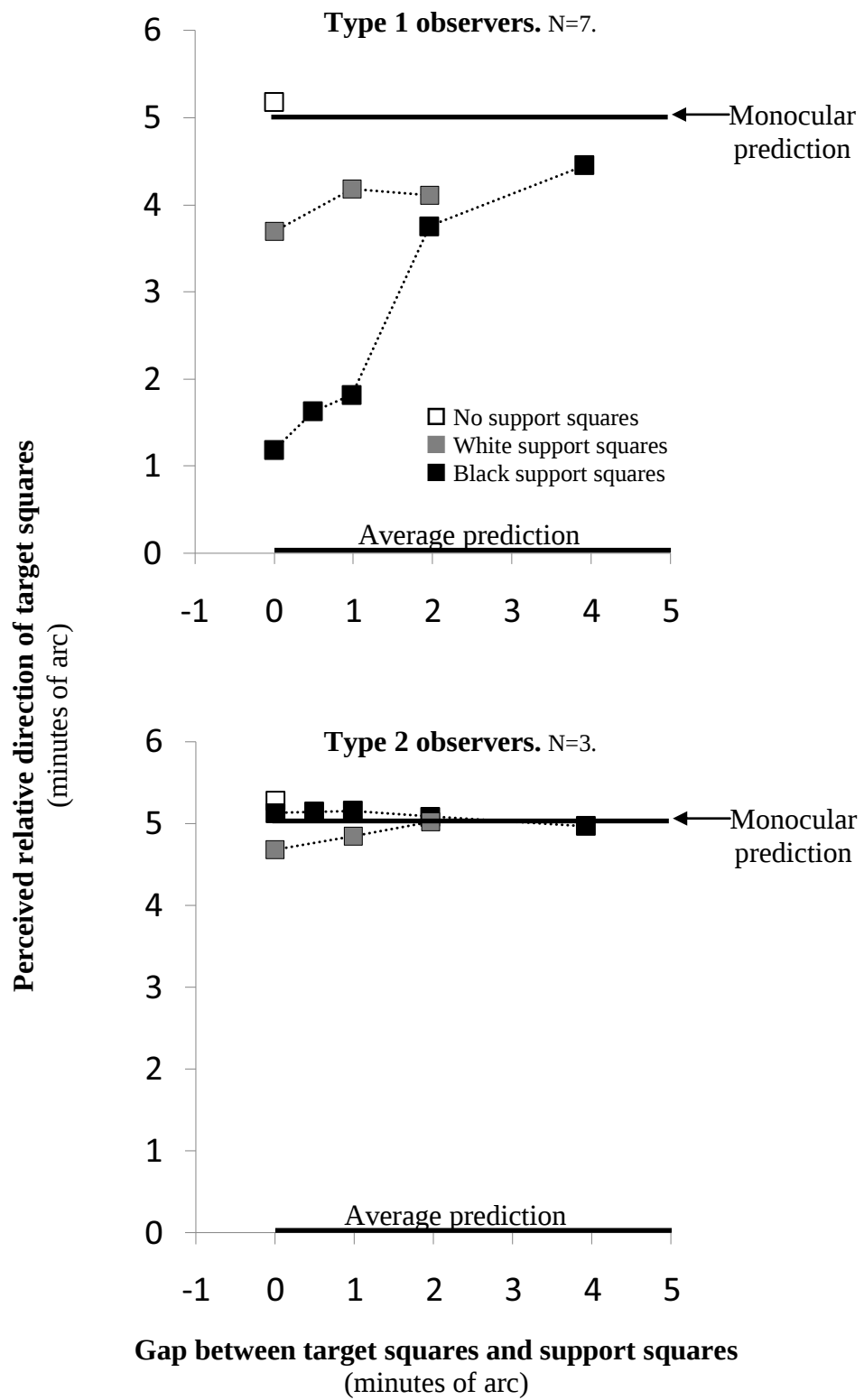


Figure 39. Results of Experiment 2.

The perceived relative direction of the target squares was not the same for all observers. The results for 7 of the 11 observers were very similar and we refer to this subset of observers as type 1. The perceived relative direction of the target squares was equal to their angular separation in one eye (the monocular prediction) for all conditions for 3 observers and we refer to this subset of observers as type 2. One observer displayed the opposite trend to the type 1 observers and is described last. The mean perceived relative direction of the target squares for the type 1 and type 2 observers is plotted separately in Figure 39 against the vertical gap between the target squares and the support squares. If the perceived relative direction of the target squares was consistent with their relative direction in one eye's view, then the alignment settings would be 5 minutes of arc, as was the case for all conditions for the type 2 observers. For the type 1 observers, the perceived relative direction of the target squares was consistent with the monocular prediction when the support squares were absent ($\square$ in Figure 39). A value of 0 for the alignment settings would indicate that the perceived relative direction of the target squares was an average of their angular separation in both eyes (average prediction). Perceived direction was closest to the average prediction when the support squares were attached to the target squares and were the same colour as the target squares for the type 1 observers ($\blacksquare$ in Figure 39). When the support squares were white and hence were opposite contrast polarity to the target squares ($\blacksquare$ in Figure 39), the perceived relative direction of the target squares was closer to the monocular prediction than the average prediction. This was the case even when the white support squares were attached to the target squares. As the gap between the support squares and the target squares increased, the perceived relative direction of the target squares shifted towards the monocular prediction. A gap of 2 minutes of arc much

reduced the effect of the support squares and the difference between the white and black support squares.

The results for the type 1 observers were analysed using a multivariate analysis of variance with planned orthogonal contrasts. The Decision-Wise error rate ($\alpha=0.05$) was controlled for each of the contrasts and 95% confidence intervals were calculated using the procedure described by Bird (2004). The perceived relative direction of the target squares was closer to the average prediction when the support squares were attached to the target squares than when the support squares were absent ($F_{(1,6)}=77.63$). With the support squares attached to the target squares, the perceived relative direction of the target was 2.5 minutes of arc closer to the average prediction when the support squares were the same rather than opposite contrast polarity to the target squares ($F_{(1,6)}=11.68$). 95% confidence intervals indicate that this difference was 0.71 to 4.3 minutes of arc. For the 1 minute of arc gap, the perceived relative direction of the target squares was 2.35 minutes of arc closer to the average prediction when the support squares were the same rather than opposite contrast polarity to the target squares ($F_{(1,6)}=78.59$). 95% confidence intervals indicate that this difference was 1.71 to 3 minutes of arc. The perceived relative direction of the target squares did not differ between the black and white support squares for the 2 minute of arc gap.

The effect of contrast polarity was reversed for 1 observer. The perceived relative direction of the target squares was consistent with the monocular prediction when the support squares had the same contrast polarity as the target squares, yet was closer to the average prediction when the support squares had opposite contrast polarity. The effect of the opposite polarity support squares diminished with separation.

3.2.3 Discussion

In Experiment 1, it was found that support features mitigate the disparity gradient constraint on fusion. This effect of the support features was replicated for 7 observers in the present experiment (type 1 observers), but was not observed for 3 observers (type 2 observers). The results of Experiment 2 show that the effect of the support squares (for the type 1 observers) was contingent on the separation of the support features from the features that define a steep disparity gradient. For a 10 minute of arc disparity, the effect of the support features was much reduced when a vertical gap of 2 minutes of arc separated the support features from the features that define a steep disparity gradient. Likewise, the extent that the disparity gradient constraint on fusion reduces the fusion limit shows a strong dependency on the separation of the features (Burt & Julesz, 1980). Hence, the results of Experiment 2 suggest that the effect of the support squares may have the same underlying basis as the disparity gradient constraint on fusion.

This conclusion is supported by the results of varying the contrast polarity of the support squares. The support features mitigated the disparity gradient constraint to a smaller extent when they had opposite contrast polarity to the features that define the steep disparity gradient. Likewise, Prazdny (1985) found that the disparity gradient constraint on fusion was reduced when the features that defined the disparity gradient had opposite contrast polarity. A possible explanation of the disparity gradient constraint provided by Tyler (1975), Wilson et. al. (1988), Scharff (1997) and McKee and Verghese (2002) is reviewed in the general discussion of Experiments 1, 2 and 3

(see section 3.4). A possible explanation for the effect of the support squares is also provided in the general discussion for these experiments.

3.3 Experiment 3: The effect of the support features when their luminance differs from the target features.

The perceived relative direction of a pair of features is not the average of their angular separation in the two eyes when the disparity gradient between the features is steep (see section 1.3.4). Experiment 1 and 2 showed that the perceived relative direction of a pair of squares (target squares) can be intermediate between their angular separations in the two eyes in the presence of a steep disparity gradient when other features with the same disparity (support squares) are proximal.

In Experiment 2, it was found that this effect of the support squares was much reduced when the support squares were opposite contrast polarity to the target squares. In the condition where the support squares were opposite contrast polarity to the target squares, the support squares were necessarily a different luminance than the target squares. It is possible that this difference in luminance between the support squares and the target squares is responsible for the reduced effect of the support squares with opposite contrast polarity to the target squares. This luminance difference explanation predicts that the effect of the support squares will be reduced when they have a different luminance to the target squares even when they have the same contrast polarity as the target squares. This prediction was tested in the following experiment.

In order for the target squares and support squares to have different luminance while having the same contrast polarity, it is necessary for the target squares and the support squares to have different values of luminance contrast. The target squares may have either lower or higher contrast than the support squares. The perceived direction of the target squares was measured for both of these conditions. In an additional set of

conditions, the target squares were presented with low or high contrast without the support squares. It was expected that the perceived relative direction of the target squares in the absence of the support squares would be closer to their angular separation in one eye (the monocular prediction) than the average of their angular separations in both eyes (the average prediction). Hence, the perceived relative direction of the target squares without support squares was measured to provide a reference against which the effect of the support squares could be judged.

The perceived relative direction of the target squares was also measured in the presence of support squares with opposite contrast polarity. In this condition, the target squares and the support squares were presented with low contrast in order to minimise the luminance difference between the target squares and the support squares. In Experiment 2, the opposite contrast polarity support squares were always white. It is also possible for the support squares to be black while having opposite contrast polarity to white target squares. Therefore, in the opposite contrast polarity condition of Experiment 3, the support squares were either darker or lighter than the background while the target squares had the opposite contrast polarity.

In Experiment 2, although the perceived direction of the target squares was consistent with the average prediction when the support squares were present for 7 observers, the support squares had no effect for 3 observers (the Type 2 observers). It is possible that the support squares would have had an effect on the perceived direction of the target squares for the Type 2 observers if the disparity gradient between the target squares was reduced. Therefore, smaller disparities were used in Experiment 3 than in Experiment 2.

3.3.1 Method

Stimuli

The stimulus was identical to that used in Experiment 1 and 2 with the following exceptions. The relative disparity between the target squares was either 3, 5 or 7 minutes of arc. The support squares, when present, were always attached to the target squares as in Experiment 1. There were two conditions in which the support squares had higher contrast than the target squares. In one of these conditions, the luminance of the target squares was 22.8 cd/m² and the luminance of the support squares was 0.24 cd/m², in which case they were both darker than the background (45.9 cd/m²). In the second condition where the contrast of the support squares was greater than contrast of the target squares, the luminance of the target squares was 68.9 cd/m² and the luminance of the support squares was 92 cd/m², in which case they were both lighter than the background. These luminance values correspond to Weber contrasts of 0.5 and 1 for the target squares and the support squares respectively. The luminance of the target squares and the luminance of the support squares were switched for the two conditions in which the target squares had higher contrast than the support squares. The target squares were presented alone in four conditions with the same luminance that was used in the conditions with the support squares (0.24 cd/m², 22.8 cd/m², 68.9 cd/m² or 92 cd/m²). For the two conditions in which the support squares had opposite contrast polarity to the target squares, the target squares were dark grey (22.8 cd/m²) and the support squares were light grey (68.9 cd/m²) or the support squares were light grey and the target squares were dark grey.

Procedure

The procedure was the same as for Experiment 1 and 2.

Observers

21 undergraduates studying psychology at the University of New South Wales participated. All were naïve to the purpose of the experiment and did not participate in Experiment 1 or Experiment 2. Their time was compensated with a small amount of course credit.

3.3.2 Results

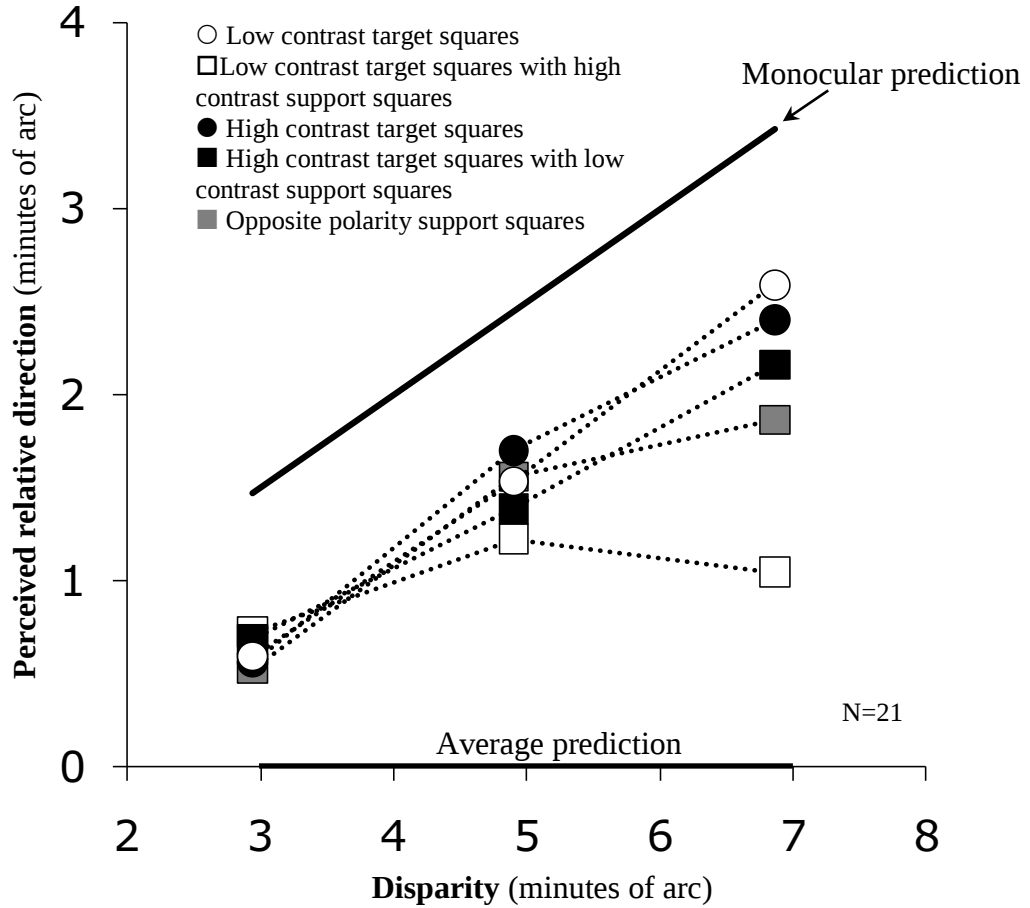


Figure 40. Results of Experiment 3.

Group data are shown in Figure 40, which plots the perceived relative direction of the target squares against their relative disparity. The perceived relative direction of the target squares was similar for all conditions for the 3 and 5 minute of arc disparities, in which case the disparity gradient between the target squares was 0.6 and 1 respectively. The bias of approximately 1-1.5 minutes of arc for the perceived relative direction of the 5 minute of arc disparity was also found in Experiment 1 in the absence of a steep disparity gradient between the target squares (■ in Figure 37). The perceived relative direction of the target squares differed between conditions for the 7 minute of

arc disparity. For this disparity, the perceived relative direction of the target squares that lacked support squares was closer to the monocular prediction than the average prediction. This was true for both the target squares with low contrast ($\circ$ in Figure 40) and the target squares with high contrast ($\bullet$ in Figure 40). The presence of low contrast support squares did not affect the perceived relative direction of the high contrast target squares ($\blacksquare$ in Figure 40). However, the presence of high contrast support squares shifted the perceived relative direction of the low contrast target squares closer to the average prediction ($\square$ in Figure 39). The support squares that had opposite contrast polarity to the target squares ($\blacksquare$ in Figure 40) resulted in a small shift of the perceived relative direction of the target squares towards the average prediction, consistent with the results of Experiment 2. In Experiment 2, there was no effect of support squares for three observers (Type 2 observers). In the present experiment, the means for 18 of the 21 observers are in the direction consistent with an effect of the support squares. Possible reasons for these individual differences are discussed in the general discussion (see section 3.4.2).

Three a priori tests were conducted for each disparity using Bonferroni adjusted alpha levels of 0.167 per test ($0.05/3$). For the 7 minute of arc disparity, the perceived relative direction of the low contrast target squares was significantly closer to the average prediction when support squares with opposite contrast polarity were present ($F_{(1,20)}=13.870$). The perceived relative direction of the low contrast target squares was significantly closer to the average prediction when high contrast support squares were present ($F_{(1,20)}=28.629$). The comparison between the high contrast target squares with or without low contrast support squares was not significant ($F_{(1,20)}=0.922$). These three contrasts were not significant for the 5 or 3 minute of arc disparities.

3.3.3 Discussion

The disparity gradient between the target squares was equal to 1.4 when the relative disparity of the target squares was 7 minutes of arc. For this disparity, the perceived direction of the target squares was closer to their relative direction in one eye than the average of their relative directions in both eyes in the absence of the support squares. The perceived direction of the target squares was shifted towards the average of their relative direction in both eyes when the support squares were present. This shift was small when the support squares had opposite contrast polarity to the target squares, which is consistent with the results of Experiment 2.

When the support squares have opposite contrast polarity to the target squares, their luminance necessarily differs from the target squares. The luminance of the support squares also differed from the luminance of the target squares for the condition where the target squares were low contrast and the support squares were high contrast and for the condition where the target squares were high contrast and the support squares were low contrast. Due to this luminance difference, it was hypothesised that the support squares may have little effect on the perceived direction of the target squares. The results showed that the low contrast support squares had little effect on the perceived direction of the high contrast target squares. However, the high contrast support squares had a large effect on the perceived direction of the low contrast target squares. The difference between these two conditions suggests that the effect of the support squares decreases when they have lower contrast than the target squares and increases when they have higher contrast than the target squares.

With high contrast support squares, the perceived relative direction of the low contrast target squares differed from the average of their relative direction in the two eyes by approximately 1 minute of arc. The target squares appeared offset to the same extent in Experiment 1 when the disparity gradient between the target squares was not steep due to a large separation between the target squares. Therefore, the results indicate that the high contrast support squares overcame the disparity gradient constraint on fusion for the low contrast target squares. This indicates that the support squares can have a strong effect on the perceived direction of the target squares when their luminance differs from the target squares. Therefore, the results suggest that the difference in luminance between the support squares and the target squares when the support squares have opposite contrast polarity is not responsible for the diminished effect of the support squares in that condition.

3.4 General Discussion

The disparity gradient constraint on fusion refers to the finding that one member of a pair of features will tend to appear double if the relative disparity of the features exceeds their angular separation (Burt and Julesz, 1980). This constraint was also observed in Experiment 1 and 2, except that the perceived direction of the features was measured rather than whether one of the features appeared double. When the disparity gradient between the pair of target squares was 2, the perceived relative direction of the target squares was closer to their angular separation in one eye than the average of their angular separations in both eyes. Despite this steep disparity gradient, the perceived relative direction of the target squares was an average of their angular separation in both eyes when each target square was near other squares with the same disparity, called support squares.

When the support squares were present, the spatial arrangement of the features was similar to that which occurs in natural scenes at the edges of occluding surfaces. At occluding edges, steep disparity gradients are defined between directionally adjacent regions of the background and the occluding surface. However, features at such edges are also proximal to features further from the edge which have similar disparity because they are part of the same surface. Therefore, the results also indicate that features at the edges of surfaces can appear in a direction that is the average of their visual lines in both eyes despite steep disparity gradients - provided that other features on the surface are proximal.

Experiment 2 demonstrated that the effect of the support features is strongly contingent on their separation from the features that define a steep disparity gradient. The results of Experiment 2 and Experiment 3 showed that the effect of the support squares was reduced when they had lower contrast or opposite contrast polarity to the features that define a steep disparity gradient. It was argued in the discussion of Experiment 2 that these results suggest that the effect of the support squares may have the same underlying basis as the disparity gradient constraint on fusion, which shows the same dependency on the separation of the features and their contrast polarity. The explanation of the disparity gradient constraint proposed by Tyler (1975), Wilson et. al. (1988), Scharff (1997) and McKee and Verghese (2002) is discussed before speculating as to the nature of the effect of the support squares.

3.4.1 The receptive field size explanation of the disparity gradient constraint on fusion

Tyler (1975), Wilson et. al. (1988), Scharff (1997) and McKee and Verghese (2002) argued that the disparity gradient constraint is explained by the following two proposals. Firstly, disparity selective neurons are unable to encode their preferred disparity when features with different values of disparity fall within their receptive field. Secondly, the receptive field size of such neurons is proportional to their disparity tuning, a hypothesis known as the size-disparity correlation. According to the first proposal, small separations between features with different values of disparity result in diplopia because then both features fall within the receptive field of a neuron required to process the largest disparity of the two features. According to the second proposal, the critical separation that results in diplopia increases with the relative disparity of the

features because neurons with larger receptive fields are required to process larger disparities.

Nienborg, Bridge, Parker and Cumming (2004) provide some evidence in support of the hypothesis that the response of disparity selective neurons is diminished when features with different values of disparity fall within their receptive field. They measured the response of neurons in area V1 of monkeys to sinusoidal variations in disparity across a surface. They found that neurons with larger receptive fields did not respond to stimuli in which the angular separation between minimum and maximum values of disparity was small so that a mixture of disparities fell within the cell's receptive field.

Physiological studies of neurons in area V1 of monkeys support the hypothesis of a size-disparity correlation. Prince, Cumming and Parker (2002) found that neurons with a wide range of receptive field sizes responded well to small disparities. However, larger disparities were preferred by neurons with proportionally larger receptive fields, as predicted by the size-disparity correlation. Psychophysical studies also provide some support for the hypothesis of a size-disparity correlation. Although receptive field size cannot be measured in psychophysical studies, Felton, Richards and Smith (1972, p.361) argued that the receptive field size of disparity sensitive neurons is related to their spatial frequency tuning. Early work using stimuli composed of only a narrow range of spatial frequencies reported that a larger range of disparities could be discriminated (Schor & Wood, 1983) and seen single (Schor et. al. 1984) than was consistent with the size-disparity correlation. However, Smallman and MacLeod (1994) and Prince and Eagle (1999) have challenged these results because the stimuli were

presented with high contrast, which may not have actually limited stimulation to a narrow range of spatial frequencies. To avoid this problem, Smallman and MacLeod (1994) and Prince and Eagle (1999) presented their stimuli at contrast threshold. Both studies measured the contrast threshold for detecting the sign of disparity for stimuli composed of only a narrow range of spatial frequencies. Smallman and MacLeod (1994) found that contrast sensitivity peaked at a disparity inversely proportional to spatial frequency, as predicted by the size-disparity correlation. Yet Prince and Eagle (1999) found that contrast sensitivity was approximately equal for a wide range of disparities for each spatial frequency tested.

Prince and Eagle (1999) proposed two stages of binocular processing in order to account for this discrepancy. They proposed that a size-disparity correlation exists at one stage of binocular processing, but does not occur for another stage of binocular processing that is only capable of effectively processing isolated stimuli. Prince and Eagle (1999) argued that the isolated Gabor patches they used could be processed by the stage of binocular processing in which a size-disparity correlation does not exist. They argued that the large patches of filtered noise used by Smallman and MacLeod (1994) required the stage of binocular processing that exhibits a size-disparity correlation. Assuming that the proposal of Prince and Eagle (1999) is correct, it seems likely that features that define steep disparity gradients would require the stage of binocular processing that exhibits a size-disparity correlation because such features are not isolated.

3.4.2 Nature of the benefit of the support squares

In Experiment 2 it was found that the benefit of the support squares is much reduced by small gaps between the support squares and the target squares. The relative disparity of the target squares in that experiment was 10 minutes of arc. For dot pairs with a relative disparity of 10 minutes of arc, Burt and Julesz (1980) found that diplopia occurred for separations smaller than approximately 10 minutes of arc. In order to account for this result, the receptive field size explanation of the disparity gradient constraint proposed that fusion depends on a disparity selective neuron with a receptive field that subtends approximately 10 minute of arc. By contrast, Experiment 2 of the present study showed that the benefit of the support squares is greatly diminished by gaps as small as 2 minutes of arc between the support features and the features that define a steep disparity gradient. On that basis, it is proposed that the support features restore fusion when they fall within the receptive field of the same neural unit invoked by Tyler (1975), Wilson et. al. (1988), Scharff (1997) and McKee and Verghese (2002) to account for the disparity gradient constraint. In the absence of the support features, two features that define a steep disparity gradient will fall within the receptive field of a neuron tuned to the largest absolute disparity of the two features. In that case, the disparity of 50% of the features within the neuron's receptive field will differ from the neuron's preferred disparity. This proportion is decreased when support features also fall within the neuron's receptive field. Therefore, it is possible that the effect of the feature that does not have the neuron's preferred disparity on the response of the neuron is also diminished.

The effect of support square contrast found in Experiment 3 is consistent with this theory if it assumed that the influence that a feature exerts on the response of a

disparity selective neuron is proportional to its contrast. According to the theory proposed in the previous paragraph, the target squares and some of the support squares stimulate the same disparity-tuned neuron. One of the target squares has this neuron's preferred disparity, while the other target square will diminish its response because it has a different disparity. The support squares serve to offset this interference, since they have the neuron's preferred disparity, and so affect the perceived direction of the target squares. In Experiment 3, the support squares failed to affect the perceived direction of target squares when the support squares were low contrast and the target squares were high contrast. Presumably, in this condition, the influence of the support squares was reduced because of their low contrast. Hence, the support squares did not offset the interference caused by the target square whose disparity differs from the neuron's preferred disparity. It is possible to test this explanation by reducing the contrast of the target square whose disparity differs from the neuron's preferred disparity. If the influence of the support squares decreases with their contrast, then the interference caused by this target square should likewise decrease with contrast. Hence, the theory predicts that low contrast support squares should affect the perceived direction of low contrast target squares.

Although there was an effect of support squares for 7 observers in Experiment 2 and 18 observers in Experiment 3 (Type 1 observers), the support squares did not affect the perceived direction of the target squares for three observers in Experiment 2 and 3 (Type 2 observers). Using a pair of vertically separated target squares similar to that used in Experiments 1-3, Scharff (1997) found that the minimum angular separation of the squares for which the squares appeared single rather than diplopic varied between observers. These individual differences in the disparity gradient that yields diplopia may

explain why the support squares failed to influence the perceived direction of the target squares for some observers in Experiment 2 and 3 of the present study (Type 2 observers). It is possible that the Type 2 observers experience diplopia for shallow disparity gradients than the observers that showed an effect of the support squares (Type 1 observers). If this is the case, then the disparity gradients that were used in Experiment 2 and 3 may have caused more interference than the support squares were able to offset for the Type 2 observers.

4 Perceived direction at the left and right edges of a surface

4.1 Experiment 4: Mapping the region affected by the Erkelens-bias

The perceived relative direction of two fused binocular features is commonly found to be an average of the angular separation of the features in both eyes (reviewed in section 1.4.3). Erkelens et. al. (1996) and Ono et. al. (2003) found that this was not the case for the perceived direction of the left or right edge of an occluding surface relative to a binocular line on the background surface (reviewed in section 1.5.3). The line and the edge appeared aligned when they were more closely aligned in the eye that viewed the monocular region of the background next to each edge than in the other eye. Based on these alignment data, Erkelens et. al. (1996) argued that the perceived relative direction of features in the “neighborhood” of a monocular region is biased towards their angular separation in the eye that views the monocular region (Erkelens-bias see section 1.5.3).

The dimensions of the “neighborhood” hypothesised by Erkelens et. al. (1996) have yet to be determined. Erkelens and van de Grind (1994) measured alignment to a binocular test line on the background surface that was horizontally separated by 48 minutes of arc from the left or right edge of an occluding surface. They found that this test line appeared vertically aligned with a binocular comparison line at the same depth when the comparison and test lines were aligned in both eyes’ views. Interpreting this result is difficult because the test line and the comparison line lay at the same depth. The lines would appear aligned when they were aligned in both eyes views if their perceived direction was an average of the angular separation in both eyes or if their

perceived direction was determined solely by their angular separation in the eye that viewed the monocular region.

Ono et. al. (2003), in their experiment 3, measured the perceived direction of a binocularly visible background line in the vicinity of a monocular region relative to a comparison line at the depth of the background or a comparison line at the depth of the occluding surface. They found that perceived alignment between the comparison line and the binocular background line was an average of the angular separation of the lines in both eyes. This suggests that the perceived direction of the binocular background line was not influenced by the monocular region. Ono et. al. (2003) did not report the horizontal location of the binocular background line, so its horizontal separation from the monocular region is unknown. Additionally, the background surface in experiment 3 of Ono et. al. (2003) lacked texture except for a monocular line within the monocular region to the side of the occluder and two additional lines within the binocularly visible region of the background. The monocular region may have a stronger influence on the perceived direction of binocular features when the surfaces are densely textured, because then the features are attached to the monocular region rather than isolated from it. It is also unknown whether the area that is affected by the monocular region varies with the width of the monocular region. Therefore, the aim of Experiment 4 was to map the transition from alignment based solely on the position of the features in the eye that views the monocular region to alignment based on the position of the features in both eyes.

This was accomplished using the stimulus shown in Figure 41. The stimulus consisted of two vertically separated textured panels. In each panel, a surface

comprising the right side of the panel occluded the right hand side of a background surface, which comprised the left side of the panel. A binocular line was located on the occluding surface of the upper panel and another binocular line was located on the background surface of the lower panel. The horizontal separation of the binocular lines from the monocular region was varied. Observers shifted the upper panel horizontally to vertically align the lines. Based on the results of Erkelens et. al. (1996), it was predicted that when both lines abutted the monocular region (target lines shown abutting the monocular region in Figure 41), the perceived direction of the lines would be strongly influenced by the monocular region so the lines would appear aligned when they were aligned in the eye that views the monocular region (monocular prediction). It was expected that the influence of the monocular region on the perceived direction of the lines would diminish as the horizontal separation of the lines from the monocular region was increased. For line-monocular region separations where the monocular region has no influence on the perceived direction of the lines, lines will appear vertically aligned when the average of their horizontal angular separation in the two eyes is zero (average prediction). A range of disparities was used to determine how this transition varies with the angular width of the monocular region.

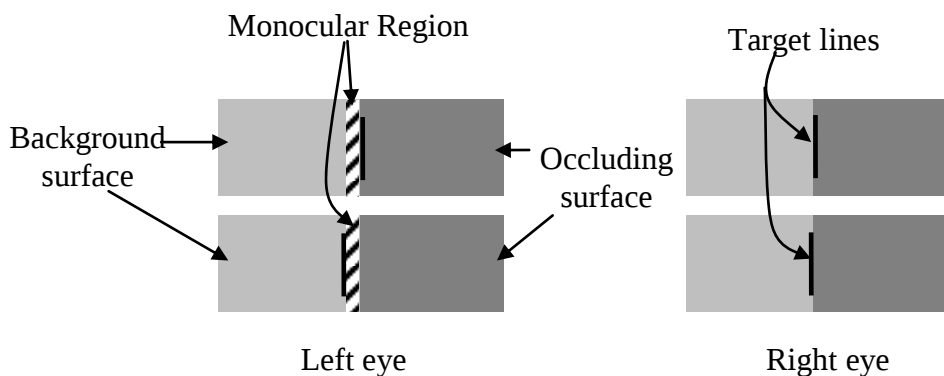


Figure 41. Schematic of stimuli for Experiment 4.

The target lines were only presented in the vicinity of a monocular region visible to the left eye in order to reduce the length of the experiment. An asymmetry of the Erkelens-bias for the left and right edges was not found by Erkelens et. al. (1996) and Ono et. al. (2003). It was expected that a few observers in the present experiment may align the target lines using the left eye, not because the monocular region was visible to that eye, but because of an ocular prevalence for that eye (ocular prevalence reviewed 1.4.3, page 47). Therefore, in the first session of testing, ocular prevalence was measured in a control condition, in which the lower and upper panels each consisted of a single surface so textured monocular regions were lacking. The horizontal separation of the target lines from the monocular region was subsequently varied for observers that did not display a strong ocular prevalence for either eye.

4.1.1 Method

Stimuli

The stimulus consisted of two textured panels, which were vertically separated by a gap of 39 minutes of arc. The texture was randomly generated with a dot size of 2.5 minutes of arc and a density of 30% white dots (luminance 140 cd/m^2), presented on a black background (luminance $<1 \text{ cd/m}^2$). The panels were 3.3° high and were seen against a black background (luminance $<1 \text{ cd/m}^2$).

In the condition with monocular regions, each panel contained two frontal plane surfaces lying at different depths (Figure 41). The surface on the right side of the panels had a crossed disparity of 9.8, 14.7 or 19.6 minutes of arc relative to the surface on the left-side of the panels. The left edge of the occluding surface was near the middle of the panel. This edge created a monocular region on the background surface which was visible to the left eye. For the upper panel, the occluding surface was 5° wide and the visible portion of the background surface was 4° wide. The widths of the surfaces in the bottom panel differed from those of the top panel by a randomly determined amount on each trial between ± 20 minutes of arcs. Since the widths of the panels were thus different, it was not possible for observers to align the lines by simply aligning the edges of the lower and upper panels. In the top panel, a red vertical line (luminance 24 cd/m^2) was imbedded in the occluding surface such that it abutted the occluding edge. In the bottom panel, a red vertical line was imbedded in the background surface abutting the left edge of the monocular region. Both lines were 2.5 minutes of arc wide and 2° high. The horizontal separation of the lines from the monocular region was varied in the

second session of testing. The separation of the line on the background surface from the left edge of the monocular region always matched the separation of the line on the occluder from the right edge of the monocular region.

In the condition that lacked monocular regions, the upper and lower panels each contained only one surface. The disparity of the lower panel relative to the upper panel was the same as the disparities used in the condition where a monocular region was present. The lines were imbedded in the centre of each panel. The upper panel was 8.33° wide. The widths of the bottom panel differed from the top panel by a randomly determined amount on each trial between ± 20 minutes of arc

Procedure

In the first session of testing, there were three disparities (9.8, 14.7 and 19.6) and two configurations (with and without monocular regions), which were presented five times in a random order. Observers were instructed to move the upper panel horizontally using the arrow keys so that the line in the bottom panel appeared vertically aligned with the line in the top panel. A trial ended when the observer signalled that the lines appeared vertically aligned by pressing another key. The first observer (CN) was also tested using a disparity of 24 minutes of arc. Subsequent observers were not tested with this disparity because CN reported that diplopia sometimes occurred for that disparity. Prior to the main experiment, observers were familiarised with the task prior to testing with 5 practice trials with monocular regions. At the end of the practice block, observers were asked which side of the panels appeared closer, which all observers reported correctly.

Observers

15 observers from the University of New South Wales community participated. All were inexperienced with experiments studying binocular vision and were naïve of the motivation for the experiment and the expected results.

4.1.2 Results

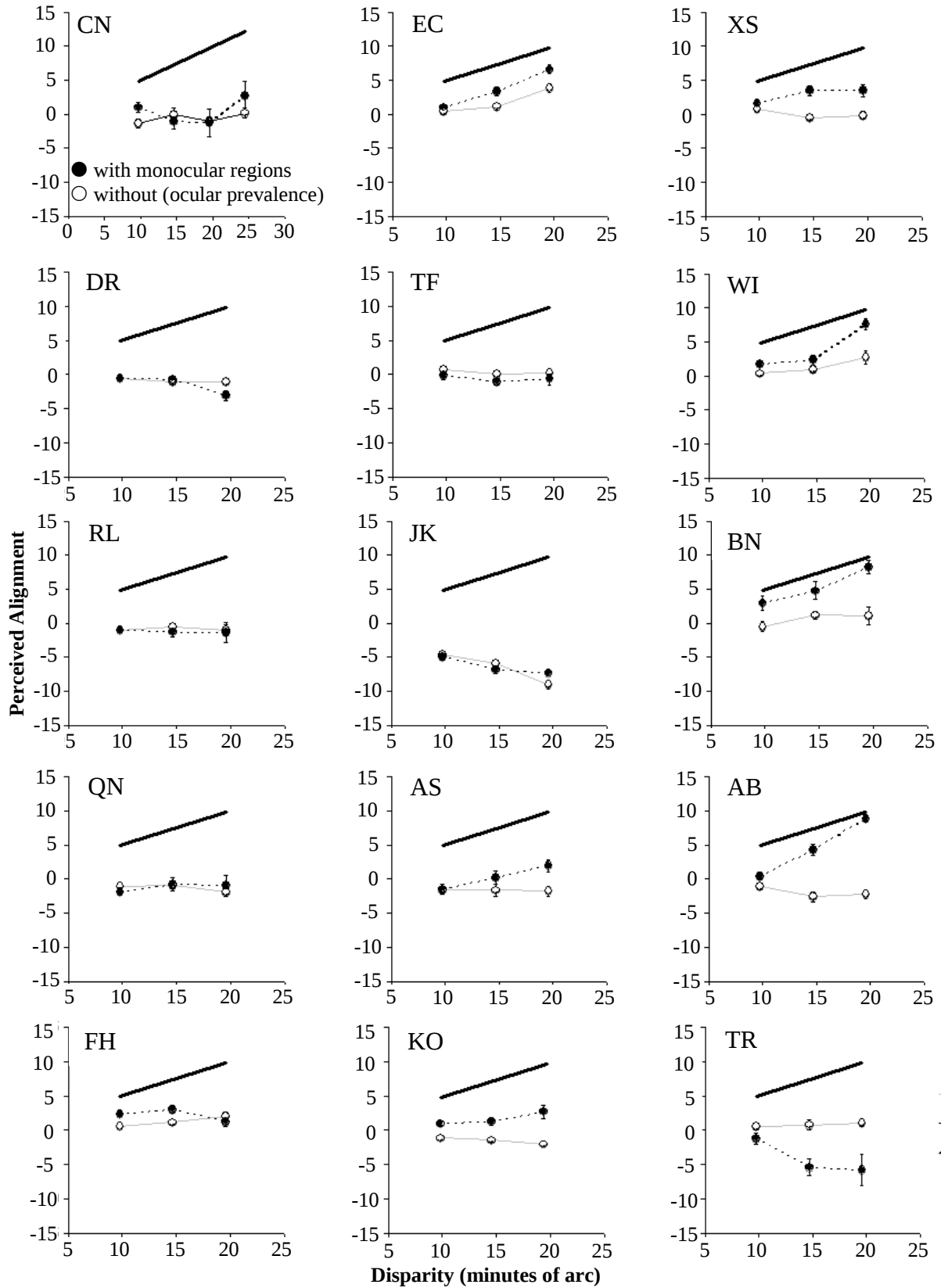


Figure 42. Results of Experiment 4. Error bars are standard errors.

The results are shown in Figure 42 for each observer because alignment differed between observers. The graphs in Figure 42 plot the mean of the alignment settings against disparity. The alignment settings are the average of the horizontal angular separation of the upper and lower lines in the two eyes. Hence, an alignment setting of zero is the average prediction and indicates that both eyes contributed equally to the perceived direction of the foreground target relative to the background line. As predicted, the lines were aligned in this way in the condition that lacked monocular regions (○ in Figure 42) for all observers except JK. Hence, the results for this control condition indicate that all observers except JK did not have a strong ocular prevalence for either eye. For JK, the lines appeared aligned when they were actually aligned in the right eye, which is consistent with a strong ocular prevalence for the right eye.

For the condition where each line abutted a monocular region (● in Figure 42), the lines were expected to appear aligned when they were aligned in the eye that viewed the monocular region. This is the monocular prediction and is shown by the diagonal line in each graph. Perceived alignment for this condition varied between observers. A t-test was conducted on the alignment settings for each observer to determine whether the settings for the control condition differed from the settings for the condition where the lines were next to a monocular region (Table 1). This analysis revealed that perceived alignment for five of the observers did not differ depending on whether the lines were presented in the centre of the surfaces or next to a monocular region. For nine observers, perceived alignment differed between the two conditions. For eight of these observers, perceived alignment when the lines were next to a monocular region was biased towards the position of the lines in the eye that viewed the monocular region (Erkelens-bias), but one observer had the opposite bias.

Table 1. Tests of the differences between the experimental and control conditions. Significant differences are shown in bold.

Observer	t	Difference	95% C .I.s	
			Lower	Upper
TR	-8.8	-4.9	-3.8	-6.1
DR	-1.5	-0.5	-1.2	0.2
RL	-0.5	-0.4	-1.6	0.9
QN	0.2	0.1	-1.2	1.4
CN	0.4	0.4	-1.5	2.3
TF	2.0	0.9	0.0	1.9
FH	2.3	0.9	0.1	1.8
EC	3.1	1.8	0.7	3.0
AS	2.8	1.9	0.5	3.3
WI	3.8	2.5	1.2	3.9
XS	5.6	2.8	1.8	3.8
KO	7.2	3.2	2.3	4.1
BN	5.5	4.8	3.0	6.5
AB	9.5	6.5	5.1	7.8

Collapsing across the three disparities, if perceived alignment in the control condition was equal to the average prediction, while alignment for the conditions where the lines were next to a monocular region was equal to the monocular prediction, then the difference between the alignment settings in these two conditions would be approximately 7.35 minutes of arc. The 95% confidence intervals include this value for observer AB and indicate that the effect of the monocular region for observer BN was also large.

These two observers returned for the second session of testing in which the separation of the lines from the monocular region was varied. The results are shown in Figure 43, which plots the alignment settings against the horizontal separation between the lines and the monocular region. The black circles are the mean of the alignment settings for the conditions where disparity was 19.6 minutes of arc. The black horizontal

line shows the monocular prediction for the 19.6 minute of arc disparity. The grey circles in the graph for observer BN are the mean of the settings for the 14.7 minute of arc disparity and the grey line shows the monocular prediction for this disparity. For a gap of 15 minutes of arc, the alignment settings were closer to the monocular prediction than the average prediction (zero). The alignment settings tended toward the average prediction as the separation between the lines and the monocular region increased. For observer BN, perceived alignment approximated the average prediction with a 30 minute of arc gap when the monocular region was 14.7 minutes of arc wide. However, with the same 30 minute of arc gap, alignment for the larger 19.6 minute of arc disparity was midway between the monocular prediction and the average prediction.

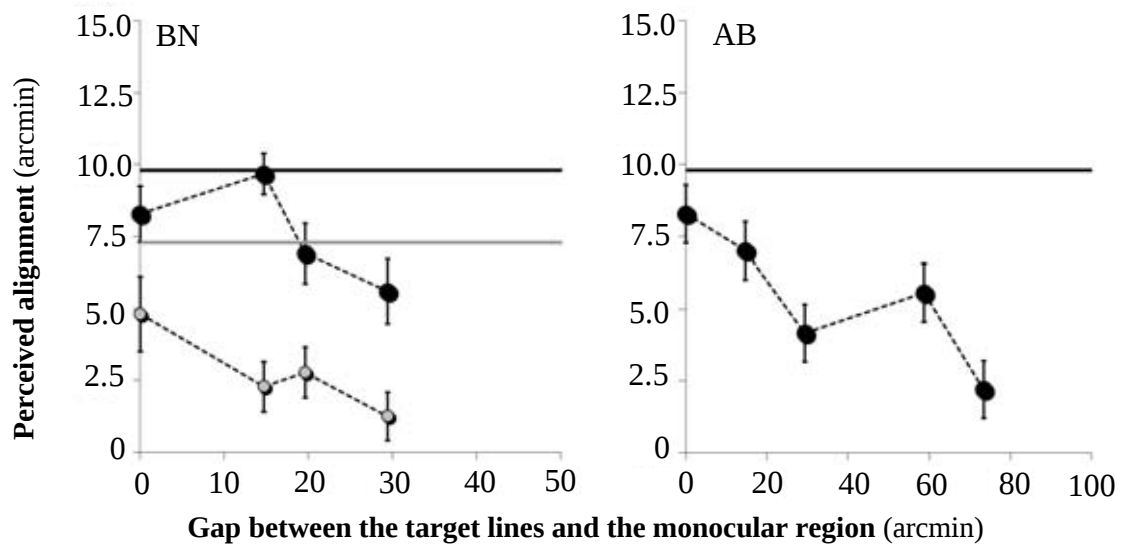


Figure 43. Results of the second session of Experiment 4. Alignment settings for the 20 minute of arc disparity ● and the 15 minute of arc disparity ●. The black horizontal line shows the monocular prediction for the 20 minute of arc disparity and the grey horizontal line shows the same prediction for the 15 minute of arc disparity. Error bars are standard errors.

4.1.3 Discussion

Erkelens et. al. (1996) and Ono et. al. (2003) found that vertical alignment between the left and right edge of an occluding surface and a line on the background surface was based principally on the position of the line and the edge in the eye that viewed the monocular region next to the edge. In the present study, the perceived relative direction of a pair of lines located next to a monocular region was biased towards their angular separation in the eye that viewed the monocular region for eight of fifteen observers (Erkelens-bias). A large Erkelens-bias occurred for two observers (AB and BN). The horizontal separation of the target lines from the monocular region was varied for these two observers using a monocular region with an angular width of twenty minutes of arc. A large bias towards the eye that viewed the monocular region also occurred for both observers with a fifteen minute of arc separation between the lines and the monocular region. This Erkelens-bias decreased as the separation between the lines and the monocular region was increased. For the 20 minute of arc disparity, a 30 minute of arc gap between the edge of the monocular region and the target lines halved the Erkelens-bias for both observers.

For one observer (BN), a large Erkelens-bias was observed with a disparity of fifteen minutes of arc, so the separation of the lines from the monocular region was also varied for this disparity for this observer. With a gap of thirty minutes of arc, the Erkelens-bias for the fifteen minute of arc disparity was almost eliminated, whereas the Erkelens-bias persisted for the same gap for the twenty minute of arc disparity. This provides some evidence that there is a relationship between the width of a monocular region and the size of the surrounding area affected by the Erkelens-bias. However,

further testing is needed, as it was only possible to compare the Erkelens-bias as a function of separation for different values of disparity for one observer because small Erkelens-biases were generally found in the present study. The magnitude of the Erkelens-biases in the present experiment, as compared to those reported by Erkelens et. al. (1996) and Ono et. al. (2003), are discussed in the introduction to Experiment 5.

4.2 Experiment 5: Perceived direction of the left and right edges of a surface and features abutting those edges.

It is commonly found (reviewed in section 1.4.3) that the perceived relative direction of two fused binocular features is an average of their angular separation in both eyes. Erkelens et. al. (1996) and Ono et. al. (2003) found that the perceived direction of the left or right edge of an occluding relative to a binocular line on the background surface is biased towards their angular separation in the eye that viewed the monocular region next to the edge (Erkelens-bias). However, the magnitude of the Erkelens-bias differed between the two studies. Erkelens et. al. (1996) reported that the line and the edge appeared aligned when the line was physically aligned with the edge in the eye that viewed the monocular region next to the edge (monocular prediction). Ono et. al. (2003) reported an Erkelens-bias that fell short of the monocular prediction (the magnitude of the Erkelens-bias was also compared between the Erkelens et. al. (1996) and Ono et. al. (2003) in section 1.5.3).

In Experiment 4 of the present study, perceived alignment was measured between a binocular line on a background surface and another binocular line on an occluding surface. Both lines abutted one side of a monocular region visible to the left eye and thus the Erkelens-bias was expected. The Erkelens-bias was found for eight of fourteen observers. Of these eight observers, the Erkelens-bias only approximated the monocular prediction for two observers. Hence, the Erkelens-bias in Experiment 4 of the present study was smaller than that found by Erkelens et. al. (1996).

It is possible that the Erkelens-bias in Experiment 4 of the present study was also smaller than that observed by Ono et. al. (2003). The results of Experiment 4 may be compared to the results of Ono et. al. (2003) by calculating a weighting factor for the eye that viewed the monocular region. A weighting factor of 100% would indicate that the alignment targets appeared aligned when they were aligned in the eye that viewed the monocular region, as was found in the Erkelens et. al. (1996) study. Hence, a weighting factor of 100% corresponds to the monocular prediction. A weighting factor of 50% for each eye would indicate that both eyes contributed equally to perceived alignment as is generally found in the absence of monocular regions for small disparities (e.g. Ono et. al. 1977; Kommerell et. al. 2003; and the control condition of Experiment 4). Hence, a weighting factor of 50% corresponds to the average prediction. Ono et. al. (2003) reported that perceived alignment to the edge of the occluder was shifted 3.93 minutes of arc towards the monocular prediction relative to the average prediction. This shift was converted to a weighting factor by first determining the difference between the monocular predictions, or in other words, the difference between alignment of the targets using solely the eye that viewed the monocular region, and alignment using the solely other eye, which was 11 minutes of arc. Then the difference between alignment using solely the eye that does not view the monocular region and the obtained alignment setting was calculated, which was $5.5+3.93=9.43$. This was then divided by the difference between the monocular predictions to give the weighting factor for the eye that viewed the monocular region $9.32/11 = 0.857 = 85.7\%$. Using this method, the results of Experiment 4 were converted to weighting factors and are shown in Table 2 below. The 95% confidence intervals reported by Ono et. al. (2003) for their experiment 3 correspond to a weighting factor between 79.9% and 91.45%,

which only overlaps the confidence intervals for the weighting factor for two observers in Experiment 4 of the present study (observers AB and BN).

Table 2. Weighting factor for the eye that viewed the monocular region for Experiment 4. Significant differences from the average prediction are shown in bold.

Observer	t	Weighting Factor	95% Confidence Intervals	
TR	-8.8	17	9	24
DR	-1.5	47	42	51
RL	-0.5	47	39	56
QN	0.2	51	42	60
CN	0.4	53	40	66
TF	2.0	56	50	63
FH	2.3	56	51	62
EC	3.1	62	55	70
AS	2.8	63	53	72
WI	3.8	67	58	77
XS	5.6	69	62	76
KO	7.2	72	66	78
BN	5.5	83	70	94
AB	9.5	94	85	103

The pattern of differences between the stimuli and procedure of Erkelens et. al. (1996), Ono et. al. (2003) and Experiment 4 of the present study can be used to identify parameters that may influence the magnitude of the Erkelens-bias. Erkelens et. al. (1996) and Ono et. al. (2003) aligned the background line with the edge of the occluder. However, in Experiment 4 of the present study, observers aligned a line on the background surface with a line on the occluder abutting the edge. The results of Experiment 4 indicated that the magnitude of the Erkelens-bias decreased with the separation of the lines from the monocular region. Hence, it is possible that the Erkelens-bias in Experiment 4 tended to be smaller than the Erkelens-biases in the Erkelens et. al. (1996) and Ono et. al. (2003) studies because alignment was not to the edge of the occluder. Therefore, in Experiment 5 observers aligned a line on the background surface with the edge of the foreground surface instead of with a line on the foreground surface.

The occluding surface in Experiment 4 of the present study was the same height as the background surface that it occluded. The area of the background surface and the occluding surface were approximately equal in Experiment 4. This differs from the stimuli used by Erkelens et. al. (1996) and Ono et. al. (2003). They used a single occluding surface that was centrally located within a larger background surface. Therefore, in Experiment 5, a single occluding surface was used that occluded the central region of a much larger background surface. Pilot data indicated that an Erkelens-bias occurred for all observers under these conditions. Therefore, the main experiment included conditions in which the background line was aligned with a line on the foreground surface at a range of horizontal separations from the edge. This would determine whether aligning the background line directly with the edge yields larger Erkelens-biases than alignment to a line abutting that edge.

4.2.1 Method

Stimuli

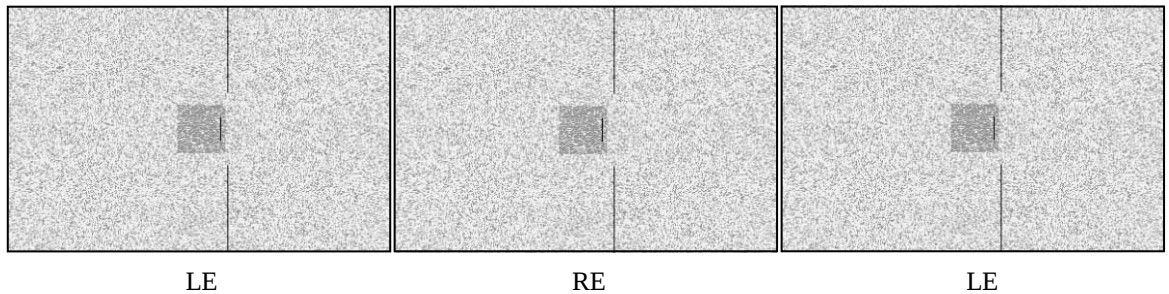


Figure 44. Stimuli used in Experiment 5.

Figure 44 shows one of the stimuli. A surface (1.6° square) occluded the central region of a large background surface (8.4° high and 13° wide). The background was a random dot surface composed of 75% light dots (105 cd/m^2) and 25% dark dots (35 cd/m^2). The proportion of light to dark dots was reversed for the texture on the occluder. Dot size was 2 minutes of arc. Disparity was manipulated by shifting the occluder left in the right eye by half the disparity and shifting the occluder in the opposite direction in the other eye by the same amount. The square had a crossed disparity of 6, 8 or 10 minutes of arc relative to the background.

A black line, 2 minutes of arc wide, was imbedded in the background surface and extended the full height of the background. This line could be moved horizontally by the observer. A vertical gap of 2.5° in the middle of the line prevented it from entering the occluded region of the background.

A black line, 2×48 minutes of arc, was imbedded in the occluding surface next to the left or right edge, except on trials where alignment was to the left or right edge.

The line, when present, abutted the edge or was horizontally separated from the edge by a gap of 2.5, 4, or 9 minutes of arc.

Procedure

At the beginning of each trial, the background line was offset by 18.6 minutes of arc to the left or right relative to the foreground target. There were three disparities (6, 8 or 10 minutes of arc), two starting locations for the background line and four gaps between the foreground target and the left or right edge of the occluder (9, 4, 2.5 minutes of arc, abutting the edge or alignment to the edge itself). Each combination of these conditions was presented five times in a random order. Observers were instructed to align the background line with the line on the occluding surface. For conditions where the line on the occluding surface was lacking, observers were instructed to align the line with the edge of the occluding surface. Data from each observer was collected in two one hour sessions, which were completed on separate days.

Observers

Six students from the University of New South Wales participated. All were naïve of the aim of the experiment and the predicted results and had not participated in any of the previous experiments.

4.2.2 Results

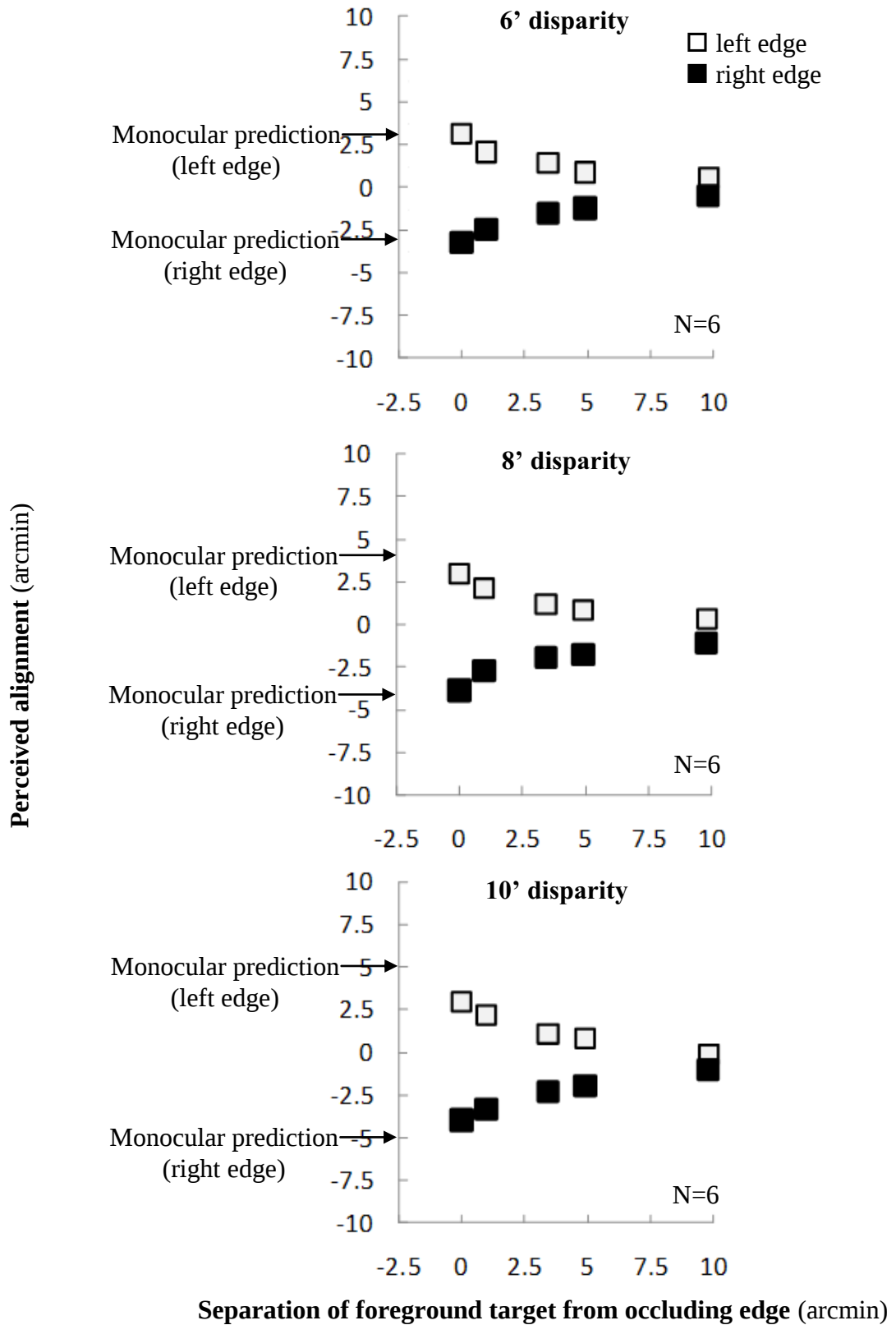


Figure 45. Results of Experiment 5.

Group data are presented in Figure 45, which plots the alignment settings against the horizontal separation of the foreground target from the occluding edge. The zero separation is the condition in which alignment was to the occluding edge and the 1 minute of arc separation is the condition in which alignment was to a line abutting that edge. The alignment settings are the average of the horizontal angular separation of the background line and the foreground target in the two eyes. Hence, an alignment setting of zero is the average prediction and indicates that both eyes contributed equally to the perceived direction of the foreground target relative to the background line. Alignment with the left edge (□ in Figure 45) and alignment with the right edge (■ in Figure 45) was biased to the right and left of the average prediction respectively by approximately 4 minutes of arc. These biases are in the expected direction (Erkelens-bias) for each edge, which are shown in Figure 45 for each disparity by small arrows. A smaller Erkelens-bias occurred for alignment with the foreground line abutting the edge of the occluder (1 minute of arc separation). The Erkelens-bias decreased with the separation of the foreground line from the edge of the occluder. The Erkelens-bias was all but eliminated by a 9 minute of arc gap between the foreground line and the occluding edge, which corresponds to the 10 arcmin separation in Figure 45. The magnitude of the Erkelens-bias did not differ between the 6, 8 and 10 minute of arc disparities (upper, middle and lower graphs of Figure 45 respectively).

The results were analysed using a two-way multivariate analysis of variance. Planned orthogonal contrasts tested for main effects of side, separation, linear and quadratic trend for disparity and their interaction. The Decision-Wise error rate ($\alpha=0.05$) was controlled for each of the contrasts and 95% confidence intervals were calculated using the procedure described by Bird (2004). The sign of the alignment

settings for the left side was reversed so that the expected direction of the Erkelens-bias was the same for the left and right edge. The main effect comparing alignment to the edge and alignment to a line abutting the edge was significant ($F_{(1,5)} = 9.856$). The 95% confidence intervals indicate that the Erkelens-bias was 0.158-1.585 minutes of arc larger for alignment to the occluding edge than a line abutting that edge. The main effect comparing the 2.5 arcmin gap to the smaller separations was significant ($F_{(1,5)} = 45.105$). The main effect comparing the 5 arcmin gap to the smaller separations was significant ($F_{(1,5)} = 34.105$). The main effect comparing the 9 arcmin gap to the smaller separations was significant ($F_{(1,5)} = 59.732$). The main effect of side ($F_{(1,5)} = 0.735$), linear trend for disparity ($F_{(1,5)} = 5.356$) and quadratic trend for disparity ($F_{(1,5)} = 0.368$) were not significant. The interaction between side and linear trend was significant ($F_{(1,5)} = 15.726$). This interaction indicates that although the Erkelens-bias for the left and right side were similar for the 6 minute of arc disparity, for the 10 minute of arc disparity the Erkelens-bias was larger for the right side than the left side.

4.2.3 Discussion

Ono et. al. (2003) and Erkelens et. al. (1996) found that perceived alignment between a binocular background line and the left or right edge of an occluding surface was biased toward the relative direction of the line and the edge in the eye that views the monocular region next to the edge (Erkelens-bias). In the present study, the magnitude of the Erkelens-bias decreased with the horizontal separation of the line from the edge and was eliminated by a separation of 10 minutes of arc. This indicates that for disparities of 10 minutes of arc or less between the occluding and background surfaces, the Erkelens-bias does not extend beyond 10 minutes of arc from the edge of the occluding surface.

The Erkelens-bias was not observed for six of fourteen observers in the previous experiment (Experiment 4) in which alignment was to a line abutting the edge instead of to the edge. The present study showed that the Erkelens-bias for alignment to a line abutting the edge was 1 minute of arc smaller than the Erkelens-bias for alignment to the edge. Hence, this difference between Experiment 4 and the Ono et. al. (2003) and Erkelens et. al. (1996) studies does not account for the absence of the Erkelens-bias for six of the observers in Experiment 4.

The Erkelens-bias in the present experiment was not proportional to the disparity between the occluding and background surfaces. This differs from the results of Erkelens et. al. (1996), who measured the Erkelens-bias for a wide range of disparities and found that the magnitude of the Erkelens-bias was equal to half the relative disparity between the occluder and the background. That the Erkelens-bias in the

Erkelens et. al. (1996) study increased with disparity ruled out the possibility that the Erkelens-bias was simply due to a response bias towards the centre of the occluder. Since, the Erkelens-bias in the present study did not increase with disparity, it is possible that the biases in the present experiment were due to a response bias towards the centre of the surface rather than the phenomenon reported by Erkelens et. al. (1996). Therefore, in the following experiment, a larger range of disparities was tested to better evaluate the Erkelens-bias as a function of disparity and several control conditions were included in order to test whether the Erkelens-bias found in the present experiment was due to the presence of a monocular region of the background next to the left and right edges of the occluding surface.

4.3 Experiment 6: The stimulus conditions for the Erkelens-bias

In Experiment 5, perceived alignment between a background line and the left or right edge of an occluding surface was biased towards the centre of the occluding surface relative to alignment based on the average of the relative directions of the line and the edge in both eyes. The direction of these biases is consistent with the proposal of Erkelens et. al. (1996) that the perceived direction of features in the neighbourhood of a monocular region is biased towards the eye that views the monocular region (Erkelens-bias see section 1.5.3). However, the magnitude of the Erkelens-biases in Experiment 5 did not increase with the relative disparity of the surfaces and hence did not increase with the width of the monocular region. Therefore, it is possible that the Erkelens-bias observed in Experiment 5 was not due to the presence of a monocular region next to the left and right edges of the occluding surface. The results may instead be due to an Erkelens-bias to respond in the direction of the centre of the square. This possibility was evaluated in Experiment 6 by measuring alignment to the edges of a square when monocular regions were either present next to the edge or lacking. If the Erkelens-bias in Experiment 6 was due to the presence of a monocular region next to the left and right edge of the square, then the Erkelens-bias will not occur when monocular regions are eliminated. Monocular regions were eliminated in two ways which are discussed below.

Monocular regions were present in the textured condition, which was similar to the stimulus used in Experiment 6. A wider range of disparities was tested than in Experiment 5, in order to better evaluate the effect of disparity on the magnitude of the Erkelens-bias. The disparities between the background surface and the occluding

surface varied between 4 and 12 minutes of arc, which lie within the fusion limit for small lines (reviewed section 1.3; Panum, 1858; Mitchell, 1966).

Textured monocular regions were lacking in the outline condition, in which only the background line and an outline of the occluding surface were visible because the texture on the surfaces was eliminated (Figure 46). If the Erkelens-bias in the textured condition were due to the presence of textured monocular regions, then the Erkelens-bias would not occur in the outline condition, since textured monocular regions were lacking. On the other hand, if the Erkelens-bias also occurred in the outline condition, then this would indicate that the Erkelens-bias was not due to the presence of textured monocular regions.

Although textured monocular regions were lacking in the outline condition, one could argue that monocular regions were present nevertheless. The basis for this argument is that the left eye always views more of the background to the left of an occluding surface than the right eye and the right eye always views more of the background than the right eye to the right of an occluding surface. Therefore, in the outline condition, the visual system may respond to the untextured region to the left of the outline of the square in the left eye's image as a monocular region visible to the left eye, on the basis that the outline of the square specifies the boundaries of an occluding surface. Likewise, the visual system may respond to the untextured region to the right of the outline of the square in the right eye's image as a monocular region visible to the right eye, on the basis that the outline of the square is an occluding surface and a monocular region is always visible to the right eye to the right of an occluding surface.

This possibility was tested in an additional set of conditions, in which the outline of the square in the central region of the stimulus was presented farther in depth than the comparison line (cross fusion of the middle and left images of the second row of Figure 46). It seems unlikely that the untextured regions to the left and right of the outline of the square would be interpreted as monocular regions in these outline behind conditions, because the outline of the square is the farthest feature in the stimulus, which is inconsistent with it being an occluding surface. Therefore, comparing perceived alignment for the crossed and uncrossed versions of the outline condition compares perceived alignment with and without a foreground surface.

In the single edge condition (Figure 46), a single edge of the occluder was retained and the observer aligned the comparison line with this edge. The Erkelens-bias was expected to be much reduced for this condition since textured monocular regions were lacking and a foreground surface is not well specified by a single edge.

4.3.1 Method

Stimuli

The textured condition (top stereogram of Figure 46), was identical to that described in Experiment 5 except that in the centre of the square was a black cross, which subtended 15 minutes of arc and had the same disparity as the square.

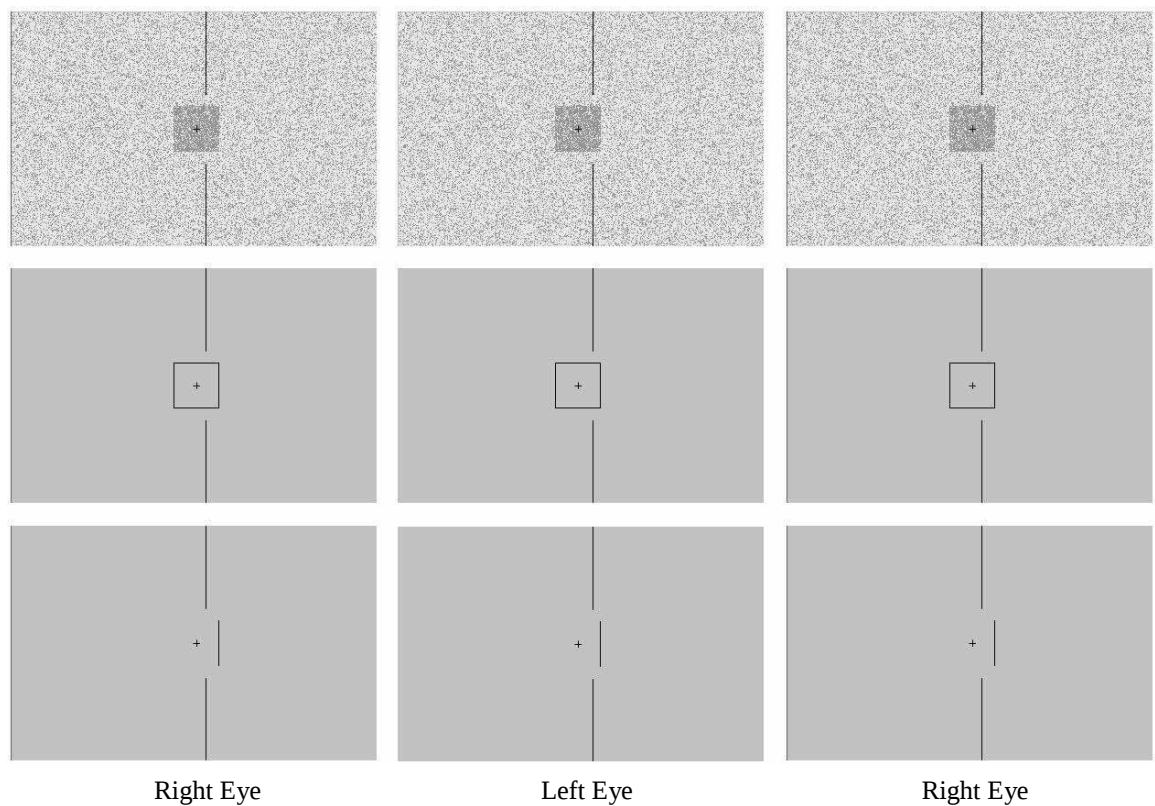


Figure 46. Stereograms of the three configurations in Experiment 6. The first row shows the textured-condition. The second row shows the outline-condition. The third row shows the single-edge condition.

In the outline condition, the surfaces lacked texture and consequently, no feature was visible to one eye that was not also visible to the other eye (middle stereogram of Figure 46). A black line, 2 minutes of arc wide, made the borders of the square visible. The luminance of the background was 70.4 cd/m².

In the single edge condition, the outline of the square was reduced to either the left or right edge (bottom stereogram of Figure 46).

Procedure

The square was presented with disparities of 4, 8 or 12 minutes of arc relative to the surround, which contained the binocular line that observers moved horizontally. For the outline condition, the central cross and the outline of the square were also presented farther in depth than the comparison line with the disparities (4, 8 or 12 minutes of arc). Likewise, the central cross and the edge in the single-edge condition were also presented farther in depth than the comparison line. At the beginning of a trial, the binocular line in the surround was presented near either the left or the right edge of the square. Observers were instructed to shift this line horizontally using the arrow keys in order to vertically align it with the edge of the square. The starting location of the lines was 24 minutes of arc to the left or right of the edge. Observers found it difficult to fixate the cross in the centre of the square while aligning the line with the edge, so observers were instructed to ignore the cross. Each combination of stimulus configuration, disparity, side, and starting position were presented 5 times in a random order.

Observers

7 observers from the University of New South Wales participated. All were inexperienced with experiments on binocular vision and were naive of the expected results.

4.3.2 Results

The results for the textured condition are described first and then the results for the outline and single edge condition are described.

Textured condition

Occluding and background surfaces textured

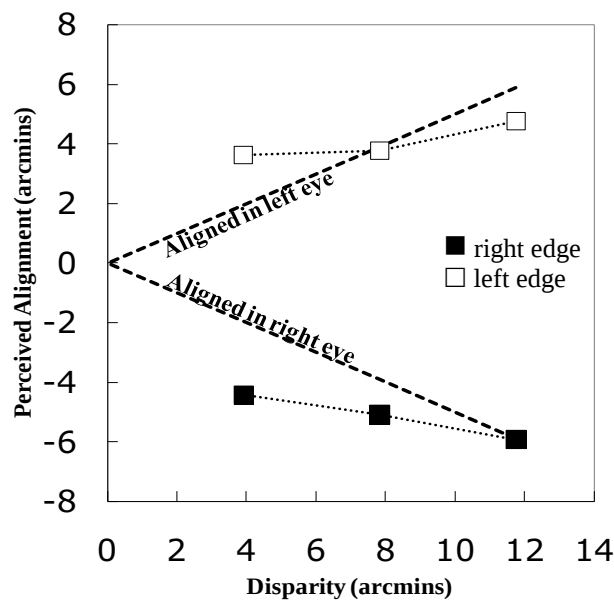


Figure 47. Group data for the textured condition in Experiment 6. The horizontal location of the comparison line when it appeared vertically aligned with either the left or right edge is plotted as a function of the disparity between the background and the occluder. $N=7$.

The group data for the textured condition are shown in Figure 47, which plots the alignment settings against disparity. The alignment settings are the average of the horizontal angular separation of the background line and the foreground target in the two eyes. Hence, an alignment setting of zero is the average prediction and indicates that both eyes contributed equally to the perceived direction of the foreground target relative to the background line. When the surfaces were textured, there was a leftwards

bias for alignment with the left edge (□ in Figure 47) and a rightwards bias for alignment with the right edge (■ in Figure 47). The magnitude of the bias was approximately four minutes of arc for the left edge and approximately 4-6 minutes of arc for the right edge. These biases lie in the same direction as the monocular prediction for each edge, which is shown in Figure 47 by the diagonal dotted lines and are in the expected direction for the Erkelens-bias. Perceived alignment was not well predicted by the position of the line and the edge in the left eye for alignment with the left edge shown by the dotted diagonal line with positive slope (monocular prediction for the left edge). Likewise, the monocular prediction for the right edge shown by the dotted diagonal line with negative slope predicts the direction of the bias for the right edge but does not accurately predict its magnitude, which increased by a smaller amount than expected across the 4, 8 and 12 minute of arc disparities (see below).

The extent to which the Erkelens-bias increased with disparity in the textured condition was analysed using a two-way multivariate analysis of variance testing for main effects of side, linear and quadratic trend for disparity and their interaction. The Decision-Wise error rate ($\alpha=0.05$) was controlled for each of the contrasts. The sign of the alignment settings for the left side was reversed so that the expected direction of the Erkelens-bias was the same for the left and right edge. The main effect of linear trend was significant ($F_{(1,6)}=31.869$) and the main effect of quadratic trend was not significant ($F_{(1,6)}=1$). The 95% confidence for the linear trend contrast was calculated using the procedure described by Bird (2004). The Erkelens-bias was 0.743-1.88 minutes of arc larger for the 12 minute of arc disparity than the four minute of arc disparity. This is less than half of the effect of disparity reported by Erkelens et. al. (1996), because if alignment were based solely on the directions in the eye that viewed the monocular

region, then the Erkelens-bias for the 12 minute of arc disparity would be 4 minutes of arc larger than the Erkelens-bias for the 4 minute of arc disparity. The main effect of side was significant ($F_{(1,6)}=10.949$), which indicates that the Erkelens-bias was larger for the right edge than the left edge.

Outline and single-edge conditions

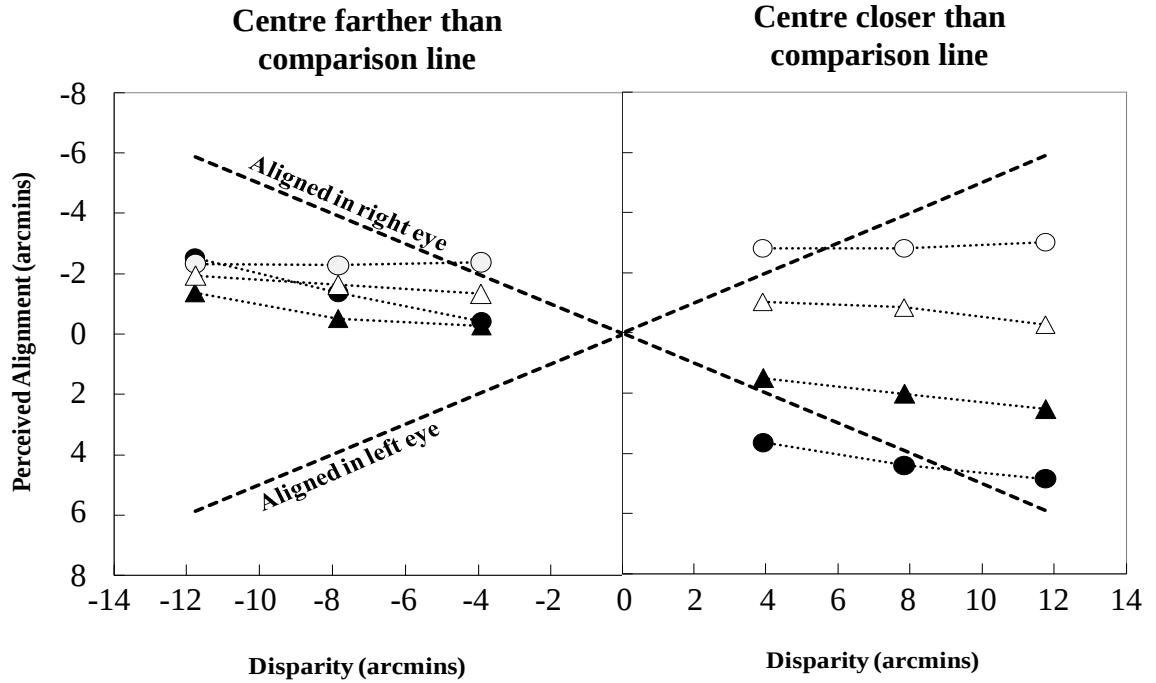


Figure 48. Group data for the outline and single edge condition of Experiment 6. The location of the comparison line in which it appeared vertically aligned with the edge is plotted as a function of the disparity between the line and the edge. Data points show: alignment in the *outline* condition for the right edge ● and for the left edge ○; alignment in the *single-edge* condition for the right edge ▲ and the left edge △. N=7.

The group data for the conditions where the texture on the surfaces was eliminated are shown in Figure 48. The results for these conditions depended on whether the comparison line was closer than the central region containing either the outline or the single edge (left graph of Figure 48) or farther in depth than the central region (right graph of Figure 48). Perceived alignment in the outline condition (● and ○) was similar to perceived alignment in the single edge condition (▲ and △) when the comparison line was closer than the outline or the edge (left graph of Figure 48). For these conditions (left graph of Figure 48), perceived alignment was biased to the left of the average of the relative directions of the comparison line and the edge in both eyes by approximately 2 minutes of arc. However, when the outline was closer than the

comparison line (right graph of Figure 48), alignment was biased leftwards for alignment with the right edge and rightwards for alignment to the left edge and is in the expected direction for the Erkelens-bias. The magnitude of the Erkelens-bias was approximately 3 minutes of arc for alignment with the left edge of the outline and approximately 4 minutes of arc for alignment with the right edge of the outline. The same bias occurred for the single edge condition but was approximately two minutes of arc smaller in magnitude than the bias for the outline condition.

The results were analysed using a two-way multivariate analysis of variance using planned orthogonal contrasts and the Decision-Wise error rate ($\alpha=0.05$) was controlled. The sign of the alignment settings for the left edge was reversed so that the expected direction of the Erkelens-bias was the same for the left and right edge. Planned orthogonal contrasts tested for main effects of side, and linear and quadratic trend for disparity magnitude. The main effect of centre closer or farther than the comparison line was tested and the main effect comparing the single edge condition to the outline condition was tested. The main effect of centre closer or farther than the comparison line was significant ($F_{(1,6)}=67.937$). The main effect comparing the single edge condition to the outline condition was significant ($F_{(1,6)}=10.647$). The main effect of side was significant ($F_{(1,6)}=13.612$), which indicates that the Erkelens-bias was larger for alignment to the right edge than the left edge. The main effects of linear ($F_{(1,6)}=1.794$) and quadratic trend ($F_{(1,6)}=0.938$) were not significant. However, the interaction between linear trend and sign of disparity was significant ($F_{(1,6)}=19.155$), which indicates that the Erkelens-bias increased with disparity when the comparison line was farther in depth the central region. The interaction between sign of disparity and

configuration was significant ($F_{(1,6)}=79.07$), which indicates that the Erkelens-bias that occurred when the central region was closer than the comparison line was larger for the outline condition than the single-edge condition. A significant triple interaction indicated that the Erkelens-bias increased with disparity when the central region was closer than the comparison line to a greater extent for the outline condition than the single edge condition ($F_{(1,6)}=9.720$). The other significant interactions reported below indicate that these effects of the sign of disparity, linear trend and configuration were larger for alignment to the right edge than alignment to the left edge. The interaction between side and configuration was significant ($F_{(1,6)}=39.774$). The interaction between side and sign of disparity was significant ($F_{(1,6)}=46.274$). The triple interaction between side, sign of disparity and configuration was significant ($F_{(1,6)}=8.076$). The triple interaction between side, linear trend and sign of disparity was significant ($F_{(1,6)}=24.470$).

4.3.3 Discussion

The perceived relative direction of a pair of features can be an average of their angular separation in the two eyes (Ono et. al. 1977; Sheedy & Fry, 1979, see section 1.4.3). However, in the present experiment, a binocular line on the background surface did not appear aligned with the left or right edge of the occluding surface when the average of the position of the edge in the two eyes was vertically aligned with the average of the position of the line in the two eyes. Relative to this average prediction, a leftwards bias occurred for alignment with the right edge and a rightwards bias occurred for alignment with the left edge, which is consistent with the Erkelens-bias reported by Erkelens et. al. (1996) and Ono et. al. (2003). The first aim of the present experiment was to evaluate the extent to which the Erkelens-bias increased with the disparity between the background and occluding surfaces. Erkelens et. al. (1996) found that the Erkelens-bias increased with disparity, whereas this was not observed in Experiment 5. In the present experiment, a larger range of disparities was used than in Experiment 5 and a relationship between the magnitude of disparity and the magnitude of the Erkelens-bias was found. However, the effect of disparity on the Erkelens-bias was only half as large as that which Erkelens et. al. (1996) found. Possible reasons for this discrepancy are discussed in the introduction to Experiment 7.

The second aim of the present experiment was to explore the stimulus conditions responsible for the Erkelens-bias. Textured monocular regions were lacking in the outline condition, yet the Erkelens-bias occurred provided that the outline was closer in depth than the comparison line. This is at odds with the claim made by Erkelens and van de Grind (1994), that Ono et. al. (1977) found that the perceived relative direction of a

pair of fused binocular features was an average of their angular separation in the two eyes rather than biased towards one eye because Ono et. al. (1977) used stimuli which were “all unstructured at the places where they were partly occluded by the foreground” (Erkelens & van de Grind, 1994, p.2964).

Since the Erkelens-bias does not depend on the presence of textured monocular regions, what then are the stimulus conditions for the Erkelens-bias? Although textured monocular regions were lacking in the outline condition, the stimulus specified the boundaries of a surface. The Erkelens-bias may depend on the presence of surface boundaries because the left eye always views a monocular region to the left of a surface and the right eye always views a monocular region to the right of a surface. Therefore, in the outline condition, the visual system may have responded to the untextured region to the left of the outline in the left eye’s image as a monocular region visible to the left eye, on the basis that the outline of the square specified the boundaries of an occluding surface. Likewise, the visual system may have responded to the untextured region to the right of the outline of the square in the right eye’s image as a monocular region visible to the right eye, on the basis that the outline of the square was an occluding surface and a monocular region is always visible to the right eye to the right of an occluding surface.

The difference in perceived alignment between the conditions where the outline was closer or farther in depth than the comparison line supports this theory. When the outline was closer than the line, a large Erkelens bias occurred for the left and right edge of the square. However, when the outline was farther in depth than the comparison line, perceived alignment was similar for alignment to the left and right edge of the outline (there was no Erkelens-bias). In these outline behind conditions, disparity specified that

the outline was the farthest feature in the stimulus and only the comparison line lay in the foreground. Therefore, it is possible that the Erkelens-bias did not occur when the outline was farther in depth than the line because then the outline of the square was responded to as texture on the background surface rather than as the edges of a foreground surface.



Figure 49. Schematic of stimuli used by Erkelens and van Ee (2007). From Erkelens and van Ee (2007).

The results of an experiment reported by Erkelens and van Ee (2007) after these data were collected also address the issue of the stimulus conditions for the Erkelens-bias. A schematic of their stimuli is shown in Figure 49. The dotted outline indicates the location of a central surface. The dark grey lines indicate the locations of two lines on the central surface. One of these lines abutted the left or right edge of the central region. The bright line indicates the location of a line in the surround region of the stimulus. Observers set the horizontal location of the line on the surround so that the central line appeared to bisect the outer lines. The disparity between the central and surround regions was varied and consequently the horizontal separation between the central line and the line on the surround differed between the eyes. Hence, the results of this experiment reveal whether the perceived relative direction of the central line and the line in the surround is biased towards their angular separation in one eye. As a result of the disparity between the central region and the surround, a monocular region was produced next to the left and right edges of the central surface. Erkelens and van Ee (2007) found that the perceived relative direction of the lines was biased towards their

angular separation in the left eye when the lines were next to the left edge and vice versa when the lines were next to the right edge. They found that the magnitude of this bias did not differ between conditions that contained textured monocular regions and conditions in which all texture was eliminated so only the three lines were visible. Hence, as was found in the present study, a bias of the perceived relative direction of features towards their angular separation in one eye (Erkelens-bias) occurred in the absence of monocularly visible texture.

On the basis of these results Erkelens and van Ee (2007, p.7) concluded that observers use “either of the two monocular 2-D images separately, but not a single cyclopean view, to assess 3-D symmetry when occlusion is involved.” Although Erkelens and van Ee (2007, p.2) state in their introduction that “dot density was varied to investigate the influence of half-occlusions [monocular regions] on bisection”, the finding that the Erkelens-bias occurred in the absence of textured monocular regions was not discussed. Erkelens and van Ee (2007) did not address the issue of why an Erkelens-bias occurred in the condition that consisted of only three vertical lines? It seems implausible that the stimulus consisting of three vertical lines alone was sufficient to specify a foreground surface. Therefore, the results of Erkelens and van Ee (2007) do not support the proposal of the present study that the Erkelens-bias occurs when the stimulus specifies a foreground surface. That the Erkelens-bias was found to occur when the stimulus consisted of only three vertical lines does not support the conclusion of Erkelens and van Ee (2007, p. 7) that the Erkelens-bias occurs “when occlusion is involved”. The only way to reconcile this result with the theory that the bias is a response to a foreground surface is to propose that a surface was assumed to be present when the stimulus consisted of only three lines. This is plausible because the

lines were always located at the edge of the occluding surface in the textured stimuli with which the lines alone condition was interleaved across over 1000 trials per observer.

4.4 Experiment 7: Bias magnitude in the Erkelens et al. (1996) study.

In Experiments 5 and 6, the perceived direction of the left and right edges of an occluding surface relative to a line on the background surface was not an average of the angular separation of the edge and the line in both eyes. Relative to this average prediction, there was an alignment bias towards the centre of the occluder, which indicates that the angular separation of the edge and the line in the eye that viewed the monocular region next to the edge made a larger contribution to their perceived relative direction than their angular separation in the other eye (Erkelens-bias). In Experiment 5, the Erkelens-bias for a 6 minute of arc disparity did not differ from that for a 10 minute of arc disparity. A larger range of disparities was used in Experiment 6, and it was observed that the Erkelens-bias was at most 2 minutes of arc larger with a disparity of 12 minutes of arc than a disparity of 4 minutes of arc. This effect of disparity is half as large as that found by Erkelens et. al. (1996), in which case the magnitude of the Erkelens-bias was equal to half the disparity between the background and the occluder.

The surfaces that Erkelens et. al. (1996) used were much larger than those in Experiments 5 and 6 of this thesis. The background surface used by Erkelens et. al. (1996) was 60° square and the occluding surface subtended 28°, whereas in Experiment 5 and 6, the background subtended 8.4° and the occluder subtended 1.6°. The large surfaces used by Erkelens supported disparities as large as 2°, whereas 12 minutes of arc was the largest disparity that was used in the previous experiments because diplopia tended to occur for the small surfaces with disparities larger than 20-30 minutes of arc. The occluding surface in the Erkelens et. al. (1996) study was a circle, whereas it was a square in Experiments 5 and 6. Additionally, Erkelens et. al. (1996) presented the

stimuli as anaglyphs, whereas a mirror stereoscope (described in the general method 2.1.1) was used to display the stimuli in Experiment 5 and 6. Due to the anaglyph technique, the monocular regions appeared to be a different colour than the binocularly visible regions of the background, which is not the case when a mirror stereoscope is used to display the stimuli. This is because the perceived colour of the binocularly visible regions of the stimulus is determined by the colour of that region in both eyes' views, whereas the perceived colour of the monocularly visible region only depends on the colour in one eye (Erkelens et. al. 1996). Therefore, in order to replicate the strong effect of disparity reported by Erkelens et. al. (1996), a large circle was presented using the anaglyph technique with the same range of disparities relative to its background that was used by Erkelens et. al. (1996).

The stimuli in the present experiment differed from those used by Erkelens et. al. (1996) in four respects. Firstly in the Erkelens et. al. (1996) study, the centre of the circle lay in the median plane of the observer. Consequently, the left and right edges of the circle lay at an eccentricity of 14° from the median plane of the observer. It is unclear in the Erkelens et. al. (1996) study whether observers turned their heads towards the target edge or kept their head straight towards the centre of the circle. This ambiguity was eliminated in the present study by presenting the circle such that the edge with which observers aligned the background line always lay in the median plane.

Secondly, the stimuli in the present experiment were not as large as the stimuli used by Erkelens et. al. (1996), for which the background surface was 60° square and the occluding surface had a diameter of 28° . However, the stimuli in the present experiment were extremely large. The background surface was 31° high and 49.9° wide

and the occluding surface had a diameter of 20°. If the size of the stimuli affects the magnitude of the Erkelens-bias, then a smaller effect of disparity may be observed than in the Erkelens et. al. (1996) study, but it would also be predicted that a larger effect of disparity would be found than in Experiments 5 and 6, because the occluding surface in the present experiment was approximately ten times larger than that used in Experiment 5 and 6 and the background surface was approximately three times larger than that used in Experiment 5 and 6.

Thirdly, in the Erkelens et. al. (1996) experiment, the background and occluding surfaces were composed of the same percentages of randomly positioned black and coloured squares (red in one eye and green in the other eye). This differed from the present experiment, where different percentages of black and coloured squares were used for the occluder and the background. Different percentages of black and coloured squares were used for the occluder and the background because Erkelens et. al. (1996) observed that perceived alignment was more precise when the occluder was made monocularly visible by adding a coloured ring at the rim of the circular occluder. Erkelens et. al. (1996) reported that apart from the precision of the settings, adding the bright rim to the occluder did not affect alignment to the left and right edges of the occluder.

Fourthly, it was not possible to equate the gap separating the end points of the background line from the rim of the occluder, because this gap was not specified by Erkelens et. al. (1996). Erkelens et. al. (1996) reported that the gap was large enough so that the disparity gradient between the line and the rim of the occluder did not cause diplopia but also small enough so that the endpoints were close to the rim. In the present

experiment, the vertical gap in the background line was chosen so that if observers aligned the background line with the rim using the eye that viewed the monocular region, then there would be a horizontal gap of at least one degree between the line and the rim of the occluder. This ensured that the gap was sufficiently large that observers could move the background line left and right without it entering the occluded region of the background.

4.4.1 Method

Display

The images intended for each eye were presented on a 76.2 centimeter LCD monitor (Dell 3007WFP) with a resolution of 2560 x 1600. The screen was viewed from a distance of 60cm, from which pixel size was approximately 1.23 minutes of arc. Head position was stabilised with a chinrest. The images for both eyes were presented on the same monitor. The texture on the surfaces was black and blue in the image for one eye and black and red in the image for the other eye and was viewed through blue-red anaglyph glasses. Faint amounts of cross talk were visible through each filter. This does not affect the conclusions drawn in this experiment and the following experiment, which used the same apparatus, because the conclusions are based on between condition differences for which cross talk did not covary. The colour in which the image for each eye was presented was counterbalanced between blocks to control for differences in luminance contrast between the blue and red filter. The results did not differ between these two blocks (see statistical analysis in results section 4.4.2).

Stimuli

The background surface was 31° high and 49.9° wide. 85% of the squares (1.23 minutes of arc) that comprised the background surface were assigned at random to be black and the remainder were blue in one eye's image and red in the other eye's image. The background surface was assigned an uncrossed disparity of 12.3 minutes of arc relative to the screen. The occluding surface was a circle with a diameter of 20°. 65% of

the squares comprising the occluder were assigned at random to be black and the remainder were blue in one eye's image and red in the other eye's image. The rim of the circle was 1.23 minutes of arc thick and blue in one eye's image and red in the other eye's image. A vertical gap in the middle of the background line prevented observers from moving the line into the occluded area of the background. The vertical gap was 14.3° high. Were the line aligned with the leftmost or rightmost point of the occluder in the eye that viewed the monocular region, then the smallest separation between the background line and the edge of the occluder would occur for the largest disparity used (2°) and be equal to 1° .

Procedure

The occluding circle was presented with crossed disparities of 0, 0.5, 1, 1.5 or 2° relative to the background surface. At the beginning of a trial, the circle was presented on either the left or right side of the screen so that its left or right edge lay in the centre of the screen. The line on the background surfaces was initially presented either 37 minutes of arc to the left or right of alignment with the centre of the screen. Observers were instructed to shift this line horizontally using the arrow keys in order to vertically align it with the leftmost point of the circle if the left side of the circle was closest to the centre of the screen or to vertically align it with the rightmost point of the circle if the right side of the circle was closest to the centre of the screen. In each block of trials, each combination of disparity, side, and starting position was presented twice in a random order. In the first block of trials, it was randomly determined whether the image for the left eye was blue and the image for the right eye was red or vice versa. The colour used for each eye was switched in the second block of trials.

Observers

Nine observers from the University of New South Wales community participated. Seven were naïve of the purposes of the experiment.

4.4.2 Results

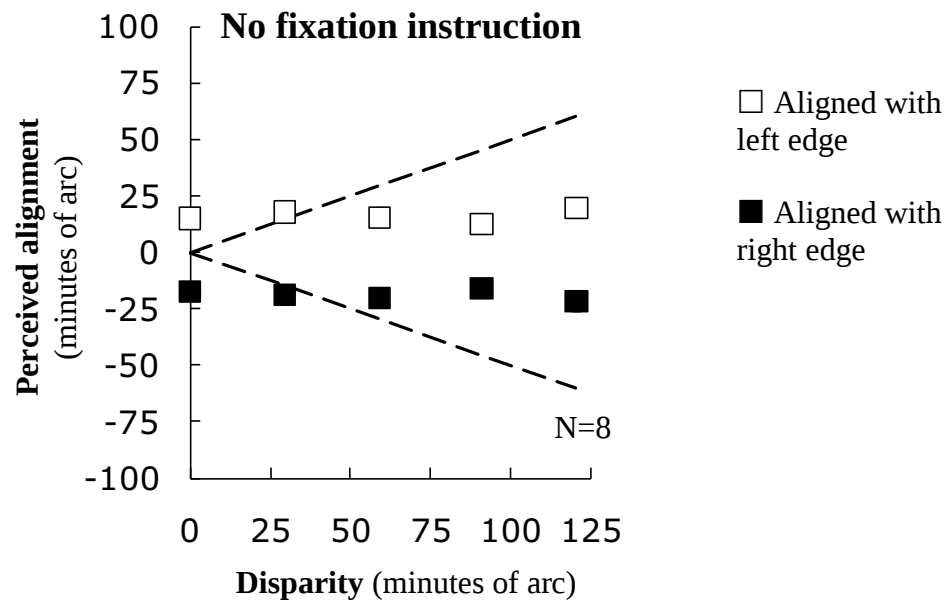


Figure 50. Results of Experiment 7.

Group data for eight of the nine observers is presented in Figure 50. The results for one observer differed from this group and are described in the next paragraph. The horizontal location of the background line is plotted against the disparity of the occluding and background surfaces. The dashed diagonal lines with positive and negative slope in Figure 50 show the values that correspond to alignment using solely the position of the line and the edge in the left eye (positive slope) or the right eye (negative slope). A value of zero indicates that the average of the position of the background line in the two eyes views was vertically aligned with the average of the position of the edge of the occluding surface in the two eyes views (average prediction). The alignment settings for alignment with the left edge of the circle (□ in Figure 50) were biased to the right of this average prediction by approximately 19 minutes of arc. The alignment settings for alignment with the right edge (■ in Figure 50) were biased to the left of the average prediction by the same amount. These biases are in the

expected direction of the Erkelens-bias. The statistical analysis reported at the end of the results section confirmed that the bias did not vary with disparity. Hence, the results for these eight observers are qualitatively different from the results reported by Erkelens et. al. (1996).

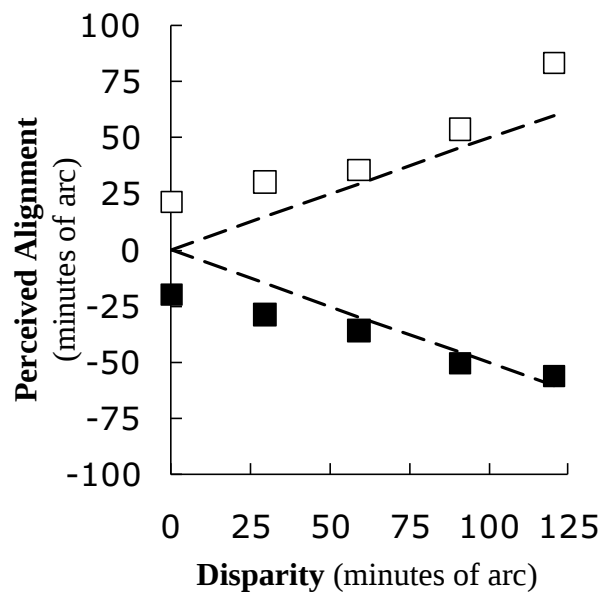


Figure 51. Results of Experiment 7 for one observer. Standard error bars are smaller than the data points. $n=8$.

The Erkelens-bias increased with disparity for one of the naïve observers. The results for this observer are shown in Figure 51. The slope of the alignment settings for this observer was calculated using linear regression in order to compare the effect of disparity on the Erkelens-bias for this observer with that reported by Erkelens et. al. (1996). The settings for both edges were combined by reversing the sign of the settings for alignment with the left edge. The slope measured 0.43 and 95% confidence intervals indicate the slope was 0.34 to 0.53, which contains the value of 0.5 reported by Erkelens et. al. (1996). Therefore, the effect of disparity for one observer in the present study was similar to that reported by Erkelens et. al. (1996). After the experiment, this observer

was asked to describe their approach to the alignment task. The observer reported a tendency to fixate the background line (The significance of this is evaluated in Experiment 8).

The results for all nine observers were analysed using a two-way multivariate analysis of variance using planned orthogonal contrasts and the Decision-Wise error rate was controlled ($\alpha=0.05$). The sign of the alignment settings for the left side was reversed so that the expected direction of the Erkelens-bias was the same for the left and right edges. The main effects of side ($F_{(1,8)}=0.171$), the colour of each eye's filter ($F_{(1,8)}=0.179$) and the starting position of the background line were not significant ($F_{(1,8)}=3.966$). The main effects of linear trend ($F_{(1,8)}=3.48$) and quadratic trend ($F_{(1,8)}=0.958$) were not significant, which indicates that averaged across the nine observers the Erkelens-bias did not increase with disparity. The interaction between side and the starting point of the background line was significant ($F_{(1,8)}=20.238$). The 95% confidence intervals for this effect indicate that the Erkelens-bias was 5.254-16.306 minutes of arc larger when the starting location of the background line was biased towards the eye viewing the monocular region than when the starting location was biased towards the other eye.

4.4.3 Discussion

The Erkelens-bias that Erkelens et. al. (1996) reported for alignment to the left or right edges of an occluder increased with disparity such that the slope of the alignment settings as a function of disparity was equal to 0.5. The purpose of the present experiment was to replicate the magnitude of this effect of disparity, since the Erkelens-biases that were found in Experiment 5 did not increase with disparity and the Erkelens-biases that were found in Experiment 6 increased with disparity by approximately half the amount that Erkelens et. al. (1996) found. In the present study, the differences between the stimuli and procedure of these previous experiments and that of Erkelens et. al. (1996) were much reduced and the large effect of disparity was observed for one of the nine observers. However, the Erkelens-bias for eight of the nine observers did not increase with disparity. Therefore, the results suggest that the discrepancy between the results of Erkelens et. al. (1996) and the results of Experiments 5 and 6 of the present study is not explained by the difference in surface size between the studies. The results indicate that the discrepancy is not explained by the larger range of disparities that was used by Erkelens et. al. (1996), or that Erkelens et. al. (1996) presented the images to the two eyes using the anaglyph technique in which case the colour of the monocular regions differed from the colour of the binocular region of the background.

The observer that exhibited the large effect of disparity reported a tendency to fixate the background line. Whether the strong effect of disparity is contingent on observers fixating the background line was evaluated in Experiment 8.

4.5 Experiment 8: Magnitude of the Erkelens-bias with fixation at the depth of the occluder or the background.

Erkelens et. al. (1996) instructed observers to vertically align a binocular line on the background surface with the leftmost or rightmost part of the edge of an occluding circle. Erkelens et. al. (1996) did not give observers instructions as to where to fixate during the alignment task so observers were free to fixate the stimulus wherever they liked. Erkelens et. al. (1996) reported that for all observers, the line appeared aligned with the edge when it was aligned with the edge in the image that contained the monocular region next to the edge. Erkelens et. al. (1996) argued that the alignment bias they reported was not contingent on where observers fixated because it was likely that fixation differed between the four observers.

Ono et. al. (2003) measured the perceived direction of the edges of an occluding surface relative to a line at the depth of the background while observers fixated a single point at the depth of the background. They found that the perceived relative direction of the edge and the line was biased towards their angular separation in the left eye for the left edge and their angular separation in the right eye for the right edge (Erkelens-bias). Ono et. al. (2003) proposed that this result depended on observers converging at the depth of the background surface. However, they did not refer to the earlier work of Erkelens et. al. (1996) in which it was argued that the Erkelens-bias does not depend on fixation. The magnitudes of the Erkelens-biases found by Erkelens et. al. (1996) and Ono et. al. (2003) was compared in section 1.5.3 by calculating the extent that the angular separation of the background line and the occluding edge in each eye contributed to perceived alignment. The eye that viewed the monocular region next to each edge contributed 100% in the Erkelens et. al. (1996) study and 85.7% in

experiment 3 of Ono et. al. (2003). Therefore, the Erkelens-bias was smaller in the Ono et. al. (2003) study, in which fixation was restricted to the background surface, than the Erkelens-bias in the Erkelens et. al. (1996) study under conditions of natural fixation. Therefore, the results of Erkelens et. al. (1996) appear to be at odds with the Ono et. al. (2003) proposal that convergence affects the magnitude of the Erkelens-bias.

In the previous experiment of the present study (Experiment 7), the stimuli and procedure was similar to those of Erkelens et. al. (1996), yet the large Erkelens-bias reported by Erkelens et. al. (1996) was replicated for only one of the nine observers. Of particular interest is that this observer reported a tendency to fixate the background line, which is consistent with the proposal of Ono et. al. (2003) that the Erkelens-bias depends on observers fixating at the depth of the background. Therefore, we wondered whether the results of Erkelens et. al. (1996) could be replicated with more observers if fixation was maintained at the depth of the background surface.

In Experiment 8, Experiment 7 was repeated except that the observers were instructed to complete the alignment task while fixating a particular point in the stimulus. Of the 18 naive observers that were recruited, 10 were randomly assigned to maintain fixation on the lower tip of the upper background line. It was predicted that the Erkelens-bias found by Erkelens et. al. (1996) would be replicated for this group of observers on the basis of the hypothesis of Ono et. al. (2003) that the Erkelens-bias occurs when fixation is at the depth of the background. The other 8 observers were instructed to perform the alignment task while fixating the edge of the occluding surface with which they aligned the background line. According to the Ono et. al. (2003) proposal, the Erkelens-bias will not occur for this group of observers since the depth

of fixation differs from the background. The apparatus, stimuli, and procedure of the present experiment were identical to that of Experiment 7 except for these instructions regarding fixation.

4.5.1 Results

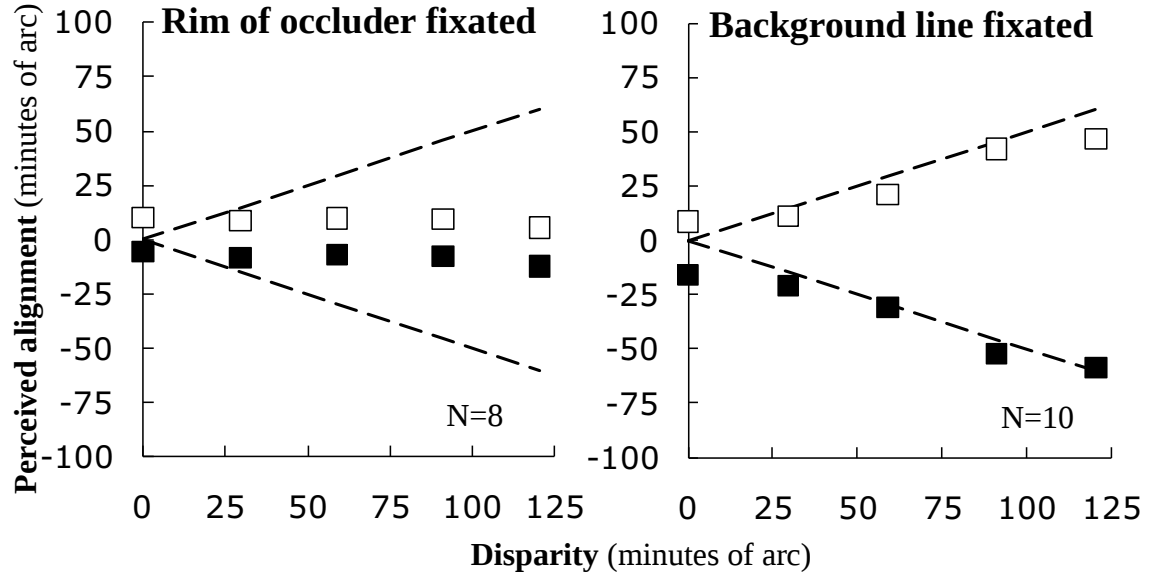


Figure 52. Group data for Experiment 8.

Group data for the observers that were instructed to fixate the rim of the occluder is shown in the left graph of Figure 52. For this condition, perceived alignment approximated the average prediction (defined in section 4.4.2), although a small leftwards bias occurred for alignment with the right edge and vice versa for alignment with the left edge (in the same direction as the Erkelens-bias). Hence, perceived alignment in this condition was similar to that in Experiment 7 when observers were not given any instructions regarding fixation. Group data for the observers that were instructed to fixate the tip of the background line is shown in the right graph of Figure 52. In this condition, the magnitude of the leftwards bias for alignment with the right edge and the rightwards bias for alignment with the left edge increased with disparity, consistent with the hypothesis of Ono et. al. (2003). The effect of disparity varied between observers in this condition and the slopes of the alignment settings for each observer are presented in Table 3. Prior to calculating the slopes, the settings for the left and right edge were combined by reversing the sign of the alignment settings for the left

edge, because the leftward shift for alignment to the right edge was the same magnitude as the rightward shift for alignment to the left edge. The slope of the alignment settings was calculated using linear regression. The slopes for the results of Erkelens et. al. (1996) was 0.5 and the slopes for 6 of the observers that were instructed to fixate the tip of the background line were not significantly different from this value, whereas the slopes for all of the observers that were instructed to fixate the rim of the occluder were significantly different from the value of 0.5 and were close to 0.

Table 3. Slope of the alignment settings as a function of disparity.

Fixate occluder				Fixate background			
	Slope	95% C. I. Lower	95% C. I. Upper		Slope	95% C. I. Lower	95% C. I. Upper
ML	-0.05	-0.15	0.05	NY	0.01	-0.08	0.09
EA	-0.03	-0.12	0.06	YJ	0.09	0.04	0.15
OC	0.03	-0.11	0.18	YM	0.12	0.04	0.20
AM	0.05	-0.03	0.12	KG	0.33	0.22	0.44
WL	0.05	-0.04	0.14	FH	0.43	0.34	0.53
SE	0.05	-0.05	0.16	PE	0.45	0.39	0.52
JJ	0.06	0.00	0.12	SF	0.47	0.41	0.53
TC	0.07	0.02	0.11	ML	0.53	0.48	0.58
				KM	0.53	0.42	0.65
				YL	0.54	0.49	0.59

The results were analysed using a two-way multivariate analysis of variance testing for differences between the two groups and their interaction with the within-group effects of alignment to the left or right edge, the colour assigned to each eye, linear and quadratic trend for disparity and the starting position of the background line. The Decision-Wise error rate ($\alpha=0.05$) was controlled for each of the contrasts, which were orthogonal to one another. The sign of the alignment settings for the left side was reversed so that the expected direction of the Erkelens-bias was the same for the left and right edge. The main effect of linear trend was significant ($F_{(1,16)}=20.632$) and as was its interaction with the between group comparison ($F_{(1,16)}=19.765$). 95% confidence

intervals for this effect were calculated using the procedure described by Bird (2004). The slopes of the alignment settings for the fixate background condition and fixate occluder conditions differed by 0.14-0.42. The main effects of side ($F_{(1,16)}=4.929$), the colour of the filter used for each eye ($F_{(1,16)}=0.186$) and quadratic trend ($F_{(1,16)}=0.836$) were not significant. The interaction between the initial location of the background line and side was significant ($F_{(1,16)}=26.716$). The Erkelens-bias was 6.278-15.01 minutes of arc larger when the starting location of the background line was biased towards the eye that views the monocular region than when the starting location was biased towards the other eye.

4.5.2 Discussion

Erkelens et. al. (1996) found that perceived alignment between a background line and the left and right edges of an occluding surface was determined solely by the eye that views the monocular region next to the edge. In Experiment 7, observers were not given any instructions regarding fixation, which is consistent with the Erkelens et. al. (1996) procedure. However, the results of Erkelens et. al. (1996) was replicated for only one of nine observers. This observer reported a tendency to fixate the background. In the present study, the Erkelens et. al. (1996) result was replicated for 6 of the 10 observers that were instructed to fixate the tip of the background line but was not replicated for any of the observers that were instructed to fixate the rim of the occluder. Hence, the results of the present experiment and Experiment 7 show that the alignment bias reported by Erkelens et. al. (1996) is contingent on where the observer fixates. This is contrary to the conclusion of Erkelens et. al. (1996, p. 2144-5) that “since the subjects were free to fixate the stimulus wherever they liked, it is most likely that the process, determining which eye is used for alignment, is related to aspects of the stimulus and not to specific retinal locations.”

Erkelens et. al. (1996) and Ono et. al. (2002; 2003) proposed different theories of perceived direction at occluding edges (reviewed section 1.5.4). These theories are described below in order to show that the effect of fixation found in the present study is more easily accounted for by the theory of Ono et. al. (2002; 2003) than the theory of Erkelens et. al. (1996). It is commonly argued (Hering, 1879/1942; Roelofs, 1959; Ono, 1979, Ono & Mapp, 1995) that the perceived direction of features is referred to a point midway between the eyes (cyclopean eye). As pointed out by Erkelens and van Ee

(1994), relative to a cyclopean eye, the left and right edges of an occluding surface have the same physical direction as the half of the monocular region of the background that is next to each edge (see section 1.5.1). Therefore, if the occluding surface and the background surface were perceived in their physical direction relative to a cyclopean eye, then the edge of the occluding surface would have the same perceived direction as part of the monocular region of the background. Erkelens et. al. (1996) and Ono et. al. (2002; 2003) both argued that the occluding surface and the background surface are not assigned the same perceived direction but proposed different means by which this is accomplished.

Ono et. al. (2002; 2003) proposed that the perceived direction of the occluding surface and the background surface is referred to the cyclopean eye. According to this theory, the perceived direction of the surfaces does not overlap because the perceived direction of the non-fixated surface is biased laterally away from its physical direction. The theory proposes that when the background is fixated, the background surface is perceived in its physical direction relative to a cyclopean eye, while the perceived direction of the edge of the occluding surface is biased laterally away from the monocular region. This proposal is consistent with the Erkelens-bias (see section 1.5.3) for the perceived alignment between the occluding edge and the background line found in the present study with fixation at the depth of the background. Ono et. al. (2002; 2003) proposed that the perceived direction of the background surface is biased laterally away from the occluding edge when fixation is at the depth of the occluding surface. Based on this proposal, an Erkelens-bias of perceived alignment between the occluding edge and the background line is predicted in the present study for those observers that were instructed to fixate the occluding surface. This was not found in the present

experiment. When observers were instructed to fixate the rim of the occluding surface, perceived alignment was based on the average of the relative direction of the edge and the line in both eyes. The absence of an Erkelens-bias with fixation on the occluding surface is consistent with the Ono et. al. (2002; 2003) theory if it is assumed that the background line lay outside of the portion of the background affected by the lateral bias of perceived direction. This seems plausible because the tips of the background line were horizontally separated from the monocular region by 2° when observers indicated that the background line appeared aligned with the edge of the occluding circle.

Erkelens et. al. (1996) proposed that the perceived direction of features in the “neighbourhood” of the left and right edges of an occluding surface are not referred to the cyclopean eye. The perceived direction of these features is instead referred to the eye that views the monocular region next to the edge, because from that reference point the physical direction of the monocular region of the background differs from the physical direction of the occluding surface. Erkelens et. al. (1996) argued that the advantage of this theory is that it is possible for both surfaces to be perceived in their physical direction simultaneously. This theory predicts that the perceived relative direction of any pair of features in the vicinity of a monocular region will match their relative direction in the eye that views the monocular region. Although the Erkelens-bias for perceived alignment in the present study with fixation at the depth of the background is consistent with this theory, it is not clear why the theory would predict that the Erkelens-bias would not occur with fixation on the occluding surface. The Erkelens et. al. (1996) and Ono et. al. (2002; 2003) theories were further tested in Experiment 9.

4.6 Experiment 9: Is perceived direction at occlusions veridical?

Erkelens et. al. (1996) and Mapp and Ono (1999) argued that it not yet known whether the perceived direction of features in the vicinity of the left or right edge of an occluding surface is veridical. The reason for this ambiguity is that in order to specify veridical alignment of the background line with the occluding edge, a reference point for that judgment is required. It is commonly argued that the reference point is a point between the eyes called the cyclopean eye (e.g. Hering (1879/1942; Ono 1979; Ono & Mapp, 1995). Erkelens et. al. (1996) argued that if the cyclopean eye were the reference point for the perceived direction of features in the vicinity of a monocular region, then it is not possible for the perceived direction of the features on both the occluding surface and the background surface to be veridical (see also Ono et. al. 2002; 2003). The basis for this argument is explained below with reference to Figure 53 and Figure 54.

Figure 53a is a bird's eye view of a line on a background surface that is aligned with the left edge of an occluding surface in the left eye's view. Erkelens et. al. (1996) found that under these conditions the background line and the occluding edge appear vertically aligned and this was replicated in the Experiment 8 provided that the observer fixated the background surface. In Figure 53b, it is assumed that the left edge is perceived in the correct location and that its perceived direction (dashed line) is referred to the cyclopean eye. Since it is known that the background line and the edge appear vertically aligned, the perceived direction of the background line is drawn overlaying the perceived direction of the left edge. The resulting perceived direction of the background line intersects a point on the background that lies to the left of its correct

location (Figure 53b). Hence, the perceived direction of the background line would be incorrect. In Figure 54a, it is assumed that the background line is perceived in the correct location and that its perceived direction is referred to the cyclopean eye. The perceived direction of the edge is drawn overlaying the perceived direction of the background line and thus lies to the right of its correct egocentric direction.

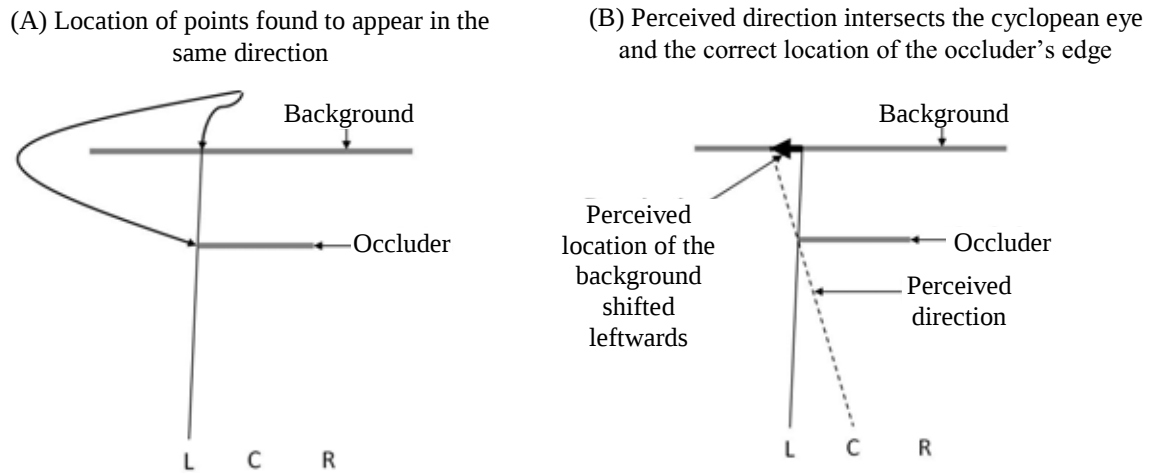


Figure 53. Location of a background line that appears vertically aligned with the edge of an occluder (A). Shows the possibility that the perceived direction of these features is referred to the cyclopean eye such that the edge of the occluder is perceived in the correct location (B).

Erkelens et. al. (1996) argued that it was possible for both the occluding edge and the background line to appear in the correct direction if their perceived direction was referred to the eye to which the monocular region is visible instead of the cyclopean eye. This possibility is shown in Figure 54b. The perceived directions of the background line and the perceived direction of the edge intersect their correct location, but are referred to the left eye instead of the cyclopean eye. Therefore, the alignment data presented by Erkelens et. al. (1996) and Ono et. al. (2003) cannot be used to determine whether the occluder and its background are perceived in the correct direction, because this depends on the reference point for their perceived direction, which is unknown.

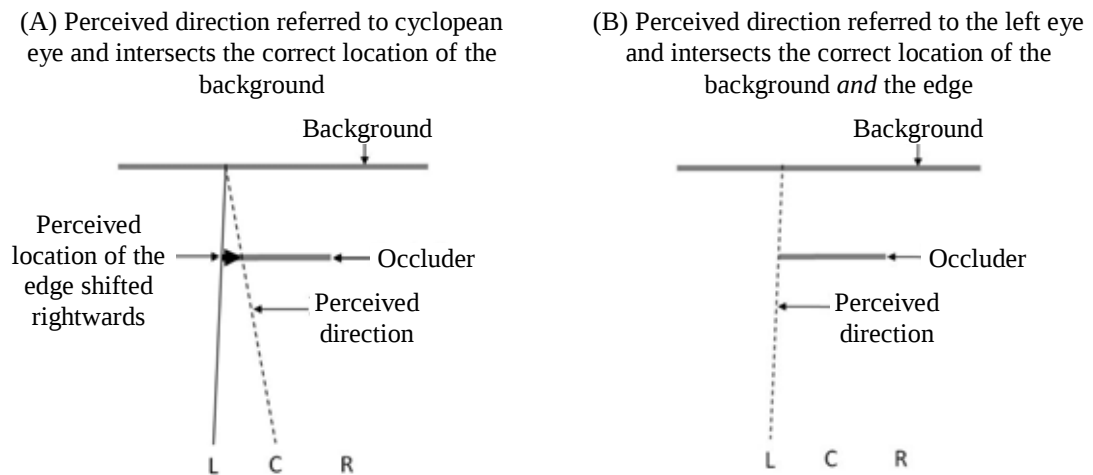


Figure 54. Perceived direction referred to cyclopean eye (A) or to the eye that views the monocular region (B).

Erkelens et. al. (1996) proposed that the perceived directions of features in the neighbourhood of monocular regions are referred to the eye that views the monocular region so that all the features in the neighbourhood of a monocular region may be perceived in the correct direction. Ono et. al. (2002; 2003) hypothesised that the cyclopean eye is the reference point for the perceived direction of features in the vicinity of monocular regions. Ono et. al. (2002; 2003) hypothesised that the perceived directions of features in the vicinity of a monocular region are laterally displaced relative to their physical direction. When the observer fixates at the depth of the occluder, the perceived direction of features on the background surface will be displaced laterally away from the edge of the occluding surface. When the observer fixates at the depth of the background surface, the perceived direction of features on the occluding surface will be displaced laterally away from the monocular region.

It is possible to test whether features in the vicinity of a monocular region are perceived in their physical direction by measuring perceived alignment between a pair

of features at the *same* depth. This is because veridical alignment of features in the same depth plane is the same regardless of whether the reference point for the judgment is the left eye, the right eye, or any point in between such as the cyclopean eye.

Perceived alignment between a feature in a monocular region and a feature at the same depth was measured by Erkelens and van de Grind (1994), van Ee et. al. (1999) and in experiment 3 of Ono et. al. (2003). These studies were reviewed in section 1.5.2. van Ee et. al. (1999) found that the perceived direction of a vertical line in a monocular region depended on its proximity to binocular features on the background surface. When the monocular line was not proximal to a binocular feature on the background surface, the perceived direction of the monocular line varied with the depth of the fixation point. Consequently, the monocular line and the binocular line appeared horizontally offset when they were physically aligned in the image that contained the monocular line. This finding is consistent with the results of studies reviewed in section 1.4.1 in which the perceived egocentric direction of small monocular features presented alone was found to vary with vergence. However, the effect of vergence on the perceived direction of a monocular line was much reduced or eliminated when the monocular line was proximal to a binocular feature as in the Erkelens and van de Grind (1994) and van Ee et. al. (1999) studies. Although Erkelens and van de Grind (1994) and van Ee et. al. (1999) did not discuss their results with respect to the issue of whether perceived direction is veridical in the neighbourhood of the left and right edges of an occluding surface, the results of those two studies are consistent with the proposal that features in the vicinity of a monocular region are perceived in their veridical direction. However, it is possible that while the perceived direction of the features in a monocular region was veridical in those studies, the perceived direction of the occluding edge was

not. This possibility is consistent with the Ono et. al. (2002; 2003) theory, which predicts that the features on either the occluding or the background surface are perceived in the correct direction, while the perceived direction of features on the non-fixated surface are laterally displaced from their true direction.

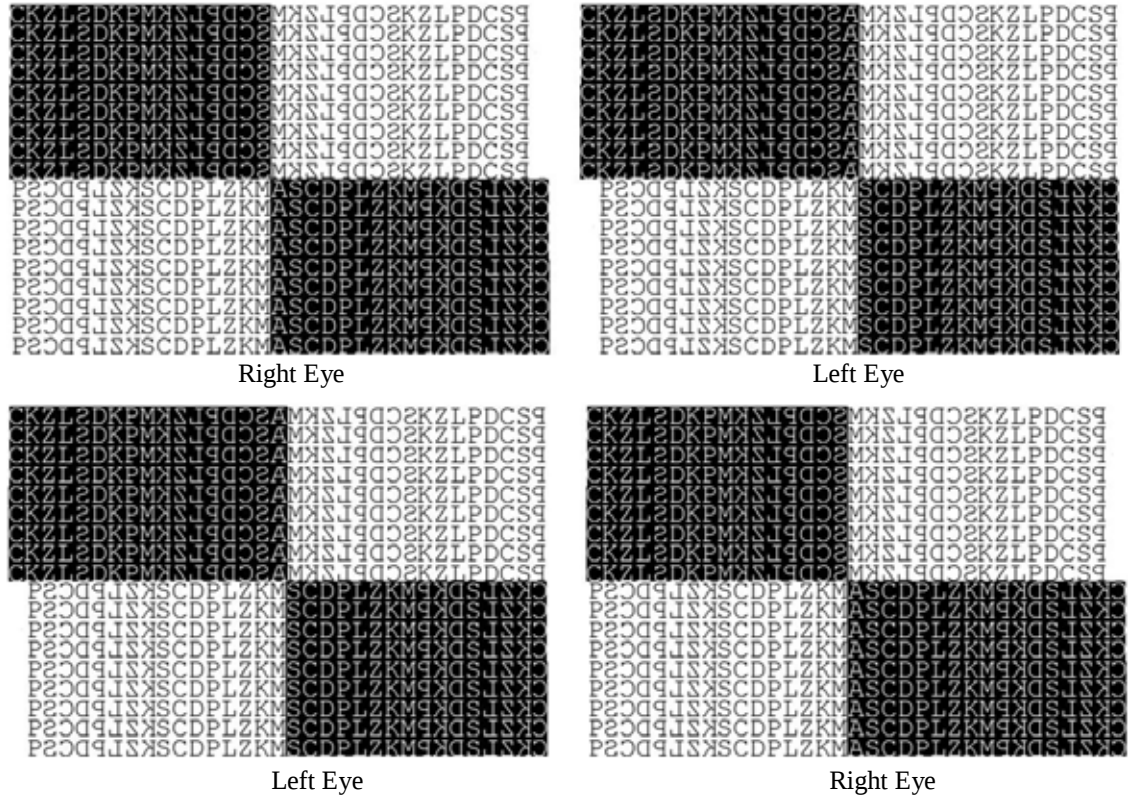


Figure 55. Stimuli used in Experiment 9. The top left and top right images are for crossed fusion. The bottom images are for uncrossed fusion.

The purpose of Experiment 9 was to determine whether perceived direction is veridical at occlusions, as argued by Erkelens et. al. (1996), or laterally biased from veridical, as argued by Ono et. al. (2002; 2003). This was accomplished using the stimulus shown in Figure 55. The stimulus consisted of two background surfaces and two foreground surfaces. In the top half of the image, a foreground surface (white) occludes the right side of a background surface (black). In the bottom half of the image, a foreground surface (white) occludes the left side of a background surface (black). The

left edge of the upper foreground surface and the right edge of the bottom foreground surface are aligned in the physical stimulus which would give rise to this stereogram. Therefore, the edges of the occluder will appear aligned if they are perceived in the correct location. This is predicted by Ono et. al. (2002; 2003) with fixation at the depth of the background surface and by Erkelens et. al. (1996) irrespective of fixation. In the centre of the images is a column of letter A's on the background surface. The upper half of this column is only visible to the left eye due to occlusion by the white surface on the top right. The bottom half of the column of letter A's is only visible to the right eye due to occlusion by the white surface on the bottom left. Although the upper and lower columns of A's are not visible to the same eye, they are vertically aligned in the physical stimulus that would give rise to the two eyes views in this stereogram. On this basis, it is possible to conclude that the perceived direction of the monocular regions is not veridical if the upper and lower column of letter A's do not appear vertically aligned.

If features near monocular regions are perceived in their correct location as proposed by Erkelens et. al. (1996), then the edges of the two occluding surfaces will appear aligned, and simultaneously, the upper and lower columns of letter A's will appear aligned. According to the Ono et. al. (2002; 2003) theory, either the edges of the surfaces or the monocularly visible letters will be perceived in a direction that is laterally displaced from their physical direction and hence will not appear aligned.

The author, who unfortunately displays a very strong ocular prevalence (see page 47) for the right eye, only rarely perceived the column of A's visible to the left eye. Therefore, suppression of the monocular regions was also measured since this

would interfere with the observer's judgment of the relative positions of the monocular regions.

4.6.1 Method

Apparatus

The stimulus was presented using the mirror stereoscope described in the general method (see section 2.1).

Stimuli

The stimulus consisted of a background surface that was partially occluded by two surfaces (Figure 55). These occluding surfaces were visible in the upper right and bottom left quadrant of the stimulus. In the centre of the stimulus, the upper right corner of the lower surface was attached to the lower left corner of the upper surface. Consequently, the left edge of the upper occluder was physically aligned with the right edge of the lower occluder. The two occluding surfaces had the same disparity as each other and a disparity of zero relative to the screen. The background surface was visible in the upper left and lower right quadrant of the stimulus. Relative to the occluding surfaces, the background surface had a crossed disparity of 11 minutes of arc that was created by shifting the background surface 5.5 minute of arc to the left on the left screen while shifting the background surface 5.5 minutes of arc to the right on the right screen.

A region of the background surface that was 11 minutes of arc wide and extended the full height of the background was hidden for one eye by the occluding surfaces. The upper part of this monocular region of the background was visible to the left eye next to the left edge of the upper occluding surface, while the lower part of the

monocular region was visible to the right eye next to the right edge of the lower occluding surface. Both monocular regions contained a single column of letter A's that were centred on the vertical midline of the screens and hence the vertical midline of the monocular regions.

The background surface consisted of white letters on a black background and the occluding surfaces consisted of black letters on a white background. The letters were 10 minutes of arc high and 7.3-10 minutes of arc wide. Mirror reversing some of the letters and placing dissimilar letters side-by-side prevented false matches. Each surface was 1.8° high and consisted of 9 rows of letters with a 1.6 minute of arc gap between rows. Each occluding surface was 17 letters across and was 2.6° wide. The width of the background surface differed between the two eyes due to the monocular region of the background next to the vertical edge of the occluding surfaces. Including the monocular region, the upper and lower regions of the background surface were each 17 letters across (2.8° wide).

Procedure

Suppression of the monocular regions was measured first. Observers were instructed to fixate the centre of the stimulus where the four surfaces intersected. Observers were instructed to press and hold the S-key when the upper column of A's was perceived and to release the S-key when the column of A's was not perceived. Observers were also instructed to press and hold the K-key when the lower column of A's was perceived and to release the K-key when the lower column of A's was not

perceived. Observers were instructed to press and hold both keys during periods where both columns were simultaneously perceived. Observers initiated the suppression task with a keypress and the stimulus was extinguished with a white screen after one minute.

A 5 minute break followed the suppression task, during which the instructions for the next task were explained to observers. Observers were instructed to fixate the centre of the stimulus where the four surfaces intersected and to judge whether the upper column of A's appeared vertically aligned or appeared side-by-side. Then observers were asked whether the left side of the top right surface appeared aligned with the right side of the bottom left surface.

Observers

Seven observers were recruited from the population of undergraduates studying first year psychology at the University of New South Wales and were all naive of the motivation for the experiment and the expected results. The visual acuity of both eyes was measured and only observers with at least 6/6 acuity in both eyes participated.

4.6.2 Results

The suppression task revealed that no suppression occurred for either monocular region for any of the observers. Six observers reported that the upper columns of A's appeared offset to the left of the lower column of A's. One observer reported that the upper and lower column of A's appeared aligned and that simultaneously, the edges of the upper and lower foreground surfaces appeared aligned. This observer also reported that the upper column of A's appeared in the same direction as the column of M's, which were the letters on the occluding surface next to the left edge of the occluder.

4.6.3 Discussion

Erkelens et. al. (1996) argued that the perceived direction of features in the vicinity of a monocular region is referred to the eye that views the monocular region instead of the cyclopean eye. The advantage of using the eye that views the monocular region as the reference point for perceived direction is that it is possible for the monocular region of the background and the edge of the occluder to appear in their physical direction while having different perceived directions (see Figure 54b). Therefore, the Erkelens et. al. (1996) theory predicts for the stimulus used in the present experiment that: (1) the left edge of the upper occluder and the right edge of the lower occluder will appear aligned since they are physically aligned; (2) the upper monocular region will appear vertically aligned with the lower monocular region since they are physically aligned. Contrary to the Erkelens et. al. (1996) theory, the monocular regions appeared laterally offset for six of the seven observers indicating that they were not perceived in their physical direction.

The upper and lower monocular regions appeared aligned for one observer, which is consistent with the Erkelens et. al. (1996) theory. However, for this observer, the perceived direction of the upper monocular region relative to the edge of the occluding surface was not consistent with the Erkelens et. al. (1996) theory. That theory states that the eye that views the monocular region will dominate the perceived direction of features in the neighbourhood of the monocular region. The left eye viewed the upper monocular region. In the left eye's view, the upper monocular region lay to the left of the left edge of the upper occluder. Therefore, the Erkelens et. al. (1996) theory predicts that the monocular region will appear to the left of the left edge of the upper occluder. Contrary to this prediction, the observer reported that the upper monocular region appeared in the same direction as the letters at the edge of the upper occluding surface.

Ono et. al. (2002; 2003) argued that the perceived direction of part of the scene in the vicinity of the left or right edge of an occluding surface is laterally biased from its physical direction. The lateral bias of the perceived direction of the monocular regions of the background in the present experiment supports this theory. Ono et. al. (2002; 2003) argued that the perceived direction of the left and right edges of an occluding surface is biased laterally from their physical direction when the observer is fixated at the depth of the background surface. This bias was not found in the present experiment since all observers reported that the left edge of the upper occluder and the right edge of the lower occluder appeared vertically aligned when they were physically aligned. This is not inconsistent with the Ono et. al. (2002; 2003) theory, since it is possible that the observers were fixated at the depth of the occluding surface. It is also possible that a lateral bias of the perceived direction of the edges of the occluding surfaces was not

found because the left edge of the upper occluder was attached to the right edge of the lower occluder. This possibility may explain why one observer perceived the monocular region visible to the left eye to lie in the same direction as the edge of the occluding surface. It is possible that if the left and right edges of the occluding surfaces were not attached, then their perceived direction would have been biased laterally to ensure that the monocular region was not perceived in the same direction as the edge of the occluder. This possibility was tested in Experiment 10.

4.7 Experiment 10: A lateral bias of the perceived direction of the edges of an occluding surface from their physical direction

Ono et. al. (2002; 2003) proposed that the perceived direction of the left and right edges of an occluding surface will be biased laterally away from their physical direction when the observer is fixated at the depth of the background surface (the Ono et. al. 2002; 2003 theory was reviewed in section 1.5.4 and in the introduction to Experiment 9, see section 4.6). The Ono et. al. (2002; 2003) theory predicts a rightward bias of perceived direction for the left edge of an occluder and a leftward bias of perceived direction for the right edge of an occluder. If these biases occur, then the left edge of an occluding surface will appear horizontally separated from the right edge of another occluding surface when these edges are physically aligned. This prediction was tested in Experiment 9 using the stimulus shown in Figure 55. The left edge of the lower occluder was found to appear aligned with the right edge of the upper occluder when these edges were physically aligned.

In the discussion of Experiment 9, it was argued that there were two possible explanations for why a lateral bias of the perceived direction of the edges of the occluding surfaces was not found that are compatible with the Ono et. al. (2002; 2003) theory. One possibility is that the left edge of the upper occluder did not appear horizontally separated from the right edge of the lower occluder because these edges were attached in both monocular views. Therefore, in the present experiment the occluding surfaces were vertically separated so that the edges were not attached. A second possibility is that observers tended to fixate at the depth of the occluding surfaces. The Ono et. al. (2002; 2003) theory proposes that the edges of the occluding

surface will be perceived in their physical direction when the observer is fixated at the depth of the occluding surface. Therefore, in the present experiment, observers were instructed to align the left edge of an occluder with the right edge of a lower occluder while fixating at the depth of the background.

It is difficult to maintain fixation on the background while performing the alignment task because fixation tends to shift towards the edges of the occluding surface because they are the targets for the alignment task. The author observed that it was easier to maintain fixation on the background while shifting fixation between two targets on the background surface. Therefore, observers were instructed to perform the alignment task while switching fixation between two horizontally separated targets that were presented on the background surface between the upper and lower occluding surfaces (see Figure 56).

An observer may fixate the background surface but base alignment of the edges on the perceived direction of those edges during brief shifts in fixation towards the edges. Since the Ono et. al. (2002; 2003) theory proposes that the bias of the edges of the occluder does not occur when the occluding surface is fixated, observers were instructed to disregard the perceived direction of the edges whenever they felt their fixation shift towards the occluders.

It is possible for the observer to be converged at the depth of the occluding surfaces while fixating a point on the background due to a crossed fixation disparity. A crossed fixation disparity may be expected because alignment of the edges of the occluding surfaces requires that the observer attends to the occluding surfaces which

have a crossed disparity relative to the background. The Ono et. al. (2002; 2003) theory predicts that the bias of the perceived direction of the edges of the occluding surfaces will not occur if a crossed fixation disparity shifts fixation from the background surface to the depth of the occluding surface. The author observed that it was easier to fixate at the depth of the background rather than the depth of the occluding surfaces when the disparity of the occluding surfaces relative to the background was large. Large surfaces were used so that a large disparity between the background and the occluding surfaces was fusible. Since large surfaces were required, the stimulus was displayed using the anaglyph setup described in the method for Experiment 7 (see 4.4.1). Using this display, it was possible to present two vertically separated occluding surfaces that were each 9.8° square. Kertesz (1981) found that the fusion limit for a surface subtending 10° was approximately 1.3° . Disparities of up to 1.13° were tested to ensure that the occluding surfaces were fusible while fixating at the depth of the background surface.

The primary aim of the present experiment was to test the prediction of the Ono et. al. (2002; 2003) theory that a lateral bias of the perceived direction of the left and right edges of occluding surfaces will occur when the observer fixates at the depth of the background. Alignment of the edges of the occluding surfaces also served as a further test of the Erkelens et. al. (1996) proposal that features in the neighbourhood of a monocular region will be perceived in their physical direction. That proposal predicts that the edges of the occluding surfaces in the present experiment will appear vertically aligned when they are physically aligned. Since the occluding surfaces lie at the same depth, it is possible to specify physical alignment of their edges without assuming that the reference point for perceived direction is the cyclopean eye or the eye that views the monocular region (see introduction to Experiment 9).

4.7.1 Method

Display

The images intended for each eye were presented on a 76.2 centimeter LCD monitor (Dell 3008WFPt) with a resolution of 2560 x 1600. The screen was viewed from a distance of 70cm, from which pixel size was approximately 1.19 minutes of arc. Head position was stabilised with a chinrest. The texture on the surfaces was black and blue in the image for one eye and black and red in the image for the other eye and was viewed through blue-red anaglyph glasses.

Stimuli

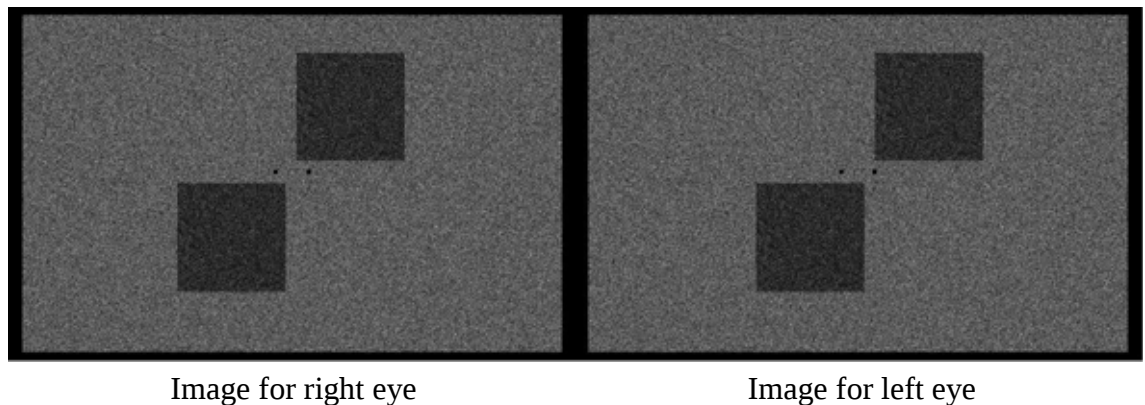


Figure 56. Stereogram of stimuli used in Experiment 10.

Figure 56 shows a stereogram of the stimulus. The background surface was 30.1° high and 48.2° wide. 85% of the squares (1.19 minutes of arc) that comprised the background surface were assigned at random to be black and the remainder were blue in one eye's image and red in the other eye's image. The background surface had an uncrossed disparity of 12 minutes of arc relative to the screen.

The occluding surfaces were 9.8° square and had a crossed disparity relative to the background equal to 0.16° , 0.48° , 0.81° or 1.13° . 65% of the squares that comprised the occluding surfaces were assigned at random to be black and the remainder were blue in one eye's image and red in the other eye's image. The lower occluding square was situated so that its top right edge lay in the centre of the background surface. A vertical gap of 2° separated the upper occluder from the lower occluder. At the start of each trial, the upper occluder was situated so that its left edge was horizontally separated from the right edge of the lower occluder by $\pm 1.5^\circ$.

Two black squares, which each subtended 24 minutes of arc, were located on the background surface and were centred on the gap between the occluding surfaces. These squares served as the fixation targets that observers were instructed to shift fixation between. One of the fixation targets was 1.5 degrees to the left of the centre of the screen and the other fixation target lay to the right of the centre of the screen by the same amount.

Procedure

Observers were instructed to shift the upper square using the left and right arrow keys so that its left edge appeared vertically aligned with the right edge of the lower square. Observers were instructed to indicate when the edges of the squares appeared vertically aligned by pressing the space bar on the keyboard. Observers were instructed to base alignment of the edges on their appearance while alternating fixation between the two small black squares on the background surface. Observers were instructed to

ignore the appearance of the edges of the squares whenever they felt their fixation dart towards the edges of the squares momentarily.

There were two blocks of trials in which each of the four disparities was presented four times in a random order. It was randomly determined whether the image for the left eye was blue and the image for the right eye was red or vice versa in the first block of trials. The colours used for the left and right eye were switched in the second block of trials.

Observers

7 naïve observers from the University of New South Wales community participated.

4.7.2 Results and Discussion

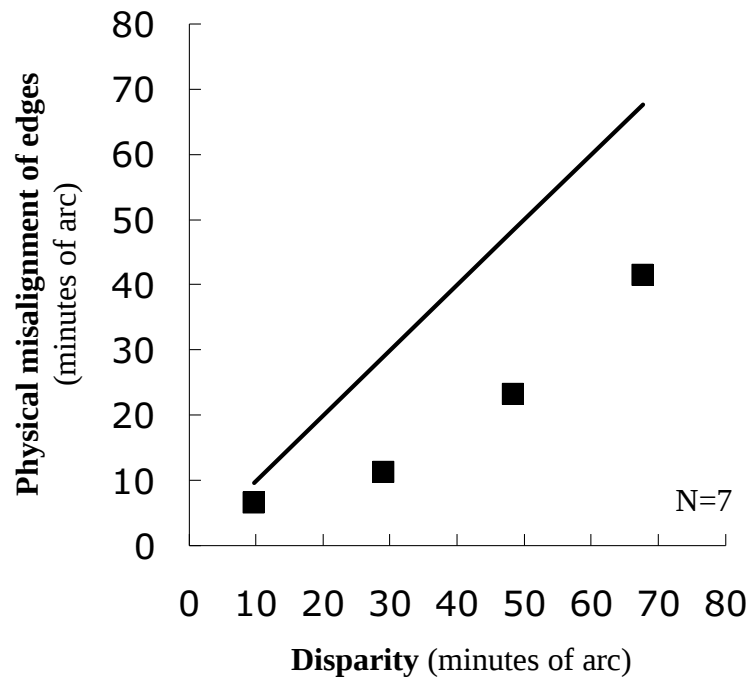


Figure 57. Results of Experiment 10.

Group data are shown in Figure 57. The physical misalignment of the left and right edges of the occluding surfaces when the observer indicated that these edges appeared aligned is shown on the y-axis. The disparity of the occluding surfaces relative to the background is shown on the x-axis. The results show that the edges of the occluding surfaces appeared aligned when the left edge of the upper occluder was to the left of the right edge of the lower occluder. This is consistent with the Ono et. al. (2002; 2003) theory, which predicts that the perceived direction of the right edge of an occluder will be biased leftwards from its physical location and the perceived direction of the left edge of an occluder will be biased rightwards from its physical location. The results do not support the Erkelens et. al. (1996) theory, which predicts that the edges of the occluding surfaces are perceived in their physical direction (the Erkelens et. al. 1996

theory was reviewed in section 1.5.4 and in the introduction to Experiment 9 see section 4.6).

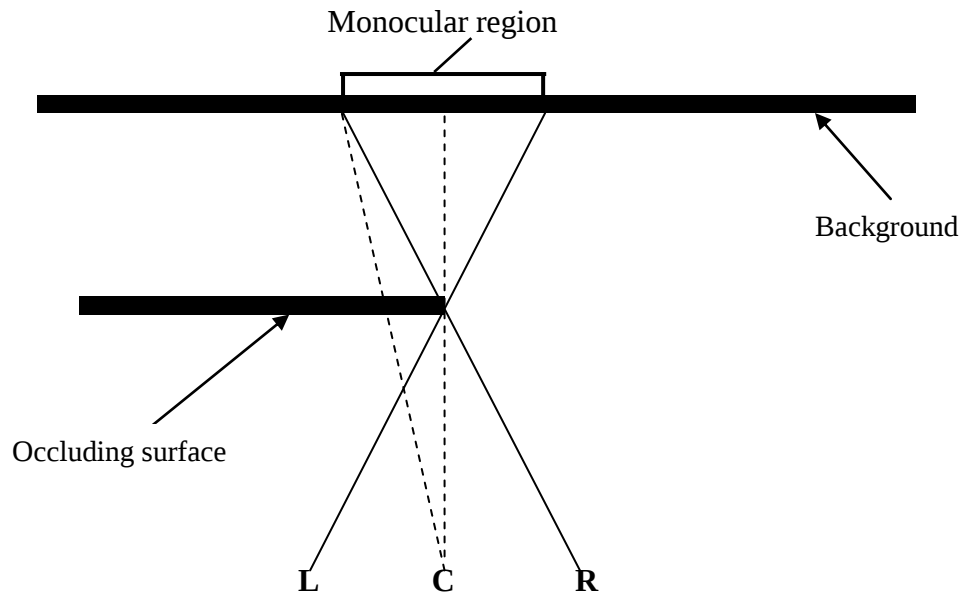


Figure 58. The portion of the monocular region of the background that has the same physical direction as the occluding surface relative to a cyclopean eye.

The Ono et. al. (2002; 2003) theory predicts that the difference between the perceived alignment of the edges and the physical alignment of the edges will increase with disparity. The width of the monocular region of the background next to the left and right edges of the occluding surfaces is equal to the disparity of the occluding surfaces relative to the background (see section 1.2). Half of the monocular region of the background has the same physical direction relative to a cyclopean eye as the edge of the occluding surface (Figure 58). Therefore, a lateral bias for the perceived direction of the edge of an occluder equal to half the disparity of the occluder will ensure that its perceived direction differs from the physical direction of the monocular region. If a bias of this magnitude occurred for the left edge of the upper occluder and the right edge of the lower occluder in the present experiment, then the edges would appear aligned when they were physically misaligned to the extent shown by the diagonal line in Figure 57.

A two-way multivariate analysis of variance controlling the Decision-Wise error rate ($\alpha=0.05$) revealed that there was a significant linear trend of bias magnitude with disparity ($F_{(1,6)}=22.27$) and a significant quadratic trend ($F_{(1,6)}=11.505$) of bias magnitude with disparity. Therefore, the results indicate that the difference between the perceived alignment of the edges and the physical alignment of the edges increased with disparity, which supports the Ono et. al. (2002; 2003) theory. The 95% confidence intervals for the linear trend in the alignment settings indicate that the slope of the alignment settings was 0.3-0.9, which differs from the predicted slope of 1. Therefore, the bias of the perceived direction of the edges of the occluding surfaces was smaller than that required for their perceived direction to differ from the physical direction of the monocular region of the background.

The Ono et. al. (2002; 2003) theory predicts that the bias of the perceived direction of the left and right edges of an occluding surface will occur when fixation is at the depth of the background but will not occur when fixation is at the depth of the occluding surface. In the introduction to the present experiment it was argued that it is difficult to maintain fixation at the depth of the background surface while aligning the edges of the occluding surfaces. Therefore, it is possible that the bias was smaller than expected because observers were not always fixated at the depth of the background. The issue of how fixation disparity may affect the bias of the perceived direction of the edges is discussed below in the general discussion of Experiments 4-10.

4.8 General Discussion of Experiments 4-10

It is commonly argued (Hering, 1879/1942; Roelofs, 1959; Ono, 1979, Ono & Mapp, 1995) that the perceived direction of features is referred to a point midway between the eyes (cyclopean eye). It is now recognised that a real eye at the location of the cyclopean eye could not view all of the features that are visible to either the left eye or the right eye (Erkelens & van de Grind, 1994; Anderson & Nakayama, 1994; Ono et. al. 2002; 2003). Features that would not be visible to a cyclopean eye occur next to the left and right edges of an occluding surface within monocular regions of the background surface. The half of the monocular region that abuts the occluding edge is hidden by the occluding surface from the perspective of a cyclopean eye (see Figure 58, page 194). For this reason, Erkelens et. al. (1996) argued that the cyclopean eye is not the reference point for perceived direction in the vicinity of the left and right edges of an occluder. Erkelens et. al. (1996) proposed that the perceived direction of features in the vicinity of the left and right edges of an occluder is referred to the eye that views the monocular region. The advantage of using the eye that views the monocular region as the reference point for perceived direction is that the occluding surface does not have the same physical direction as features on the background surface that are visible to either the left or right eye.

A prediction of the Erkelens et. al. (1996) theory is that the perceived relative direction of any pair of features in the vicinity of a monocular region will match their relative direction in the eye that views the monocular region. Erkelens et. al. (1996) measured the perceived direction of the edges of an occluding surface relative to a line

on the background surface by instructing observers to vertically align the line with the edge. Erkelens et. al. (1996) found that the background line appeared vertically aligned with the edge when the line and the edge were vertically aligned in the eye that views the monocular region next to the edge, as predicted by the Erkelens et. al. (1996) theory. This result is referred to as an Erkelens-bias since the position of the line and the edge in the eye that viewed the monocular region made a larger contribution to their perceived relative direction than the position of the line and the edge in the other eye.

Ono et. al. (2003) also found an Erkelens-bias for perceived alignment between a background line and the left and right edges of an occluder. However, the Erkelens-bias was smaller in the Ono et. al. (2003) study than in the Erkelens et. al. (1996) study. Comparing the Erkelens et. al. (1996) and Ono et. al. (2003) studies suggested that fixation may affect the magnitude of the Erkelens-bias. Ono et. al. (2003) instructed observers to fixate a specific point in the stimulus located at the depth of the background. A pair of nonius lines flanked the fixation point vertically. Observers were instructed to monitor the perceived alignment of the nonius lines while simultaneously aligning the comparison line with the edge of the occluder. On the other hand, no fixation instructions were given in the Erkelens et. al. (1996) study and the largest Erkelens-bias of perceived alignment was found in that study. The stimulus and procedure of Experiment 7 was similar to that of the Erkelens et. al. (1996) study yet the results of Erkelens et. al. (1996) were only replicated for one of the nine observers. Experiment 8 suggests that the large Erkelens-bias of perceived alignment found in the Erkelens et. al. (1996) study was contingent on where observers fixated. In Experiment 8, the same stimulus was used as in Experiment 7 but observers were instructed to fixate either the tip of the background line or the edge of the occluding surface. Perceived

alignment between the occluding edge and the background line was biased towards their relative direction in the eye that viewed the monocular region for observers that were instructed to fixate the background line. This Erkelens-bias did not occur for observers that were instructed to fixate the occluding surface. This effect of fixation suggests that the conclusion of Erkelens et. al. (1996) that their results did not depend on where observers fixated is incorrect. The possibility that the observers in Experiment 4, 5, 6 and 7 did not always fixate the background surface may explain why the Erkelens-bias in those experiments was smaller than the Erkelens-bias found in Experiment 8, in which observers were instructed to fixate the background surface. Since the Erkelens-bias of perceived alignment is reduced when observers do not fixate the background surface, a tendency to not fixate the background would likewise reduce the extent that the Erkelens-bias of perceived alignment increased with the disparity between the surfaces. Hence, the effect of disparity in Experiments 5 and 6 may have been smaller than expected because observers in those experiments did not always fixate the background.

The large Erkelens-bias of perceived alignment found in Experiment 8 with fixation at the depth of the background is consistent with the Erkelens et. al. (1996) proposal that the perceived direction of features is referred to the eye that views the monocular region. However, the Erkelens et. al. (1996) theory does not explain why the Erkelens-bias of perceived alignment did not occur with fixation on the occluding surface in Experiment 8 or when observers were given no instructions regarding fixation in Experiment 7. On the other hand, the effect of fixation is consistent with an alternative theory proposed by Ono et. al. (2002; 2003). Ono et. al. (2002; 2003) proposed that the perceived direction of features is referred to the cyclopean eye. They

argued that the entire monocular region is incorporated into a cyclopean view of the visual scene by means of lateral biases in the perceived direction of parts of the scene away from their physical direction relative to a cyclopean eye. Ono et. al. (2002; 2003) hypothesised that this lateral bias will occur for features on the background when the occluder is fixated and will occur for features on the occluder when the background is fixated. Therefore, the Ono et. al. (2002; 2003) theory predicts that the perceived direction of the occluding edge will be biased laterally with fixation at the depth of the background but not with fixation at the depth of the occluder. Consistent with both of these predictions, an Erkelens-bias of perceived alignment between the occluding edge and the background line occurred in Experiment 8 for observers that were instructed to fixate the background line, but did not occur for observers that were instructed to fixate the occluding surface.

Experiment 9 provided a further test of the Erkelens et. al. (1996) and Ono et. al. (2003) theories. The Ono et. al. (2003) theory predicts that the perceived direction of features on the non-fixated surface will differ from their physical direction. Ono et. al. (2003, p. 261) argued that the Erkelens-bias of perceived alignment between a background line and the left and right edges of an occluding surface “clearly indicate that displacement of a binocularly fused stimulus occurs on the surface of the nonfixated plane.” However, Erkelens et. al. (1996) argued that the same bias of perceived alignment supported the proposal that the edge of the occluding surface is perceived in its physical direction relative to the eye that views the monocular region. Experiment 9 showed that a pair of monocular regions that were physically aligned appeared horizontally offset from one another, which supports the Ono et. al. (2002; 2003) theory and does not support the Erkelens et. al. (1996) theory. Likewise,

Experiment 10 showed that the left edge of an occluder appeared aligned with the right edge of an occluder when these edges were physically misaligned, which supports the Ono et. al. (2002; 2003) theory and does not support the Erkelens et. al. (1996) theory.

What impact do these results have on the controversy regarding the reference point for perceived direction? Ono et. al. (2003) speculated that the cyclopean eye is the reference point for perceived direction at the left and right edges of a surface. Erkelens et. al. (1996) speculated that the eye that views the monocular region is the reference point for the perceived direction of features in the vicinity of that monocular region. Hering's (1879/1942) compelling demonstration (reviewed section 1.4 see Figure 19) shows that the perceived direction of features can be referred to a point midway between the eyes (cyclopean eye). The theory that perceived directions are referred to the cyclopean eye leads to the counterintuitive prediction that when a feature is visible to one eye only, its perceived direction is affected by the posture of the eye that does not view the feature. There is much experimental evidence for this effect of the non viewing eye on the perceived direction of a monocularly visible feature (reviewed section 1.4.1; e.g. Ono et. al. 1972; Ono & Gonda, 1978; Barbeito, 1981; Ono & Barbeito, 1982; Barbeito & Simpson, 1991). For a binocularly visible feature presented against empty space, the reference point for perceived direction has been determined to be the cyclopean eye (Mitson et. al. 1976; Barbeito & Ono, 1979; reviewed section 1.4.1). Finally, the perceived relative direction of a pair of fused binocular features approximates the angle that they would subtend at a cyclopean eye (Ono et. al. 1977; Mapp & Ono, 1995; see section 1.4.3). Therefore, there is much evidence to support the conclusion that the cyclopean eye is the reference point for perceived direction - at least for features that are not in the neighbourhood of the left and right edges of a surface as

contested by Erkelens et. al. (1996). Erkelens et. al. (1996) found that the perceived direction of the left or right edge of a surface relative to a line on the background surface does not match the angle that the line and the edge would subtend at a cyclopean eye. Hence, if the perceived direction of the features was referred to the cyclopean eye, then either the edge or the line would appear in the wrong direction relative to the observer (the logic of this conclusion was set out in detail in section 4.6). On the other hand, if the perceived direction of the edge of the surface and the background line was referred to the eye that viewed the monocular region next to the edge, then the line and the edge could both appear in the correct direction while having the perceived relative direction found by Erkelens et. al. (1996). The basis then for the Erkelens et. al. (1996) proposal is therefore the expectation that we perceive features at the left and right edges of a surface in the correct direction. Experiments 9 and 10 reveal that this is not the case. The edge of the foreground surface and monocular region of the background are not perceived in the correct direction. This leads to the conclusion that the perceived direction of features is referred to the cyclopean eye, even at the left and right edges of a surface.

Ono et. al. (2002; 2003) proposed that: (1) features on the fixated surface are perceived in their physical direction relative to a cyclopean eye; (2) to ensure that the perceived direction of the occluding and background surfaces differs, the perceived direction of features on the non-fixated surface is biased laterally away from the boundary between the surfaces with respect to their physical direction relative to the cyclopean eye. These proposals do not specify what the perceived direction of the surfaces will be when the depth of fixation does not match the depth of either surface due to a fixation disparity. One possibility is that fixation disparity does not affect the

perceived direction of the surfaces. The surface that is closest to the depth of fixation will be perceived in its physical direction relative to a cyclopean eye, while the perceived direction of features on the other surface are biased laterally away from the boundary between the surfaces with respect to their physical direction relative to the cyclopean eye so that features on the occluding and background surfaces do not have the same perceived direction. Ono et. al. (2003) raised the possibility that a fixation disparity might affect the magnitude of the Erkelens-bias of perceived direction. Ono et. al. (2003) argued that the basis for this possibility is that the discrepancy between the perceived and physical direction of a monocular feature presented alone and correlates highly with fixation disparity (Ono et. al. 1972; Ono & Gonda, 1978); reviewed section 1.4.1). A crossed disparity while fixating the background surface would shift the depth of fixation towards the occluding surface. Since the discrepancy between the physical and perceived direction of a monocular feature diminishes as the depth of fixation approaches the depth of the monocular feature, the lateral bias of the perceived direction of the occluding surface may diminish if a crossed fixation disparity shifted fixation away from the background towards the occluding surface. This possibility may be evaluated in future research by either measuring the perceived direction of the left and right edges of an occluder as a function of the depth of fixation relative to the background or by correlating the magnitude of the Erkelens-bias and fixation disparity.

Fixation disparity provides a possible explanation for the difference in the magnitude of the Erkelens-bias of perceived alignment between the Erkelens et. al. (1996) and Ono et. al. (2003) studies. The extent that a given fixation disparity would shift the depth of fixation toward the depth of the occluder decreases as the relative disparity between the surfaces increases. Larger relative disparities between the

background and occluding surface were used in the Erkelens et. al. (1996) study (up to 2°) than in the Ono et. al. (2003) study (15 minutes of arc in Experiment 3 and 11 minutes of arc in Experiment 2). Therefore, if fixation disparity affects the magnitude of the Erkelens-bias of perceived alignment, then a fixation disparity of a few minutes of arc would reduce the Erkelens-bias of perceived alignment more for the small disparities used by Ono et. al. (2003) than the large disparities used by Erkelens et. al. (1996).

The minimal stimulus conditions for the Erkelens-bias of perceived alignment were investigated in Experiment 6. The stimuli used by Erkelens et. al. (1996) and Ono et. al. (2003) contained monocularly visible texture within the monocular region of the background next to the edges of the occluding surface. The results of Experiment 6 of the present study and the results of Erkelens and van Ee (2007) eliminate the possibility that the Erkelens-bias of perceived alignment at the edges of an occluding surface depends on texture within the monocular region. In both studies, an Erkelens-bias of perceived alignment was found when the monocular region of the background lacked any texture. It was proposed in Experiment 6 that the Erkelens-bias of perceived alignment simply depends on the stimulus specifying the boundaries of a foreground surface because the left eye always views a monocular region to the left of a foreground surface and the right eye always views a monocular region to the right of a foreground surface. In support of this account, Experiment 6 showed that the Erkelens-bias was eliminated when the outline of a surface was presented as the farthest feature in the scene, which is incompatible with it being a foreground surface.

The largest Erkelens-biases of perceived alignment between the occluding edge and the background line were found in the Erkelens et. al. (1996) study and in Experiment 8 of the present study. Disparity gradients equal to 2 occurred between the edge of the occluding surface and binocularly visible texture on the background surface in both of those experiments. The possibility that these steep disparity gradients contributed to the Erkelens-bias of perceived alignment was dismissed by Erkelens et. al. (1996), because the disparity gradient between the occluding edge and the background line was not steep. However, this ignores the fact that the disparity gradient between the edge and the binocularly visible texture on the background surface was steep. One might also argue that the disparity gradient at the edges between the surfaces did not contribute to the Erkelens-bias of perceived alignment because steep disparity gradients have been shown to induce diplopia and trials in which diplopia was observed were aborted in the Erkelens et. al. (1996) study. However, judgments of diplopia are more difficult for features that are part of a surface than for features presented alone (see Duwaer, 1983; McKee & Vergheze, 2002). Furthermore, it is also possible that diplopia might rarely be experienced for densely textured surfaces because one of the diplopic images of the surface is suppressed. Suppression of one of the diplopic images of a surface may be expected on the basis that the perceived direction of the two diplopic directions of a surface are expected to overlap. Steep disparity gradients were lacking in experiment 2 of the Ono et. al. (2003) study since the background next to the edge of the occluder was black except for a single line located in the monocular region. In that study, if the eye that viewed the monocular region next to the edge dominated perceived alignment, as was found with steep disparity gradients in the Erkelens et. al. (1996) study and in Experiment 8 of the present study, then the Erkelens-bias of perceived alignment would equal 7.5 minutes of arc. The obtained Erkelens-bias was

equal to 0.81 minutes of arc. Hence, experiment 2 of the Ono et. al. (2003) study does not eliminate the possibility that steep disparity gradients are responsible for the large Erkelens-biases of perceived alignment found in the Erkelens et. al. (1996) study and in Experiment 8 of the present study. Steep disparity gradients were also lacking in the outline condition of Experiment 6 of the present study because the left and right edges of the outline of the surface were not proximal to any features on the background surface. The Erkelens-bias in this experiment was larger than that found in experiment 2 of the Ono et. al. (2003) study, but was also smaller than that found with steep disparity gradients in Experiment 8 and in the Erkelens et. al. (1996) study. It was argued in the preceding paragraphs that the difference in the magnitude of the Erkelens-bias between these studies may also be attributed to the depth of the observer's fixation. Hence, future research that compares the Erkelens-bias of perceived direction at the left and right edges of an occluder in the presence or absence of steep disparity gradients should ensure that the observer is converged at the same depth in both conditions.

The Ono et. al. (2002; 2003) theory predicts that with fixation at the depth of the background, a leftwards bias of perceived direction will occur for the right edge of an occluder while a rightwards bias of perceived direction will occur for its left edge. Consequently, it is predicted that the difference between the perceived directions of the left and right edge of an occluder is smaller than the difference between their physical directions. This discrepancy between the perceived and physical difference in direction between a pair of features on the same surface was described as a *compression* of perceived direction by Ono et. al. (2002; 2003).

The problem of how the Erkelens-bias of perceived direction is distributed across the occluding surface has until now not been addressed. One possibility is that the lateral bias decreases slowly across the occluding surface in order to minimise the compression of perceived direction between adjacent features. However, a slow decrease in the discrepancy between the perceived direction of a feature and its physical direction with separation from the edge of the occluder would maximise the region of the occluder that is affected by the lateral bias of perceived direction. To reduce the area of the occluder affected by the lateral bias of perceived direction, the rate that the bias diminishes with separation from the edge must increase, thereby increasing the compression of perceived direction between adjacent features. An interesting question is whether the lateral bias of perceived direction is distributed to minimise either: (1) the compression of perceived direction between adjacent features; or (2) the area of the occluder that is affected by the lateral bias of perceived direction.

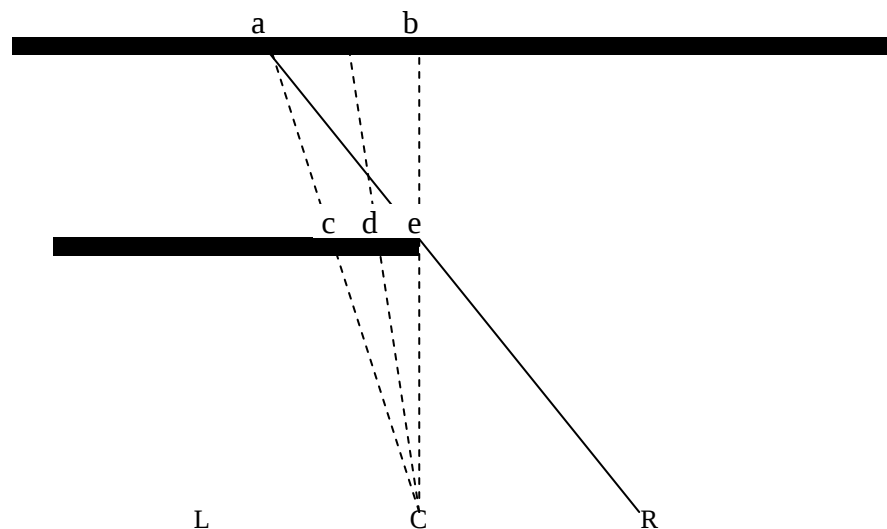


Figure 59. The portion of the occluder that lies in the same direction relative to a cyclopean eye as the background visible to one of the eyes.

There exists a minimum region of the occluder that is predicted to be affected by the lateral bias of perceived direction by the proposals of Ono et. al. (2002; 2003). Ono

et. al. (2002; 2003) argued that the perceived direction of features in the vicinity of the left and right edges of an occluder is referred to the cyclopean eye. From that reference point, the physical direction of the half of the monocular region of the background that is next to the edge of the occluder (a-b in Figure 59) is the same as the physical direction of a portion of the occluder (c-e in Figure 59). Ono et. al. (2002; 2003) argued that with fixation at the depth of the background, the features in the monocular region are perceived in their physical direction relative to cyclopean eye, while the perceived direction of the occluder is shifted laterally so that the perceived direction of the two surfaces does not overlap. Therefore, the portion of the occluder that is affected by the Erkelens-bias must exceed that which would hide part of the monocular region from a cyclopean eye in order to be compatible with the Ono et. al. (2002; 2003) theory.

The results of Experiment 4 and 5 address these questions concerning the distribution of the Erkelens-bias of perceived direction across the occluder. In both experiments, the perceived direction of a line on the occluding surface was measured relative to a line on the background surface. The lateral separation of the line on the occluding surface from the edge was varied. The portion of the occluder that would hide part of the monocular region from a cyclopean eye was either 10 or 15 minutes of arc wide in Experiment 4 and was 3, 4 or 5 minutes of arc wide in Experiment 5. An Erkelens-bias of perceived alignment was found when the line on the occluding surface was located within this portion of the occluder as required by the theory of Ono et. al. (2002; 2003). The Erkelens-bias of perceived alignment was also found when the line on the occluder lay outside of the portion of the occluder that would hide part of the monocular region from a cyclopean eye. In Experiment 5, an Erkelens-bias was found when the line on the occluder was separated from the edge of the occluder by 5 minutes

of arc. For that stimulus, the portion of the occluder that would hide the monocular region from a cyclopean eye was 3 minutes of arc wide. In Experiment 4, when the portion of the occluder that would hide a cyclopean eye was 10 minutes of arc wide, an Erkelens-bias of perceived alignment was found when the separation of the line on the occluder was 30 minutes of arc. These results support the conclusion that the area of the occluder affected by the lateral bias of perceived direction away from the physical direction of the features is not minimised, because the Erkelens-bias was found even when the line on the occluder did not lie within the region that would hide the monocular region from a cyclopean eye. The results also indicate that the Erkelens-bias of perceived direction on the occluding surface is not distributed to minimise the discrepancy between the perceived and physical difference in direction between adjacent features. Were this discrepancy minimised, the Erkelens-bias would gradually decrease across a wide range of separations. Contrary to this prediction, the Erkelens-bias of perceived alignment in Experiment 5 was eliminated by a separation of 9 minutes of arc between the line on the occluding surface and the edge of the occluding surface. The results indicate that the Erkelens-bias is distributed across the occluding surface in a compromise between minimising the area of the occluder that is affected by the Erkelens-bias and minimising the discrepancy between the perceived and physical difference in direction between adjacent features.

4.9 Summary of recommendations for future experiments

The main finding of the experiments reported in section 4 is that at the left and right edges of a surface, features on either the occluding or the background surface are not perceived in their physical direction. Relative to their physical direction, the perceived direction of the features is biased laterally away from the boundary between the surfaces. It was argued in the General Discussion of Experiments 4-10 (section 4.8) that this finding supports the Ono et. al. (2003) theory of perceived direction and is incompatible with the theory advanced by Erkelens et. al. (1996) (for a review of these theories see section 4.8 or section 1.5.4). A resolution of a number of issues raised in the General Discussion of Experiments 4-10 require further experiments and are summarised below.

Fixation disparity

The perceived direction of the left and right edges of an occluding surface, relative to a line on the background surface, differed between the experiments reported in section 4 and between the experiments reported by Erkelens et. al (1996) and Ono et. al (2003). The results of Experiment 7 indicate that the depth at which the observer is fixated may account for some of these discrepancies between the experiments. In Experiment 7, when the background surface was fixated, the perceived relative direction of the occluding edge and the background line was more similar to their angular separation in the eye that viewed the monocular region next to the edge than to their angular separation in the other eye. We refer to this result as an Erkelens-bias because

the eye that viewed the monocular region had a stronger influence on perceived alignment of the features than did the other eye. In Experiment 7, when the occluding surface was fixated, the perceived relative direction of the occluding edge and the background line was an average of the angular separation of the edge and the line in both eyes. Hence, Experiment 7 showed that an Erkelens-bias of perceived direction occurs when the background surface is fixated and is eliminated when the occluding surface is fixated. However, it is not yet known whether the magnitude of the Erkelens-bias of perceived alignment is reduced when small fixation disparities shift the depth of fixation away from the depth of the background surface. The effect of fixation disparity on the Erkelens-bias of perceived alignment may be examined by either measuring the perceived direction of the left and right edges of an occluder as a function of the depth of fixation relative to the background or by correlating the magnitude of the Erkelens-bias and fixation disparity. In order to vary the depth of fixation relative to the background surface, vergence eye movements must be prevented. This could be achieved by presenting the stimulus for a duration of approximately 150 ms or less, which is shorter than the reaction time of vergence eye movements to the presentation of a stimulus (Ginsborg, 1953; Rashbass & Westheimer, 1961).

Steep disparity gradients

Steep disparity gradients (see section 1.3.4) have been shown to affect the perceived direction of pairs of lines and dots (Tyler, 1975; Braddick, 1979; Burt & Julesz, 1984). In the General Discussion of Experiments 4-10, it was noted that an Erkelens-bias of the perceived direction of the left or right edges of an occluding surface has been found using stimuli that lack steep disparity gradients (see experiment 2 of

Ono et. al. 2003 and Experiment 6 of the present study). However, the Erkelens-bias of perceived direction found in these experiments that lacked steep disparity gradients was much smaller than the Erkelens-bias found in experiments that contained steep disparity gradients (Erkelens et. al. 1996; Experiment 8 of the present study). As was pointed out in the General Discussion of Experiments 4-10, it is possible that these differences in the Erkelens-bias may be due to differences in fixation disparity. However, it is also possible that large Erkelens-biases require steep disparity gradients. What is needed to resolve this issue is an experiment where the perceived direction of the edges is measured with or without steep disparity gradients, while ensuring that fixation disparity does not differ between these two conditions. This also requires that the stimulus be presented for less than 150ms in order to equate the depth of fixation between the two conditions.

Distribution of the distortion of perceived direction across the surfaces

Experiment 9 and 10 show that in the vicinity of the left and right edges of an occluding surface, features on either the background surface or the occluding surface can appear in a direction that differs from their physical direction. Relative to their physical directions, the perceived directions of the left and right edges of an occluding surface can be biased towards the centre of the surface. An interesting issue raised in section 4 is to how this distortion of perceived direction is distributed across the occluding surface. It was argued in the General Discussion that the results of Experiment 4 and 5 show that the distortion of perceived direction is not distributed so as to minimise the discrepancy between the perceived and physical difference in direction between adjacent features. It was also argued that those experiments showed

that the distortion of perceived direction was not distributed so as to minimise the area of the surface that is affected by the distortion. Our understanding of how the distortion is distributed across the surface would be improved by further experiments that measure the perceived direction of features at different distances from the left and right edges of surfaces. Interesting issues that remain to be resolved are how these distributions vary as a function of surface width, feature density and the disparity between the surfaces.

5 References

- Anderson, B. (1994). The role of partial occlusion in stereopsis. *Nature*, 367, 365-368.
- Anderson, B. & Nakayama, K. (1994). Toward a general theory of stereopsis: Binocular matching, occluding contours, and fusion. *Psychological Review*, 101, 414-445.
- Asher, H. (1953). Suppression theory of binocular vision. *British Journal of Ophthalmology*, 37, 36-49.
- Assee, A. & Qian, N. (2007). Solving da Vinci stereopsis with depth-edge-selective V2 cells. *Vision Research*, 47, 2585-2602.
- Banks, M., van Ee, R. & Backus, B. (1997). The computation of binocular visual direction: a re-examination of Mansfield and Legge (1996). *Vision Research*, 37, 1605-1610.
- Barbeito, R. (1981). Sighting dominance: An explanation based on the processing of visual direction in tests of sighting dominance. *Vision Research*, 21, 855-860.
- Barbeito, R. & Ono, H. (1979). Four methods of locating the egocentre: A comparison of their predictive validities and reliabilities. *Behavior Research Methods & Instrumentation*, 11, 31-36.
- Barbeito, R. & Simpson, T. (1991). The relationship between eye position and egocentric visual direction. *Perception & Psychophysics*, 50, 373-382.
- Bird, K. (2004). *Analysis of Variance via Confidence Intervals*. London: Sage Publications Ltd.
- Boman, D. & Kertesz, A. (1985). Effect of stimulus parameters on fusional and stereoscopic performance. *American Journal of Optometry and Physiological Optics*, 62, 222-227.
- Braddick, O. (1979). Binocular single vision and perceptual processing. *Proceedings of the Royal Society of London, B*, 204, 503-512.
- Brainard, D. (1997). The psychophysics toolbox. *Spatial Vision*, 10, 433-436.
- Burt, P. & Julesz, B. (1980). A disparity gradient limit for binocular fusion. *Science*, 208, 615-617.
- Charnwood, J. (1949). Observations on ocular dominance. *The Optician*, 116, 85-88.
- Dodge, R. (1903). Five types of eye movments in the horizontal meridian plane of the field of regard. *American Journal of Physiology*, 8, 307-329.

- Duwaer, A. (1983). Patent stereopsis with diplopia in random-dot stereograms. *Perception & Psychophysics*, 33, 443-54.
- Enright, T. (1988). The cyclopean eye and its implications: Vergence state and visual direction. *Vision Research*, 28, 925-930.
- Erkelens, C. (1988). Fusional limits for a large random-dot stereogram. *Vision Research*, 28 345-353.
- Erkelens, C. (2000). Perceived direction during monocular viewing is based on signals of the viewing eye only. *Vision Research*. 40, 2411-2419.
- Erkelens, C. & van de Grind, W. (1994). Binocular visual direction. *Vision Research*, 34, 2963-2969.
- Erkelens, C. & van Ee, R. (1997a). Capture of visual direction: an unexpected phenomenon in binocular vision. *Vision Research*, 37,1193-1196.
- Erkelens, C. & van Ee, R. (1997b). Capture of visual direction of monocular objects by adjacent binocular objects. *Vision Research*, 37,1735-1745.
- Erkelens, C. & van Ee, R. (2007). Monocular symmetry in binocular vision. *Journal of Vision*, 7, 1-9.
- Erkelens, C., Muijs, A. & van Ee, R. (1996). Binocular alignment in different depth planes. *Vision Research*, 36, 2141-2147.
- Fahle, M. (1982). Binocular rivalry: Suppression depends on orientation and spatial frequency. 22, 787-800.
- Fender, D. & Julesz, B. (1967). Extension of Panum's fusional area in binocularly stabilized vision. *Journal of the Optical Society of America*, 57, 819-830.
- Felton, T., Richards, W. & Smith, R. (1972). Disparity processing of spatial frequencies in man. *Journal of Physiology*, 225, 349-362.
- Forte, J., Peirce, J. & Lennie, P. (2002). Binocular integration of partially occluded surfaces. *Vision Research*, 42, 1225-1235.
- Gillam, B. & Borsting, E. (1988). The role of monocular regions in stereoscopic displays. *Perception*, 17, 603-608.
- Gillam, B. & Nakayama, K. (1999). Quantitative depth for a phantom surface can be based on cyclopean occlusion cues alone. *Vision Research*, 39, 109-112.
- Gillam, B. Blackburn, S. & Cook, M. (1995). Panum's limiting case: Double fusion, convergence error, or 'da Vinci stereopsis'. *Perception*. 24, 333-346.

- Gillam, B. Cook, M. & Blackburn, S. (2003). Monocular discs in the occlusion zones of binocular surfaces do not have quantitative depth – A comparison with Panum's limiting case. *Perception*, 32, 1009-1019.
- Ginsborg, B. (1953). Small voluntary movements of the eye. *British Journal of Ophthalmology*, 37, 746-754.
- Hering, E. (1879/1942). *Spatial sense and movements of the eye*. Trans. C. A. Radde. (Baltimore: American Academy of Optometry). Originally published 1879.
- Hirsch, M. & Weymouth, F. (1948). Distance, discrimination; effect on threshold of lateral separation of the test objects. *Archives of Ophthalmology*, 39, 224-231.
- Hochberg, J. (1964). Contralateral suppressive fields of binocular combination. *Psychonomic Science*, 1, 157-158.
- Howard (2002). *Seeing in depth. v. 1. Basic mechanisms*. Toronto: I Porteous.
- Howard, I. & Templeton, W. (1966). *Human spatial orientation*. New York: Wiley.
- Howard, I. & Rogers, B. (2002). *Seeing in depth. v. 2. Depth perception*. Toronto: I Porteous.
- Howard, I. & Wade, N. (1996). Ptolemy's contributions to the geometry of binocular vision. *Perception*, 25, 1189-1201.
- Jaschinski, W., Jainta, S. & Schürer, M. (2006). Capture of isual direction in dynamic vergence is reduced with flashed monocular lines. *Vision Research*, 46, 2608-2614.
- Julesz, B. (1960). Binocular depth perception of computer-generated patterns. *The Bell System Technical Journal*, 39, 1225.
- Julesz, B. (1964). Binocular depth perception without familiarity cues. *Science*, 24, 145, 356-362.
- Kaye, M. (1978). Stereopsis without binocular correlation. *Vision Research*, 18, 1013-1022.
- Kertesz, A. (1981). Effect of stimulus size on fusion and vergence. *Journal of the Optical Society of America*, 71, 289-293.
- Khokhotva, M. Ono, H. & Mapp, A. (2005). The cyclopean eye is relevant for predicting visual direction. *Vision Research*, 45, 2339-2345.
- Kommerell, G., Schmitt, C., Kromeier, M. & Bach, M. (2003). Ocular prevalence versus ocular dominance. *Vision Research*, 43, 1397-1403.
- Kulikowski, J. (1978). Limit of single vision in stereopsis depends on contour sharpness. *Nature*, 276, 126-127.

- Lawson, R. & Gulick, W. (1967). Stereopsis and anomalous contour. *Vision Research*, 7, 271-297.
- Lee, H. & Dobbins, A. (2006). Perceiving surfaces in depth beyond the fusion limit of their elements. *Perception*, 35, 31-39.
- Levelt, W. (1966). The alternation process in binocular rivalry. *British Journal of Psychology*, 57, 225-238.
- Mansfield, S. & Legge, G. (1996). The binocular computation of visual direction. *Vision Research*, 36, 27-41.
- Mapp, A. & Ono, H. (1999). Wondering about the wandering cyclopean eye. *Vision Research*, 39, 2381-2386.
- Mapp, A., Ono, H. & Khokhotva, M. (2007). Hitting the target: Relatively easy, yet absolutely difficult. *Perception*, 36, 1139-1151.
- Marr, D. & Poggio, T. (1976). Cooperative computation of stereo disparity. *Science*, 194, 283-287.
- McKee, S. & Verghese, P. (2002). Stereo transparency and the disparity gradient limit. *Vision Research*, 42, 1963-77.
- McKee, S. & Westheimer, G. (1980). Stereogram design for testing local stereopsis. *Investigative Ophthalmology and Visual Science*, 19, 802-809.
- McKee, S., Bravo, M., Smallman, H. & Legge, G. (1995). The uniqueness constraint and binocular masking. *Perception*, 24, 49-65.
- Mitchell, D. (1966). Retinal disparity and diplopia. *Vision Research*, 6, 441-451.
- Mitson, G., Ono, H. & Barbeito, R. (1976). Three methods of measuring the location of the egocentre: their reliability, comparative locations and intercorrelations. *Canadian Journal of Psychology*, 30, 1-9.
- Nakayama, K. & Shimojo, S. (1990). Da Vinci stereopsis: Depth and subjective occluding contours from unpaired image points. *Vision Research*, 30, 1811-25.
- Nienborg, H., Bridge, H., Parker, A. & Cumming, B. (2004). Receptive field size in V1 neurons limits acuity for perceiving disparity modulation. *The Journal of Neuroscience*, 24, 2065-2076.
- Ogle, K. (1950). *Researches in binocular vision*. (Philadelphia: Saunders).
- Ono, H. (1979). Axiomatic summary and deductions from Hering's principles of visual direction. *Perception & Psychophysics*, 25, 473 – 477.

- Ono, H. & Angus, R. (1974). Adaptation to sensory-motor conflict produced by the visual direction of the hand specified from the cyclopean eye. *Journal of Experimental Psychology*, 103, 1-9.
- Ono, H. & Barbeito, R. (1982). The cyclopean eye vs. the sighting-dominant eye as the center of visual direction. *Perception & Psychophysics*, 32, 201-210.
- Ono, H. & Gonda, G. (1978). Apparent movement, eye movements and phoria when two eyes alternate in viewing a stimulus. *Perception*, 7, 75-83.
- Ono, H. & Mapp, A. (1995). A restatement and modification of Wells-Hering's laws of visual direction. *Perception*, 24, 237-252.
- Ono, H. & Weber, E. (1981). Nonveridical visual direction produced by monocular viewing. *Journal of Experimental Psychology: Human Perception and Performance*, 7, 937-947.
- Ono, H., Angus, R. & Gregor, P. (1977). Binocular single vision achieved by fusion and suppression. *Perception & Psychophysics*, 21 513-521.
- Ono, H., Mapp, A. & Howard, I. (2002). The cyclopean eye in vision: the new and old data continue to hit you right between the eyes. *Vision Research*, 42, 1307-1324.
- Ono, H., Mapp, A. & Mizushina, H. (2007). The cyclopean illusion unleashed. *Vision Research*, 47, 2067-2075.
- Ono, H., Wade, N. & Lillakas, L. (2002). The pursuit of Leonardo's constraint. *Perception*, 31, 83-102.
- Ono, H., Lillakas, L. Grove, P., & Suzuki, M. (2003). Leonardo's paradox as the constraint that two opaque objects cannot be seen in the same direction. *Journal of Experimental Psychology: General*, 132, 253-265.
- Ono, H. Wikinson, A., Muter, P. & Mitson, L. (1972). Apparent movement and change in perceived location of a stimulus produced by a change in accommodative vergence. *Perception & Psychophysics*, 12, 187-192.
- Palmer, D. (1961). Measurement of the horizontal extent of Panum's area by a method of constant stimuli. *Optica Acta*, 8, 151-159.
- Panum, P. (1858). Physiologische Untersuchungen über das Sehen mit zwei Augen (Kiel: Schwerssche Buchhandlung).
- Prazdny, K. (1985). On the disparity gradient limit for binocular fusion. *Perception & Psychophysics*, 37, 81-83.
- Prince, S., Cumming, B. & Parker, A. (2002). Range and mechanism of encoding of horizontal disparity in macaque V1. *Journal of Neurophysiology*. 87, 209-221.

- Prince, S., Eagle, R. & Rogers, B. (1998). Contrast masking reveals spatial-frequency channels in stereopsis. *Perception*, 27, 1345-55.
- Rashbass, C. & Westheimer, G. (1961). Disjunctive eye movements. *Journal of Physiology*, 159, 339-360.
- Rohaly, A. & Wilson, H. (1993). Nature of coarse-to-fine constraints on binocular fusion. *Journal of the Optical Society of America A*, 10, 2433-2441.
- Roelofs, O. (1959). Considerations on the visual egocenter, *Acta Psychologica*, 16, 226-234.
- Rose, D. & Blake, R. (1988). Mislocalisation of diplopic images. *Journal of the Optical Society of America*, 5, 1512-1520.
- Roumes, C. Plantier, J. & Menu, (1997). The effects of spatial frequency on binocular fusion: From elementary to complex images. *Human Factors*, 39, 359-73.
- Scharff, L. (1997). Decreases in the critical disparity gradient with eccentricity may reflect the size-disparity correlation. *Journal of the Optical Society of America A*, 14, 1205-1212.
- Schor, C. & Wood, I. (1983). Disparity range for local stereopsis as a function of luminance spatial frequency. *Vision Research*, 23, 1649-1654.
- Schor, C. Wood, I. & Ogawa, J. (1984). Binocular sensory fusion is limited by spatial resolution. *Vision Research*, 24, 661-665.
- Schor, C. Wesson, M. & Robertson, K. (1986). Combined effects of spatial frequency and retinal eccentricity upon fixation disparity. *American Journal of Optometry*, 63, 619-626.
- Sheedy, J. & Fry, G. (1979). The perceived direction of the binocular image. *Vision Research*, 19, 201-11.
- Shimojo, S. & Nakayama, K. (1990). Real world occlusion constraints and binocular rivalry. *Vision Research*, 30, 69-80.
- Shimono, K. & Wade, N. (2002). Monocular alignment in different depth planes. *Vision Research*, 42, 1127-1135.
- Shimono, K., Tam, W., Asakura, N. & Ohmi, M. (2005). Localization of monocular stimuli in different depth planes. *Vision Research*, 45, 2631-2641.
- Shipley, T. & Rawlings, S. (1970). The nonius-horopter – I. History and theory. *Vision Research*, 10, 1225-1262.
- Smallman, H. & MacLeod, D. (1994). Size-disparity correlation in stereopsis at contrast threshold. *Journal of the Optical Society of America, A*, 11, 2169-83.

Tyler, C. (1975). Spatial organisation of binocular disparity sensitivity. *Vision Research*, 15, 583-590.

Van Ee, R., Erkelens, C. (2000). Is there an interaction between perceived direction and perceived aspect ratio in stereoscopic vision? *Perception & Psychophysics*, 62, 910-926.

Van Ee, R., Banks, M. & Backus, B. (1999). Perceived visual direction near an occluder. *Vision Research*, 39, 4085-4097.

Verhoeff, F. H. (1935). A new theory of binocular vision. *Archives of Ophthalmology*, 13, 151-175.

Wells, W. (1792). *An essay upon single vision with two eyes: Together with experiments and observations on several other subjects in optics*. In Microform 1975 (New York: Readex Microprint Corporation).

Westheimer, G. & Levi, D. (1987). Depth attraction and repulsion of disparate foveal stimuli. *Vision Research*, 27, 1361-1368.

Wheatstone, C. (1838). Contributions to the physiology of vision. Part the first. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 128, 371-394.

Wheatstone, C. (1852). Contributions to the physiology of vision. Part the second. On some remarkable, and hitherto unobserved, phenomena of binocular vision. *Philosophical Transactions of the Royal Society of London*, 142, 1-17.

Wilcox, L., Harris, J. & McKee, S. (2007). The role of binocular stereopsis in monoptic depth perception. *Vision Research*, 47, 2367-2377.

Wilson, H. Blake, R. & Pokorny, J. (1988). Limits of binocular fusion in short wave sensitive ("blue") cones. *Vision Research*, 28, 555-562.

i