

ANGLIA RUSKIN UNIVERSITY

**HOW DOES VISUAL CROWDING INTERFERE WITH
DEPTH DISCRIMINATION?**

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DEDICATION

To my daughter and wife, Joan-Brianna Ocansey and Lydia Ocansey for having been away from them during the writing of this thesis, and Lydia for her constant prayers and endless love and support throughout my PhD studies.

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ANGLIA RUSKIN UNIVERSITY

ABSTRACT

FACULTY OF SCIENCE AND TECHNOLOGY

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HOW DOES VISUAL CROWDING INTERFERE WITH DEPTH DISCRIMINATION?

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The presence of flanking targets can impair depth discrimination, presumably through a form of lateral interaction or visual crowding. This study investigates how stereoscopic crowding interferes with foveal depth discrimination when tests and flanking stimuli of different spatial configuration are located on and off the horopter in normal subjects by using psychophysical means.

The magnitude of crowding increased when the flanking bars were in close spatial proximity to the test, between 1 to 2 arc min, and returned to unflanked levels for wider separations of 4 arc min and beyond. The magnitude of crowding depended on the extent to which the test and the flanking bars width matched. When flankers were placed at the optimum crowding distance (OCD) and displaced off the horopter, crowding reduced but the flanker effect was restored at greater flanker disparity. On the contrary, flankers positioned at the least crowding distance (LCD) at the onset generally showed an increase in thresholds from the fixation plane with increasing flanker disparity. Crowding was produced at similar small test-flanker separation for the range of 0.5 to 4 cpd flanker spatial frequency composition used. The magnitude of crowding was greater for test and flanker of similar spatial frequency, though some crowding was produced when their spatial frequency differed.

Overall, the results confirm previous reports showing that depth discrimination thresholds increase in the presence of flanking contours, but in addition suggest that disparity integration relative to the fixation demonstrates a dichotomy of fine and coarse mechanisms driven by salience attraction. Additionally, the results show that the crowding effect can be reduced by depth cues related to the width, and disparity of flanking stimuli. The crowding effect may be attributed to the action of local disparity interactions, but suggest the involvement of Gestalt factors (for larger flanker widths) and luminance flux (for thinner flanker widths) factors.

Keywords: stereopsis, stereoacuity, Gabors, crowding, depth discrimination, disparity, horopter, separation, threshold.

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CHAPTER ONE

GENERAL INTRODUCTION

Context of the Study

The visual system is adept at discriminating simple fine details in the visual field (i.e. visual acuity) and at performing higher visual tasks such as the relative lateral object location (Vernier acuity), or relative depth localisation (stereo acuity). Often, the keenness of these tasks is used as an indication of functional integrity of the visual system and its processes (Harwerth and Schor, 2002; Momeni-Moghadam et al., 2011). It is usual therefore, to find that many investigations to understand visual information perception and processing, focus on monocular and binocular measures of object detection, recognition, resolution and localisation (Levi, 2008). However, because objects are not seen in isolation, but as a manifold of intricately interconnected visual cues, the determination of the threshold for these spatial tasks is affected by the interaction with other objects in the visual field (Levi, 2008; Pelli, 2008, Westheimer, 2012). Limitations to visual performance are attributed to various factors including the anatomy and physiology of the eye, the type and form of the object to be discerned and the spatial relationship between the objects to be separated; known as spatial interaction (Levi, 2008; Whitney and Levi, 2011).

Contour interaction (i.e. when the distractors are simple features such as lines) (Flom et al., 1963a) or visual crowding (i.e. when the surrounds are more complex, such as letters) (Townsend et al, 1971) are well-known phenomena in spatial interaction, but for simplicity all such interactions are referred to as crowding in this study. Crowding generally refers to the detrimental effect of surrounding features (or contours) on the spatial discrimination of visual objects (Flom et al., 1963a; Flom et al., 1963b, Bouma, 1970; Bouma, 1970; Townsend et al, 1971). Crowding is manifest clinically by the reduction in high contrast visual acuity that occurs when measured using a full letter chart compared to acuity when

measured with single, unflanked letters (Flom et al., 1963a). Crowding can also occur for two-bar resolution tasks (Takahashi, 1967), Vernier acuity (Westheimer and Hauske, 1975; Levi and Klein, 1985; Levi et al., 1985), line orientation discrimination (Westheimer et al., 1976), and stereopsis (Butler and Westheimer, 1978). These latter two are considered hyperacuity tasks, because their thresholds are much smaller than the diameter of a single foveal cone, and are therefore considered to reflect cortical processing (Barlow, 1981; Westheimer, 1981). Consequently, extensive work has been dedicated towards investigating crowding under varying conditions in an effort to understand the underlying cortical mechanisms responsible (Butler and Westheimer, 1978; Levi, 2008; Whitney and Levi, 2011).

In 2-dimensional space (2-D), crowding has been subjected to a significant amount of research and the findings are well known and documented (Levi, 2008). The application thereof has led to the development of useful clinical tools, such as crowded letter charts which optimise crowding properties to improve the screening of patients with disorders of binocular vision, notably amblyopia (Gräf et al., 2000; Vision in Preschoolers Study Group (VIP); 2003). Though it is common for clinicians to infer stereoscopic meaning from monocular tasks, this could be problematic since the relationship is not always direct (Harwerth and Schor, 2002). Further, there is evidence that some processing mechanisms operate only in the stereoscopic domain, making binocular inferences from monocular measures not always tenable (Butler and Westheimer, 1978; Westheimer and Truong, 1988). Previously, investigation of 3-dimensional (3-D) crowding was hindered by the intrinsic difficulty in manipulating the 3-D space, without introducing confounding effects and monocular cues (Fox, 1970). The lack of adequate information on stereopsis coding mechanisms, and the application thereof, has prompted interest in the area of stereoscopic crowding. The work described in this thesis investigated stereo based crowding, in an attempt to increase our knowledge on the mechanisms underlining the interaction, and where possible, to apply the results clinically.

The majority of work carried out on crowding in depth has concentrated on observations made on or near the fixation plane (Westheimer and McKee, 1978; Butler and Westheimer, 1978; Fox and Patterson, 1981; Westheimer and McKee, 1980; Westheimer and Truong, 1988). The consensus has been that subtle depth judgments and optimal crowding occur in a region near the plane of fixation in the visual field. The dearth of information about crowding stimulus configuration in the stereoscopic domain require that further investigations are conducted to understand the processes involved and how the information might be useful clinically.

In this study, by using high contrast line or bar stimuli, the spatial extent and degree of crowding was investigated. The influence of stimulus spatial dimensions on the crowding interaction was further investigated by employing disparity increments of both the test and flanking stimuli, on and off the fixation plane. Further, since the origin of stereoscopic depth perception is cortical, stimuli that comprised of different spatial frequencies (Gabor stimuli) were also employed in order to assess different psychophysical visual processing channels in an attempt to understand the behavior of underlying neuronal processes that code for disparity.

Hyperacuities

Ordinarily, visual acuity refers to the ability of the human visual system to discriminate fine details in the visual field. The determination of visual acuity requires that the sensitivity of the visual system response to features is measured. In a more encompassing definition, visual acuity includes tasks such as detection, resolution, recognition and localisation (Harwerth and Schor, 2002; Kniestedt and Stamper, 2003). Distinctions are made between three (3) main visual acuities, namely minimum visible, minimum resolvable, and minimum recognisable. Minimum visible denotes the ability to detect the presence of a single feature or visual stimulus. Target visibility may be improved by increasing its luminance in relation to the background or by increasing its size or both. The basis for minimum visible therefore

is the detection of brightness difference. Minimum resolvable, the criterion of the presence or internal arrangement of identifying features in a visible target, tests the ability to discriminate the minimum separation between features of an object. This is demonstrated by the detection of “doubling” of stimulus consisting of two lines, dots or grating or the gap in the Landolt C. Recognition threshold measures the ability to correctly identify an object such as a letter or similar optotype. This is measured clinically with Snellen letters (Westheimer, 1979a).

In the description of the resolution power of the eye, we ascribe criteria for the relative location of a visible feature in the visual field, thus the ability to ascribe position or locate a test stimulus in space is measured. Examples are the minimum detectable lateral displacement of a line target (Vernier acuity) or discriminating relative depth positions of targets (stereo acuity) (Westheimer, 1979a; Fendick and Westheimer, 1983). Westheimer (1979a) distinguished between ordinary visual acuity (resolution) and hyperacuity (the spatial localisation power of the eye) based on the latter’s superiority over other acuity tasks (see Fig. 1.0 (A)). Spatial hyperacuity tasks include line separation discriminations, bisection acuity, orientation discrimination, motion displacement and disparity discrimination. However, since spatial localisation thresholds are much smaller than the resolution limit of the retina, various theories have systematically been put forward to explain the specialisation involved in such tasks.

Early theories pointed to the coupling of anatomical and functional properties between individual retinal receptors. The sensitivity effect for hyperacuity signals was understood as purely retinal. Helmholtz (1866) proposed that for a visual resolution task such as grating resolution, energised cones must be pooled. Lotze (1886) introduced the idea of ‘local signs’. He stated that the perception of a point stimulus on the retina is mediated by receptors connected to that point. He described a point-to-point connection of the local action to explain the finesse of hyperacuity tasks (cited by Graham, 1966). Arguably, the proposals of Helmholtz (1866) and Lotze (1886) fail to sufficiently account for hyperacuity

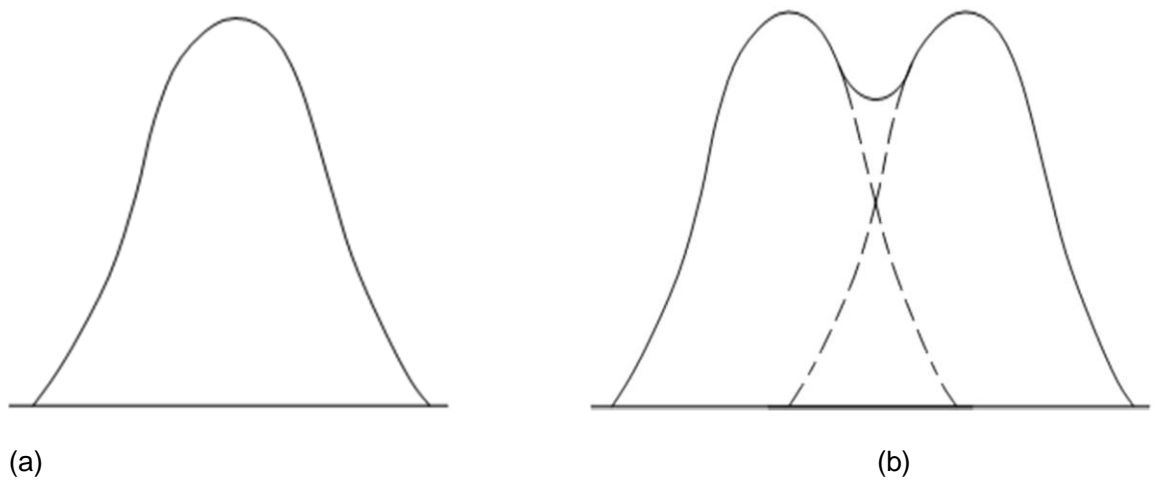
due to the limitation imposed by the diameter of foveal cone receptors. When optimum conditions prevail, depth discrimination thresholds as low as 2 to 5 sec arc, which can equal monocular localisation thresholds in trained observers, have been measured (Berry, 1948; Stigmar, 1970; Westheimer and McKee, 1977). These thresholds are up to 10 times less than the distance between foveal cones (i.e. 20 times smaller than the size of a 6/6 letter on a Snellen VA chart) (Westheimer, 1976; 1979a). Clearly, the discrepancies in hyperacuity threshold and the size of retinal receptor cannot not be explained by any optical or retinal mechanism correction.

To account for the limitation imposed by the cone size for hyperacuties, Hering (1899) proposed an 'averaging' process in which he emphasised that spatial position signals (local signs) associated with individual receptor elements are 'averaged' to yield a localisation threshold smaller than the diameter of a single cone. Anderson and Weymouth (1923) expounded this hypothesis by suggesting that "retinal mean local sign" is a more plausible mechanism. While agreeing that the retina contained narrow receptors with individual connections, features can have exquisite precision in their assigned local sign, and the whole dilemma of measuring the acute grain of visual space revolves around the extraction of this information from along the length of the stimulus (Anderson and Weymouth, 1923). Subsequently, the length of test stimulus (size) was considered a vital aspect of determining the hyperacuity threshold. In that regard, it was explained that spatial position signals associated with individual receptive elements stimulated by a test line, were averaged along the length of the test to yield more precise threshold. Indeed, there was evidence to show that Vernier and stereo acuity improved with an increase in target length, even though the influence of target length on stereo acuity was later found to be limited (Hering, 1961; 1899; Anderson and Weymouth, 1923, McKee, 1983). Westheimer (1975) averred that the binocular apparatus constitutes a powerful tool to extract, and refine depth signals with very precise local signs if required. Stereo acuity is therefore deemed to have most access to the smallest distinction between local signs, and as such the most precise of all the localisation

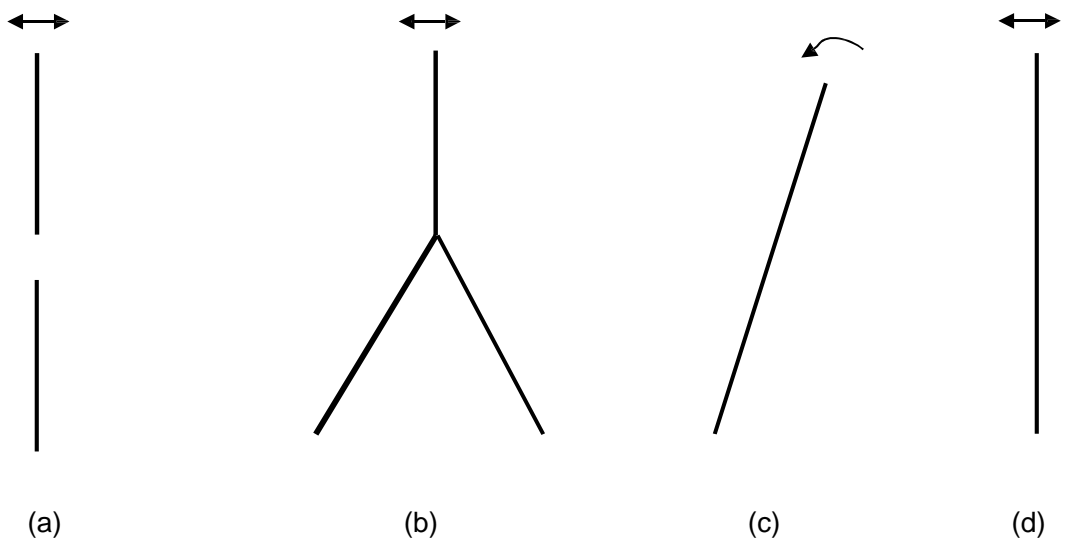
tasks. Westheimer (1979a) used the term hyperacuity to distinguish low threshold visual tasks from ordinary visual acuity. Later, he suggested the recognition of a “centroid” of a retinal light distribution as possible mechanism. He reasoned that the phenomenon is based on the pattern of activity among excited neurons due to the recognition of the centroid (Westheimer, 1979b).

Hyperacuities can be determined by well controlled psychophysical measurements, and are found to be affected by similar conditions such as method of presentation (Lindblom, and Westheimer, 1992), velocity of targets (Westheimer and McKee, 1978), crowding or interference (Westheimer and Hauske, 1975; Butler and Westheimer, 1978). The similarities in the spatial interaction of hyperacuities support the proposition that a common visual mode of processing may subserve both Vernier and stereo acuity (Berry, 1948; Westheimer, 1979b). Westheimer (1979b) however, makes a distinction, and points out that monocular Vernier measurements (Fig. 1.0 (B)) cannot be equated to stereo acuity. He asserts that while Vernier acuity can be estimated to a large extent monocularly, stereo acuity should be devoid of monocular cues and requires single binocular vision to achieve best stereopsis, as was suggested by Julesz (1971).

As described, the limitations imposed by the eye’s optics and retinal constraints fail to adequately account for the precision in discriminating disparity signals. More recent work has therefore focused on higher level cortical explanations. The trend reflects the advancement in scientific research and technology which have allowed more vigorous testing of existing theories and the development of theories which hitherto were a matter of conjecture. In order to further understand our visual impression and sensory information processing, there is the need for further characterisation. Since our impression of an object, and for that matter, disparity detection is remarkably affected by the presence of other objects, studying mechanisms that underline their interaction may help in unearthing the neural underpinnings of spatial discrimination.



A



B

Fig. 1.0 Spatial Resolution Tasks. (A) Difference between visual localisation (a) and resolution (b) (B) Hyperacuity tasks include line separation discrimination (a) bisection acuity (b), and orientation discrimination (c, d) (Redrawn from Westheimer, 1979b)

Binocular Vision and Stereopsis

Binocular (single) vision, is a prerequisite for acute stereopsis and generally refers to the ability to code depth from inter-retinal image overlap (Wheatstone, 1838; Panum, 1858; Julesz, 1960). Binocular vision has several functional advantages including a larger field of view compared to either monocular fields, a 'spare eye' in case distortions are caused by optical or pathologic defects in fellow eye, binocular summation and stereopsis (Bishop, 1987; Harwerth, and Schor, 2002).

When an observer fixates along the primary line of sight (plane of fixation), the primary visual direction (oculocentric direction) is imaged on the center of the fovea (Julesz, 1960; Harwerth and Schor, 2002). Secondary lines of sight (non-fixated) have retinal image locations relative to the primary line of sight. However, the concept of binocular vision (Julesz, 1960) gives one impression of the visual field, with reference to one hypothetical eye located about the midway between the two eyes (the ego centre, or cyclopean eye). Objects located at small distances in front of, or behind the plane of fixation are imaged at retinal locations with different angular distances from the observer. The horopter then defines the location of objects that are imaged onto corresponding retinal points (i.e. correspond to objects on the fixation plane) (Vieth, 1818). The theoretical horopter is the location of object points that are images on corresponding retinal points traced along the horizontal meridian through the fovea by an arc passing through the fixated objects, to peripheral objects that stimulate corresponding retinal points (i.e. the specific locations of objects in physical space that have zero retinal image disparity) (Vieth, 1818). The empirical (objective) horopter is defined by the location of object points in the mid-sagittal plane that are imaged on corresponding points along the vertical meridian (see Fig.1.1) (Wheatstone, 1838, Panum, 1858). The area that lies in front of, and behind the horopter where single binocular vision is still achieved, is known as Panum's fusional area (Panum, 1858). The empirical horopter can be determined in several ways including; using a method of identical visual direction, determination of the position of most acute stereoscopic depth perception

for a range of eccentricities, or estimating the sensory fusion range of Panum's fusional area (Panum, 1958) (Fig. 1.2(A)). This implies that objects not located on the horopter but which lie within the range of Panum's fusional area, will result in the impression of single binocular vision (Panum, 1958). Objects located nearer or farther away from the horopter produce binocular retinal disparities, which are the unique binocular stimulus for stereoscopic depth perception. Binocular disparities are described as uncrossed (distal) or crossed (proximal) relative to the horopter. Perceptually, uncrossed disparities gives rise to a sense of relative 'far' depth, or, if the disparity is large to uncrossed diplopia. Crossed disparities give rise to the perception of 'near' depth, or crossed diplopia (see Figs 1.2(B)). However, the ability to experience fine stereopsis require that all the underlying binocular vision processes are functioning normally, which include normal visual acuity in both eyes, central fixation, bifoveal fixation, and the neural mechanisms to extract stereopsis (Bishop, 1987; Howard and Rogers).

The term 'stereopsis' comes from the Greek word 'stereos' which means solid, to imply the perception of the visual space 3-D, and refers to the relative localisation of objects in depth (perception of relative distance or depth separation) (Wheatstone, 1938; Bishop, 1987). As described, because humans have eyes that are horizontally situated on the face, each eye receives a slightly different view of the visual field (horizontal disparity), resulting in an overlap of the visual field of the two eyes. Consequently, the binocular system ensures a unified representation of the visual field. The binocular system allows the extraction and elaboration of depth signals in relation to retinal images (Ogle, 1962; Westheimer, 1979b). It is the neural processing of these relative horizontal binocular disparities that gives rise to the impression of depth (Wheatstone, 1838; Ogle, 1952, 1953, 1963 Tyler, 1975; Westheimer and McKee, 1979). To understand the mechanism of depth perception, it is relevant to discuss its developmental processes.

Stereopsis is not present at birth and available evidence does not reveal a clear cut period at which the development in humans starts and ends (Ciner et al., 1991; Birch and Petrig,

1996; Giaschi *et al*, 2013). Several investigations into the development of stereopsis have used a variety of tests, principally commercial stereo tests resulting in considerable differences in the time-course of stereopsis development. Visual tracking of small targets and anecdotal clinical evidence suggests that stereopsis emerges between 2 and 5 months after birth (Birch and Petrig, 1996, Daw; 1998). Stereo acuities of 60 min arc have been measured in infants at 6 month, and found to increase thereafter up until about 4 years of age (Daw, 1998). On the other hand, Birch and Petrig (1996) found that stereopsis matured by 6 to 7 months in humans when they employed visually evoked potential (VEP) measurements. Despite the variety of studies, there is general agreement among investigators that stereopsis reaches adult level by the age of 9 (Fox, Patterson and Francis, 1986; Ciner, 1991; Birch and Petrig, 1996, Daw; 1998). Binocular fusion is reported to follow a similar developmental time course and has functional and clinical implications on stereopsis (Ciner, 1991; Daw, 1998).

It must be noted that a distinction is made between the period of maturation for 'fine' stereopsis, and 'coarse' stereopsis in human. Fine stereopsis is reported to mature after 4 years, while coarse stereopsis matures after 8 years (Giaschi, *et al*, 2013). The knowledge of 'fine' and 'coarse' scales of stereopsis dual processing has been applied in understanding people with binocular vision abnormalities (e.g. amblyopia and strabismus), but who may have retained some residual stereopsis (coarse stereopsis). This concept is discussed in another section later in this discussion.

Distinction must also be made between 'relative depth (distance) perception' and 'stereopsis'. The former could be appreciated with monocular and binocular cues, whereas the latter is experienced only as a result of binocular retinal disparity. Broadly speaking, depth perception/sensation is a more encompassing concept, and stereopsis can be regarded as an aspect of depth perception (Gonzalez and Perez, 1998). In this thesis however, as is the case in other literature, the terms are used interchangeably and they imply similar meaning unless otherwise specified.

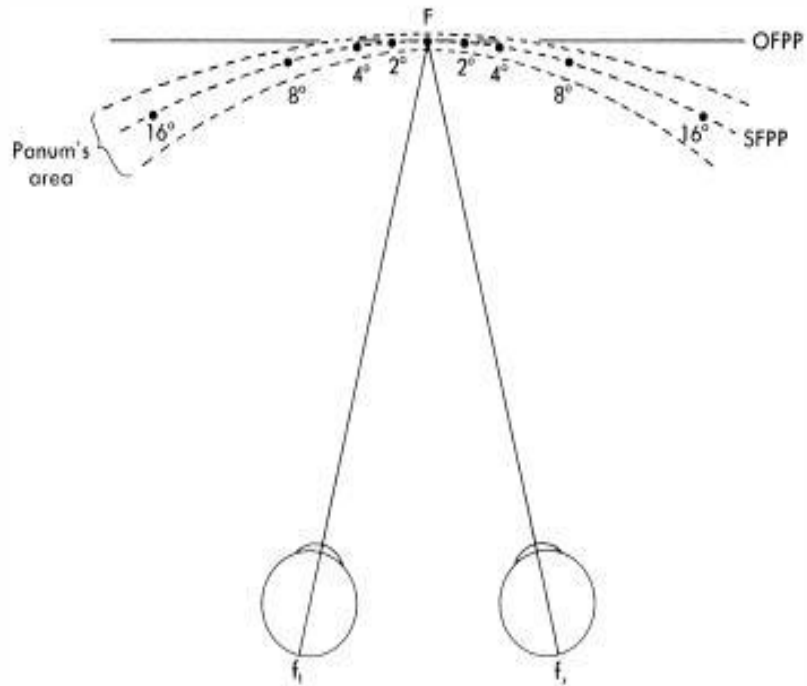
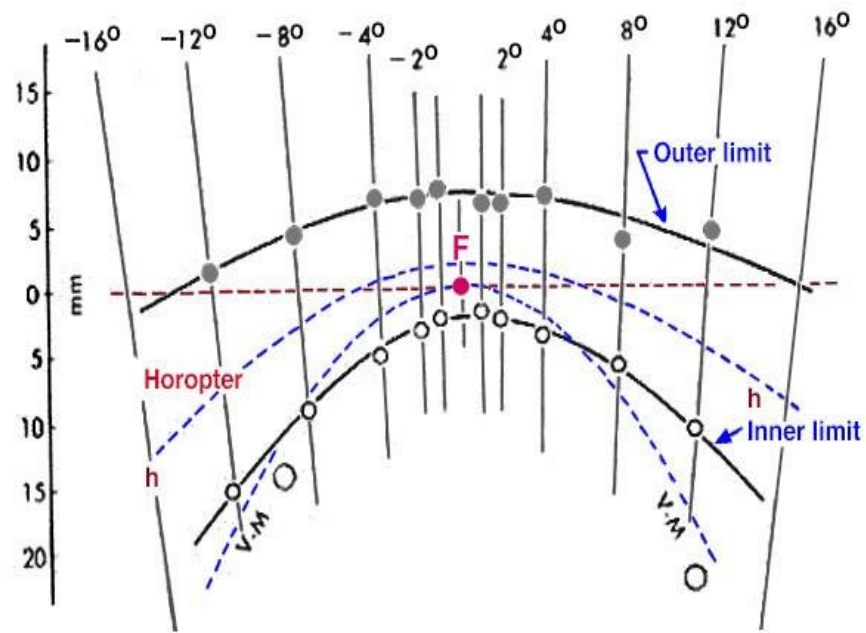
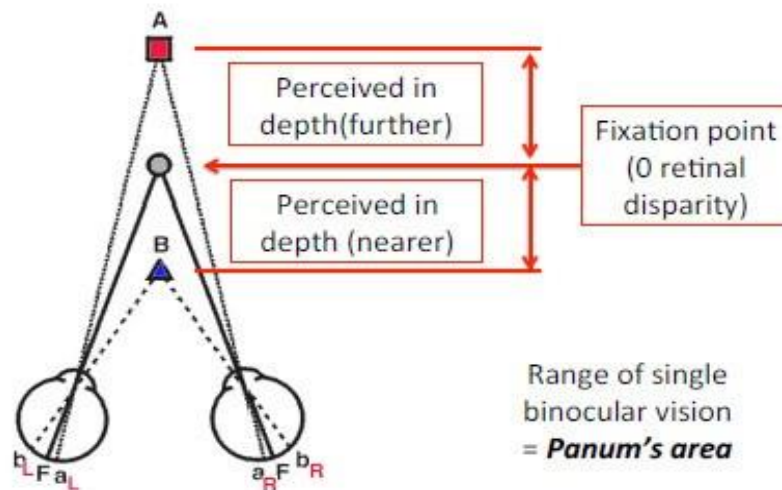


Fig. 1. 1. Panum's Fusion Area as Measured by Horopter Method (Hering, 1961) (From Harwerth and Schor, 2002). F , fixation point; SFPP, subjective frontoparallel plane. OFPP, objective frontoparallel plane. The horizontal extent of these areas is small at the center (6 to 10 minutes near the fovea) and increases toward the periphery (around 30 to 40 minutes at 12 deg from the fovea). The vertical extent has been variously assessed by different researchers. However, more recent research suggests that Panum's area is considerably larger (e.g. Julesz, 1986). Moving RDS, which are most effective in retaining fusion while the disparity is increased, have shown that disparities of as much as 2 to 3 deg can be fused.



(A)



(B)

Fig. 1. 2. The Horopter (From Kalloniatis and Luu, 2007; Harwerth and Schor, 2002). The horopter is a curved line which represents the points which are the same distance from the observer as the object of focus. Panum's area specifies the zone around the horopter (lower and upper limits) where retinal images will be fused into a single object (A). Perceived depth relative to the fixation.

Neurophysiological Basis of Stereopsis and Crowding

Wheatstone (1838) first proposed that disparities between inter-ocular images were sufficient cues for the sensation of stereoscopic depth. However, because human observers are able to differentiate depth differences corresponding to retinal disparities of the order of secs of arc of visual angle, the mechanism necessary to extract the correct signals must lie beyond the level of the retina. Various authors have related physiological (Qian, and Zhu, 1997), computational (Poggio and Poggio, 1984) and psychophysical (Butler and Westheimer, 1978) investigations using cat (Hubel and Wiesel, 1962; Barlow et al., 1967; Anzai et al., 1997), macaque monkey (Baker et al., 1974; Crawford et al., 1975; Connolly and Van Essen, 1984) and human observers (e.g.s. Freeman and Ohzawa, 1990; Kiorpes and McKee, 1999) to understand the neural mechanisms of stereoscopic depth perception in humans

From an anatomic viewpoint, objects that are located in front of, or behind the fixation plane will have their retinal images located on the nasal or temporal retinae respectively. Strict partial decussation in each nasal and temporal hemiretina means corresponding retinal points should be represented monocularly in inter-hemispheric parts of the cerebrum. Intercortical pathways passing through the splenium of the corpus collosum later permit merging of the signals upon single cortical neurons (Barlow et al., 1967; Blakemore and Campbell, 1969; Blakemore, 1970; Blakemore and Hague, 1972; Sherman and Koch, 1986). The human cerebrum has six layers. Layers 1, 4 and 6 receive signals from the nasal retinal fibres of the contralateral retina. The other three layers receive signals from the temporal ipsilateral retina. The projections from the retina ganglion cells to the lateral geniculate nucleus (LGN), and later the primary visual (striate) cortex (V1) are registered in the sense that a given point in the visual field is represented by the same point of all LGN layers along the same projection line perpendicular to the layers. In addition, the LGN receives feedback from the visual cortex (Sherman and Koch, 1986). For example, in cats, it has been reported that damage to the cortex shows matching degeneration in some fibres in both the cortex

and LGN (Guillery, 1967), and in humans, roughly 50 percent of synapses in the LGN are derived from cells in VI (Sherman and Koch, 1986). Though optic nerve fibers from the two eyes are first in near proximity to the LGN, individual layers of each LGN are monocular. Consequently, binocular combination of visual information has focused on higher cortical centres.

Detailed physiological, psychophysical and histological investigations demonstrate the existence of at least two major parallel pathways through which visual information from the LGN is received in the V1, and then projected to higher visual areas in the extra striate visual cortex (Fig.1.3). These are magnocellular and parvocellular pathways (Harwerth and Schor, 2002) Stereopsis and motion are thought to be mediated by the magnocellular pathway, and associated with two dorsal layers of the LGN. From the V1 magnocellular layers are projected to extra striate cortical areas such as the middle temporal area (MT) and medial superior temporal area (MST). The parvocellular pathway, associated with the ventral layers of the LGN is subdivided into the blob and interblob streams which mediate colour and form perception. From the V1 parvocellular layers are projected to extra striate cortical areas V2, V4, and inferiotemporal area (IT) (Hubel and Livingstone, 1987).

Hubel and Wiesel (1962) recorded from single cells in the cat visual system and found that some cells in the first stage of binocular convergence (V1) fire optimally only when stimulated by corresponding retinal regions. Their study provided information on spatial parameters that elicited optimum excitation of cortical cells by investigating and mapping the receptive fields of cells in the visual cortex of cats. Based on the Hubel and Wiesel (1962) findings, Barlow and his colleagues (Barlow et al., 1967) first demonstrated disparity-tuned cells in the visual cortex in cats and later more extensive recording (V1 and V2) in monkeys (Hubel and Wiesel, 1970; Poggio and Fischer, 1977) which revealed neurons that were optimally excited by spatially distant objects that fall within their 'receptive fields'.

The receptive field (RF) defines the area of the visual field that a stimulus must occupy to excite a cell (Hubel and Wiesel, 1962; Barlow et al, 1967). Each single cell therefore has its

own receptive field, and binocular cortical cells have two receptive fields, one for each eye. Cortical visual cells receiving input projections from the LGN were categorised into two groups according to their receptive field properties. Identified cells had rectangular (elongated) RFs unlike the circular RFs found in retina and LGN along various directions with either, ON (excitatory) or, OFF (inhibition) center and antagonistic surround.

Hubel and Wiesel (1962) first discovered two different types of V1 cells which they termed simple and complex cells. Both types are excited by stimuli of different spatial properties and orientations. Simple cells (mainly found in V1 layers 4 and 6) have RF that comprise spatially distinct subregions of ON and OFF (distinct inhibitory and excitatory regions) that respond to either offsets or onsets of flashed stationary bars of light. Also, simple cells show linearity of spatial summation within separate inhibitory and excitatory regions, and demonstrate antagonism between inhibitory and excitatory regions. As such, responses of simple cells to moving or stationary spots of lights can be predicted from excitatory and inhibitory cell maps. Complex cells (mainly found in V1 layers 2, 3 and 5) have spatially uniform receptive fields. That is, they have no clear distinct inhibitory and excitatory regions inside their RFs, and are excited by changes in light illumination (both bright and dark bars). Complex cells are ineffectively excited by spots of light covering their entire RF (stimulus with uniform intensity), and thus are insensitive to contrast polarity but are more broadly selective to stimulus orientation. While simple cells receive input from the magnocellular pathway, complex cells receive input from parvocellular pathway, respectively. Both cells were subsequently found to be sensitive to retinal image disparities (Kuffler, 1953; Hubel and Wiesel, 1962; Barlow et al., 1967; Ohzawa et al, 1990).

The activity pattern of neurons that detect disparity information were studied by linking it to specific visual percept. (e.g. Barlow et al, 1967; DeAngelis et al, 1995a; 1995b). The use of different stimuli produced changes in disparity tuning functions (responses of a cell measured as impulse per second plotted against disparity) of cortical cells in V1. To date, six (6) main groups of neurons have been described in macaque monkeys in the areas V1,

V2 and other visual areas based on their response to disparity using dynamic random dot stereograms (RDS) and solid bars (Poggio and Fischer, 1977; Poggio and Poggio, 1984; Ohzawa et al, 1990; Freeman, 1990). They include tuned excitatory, tuned inhibitory, near cells, far cells, tuned near and tuned far cells (Fig. 1.4).

For tuned excitatory cells, their disparity tuning function displays binocular facilitation over a narrow range of disparity located around zero disparity, and shows binocular suppression for both crossed and uncrossed disparities. That is, they are narrowly tuned for disparity around the horopter and show symmetry around zero disparity for the narrow tuning width. Tuned inhibitory cells also signal for disparities located on the horopter and demonstrate a similar disparity tuning function as tuned excitatory cells, only that the peak is for uncrossed disparity. They show characteristic suppression points over a narrow range of disparities around zero disparity, and facilitation for other uncrossed or crossed disparities. Tuned far cells show similar functions as tuned excitatory cells, however they display a peak at uncrossed disparities. Tuned near cells are a homologue to tuned far cells, but have their peak at crossed disparities. In other words tuned far and tuned near cells would be ideal to code for disparity located behind of, and in front of the horopter respectively, and demonstrate reciprocity inhibition to their firing (Lehky and Sejnowski, 1990). Whilst far cells are activated by uncrossed disparities over a wide range disparities and suppressed by crossed disparities, the opposite holds true for near cells. As described these disparity sensitive neurons are known to be associated with the “magno” pathway, being particularly prominent in the V2 and also in the extra striate area of MT (Poggio and Poggio, 1984; Hubel and Livingstone, 1987).

From the foregoing discussion, it can be noted that stereopsis can be traced to the V1 (Brodmann area 17). However, there is a consensus for a two-stage model of discrimination, in which the first stage involves the detection of simple features (in V1), and a second stage where integration of features beyond V1, perhaps in areas V2 and MT (Crawford et al., 1984; Lehky and Sejnowski, 1990; Read, 2005).

Most cells in V1 are selective to spatial frequency (simple cells are phase sensitive while complex cells are phase insensitive) and orientation. The magnitude of response of a given cell to different spatial frequencies forms a tuning curve which peaks at some certain optimal frequency and reduces when the spatial frequency is either higher or lower than optimal. These cells form a continuum in terms of their optimal spatial frequencies ranging from low spatial frequency of about 2 cpd (cycles per degree) to high spatial frequency of about 10 cpd. V1 cells are capable of neuronal adaptation (or fatigue), a reduction in firing rate after prolonged excitation (Blakemore and Julesz, 1971; Blakemore and Hague, 1972). This implies that the perceived spatial frequency of an object is the result of the comparison among different channels in the visual system, each preferring a specific range of spatial frequencies, where the bandwidth of spatial frequency tuning is defined as the frequency difference between the two frequencies where the amplitude of the response is half of the peak. From the discussion above, we note that in the visual cortex the neurons selectively tuned to different spatial frequencies can be considered as a set of band-pass filters. The incoming visual signals are filtered and processed in parallel by an array of filter channels. In other words, the visual signals are analysed not only in spatial domain or location, but also in the spatial frequency domain (De Valois et al., 1982).

For a disparity integration (crowding) mechanism, two main conflicting conceptual modes of operation have been argued. First is an inert, additive theory of depth disparity differences within some integrating region in the visual cortex, and second, and an active inhibition theory between depth signals elicited by disparate signals within a small slice of the visual field (Blakemore and Hague, 1972; Freeman and Ohzawa 1990; Ohzawa et al., 1990). According to the former, crowding by surrounding flankers in the fixation plane dilutes the depth signals, therefore greater disparities are needed to reach thresholds (Wilkinson et al., 1997). The latter model gives credence to the interaction of a test with surrounding flankers which inhibit the extraction of depth information related to the test (Butler and Westheimer, 1978; Westheimer and McKee, 1978; Westheimer, 1986; Tyler and Likova, 2007).

The findings of some psychophysical experiments correlate with some neurophysiological studies that point out that responses of substrates in the V1 could be enhanced or repressed by the surrounds. Both additive (pooling) and inhibitory mechanisms have successfully been used to explain crowding in visual tasks (Sayim et al., 2010). In former model, depth information from flankers and test are pooled and averaged. As such, well placed flankers act to reduce the neural activity of the test to occasion elevated thresholds (Badcock and Westheimer, 1985; Kumar and Glaser, 1992a). That is, stereo acuity is better when the test is presented alone compared to when flankers are present. In the later model, flankers act to decrease neural activity connected to the test when flankers are positioned within the inhibitory zone of the receptive field of the neural mechanisms associated with the test. Consequently, poorer stereo acuities are recorded compared to when flankers are present within the surround of the test (Westheimer and Hauske, 1975).

More recently, there are propositions that suggest that perceptual Gestalt grouping factors are an important factor in the modulation of foveal crowding (Kooi et al., 1994; Manassi et al., 2012; Herzog et al, 2015). Proponents posit that cortical processing of local disparities cannot sufficiently explain crowding, rather there is the involvement of mid-level perceptual grouping. In that sense, flankers positioned around a test would act to increase the threshold when the test and flankers are perceived as part of a group, but ungrouping will enhance performance (Mitchison and Westheimer, 1984; Deas and Wilcox, 2014). For example, when horizontal lines were added below and above a stereoscopic test such that the configuration resembled a rectangle, there was reduction in stereo acuity despite the fact that the same disparity information was available from the onset when the test was presented alone (McKee, 1983). Recent work with supra-threshold stereo-targets support the idea that depth perception may be degraded by Gestalt group factors (Deas and Wilcox, 2014). Nevertheless, the influence of Gestalt grouping on stereoscopic crowding has not been studied extensively.

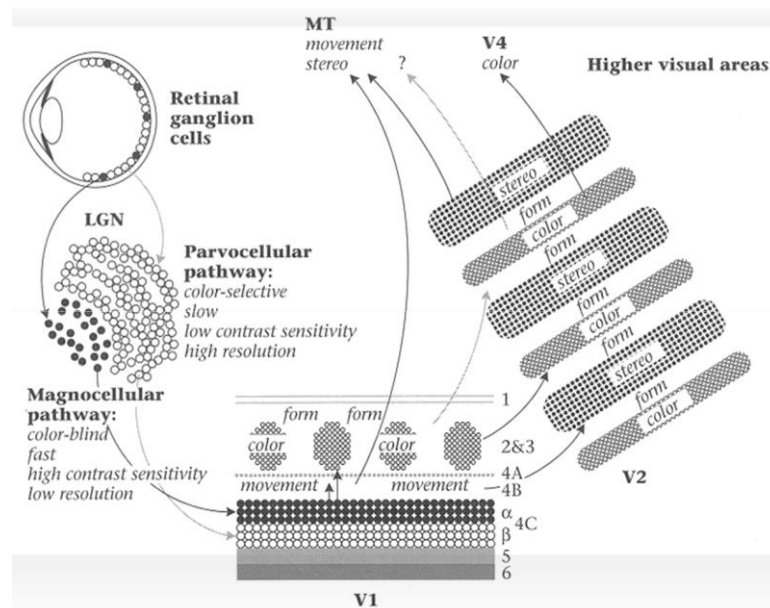


Fig 1. 3 The Visual Cortex (From Hubel and Livingstone, 1987). Visual signals from the nasal retina of the left eye and temporal retina of the right eye (representing the left visual field of both eyes) are projected to the right visual cortex. In a similar way, visual signals from the nasal retina of the right eye and temporal retina of the left eye (representing the right visual field of both eyes) are projected to the left visual cortex (not displayed). Projections are made from the primary visual cortex ([V1] Brodmann's area 17), the secondary visual cortex ([V2] Brodmann's area 18), and the visual areas V3 and V5 (Brodmann's area 19). V1 is involved in basic visual features and stereopsis, V3, MT/V5 are media motion detection, spatial localisation, eye and hand movement, and V4 mediate color.

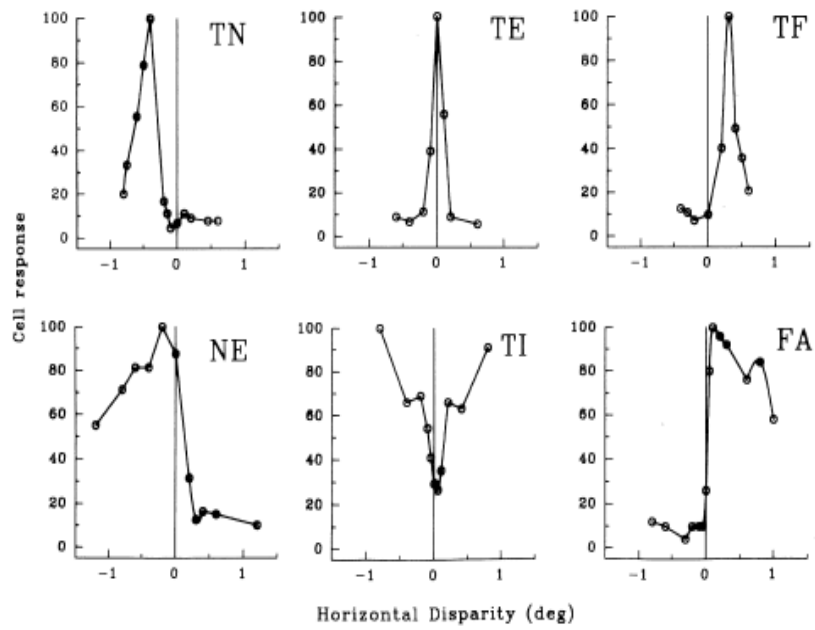


Fig. 1. 4. Disparity Tuning Function of Visual Cells (From Gonzalez and Perez, 1998). Each panel one of six (6) main groups of neurons described in the visual areas based their response to disparity using dynamic RDS and solid bars (Poggio and Fischer, 1977; Poggio and Poggio, 1984). They include tuned near cells, excitatory, tuned far cells, tuned near, tuned inhibitory and tuned far.

Measurement of Stereopsis (Stereo Acuity)

Stereopsis development in humans can be disrupted by developmental factors including amblyopia (Daw, 1998; Kiorpes and McKee, 1999; Giaschi *et al* 2013), refractive error (Westheimer and McKee, 1980a), difference in retinal image contrast (Legge, and Gu, 1989) and strabismus (Levi, 2008). Clinically, assessment of stereopsis is one way to gain a functional outlook of the binocular system and to monitor the success of treatment of binocular anomalies (Fricke and Siderov, 1997; Momeni-Moghadam et al., 2011). A number of stereograms have been developed for age-specific assessment, screening and monitoring of therapy. Local contour stereograms such as the Titmus stereofly test (Stereo Optical CO) and global random dot stereograms (RDS) (e.g. Lang stereotest (Haag-Streit Service Inc.), Frisby (Clement Clarke International), Random-Dot E (Stereo Optical Co.), TNO (Lameris Ootech) are used in screening and measuring stereopsis in the clinic. It has been observed that the measurement of clinical stereo acuity is influenced by the type of stereogram used, thus the pattern and parameters of the stimulus configuration embedded in the test design influence the level of stereo acuity measured (Harwerth and Schor, 2002). Non-random dot stereograms rely on the presence of monocular visible contours assumed to be matched locally (*local stereopsis*) (Westheimer and McKee, 1980; Harwerth and Schor, 2002) and RDS, first used by Julesz (1960), are thought to require a more global process (*global stereopsis*). RDSs contain no monocular depth cues and are thought to elicit stereoscopic depth through a process of comparing corresponding and disparate points by associating identical features over a large retinal area (Westheimer and McKee, 1979; Westheimer, 2012). However, some current tests of stereopsis suffer from resolution ambiguities and crowding in feature articulation (Harwerth and Schor, 2002; Westheimer, 2012), suggesting a need for improvement in test designs.

Horizontal retinal disparities are quantified in stereoangles (η), and measured clinically as the smallest detectable stereoscopic depth (stereo acuity). From the geometric perspective (Fig. 1.5), the situation can be simplified as an object positioned in the plane of fixation at

distance d from an observer with interpupillary distance, a . In normal humans, the average inter-ocular distance between the two eyes is between 58 and 70 mm (Howarth, 2011). This creates a disparity due to the slightly different view of the object from the right and left eyes. The magnitude of the disparity is equal to the difference in the longitudinal visual angles (α_1 and α_2), or the convergence (parallax) angles (δ_1 and δ_2). The stereo angle, η can be calculated from the angular difference in location of common objects in the two half-views of the stereogram (see Fig 1.5).

Stereo acuity is defined in relation to the subjective location of the object, and as the function shows (Fig. 1. 5), for any given fixation distance, the relationship between the depth interval and retinal disparity is linear, thus disparity increases with increasing depth interval but the relationship varies with fixation distance by the square of the distance. In other words, disparity and therefore stereo acuity increases with increasing viewing distance. That is, the magnitude of the disparity depends on the fixation distance (d), the depth interval (Δb) and the interpupillary distance (a). In testing for stereo acuity therefore, to maintain the relationship between perceived depth and disparity, or stereo angle and viewing distance, an observer's horizontal disparity must be scaled with the viewing distance.

Presently, there is no single standardized clinical test to measure stereo acuity in normal subjects or used to detect binocular deficits in children unlike the use of standardised visual acuity tests to measure monocular visual deficits (Harwerth and Schor, 2002). Poor visual acuity generally relates to reduced stereo acuity. Again, both stereo acuity and visual acuity decrease from the fovea to the periphery of the retina. Spectacle blur has also been shown to have a detrimental effect on stereo acuity more than the effect on visual acuity (Westheimer, 1982; 1979a; Fendick and Westheimer, 1983). However, it may not be useful to make assumptions from the measures of visual acuity alone, since angles for disparity detection are usually smaller than resolution angles for visual acuity (Westheimer, 1979a). Thus, the relationship between visual acuity and stereo acuity is nonlinear making reliance on visual acuity to predict stereo acuity unreliable. Given this, it may be presumptuous to

assume that stereo acuity in children with amblyopia may be better or worse using predicted values from visual acuity assessment alone. Consequently, this thesis seeks to answer questions about stereo based visual crowding, and stimulus characteristics which could be important in developing stereograms for detecting binocular vision dysfunctions.

Conventionally, stereograms (Fig. 1.6) are used as screening tools for distinguishing normal from abnormal binocular vision such as stereoblindness, microstrabismus, monofixation and all forms of amblyopia (Fricke and Siderov, 1997). Stereograms consist of 2-D monocular images seen separately by the left and the right eye but are combined into 3-D percept in depth. The design is such that interocular images contain reference elements or features in relative locations in other eyes view. As a result, features that are offset in their relative spatial locations are perceived by the right and left eye separately. The offsets or relative binocular disparity causes the experience of stereoscopic depth sensation.

Clinically, stereo thresholds in the region of 15 to 30 arc sec are expected for an observer with normal binocular function (Bishop, 1987; Harwerth, and Schor, 2002). However, this range is usually lower than the smallest detectable disparity present in most clinical tests. Similarly, in the laboratory, for untrained observers stereo acuities are typically worse than 30 sec arc. But in a well-controlled laboratory experiment and well trained subjects thresholds can measure as low as 2 to 7 sec arc (Berry 1948; Stigmar, 1970).

The limited information on stimulus parameters may be the reason for discrepancies in stereo acuity measured with different stereograms, sometimes on the same observer (Harwerth, and Schor, 2002). This has led to the suggestion of a standardized stereotest to be developed to provide information for clinical decision. This makes it important that in addition to traditional visual acuity tests, stereograms that offer an alternative to assess the integrity of binocular functions are developed. It is hoped that the findings from this thesis will highlight significant aspects of crowding in stereopsis, and contribute to our understanding of how objects are spatially discriminated in depth.



(a)



(b)



(c)



(d)



(e)

Fig. 1. 6. Commercially Available Clinical Stereotests

a)The Wirt stereotest, (b) Frisby test, (c) Randot stereotest, and Lang II, (d) Random dot and (e) Random dot E (Fricke and Siderov, 1997; Momeni-Moghadam et al., 2011)

Coarse and Fine Stereopsis

It has long been established that the fundamental cue for stereopsis is the small horizontal retinal image difference due to the separation of the two eyes, which results in the visual impression of depth (Wheatstone 1838; Panum, 1958). As discussed earlier, retinal disparities that contribute to stereopsis range from small disparities that are considered to operate across 'fine' scales to larger disparities that operate across 'coarse' scales, which may be processed via different processes and have different developmental time courses (Menz and Freeman, 2003; Giaschi et al, 2013). Based on these observations two forms of stereopsis have been described, namely 'patent' and 'qualitative'. Patent (fine) stereopsis results from small disparities which require fusion and a stable binocular system, while qualitative (coarse) stereopsis may result from large disparities in the absence of sensory fusion, even from diplopic images (Fig. 1.7) (Ogle, 1952, 1953, 1963, Blakemore, 1970). Ogle's definition of fine stereopsis referred to the quality of the stereopsis such that increasing the disparity resulted in a commensurate increase in the perceived depth. Whereas qualitative stereopsis gave an impression of 'in front' or 'behind' but without the close link with the amount of disparity. Therefore fine stereopsis involves precise depth discriminations from disparities not exceeding 2 degrees of arc (Poggio and Fischer, 1977; Giaschi et al., 2013) while coarse stereopsis results from disparities within the range up to 7 degrees for crossed and up to 12 degrees for uncrossed disparities (Westheimer and Tanzman, 1956; Blakemore, 1970; Menz and Freeman, 2003; Giaschi et al., 2013).

Systematic scientific investigations have suggested different neural mechanisms seem to process fine (first order) and coarse (second order) stereoscopic (Menz and Freeman, 2003), and therefore respond to different stimuli detail. That is, first order stereopsis responds to luminance based disparity signals and coarse stereopsis responds to the information provided by the stimulus contrast envelope (Wilcox and Hess, 1994; 1998). Also, coarse stereopsis is found to be more robust to a stimulus that produces large differences

in interocular images and accounts for the large upper limits of stereopsis processing (Farell et al., 2004).

Fine and coarse mechanisms of stereopsis are thought to play different roles in depth perception (Marr and Poggi, 1979; Schor and Wood, 1983; Harris et al, 1997) depending on the spatial task. In essence, the two mechanisms operate in a synergetic manner in normal adult (Wilcox and Hess, 1998). The fine stereo mechanism operates when there is no ambiguity in the images being compared in both eyes, and the coarse stereo mechanism operates as a backup system which is used when there is ambiguity in the stimulus (e.g. random dots) or the disparities are outside the fusion limits (Julesz, 1971; 1986). It is also speculated that coarse stereopsis could be involved in the development of coordinated binocular eye movements in infants (Ciner, 1991; Giaschi et al, 2013). The coarse stereopsis mechanism may be used by the developing visual system to ensure binocular fusion, and subsequently, used to align the eyes which ensures the eventual development of high resolution fine stereopsis (Giaschi et al, 2013). Giaschi and colleagues (2013) demonstrated differences in discrimination of coarse and fine disparities in young subjects (5 to 12 years) with normal and amblyopic vision. Their study suggested that coarse stereopsis could be physiologically spared to provide critical depth information in amblyopic children who do not possess high resolution fine stereopsis due to their amblyopic abnormality (see Fig 1.8)

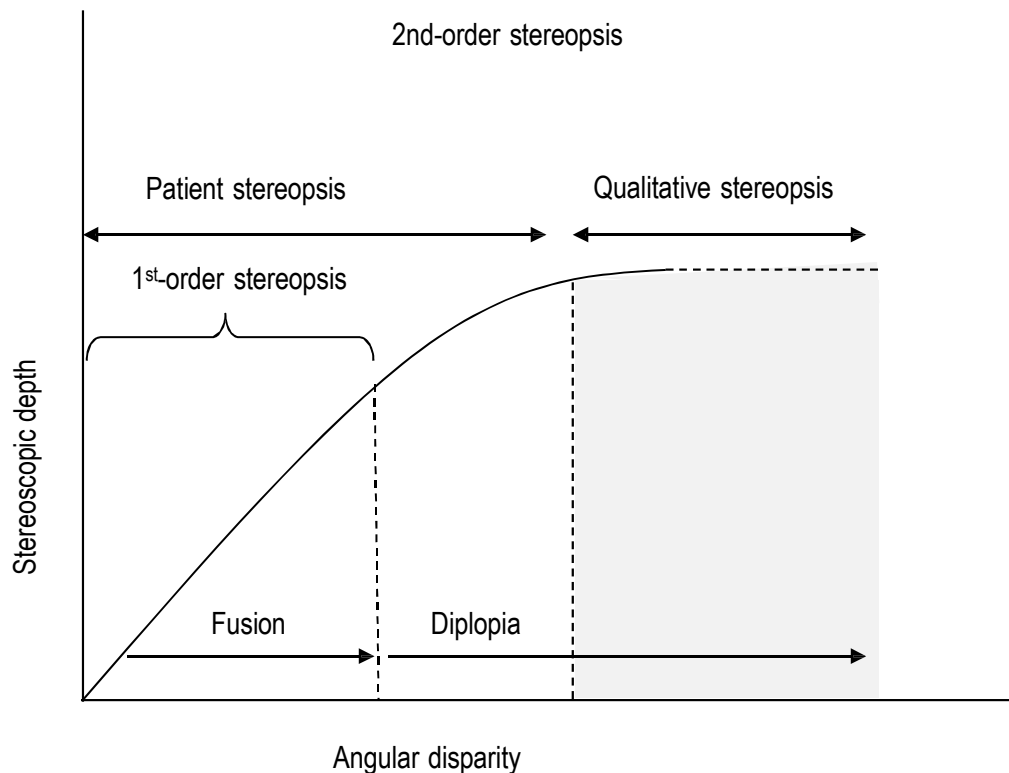


Fig. 1. 7. Illustration of Range of Stereopsis

A schematic representation of Ogle's (1952; 1953) categorisation of patient and qualitative stereopsis as re-illustrated by Wilcox and Allison (2009), showing perceived depth as function of angular disparity. The range of stereopsis is a function of fusion and diplopia.

Local and Global Stereopsis

Stereoscopic depth perception, in its simplest form, refers to the ability to detect a stimulus as appearing in front of, or behind a reference target based solely on differences in horizontal retinal disparity (Westheimer and McKee, 1980a). Stereopsis can be categorised as either local or global (Julesz, 1971; Richards and Kaye, 1974; Gantz and Bedell, 2011) (see Fig. 1.9).

Local stereopsis usually yields fusion and requires a high degree of binocular similarity of images in each eye (disparate images). Therefore, local stereopsis is customarily associated

with a single or only a few isolated features (Mitchell and O'Hagan, 1972; Westheimer and McKee, 1980a; Fahle and Westheimer, 1988), and assign depth values to individual features in the stimulus (Westheimer, 1986). The range of disparities for local stereopsis is less than 0.5 deg (Ogle, 1962; 1963, Richards and Kaye, 1974). Local stereograms composed of high contrast features or contours such as lines or bars can easily be detected by all individuals with normal binocular vision, and subjects with binocular abnormalities but who still have some binocular function. Many clinical stereo tests are based on local contour stereogram designs (e.g. Titmus fly test and Randot test) (Saladin, 2005). In the laboratory, stereo-thresholds measured under local stereopsis can be very low, usually less than 10 sec arc in trained observers under exposure durations less than 500 ms (Berry, 1948; Ogle, 1960; Stigmar, 1970; Westheimer and McKee, 1980a).

On the other hand, global stereopsis is disparity based, and stereopsis is experienced by comparing multiple identical elements between the right and left eye to make a depth judgement (Julesz, 1971). Global stereopsis does not require similar targets in each eye and these targets are generally not fused but appear diplopic (Westheimer and Tanzman, 1956). Therefore, global processes assign depth values to the overall configuration and are relatively unaffected by depth values of the individual features. The range of disparities that gives rise to global stereopsis is much larger than 0.5 deg. (Ogle, 1962; 1963; Richards and Kaye, 1974). Julesz (1971) developed the RDS for measuring global stereopsis and showed that stereopsis may still be experienced without monocular cues. It was previously assumed that the depth location of an object was obtained by comparing the disparity between the right and left images without actually experiencing the sensation of depth. In other words, it was as if the visual system processed information about an object's characteristics and location first, before that information was used for depth perception. However, Julesz and others (Julesz, 1971; Blakemore and Julesz, 1971; Westheimer and McKee, 1979) showed that depth perception can be experienced from binocular pattern differences (disparities) that are not visible monocularly. A clear example of this is how the visual system solves the

many identical features in RDS by associating retinal images in the right and left eyes (Westheimer, 1979b; 2012; Westheimer and McKee, 1980a).

Though global stereopsis measures very fine stereopsis, there are disadvantages that arise from the design of the test (Westheimer, 2012). Firstly, the structure global stereograms limits the minimum disparity that can be presented compared to values found in local forms. As such, untrained observers (e.g. children) have challenges making depth judgements in them. Secondly, there are restrictions on the range stimulus disparity used because disparities can only be created to scale to the size of elements in the pattern. Thirdly, there is ambiguity and crowding in matching elements, which results in multiple false matches. Because the minimum inter element separation required depends on element size, this creates ambiguity and crowding when comparing the features, especially for untrained observers and observers with abnormal binocular vision (Fendick and Westheimer, 1983; Westheimer, 2012). For example the minimum separation found to optimise threshold in a simple stereogram by Westheimer and McKee (1980a) was 10 min arc, but this separation might be too coarse and not in good accord with the purpose of global stereopsis.

Based on the manner local and global stereopsis operate, different authors postulate that stereopsis involves separate local and global modes of processing, while others argue to the contrary (Richards and Kaye, 1974). Gantz and Bedell, (2011) reported different depth experiences for global and local stereopsis based on the density of the RDS used. They showed that stereo-thresholds increased for a test superimposed on a RDS at small separations (making it global) and large separations (making it local). Gantz and Bedell, (2011) concluded that the same disparity mechanisms process local and global stereopsis. From the discussion, the general consensus is that the type of stereopsis operated depends on the density of features embedded in the stimuli being used, but the two processing mechanisms cannot be entirely separated (Richards and Kaye, 1974). It must be stressed that one can have local stereopsis in the absence of global, but not vice-versa. Additionally, it has been demonstrated that early onset strabismus can result in the loss of global

stereopsis, though gross local stereo capability from coarse disparity mechanisms may remain (see Fig. 1.8, study by Giachi et al., (2013) which showed the sparing of coarse stereopsis).

Most past investigations that differentiated local and global stereopsis mechanisms used narrow or wide stimulus targets and made a link between stimulus size and mechanisms of local and global stereopsis (Richards and Kaye, 1974). It was argued that narrow stimulus size detectors encode for small disparity mechanisms and wide stimulus size encode for large disparity mechanism. This present study which investigated the size of stimuli parameters and configuration on depth discrimination may show a continuum of local and global mechanism.

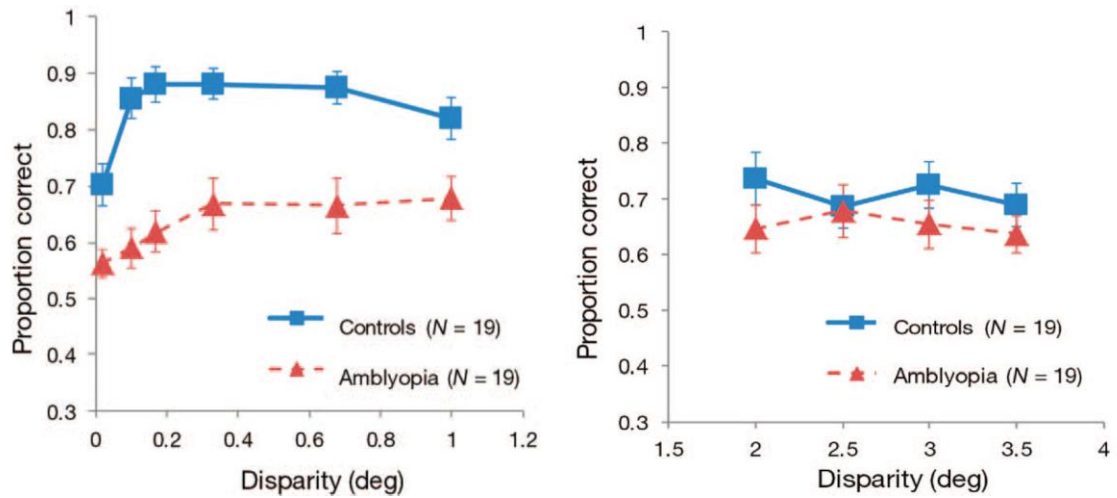
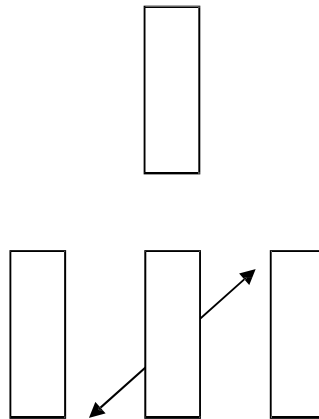
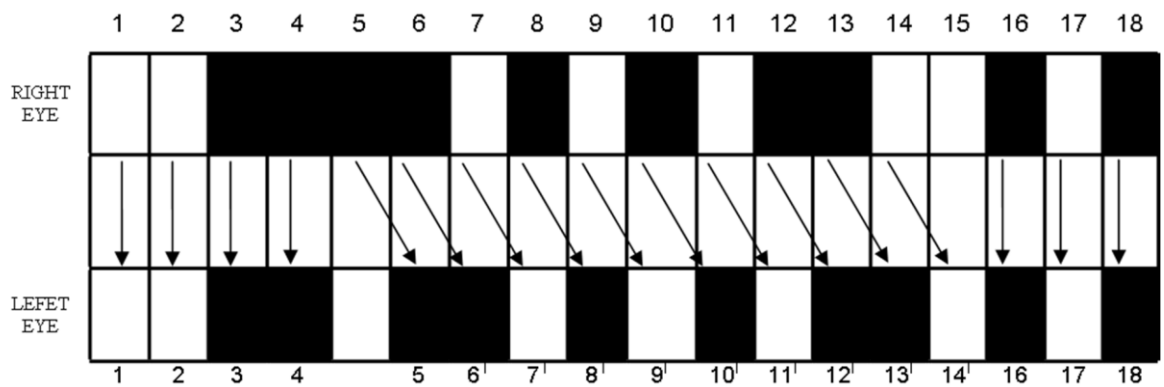


Fig. 1. 8. Fine and Coarse Disparity Discrimination in Amblyopes (Giachi et al, (2013). Based on an assumption that coarse stereopsis develops before fine stereopsis and maybe physiologically immune to early abnormalities of the binocular cooperation and deprivation, the authors showed that the disparity range at which diplopic (coarse) stereopsis occurred was between 1 and 2 degrees and observed that there was no significant difference in the coarse discrimination among the normals and amblyopic subgroups. But in the fine disparity range, amblyopic subjects performed comparatively worse, especially for strabismic related cases. Based on their results, they suggested that under some conditions, coarse stereopsis that occur from large disparities maybe physiologically spared when fine stereopsis is disrupted by early visual development in amblyopia.



(A)



(B)

Fig. 1. 9. Local and global stereograms (From Westheimer, 2012). Stereograms are categorised based on the density of feature elements needed to create disparity. Local tests (A) are composed of few features or contours such as lines, with which low thresholds can be measured. Depth sensation is experienced by detecting a feature such as a bar (arrowed) as appearing in front or behind of other features. Global tests (B) have multiple identical feature elements embedded in them. Depth sensation is experienced by matching the many identical features between the right and left eye. The differences their retinal image disparity makes it appear as uncrossed or crossed.

Crowding in 2-DTasks

Crowding is frequently interchanged with the term 'masking' (Levi, 2008). Masking is either described as 'lateral masking' to refer to any effect on the detectability, discriminability or recognition of a test by non-overlapping spatially adjacent patterns (masker) or 'pattern masking', to refer to when the masker with the same orientation and properties as the test overlap (Legge and Foley, 1980; Polat and Sagi, 1993). In lateral masking, the spatial discrimination of a test stimulus is increased when high contrast flankers are positioned close to the test, but decreases at larger separations (Polat and Sagi, 1993). In pattern masking, the discriminability of a test stimulus increases exponentially with an increase in flanker contrast, compared to when no flankers are present (Legge, Foley, 1980). Generally, the synonymous use of 'crowding' with 'masking' introduces a presumptive underlying link between their modes of operation, or possibly reflect the same mechanism. However, most traditional crowding studies have used letters as tests and flankers, and masking studies have used Gabor patches as tests and flankers (Gabor-by-Gabor) (e.g. Polat and Sagi, 1993, Legge, 1979; Legge and Foley, 1980; Pelli et al., 2004; Levi, 2008).

The effects of crowding for 2-D tasks are ubiquitous in the literature. In the most classic of experiments, the ability to identify letters (i.e. visual acuity) is found to be impaired when surrounded by other optotypes or contours (Bouma, 1970; Townsend et al., 1971). Crowding is found to be more extensive in the peripheral visual field than in central vision (Bouma, 1970; Toet and Levi, 1992). The magnitude of the crowding effect critically depends on the separation between the test and flankers. In the fovea, the spatial extent of crowding or critical separation, only extends over a few minutes of arc (Flom et al., 1963a, 1963b; Westheimer and Truong, 1988; Ehrt et al., 2005; Danilova et al., 2007; Siderov et al., 2013). The strength of crowding is greater for vertical and horizontal stimulus orientations compared to oblique orientations (Toet and Levi, 1992; Whitney and Levi, 2011).

Monocular tasks such as Vernier acuity and judgement of tilt for foveal tasks are highly susceptible to crowding (Westheimer and Hauske, 1975; Westheimer et al., 1976). For Vernier acuity, critical distance of about 3 to 6 min arc has been found at the fovea and up to 0.5 times the eccentricity of the test in the periphery (Bouma, 1970; Westheimer and Hauske, 1975; Westheimer et al., 1976). Individuals with amblyopia exhibit extensive crowding in the central visual field, worse in strabismic amblyopes than anisometric amblyopes (Hess et al., 2001).

The magnitude of crowding is probably related to the cortical representation of retinal receptors (i.e. the cortical magnification) (Levi et al., 1985), but also, the strength of the effect at the particular eccentricity in the visual field, corresponds to the spatial properties of the stimulus (Kooi et al, 1994). Optimum crowding occurs when the test and flankers share similar low-level properties such as colour, contrast polarity, spatial frequency and orientation (Westheimer et al., 1976; Kooi et al, 1994; Chung, 2001). 2-D crowding has been shown to be elicited with a wide range of different stimuli, from simple Gabor patches (Parkes et al., 2001), to more sophisticated targets, such as faces (Louie et al., 2007). In the fovea, Levi et al (1985) showed that crowding scaled with spatial frequency or target size while more recently Danilova and Bondarko (2007) and Siderov et al. (2013) found no such scaling in the fovea.

Limitations in resolution due to retinal receptor density has long been suggested to explain the modes of neural processing for monocular tasks. During the first stage of resolution, optical (linear) filtering and visual quasi-linear filtering factors such as spatial frequency channels limit the spatial structure that can be processed. At the second stage, resolution is limited by non-linear visual processes of pooling, integration and attentional resolution that group and piece together features that are signalled at the first stage, limiting features that are perceived individually. However, there is evidence that points to the involvement of cortical origins (neural inhibitory interaction) after presenting a test and flankers to opposite

eyes (dichoptic testing) which still produced crowding (Flom et al, 1963a, Flom et al, 1963b; Westheimer and Hauske, 1975). Because crowding usually results in an interference rather than a facilitation, investigations to understand the underlying cortical processes have focused on the spatial aspects of this interference.

Effects of Crowding on Stereo Acuity

Stereo acuity is known to be affected by spatial interference more than other hyperacuity tasks (Westheimer and Hauske, 1975). Since stereo acuity values are much smaller than the dimension of foveal cones, investigations have focused on the neural coding responsible for depth perception. The goal is normally accomplished by manipulating spatial features, such as target separation, target dimensions and feature density (Butler and Westheimer, 1978; Westheimer and McKee, 1980; Livne and Sagi, 2007). In 3-D crowding studies, similar stimulus lines, bars, squares or dots are used (Butler and Westheimer, 1978; Mitchison and Westheimer, 1984; Westheimer and Truong, 1988; Kumar and Glaser, 1992a).

The consensus amongst investigators is that the lateral separation between the stereoscopic test and reference/surrounding targets is critical in the amount of crowding produced, the magnitude of which varies as a function of the separation and eccentricity (Hirsch and Weymouth 1948; Berry, 1948; Butler and Westheimer, 1978; Westheimer and McKee, 1980). The influence of spatial properties on stereo based crowding have been demonstrated by several authors (e.g.s. Butler and Westheimer, 1978, Westheimer and McKee, 1978; Westheimer and McKee, 1980; Fendick and Westheimer, 1983; Westheimer and Truong, 1988). Similar to other hyperacuity tasks, stereo-thresholds vary across the visual field, keenest at the central field (4 to 6 or 2 to 3 arc min on opposite sides of the fixation plane) and degrade towards the periphery (Westheimer and McKee, 1978; Westheimer and Truong, 1988). Most previous studies have however investigated stereo crowding in the fixation plane (Rawlings and Shipley, 1969; Butler and Westheimer, 1978; Westheimer and McKee, 1980; Fahle and Westheimer, 1988; Kumar and Glaser, 1992a).

Teichner and colleagues (1956) were one of the earliest investigators to study the influence of separation between a test and reference stereo targets on stereothreshold. They suggested that within the limits of distance, the effect of separation (1.4 to 114.6 min arc) on commonplace (ordinary) depth perception may be considered negligible compared to the influence of other factors such as viewing distance and refractive status. They hypothesised that the presence of other depth cues may compensate for the angular change in separation and still make it possible to correctly predict the depth direction of the test. The observations followed on from an experiment, where they varied the viewing distance and found that separation test and comparison reference only had a significant and reliable effect on depth judgement at the widest separation (>114.6 min arc). They attributed this effect to refractive status (visual acuity) rather than any influence of separation. It must however be stressed that Teichner et al. (1956) experiments were conducted in an outdoor environment, so the long viewing distance used might have affected visual acuity, making small targets separations indistinguishable. Notwithstanding their findings, they concluded that both stereoscopic and Vernier acuity cues were involved in the depth perception of the test target and not only monocular cues.

Rawlings and Shipley (1969) studied the effects of test – reference separation on stereoacuity across the visual field by having subjects compare tests in the fovea and periphery. They made their subjects discriminate two points of light which had a lateral separation up to 60 sec arc. Stereoacuity recorded for different point separation were 0 deg - 21 sec arc, 2 deg - 82 sec arc, 4 deg - 155 sec arc, 6 deg - 193 sec arc, and 8 deg - 345 sec arc. Their results also showed maximum sensitivity at the fixation, and discontinuity in the stereo-threshold curve at retinal eccentricities near 4 to 6 deg, with the threshold rapidly deteriorating towards the periphery. Later studies supported their findings and showed that hyperacuity thresholds (stereo and Vernier etc) decrease as function of increased separation relative to the fixation, and faster than those of visual acuity (Westheimer and McKee, 1978; Westheimer, 1979b; Fendick and Westheimer, 1983; Levi et al., 1985;

Westheimer and Truong, 1988). Fendick and Westheimer (1983) in a later study compared practice-stabilized stereo-thresholds in normal observers at optimal test-reference separations. Their stereo test target comprised of small squares displayed in pairs at the fovea and retinal eccentricities 2.5 and 5 deg. Their findings revealed a steeper deterioration in stereo acuity between the fovea and 2.5 to 5 deg eccentricities, supporting reduction in relative depth discrimination as a function of eccentricity. Fendick and Westheimer (1983) however contended that the decrease of stereo-threshold at more peripheral locations was more gradual than had been previously reported. They also stressed that the deterioration was not related to visual acuity as suggested by Teichner et al. (1956). Fendick and Westheimer (1983) aggregated best performance across meridians and subjects which indicated average stereo thresholds of 6 arc sec at the fovea and 21, 36 and 80 arc sec at retinal eccentricities of 2.5, 5, and 10 deg, respectively. Both horizontal and vertical separations demonstrated a similar effect on threshold, though a closer inspection of their data reveals that test stimuli that were horizontally separated showed a steeper deterioration in threshold.

From the foregoing research, it was found that acute stereo acuity requires a test target and reference target to be located close to one another (Westheimer and McKee, 1979; McKee, 1983). Large separations would presumably make depth discrimination harder as one would need to rely on more of an absolute stereo and performance varied along the visual field (Hirsch and Weymouth, 1948; Rawlings and Shipley, 1969; Westheimer and McKee, 1979; Fendick and Westheimer (1983). This is unlike in 2-D VA tasks, where optimal performance in recognising a letter occurs with the letter in isolation. These results suggest that if stereoscopic targets are moved away from fovea to the periphery, wider separations between test and reference target for optimal performance are needed (Westheimer and Truong, 1988). Since stereo-thresholds got worse with test and reference separation and relative to the fovea, the observed effect prompted further investigations into depth interactions using flanking contours.

References can be made to the studies of Butler and Westheimer (1978), who demonstrated that stereo crowding varies as a function of the test-to-flanker separation, being maximum when the test-flanker separation was between 2 - 3 min arc. Other authors have reported larger separations for optimum stereo crowding (Westheimer and McKee, 1980; Fahle and Westheimer, 1988; Kumar and Glaser, 1992a). These studies showed that when the test-flanker separation is set at the optimum separation, the crowding effect can degrade the stereo-threshold up to about six times compared to when no flankers are present (Butler and Westheimer, 1978). Subsequently, Westheimer and McKee (1980) demonstrated that crowding in depth does not depend on the number of stimulus features used (so called ramp density), but on the separation between the stimulus features (i.e. test and flanker disparity density). Later investigations also reported no significant difference between vertical and horizontal separations of the features (Westheimer and McKee, 1980; Fahle and Westheimer, 1988; Kumar and Glaser, 1992a). However, in another study, Fahle and Westheimer (1995) reported that the length of the ramp density could influence the discrimination threshold, suggesting a global factor in disparity processing.

More recently Gantz and Bedell (2011) investigated the effects of feature density on stereo-threshold. By measuring the relative depth of a small disparate line superimposed on a random stereogram which varied in density from 0.07% to 28.3%, they reported that thresholds increased at low and at high background densities. They reasoned that the increase in threshold at lower densities (larger spacing between elements) was due to increased spacing between the background reference targets which became less useful for relative disparity detection. The increase in threshold at higher densities (smaller spacing between elements) was attributed to the crowding effect. Their findings which revealed increased threshold at smaller separations of the random stereogram due to crowding compared well the previous finding by Hirsch and Weymouth (1948) earlier work. Gantz and Bedell (2011) contended that that judging by the nature of the observation for both a high

and low ramp density, a similar cortical mechanism may be responsible for the processing both local and global stimuli.

Other studies have revealed that stereo based crowding is affected by the depth location of disparate stimulus features (i.e. shows depth tuning) (e.g. Butler and Westheimer, 1978; Fox and Petterson, 1981, Kooi et al., 1994, Astle et al, 2014). The depth tuning function suggests that neurons that encode depth may be sharply tuned to receive and carry visual inputs from a small area of visual space around the plane of fixation (Butler and Westheimer, 1978). These disparity tuning effects have not yet been demonstrated for other hyperacuity tasks, suggesting that it might operate only in the stereo (disparity) domain. Westheimer (1986) later described what he called the 'inducing effect' (or salience) of displaced features in depth, which strongly affected the stereo-threshold. This present study will seek to extend these results and further investigate the effect of salience of crowding.

Many of the previously reported studies quantified the critical spacing, and the spatial extent of crowding. The goal was normally accomplished by the use of spatially adjoining flanking targets which had similar properties as that of the test. However, we are interested in examining the effect of size in stereo crowding. This would have some bearing on more recent results which show that for Vernier tasks crowding may be alleviated with flanker size (Banks and White; 1984; Manassi et al., 2012; Herzog et al., 2015), something which has not been shown in stereo crowding. Studies related to crowding on the horopter and off the horopter are discussed in more detail under the relevant sections in Chapters 3 and 4.

Fundamentally, the differences in crowding observations reported here evidently show that much more specialisation is needed to discriminate the relative depth positions, compared to monocular tasks. This perhaps provides further support for the distinction between stereo acuity and other acuity tasks (Fendick and Westheimer, 1983; McKee, 1983). Further, differences in results obtained may be explained by the influence of practice, and restriction of the parameters in the stimuli used. Differences in the test type, such as squares, lines, bars and point stimuli may also have played a role in discrimination thresholds reported. On

the other hand, it demonstrates that individuals have different sensitivity to threshold discrimination in different stimuli, and supports the view that further spatial characterisation of crowding in depth is needed.

Research Gaps and Aims of the Study

Whilst there are relatively few stereo based crowding studies which have addressed the question about the critical spacing required to produce crowding, information about the influence of reference and flanker configurations and dimensions on crowding are uncommon, leaving a gap in the intellectual discourse concerning crowding in depth. Crowding in Vernier tasks have been demonstrated to respond well to stimuli dimensions, with crowding being optimum when test and flankers are similar in shape and size (e.g. Kooi et al., 1994). And since it is known that stereo precision is greatly influenced by factors such as size (e.g. McKee, 1983), it is of interest in the present study to investigate the influence size tuning of the discrete features in the stereo stimuli on discrimination threshold. While the few classical studies on crowding in depth used tests and flankers that had similar shapes, we deem it important to address the question “to what extent does test stimulus and flankers need to be similar in size for crowding to optimally interfere with the discrimination of a stereo test?”.

Stereo-thresholds are known to demonstrate a pattern of elevation outside the plane of fixation with pedestal disparity. This present study investigates the influence of displaced discrete features in stereo stimuli on crowding.

Therefore, the main aim of this study was to investigate the effects of visual crowding on stereopsis on and off the horopter by psychophysical means. Three experimental objectives were developed to achieve this aim;

1. Investigate the influence of lateral separation between test and flanking stimuli (i.e. crowding), on depth discrimination thresholds on the fixation plane.

2. Investigate the influence of lateral separation between test and flanking stimuli (i.e. crowding) and separation in depth, on depth discrimination thresholds off the fixation plane.
3. Evaluate the stereo interaction using stimuli composed of different spatial frequencies (Gabor stimuli) as a function of the disparity of test and flanker stimuli.

The experimental objectives were formulated in order to address the key research question of how to understand the neural coding of depth information in the visual system by employing psychophysical methods, and how the finding may be useful in developing new ways to detect anomalies in the binocular processing of signals.

Specifically, the following questions are addressed;

1. What are the critical lateral distances between a stereoscopic test and adjoining flankers that will produce optimum crowding, and the separation that will release crowding on the plane of fixation?
2. What is the effect of disparity (relative depth separation) of the flankers, and disparity of the constructed stimulus, on crowding?
3. What is the influence of the size of the flanking bars on depth discrimination threshold on, and off the plane of fixation?
4. How does the interaction differ when measured with different stimuli probing different putative pathways and depths of disparity processing in the visual cortex?

Thesis Structure

This thesis is organised into six chapters.

Chapter 1 is an introduction to the thesis and presents the research background, review of the theoretical knowledge and existing literature on the subject. The chapter states the objectives, research questions, gaps in research, and the original contribution of this work.

Chapter 2 outlines the general methodology employed in the study. It covers the materials, generation of stimuli, subjects, experimental procedures and how the data were analysed.

Chapter 3 begins the first experimental work. The chapter briefly introduces crowding in depth, with reference to the fixation plane, builds the premise for the experiments contained in the chapter and the rational for it. Briefly related methodology, procedure, results, discussion of results, and conclusions are collated.

Chapter 4 extends the experiments to interactions off the fixation plane. The chapter contains a brief introduction of concepts relating to depth perception off the horopter, methods and procedures employed, results, and discussion and conclusion.

Chapter 5 explores the crowding phenomenon using different stimuli (Gabor patches). Brief introduction of the notions relating to depth information processing along the visual pathway, methodology, procedure, results, discussion of results, and conclusions are presented.

Chapter 6 presents the general discussion of results from all the experiments, the overall conclusion and recommendations for future work.

CHAPTER TWO

GENERAL METHODS AND MATERIALS

Apparatus

Standard psychophysical methods were employed to investigate characteristics of stereoscopic depth-crowding. Stereoscopic test and reference stimuli with interfering flankers set at varying disparity directions and magnitudes were created using a custom written programme in Matlab (version 10). The stimuli were presented to observers on a visually flat single, gamma corrected monochromatic 21" Sony Trinitron colour graphic video monitor display (Model: GDM-F520). The stimuli were loaded using a frame store memory of the Cambridge Research Systems (CRS), Visual Stimulus Generator (VSG 2/5) graphic card. Stimuli were presented to each eye separately using a liquid crystal shutter goggle synchronized to the video display unit. In principle, the display system works in a similar fashion to the traditional phase haploscopes (Holloway and Lastra, 1993; Howard and Rogers, 1995). The video haploscope presents alternate, non-interlaced video frames to each eye, controlled by a shutter system synchronised to the monitor frame rate. The monitor refresh rate was 120 Hz (each eye saw a flickerless image of the stimuli at 60 Hz) while that of the shutter operated at 60 Hz.

Stimuli

The stereoscopic stimuli for the experimental objectives 1 and 2 (written as Chapters 3 and 4) were relatively narrow luminous vertical bars (white on dark background) set at varying disparity levels depending on the experiment. The luminance of the target and reference was the same and measured 52 cd/m² in dim illumination. The mean luminance of the display measured 4cd/m². Appendix Table C.1 gives summary data for luminance calibrations. The transmission rate for the shutter goggle was 15%. The luminance contrast for the target and the background was specified by the formula $(I - I_b)/I_b$, with I and I_b

representing the luminance of the target and the background, respectively (Lit et al, 1971). The luminance of the display was calibrated using a Pritchard Spectrophotometer (PR-650 Spectrascan Colorimeter). In conducting experimental objective 3, (written as Chapter 5), additional stimuli characterised as sinusoid luminance modulation with a Gaussian envelope (Gabor patches) were used. Varying spatial frequencies and standard deviations were employed depending on the experiment. The test target and reference elements for each eye had the same dimensions, the specification of which depended on the objectives of the experiments (Fig. 2.0 (A)). In crowding experiments, flanking bars or Gabors stimuli were placed symmetrically on either side of the target bar only. The stimuli were positioned at equal vertical and horizontal distances from the middle of the monitor display, with vertical separation between them so that stereoscopic stimuli always appeared at the center of the video display. Depending on the separation required for a subject for stereoscopic threshold discrimination, both the reference and the target were shifted by equal distances, vertically from the centre of the video display in the opposite direction. The separation between their endpoints depended on the observer's pre-determined optimum vertical separation. Changes in the dimensions of stimuli depended on the objective of the experiment hence specific configurations are given for the various experiments. The target bar appeared at eight disparate positions, four equally spaced positions in front or behind the reference bar or at the fixation plane, and one in the same depth plane as the reference bar (zero disparity). Binocular fixation at the plane of the reference element was maintained between trials by fixating at a relative position of Nonius stimuli which was composed of a pair of luminous bars vertically aligned and separated by a fixation point which always appeared at the centre of the monitor display. The diameter of the fixation point was 30 sec arc and the dimensions of the vertical bars were 1.4 min arc wide and 7 min arc long. They were surrounded in a square frame of size 28 min arc (Fig. 2.0 (B)). The Nonius stimuli which were programmed to flicker in synchrony with the shutter goggles, were seen one by each eye and presented just prior to a trial and disappeared when the test stimulus was presented.

Good control of horizontal oculomotor vergence was achieved by asking subjects to fixate in-between the two Nonius bars and keep them vertically aligned. Alternate presentation were made so that they did not interfere with depth discrimination task. The Nonius did not leave after-images due to the relatively low luminance level, as this was checked throughout the data collection period.

Binocular disparity of the stereoscopic stimuli was produced by a programmed presentation of alternate, non-interlaced video frames to each eye which was viewed through shutter goggles, synchronised to the monitor frame rate. The range of binocular disparity offsets of the test target from the reference element was produced by introducing pixel offsets in the location of each of the eye's view of the target stimuli. The binocular disparities used depended on the particular experiment. The presentation of the disparity target offsets was randomized between trials and runs. The number of frames per field (where the field is the shortest possible presentation of an image) was set to 1 for all experiments (other values are only used for debugging/testing).

The liquid crystal shutter type stereoscopic goggle used has advantage of no limitation of viewing angle and distance compared to auto stereoscopic display such as the barrier and lenticular types. Nevertheless, the view separation mechanism leads to *system crosstalk*; an expected small proportion of about 1-3% of one eye image being seen by the other eye as well (Woods, 2010). Though this was not measured for the goggle used, its effects on image quality, depth quality and visual comfort was checked and it did not have effect on observers overall viewing experience.

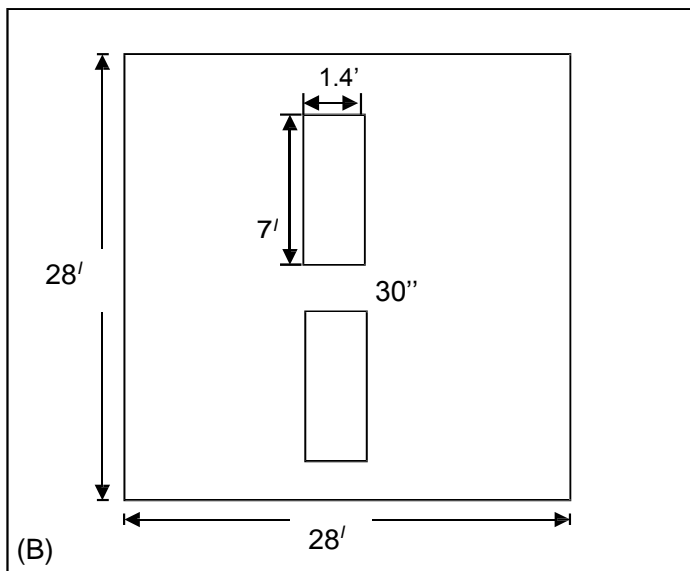
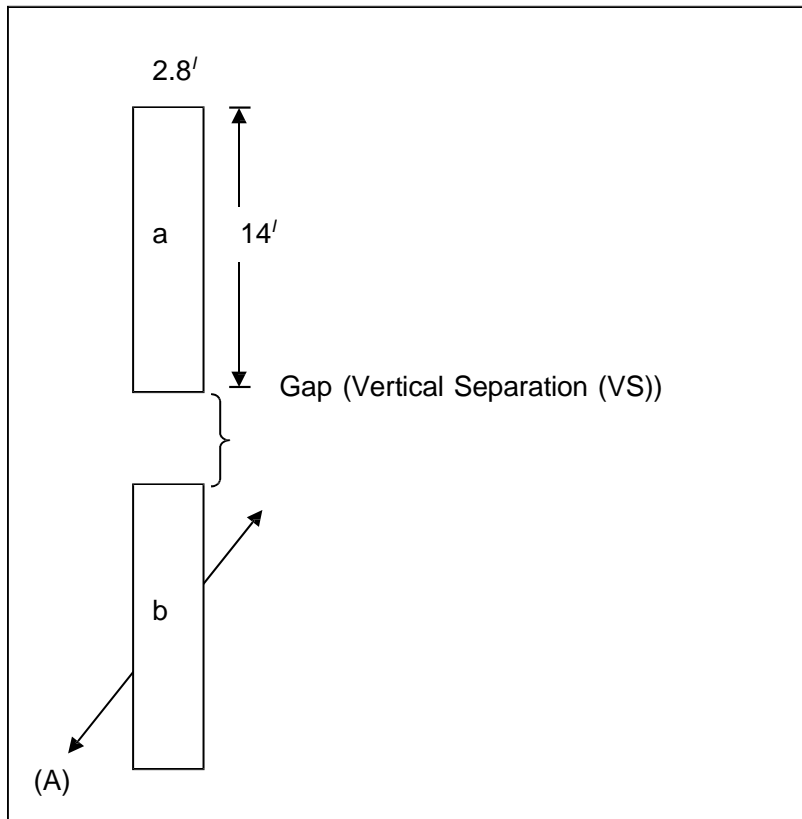


Fig. 2. 0. *Stimulus and Nonius Targets. (A) Stereoscopic stimulus pair. Reference (a), test (b) and (B) Nonius stimuli (Drawn and does not represent actual stimuli)*

Calibration

To ensure that correct stimuli configurations and disparity settings in the condition file were displayed on the monitor, disparity values were measured on the monitor display and fitted with a curve and found to be linear at the test distance. The procedure required that each disparity was presented repeatedly for stimulus dimensions as well as distance between the target and reference to be measured on screen. To determine the range of disparities to use, preliminary observations were made to find the approximate range of disparity values in which the stimulus of the highest disparity was always perceived, and the stimulus with the lowest disparity was seldom perceived. Stimuli dimensions were also selected based on the range of normal values found in literature (e.g. McKee, 1983), which were also pretested during calibration. Fig. 2.1 shows pretested data for stimuli configuration for at least one observer. Though the data does not seem to show effect of stimulus width and length on threshold for at least one observer, the information garnered from it was useful for stimuli dimension selection and calibration. Monitor calibration and gamma correction were done before experiments with Gabor patches. This was done to avoid unwarranted visual outputs caused by luminance artefacts. The range of possible luminance output from each colour gun of the monitor was measured using OptiCal photometer head. The monitor's gamma non-linearity was corrected using generated estimates and a curve fitting procedure was used to create a software lookup tables in the VSG. The linearised output thereafter was also checked. The Mean luminance measured was 52 cd/m². Again, to minimize the influence of contrast on depth discrimination threshold, contrast for each of the stimuli were held constant at the maximum available contrast (Siderov and Harwerth, 1993). The screen resolution was verified to ensure that images were accurately presented on the monitor.

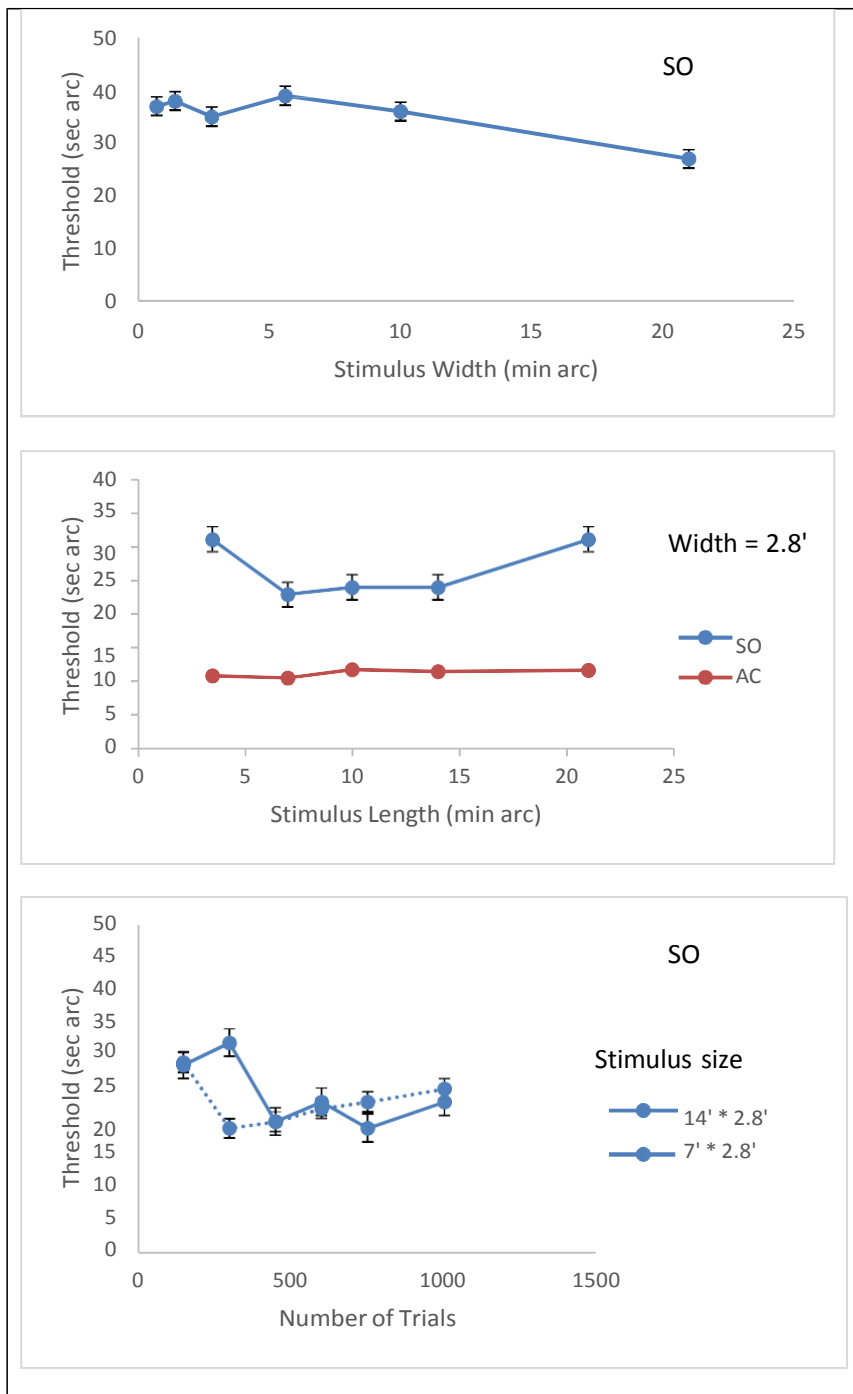


Fig. 2. 1. Pretested Stimuli Dimensions

Graph shows thresholds plotted as a function of stimulus (A) width, (B) length and (C) practice thresholds before actual data collection commenced. The colours represent individual performance, blue for SO and red for AC.

Method of Constant Stimuli

The psychophysical method of constant stimuli (Woodworth and Schlosberg, 1971) was employed to determine the stereoscopic depth discrimination thresholds. The method involves the repeated use of the same stimulus levels throughout the experiment to determine the range of binocular disparity that encompasses the psychometric function. Usually, this range is divided into steps of equal magnitude in disparity and presented randomly. Observers were asked to respond to the apparent depth of the test stimulus as either 'in front' or 'behind' the reference stimulus. Subsequent data analysis plotted the percentage correct 'in front' responses. Catch trials where the test stimulus had no disparity were also included.

The method of constant stimuli has advantages over other methods of psychophysical measurements such as the method adjustment, method of limits and the staircase method. (Woodworth and Schlosberg, 1954). Firstly, it removes errors due to anticipation and habituation by the use of randomised presentation of disparities. Habituation refers to the tendency for participants to keep saying 'in front' or 'behind' without actually experiencing the required depth. Anticipation on the other hand refers to the propensity to expect a change, prompting an observer to switch from saying 'in front' to 'behind'. Again, participants had specific times intervals to view and make judgments about the perceived depth of test presented. Additionally, the method allows for the elimination of the possibility of observers using oculomotor skills as a cue to depth discrimination as interocular depth disparities were randomly varied.

Observers and Visual Condition

In all, eight observers (five males and three females) aged over 18 years old, participated in the experiments. Participants comprised both trained ($N = 3$) and naïve ($N = 5$) observers, including the author. They had normal binocular vision (no significant heterophoria) and stereoacuity less than 30sec arc which was assessed clinically with the TNO (Lameris

Ootech) (Fricke and Siderov, 1997) stereoacuity test. All observers were emmetropic or corrected to 6/6 Snellen acuity or better. Appendix Table C.2 shows the visual data of participants. Observers viewed the stimuli through their natural pupils, glasses (when required) and appropriately orientated shutter goggles. Normal head position was maintained by a headrest and keeping fixation within the frame of the Nonius stimulus.

Experimental Procedure

The psychophysical procedure employed was the single exposure, two alternative, forced-choice paradigm. The observer's task was always to indicate whether the 'test' (lower central target in the display) was in front of the 'reference' (upper central target) or behind at eight possible disparities. The observer indicated 'target in front' or 'target nearer' by pressing the left button of a response box (CRS CT-6) upwards (or away from themselves). The observer indicated 'target behind' or 'target farther' by pressing the right button of the response box upwards (or away from themselves). Binocular fixation was maintained between trials by fixating at a relative position of Nonius bars. The Nonius stimuli ensured that observers vergence were correct by fixating at the fixation point and keeping the vertical bars aligned in between trials. This served to maintain control of horizontal oculomotor vergence. The observers were instructed to wait until the upper and lower Nonius bars appeared stable and aligned (in a straight line with each other) and then press the central button of the response box upwards (away from themselves) to make the stereoscopic stimulus display appear. The Nonius pattern was symmetrically placed around the position occupied by the stereoscopic stimulus and was always absent when the stereoscopic stimulus was present (i.e. it appeared consecutively and therefore did not interfere with depth discrimination thresholds). It was not possible to guarantee the length of time between the Nonius and stereoscopic stimuli presentation as the observers choose how long to view the Nonius display. However, the uncertainty in this duration is small in practice typically much less than a second. The apparatus set up ensured uniform illumination and the ambient laboratory

room illumination was kept low to ensure stereoscopic stimuli and Nonius displays were clearly visible to observers.

If the observer pressed the central button of the response box downwards (towards themselves) then the experiment was aborted and the data file is completed with the summary statistics for the number of trials run before that experimental session was aborted. If the observer does not press the central button downwards at any time, then the experiment runs for the number of trials specified by the value in the condition file. Observers viewed the stimuli at a distance of 13.5m from the computer display with the help of a mirror (Fig. 2.2). Shorter calibrated distances were used when Gabor's stimuli were employed. The display was presented for 300 msec at a self-paced rate by pressing the central button of the response box when they were ready to start a trial. A period too short for vergence eye-movements to be elicited (Westheimer and Hauske, 1975; Westheimer and McKee, 1980a, Westheimer, 2012). Presentation times were controlled precisely by setting the rate of presentation in the condition file. Conditions required for each experiment were specified by setting the required parameters in a condition file.

Feedback

By using the two-alternative-forced choice method, observers responded to the perceived stimulus directions, crossed (in front) or uncrossed (behind) using a response button box. In each trial, the target stimulus of the stereoscopic test stimuli could appear with crossed, uncrossed or no disparity (catch trials). However, the experiment only allowed for observers to choose either crossed or uncrossed depth perceptions. After each target presentation, the subject pressed a button to indicate whether the bottom bar had appeared in front or behind the lower reference line in depth. A high pitched beep sound (correct response) and low pitch beep sound (wrong response), and no sound (no disparity) provided immediate feedback to the observer. The feedback sound could be switched off. No feedback and

reverse feedback were used to monitor performance after observers had proficiency in the task.

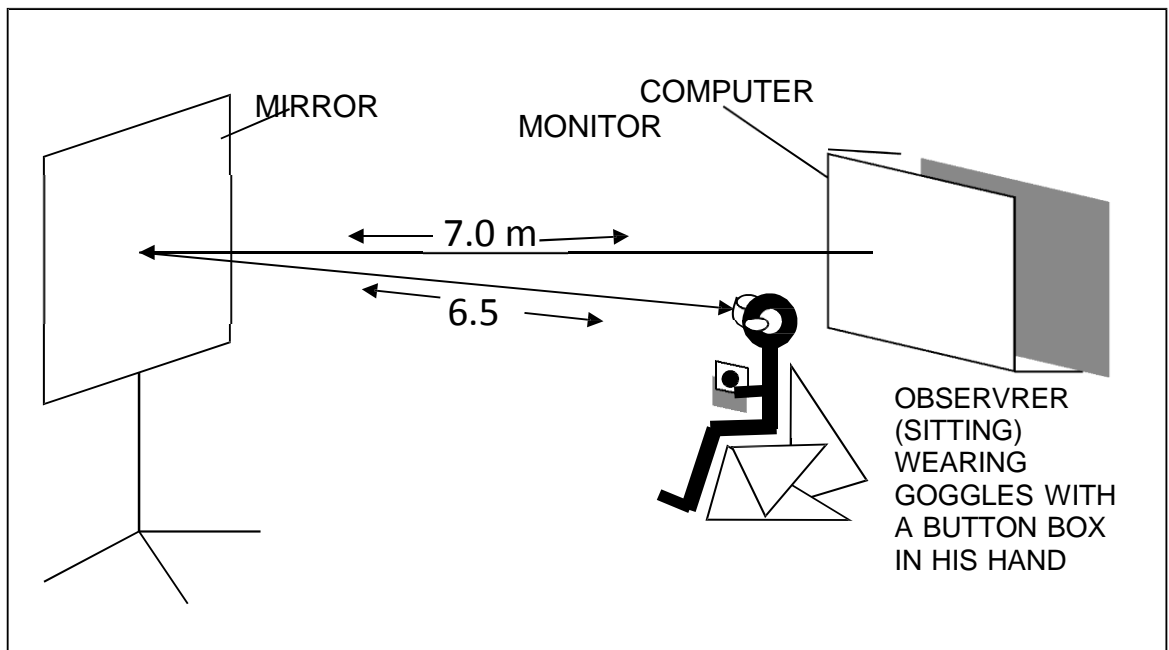


Fig. 2. 2. Experimental set-up (Drawn and does not represent actual set-up). Showing the position and distance of the observer relative to the computer screen.

Training

In hyperacuity tasks, learning effects are important in determining discrimination thresholds (McKee and Westheimer, 1978). Participants were given sufficient training in the tasks involving the simple stereoscopic test (i.e. test and reference) to minimize learning effects and ensure stable thresholds. In that regard, observers were trained for 2 to 3 weeks during which between 1500 and 2000 trials were completed and after which their baseline threshold with the basic stereoscopic discrimination test (test and reference stimuli only without the flankers) was stabilised. Subsequently the baseline threshold was monitored and remained relatively stable throughout the experimental period. For instance, observer OS threshold which measured 60 sec arc (500 trials) at the beginning of the training period was reduced to 40 sec arc (1000 trials), 30 sec arc (1500 trials) and stabilised at 18 sec arc after over 2000 trials. Fig. 2.3 shows the decrease in stereothreshold with increases in the total number of practice trials (this excludes observations made during the stimuli dimension calibration and testing) for the bar and Gabor stimuli for the same observer.

Ethical and Legal Considerations

Ethical guidelines and procedures involved in such non-invasive psychophysical experiments were followed. The research adhered to the Helsinki Declaration on Research regarding Human Subjects. Ethical approval was given by the Faculty Research Ethics Panel (FREP) of ARU having conformed to ARU institutional research procedures prescribed by the Research Ethics Sub Committee (RESC). Participation was voluntary, and observers signed an informed consent agreement after the risks, though minimal have been explained to them. Participants maintained the right to elect to withdraw from the experiment without any repercussions. At all times, participants' confidentiality was assured. Though the results of this study may be published in a scientific journal or reported at scientific meetings, at no time will participants be identified.

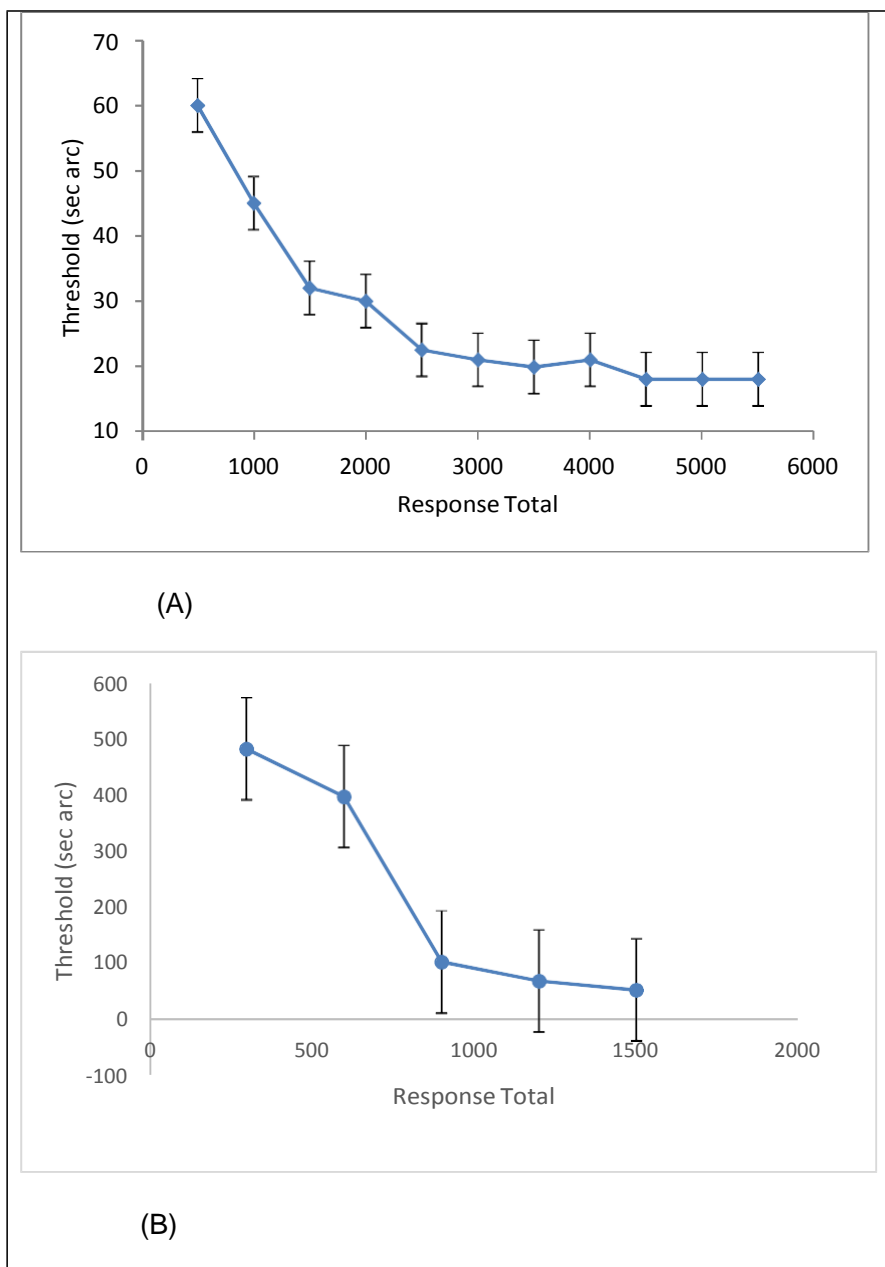
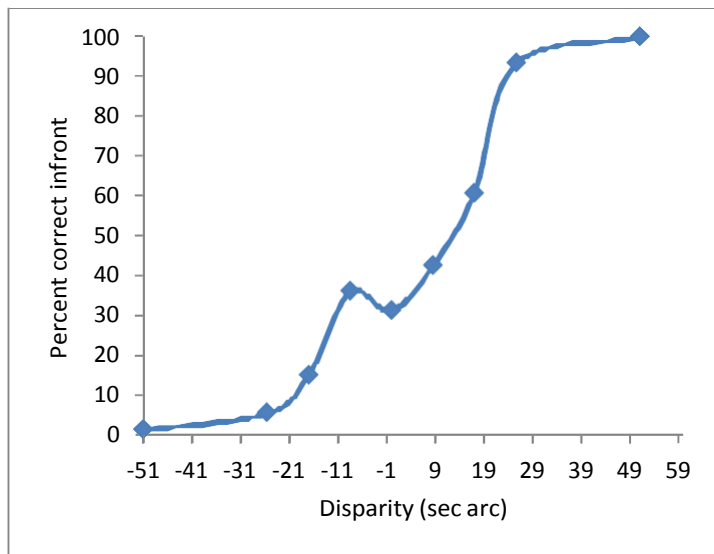


Fig. 2. 3. Practice Thresholds. Thresholds for (A) Bar stimulus and (B) Gabor stimulus for one participant.

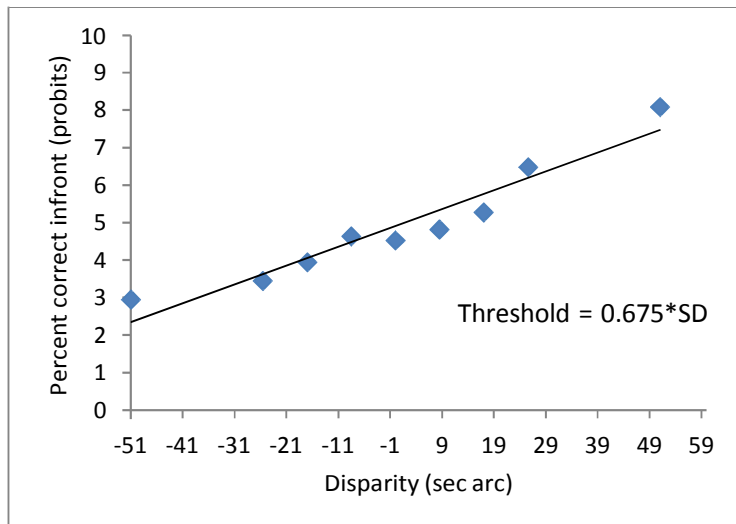
Data Analysis

Experiments were run in sessions of up to about 1-2 hours per day, and responses for each run were stored. Through the method of constant stimuli, the percentage of detection as a function of binocular disparity was determined. During the experiment, count of the number of 'in front' responses and 'behind' responses was kept. Two different statistical approaches were used to analyze the data, by way of Ogive (stimulus of seeing curve) curve and Probit Analysis. The Ogive (psychometric function) is a graphical method which involves plotting the percentage of 'in front' responses verses the disparity of the targets. A typical sigmoid curve is obtained from which the stereo threshold could be determined and the Standard deviation (SD) calculated. However, because of the uncertainty in drawing a perfect curve through the points, the data were fitted by probit analysis (Finney, 1971). The probit analysis involves first converting the percentage of 'in front' responses to probits (Finney's Table). The probit values were then plotted against disparity in sec arc. The threshold was the disparity range detected between 75% and 50% of the time. The absolute threshold was estimated as the semi-interquartile range ($= 0.675$), thus the disparity for which the proportion of trials resulting in 'in front' responses lied between 50% to 75% of the fitted psychometric functions, as well as standard error of this value was estimated from the frequency of seeing curve (psychometric function) by probit fitting. Error bars on graphs indicate the magnitude of \pm standard error, reflecting the larger of the within run and between run variances of data presented. Fig. 2.4 indicates how data were analysed. In the graphs plotted, each of the plotted points is the results of at least 500 forced choice responses.

Stereoacuity is calculated as the reciprocal of the threshold, thus a high stereo threshold means a low stereoacuity and vice-versa. Summary statistics were computed by SPSS (IBM SPSS Amos 22) and graphs drawn and presented by Excel (2013).



(A)



(B)

Fig. 2. 4. Method of Data Analysis. (A) Frequency of seeing curve (psychometric function) constructed by ogive method, shows stimulus disparity (sec arc) on the x-axis and frequency of detection on the y-axis. (B) Probit furnished psychometric function to estimate the stereoscopic threshold that lie between 50% - 75% correct responses. Negative and positive values represent uncrossed and crossed disparity respectively

CHAPTER THREE

INFLUENCE OF LATERAL SEPARATION, FLANKER AND REFERENCE BAR CONFIGURATION ON FOVEAL DEPTH DISCRIMINATION

INTRODUCTION

The human binocular visual system has the ability to discriminate extremely small differences in the relative depth of targets in visual space and does so with remarkable accuracy (Berry, 1948; Stigmar, 1970; Westheimer and McKee, 1979; McKee, 1983). This attribute of the binocular visual system, referred to as stereoscopic depth perception stems from a physiological mechanism that extracts relevant information from the right and left eyes images and combines these two images to form a single binocular percept. As a result of the horizontal positioning of the two eyes, two objects located in front of an observer but at slightly different fixation distances (i.e. at different depths), the relative positions of their respective retinal images will differ slightly in the two eyes resulting in a horizontal retinal disparity, which is the fundamental cue to stereoscopic depth perception (Wheatstone 1838; Ogle, 1952, 1953). The depth discrimination threshold is the smallest detectable retinal disparity that still yields a reliable stereoscopic depth percept and connotes the angular sum of the displacement of retinal images of a target in the two eyes. Stereoscopic depth discrimination is most acute for stimuli separated by only a few minutes of arc and located on or near the fixation plane and can be of the order of a few arc seconds of disparity (Berry, 1948; Blakemore, 1970; Butler and Westheimer, 1978; Westheimer, 1986; Westheimer and Truong, 1988).

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Similar to other spatial acuity tasks (e.g. visual acuity, Vernier acuity and judgment of tilt of short lines) (Flom et al., 1963a; Flom et al., 1963b; Bouma, 1970; Levi, 2008; Pelli, 2008), stereoscopic acuity is also impeded by the presence of flanking targets ostensibly through a form of lateral interaction or visual crowding.

Crowding is believed to have a cortical locus as previous investigations demonstrated that crowding can still be produced with dichoptic images by presenting a target and flankers separately to each eye (Flom, et al., 1963a; Butler and Westheimer, 1978; Tripathy and Levi, 1994), suggesting signals bypass early stages of visual processing to arise in the visual cortex. Visual crowding therefore provides an investigative tool to ascertain the neural underpinning of depth perception, by studying factors that influence depth discrimination thresholds (Butler and Westheimer, 1978; Westheimer and McKee, 1980b; Mitchison, and Westheimer, 1984; Levi et al., 1985, Westheimer, and Truong, 1988; Kumar and Glaser, 1992a; Gantz, and Bedell, 2011).

Crowding is one mechanism that has been extensively studied in recent years in an effort to understand the neural underpinnings behind the spatial interaction, and in that regard, understand the mechanism by which the visual system collates visual information from the environment. Unlike masking, crowding is understood to be an interference, but not a destructive process, which will not make the test target indistinguishable (Legge and Yuanchao, 1989; Polat and Sagi, 1993). Therefore to clearly understand the mechanism of the interaction, it is useful to link important parameters in the physical stimulus, the binocular disparity and the associated perceptual depth sensation. Thus, to understand the modes of depth processing, experiments that characterise the binocular and spatial extent of the crowding features have been conducted (Butler and Westheimer, 1978; Westheimer and McKee, 1980a; Livene and Sagi, 2007).

Generally, visual crowding refers to the deleterious impairment of nearby contours (or targets) on the spatial discrimination of objects in the fovea and peripheral visual field (Flom et al., 1963a; Flom et al., 1963b; Bouma, 1970; Levi, 2008; Pelli, 2008; Bernard and Chung,

2011). In depth perception, crowding reduces the perceptual discrimination of the depth position of targets surrounded by similar targets, especially for objects positioned at close spatial proximity to the plane of fixation (Westheimer and Truong, 1988; Butler and Westheimer, 1978). Though crowding has been demonstrated to impair the ability to discriminate targets in spatial vision especially in 2-D tasks (Levi, 2008), observations about the perceptual interference of crowding on targets seen in depth (3-D) remains scarce (see Chapter 1 for a summary of what was evidenced for studies conducted on 2-D and stereoscopic based crowding).

The crowding effect on the depth discrimination threshold for a vertical test line relative to a fixated reference line, in the fixation plane, was demonstrated by Butler and Westheimer (1978). Their configuration comprised computer generated luminous lines 10 min arc in length and 30 sec arc thick positioned one above the other with a gap of about 3 min arc between them. The test was surrounded by two laterally placed similar flanking lines, but 4 min arc shorter. The interference on depth discrimination of the test line by the flanking lines was investigated by varying their lateral separation from the test line, by adjusting the relative depth of the flanking lines and by varying their temporal presentation times. They found that crowding was evident for a small range of test to flanking line separations of about 1 to 6 min arc, (peaking at 2-3 min arc separation) and occurred only when the flanking lines appeared in the same depth plane as the reference line. Crowding was absent when the flanking lines were coupled with the disparity of the test target (i.e. made to appear in the same depth plane as the test) (Fig. 3.0). Butler and Westheimer (1978) concluded that inhibition of depth signals due to lateral interaction of the disparities of the stimuli caused crowding.

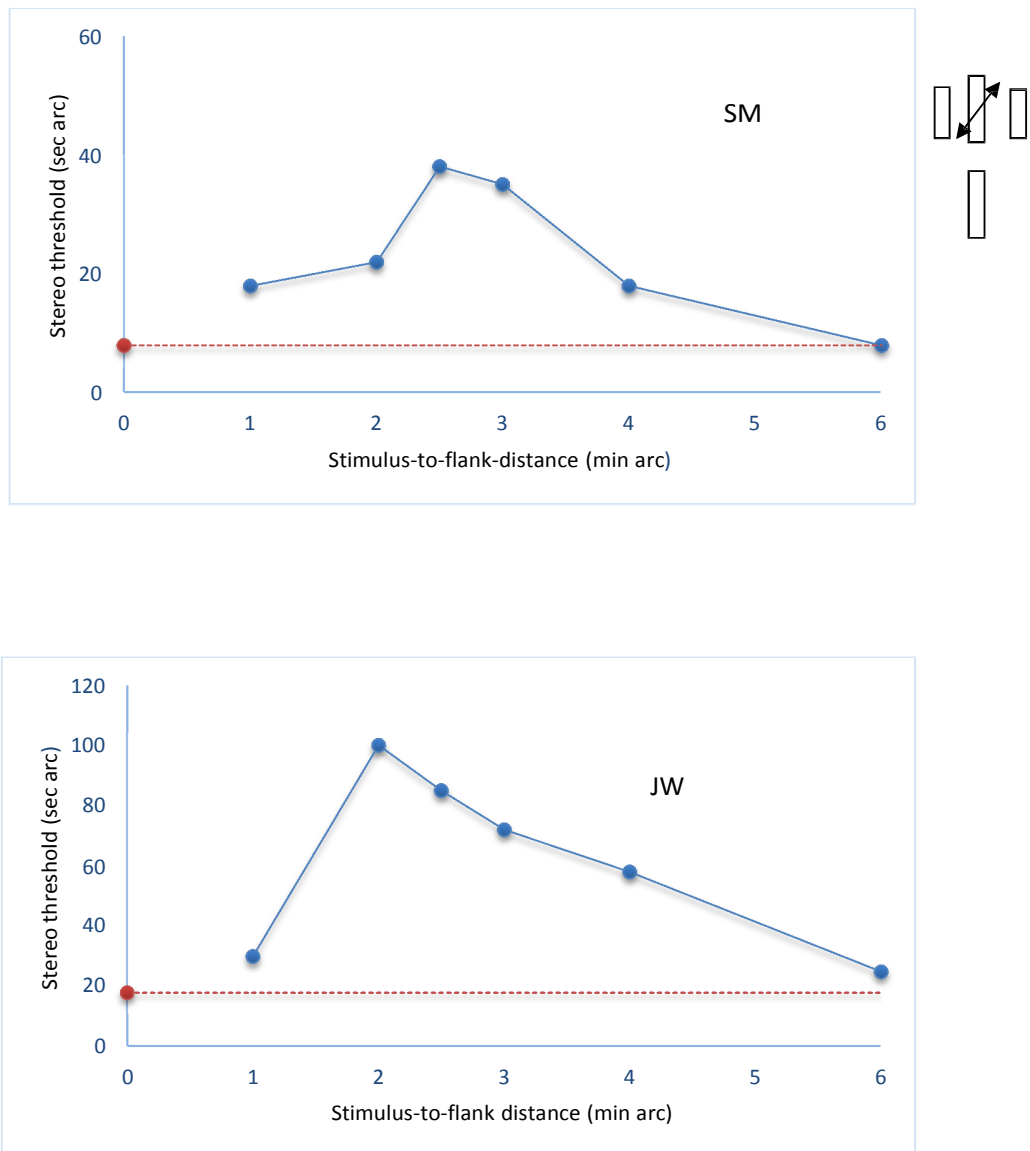


Fig. 3.0 Variation in Crowding with stimulus-to-flank distance for 2 subjects (Redrawn from Butler and Westheimer (1978), fig. 1). The inset in the top panel represents the stimulus configuration used. The upper test line was displaced in depth, relative to the lower reference line. Stimuli were presented for 200ms. In each panel, the solid line represents stereo-thresholds for the discrimination of the test plotted against the distance (min arc) of the test line to the flankers surrounding them. Dashed line indicates depth discrimination threshold for each subject when no flankers were present. All stimuli except the upper test line were always presented in the plane of fixation.

Butler and Westheimer's (1978) results showed that optimum crowding did not require the flanking stimuli to be closest to the stereoscopic test. The crowding function appeared tuned with better thresholds obtained when the flanking stimuli were too close or too far from the target. For flankers too far from the test target, the explanation is relatively simple, as any interference from the flankers would be assumed to be beyond any putative mechanisms that would induce crowding. However, for small flanker–test separations the explanation is less certain and questions as to whether the flanking lines themselves acted as reference, rather than flanking targets arise. Other work has shown that unequal lengths of flankers in a stereoscopic task may be used to aid depth discrimination when flankers are close to the test (Kumar and Glaser, 1992b). These questions are subjected to further investigations in this study.

Kumar and Glaser (1992a) tested a longer range of test-flank separations and observed that flanking lines can facilitate rather than impede depth discrimination thereby improving the stereo threshold, depending on the number of flankers used and the lateral distance the flankers are placed from the stereoscopic target. Employing a range of separations up to 40 min arc, they discovered that observers were able to use the flanking lines as additional references to improve thresholds up to 10 fold. One, two, and four flanking lines progressively facilitated the thresholds. Consistent with the findings of Butler and Westheimer (1978), a single flanking line resulted in depth thresholds up to 20 sec arc for separations to 1 arc min, and they attributed crowding as the probable cause in the degradation in stereo acuity found. Improvement in thresholds was attributed to the use of the flanking lines as better references for relative depth judgement.

Few other studies have inquired into the comparative influence of test-flanker separation and density of isolated features embedded in stimulus configuration (Hirsch and Weymouth, 1948; Westheimer and McKee, 1980; Fahle and Westheimer, 1995; Gantz and Bedell, 2011). Westheimer and McKee (1980a) increased the number of discriminable tests and

made observations that supported the proposition that depth discrimination thresholds depend more on feature separation than number of features in the stimulus. Using a test composed of small bright squares, 2 min arc on a side, Westheimer and McKee (1980a) first examined the crowding effect by varying the distance between the nearest sides of the test squares. Consistent with other separation results (Hirsch and Weymouth, 1948; Butler and Westheimer, 1978), the stereo-threshold increased when the separation between the test square and its nearby square was increased or decreased beyond an optimum range. Stereo acuity was optimal for a narrow range of target separations 10 to 20 min arc. When they crowded their square test in 3 × 3 matrix, they showed that the presence of extra reference square targets degraded the stereo acuity at small separations as thresholds rose quite considerably when test - reference distances were narrowed to less than 10 min arc, making the configuration appear more crowded. Significantly, they found that, consistent with the results of the stereo square pair, the separation for best performance was 10 min arc. However, contrary to previous results of Butler and Westheimer (1978), Westheimer and McKee (1980a) found that thresholds progressively increased for smaller and smaller test – reference separations less than about 10 min arc and also, albeit not as dramatically when the separation widened outside the range for best performance (Fig. 3.0.1). Although crowding may explain the threshold elevation for small test – reference separations, it is less clear what caused the worsening in thresholds at wider separations, especially for the stereo square pair. It may be that at the wider separations, the flanking square became a poor reference target, and hence the relatively higher thresholds represented a near absolute depth discrimination of the test square. This proposition is subjected to further investigation in this study.

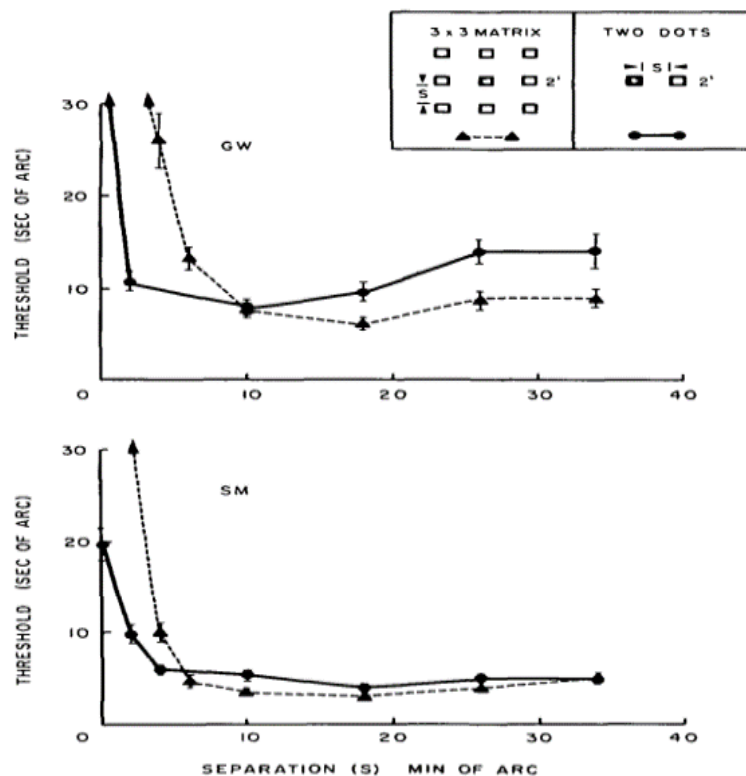


Fig. 3.0.1 Effect of Feature Configuration on Crowding (from Westheimer and McKee (1980a), fig. 3.)

The top and bottom panels show for a single observer each, threshold (sec arc) for depth discrimination plotted as a function of edge-to-edge separation (min arc) of two small squares, 2 min arc on a side compared to a more crowded configuration. Exposure duration was 500 msec. The effect of crowding is more pronounced at smaller separations and for multiple-target test than for the simple two-square target, but for wider separations the reverse is true.

Fahle and Westheimer (1988) subsequently found that the discrimination threshold for the relative depth of two fixed test targets increased when a third point target was inserted between them, linearly to increase the depth ramp. On the contrary, the addition of the same point target to two fixed reference targets did not show any change in the discrimination threshold. In contrast to later findings of Kumar and Glaser (1992a), the depth discrimination threshold showed a positive correlation and continued to increase as more elements were inserted between the ramps, for both horizontal and vertical configurations. Fahle and Westheimer's (1988) results agreed with other findings that the separation between adjoining targets (called the disparity density) was the most crucial factor which determined crowding as opposed to the number of features (Butler and Westheimer, 1978; Westheimer and McKee, 1980). In a later study, however, Fahle and Westheimer (1995) pointed out that increasing the length of the disparity ramp (i.e. increasing the number of features) may play a role in the sensitivity of the disparity threshold, and suggested a possible global factor in the processing of depth discrimination. Their finding showed that the length of the depth ramp is a significant factor as previously demonstrated by Mitchison and Westheimer (1984) who found that the depth discrimination threshold for detecting a slant between two columns of dot elements, thus a short ramp at specific lateral separations between them was lower than when the two dot elements were fixed within a long row of dots.

In the aforementioned studies, the dimensions of the interacting features, and their influence on the depth discrimination thresholds were not well elucidated leaving gaps for further investigations. There is evidence through psychophysical means that the interaction between a stereo test and contiguous flankers does not only hinge on spatial separation (Kumar and Glaser, 1992a, Butler and Westheimer, 1978; Westheimer and McKee, 1980a; Fendick and Westheimer, 1983), but also on several factors including relative orientation (Andrews et al., 2001; Farell, 2006) and feature properties such as colour (chromaticity) (Kennedy and Whitaker, 2010), texture (Frisby and Mayhew, 1978; Gantz and Bedell, 2011;

Gómez et al., 2011), spatial frequency composition (Schor, and Howarth, 1986; Brown and Weisstein, 1988; Siderov and Harwerth, 1993; Farell and McKee, 2004), direction of movement (Westheimer and McKee, 1978), shape (Kooi et al., 1994), contrast (Kooi et al., 1994; Chung and Mansfield, 2009) as well as the visual status of the observer (Siderov and Fricke, 1997; Momeni-Moghadam et al., 2011). Richards and Kaye, (1974) and Mitchell and O'Hagan (1972) have suggested the importance of size effects, and questioned whether the stereoscopic mechanism relies more on the edges of vertical bars than the centre of the test. To further enhance the understanding of the neural signage of depth-crowding interaction, it is important that research involving the influence of stimulus parameters on any such interaction is undertaken.

Though Berry (1948) and Westheimer (1979b) distinguished Vernier acuity from stereo acuity, both tasks are based on discriminating relative direction differences, and it has been thought subserved by a common mechanism and therefore have visual functions which are closely related (Westheimer 1979b). To that regard, the approach here is to review the effects of stimulus size on spatial measurements, since both Vernier and stereoscopic tasks are affected by interference (Levi, 2008).

The earliest investigation of the effect of test dimensions on Vernier and stereo acuity focused on the length of the stimulus (French, 1920; Weymouth et al, 1923; McKee; 1983). Target length was regarded as the most important factor to consider for fine Vernier and stereo acuity. However, Andersen and Weymouth (1923) first demonstrated that test length had no significant effect on stereo thresholds. In their experiment, they employed a stereoscopic test made up of three vertical lines separated by 26 min arc horizontally from each other. They found that the shortest test length yielded a threshold of 3 sec arc and only increased to 2 sec arc when the test length was increased to subtend 3 deg. visual angle. Interestingly, when the test and reference were well separated, the shortest test length still produced fine depth discrimination thresholds of 2 sec arc. Sigmar (1970) also showed that altering the test length did not lead to significant improvement in Vernier threshold, but the

mean threshold increased from 2.9 sec arc for a test length of 14 min arc to 4.2 sec arc for a test length of 50 min arc.

McKee (1983) later investigated the effects of test dimensions on stereo acuity and made a prediction towards the best test length to determine optimum stereo acuity. Using a configuration consisting of three bright vertical lines separated laterally by 13 min arc, she found improvement in stereo acuity when the initial small test length of 5 min arc was increased by a factor of two, but showed little improvement when increased more than 20 min arc. McKee (1983) suggested that the best test length ought to be between 10 to 15 min arc to produce stereo acuity less than 5 sec arc. Her conclusions supported the earlier findings of Andersen and Weymouth (1923).

Previous results about the fineness of all hyperacuity thresholds (French, 1920; Weymouth et al., 1923; Sigmar, 1970) were explained on the basis of the recruitment of spatial position signal 'local signs' (see Hyperacuity section in Chapter 1). The assumption was that as the vertical dimension of the test stimulus is increased, more foveal cones were stimulated or recruited to improve localisation and hence lead to better thresholds. Individual receptor elements connected to a long vertical test would act to stimulate more positional signals related to horizontal disparity, and then average them to yield a precise location acuity greater than the diameter of a single cone. However, further increases of the length of the target beyond the fovea would stimulate extra foveal cones leading to no appreciable increases in thresholds. As a point of departure, McKee (1983) explained her findings as a consequence of some sort of "summation" of positional signals along the length of the test which accounted for the improvement in thresholds. She discounted the explanation based on the averaging of disparity signals from multiple point sources, and stressed that it was not the quantity of light that was summed when the test is increased but rather signals about the positional distribution of the test.

Based on the McKee (1983) explanation, it would be expected that altering the width of a stereo-stimulus would decrease stereo-thresholds. While McKee (1983) reported that increasing the test lines horizontally (i.e. their width) yielded no appreciable improvement in stereo acuity, she did not show experimental data to support this statement. The argument is that by widening the test horizontally there will be an increase in the light distribution along the width, but as it is only the endpoints of the horizontal line that contain depth signals (horizontal disparity) there should be no appreciable effect on threshold. Berry et al (1950) had also investigated the effect of test widths on Vernier threshold and found no substantial change in the threshold with increases in angular widths from 27 to 424 sec arc. Their findings are however in contrast to the observations of Foley-Fisher (1977) who demonstrated that Vernier thresholds may be influenced by widening the width for high contrast tests and revealed the optimum line width of 15 min arc for producing best performance. Earlier French (1920) had also suggested that lengthening line widths may improve Vernier threshold when he was investigating separation and test length, and found that precision was more difficult for a thinner line of 52 sec arc compared to thicker line of 444 sec arc. Foley-Fisher (1977) in explaining his findings argued that when the widths are widened more than the minimum, the visual system will regard both sides as independent sources of information. The information is additive across the width, resulting in better performance. However, he reckoned that the addition will only occur within 10 to 20 min arc of the fovea.

While there seems to be a consensus on the influence of the stimulus length on depth discrimination thresholds, there is no agreed view on the influence of stimulus widths other than restrictions imposed by physiological explanations (see Chapter 1). Again, while the apparent inconsistencies in the results aforementioned could be attributed to the differences in stimuli to investigate the effects, there is no available evidence to indicate the effect on depth discrimination when the widths of flanker (nearby targets which carry disparity) are changed. More recently however, there is strong opinion supporting the influence of

grouping (shape manipulations, including figures with longer width) on depth discrimination of a test (Livne and Sagi, 2007; Deas and Wilcox, 2014). To that end, this study will further investigate the effect of varying the widths of flanking bars on depth discrimination of a test in the fixation plane.

Generally, the dearth of information about stimulus parameters and differences in study results support the view that more information is needed to understand crowding in depth (stereo-crowding interaction) based on the mechanisms of depth signal processing by the visual system. Such an endeavor can be achieved with the deliberate manipulation of a stereo test design with the aim to characterize the spatial of features of the stimuli elements. Ultimately, the goal is to understand the neural basis of depth discrimination and crowding since configuration effects reflect integrative processes within the visual system (Livne and Sagi, 2007). If the magnitude of the effect depends on the relationship between the features in stimuli, the present investigation, which investigates the influence of stimulus configuration on depth discrimination thresholds and crowding, is worthwhile.

Rationale

Although some aspects of crowding in stereoscopic vision are known, the interest of the present work is to study further the nature and characteristics of stereo crowding in a stimulus configuration consisting of a test bar surrounded by flanking bars at optimum stimulus conditions (Richards, 1972; Mitchell and O'Hagan, 1972; Butler and Westheimer, 1978; Westheimer and McKee, 1980a; Mitchison and Westheimer, 1984; Westheimer, and Truong, 1988; Kumar and Glaser, 1992a). We investigated the lateral interference, of flanking and reference bar configuration on depth discrimination thresholds in an attempt to characterize the spatial extent of crowding at the fixation plane.

First, we designed an experiment similar to that used by Butler and Westheimer (1978) to examine the influence of horizontal retinal disparity (lateral separation) of flanking targets

(i.e. crowding) on the depth discrimination thresholds under optimum test–reference conditions. The aim was to examine if our experimental setup would produce similar crowding consistent with previous findings. That is, find the critical lateral distance between the stereoscopic test and adjoining flanking bars that will produce optimum crowding when positioned on the plane of fixation.

Second, in order to specify more accurately the influence of the flanking bar and reference bar configuration on crowding, and to clarify if the flanking bars become relatively more useful cues for depth discrimination than the reference bars at smaller test-to-flank separations (Butler and Westheimer, 1978), the reference bar of the stereo pair was omitted in another experimental design. We propose that, if the reference target is present, and the visual system regards the reference as useful for relative depth discrimination, visual attention (decision process) should not be interested or change from using the designated reference element to use the flanking bars as depth cues when the flankers lie in close spatial proximity to the stereo test. If depth perception is affected by disparity signals in the fixation plane, we expected an inhibition due the interaction from similar flanking bars targets close to the stereoscopic test bar, but facilitation if the reference bar is omitted and flanking bars are used as ‘ad hoc’ reference targets for discrimination.

Third, depth discrimination thresholds of the test in the absence of all other close features were measured. The results could then be compared to results where flankers were used particularly for conditions employing wide test flanker separations (Westheimer and McKee, 1980a).

Further, while there is some evidence that increasing the length of the test stimulus in a test-reference configuration can lead to improved stereo acuity, the influence of increasing the width of stereo test stimuli are less consistent. Physiological evidence exists showing that the responses of some cortical cells in both cat and monkey (e.g. hypercomplex cells) depend on the dimensions of the stimulus (Hubel and Wiesel, 1959, 1962; 1970). There is also evidence that some neurons in the visual cortex are specifically tuned to the size of the

stimulus and increase their relative excitation at set dimension for that particular cell (Blakemore and Campbell, 1969; Mitchell and O'Hagan, 1972). In this study, we were interested to find out if, when the flanking bars induce crowding in the stereo task, such that it participates in calling the depth location of the test (crowding), whether changing the widths will affect the threshold. We were motivated by the assumption that, in hyperacuity tasks the distinctness of a border or edge could be very important in the spatial discrimination of a test from its neighbours (Richards, 1972; Richards and Kaye, 1974; Foley-Fisher, 1977), and in a stereo configuration that permits crowding, it will help clarify whether the mechanism for depth discrimination uses as a metric, edge-to-edge or centre-to-centre interactions. In an experiment, the width of the flanking bars were manipulated to examine their tuning effect on the interaction by measuring depth discrimination thresholds for different flanking bar widths. If crowding is an integrative process involving local and global factors where disparity information are pooled, we expected the size (width) of the flanking bars (crowding bars) to have an influence on depth discrimination threshold on the plane of fixation. It will seem that the edge-to-edge interactions will serve as vital cue for depth discrimination in this instance, but the mechanism may shift to a center-to-center interaction due the pooling effect when the sizes are widened. We assumed that deleterious effects of the flanking bars will be maximum when the stereoscopic test and flankers have similar sizes (widths) due to crowding (Kooi et al, 1994), but depth discrimination thresholds will decrease when the size of the flankers are widened to perceptually look distinct from the test bar due grouping or compulsory pooling of their disparity information to evade crowding

Lastly, if the reference bar is restricted to the fixation plane, and the instruction is to use it for relative judgment of the depth location of the test target, we propose that any change in the size of the reference target should not affect the discrimination threshold of the test.

The investigations here, using stereo configurations that permit optimum performance and restrict performance based on the interaction of spatial properties, may potentially be helpful

to provide additional information on stimulus parameters in the design of stereo configurations.

METHOD AND APPARATUS

The methods employed in this Chapter have been described in detail elsewhere (Chapter Two) and therefore only a brief description is given here. Stimuli were displayed on a suitable high resolution monitor using the psychophysical method of constant stimuli, and data collated by means of a two-alternative forced choice paradigm to determine stereoscopic depth discrimination thresholds.

Stimuli

The basic stereoscopic stimuli for the experiments were two relatively thin, luminous vertical targets (test and reference bars) (broad-band) displayed with the test bar directly below the reference and separated by a small spacing that varied slightly between observers. The construction of the stimulus was similar to the one used by Butler and Westheimer (1978), but with important differences (Fig. 3.0.2). For Expts. 3.1 to 3.4, the dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. The test bar was presented in randomly interleaved trials (mixed by alternating between them) at one of 9 possible positions disparities of 8.5, 17, 25.6, and 51 sec arc) either in front of, or behind the fixation plane and one position on the fixation plane (i.e. no disparity). Crossed disparities were recorded as positive and uncrossed disparities negative. Binocular disparity of the target bar was produced by introducing small lateral pixel offsets of the bar targets in opposite directions and presented, in an alternate non-interlaced fashion, to each eye through an electric shutter goggle system. Where appropriate, flanking bars of the same height and width as the test and reference bars could also be displayed and were positioned adjacent and parallel to the target bar only. The edge-to-edge distance of the test to flanking bars could be varied systematically (Fig. 3.0.2 panels 3.2, 3.3). For Expts. 3.5 and 3.6,

changes in the size (width) of the flanker and reference bars, from 0.5, 1, 2, 4 to 6 min arc, were introduced while maintaining the edge-to-edge separation between the test and flanker bars so that the change in width occurred independently of the separation distance (fig. 3.0.2 panels 3.5, 3.6).

In order to ensure fixation was aligned to the plane of the monitor, prior to each trial, observers binocularly fixated on a central fixation spot of 30 sec arc displayed in the middle of a pair of vertical Nonius bars, 1.4 min arc wide and 7 min arc long. The Nonius bars and fixation point were surrounded by a thin square frame of size 28 min arc and were presented just prior to a trial and disappeared when the test stimulus was presented (see Chapter two). Stimuli displayed on a high resolution monitor were presented to the observers' eyes separately via a shutter goggle system.

The ambient laboratory room lighting conditions were kept low, to avoid disturbances of reflection from the computer screen and ensure that the stereoscopic stimuli and Nonius display were clearly visible to observers (Kumar and Glaser, 1992).

A custom written Matlab (version 10) script was used to create the stimuli and control display and presentation times. Parameters for stimuli configurations and properties required for each experiment were specified in a programmed condition file and are described in the experiments described herein.

Subjects and Visual Condition

For each experimental condition, at least three adult observers participated, but in all five adult observers (AC, JO, SO, MC and MR) were used. Observers had normal or corrected to normal visual acuity (6/6 Snellen acuity or better) and normal stereopsis (< 30 sec arc assessed using the TNO stereotest) (Lameris Ootech) (Fricke and Siderov, 1997). Observers viewed the display monitor through their natural pupils, and the shutter goggles

were appropriately positioned on the face by maintaining the head position in the primary gaze.

Procedure

All experiments were performed at a distance of 13.5m measured from the computer display to the observer and stimulus was presented for 300 msec at a self-timed rate.

The observer's task was to indicate whether the test bar appeared in front of, or behind the reference bar by pressing buttons on a response box. Before each trial, observers were instructed to fixate on the position of the fixation spot, and to ensure that the Nonius lines appeared aligned, before they pressed the task button of the response box to display the stereoscopic stimuli. For each trial, the test appeared with either crossed or uncrossed disparity or no disparity, relative to the reference target. Feedback was provided immediately after the decision about test depth direction by a high and low pitch sound for correct and incorrect responses respectively, and no sound when the stereo target had no disparity. All observers undertook several pre-trial sessions up to 2 to 3 weeks prior to actual data collection during which time up to 10 hours of training was completed. This training was done to minimise any learning effects; nevertheless, this potential confound was also monitored throughout the data collection period by measuring the baseline stereo acuity periodically. Data collection commenced only after stable thresholds values were recorded after training (see chapter two). Data collection was done in sessions, twice a week with each session lasting about 1 -2 hours. A minimum of 250 responses were obtained for each run.

Experiment 3.1

An initial control experiment determined the vertical separation of the test and reference stimuli for optimum depth discrimination for each observer. The stereoscopic stimulus composed of a simple two-bar test and reference targets aligned in a top-bottom

configuration (Fig. 3. 0.2 (3.1)). The separation between the test and reference bar was increasingly varied from abutting to separations of 3.2, 7.12, 14.22, 21.34 min arc to determine the separation that resulted in best performance for each observer. The reference was always presented in the fixation plane. Observers were required to make a forced-choice response as to whether the test bar appeared in front of or behind the reference bar through a response box. This simple depth discrimination task also served as a control condition without the presence of flanking stimuli.

Experiment 3.2

Expt. 3.2 investigated the spatial interactions around the plane of fixation using stereoscopic configurations that would result in maximum interference. Two vertical flanking bars of the same length, width and contrast as the test bar were used to induce crowding (Fig. 3.0.2 (3.2)). The flanking bars were positioned symmetrically parallel to the lower test bar only. The stereoscopic stimuli together with the flanking bars were presented simultaneously at the same brief duration. The lateral distance from the edge of the test bar to each of the flankers, thus test-to-flank separation, was systematically varied to determine the test-to-flank distance resulting in maximal crowding. The lower test bar appeared at one of the eight positions in depth, and observers responded to the depth position of it, either in front of or behind, relative to the upper reference bar. The two flanking bars and reference bar always appeared in the plane of fixation (fronto-parallel plane). Five observers (AC, JO, MC, MR and SO) were involved in this experiment.

Experiment 3.3

Expt. 3.3 was an additional control condition to confirm that the flanking bars did not become default reference targets for the stereoscopic task. As the edge-to-edge separation of the flanking bars was reduced in Expt. 3.2, they may have become relatively more useful depth

cues than the reference bar for the depth discrimination task. The stimulus configuration used was the same as used in the crowding experiment previously described (Expt. 3.2), except that the upper reference bar was omitted. The edge-to-edge separation of the flanking bars from the test bar was systematically varied just as in Expt. 3.2. The observers' task was similar to the task in Expt. 3.2, to judge whether the middle test appeared in front of, or behind the plane of fixation, but using the two flanking bars as relative reference elements (Fig. 3. 0.2 (3.3)). Four observers (AC, SO, JO, MR) participated in this experiment.

Experiment 3.4

In Expt. 3.4, the reference and flanking bars were omitted and only the test bar was displayed. The observers' task was to determine the depth of the test bar without the aid of a reference (notwithstanding the edges of the monitor frame provide a distance relative reference). The test was displayed with given disparity and moved in depth to determine the absolute thresholds for the test bar. It was useful to do this control to compare the discrimination threshold of this experiment to baseline values of the basic test-reference configuration. Here, the fixation spot and the Nonius stimulus, which always appeared just prior to the test, served as a reference to the plane of fixation. Three observers (AC, SO, JO) participated in this experiment.

Experiments 3.5 & 3.6

Expts. 3.5 and 3.6 investigated whether the width of the flanking bars had an influence on the stereo thresholds under crowded conditions. For Expt. 3.5, the configuration was the same as in Expt. 3.2 but the width of the flanking bars was varied while the edge-to-edge separation of the flanking bars to the test bar was kept at each observer's determined optimum crowding distance. When the width of flankers was being varied, care was taken to account for the relative increase in the width of the flankers so that the optimal edge-to-

edge separation for each observer remained the same. In Expt. 3.6, the same configuration as in Expt. 3.2 was used, except the width of the reference bar which was varied. In both experimental conditions, observers were required to make a forced-choice response as to whether the test bar appeared in front of, or behind the reference bar using a response box. Three observers (AC, SO, JO) participated in these experiments

Analysis

For each experimental run, a count of the number of 'in front' and 'behind' responses was stored in a file. The percentage of correct 'in front' responses as a function of binocular disparity was first determined by constructing the frequency of seeing curve. Standard error was estimated from the psychometric function by probit fitting (Finney, 1971). Observers' thresholds were calculated as the semi-interquartile range ($=0.675$), that is the disparity for which the proportion of trials that occasioned 'in front' responses between 50% - 75% of the fitted psychometric functions. Data points represent at least 500 responses, and sometimes as many as 1000 responses. Error bars indicate ± 1 standard error (SE) of the mean.

The magnitude of crowding was examined by comparing stereo-threshold measured in the presence of flankers to the stereo-threshold measured when the flankers were omitted (i.e. the baseline threshold for the stereo pair). In the main crowding experiment, peak crowding was defined as the greatest detrimental effect of the flankers on the baseline threshold. Extent of crowding is the smallest test-flanker separation at which the flanked stereo-threshold was not statistically significantly different, relative to the baseline stereo-threshold. A one-way repeated measures Analysis of Variance (ANOVA) performed examined differences in the strength of the effect of separation (including a condition when the flankers were not present) on depth discrimination thresholds. When required, a follow up post hoc Turkey's Honestly Significant Difference (HSD) test ($\alpha=0.5$) was carried out to determine effect of flankers at each test-flanker separation. When interpreting the results however, the *p value* must not be used in isolation. Limitation associated with the few subjects' used in

the experiments, and subjective bias in performance, which are not unusual in psychophysical studies may hide the magnitude of observed effects and its variability if not jointly interpreted with alternative graphical presentation, ratios or main performances reported (Twa, 2016).

Estimation of Depth Bias

In the crowding experiment conducted (Expt. 3.2), the flankers were always positioned in the fixation plane. Flanker effects in causing bias in discriminating the depth direction of the test relative to the reference was determined. Induced depth bias was calculated as the shift in the mean of the fitted psychometric function of the in front responses. The shift in the mean represents the position the test needed to be moved either in front of or behind the reference bar in order for it to have been perceived to be in the same depth plane as the reference (i.e. align with the reference) (Westheimer, 1986). Therefore, it can be regarded as estimation of the point of subjective equality (PSE).

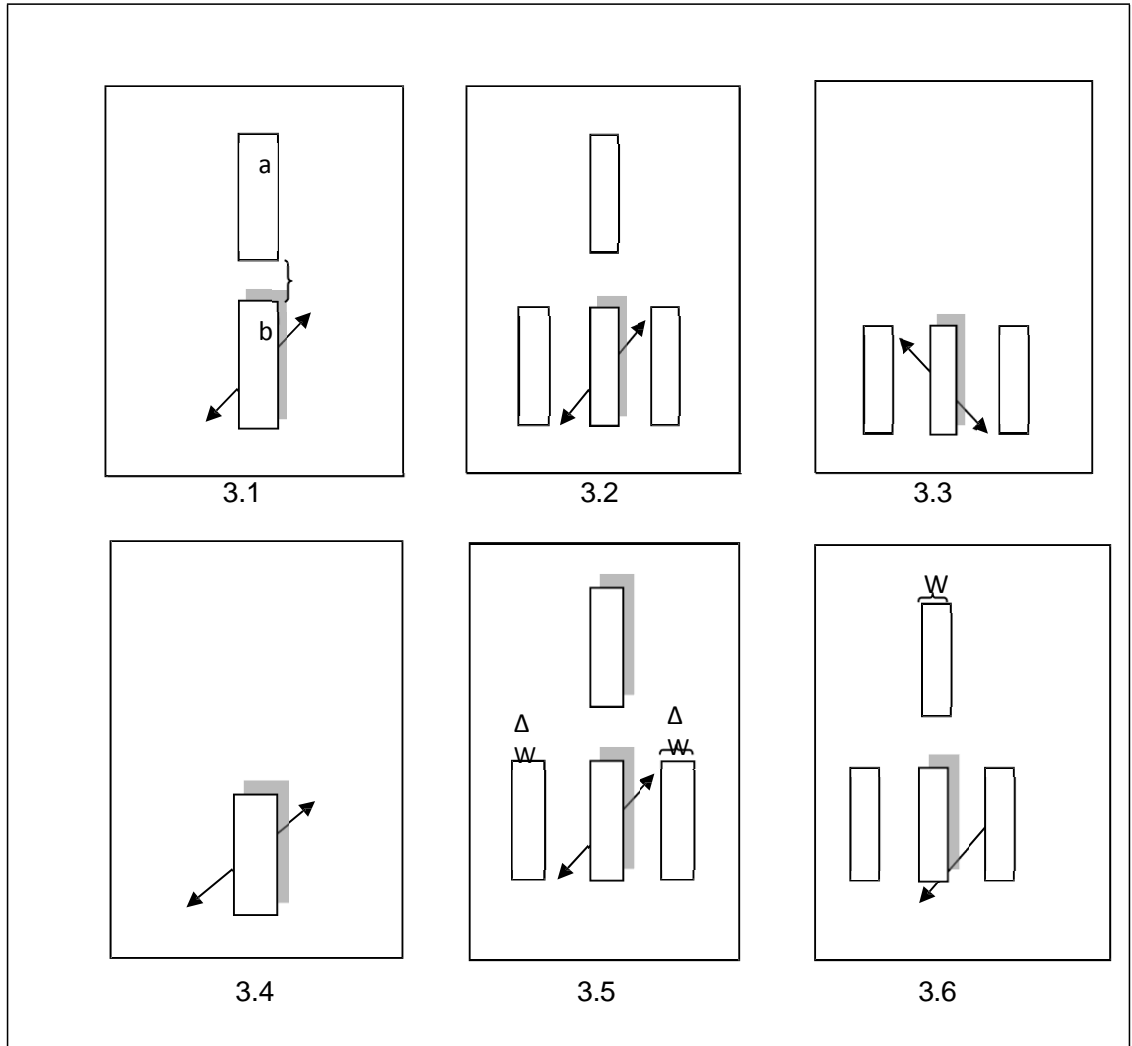


Fig. 3. 0. 2 Test conditions for the Experiments are depicted in each of the panels. In experiment 3.1, to determine optimal vertical separation, the configuration consisted of test bar (b) (lower bar) and the reference bar (a) (upper bar) aligned in a top-bottom configuration. Only the test moved in depth as depicted by the arrows. Expts. 3.2 and 3.3 determined the influence of crowding on depth discrimination thresholds. In (3.2) two flanking bars were symmetrically placed around the lower test and in (3.3) the reference element was omitted and all features simultaneously presented for the same duration. In Expt. 3.4, only the test was moved in depth to measure the stereo-threshold free from local references. In Expts. 3.5 and 3.6, the width of the flanking bars at the optimum crowding distance (OCD) and reference bar was varied respectively in the size tuning experiment.

RESULTS

Experiment 3.1. Optimum Vertical Separation

The results of all 5 observers (SO, AC, JO, MR and MC) are reported here. Thresholds were consistently stable after 1500 – 2000 training trials. Individual results are shown in Fig. 3.1 (A), where the stereo-threshold (sec arc) is plotted against the vertical separation of the test and reference bar (min arc). Stereo acuity was finest for a narrow range of test and reference separations, between 7 to 14 min arc, consistent with previous reports that for best stereo acuity, the test and reference targets should not be abutting but separated slightly by a few min arcs (Westheimer and McKee, 1980a; Fendick and Westheimer, 1983). Stereo acuity showed a relatively sharp decline when the test and reference bars were abutting, and a more gradual decline when the bars separation extended beyond the optimum range (Fig. 3.1 (B)). Connecting the end points of the test and reference bar, thus forming a continuous long bar, made it more difficult for observers to perceive 2 discrete targets resulting in the relatively poorer stereo acuity under this condition. At wider test and reference separations, the reference bar became relatively less useful for helping to judge the depth of the test (Anderson and Weymouth, 1923; McKee, 1983). The test and reference bar separations that produced optimum stereo-thresholds were, for each of the observers, were AC and MR 7 min arc, JO, and MC 14 min arc and SO 21 min arc. The optimum stereo-thresholds were AC 13 sec arc, JC 14 sec arc, MC 20 sec arc and SO and MR 21 sec arc. A one-way ANOVA done revealed that there was a statistically significant effect of test-reference vertical separation on discrimination [$F(4, 20) = 3.788, p = 0.019$]. A Tukey post-hoc test ($\alpha=0.5$) revealed that effect of vertical separation on depth discrimination was statistically significantly between abutting [$(60.4 \pm 12.8 \text{ sec arc})$] and 7 min arc [$(25.8 \pm 3.9 \text{ sec arc}, p = 0.032)$] and 14 min arc [$(23.2 \pm 1.7 \text{ sec arc}, p = 0.019)$] separations compared to other separations that showed no statistically significant effect on discrimination.

These depth discrimination values are within the predictable range for the stimulus configurations and exposure duration used in this experiment (Westheimer and McKee, 1980a; Westheimer and Pette, 1990). The separation for each observer that gave the best depth discrimination was used as the optimal vertical separation for the stereoscopic stimulus configuration in the next and subsequent experiments. The threshold obtained for this experiment, was checked when other experimental data were being collected, and remained stable throughout the data collection period, which lasted several months. Where relevant, this threshold value is depicted as dashed lines on subsequent figures (see Fig.3) and is labelled as control or baseline threshold.

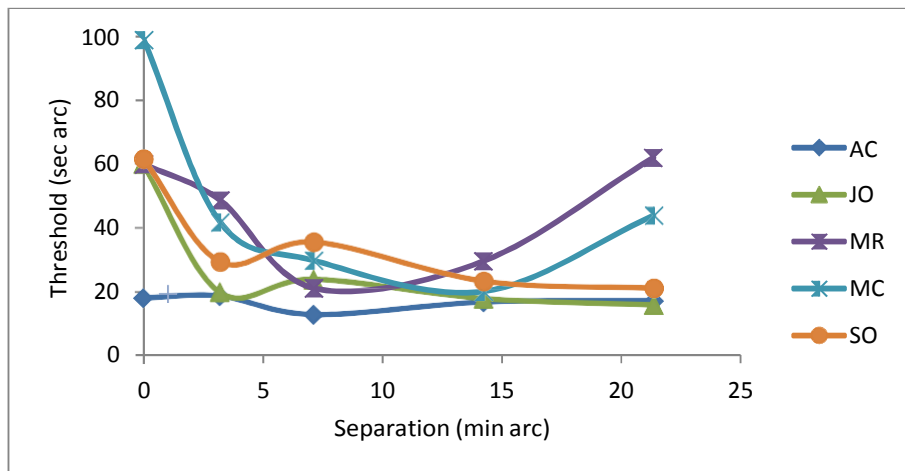
Experiment 3.2 and 3.3 Crowding in Depth

Fig. 3.2A depicts the results for Expt. 3.2 showing, in each panel, the individual stereo-thresholds for 5 observers plotted as function of the edge-to-edge test-to-flanker separation. Also shown are the baseline stereo-thresholds for each observer (dotted lines). Stereo acuity is degraded by the presence of the flanking bars, and the deterioration in stereo acuity is dependent on the test-to-flanker distance in a somewhat non-monotonic fashion. Thus, thresholds increased with decreasing test-flanker separations. Individual results showed two patterns among the observers. For observers JO, MR and MC crowding occurred at the closest flanker distance of 1 min arc away from the test, but reached a peak at a test-to-flanker distance of 2 min arc. At this separation, observer JO showed about a fivefold elevation in threshold (from 14 to 69 sec arc) compared to observers MC and MR who showed about eight fold increases in threshold over their respective control values (from 20 and 21 sec arc to 225 and 182 sec arc respectively). For all 3 observers, the crowding effect decreased quickly for greater test-to-flanker distances up to about 4 min arc and more slowly up until at a test-to-flanker distance of about 6 min arc when the effect considerably dissipated to values equalling the control condition when no flankers were present. For observers AC and SO, the peak crowding effect occurred when the flankers were 1 min arc

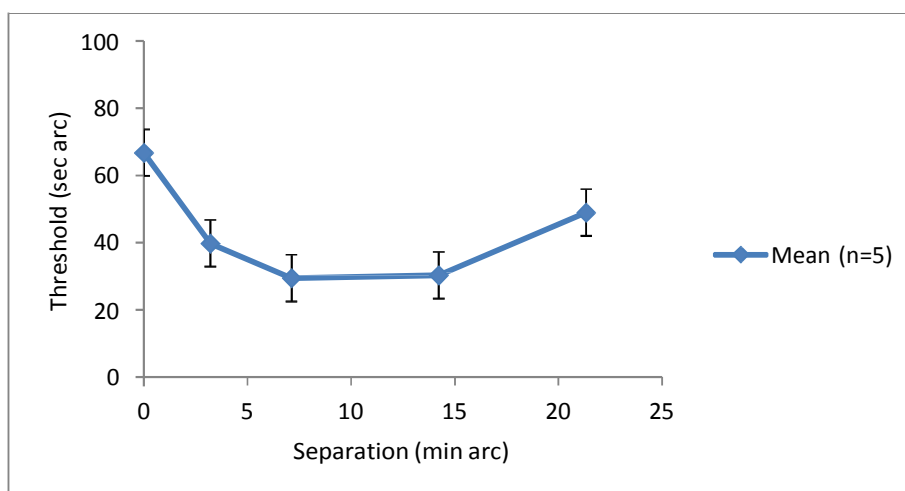
away from the test target. For observer AC, who is a trained stereo observer, his threshold at the maximum crowding separation was three times more than his control values (13 to 43 sec arc). Whilst, the performance for observer SO was consistent with the findings of the first three observers, showing an eight fold threshold elevation at the peak crowding separation (from 21 to 168 sec arc). For observers AC and SO the crowding effect dropped-off sharply for test-to-flanker distances up to about 4 min arc and then showed no appreciable increase over control values. Though, unlike AC, and SO whose crowding effect disappeared completely with the increase in test-to-flanker separations beyond 4 arc min, thresholds for JO, MC and MC at the largest test-to-flanker distance were still slightly above their respective baseline values. Fig. 3.2B shows the mean results averaged across all 5 observers. A one-way ANOVA was used to analyse the effect of test-flanker separation (including when no flankers were present condition) on crowding. There was a statistically significant effect of separation on discrimination [$F(5, 24) = 4.654, p = 0.004$]. A Tukey post-hoc test revealed that effect of separation was statistically significant when the flankers were 1 min arc [$(116.6 \pm 30.8 \text{ sec arc}, p = 0.030)$] and 2 min arc [$(115.5 \pm 38.2 \text{ sec arc}, p = 0.033)$] away from the test compared to other separations which were not statistically significant ($p > 0.05$).

The overall results of the control condition in Expt. 3.3 show that removal of the reference element reduces the relative crowding effect of the flanking bars on stereo-thresholds, although there were individual variations amongst the 4 observers (AC, SO, JO, MR) (Fig. 3.3A). For all 4 observers, the same test-to-flank distance of 1 min arc as found in Expt. 3.2 produced maximum threshold values. The peak crowding for this control condition also varied as a function of the test-to-flank separation distance. Inspection of the individual results (panels in Fig. 3.3A) also show that except for observer MR, the control configuration was not as effective in producing crowding as the configuration used in Expt. 3.2. Optimum depth thresholds recorded were 31, 87, and 40 sec arc compared to 43, 169 and 60 sec arc

for observers AC, SO and JO respectively. Observer MR quite atypically recorded more effect of crowding at the optimum crowding distance (281 sec arc) than when the reference bar was present (107 sec arc). Nevertheless, what is consistent among the observers' performance is that the crowding effect derived from the presence of the flankers dissipated at the same stimulus distance of about 4 min arc as found in Expt.3.2. A one-way ANOVA analysed revealed that the effect of test-flanker separation (including when no flankers were present condition) showed no statistically significant effect of separation on discrimination [$F(5, 18) = 2.137, p = 0.107$]. Mean threshold however appreciably decreased from the close separation of 1 min arc (112.2 ± 57.5 sec arc) to the uncrowded separation of 6 min arc (23.5 ± 3.5 sec arc).



(A)



(B)

Fig. 3. 1 Expt. 3.1. Stereo-thresholds for Test-Reference Vertical Separation.

(A) Individual thresholds (sec arc) for the stereoscopic depth discrimination task described in the text as a function of the edge-to-edge vertical separation (min arc) between the test and reference targets (inset). (B) Mean thresholds (sec arc) averaged across all 5 observers plotted against the edge-to-edge vertical separation (min arc) between the test and reference bar. Error bars represent +/- 1 standard errors.

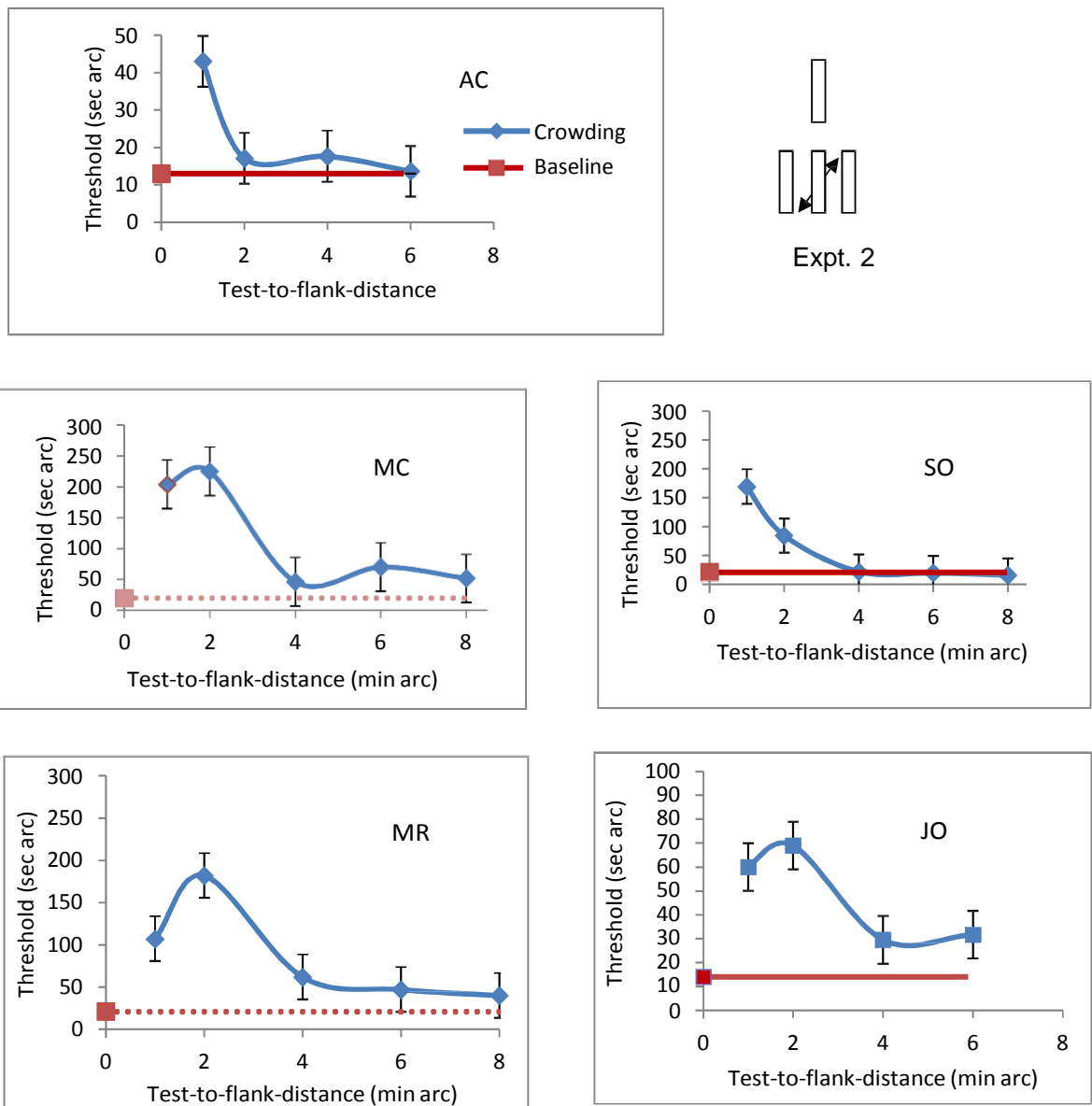


Fig. 3. 2A. Expt. 3.2. Influence of Bar Crowding on Depth Discrimination.

Each panel shows for each individual observer, the depth discrimination thresholds (sec arc) plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc). Also shown in the inset is the stimulus configuration. Dotted lines indicate the threshold when the flanking bars were not present. Error bars represent ± 1 standard errors. Data for AC and JO are plotted on different scales to show their effect as they were normally good observers.

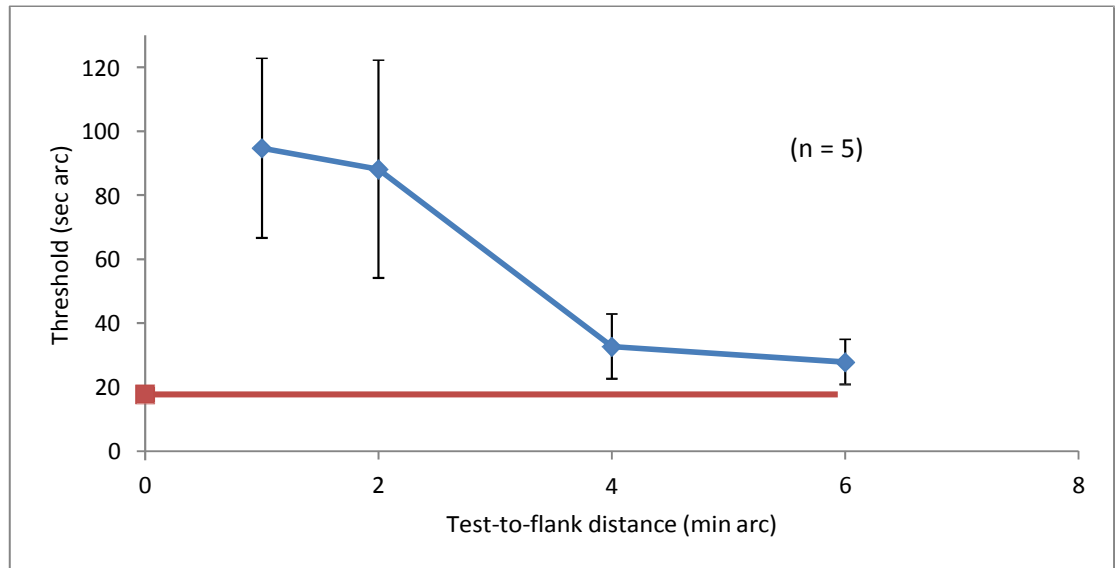


Fig 3.2B. Expt. 3.2. Mean Effect of Bar Crowding on Depth Discrimination. Mean depth discrimination thresholds (sec arc) averaged across the 5 observers, plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc). Dotted lines indicate the threshold when the flanking bars were not present averaged across the same 5 observers. Error bars represent ± 1 standard errors.

Depth Bias

In the basic test and reference task discrimination (Expt. 3.1), all the subjects except SO demonstrated crossed disparity bias, thus they judged the test often time to be 'in front of' the reference bar compared to 'behind' responses. However, when the flankers were present (Expt. 2) and were within the test-flanker distance that produced crowding (Fig. 3.2A), their presence seemed to have induced positional shifts in the test location, resulting in subjects often judging the test to be further in front of the reference. For one subject (AC) though he showed a 'front' bias for the stereoscopic pair (in Expt. 3.1), but subsequently displayed 'behind' bias when the flankers were in place, his bias appeared to consistently shift to a more front bias effect when the flankers were at small distances. In fact, generally at larger distances at which the observers recorded no crowding, the inducing ability of the flankers to cause a shift in the bias in target discrimination was generally not as substantial (except for MR and MC) (Table 3.1 shows the bias calculated as induced effect by the flankers).

Table 3. 1. Observers' Bias

Test-Flank distance (min arc)	Bias (sec arc)				
	SO	AC	JO	MR	MC
0*	5	- 4.8	- 2.9	- 12	- 2.4
1	- 20	5.1	- 32	-19	-18
2	- 28	10	- 4.2	-34	- 81
4	4	15	12.8	-13.8	-11.5
6	- 3.3	9	2.3	- 30	- 40
8	- 3.1	12	2.3	- 29	- 6

In the table negative and positive numbers represent 'in front' and 'behind' bias respectively when the flaking bars were positioned at the plane of fixation. Zero (0) test-flanker represents when bias measured with the stereoscopic pair at each observer's best separation when there were no flankers in place.*

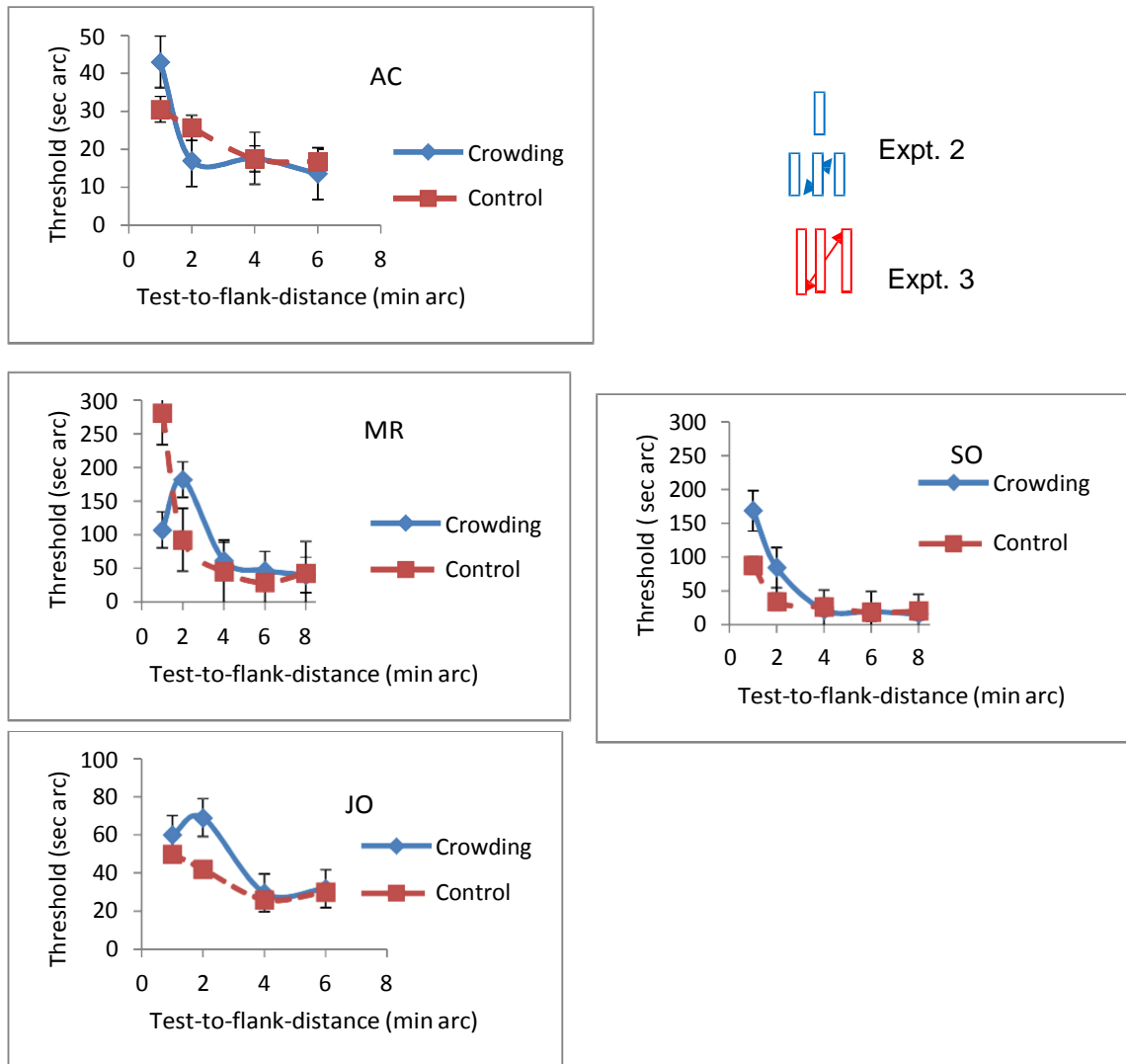


Fig. 3. 3A. Expt. 3.3. Comparative Influence of Configuration on Depth Discrimination. Each panel shows for each individual observer, the depth discrimination thresholds (sec arc) plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc). Also shown in the inset is the stimulus configurations used in Expt. 3.2 (blue) and Expt. 3.3 (red). The solid blue lines are the data derived from Expt. 3.2 replotted and labelled 'Crowding' and the red dashed lines (labelled 'Control' are the data in the current experiment where the reference bar was omitted leaving the two flanking bars as references for relative depth discrimination. Error bars represent ± 1 standard errors. Data for AC and JO are plotted on a different scales to show their effect as they were normally good observers.

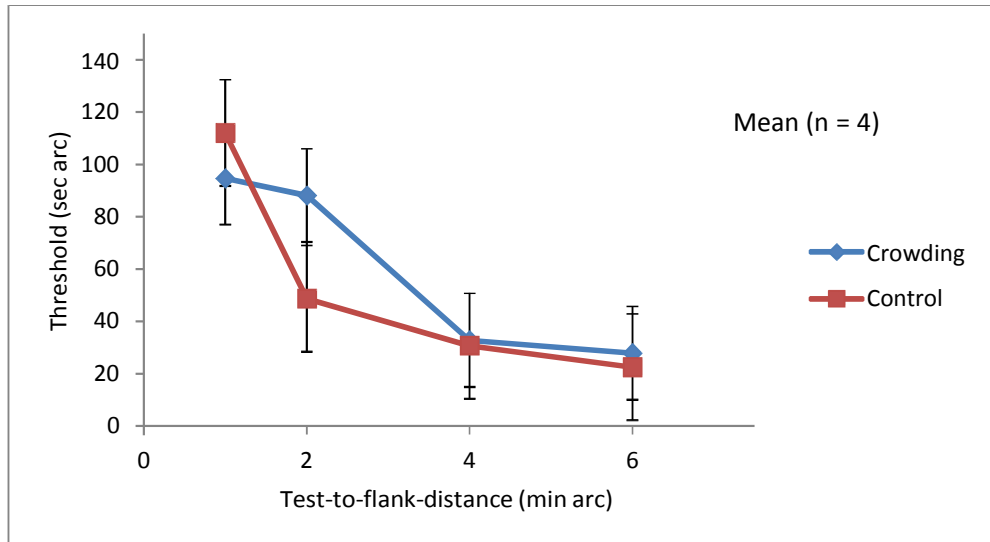


Fig. 3.3B Mean Comparative effect of Bar Crowding Configuration on Depth Discrimination. Data from Fig 3.3A averaged across all 4 observers. Depth discrimination thresholds (sec arc) are plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc). The solid blue lines are the mean 'Crowding' data and the red lines are the mean 'Control' data where the reference bar was omitted leaving the two flanking bars as references for relative depth discrimination. Error bars represent +/- 1 standard error.

Experiment 3.4. Threshold for Depth of Single Test Target

The results of Expt. 3.4 for 3 observers are shown in Fig. 3.4. Each panel depicts individual stereo-thresholds for the test displayed in isolation (labelled 'Absolute') together with the results from the previous experiments, Expts. 3.2 ('Crowding') and 3.3 ('Control'). Results amongst the 3 observers demonstrated differences in the discrimination of the test. For observer AC, the stereo acuity for this task was worse than the stereo acuity recorded for both the crowding and control conditions (threshold of 55 sec arc), but for observer JO the stereo acuity was better than both other conditions with threshold of 42 sec arc (i.e. when the reference and the flanking bars were present (Expt. 3.2) and when the reference bar was omitted (Expt. 3.3)). For observer SO however, his performance was somewhat between the peaks of the two conditions (threshold of 110 sec arc). Consistent among the observers however, was that absolute thresholds were always above baseline values, and worse than when the flanking bars were present.

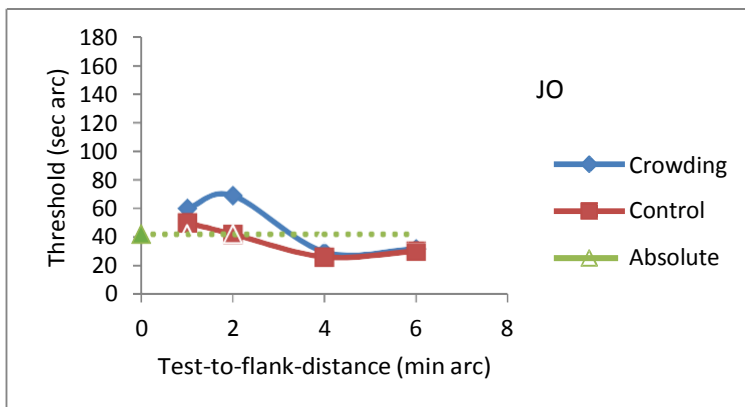
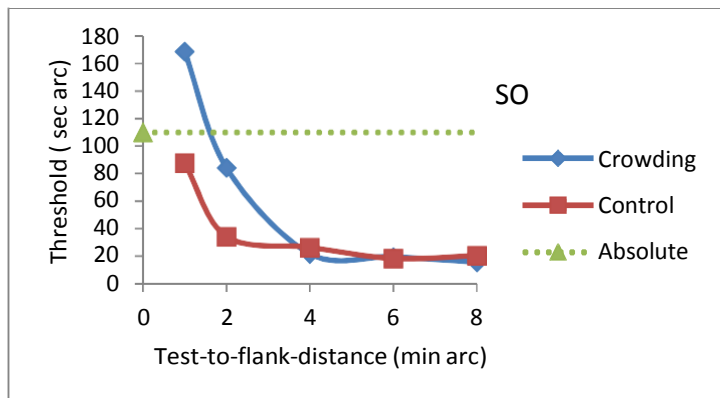
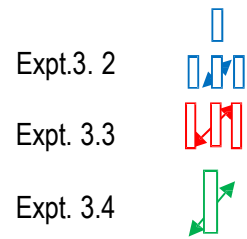
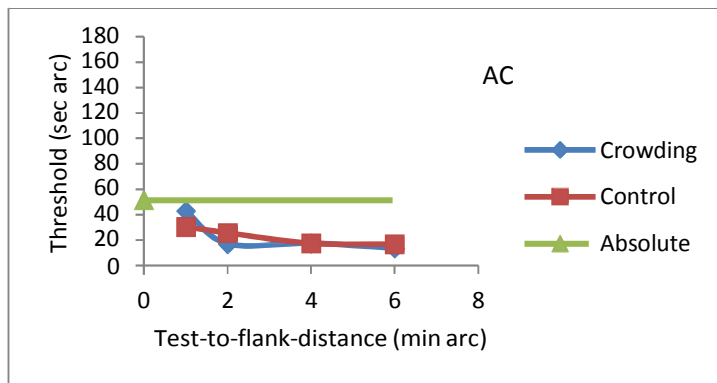


Fig. 3. 4 Expt. 3.4. Disparity Discrimination Threshold (Absolute) for a Single Test bar.

The average threshold is shown on the y-axis, and indicated as the dashed line across the x-axis. The test bar measured 14' Long and 2.8' Wide. Also shown in the inset is the stimulus configurations used in Expt. 3.2 (Crowding, blue line) and Expt. 3.3 (Control, red line). The green dashed lines (labelled 'Absolute') are the data in the current experiment where the reference bar and the flankers were omitted leaving the isolated test bar to be discriminated in depth. Error bars are not shown for clarity.

Experiments 3.5 and 3.6. Influence of Flanker and Reference bar Width

Configuration on Crowding

The results of 3 observers who took part in this experiment are shown in Figs. 3.5A and 3.5B. The results showed a similar function, a decrease in stereo-threshold value at thinner flanker widths, that approached baseline threshold when no flankers were present, followed by elevation in threshold as the flanking bar width was increased to match the original flanker width, and then a reduction in threshold at wider flanker widths. While observers AC and JO recorded much better stereo acuity and displayed a flatter function, observer SO displayed a much steeper function to indicate worse crowding for similar test and flanker width. However, consistent among all the observers, crowding was optimum for similar width of test and flanking bars configuration. A more consistent observation among the observers was that when the width of the flanks were less than a minute, the crowding showed little or no effect on thresholds (AC, 13; JO, 22; and SO, 24 sec arc), then marginally increased when the flanker width was increased to about 1 min arc (AC, 18; JO, 49; and SO, 42 sec arc). For observers AC and SO, when the flanker size (width) was about half the size of the original test, the flankers induced about half of the maximum crowding found when the flanking bars and test were the same size (width) (See Fig. 3.2A). Conversely, for observer JO, for similar flanker dimensions, his thresholds were comparable to what was recorded at optimum crowding in Expt. 2 (i.e. flanking bars were only half the size of the original). For observers JO and SO, maximum crowding occurred when the width of the flankers was increased to 2 min arc, while for AC, optimum crowding was produced at 4 min arc flanker width. For all observers, subsequent widening in the width of the flankers degraded the crowding effect, as portrayed by the flattening of their functions. Interestingly, when the width of the flanking bars approached the pretested size (original width) used in Experiment 2, the interaction demonstrated a similar crowding effect, with thresholds reaching 36, 69 and 110 sec arc (compared to 42, 60 and 168 sec arc in Expt. 3.2) for AC, JO and SO respectively.

One way ANOVA performed revealed no statistically significant main effect of change in the width of flankers on discrimination threshold [$F(4, 10) = 2.572, p = 0.103$]. Mean performance from changing the width from the thinnest 0.5 min arc [$(19.7 \pm 3.5 \text{ sec arc})$] to near the original (2 min arc) was [$(83.7 \pm 32.7 \text{ sec arc}, p = 0.095)$] and the thickest width [$(25.3 \pm 7.3 \text{ sec arc}, p = 0.0127)$], clearly suggesting that the width of the flankers strongly affected crowding.

Results of Expt. 3.6 for each individual and results averaged across the three observers are shown in Figs 3.6A and 3.6B respectively. Consistent among the observers, changing the width of the reference bar did not have much effect on depth discrimination, except when the reference bar was made very thin. As indicated by individual sample results, when the width of the reference bar was reduced to less than a minute (0.5 min arc), the performance of all three observers (AC, SO, JO) worsened (similar to the effect seen in Expt. 3.3, when the reference bar was omitted), thus showing that such a reference dimension makes the target less effective to serve as reference target. When the width of reference bar was increased to 1 min arc, the threshold improved and levelled off at widths greater than 2 min arc. One-way ANOVA revealed no statistically significant effect in changing the width of reference bar on discrimination [$F(4, 10) = 0.945, p = 0.477$]. Quite appreciably however, mean threshold at the thinnest width 0.5 arc min [$(56.7 \pm 14.7 \text{ sec arc})$] reduced to [$(32.7 \pm 8.7 \text{ sec arc})$] at the thickest width.

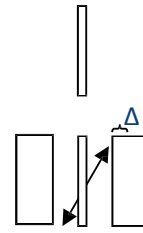
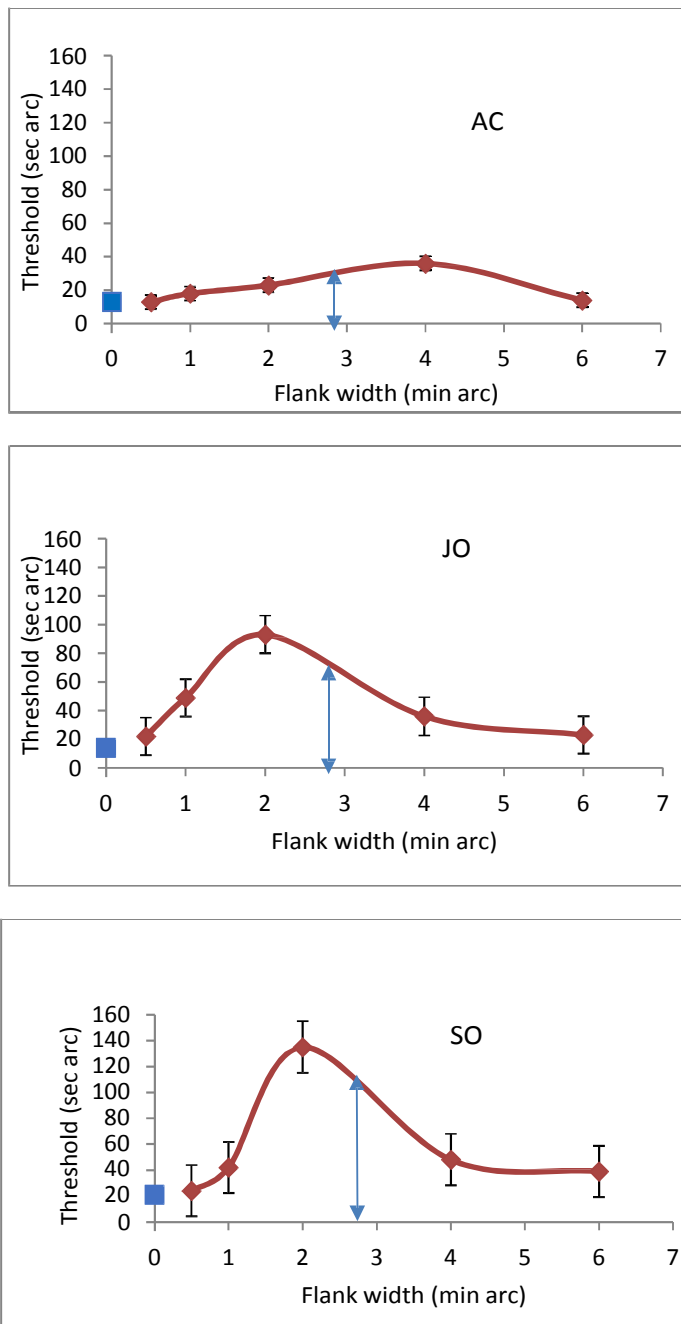


Fig. 3. 5A. Expt. 3.5. Effects of Width of Flanking bars on Depth Discrimination at OCD. Each panel shows for each individual observer, thresholds (sec arc) for the depth discrimination of the lower test target plotted as a function of the width of the surrounding flanking bars. Also plotted is the baseline threshold (on y-axis) and the arrow indicate when the stereoscopic target pair and flankers had equal size. Shown in the inset is the stimulus configurations used in Expt. 3.5. Error bars represent ± 1 standard errors.

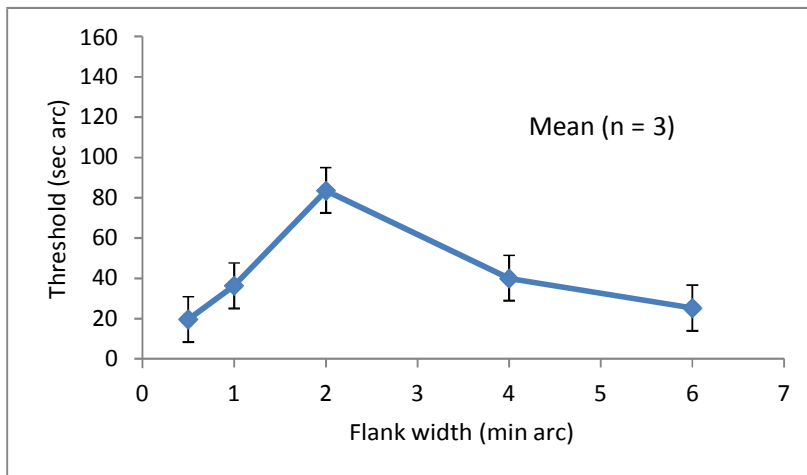


Fig 3.5B. Expt. 5 Mean Effects of Tuning the Width of Flanking Bars on Crowding at OCD. Thresholds (sec arc) averaged across the 3 observers for the depth discrimination of the lower test target are plotted against the width of the surrounding flanking bars. Error bars represent +/- 1 standard error.

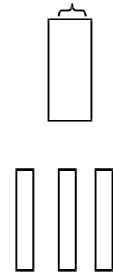
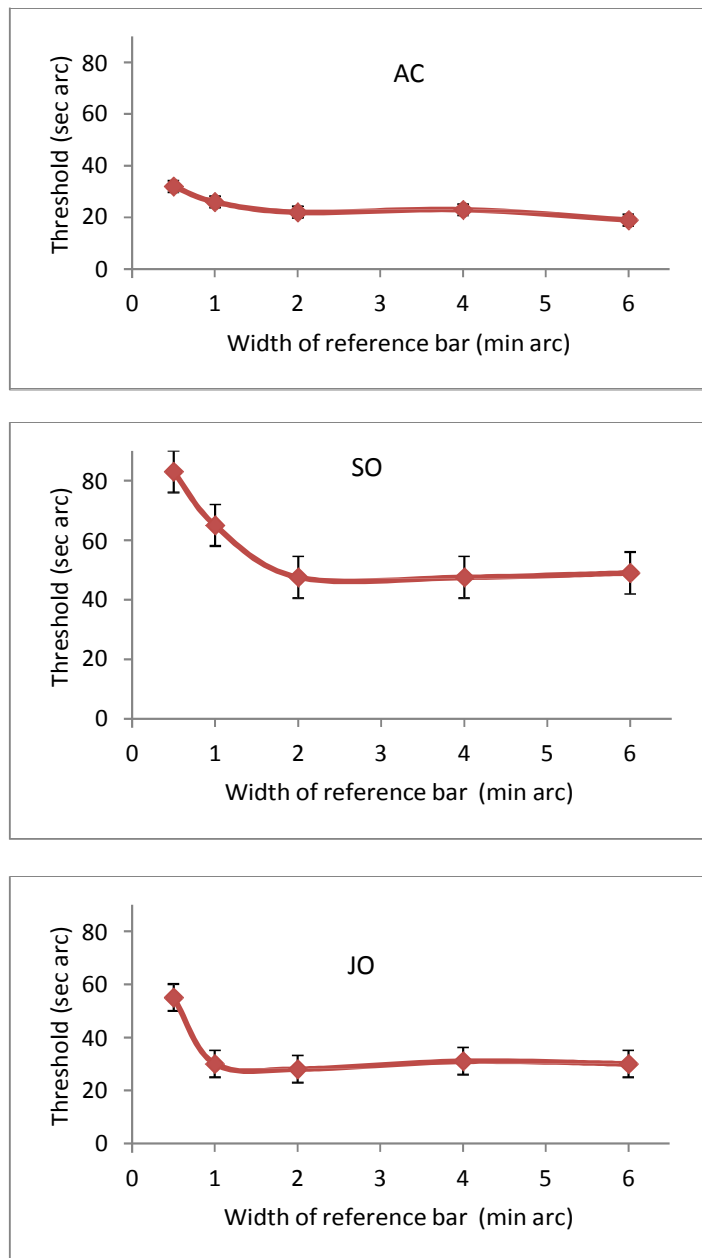


Fig. 3. 6A. Expt. 6. Effects of Width of Reference bar on Crowding at the OCD.

Each panel shows for each individual observer, thresholds (sec arc) for the depth discrimination of the lower test target of stereoscopic stimulus are plotted as function width size of the reference bar. Also shown in the inset is the stimulus configurations used in Expt. 3.6. Error bars represent ± 1 standard error.

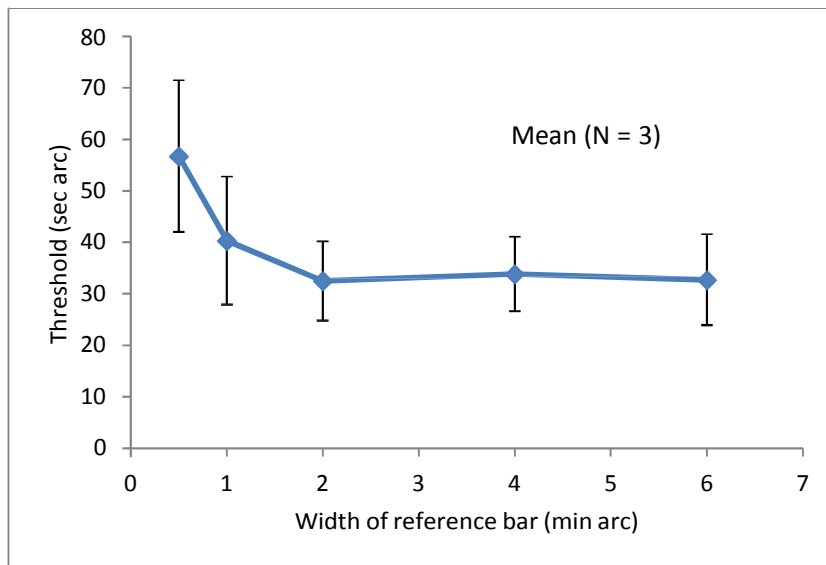


Fig 3.6B Expt. 3.6. Mean Effects of Tuning the Width of Reference bar to Crowding at the OCD. Data averaged across 3 observers, showing thresholds (sec arc) for the depth discrimination of the lower test target of are plotted as function width size of reference bar. Error bars represent +/- 1 standard error.

DISCUSSION OF RESULTS

The results presented here addressed how the depth discrimination of a test target is influenced by its interaction with nearby flanking features in a stereoscopic configuration in the fixation plane, through presumably a form of lateral interaction. The spatial extent and spatial characteristics of this interaction were examined by manipulating stimuli parameters in a simple stereoscopic configuration.

Optimum Vertical Separation

Berry (1948) and Westheimer and McKee (1980a) have shown that vertical separation between test and reference targets affects stereo thresholds. In the present study, across observers, a range of vertical separation between test and reference elements of 7 to 21 min arc produced the best stereo-thresholds. Our finding (Fig 3.1A) is consistent with previous studies suggesting that best depth discrimination thresholds are obtained with a range of test and reference separations of 10 to 30 min arc (Hirsch and Weymouth, 1948; Westheimer and McKee, 1979; Westheimer and McKee, 1980a, McKee, 1983).

Relative depth discrimination involving a two-line stereo test and reference configuration is quite simple and acute (Westheimer, 1979b; Westheimer and McKee, 1979). Indeed, within the range of test and reference separations used here, stereo-thresholds between 13 and 22 sec arc were recorded which are similar to thresholds obtained under ideal conditions in trained observers (Westheimer and McKee, 1980a, McKee, 1983). Our results are also in agreement with depth discrimination thresholds determined as a function of separation for other targets, usually lines and small squares (Westheimer and McKee, 1980a; Kumar and Glaser, 1995). Kumar and Glaser (1995) measured thresholds less than 20 sec arc for observers using lines separated by 2.5 min arc. Similar thresholds have also been found for two-line Vernier tasks, supporting a possible relationship between stereoscopic discrimination and Vernier tasks (Westheimer, 1975; 1979b). Since the investigations here were of foveal discrimination, the narrow range of separation and fine stereo acuity obtained

supports the fine nature of foveal discrimination tasks. If the test and reference were moved out of fixation plane, greater separation would have been required between the stereo pair to measure best stereo acuity (Westheimer and Truong, 1988). This inference is supported by the elevation in thresholds at wider separation beyond the optimum range found.

Spatial Extent and Characteristics of Crowding in Depth

In order to confirm and then extend previous results on the effect of crowding on stereoscopic depth threshold, we used stimuli and a paradigm similar to that employed previously (e.g. Butler and Westheimer, 1978). Consistent with those previous results, in our first experiment (Fig. 3.2A), we showed that flanking bars of the same length and width as the test bar and laterally and symmetrically positioned around the test bar, reduced the ability to judge the relative depth of the test bar. The crowding effect occurred when the flanking bars were in close proximity to the test bar and at the same depth plane as the reference bar (i.e. plane of fixation). The degree of the crowding produced by the flanking bars varied significantly as a function of the test-flank separation. As the distance between the flanking bars and the test bar was increased, the crowding effect decreased. The presence of the flanking bars reduced the depth resolution capacity of the visual system, but the strength of the interference depended on the specific distance for each observer. The test-to-flanker distance that produced the maximum crowding effect was 1 to 2 min arc.

Our crowding stimuli produced comparable test-flanker distances to those measured by Butler and Westheimer (1978) for their observers. They showed that the addition of flanking lines can degrade stereo acuity, and demonstrated that the threshold for a vertical test line adjudged relative to a reference line at the fixation plane was remarkably elevated by flanking lines. In their study, the crowding effect reached its apex, when the test-flanker separation reached about 2.5 min arc. Westheimer and McKee (1979b) also demonstrated that the depth discrimination threshold for a vertical line flanked by two comparison lines increased sharply as the distance between them was reduced below 5 min arc, and for

separations below 3 min arc, depth judgment became difficult. Kumar and Glaser (1995) and Gantz and Bedell (2011) have demonstrated similar crowding effects on depth discrimination. The findings here are in good accord with previous reports that targets separated from a stereoscopic test by less than 6 to 8 min arc will influence the depth discrimination of the test. (Butler and Westheimer, 1978; Westheimer and McKee, 1979; Westheimer and Levi, 1987). Further, the interactions observed in this study are consistent with other findings that revealed that lateral interaction between test and flankers is insignificant at greater separations of 6 -15 arc min (Butler and Westheimer, 1978; Westheimer and Levi, 1987, Gantz and Bedell, 2011).

The results of Butler and Westheimer (1978) study which we replicated here (albeit not for all observers, Expt. 1) showed that for very close test – flanker separations the crowding effect diminished and thresholds returned almost to those seen in the non-flank condition. We further investigated whether, for very close test – flanker separations, observers could use the flanking bars as reference targets therefore overcoming the crowding effect (Yantis, 2000; Freeman et al., 2001). When the reference bar was omitted, and the experimental task repeated, the similarity in the results (Fig 3.3B) coupled with the lower thresholds observed (compared to Expt. 3.2), indicated that the flankers without the reference bar enhanced relative depth discrimination of test. This finding confirmed that the results seen in Expt. 3.2 were due to a lateral interference of the flanker bars on the test and on average observers did not use the flanking bars at smaller separations in Expt. 3.2, but still relied on the reference bar when both were present. This observation does not support the explanation that shape effects (since test and flankers had equal length and width) (e.g. Kumar and Glaser, 1992b) accounted for the observation at close separations in Butler and Westheimer (1978) study. The results are however in good accord with the Butler and Westheimer (1978) assertion that the extent of crowding is maximal at a particular test-flanker separation, and we have shown here that it may also depend on the configuration

used. Though analyses of the results for this control experiment did not reveal statistical significance, results among the observers were consistent, a decrease in stereo-threshold from the close separation (1 min arc) to the uncrowded separation (6 min arc) by a mean ratio of 6.6 to 1.4 to over baseline values. The similar functions obtained for both conditions (Fig. 3.3B) suggests that the same processing mechanism was employed by the visual system.

Reviewing individual data (Fig. 3.2A) superimposed on the findings of previous investigations reveal two paradigms. In the first paradigm (observers MC, MR and JO), when the flanking bars were at a close distance from the test target (1 min arc), some crowding was produced. Then, the magnitude of the crowding increased as the flankers were placed further away from the test, until at a particular test-to-flanker distance (2 min arc), crowding reached a peak. Further, wider test-to-flanker separations yielded a progressively smaller crowding effect, until the effect considerably dissipated at larger test to flanker distances of 4 min arc. In the second paradigm (observers AC and SO), the presence of the flanking bar progressively degraded stereo acuity from close test-to-flanker distance (1 min arc) where crowding was optimal. The magnitude of the crowding then sharply declines as the flankers are placed away from the test, until, at a wider test to flank distance (4 min arc), rather similar to the observation in the first pattern, the effect substantially dissipates. The former paradigm is very similar to the Butler and Westheimer (1978) finding and the latter is typical of the Westheimer and McKee (1980a) finding. Notwithstanding, the similarity in the trend of both functions affirms use of the same mode of processing by the visual system.

The nature of the mechanism that encodes for this crowding influence has not yet well been agreed or understood. Crowding has been suggested to reveal integrative processes within the visual system (Butler and Westheimer, 1978; Levi, 2008; Sayim et al., 2010). Two basic alternative models of processing have been advanced to explain crowding in depth. First, a passive pooling mechanism where disparity signals are pooled and averaged within some integrative area in visual cortex (e.g. Badcock and Westheimer, 1985), or second, an active

inhibition mechanism of depth signals between disparate features within small area of the visual space (Blakemore and Hague, 1972; Butler and Westheimer, 1978; Poggio and Fischer, 1977; Poggio and Poggio, 1984; Badcock and Westheimer, 1985; Freeman and Ohzawa 1990). In the additive model, the disparity signals of the test and nearby flankers are summed. As a consequence, the presence of the pair of flanking bars in the fixation plane would serve as a prelude to weaken the depth signals of the test bar and hence, a greater disparity of the test bar would be required to reach the depth-difference threshold. Clearly, the plausibility of this additive model cannot easily be assumed to explain some of the crowding effect which shows a rise followed by sharp fall of threshold at increasing test-to-flanker distance (Butler and Westheimer, 1978). On the contrary, this particular type of interaction is compatible with the notion of inhibitory type (Butler and Westheimer, 1978; Westheimer and McKee, 1978; Tyler and Likova, 2007). During the inhibitory process, nearby flanking bars actively mitigated against the elaboration of the depth signals of the test because of competing visual direction at small separations. Perhaps the magnitude of effect is optimum at a certain test-flanker separation for each observer, and may be affected by stimuli configuration and task involved as has been alluded to. Recounting the manner in which the models are operationalised, and due to the modus of the interaction described here, it is more likely that the former mechanism could be ascribed for the crowding found here.

Absolute threshold

As an additional control condition, we measured the depth discrimination threshold of a test bar in the absence of all other local reference or flanking bars. The results showed relatively high depth discrimination thresholds pointing to the importance of the reference bar in the configuration for relative discrimination (Fig 3.4) (Kumar and Glaser, 1992a). Mitchison and Westheimer (1984) argued that if the judgment of depth of a test bar has to be made and nothing else is visible, the visual system will define a hypothetical fronto-parallel plane in

making a decision about the perceived depth of the test. Again, the higher absolute depth discrimination thresholds are consistent with results of other studies which showed that observers are relatively poor at discriminating a single test stimulus in depth and widely vary among observers and even within the individual (Kumar and Glaser, 1992a). This result supports the suggestion that the stereoscopic system requires a minimum of two features in close proximity to produce relatively low thresholds (Westheimer and McKee, 1979; McKee, 1983). In addition, the higher absolute depth thresholds we found further explains the results of other studies, where, for stimuli with features that are widely separate, depth discrimination thresholds have been noted to worsen (McKee and Westheimer, 1980a).

Do Flankers Induce Depth Bias Effects in the Fixation?

The depth positional bias (depth direction bias) exhibited by the observers is not uncommon in depth discrimination tasks. Similar effects have been previously reported, which were generally skewed towards crossed disparity responses (Richards and Foley, 1971; Lehmkuhle and Fox, 1980; Mustillo, 1985). What is noticeable here and which has not previously been reported for the interaction we investigated is that the positional shifts were more towards crossed bias at small test-flanker separation. The increasing strength of the front bias at small distances seems to indicate an 'exertion or pull' on the test by the flankers towards the crossed direction. The pulling effect distracted the extraction of signals about the depth information of the stereo test, with the magnitude being greater around the fixation plane. As observed in Expts. 3.2 and 3.3, measured stereo-thresholds were highest within the range of distances that resulted in increasingly greater depth bias. It must be stressed that the flankers were always positioned in the fixation plane (i.e. had no disparity). Previous findings regarding induced bias have been caused by flankers which carried disparity (i.e. had different depth plane from the test) (Fox and Patterson, 1981; Westheimer, 1986). Such disparate flankers can be argued to distract the position of the assigned reference plane(s)

in the stimulus (Westheimer, 1886). When that happens, positional bias is seen as a mechanism adapted by the visual system to realign the reference plane for discrimination. Still, other authors suggest a mechanism of “preferential attention” and “figure-ground” processing to explain depth bias. In preferential attention hypothesis, spatial features nearer to the observer receive proximal attention, and therefore their location is resolved first by the visual system. Such a mechanism is suggested to have developed as an adaptive response to proximal stimulation. The ‘figure-ground’ theory posits that when a stimulus is perceptually perceived as figure, the position of the test is judged to be on top (in front of) of the ground, and hence, closer in depth to the observer (Fox, 1970; Lehmkuhle and Fox, 1980). The effect is greatest near the fixation plane due to competing visual directions from the features in the stimuli (Fox, 1970). In this study, we attribute the front depth bias observed to the ‘front effect’ since the effect was great at the distances where crowding was maximal.

While presumably fixation disparity could account for some small changes in discrimination around the fixation in some of our subjects (Duwaer and van den Brink (1982; Mustillo, 1985), the consistency in the data set show that such an assumption cannot be tenable for all the observers. Duwaer and van den Brink (1982) explained that changes in threshold in near-horopter measurements may be due to increased ‘noise’ or ‘loss of sign’ (that is break in the ability to tell the depth direction of a test target). However, this noise effect would be absent or minimal for vertically arranged (horizontal disparities) bars and the range of distances and disparities tested (Farell et al., 2004).

Does the Flanker and Reference Bar Width Matter for Crowding?

The results of Expt. 3.5, where the width of the flanking bars was varied, revealed that depth discrimination thresholds under crowded conditions depended on the extent to which the test and the flanking bars matched in size (degree of similarity between them) (Fig. 3.5). Though no statistical significance effect was found, this was perhaps due to the difference in performance of the observers who demonstrated differences in the width sizes for peak

crowding. The few subjects used in the experiment and bias (especially AC results) mitigated against statistical significance, but not against the finding that width of the flankers influences crowding. Thinner flankers caused less crowding resulting in better stereo acuity. When the flankers were the same size as the test, stereo acuity was worse due to the increase in crowding and then subsequently decreased when the flanker widths were increased.

The results suggest that the neurons that process depth discrimination are subject to an interaction from other neural mechanisms (i.e. crowding), and thus sensitive to images of a particular size (Richards and Kaye, 1974). Feature component effects (i.e. shape and depth position) have been reported by Kooi et al. (1994) when they studied the similarities and differences crowding in 2-D Vernier tasks. Size effects can be also inferred from the study of Mitchell and O'Hagan (1972) that reported neurons most sensitive to optimum size vary from cell to cell, and from the results here, perhaps among individuals depending on the stereo sensitivity. Further psychophysical evidence for the presence of size detecting neurons can be deduced from an experiment by Parlee (1969) who measured the amount of masking produced by a single line of variable length on a single test line of a fixed length (2.82"). Her results indicated that the masking effect was greatest when the masking line achieved the same size as the test line, but the detectability of the test line increased as it was made larger. Again with the largest masking line, which was 1.7 times the length of the test line the detectability of the latter line was also increased in comparison to its detectability when the two lines were of the same length. The finding of this study fits the explanation that under conditions of maximal crowding, when the size of the test remains unchanged, reducing the widths of the flanking bars relieves crowding while increasing the flanker width will also result in less crowding and improved thresholds. It seems that the interaction of test and flankers are additive or pooled to produce improved performance. That is, depth information from the various parts of the stimulus was pooled in the centre in order extract an 'average' disparity for depth judgement (Richards, 1972; Mitchell and O'Hagan, 1972).

Such interactions will be consistent with discrimination in the central part of the fovea (10 to 20 min arc). A larger stimulus so that the edges fall outside the central fovea area will result in the inhibition of their signals. Such inhibitory effects may occur over wide area of the receptive field, with greater disparities than those used here (Richards and Kaye, 1974; Foley-Fisher, 1977).

On the other hand, other investigators posit a mid-level processing of signals based on Gestalt group factors as the more probable mechanism (e.g. Sayim et al., 2010; Deas and Wilcox, 2014). According to Gestalt grouping proponents, features in a stimulus are analysed and perceived as part of a group. From the results here, it can be reasoned that making the flankers thicker or thinner caused them to be perceived more distinctly from the test, which reduced the crowding effect and made the depth discriminability of the test easier. However, when the size of the test and the flanking bars were made similar, the stereoscopic system was unable to extract the disparity signals from the target pair with the same precision. By Gestalt explanation, narrowing or widening the size of the flanking bars to appear distinct from the stereoscopic test aided in ungrouping of the disparity cues in the stimulus and that improved performance. As suggested by Kooi and his colleagues, it seemed the visual system was responding to some compulsory grouping due to similarity in shapes (Kooi et al, 1994). The observation in this study is in good accord with the influence that Gestalt grouping cues could have in spatial vision processing, and hence may have played a role in the depth crowding reported here. Based on our results, we suggest that a disparity pooling and Gestalt grouping cues are involved in the depth discrimination of the precise configuration used in the experiments.

The effect could further be interpreted as due to a luminance modulation (flux) of the test and flanking bars (Kumar, 1995; Kumar and Glaser, 1995). Kumar and Glaser (1995) found that at the optimum crowding distance, stereo-thresholds reduced when the luminance of the test was greater than that of the flankers. With further increase in the relative luminance of the test, the performance of their observers eventually deteriorated. The effects as was

reported by Kumar and Glaser (1995) was not because of the difficulty in seeing the features which were individually clearly visible for all the luminance tested but due to the luminance modulation of the features in their stimulus. In our configuration, wider flanker widths will potentially have more luminance energy across the stimulus relative to the test, thus potentially brighter than the test. The differences in the luminance of the test and flankers can be argued to have aided in test-flank border or edge detection, and hence facilitate the spatial discrimination (Comerford, 1974; Kumar, 1995). The lower threshold recorded for thinner flankers (i.e. less energy) could be due to the high-contrast of the test which will have greater salience (pop out), and therefore evade crowding (Richards, 1972; Felisberti et al., 2005). Therefore, the results found here is succinctly summed by Kooi et al (1994) *“similarity in the component orientations (i.e. shape and depth) of the test target and flanks appears to be the primary factor determining the degree and extent of spatial interaction; the flux of the flanks seems to be secondary at best”*.

The reference bar width tuning experiment (Expt. 3.6) is consistent with the previous results and demonstrates the reliance of the stereo-depth mechanism on the reference bar for discrimination (Westheimer, 1979b, Kumar and Glaser, 1992a). Changing the width of the reference bar only produced a slight elevation in threshold at wider widths. The leveling of threshold for wider bars reveals that the width of the reference bar had little or no influence on the magnitude of the crowding, but rather the information provided by the bordering edge to the test bar was the important cue for depth discrimination. This is in agreement with Butler and Westheimer's (1978) report that adjoining contours will affect depth discrimination thresholds only when they surround the test, but produce no crowding effect when placed around a reference. The slightly higher thresholds recorded using thinner reference bar widths could be attributed to the ineffectiveness of the visual system to use the smaller size of the reference bar for relative judgment due to the large difference in size of the test and the reference bar, which effectively reduced the contrast of the reference bar.

When the foregoing discussions are taken together, there is evidence to reason that the mechanisms that subserve the processes of crowding in stereopsis could contain a number of different mechanisms selectively tuned to different bar widths, but these mechanisms operate in parallel (possible matching or coupling) as suggested by Wilson and Bergen (1978).

CONCLUSIONS

By employing a configuration that permitted the production of maximum crowding, we have experimentally characterized the influence of interacting features on depth discrimination threshold.

This study has demonstrated the influence of surrounding flanking bars on a stereoscopically localised test in a 'depth-crowding' interaction. We report that flanking bars with similar features to a test target can affect depth discrimination threshold, and their interaction depends on a number of factors including separation and stimuli dimensions. It was clear that, maximum crowding was produced at a specified test to flanker distance close to the plane of fixation. The results revealed that the test to flanker separation required to produce optimum crowding was 1 to 2 min arc. Crowding was found to decline sharply to reach baseline depth discrimination thresholds at 4 to 6 min arc distance where the flanking bars do not significantly interfere with depth discrimination. Observations for different bar crowding configurations (with and without a designated reference) were attributed to the action of the same processing mechanisms. These findings confirm previous results showing that depth discrimination thresholds are reduced in the presence of flanking contours.

Additionally, the findings are in good accord with the suggestion that crowding does not depend exclusively on stimulus spatial separation, but on the configuration of other spatial features. Though separation has long been known as the dominant factor underpinning depth-crowding, we have now demonstrated that the effect needs to be contextualised with

reference to the dimension (width), configuration of stimuli used and observer. There was a positive influence of flanker configuration, but not reference bar configuration on crowding. Our findings suggest that apart from the separation effects, other features of the configuration with respect to stimulus size (width) cannot be discounted when discussing stereoscopic depth-crowding. The magnitude of the crowding and accuracy of the depth discrimination depended on the extent to which the test and the flanking bars matched. Altering the width of the flanking bars to look thinner or thicker at the crowding distance was able to relieve the crowding.

The behavior of the interaction described in this study is attributed to local processing mechanisms of inhibition and spatial pooling, but Gestalt group factors (for thicker flanker widths) and contrast modulation (for thinner flanker widths) influenced the depth discrimination when flanking bar widths are varied which aided the visual system to perceptually ungroup the stimulus elements. The differences in performance among the observers could stem from the specialization required for depth discrimination than other acuity tasks, their depth discrimination experience and their subjective sensitivity to depth thresholds. But since the origin of crowding is known to be cortical, it is imperative that further investigation are conducted using stimuli configurations that mimic the characteristics of receptive field properties of neurons in the visual cortex by bypassing lower cortical centers to access more higher processing centers of the visual system.

CHAPTER FOUR

FURTHER INVESTIGATIONS INTO STEREOSCOPIC DEPTH-CROWDING OFF THE HOROPTER

INTRODUCTION

The horopter defines the spatial location of objects in the fixation plane that stimulate corresponding retinal points, and represents the locus of objects that appear to be fused binocularly (Ogle, 1953; Moses and Hart, 1987). Objects nearer or farther away than the fixation plane will stimulate disparate retinal points, causing binocular disparity (retinal disparity) in their retinal images leading to the perception of depth (Ogle, 1952; Blakemore, 1970). The general understanding is that thresholds for perceived depth discrimination increase with distance from the horopter (Rawlings and Shipley, 1969; Blakemore, 1970; Fendick and Westheimer, 1983; Westheimer and Truong 1988). However, Ogle (1952; 1953) first proposed that stereoscopic depth can be separated based on precise relative depth perception from small disparities (up to 10 min arc at the fovea), which he called patent or quantitative stereopsis, or depth perception from a large range (up to 10 deg) of diplopic disparities, which he called qualitative stereopsis (from about 15 min arc at the fovea). Subsequently, collective investigations (Blakemore, 1970; Poggio and Fischer, 1977; Marr and Poggio, 1979) have provided support for Ogle's distinction. Poggio and colleagues (Poggio and Fischer, 1977; Marr and Poggio, 1979) agreed with Ogle (1952; 1953), but further differentiated responses elicited with small disparity changes on or near the horopter which produced acute discrimination, and responses to large disparities off the horopter. Marr and Poggio (1979) predicted that the disparity range over which depth is processed is proportional to the receptive field size of the disparity coding mechanisms. The putative mechanism put forward to explain this observation posited optimal stimulation of neurons in the visual cortex which have positional requirements. Therefore, increment stereo-thresholds would correspond to depth information processed by disparity-tuned

mechanisms (Marr and Poggio, 1979). In that regard, Ogle's distinction in stereopsis is due to processing by a set of mechanisms tuned to process a restricted range of disparities around the fixation point and at farther distances off fixation.

Previous studies that measured thresholds off the horopter often used local stereoscopic test and reference targets. However, depth detection can be influenced by spatial context, when other objects are near the vicinity of the test and they interact. Test and flankers, which vary in their lateral separation, relative depth position and size may influence the stereo-threshold (Kooi et al., 1994). The influence of these factors in perceived depth discrimination outside the fixation plane has not been well investigated. The idea that lateral separation, relative depth separation, and different sized flankers can influence perceived depth discrimination of the test stimulus is in accord with a number of studies (Richards and Kaye; 1974; Butler and Westheimer; 1978; Lehmkuhle and Fox; 1980; Fox, 1981, Fox and Patterson, 1980 Mitchison and Westheimer, 1984; Westheimer, 1986; Kooi et al, 1994; Astle et al., 2014; Funke et al 2015). This present study overcomes a number of confounds in previous studies by coupling the effects of lateral separation and relative depth separation between the test and flankers. We employed a stereoscopic configuration that allowed optimum crowding (interaction) (where crowding is maximal), and manipulated several spatial features to investigate perceived depth and crowding off the horopter. We also investigated the sensitivity of the disparity detecting system to the dimensions of the stimuli based on a grouping hypothesis (Richards and Kaye, 1974; Kooi et al, 1994). The manipulation of these spatial features in the presence of crowding enabled the investigation of perceived depth and the possible underlying mechanisms when integrating disparities.

Psychophysical evidence from spatial discrimination tasks supports the view that optimum disparity detection is based on the relative disparities of adjoining targets (Westheimer and McKee, 1978; Mitchison and Westheimer, 1984, Westheimer, 1986; McKee, et al., 1990; Kumar and Glaser, 1992a). The perceived depth threshold could be regarded as the

difference between the absolute disparities of adjoining targets in the stimuli. While some studies have explored stereoscopic depth-crowding in features in the fixation plane based on relative disparity discrimination (Butler and Westheimer, 1978; McKee and Westheimer, 1980a), it is not clear what would happen when perturbing targets are positioned at different depth locations outside the fixation plane relative to the test, and the extent to which such configurations would exert influence on stereoscopic depth-crowding.

When the perceived depth of a stereoscopic test is considered, incremental discrimination thresholds are known to increase rapidly with increase in pedestal disparity (Ogle, 1953; Blakemore, 1970; Badcock and Schor, 1985; Westheimer, 1986; McKee et al, 1990, Siderov and Harwerth, 1993; 1995). However, when the stimulus consists of a test and reference/s presented at the same depth plane, i.e. if they are located in the same depth plane, it would be easier to locate the depth position of the test, and hence optimise performance (Ogle, 1952; Mitchison and Westheimer, 1984; Kumar and Glaser, 1992a; 1992b). For example, Mitchison and Westheimer (1984) showed that the stereo-threshold for a line test reduced by a factor of two when the reference surface was at the same depth as the comparison line or close to it, but increased when they were given opposite disparity. From the above studies, one can assume that the depth position of the reference, relative to the test is crucial for the visual system to extract the exact information for the depth location of the discriminable test.

When we consider not just moving the test/reference off the horopter, but the whole constructed stereoscopic stimuli (i.e. test, reference and flankers), the situation changes. Though a search of the literature does not readily yield any reported findings concerning this, Ogle and colleagues (Ogle, 1952; Marr and Poggio, 1979) suggested that the pedestal movement for a stereoscopic configuration will be subjected to processing by depth information channels for the range of disparities used. Other authors have adduced evidence that demonstrates that the perceived depth of a test object (e.g. a line) could be

influenced by the presence of background/flanking references not related to the task (Westheimer, 1986, Kumar and Glaser, 1992a, 1992b). In those studies, it was argued that the addition of flanking lines would reduce the incremental threshold if the observer learns to use the new information (e.g. from flanking bars) as depth cues. More recently, other authors have reported increases in discrimination thresholds when additional features are added to the stimulus, but ascribed the increases in threshold to the features acting as detractors (Parkes et al., 2001; Felisberti et al., 2005).

Studies by a number of authors (Butler and Westheimer, 1978; Mitchison and Westheimer, 1984; Westheimer 1986; Westheimer and Levi, 1987; Kumar and Glaser, 1992a) suggest that when targets are laterally separated by less than 15 min arc, changes in depth separations (test-flanker disparity) would affect the stereo-threshold assigned to individual features that are in the different depth planes. This effect can be observed in studies that presented flanking lines or bars at single depth in front of (Butler and Westheimer, 1978; Felisberti et al, 2005; Sayim et al 2008), or behind (Felisberti et al., 2005; Kooi et al., 1994; Sayim et al., 2008) the test stimulus. The flankers induced effects that either cause a decrease or increase in discrimination threshold. Investigation of flanker effects is premised on the work of Jeansch (1911) who first demonstrated that, the outer lines of three equidistance vertical lines from an observer at the onset, will appear to recede when the outer flanks are moved away from the observer. Other references can be made to a stereo version of the Craik-O'Brien-Cornsweet illusion, which showed how reference elements can influence perceived depth (Anstis et al., 1978), and Westheimer (1986) who demonstrated that displaced flanking lines off the horopter can act to influence the stereoscopic threshold.

Butler and Westheimer (1978) investigated how close flanking lines must be displaced in depth and still interfere with depth discrimination of a test bar in the fixation plane. Their subjects discriminated the depth position of a spatially displaced bar relative to the position of a fixed reference bar. They found that the flanking bars caused optimum crowding when

the flankers were at the same depth location as the reference (i.e. on the horopter). The crowding effect dropped-off quite rapidly from the fixation plane as a louver of flanking lines was increasingly presented off the horopter to about 0.5 min arc when the crowding effect reduced considerably. The effect was symmetrical around the horopter. They attributed the decline in threshold to reducing interference from the displaced flankers. They suggested that nearby similar targets activate the inhibitory regions of neurons tuned to the disparity of the test and thereby decrease the neural activity corresponding to discrimination. Butler and Westheimer (1978) concluded that signals that carry depth information are tuned to the horopter, but the area of the function is very narrow. Similar symmetric findings have recently been reported Astle et al. (2014) using Gabor gratings. Though the Butler and Westheimer (1978) study provides insight into the probable interaction between a stereoscopic test and displaced flanking bars off the horopter, the range of flanking bar disparity used was only up to about half a minute, so it not clear what would have happen if larger disparities than those used in their investigation are employed. For instance, Kumar and Glaser (1992a) suggested that induced effects from flanking bars due to their relative disparity will act to decrease the stereo-threshold, but the thresholds will subsequently rise with increasing disparity of the flanking lines. Such findings have been reported indirectly by some authors (Fox, 1970; Lehmkuhle and Fox, 1980; Fox and Patterson, 1981; Funke et al., 2015). Fox (1970) found that separating the interacting stimuli in depth will substantially modify their interaction. However, unlike Butler and Westheimer (1978) and Astle et al (2014) he found that, the effect was asymmetric around the fixation plane. When the flankers were displayed behind the test, the interaction declined as a monotonic function of the relative depth separation. However, when their relative depth position positions were reversed and the flankers appeared in the depth plane in front of the test, the magnitude of the interaction tended to increase. More recently, in another investigation not directly related to stereoscopic crowding, but relevant to it, Funke et al. (2015) studied how introducing stereoscopic disparity to some elements of visual displays can be used to declutter symbols in air traffic

displays. Using a dichoptic presentation, their subjects were required to correctly identify a set of letters surrounded by compatible flankers. The flankers were made to appear at depth positions measured to be 1mm, 8mm in front of, or behind the test letters, and on the same depth plane as the letters. They observed asymmetric flanker effects which were consistent with the finding by Fox (1970). Their findings revealed that response time (RT) to letter recognition was elevated when the test and flankers were in the same depth plane. The effect was eliminated when the flankers were made to appear behind the letters. On the other hand, when the flankers were made to appear slightly in front of the letters, the effect also dissipated, but was restored when the flankers were placed farther in front of the letters.

In a similar masking experiments Fox and Patterson (1981) demonstrated similar influences of depth separation and lateral interference. Their subjects made a forced-choice resolution task (i.e. subjects had to respond to the direction of the gap in the C) and clarity ratings of a briefly presented Landolt C test stimulus and a continuously visible circular annulus. Consistent with previous findings, they found that when both the test and interfering annulus were in the same depth plane, considerable interference in recognising the direction of the in the C was produced. The interference effect was optimum at close separations, and showed a monotonic decline when the lateral separation between the outer contour of the test and inner contour of the annulus was increased. The relative depth separation between the test C and the interfering annulus has substantial influence on the magnitude of the interference. When the test stimulus appeared in the depth plane behind the inducing annulus (i.e. farther from the observer), the magnitude of the interference also tended to decline following a monotonic function. When the depth test appeared in the depth plane in front of the annulus, the inference effect was restored and thresholds increased. Their finding agrees with the findings by Fox (1970) and Funke et al (2015). This asymmetry in perceived depth discrimination has been attributed to a 'front effect' cue in spatially close targets (defined as perceiving a target which occupy different depth planes from its

neighbouring similar targets, with competing visual directions to be closer to the observer). It is suggested that front effects might reflect bias of the visual system to give preferential treatment to the stimulus that is in front of another and closer to the observer due to the 'figure-ground' perception by the stereoscopic system (Fox, 1970; Lehmkuhle and Fox, 1980; Fox and Patterson, 1981; Astle et al, 2014). In the present study, we investigated the possible influence of front effect for 'depth bias' of the test stimulus, on the putative bias mechanisms underlying stereoscopic depth-crowding.

Based on the reported finding of Jeansch (1911) and on his own study (Mitchison and Westheimer, 1984), Westheimer (1986), used vertical test lines and flanking lines displaced up to 100 sec arc in depth to study induced depth effects by the displaced flankers. He found that flanking lines induced an effect they termed 'salience' (defined as the depth attraction or repulsion between targets that occupy different depth planes) (Ogle 1962; Mitchison and Westheimer, 1984). Westheimer (1986) demonstrated that the depth discrimination threshold of the test lines relative to displaced flanking lines increased when tests and flanking lines carried similar disparities (i.e. displayed in the same depth direction), but decreased when the standing disparity between the test and flanking lines (target-flanker disparity or depth separation) and lateral separation were made larger. For one observer, the threshold reduced from 13.4 to 10.8 sec arc when the test-to-flanker lateral distance was changed from 12 to 24 min arc and flanker disparity changed from 50 to 100 min arc. The flanking lines induced a positive directional influence (i.e. same depth direction) as test line. The effect was symmetrical around the fixation plane. Westheimer (1986) concluded that at small test-flanker separations, there is induced salience 'attraction', but 'repulsion' at large test-flanker separations. However, the results of the Westheimer (1986) study co-varies lateral distance and depth separation, making it difficult to differentiate between flanker effects due to lateral separation in the same depth plane or separation in different depth planes. Mitchison and Westheimer (1984) had argued that when the flanking lines are

displaced, they distract the locus of the reference plane. Saliency therefore becomes a corrective mechanism which the visual system adopts to realign spatially displaced features when assigning depth values. In a later study, Westheimer and Levi (1987) used horizontal-line-and-point configuration and found similar finding as Westheimer (1986) with saliency attraction ranging between 3 to 8 among their subjects, but in addition demonstrated the interaction was positively affected by contrast reversals and length variation of the test.

In the above reported studies, two possible competing hypotheses have been posited to explain flanker effects, a 'front effect' (Fox, 1970) or 'saliency' mechanism (Ogle, 1962; Westheimer, 1986; Westheimer and Levi, 1987). Both mechanisms have been used to account for the elevation in thresholds when flankers are displaced in front of the test. According to some authors (Ogle, 1963; Mitchison and Westheimer, 1984; Westheimer, 1986) saliency creates a somewhat hypothetical depth cue that visual system uses to detect the depth position of the test. Authors like Fox and colleagues (Fox, 1970; Lehmkuhle and Fox, 1980; Fox and Patterson; 1981) also suggest front effect cues to explain the elevation in stereo-threshold due to competing visual direction at close separations. What is similar in the operation of these two mechanisms is that thresholds correspondingly increase at small separations for both saliency and the front effect. Since saliency is a perceptual mechanism, it seems front effects are the resultant physical attribute of the saliency. Nevertheless, this assumption has not been explored in any study concerning stereoscopic depth-crowding. In this present study, we investigated the assumption that increasing saliency (i.e. due to increasing relative test-flanker depth separation) will duly increase front effects to induce corresponding depth bias of the test stimulus in the depth direction of the inducing flankers.

Depth detection has been shown to be affected by the dimensions of the stimuli (Richards and Kaye; 1974; McKee, 1983; Kooi et al, 1994; Livne and Sagi, 2007; Deas and Wilcox, 2012). Results adduced in the previous chapter (i.e. Chapter 3) suggest that the width of flanking bars is an important feature in resolving disparities, and could aid in reducing

crowding. Here, we tested the same hypothesis on incremental depth discrimination thresholds. The present findings and findings from other studies (Andriessen and Bouma, 1976; Wood, 1983; Nazir, 1992; Kooi, et al., 1994; Farell, 2006) lead to the suggestion that crowding is optimally produced when a test and nearby objects have similar sizes. Stereo-thresholds however reduce when flankers have different widths due to possible involvement of mid-level compulsory grouping mechanisms which increase the saliency or 'pop out' of the test (Kooi et al, 1994; Felisberti et al., 2005; Legge et al., 2007; Sayim et al., 2008). If indeed flanker width is an importance parameter to be considered by a putative stereo mechanism, then the stereoscopic mechanism must be interested in the flanker size in any interaction off the horopter. Presently, we do not know of any studies detailing this task we are presently investigating in the stereoscopic domain.

There is a general belief that integrative depth information processed by relative disparity mechanisms have useful clinical implications (Neri et al., 2004; Levi and Carney, 2011). There is also the prospect of revealing the neural mechanisms that encode for spatial discriminations (Richards, 1977, Blakemore, 1970; 1992; Andrews, Glennerster and Parker, 2001) and further our understanding of stereo mechanisms. Indeed, Marr and Poggio (1979) proposed the resolution of ambiguities in random dot stereograms (RDS) using relative disparities, while Julesz (1971) proposed disparity interaction to address the correspondence problem in the stereo task. The present experiment extend this interaction in the domain of stereoscopic depth-crowding. The dearth of information on the spatial scope of stereoscopic depth-crowding defined by displaced stimuli supports the present study designed to investigate these interactions by measuring depth discrimination thresholds. Simply, because crowding is an integrative process, but places a sensory limit on the ability to discriminate the spatial location of a test due to the presence of nearby flankers, the interest here is to study disparity interactions that will act to release or increase crowding, whilst examining the mechanisms that mediate those disparity interactions.

Rationale

Whilst previous studies provide some evidence that the sensitivity of the disparity detecting system can be influenced by relative disparity cues of flanking targets not directly related to the task, the role of flanking or crowding elements in stereoscopic depth-crowding must be disentangled. On reviewing the literature, only a few studies that detail these effects can be cited. The present investigation was therefore undertaken to characterise how stereoscopic crowding and perceived depth are affected by spatial interaction off the horopter. The general investigative assumption is that, if depth information is processed by a set of mechanisms tuned to a restricted range of disparity, then incremental stereo-threshold measured for relative disparity integration has the prospect of revealing disparity tuned mechanisms (Richards and Kaye, 1974; Marr and Poggio, 1979).

We therefore performed experiments to clarify and address a number of issues. For instance, in the Butler and Westheimer (1978) study, they demonstrated release from crowding when the flanking louver elements they used were presented at single depth in front of the horopter. However, the disparity range used was within a few seconds of arc, so it is not evidently clear if the same mechanism that codes for the disparity tuning function they found would operate if a larger range of disparities is used, and the flankers presented farther outside the function tuned around the fixation plane. There is also the suggestions that the horizontal louver pattern used in that study may not have been a good stimulus (Astle et al., 2014), due to possible false matching of the retinal images. In this study, we avoided this potential problem by using flankers similar to the test in both orientation and dimension. In a series of experimental designs, we characterized the influence of test-flanker disparity (test-flanker depth separation) for a broader range of disparities. We hypothesised that, if indeed precise stereoscopic discrimination operated around a region around the plane of fixation and has a narrow tuning function, crowding would decrease when the flankers are displaced within a small distance outside the fixation plane, but the threshold

would increase with a larger range of disparities outside the scope tuned to the fixation plane based on the mechanism of salience (Gogel 1963; Mitchison and Westheimer, 1984; Westheimer, 1986).

In Westheimer's (1986) study, distance (lateral separation) and flanker disparity (test-flanker depth separation) were co-varied, making it difficult to attribute the observed effect to either the disparity of the flankers or distance factors. In this study, we delineated the distance and disparity component in an attempt to examine the influence of both on the interaction. We predicted that the discrimination threshold would increase when the lateral distance between the test and inducing (displaced) flankers are small due to lateral interference and 'salience attraction', but decline when the distance between them is increased due to decreased interference and 'salience repulsion' between their edges.

Front bias effects have been reported in depth discrimination tasks, and are thought to underline asymmetry in the stereoscopic system (e.g.s. Lehmkuhle and Fox, 1980; Fox and Patterson; 1981). The effect has mainly be explained based on 'front effect' by targets that occupy proximal depth planes. 'Salience' has also been adduced to explain perceptual effects between targets that occupy different depth locations in space. Here, we propose that the "front effect" maybe perceptually driven, a resultant physical attribute of the salience mechanism. We examined this proposition by predicting that inducing flankers (due to salience) would increasingly cause 'front bias' effects of test in the depth direction of the flankers (due to the resultant front effect cues by the flankers).

Further, we questioned whether it is awareness of the test-flanker configuration on the horopter which is required to produce crowding, or, if the relative change in the stimuli (all features) depth location would still drive the crowding effect off the horopter. We achieved this by measuring the depth discrimination threshold for the incremental disparity of an optimum crowded stimuli, and for a configuration that produced none or little crowding. We

show that the depth discrimination threshold for the stimulus pedestal systematically decreases when presented in front of the test with increasing pedestal disparity until they are sufficiently presented outside the fixation, possibly outside the function tuned to the horopter, before the thresholds rise steadily.

Lastly, we tested the proposition that incongruent test - flanker dimensions would aid in ungrouping the stimuli, and therefore affect the discrimination threshold for a test stimulus when the perturbing flankers are located off the horopter (Andriessen and Bouma, 1976; Kooi et al., 1994).

We believe that knowledge of the characteristics of disparity interaction relating to stereoscopic depth-crowding off the horopter may reveal important aspects of the processes underlying spatial discriminations. The approach to this study was that crowding is an attribute of contextual processing of disparity features embedded in a configuration, each of which may contribute to the threshold. Therefore, this part of the study focuses on elaborating on the influence of individual disparity features in the stimulus on stereo-threshold, with the possibility of reducing in crowding. This study can therefore be regarded as a tangible link between earlier studies which detailed interactive aspects of stereoscopic configurations on the fixation plane, spatial interactions off the horopter, and less explored stereoscopic crowding off the horopter. There is reasonable belief that detailed characterization in our experimentally designed stimulus within the range operationally permissible by our apparatus will constitute a step towards understanding a more global disparity processing.

METHOD AND APPARATUS

The methods employed in this Chapter are similar to the one used in Chapter Three, and described in detail elsewhere (Chapter Two). This section describes additional and methodological variations peculiar to individual experiments in this chapter.

Stimuli

Stimuli were generated and presented on a high resolution single, monochromatic video monitor using a stereoscopic video system. The basic stereoscopic stimuli for the experiments were two relatively thin, luminous vertical targets (test and reference bars) (broad-band) displayed with the test bar directly below the reference and separated by a small spacing that varied slightly between observers. Flanking bars were symmetrically placed around the test only. The original dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. However, in the experiment where the objective was to determine the influence of the widths of the flanking bars, the widths of the flanking bars were systematically varied from 0.5, 1, 2, 4 to 6 min arc. Binocular disparity of the test bar was produced by introducing small lateral pixel offsets of the bar tests in opposite directions and presented, in an alternate non-interlaced fashion, to each eye through an electric shutter goggle system. Binocular disparity of the reference and flankers was produced by introducing shifts in image to each eye through a shutter goggle system (i.e. programmable delay of the horizontal sweep of the video image of one eye). On any one trial, the test bar was presented in randomly interleaved trials (mixed by alternating between them) at one of 8 possible disparities (8.5, 17, 25.6, and 51 sec arc) either in front of, or behind the fixation plane, and one on the fixation plane. The pedestal depth positions used were 0 (at the plane of fixation), 0.5, 1, 2 and 4 min arc in both crossed (positive) and uncrossed (negative) depth directions. The pedestal disparity was quasi-randomly varied between runs, but not between trials. Prior to each trial, observers binocularly fixated on a central fixation spot of 30 sec arc displayed in the middle of a pair of vertical Nonius bars,

1.4 min arc wide and 7 min arc long. This ensured that bifoveal fixation was aligned to the plane of the monitor screen. The Nonius bars and fixation point were surrounded by a thin square frame of size 28 min arc and were presented just prior to a trial and disappeared when the test stimulus was presented (see Chapter two). The ambient laboratory room lighting conditions were kept low, to avoid glare from the monitor screen and ensure the stimuli and Nonius display were clearly visible to observers.

A custom written Matlab (version 10) script was used to create the stimuli and control presentation. Parameters for the stimuli and the required configuration for each experiment were specified in a programmed condition file and are described in the experiments described herein.

Subjects and Visual Condition

In all, five adults observers were recruited for the study (SO, AC, VO, PI and JO), and at least three participated in each experiment. Three were naive subjects. All observers were staff and students of ARU, including the author. Participants had normal visual acuity of 6/6 or had their vision corrected to normal levels using conventional glasses or contact lens. Stereoacuity (less than 30 sec arc) was measured clinically with the TNO stereotest (Lameris Ootech) (Fricke and Siderov, 1997) in each of the participants. All observers were well practiced for making relative depth discrimination judgements, and had performed several thousands of trials prior to the actual data collection.

Procedure

All experiments were performed at a distance of 13.5m measured from the center of the monitor display to the observer. Observers positioned the shutter goggles as required and viewed the monitor display through natural pupils (wore glasses if required), while maintaining their head position in the primary gaze. The stimulus was presented for 300 msec at a self-timed rate. The psychophysical procedure of a single exposure, forced-choice

paradigm was used to collect data. Observers were instructed to indicate whether the test (bottom bar) appeared in front of, or behind the reference (top) bar by setting a response box. During a short response period, immediately following the presentation of the stimulus, observers pressed the appropriate response button to indicate that the relative depth of the test stimulus. In each trial, the test could appear with either crossed or uncrossed disparity or no disparity, relative to the reference. However, observers were allowed to choose only between crossed or uncrossed responses. Catch trials were introduced to assess depth direction bias. Immediate feedback was provided by a high and low pitch sound for correct and incorrect responses respectively, and no sound when the test had no disparity. At the end of the specified number of trials, the data file for the experiment was completed with the summary statistics for the experimental session. The required parameters for each experiment run was specified in a programmed condition file. Before each trial, observers were instructed to use the Nonius display, which preceded the stimulus, to ensure their subjective eye position was aligned with the plane of the monitor was. They were instructed to wait until the upper and lower Nonius bars appeared aligned and then to press the start button to initiate the test stimulus display.

Data were collected during experimental sessions of up to about 1-2 hours per day. At least 150 responses were obtained for each data collection run. Before actual data collection commenced, observers were trained on the simple two bar stereoscopic stimulus to achieve stable thresholds.

Experiments 4.1A and 4.1B

Expts. 4.1A and 4.1B were performed to determine the influence of test-flanker disparity (i.e. relative depth separation) on crowding. In other words, we measured how close the disparity of flankers must be to the test and still interfere with depth discrimination of the test bar. Prior to this, we had measured the test-flanker lateral separation on the fixation plane where significant crowding was produced for each participant (see Chapter 3), and found that

optimum (i.e. maximal) crowding occurred for a test-flanker separation of between 1-2 min arc. As a common feature for all observers, at 2 min arc test-flanker separation, we found significant threshold elevation of between a three to eightfold increase relative to the unflanked thresholds. To ensure the effect of test-flanker disparity on crowding was effectively measured, a common test-flanker separation of 2 min arc (referred to as the Optimum Crowding Distance (OCD)) was used in this experiment (see Fig 4.0 (4.1A)). As is the case in Chapter 3 the test and reference bars were aligned in a bottom-top configuration respectively and flankers symmetrically placed around the test only, at the specified test-flanker distances. To tune the disparity of the flankers to that of the test, in any one experimental session, the test-flanker separation was held constant while the disparity of the flankers (depth separation) was changed. In separate runs, the flanking bars were presented with different single disparities in front of the test ranging from 0 to 2 min arc. Trials with different disparities of the test bars as described were presented relative to the reference target, while the flankers disparities were changed in between runs (quasi randomised) and a series of responses elicited. For all trials, the reference bar always appeared in the fixation plane.

In order to further examine the effect of the test-flanker disparity on the depth discrimination threshold, while releasing the influence of flanker-test separation, Expt. 4.1B (see Fig 4.0 (4.1B)) was conducted with a larger test-flanker separation. We have shown that on the horopter (in Chapter Three), when the test and flankers are separated by 6 min arc, little or no crowding was evident. Therefore, in Expt. 4.1B, the test-flanker separation was fixed at 6 min arc (referred to as the Least Crowding Distance (LCD)) and for any experimental session, the disparity of the flankers was changed from 0 to 4 min arc. Larger test-flanker separation of up to 18 min arc were also tested for two observers. Larger distances allowed for larger disparity offsets of the flankers to be tested off the horopter.

In accompanying control trials for Expts. 4.1A and 4.1B, similar flanker disparities were presented behind the plane of fixation, and also randomised between crossed and uncrossed disparities in interleaved trials. Randomising the flanker disparities addressed the question as to whether the fixed depth location of the flankers in front of the test possibly provided a non-stereoscopic (i.e. convergence) cue to the visual system prior to the brief display of the test bar.

Experiments 4.2A and 4.2B

The stimuli used in Expts. 4.2A and 4.2B were the same as those used in Expts. 4.1A and 4.1B respectively. In Expt. 4.2A (Fig 4.0 (4.2A)), the test-flanker separation was fixed at 2 min arc while for any experimental session, the whole stimulus was given single incremental disparities ranging from 0 to 2 min arc in the crossed direction in front of the fixation plane. The comparative Expt. 4.2B (Fig 4.0 (4.2B)) involved the same configural arrangement but the test and flanking bars were separated laterally by 6 min arc. Thereafter, for any one experimental session the disparity of stimulus was changed from 0 to 4 min arc and presented at a single disparity in front of the horopter for each series of trials. The task of the observer remained the same, to respond as to the perceived depth of the test bar in front of or behind the reference.

Other Control Experiments

Experiments 4.3A and 4.3B

In Expt. 4.3A (Fig 4.0 (4.3A)), the configuration arrangement remained the same as used in previous experiments, except that the flanking bars were now fixed in the fixation plane. Thus, the flanking bars had no disparity, and only the stereoscopic pair of test and reference bars were displaced at a single depth in front of the fixation for any one experimental session (i.e. measured increment threshold depth for the test and reference bars). The crowding distance of 2 min arc was maintained and the stereoscopic pair presented at depth pedestals

ranging from 0 to 4 min arc. Observers maintained fixation using the fixation spot of the Nonius stimuli.

In Expt. 4.3B (4.0 (4.3B)), the flanking bars were omitted and only the stereoscopic stimulus pair consisting of test and reference given pedestal disparity and moved out of the fixation plane. The vertical separation between the test and the reference bars was maintained at each observers best determined separation. In separate trials, the stereoscopic stimulus was displayed at single disparity in front of the fixation plane ranging from 0 to 4 min arc.

Experiment 4.4

In Chapter Three, we found that changing the width of the flanking bars improved depth discrimination of the test. In this experiment, (Fig. 4.0 (4.4)), we inquired if changing the width of the flanking bars when positioned off the horopter will influence the discrimination threshold, and if the change will scale with the depth location of the flanking bars. In order to avoid and overlap of the flankers with the test stimulus when varying flanker width the flanking bars were fixed at a test-flanker separation of 6 min arc. Different runs were conducted depth locations of 1, 2 and 4 min arc of the flankers disparity in front of the test during which the width of the flankers were altered. As in previous experiments, observers indicated whether the test appeared in front of, or behind the reference. Initial fixation was controlled through the use of the Nonius display which always appeared prior to each trial.

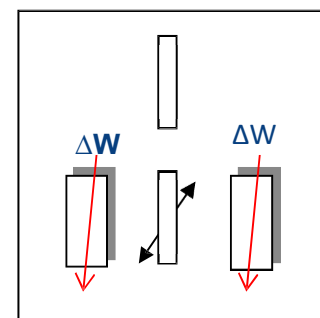
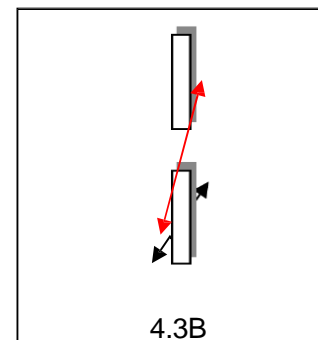
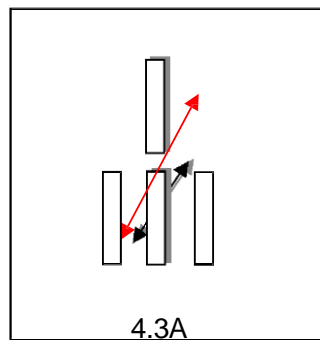
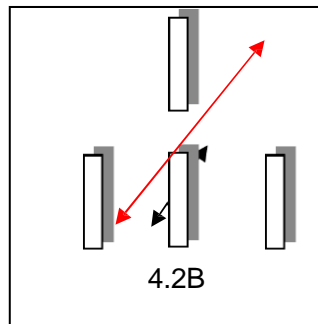
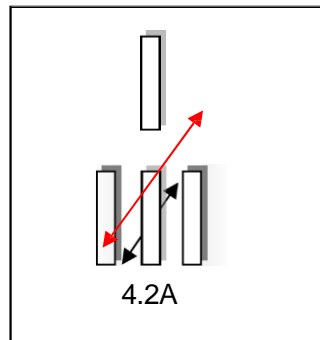
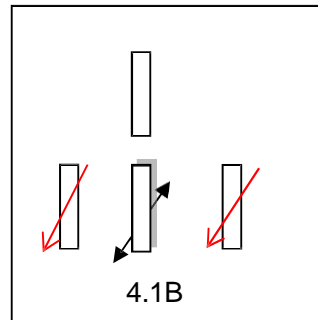
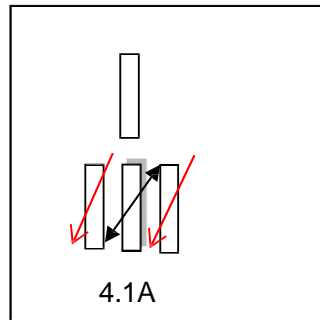


Fig. 4. 0. Test conditions for the Experiments are depicted in each of the panels. In Expts. 4.1A and 4.1B, to determine effect of test-flanker disparity on crowding, the flankers were fixed at the OCD and LCD respectively and only the flankers were moved in depth as depicted by the arrows. In Expts. 4.2A and 4.2B, to determine the incremental disparity threshold of stimulus, the configuration was the same as used in 4.1A and 4.1B except that the whole stimulus was given disparity and moved out of the fixation plane. Expts. 4.3A and 4.3B determined the discrimination threshold for the pedestals of the stereoscopic pair. In (4.3A), no flankers were present, while in 4.3B, the test-flanker distance was fixed at OCD. Expt. 4.4 tested test-flanker dissimilarity on incremental threshold for the non-crowding stimulus.

Analysis

Thresholds were calculated by first constructing a frequency of seeing curve from the correct in front responses which were stored in a data file during trials. The data was then fitted with a probit function (Finney, 1971) to compute the depth discrimination threshold (see Chapter Two) by estimating the semi-interquartile range (≈ 0.675). That is, the disparity for which the proportion of trials that occasioned between 50% - 75% of correct in front response from the psychometric functions was used as the threshold. In the graphs of results presented, each data point plotted represents an average of 300 responses. Error bars indicate the magnitude of ± 1 standard error (SE) of the mean.

Repeated Measures Analysis of Variance (ANOVA) was calculated to determine differences in the strength of the effect of depth separation (including a condition when the flankers were not on the fixation) and lateral separation when indicated on depth discrimination thresholds. However, the case has been made in Chapter 3 that, the purpose of the experiments here was to measure depth discrimination thresholds through constant stimulation, and plot discrimination threshold for psychophysical inference. Therefore, results of the statistical significance *p value* must be looked at in comparison to graphical presentation of data, ratios or main performance (Twa, 2016) as the magnitude of the effects measured may be hidden by the fewer and bias associated depth discrimination tasks.

Estimation of Depth Bias

In the crowding experiments as described, the configuration involves a reference and test bar in top-bottom configuration. At the outset, two flankers are laterally positioned around the test target at the fixation plane and equidistant from the observer. The test is then displayed at random in one of eight disparate positions, either in front of, or behind the fixation plane, and one in the same plane of the fixation in an interleaved manner. Observers respond to the depth position of the test relative to the reference. In subsequent runs, the flanker are moved to different depth positions in front of the fixation in a quasi-randomised

fashion while test and reference always appears at the fixation plane. Data for an aggregate of 300 trials at each flanker depth position are used to construct a probit fitted frequency of seeing curve for correct in front responses only. Flanker effects in causing bias in discriminating the depth direction of the test relative to the reference are determined with respect to each flanker depth position. Induced depth bias is calculated as the shift in the mean of the fitted psychometric function. The shift in the mean computes the position the test needed to be moved either in front of, or behind the reference bar to achieve co-planarity (i.e. align with the reference (Westheimer, 1986)). Therefore, it can be regarded as an estimation of the point of subjective equality (PSE). This method is similar to the 'annulling' methods employed by Westheimer (1986), the only difference being that study flankers bias effects caused by flanker depth were annulled by presenting one of two equal and opposite disparity before difference in means of two subsequently constructed psychometric functions were used to calculate induced changes in the depth direction of the test target.

RESULTS

Expts 4.1A and 4.1B: Disparity Tuning of the Flanking Bars to Crowding (Influence of Relative Depth Separation on Crowding)

Experiment 4.1A

The results of all five observers are shown in Figure 4.1A, where stereo-thresholds are plotted as a function of test-flanker disparity. For all participants, stereo thresholds consistently revealed a function which shows a systematic reduction in threshold from the fixation plane to unflanked levels with increasing crossed flanker disparity (i.e. flankers closer to the observer than the test target), until the flankers were displaced to about 0.5 min arc (for AC, PI and JO) or 1 min arc (SO and VO) from the fixation plane. Subsequently, presenting the flankers with greater disparities outside of the fixation plane (i.e. beyond 1 min arc), yielded an elevation in stereo-thresholds comparable to thresholds in the fixation plane.

Accompanying control data for uncrossed flanker disparities for three observers (SO, AC, VO) revealed that the resulting function was symmetric around the horopter, but stereo-thresholds were generally lower when the flankers were presented behind the fixation plane. For one observer (SO), thresholds were 32 and 40 sec arc and 96 and 100 sec arc at 1 and 2 min arc for uncrossed and crossed disparities, respectively. For the second observer (AC), stereo-thresholds were 13 and 38 sec arc and 12 and 45 sec arc at 1 and 2 sec arc for uncrossed and crossed disparities, respectively. For observer VO, stereo-thresholds were 45 and 64 sec arc and 60 and 92 sec arc at the same flanker depth positions.

In the randomised trials (i.e. where the flanker disparity was presented either in front of behind the fixation plane at random), for observer VO stereo-thresholds were lower compared to only crossed positions, but for SO and AC, thresholds were lower compared to both crossed and uncrossed positions. In all observers however, the disparity tuning showed a similar trend in the function for crossed, uncrossed and randomised trials. The one-way ANOVA calculated revealed that there was no statistically significant effect of test-flanker depth separation on discrimination [$F(4, 20) = 1.127, p = 0.372$].

Experiment 4.1B

The results of all five observers are reported in Fig. 4.1B, showing stereo-thresholds measured as a function of test-flanker disparity. As the individual and averaged data shows, in contrast to the crowding stimulus, stereo-thresholds do not reveal a reduction around the fixation, but rather a systematic rise with increasing crossed flanker disparity. The crowding effect dropped slightly for some observers beyond 2 min arc disparity.

The corresponding control trials which measured the sensitivity of the stereo system to uncrossed flanker disparity revealed individual differences. Data for observers (AC, VO) indicated that stereo-thresholds were generally lower with uncrossed compared to crossed disparities, but for one observer (SO) who recorded higher thresholds for uncrossed

positions. For the randomised trials, stereo-thresholds were generally lower in all observers compared to discrete crossed or uncrossed runs yet showed a similar function (Fig. 4.1A (for observers SO, AC and VO). A one-way repeated measures ANOVA revealed that effect of test-flanker relative depth separation (including a condition when the flankers were on the fixation) on depth discrimination thresholds were not statistically significant [$F(4, 20) = 1.878, p = 0.154$].

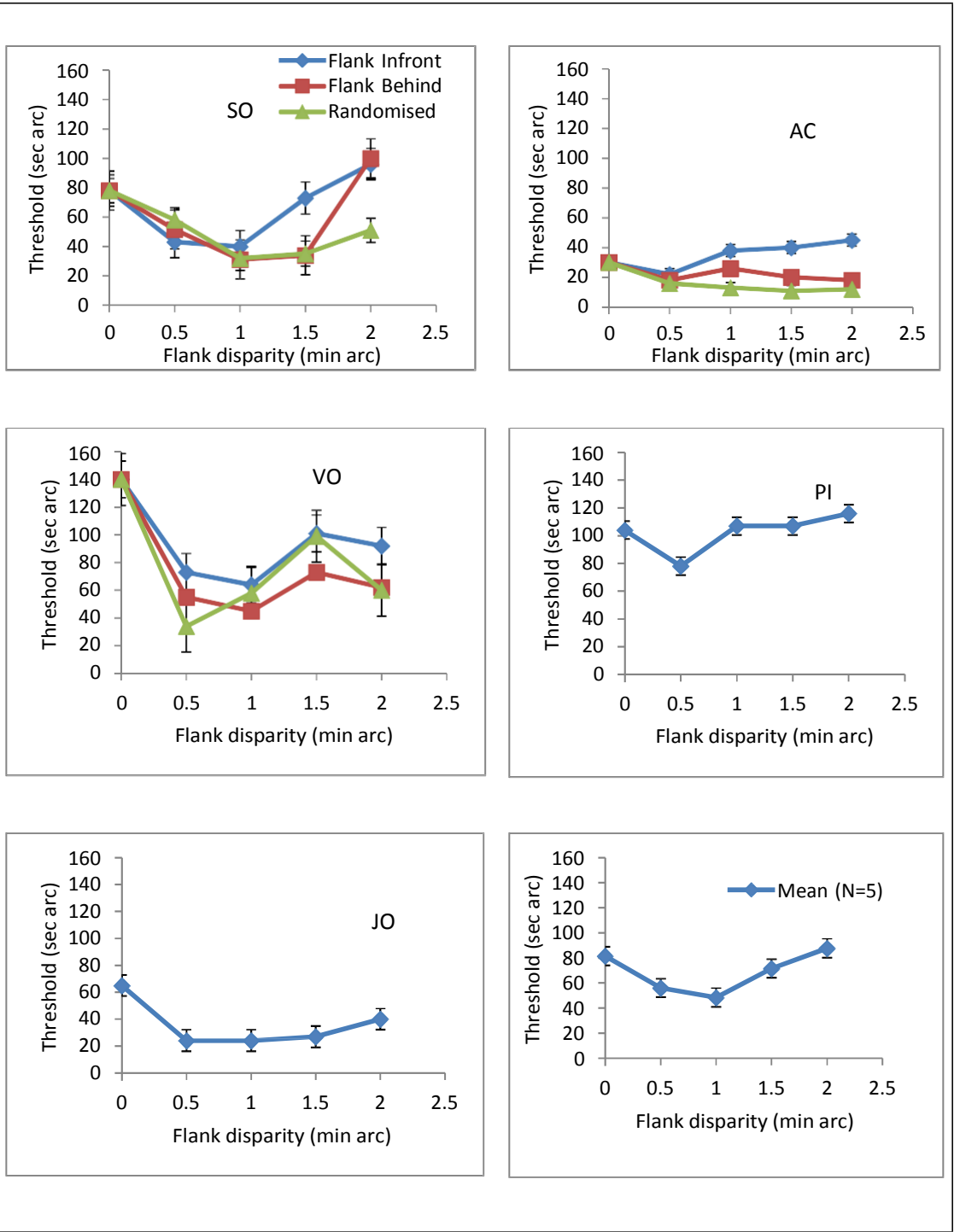


Fig. 4. 1A Expt. 4.1A. Influence of Test-Flanker Disparity for the Crowding Stimulus.

Each panel shows, for each individual observer, stereo-thresholds (sec arc) for the test in the presence two symmetrically placed flankers at the OCD plotted as function of the test-flanker disparity (min arc). The colours in the first three panels represent the control conditions, and indicate different depth direction of the flankers. The last panel (blue line) show data averaged across all five observers for infront flankers. The stereoscopic test was displayed with disparity relative to reference which appeared in the fixation plane, while the flanking bars were displaced in depth. Error bars indicate ± 1 standard error.

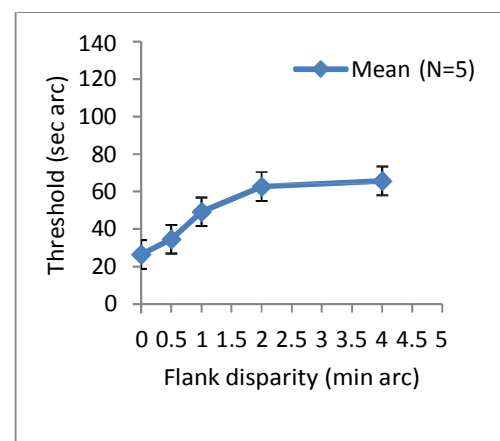
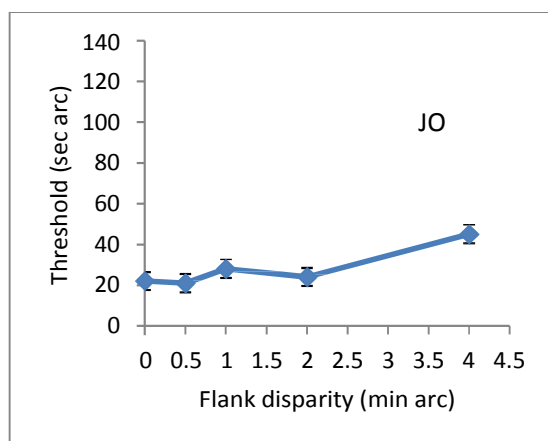
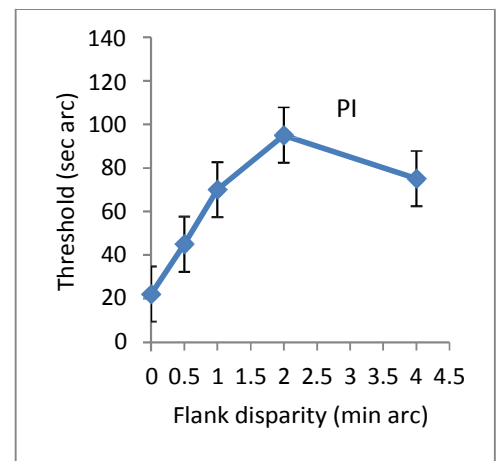
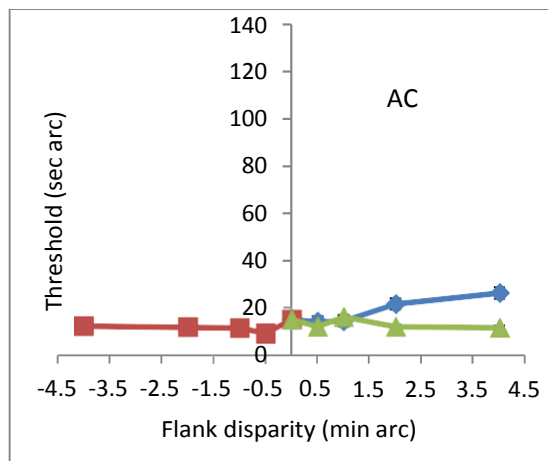
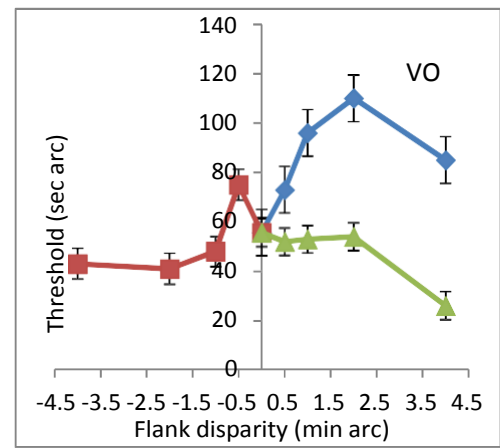
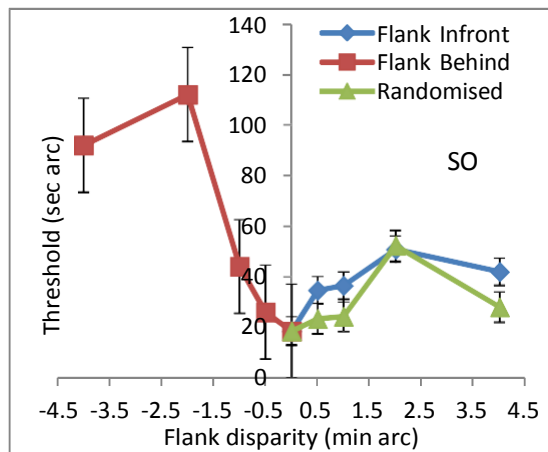


Fig 4.1B Expt. 4.1B. Influence of Test-Flanker Disparity for the Non-crowding Stimulus. Each panel shows for each individual observer, stereo-thresholds (sec arc) of the test in the presence two symmetrically placed flankers at LCD is plotted as function of the test-flanker disparity (min arc). The colours in the first three panels are control conditions, and indicate different depth direction of the flankers. The last panel (blue line) show data averaged across all five observers for infront flankers. The stereoscopic test was displaced with disparity relative to the reference which appeared in the fixation plane, whiles the flanking bars were displaced in depth. Error bars indicate ± 1 standard error.

Distance Effects and Induced Depth Bias

For two observers (SO and AC) the test-flanker separation was increased up 18 min arc. The results are shown in Fig. in 4.1C., and indicate that the test-flanker interaction is still affected by both the lateral separation and depth separation even with quite wide test-flanker separations. The crowding effect decreased monotonically with increasing lateral separation. The magnitude also increased with greater depth location of the flankers (i.e. greater relative depth separation). Thus, flankers displaced by 2 min arc off the fixation plane induced more crowding effects than when displaced by 1 min arc disparity. For both effects, crowding was greater when the separation was small and declined when the separation was increased.

Induction (bias) by the flankers on the depth direction of the test stimulus due to the interaction described was characterised. The averaged experimental findings across all 5 observers of the spatial distribution of the biases is indicated in Fig. 4.1D, where bias is plotted as a function of separation. Though induction effects are often very small, the data reveal that greater test-flanker depth separation (i.e. increasing degree of flanker depth off the horopter) induces more apparent depth bias in the direction of the flanker disparity. The magnitude of the bias is stronger at small test-flanker lateral separations. The bias demonstrates a strong effect when the lateral separation was less than 4 min arc, and at the critical OCD of 2 min arc, the bias increases by about a factor of two with each 1 min arc test-flanker disparity increase. At larger lateral separation beyond 4 min arc, bias diminished and show similar bias for fixation, 1 min arc and 2 min arc, except when the depth separation was 2 min arc, which still shows some effect. A two-way ANOVA was conducted that examined the interaction of the effect of lateral separation and relative depth separation on discrimination threshold. There was no statistically significant interaction between the effects of lateral separation and depth separation on depth discrimination, [$F(4, 10) = 0.176, p =$

0.936]. There was also no statistically significant difference in discrimination threshold between depth separation [($p = 0.148$)], and lateral separation [($p < 0.07$)].

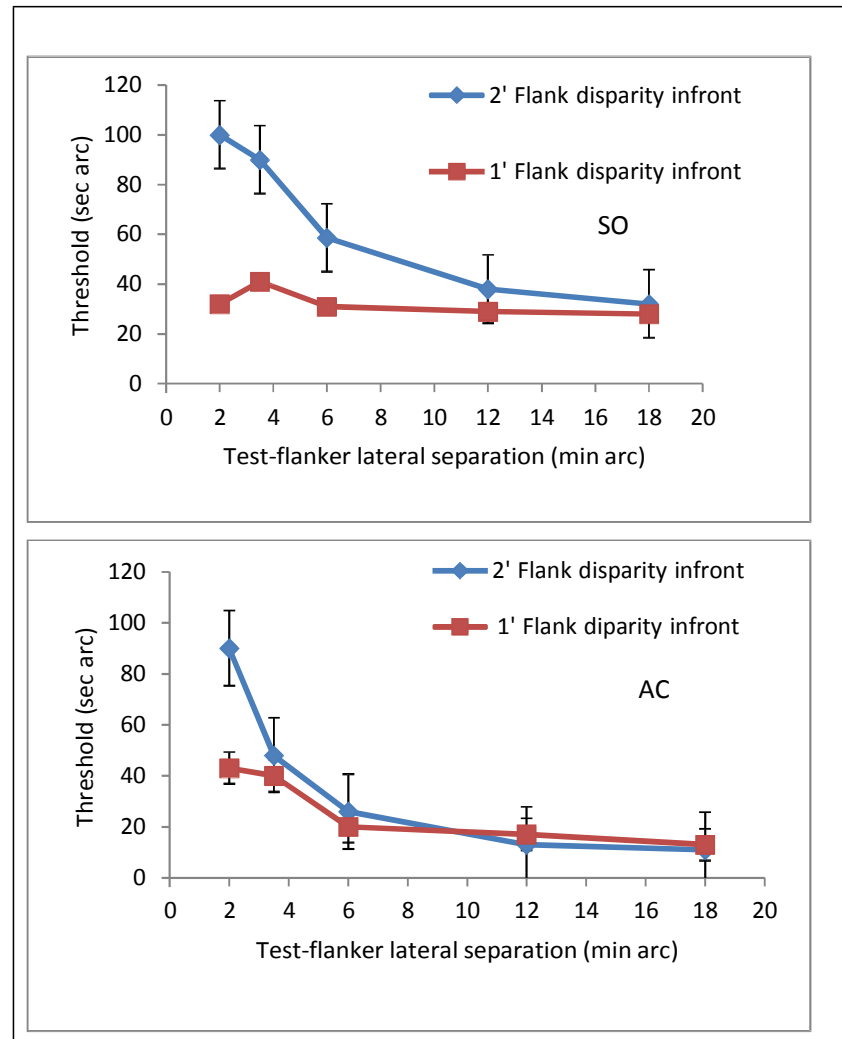
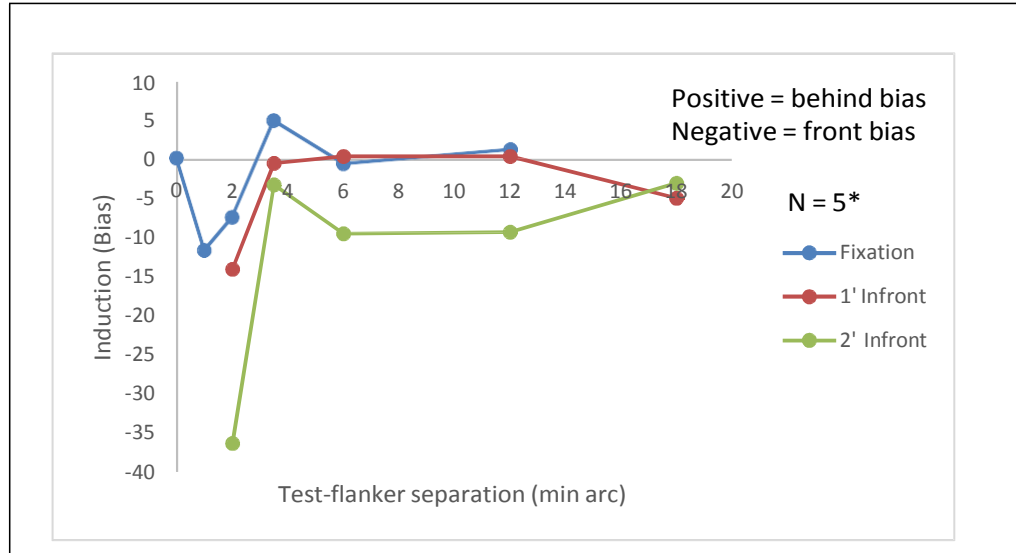


Fig. 4.1C. Depth Separation (Test-Flanker Disparity) and Lateral Separation Effects. Each panel shows for each individual observer, depth discrimination thresholds plotted as function of the lateral distance between the test and displaced flankers. The colours represent different depth positions of the flankers in front of the test and error bars indicate ± 1 standard error. The data show that the magnitude of the interaction depended on both the depth position of the flankers, and lateral separation between the test and flankers.



**only two subjects were tested for 12-18 min arc separations (x-y intersection (0 on x-axis indicates when the test and flankers were abutted on the fixation plane)*

Fig 4.1D. Induced Depth Bias. Bias averaged across the 5 observers, plotted as function of the test-flanker lateral separation. Negative indicate crossed disparity bias (situation where the apparent depth of the inducing flankers pulls the test towards itself, indicating attraction) and positive uncrossed disparity bias. The colours represent different depth positions of the flankers in front of the test stimulus. The data reveal that the magnitude of the bias depended on the depth position of the flankers in front of the fixation, and scaled at the OCD.

Experiment 4.2A and 4.2B: Threshold for ‘Crowding’ and ‘Non-crowding’ Stimulus’ off the Horopter

Results for five observers who participated in Expt.4.2A are shown in Fig. 4.2A, where the stereo-threshold is plotted as a function of the stimuli disparity. As found in Chapter 3, the crowding effect is greatest in the fixation plane, but drops off (e.g. from 80 to 33.6 sec arc for the averaged data) as the stimulus was moved out of the fixation plane (i.e. closer to the observer) to about 0.5 to 1 min arc in front for different observers. Subsequent stimuli pedestals show a more gradual rise in threshold, and comparable thresholds to that in the fixation at greater disparity. Analysis by one-way ANOVA revealed no statistically significant main effect of change in level of stimulus depth position on discrimination threshold [$F(4, 20) = 1.291, p = 0.307$]

In Expt.4.2B (see Fig.4.2B), the flankers caused little or no interference in the fixation plane, but in contrast to results in Expt. 4.2A, the crowding effect did not show a reduction around the fixation plane, but rather revealed an increase from the fixation plane to about 1 min arc in front for some observers (SO, VO, PI). Observer performance beyond 1 min arc disparity varied for example observers VO and PI, who recorded greater crowding effects with the flanker disparity, their stereo-threshold declined. Analysis by one-way ANOVA revealed no statistically significant main effect of change in level of stimulus depth position on discrimination threshold [$F(4, 20) = 0.385, p = 0.817$].

Experiments 4.3A and 4.3B: Incremental Threshold for the Stereoscopic Pair

Mean data for three observers are shown in Fig. 4.3(A), showing stereo-threshold plotted as a function of pedestal disparity of the stereoscopic pair (test and reference bars). Crowding is optimum on the horopter, but further increments in disparity of the stereoscopic pair reveal that stereo-threshold drops sharply and remains low or shows no appreciable increase when the disparity of the stereoscopic pair was increased. Analysis by one-way ANOVA revealed no statistically significant main effect of change in level of stimulus depth position on

discrimination threshold [$F(4, 10) = 0.831, p = 0.535$]. In Expt. 4.3B, as indicated in Fig 4.3(B), in concordance with previous pedestal disparity measurements (Blakemore, 1970; Andrews et al, 2001), thresholds increased but the rise was gradual as opposed to a rapid rise, probably due to the small range of pedestal disparities used. One-way ANOVA revealed no statistically significant main effect of change in level of stimulus depth position on discrimination threshold [$F(4, 10) = 0.647, p = 0.642$]

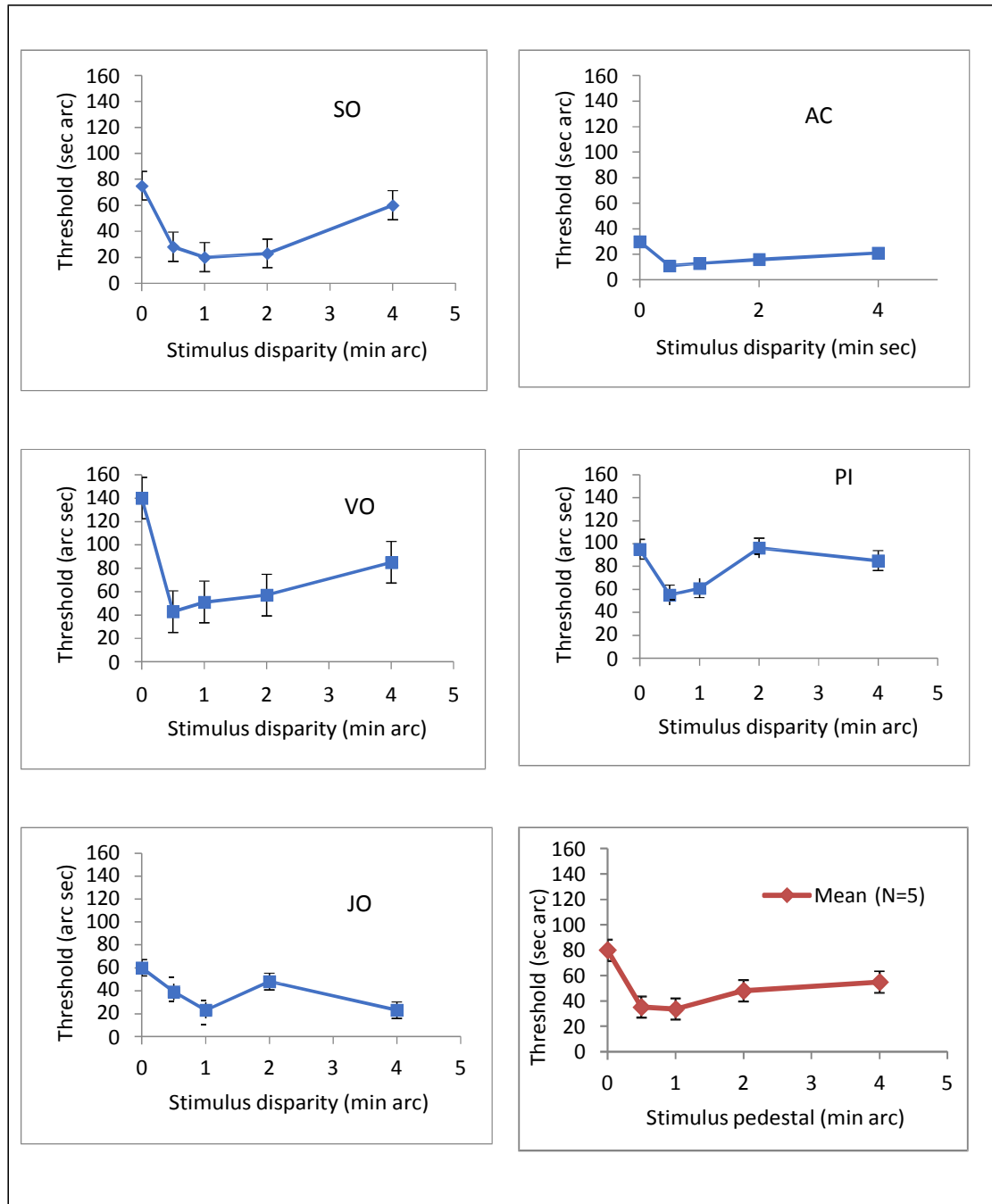


Fig. 4. 2A. Expt. 4.2A. Incremental Threshold for the Crowded Stimulus.

Each panel shows for each individual observer, stereo-thresholds (sec arc) plotted as a function of the stimulus disparity (min arc). The last panel (red line) shows data averaged across five observers. The entire configuration was presented for 300 msec while fixation was maintained in the fixation plane using the Nonius stimulus. Error bars indicate ± 1 SE.

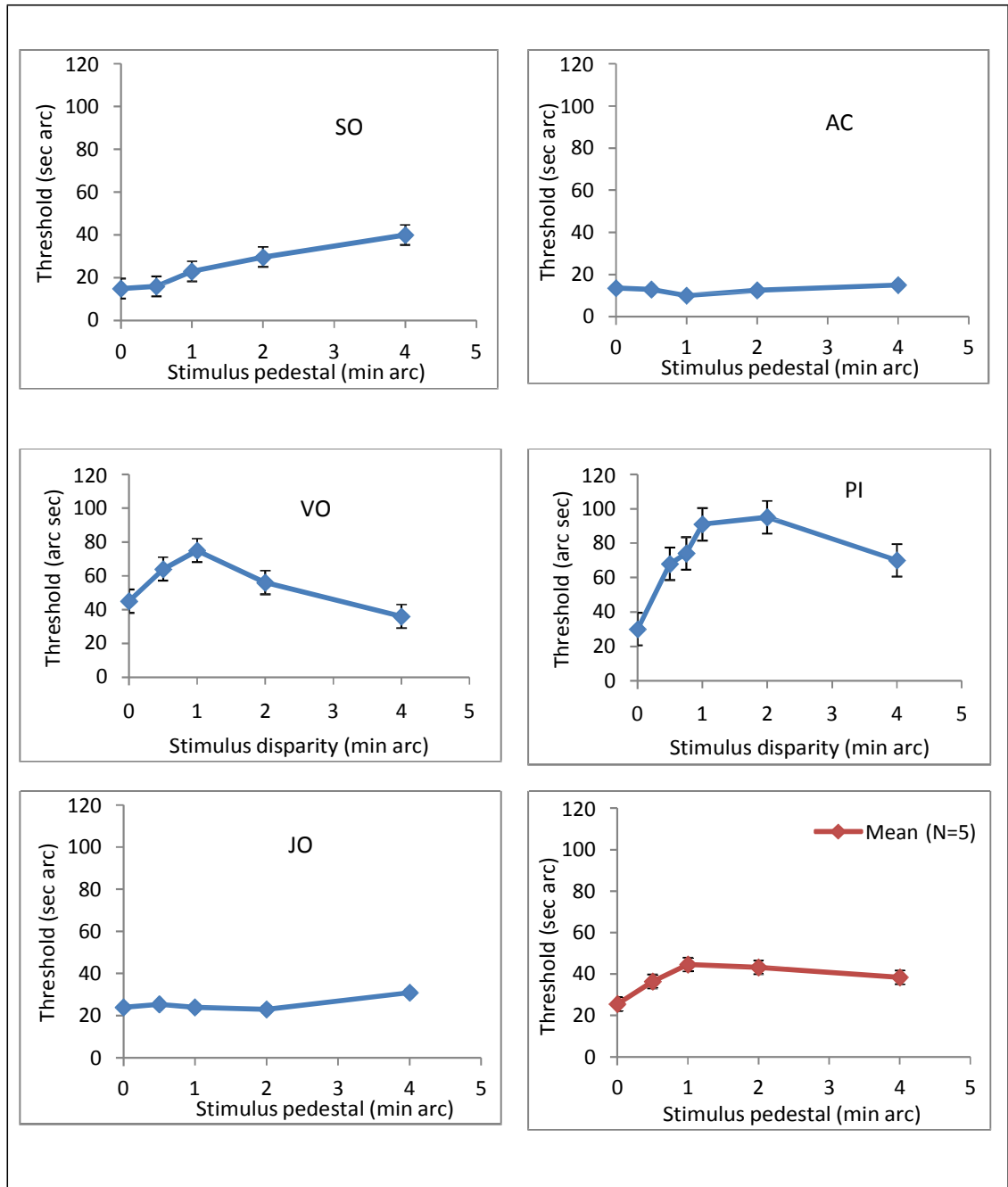


Fig. 4. 2B. Expt. 4.2B. Incremental Threshold for the Non-Crowding Stimulus. Each panel shows for each individual observer, stereo-thresholds (sec arc) is plotted as function of the stimulus disparity (min arc). Last panel (red) show sample data averaged across five observers. Stimulus presentation and duration was the same as in Expt 4.2A. Error bars are ± 1 standard error.

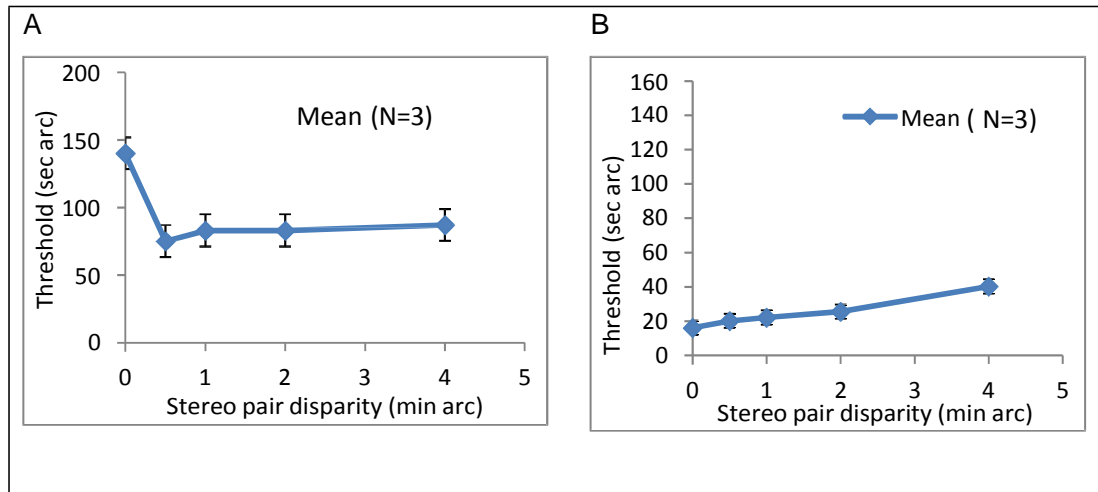


Fig. 4. 3 Expt. 4.3A and 4.3B. Incremental Threshold for the Stereoscopic Pair (Test and reference). In (A) flanking bars were fixed in the fixation plane. In (B) Flanking bars were omitted. Each panel shows for each individual observer, depth discrimination thresholds (sec arc) plotted as a function of test target and reference disparity. Stimulus presentation and duration was the same as previous. Error bars represent ± 1 standard error.

Experiment 4. 4: Does the Flankers' Width Tune to Crowding?

The data for four observers are shown in Fig 4.4. Varying the width of the flankers improved performance of the observers. Stereo-thresholds reduced when the width of the flankers was altered to look thinner than the test target, then increased to the optimum threshold, for the test-flanker distance used, when the width of the flankers matched that of the test. Subsequently, widening the width of the flankers for them to appear distinct from the test reduced the threshold. However, the change in threshold with changes in flanker width did not appear to scale with the test-flanker disparity (flanker depth position). For example, performance was better when the flankers were positioned at 2 min arc from the fixation plane, compared to when they were positioned at 4 min arc. A two-way ANOVA revealed that the interaction between effect depth position of flankers and change in width of flankers on discrimination threshold was not statistically significant, [$F(8, 30) = 0.354, p = 0.926$]. There was also no statistically significant difference in effect of width [$(p = 0.302)$], and flanker depth position [$(p < 0.124)$]. However, pairwise comparison revealed that there was statistically significant effect from changing the size from the original width (2.8 min arc) to the thickest width (8.4 min arc) [$(p = 0.05)$] at all flanker positions compared to other changes that showed no statistically significant effect [$(p > 0.05)$].

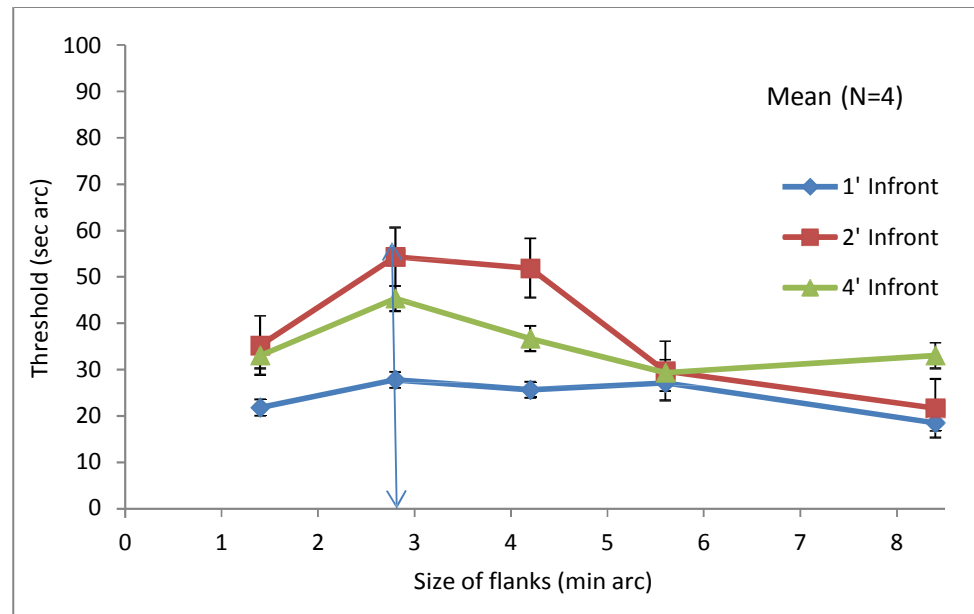


Fig. 4. 4A. Expt. 4.4A Influence of Flanker width on Stereo-threshold. Stereo-thresholds (sec arc), averaged across the 4 observers, plotted as a function of the width size of the surrounding flanking bars which were displaced in depth in front of the test. Stimulus presentation and duration was the same as previous. The arrow indicates where the test and flankers had equal widths. The colours represent different depth positions of the flankers in front of the test. Error bars indicate ± 1 SE.

DISCUSSION OF RESULTS

This work highlights aspects of stereoscopic spatial interaction (crowding) concerning stimuli presented outside the fixation plane, and the role played by nearby targets when different disparity signals are assigned. Our aim was to investigate how crowding and perceived depth are affected by off the horopter spatial interaction, and performed a number of experiments towards this end.

Consistent with previous reports (Butler and Westheimer 1978; Astle et al., 2014), when there was optimum crowding stereo-threshold was elevated in the fixation plane, then decreased when the flankers were presented slightly in front of the test which we presume to show that crowding on the plane of fixation may be relieved when the flankers are shown in depth (Fig. 4.1A). Surprisingly however, when the flanker disparity was increased further, the crowding effect returned and stereo-threshold was elevated once again. The flanking bars also produced a depth bias of the test in the direction of the perceived depth of the flankers (Fig. 4.1D). When all elements of the stimulus configuration was shown with a pedestal disparity, the effects were similar, a decrease and then increase in the stereo-threshold (Fig. 4.2A). When the test and flanker separation was increased to the least crowding distance, the stereo-threshold interestingly showed a progressive increase from the fixation (Fig. 4.1B), which was similar to the pedestal threshold of the non-crowding configuration (Fig. 4.2B). Additionally, the findings reveal that the interaction was pulled along the width of flankers (i.e. affected by the width of the flankers), as dissimilar flanker width improved performance.

We know of similar studies that have shown that crowding effects decline when flankers are presented at small depth planes in front of the horopter (Butler and Westheimer 1978; Astle et al., 2014), but the subsequent elevation in threshold at the greater flanker disparities (than those tested by Butler and Westheimer (1978)) observed in this study is a new finding, which perhaps supports the fine and coarse dichotomy in stereopsis (Ogle, 1952, Marr and Poggio,

1979). Since the crowding effect depended on the relative depth and lateral separations of the stimuli (Fig. 4.1C), it is possible that the perceptual mechanism of salience drives the perceived 'front effect' (Fox, 1970; Lehmkuhle and Fox, 1980; Fox and Patterson, 1981) and induced 'depth bias' in the depth direction of the test stimulus. These results obtained here concerning lateral interaction and relative test-flanker disparity (relative disparity) interaction can best be interpreted by referring to previous studies (Westheimer, 1986; Westheimer and Levi, 1987, Stevenson et al., 1991) which sought to provide insight into perceived depth using relative disparities. The present research has extended these findings in the domain of stereoscopic crowding.

Influence of Test-Flanker Disparity on Crowding

Previous studies indicate that presenting a stereoscopic test stimulus and flankers in different depth planes can influence the stereo-threshold (Fox, 1970; Bulter and Westheimer, 1978; Kooi et al., 1994; Felisberti et al., 2005; Astle et al., 2014; Funke et al., 2015). The general understanding is that presenting flankers and test/reference in the same depth plane produces crowding. However, studies which presented the flankers behind (e.g. Fox, 1970; Butler and Westheimer, 1978; Felisberti et al., 2005) or in front of (e.g. Bulter and Westheimer, 1978; Kooi et al., 1994) the test have recorded contrasting results. From these studies, it is not clear how the interactions reported related to stereoscopic crowding, and the degree to which it is affected by different spatial factors. Based on this, we designed experiments that allowed us to assess the spatial factors that affected the interaction off the horopter in the presence of crowding, and examined the underlying mechanism.

In this study, crowding was produced in the fixation plane. The crowding effect reduced when the flanking bars were presented at different disparities to the test up to about 1 min arc, before the stereo-threshold increased again when the flankers' disparity was increased up to 2 min arc. Reduction in thresholds at small relative depth separations is consistent with the previous findings (Fox (1970), Butler and Westheimer (1978), Kooi et al, 1994),

Felisberti et al. (2005), Astle et al. (2014) and Funke (2015)). The subsequent restoration of the flanker effect as flanker disparity is increased is also in accordance with the findings of Fox (1970), Kumar and Glaser (1992a), Funke et al. (2015). In the Butler and Westheimer (1978) study, which measured the disparity tuning of a foveal test using orthogonal line flankers distributed over a limited range of disparities, the bandwidth of their tuning function was much narrower compared to our results (thresholds halved when an average test-flanker disparity of approximately 23 arc sec was introduced. Kooi et al. (1994) also found that presenting a test at a single fixed depth in front of flankers increased the accuracy of responses and decreased the spatial extent of crowding for a peripheral letter recognition task). Various authors (e.g. Butler and Westheimer, 1978) attributed flanker effects to activation of 'inhibitory' or 'integratory' regions of neurons tuned to disparity during stimuli integration which decrease or increase the neural activity corresponding to detection (Butler and Westheimer, 1978; Badcock and Westheimer, 1985; Kooi et al, 1994). Butler and Westheimer (1978) averred that this mechanism is sharply tuned to the fixation plane.

The results here were obtained by measuring crowding over a larger range of crossed disparities, which revealed that stereo-threshold elevates when the test-flanker disparity is increased beyond 1 min arc. It is possible than in the Butler and Westheimer (1978) study because they used flankers that were orthogonal to the test rather than having the same orientation and size, crowding could have greatly reduced in this situation, and did not demonstrate the effects we have reported at larger test-flanker disparities. Moreover, the reduction in stereo-threshold followed by an elevation when test-flanker disparity is increased, possibly reveals a two scale disparity-based tuning function. This suggests that the strength of crowding changes with the magnitude of the test-flanker disparity. If indeed the stereoscopic system is sharply tuned to encode for depth information around the plane of fixation (Butler and Westheimer, 1978; Blakemore and Hague, 1972), then there may exist a different mechanism that results in an elevation in threshold when the flankers are

given greater disparities. A drop-off in threshold around the fixation plane, followed by an elevation suggests a possible interaction of two processing mechanisms, one tuned around the fixation plane which process small disparities and one tuned to process larger disparities away from the fixation plane. Such a suggestion is in accord with the proposed fine and coarse dichotomy in stereopsis (Ogle, 1952, Marr and Poggio, 1979).

Could the elevation in stereo-threshold at greater relative test-flanker depth separations be a result of some 'distal crowding' or 'an induction' by the flanker on the test? Authors like (Ogle, 1963; Mitchison and Westheimer, 1984; Westheimer, 1986) posit the concept of 'salience', to explain the interaction based on relative depth separation. They describe the situation where the depth difference in the position of test and flankers creates induction effects of 'attraction' and 'repulsion' depending on the lateral separation between them. The salience concept has successfully been used to explain the symmetric effect in depth discrimination (Westheimer, 1986). Other authors postulate a 'front effect' to explain the asymmetry in depth discrimination in spatially close targets (Fox, 1970; Lehmkuhle and Fox, 1980; Fox and Patterson, 1981). Because both mechanisms are affected by similar spatial characteristics, that is operationalised at small separations, increases with crowding and affected by relative depth separation, we hypothesised that 'front effect' is the physical attribute of 'salience attraction' which is a perceptual mechanism.

We tested this disparity induction assumption by using relatively wide test and flanker separations where there was no interference on the fixation plane at the onset. In that experiment (Fig. 4.1B), it was observed that there was no reduction in stereo-threshold, but rather progressive elevation away from the fixation plane. Though there was no interference in the fixation plane for this relatively wide separation, the increase in stereo-threshold when the flankers were given disparity is not surprising due to salience. Kumar and Glaser (1992a) have suggested that targets separated less than 15 min arc will interact when they are given disparity. Elevation in stereo-threshold for similar configurations have, in the past, been

variously attributed to cue conflict, target saliency and grouping effects (Westheimer, 1986; Livne, and Sagi, 2007; Deas and Wilcox, 2012). Here, because there were no other cues available other than flanker disparity, the observed effect can be attributed to salience or induction due to test-flanker disparity or depth separation.

In another control experiment (Fig. 4.3 (A)), where the flankers were fixed on the fixation plane, and only the test and reference pair moved in depth from the fixation, the flankers induced slight effects in the stereo-threshold which remained largely stable, and comparable to when the flankers were not present at all. In explaining this, it could be assumed that, when the two flanking bars are fixed in the fixation plane, their contribution to the identical environment to salience will be very small leading to reduced and stable thresholds (Mitchison and Westheimer, 1984). Where the flankers were displaced from the fixation plane, their equal salience in relation to the test led to the elevation in stereo-threshold.

Previous studies have suggested that crossed disparities are processed more efficiently than uncrossed disparities, while others attribute this to differences between observers' stereo acuity (e.g. Lasley et al, 1982; Mustillo, 1985). However, if the interaction observed was based on salience, we would have expected thresholds to be higher in the depth direction of the flankers when flankers had crossed disparity compared to when it they were presented with uncrossed disparity, which indeed was the case in most of our observers (Fig. 4.1A). Again, reduction in stereo-threshold in the presence of crossed flanker disparity could reflect a systematic change in vergence position prior to stimulus presentation. However, in the randomised trials, thresholds were generally lower with uncrossed disparity in the flankers and showed a similar function to when the flankers had crossed disparity, suggesting that for the conditions tested, it was not the crossed position of the flankers (due to fixation disparity) which was responsible for the lowering of threshold. The consistency in the data set also supports this assumption. Differences in crossed and uncrossed flanker disparity function could therefore reflect asymmetry in the underlying neural mechanisms.

In doing this experiment, care was taken to ensure that changes to the disparity of the flankers did not affect the edge separation between the test and flankers, and the similarity in the tuning functions when the flankers were given uncrossed disparity or randomised between crossed and uncrossed disparities suggest that the effect was a result of a mechanism due to the test-flanker disparity. Astle et al., 2014 ruled out effects due to the 3-D distance between the test and flankers as result of the perpendicular movement of the flanks to the screen.

Distance Effects and Depth Bias (Further Evidence of Saliency)

Distance effects are not uncommon for vertical display of stereoscopic targets, where the targets' contours carry disparity signals and interact. According to Westheimer (1986), when the targets are a few minutes of arc apart, the effect will be equivalent to pooling of their disparity signals. The increases in stereo-thresholds when the test and flankers had small test-flanker depth separation (test-flanker disparity) and laterally separated by a few min arc can be interpreted as their disparities being somewhat pooled (Badcock and Westheimer, 1985). Disparity pooling supports the idea of a saliency 'attraction' mechanism earlier described. However, when the separation between test and flankers was widened to more than 6 min of arc, the effect was in the opposite direction, acting to repel each other in depth (Westheimer, 1986). These results are consistent with the proposition of Mitchison and Westheimer (1984) that the weight of the interaction (due to the action of saliency) is inversely proportional to distance between the test and the flanking bars.

We had proposed that if 'saliency attraction' and 'front effect' are linked such that saliency leads to the front effect, increasing the relative test-flanker depth separation will induce depth bias in the depth direction of the flankers. We found more depth bias with corresponding increases in the test-flanker disparity (increasing crossed disparity) in the depth direction of flanking bars. The bias effect scaled at the OCD by a factor of two with each minute arc increase in flanker depth. The saliency attraction effect reduced with

increasing lateral separation between the test targets and flankers (see Fig. 4.1D). This observation supports the proposition that the 'salience attraction' (due to increasing flanker disparity) induces corresponding increase in 'front effect' of the test when the separation between the targets in the fixation are small, the effect being maximum when there is optimum crowding. This result is consistent with our prediction in the fixation plane (see Chapter 3), that greater flanker disparity would induce even more biases in the direction of the flanker disparity.

Observations Due to the Incremental Disparity of the Configuration

By keeping the flanking bars fixated, and moving all parts of the stimuli out of the fixation plane, it was reasonable to attribute the observed effect to the action of mechanisms tuned to the processing of disparity to which they were moved (Ogle, 1952; 1953; Blakemore, 1970; Badcock and Schor, 1985). As predicted, the incremental disparity stereo-threshold for the 'crowding' stimulus was characterised by two main trends; a drop in threshold around the fixation, and a steady rise as the pedestal disparity was increased from the fixation plane (Fig. 4.2A). Depth discrimination thresholds for the 'non-crowding' stimulus on the other hand, showed a progressive elevation from the fixation (Fig.4.2B). These results are consistent with the earlier findings (i.e. the flanker effects observed with test-flanker disparity in Expts. 1A and 1B). Thus, a classic increment disparity threshold function which shows a decrease in stereo-threshold around the fixation, then a sharp elevation with increasing pedestal disparity (Ogle, 1953; Blakemore, 1970, Westheimer and McKee, 1978; Westheimer, 1979; Badcock and Schor, 1985; McKee et al., 1990; Andrews et al., 2001).

Influence of Disparate Flanker Width on Stereo-threshold off the Horopter

We characterised the graded influence of test-flanker dissimilarity on the magnitude of crowding off the fixation plane. We found that performance improved by varying the width of the flankers to appear thinner or thicker than the test (Fig. 4.4). This finding is consistent with the previous finding in the fixation plane (Chapter three), where changing the width of the flankers aided to ungroup the stimuli (due to the pop-out of the test) (Felisberti et al, 2004; Kumar, 1995; Kumar and Glaser, 1995). However, the flanker effect did not scale with the flanker depth position. These findings reveal the strong influence of contrast (for thinner widths) and compulsory grouping (for thicker widths) on crowding, and support postulations that posit a grouping hypothesis to explain crowding (Andriessen and Bouma, 1976; McKee, 1983, Kumar and Glaser, 1992b; Kooi et al., 1994; Livne, and Sagi, 2007).

From the foregoing observations, it is clear that smaller depth-differences can be discriminated on or near the fixation plane, where Butler and Westheimer (1978) had demonstrated that depth information is sharply tuned to the fixation plane. Here, our results provide support for the idea that relative depth sensitivity is acute around the horopter, but when discrimination is extended beyond the function tuned to the fixation plane, one runs into a different mechanism tuned to a potentially coarse mechanism. The sharp rise in stereo-threshold possibly marks a transition from disparities which give rise to fine spatial discrimination to disparities which give rise to coarser discrimination (Westheimer and McKee, 1978; Westheimer, 1979; Badcock and Schor, 1985; McKee et al, 1990). These findings can be related to the idea 'fine- to-coarse' scales interaction in stereopsis proposed by Marr and Poggio (1979) when discriminating relative disparities.

While these findings are uncommon with the relatively broad-bandwidth stimuli (spatial frequency bandwidth is broad compared to that of individual channels) used in this experiment, it may be difficult to attribute the observation to a size-disparity processing or scale-dependent resolution mechanism. Farell et al. (2004) have suggested that incremental

threshold observations with broad bandwidth stimuli can be as a result of the spatial-frequency components of the stimuli. They averred that there is the possibility of intrinsic alteration on frequency components of the stimuli from one pedestal disparity to another during measurement and reckoned that high-spatial frequency components would act to reduce threshold at small pedestal and low-spatial frequency would limit thresholds at large pedestals. Further investigations using stimuli capable of broader range of frequency bandwidth and contrast manipulations are needed to evaluate channels contributions to crowding off the horopter in the domain of disparity signals. On the other hand, the findings of this study highlight that crowding has a positional requirement and is influenced by off the horopter pedestals.

CONCLUSION

Using a simple stereoscopic configuration made up of vertical bars, that allowed crowding and the manipulation of spatial features, we have been able to characterise further crowding effects off the horopter using disparity information. The role played by local interactions when flanking bars which carry different disparity signals have been highlighted. In the end, based on the data adduced the effect could be simple, such as reduction or increment in the stereo-threshold through contour or edge interaction. Though the interactions observed are as a result of the peculiar configuration used here, and spatial properties of the stimuli, it has enabled us make proposals about crowding off the horopter.

We attribute the observed effects to the depth position of the targets through the interaction of their local disparities (which acts through salience). The effects were, fine scales tuned to a small area around the horopter, and broader or coarse scales farther away from the horopter. The findings support the idea of a local disparities mechanism of 'salience attraction' which induces 'front effect' and 'depth bias' at small separations in the stereo mechanism. The disparity information was pulled along the width of the flankers.

While increases in stereo-threshold with pedestal disparity have been attributed to the proportion of neurons in the primary visual cortex which encode for different absolute disparities (Barlow et al., 1967), a dip around the fixation plane, followed by a rise possibly underpins different neural mechanisms that sub serve small (fine scale) and large disparities (coarse scale) during on and off the horopter movements.

The results constitute an important step in understanding a more global processing of disparity signals (i.e. off the horopter processing of disparity signals) and may support existing models of disparity mechanisms arising out of such stimuli (Lehky and Sejnowski, 1990; Lehky et al., 1990; Mikaelian and Qian, 2000). Indeed, the basic design of a global stereogram comprises local features which, when processed by the stereoscopic system, gives rise to the impression of depth.

Nevertheless, the stimuli used here were of broad bandwidth in nature, further investigations with a more definite stimuli such as Gabor patches (composed of different spatial frequencies) which has the advantage of probing different pathways of disparity processing in the visual cortex.

CHAPTER FIVE

INFLUENCE OF SPATIAL FREQUENCY ON STEREOSCOPIC CROWDING ON, AND OFF THE HOROPTER

INTRODUCTION

The seminal work of Wheatstone (1838) and Ogle (1952, 53) provided evidence that horizontal retinal disparity is the fundamental cue to stereoscopic depth perception, the strength of which directly depends on the magnitude of the disparity causing it (Blakemore, 1970; Badcock and Schor, 1985). To measure the stereo-threshold of a local test target, the smallest detectable retinal disparity that still yields reliable stereoscopic depth percepts are measured (Westheimer and McKee, 1980a). Previous reports support a link between retinal disparity sensitivity and the sensitivity of the visual system to spatial frequency composition of a test target (Stigmar, 1971; Westheimer and McKee, 1980b; Schor and Wood, 1983). Due to the postulated series of overlapping spatial filters in the retina, disparity is thought to be computed in signals filtered through visual channels tuned to different spatial frequency composition, with a matching increase in spatial scale as a function of retinal eccentricity (Julesz and Miller, 1975; Marr and Poggio, 1979; Mayhew and Frisby, 1981). Therefore, the stereo-threshold varies with the spatial frequencies of the test target being discriminated, and relative to the spatial location from the fixation plane. Based on this idea, several authors have systematically used different investigative methods and spatial tasks, to investigate the effect of spatial frequency on stereo acuity, which have provided some empirical data to support the idea (e.g. Mayhew and Frisby, 1981; Schor et al., 1984; Badcock and Schor, 1985).

It is also generally known that the stereo-threshold of a spatially localised discrete test target is influenced by the properties of surrounding flanking targets through a phenomenon known as crowding (Flom, 1963; Bouma, 1970; Butler and Westheimer, 1978; Kooi et al., 1994). That is, depth discrimination of the test target is impaired by interference from surrounding

flankers. The effect of flankers on test target depth discrimination is either a reduction or elevation in the stereo-threshold depending on the task, and the spatial properties of the test and flankers (Polat and Sagi, 1993; Chung et al., 2001). Both reduction and elevation effects of flanking targets on depth discrimination has been recorded for tasks using broadband targets such as bars (Butler and Westheimer, 1978; Kumar and Glaser, 1992a), and for limited spatial frequency stimuli such as Gabor patches (Polat and Sagi, 1993), providing information about probable neural mechanisms that are involved in processing depth information. However, it still remains unclear the exact channels that are involved in depth information processing for spatial frequency-defined test target and flanker. Current models posit matching and coupling of channels to explain depth discrimination (Mayhew and Frisby, 1981; Schor et al 1984). Fortunately, because crowding is an integrative process, it represents a useful method to investigate models that posit matching and coupling of channels, through stimuli manipulations such as spatial frequency, contrast and size. The manipulation of stimulus parameters allows us to examine their effects on the discrimination of a test target, and to imply the possible channels underlying the interaction since the effects of stimulus properties of spatial frequency, contrast and size are now well understood. It is germane therefore, for the current study which examined the influence of spatial frequency on stereo-based crowding.

A common psychophysical investigative assumption to start from is that stimulus dimensions are processed through channels which are size sensitive (e.g.s. Stigmar, 1971; Westheimer and McKee, 1980b; Schor and Wood, 1983). Many other investigators have reported that stereo-threshold increases with increasing size of the spatial frequency defined-stimulus (e.g. Wilcox and Allison, 2009). Evidence for these channels in spatial vision have been found for grating spatial frequency and orientation (Blakemore and Campbell, 1969); lateral motions (Levinson and Sekuler, 1980), motion in depth (Beverley and Regan, 1975) and static retinal disparity (Felton, Richards and Smith, 1972). Early evidence for disparity tuned channels in human vision was reported by Blakemore and Julesz (1971), who found that

adaption to Random-Dot Stereograms (RDS) produced shifts in the apparent depth of the subsequently viewed stereograms. They argued that the shifts indicated that relatively narrow disparity tuned mechanism had been adapted. Further evidence was provided by experiments that revealed disparity specific-elevation of contrast threshold after adaptation to sine-wave gratings (Felton et al., 1972; Blakemore and Hague, 1972). Felton et al. (1972) for instance, found the greatest threshold elevation when the grating periods were double the disparity, and suggested that disparity selective neurons pool information across the full extent of the test target itself and not the edges. Blakemore and Hague (1972) in another experiment revealed disparity-specific elevation of contrast threshold after adaptation to sine-wave gratings. These findings support a theory that posits disparity-tuned mechanisms with optimum sensitivity covering a narrow range of spatial frequency (Felton et al., 1972; Marr and Poggio, 1979).

Foveal crowding is argued to be a form of masking (Legge, 1979; Lehmkuhle and Fox, 1980; Legge and Foley, 1980; Levi et al., 2002). One of the putative models to explain spatial frequency based masking posits that spatial-frequency filters operate in parallel, and the output of each of these filters passes through a compressive contrast nonlinearity (Wilson and Bergen, 1979; Legge and Foley, 1980; Halpern and Blake, 1988). However, there is a seemingly similar effect of spatial frequency and contrast on masking and crowding (Richards, 1972; Banks and White, 1984; Polat and Sagi, 1993; Chung et al., 2001) leading to the suggestion that crowding can be explained by simple spatial frequency based masking mechanisms. Indeed, there is evidence that crowding is optimum when the test stimulus and flankers have similar stimulus properties such as size, shape, orientation and spatial frequency (Andriessen and Bouma, 1976; Schor and Wood, 1983; Kooi et al., 1994; Chung et al., 2001; Farell, 2006), suggesting that crowding, like masking, might be spatial frequency selective. Another common spatial characteristic is the narrow spatial tuning of their effects (Polat and Sagi, 1993). The narrow tuning of crowding to the horopter reported by Butler and Westheimer (1978) in their classic stereo based crowding paradigm has been

suggested to result from a form of lateral masking, because the effect was only produced when the test and flankers had the same relative depth, had narrow lateral separation and were presented within a short temporal window.

Studies of Gabor-by-Gabor lateral masking showed that detection thresholds of a Gabor test target are raised in the presence of nearby flanking Gabors (e.g. Polat and Sagi, 1993; Zenger and Sagi, 1996). Detection thresholds reduces when the spatial frequency composition of the test and flankers become dissimilar and greatest when the spatial frequency composition of the test is similar to that of the flankers (Polat and Sagi, 1993; Chung et al., 2001). Polat and Sagi (1993) found that detection threshold of a test patch was lower when it was flanked by high contrast Gabor patches. Spatial scaling and maximum facilitation (approximately half the non-flanked threshold) was noted when the flankers were laterally separated from the test patch by a distance equal to two to three standard deviation (SD) of the Gabor patch. Larger separations (up to 8 or 12 times of the SD produced measurable facilitation, while small separations produced inhibition. Polat and Sagi (1993) concluded that spatial scaling is an important general principle in spatial vision which expresses a uniform operation of the visual system across all scales. Chung et al. (2001) compared the spatial frequency properties (range 0.63 to 10 cycle per letter) and contrast dependency of pattern masking and crowding at the fovea and 5 deg. Their subjects detected the contrast for identifying the middle test letters in strings of three letters (letter trigrams) which were subsequently compared to thresholds obtained for unflanked letters. Threshold elevation was substantial and peaked when the frequencies of the test and its flanking letters were similar, and diminished as the difference between their frequencies increased. In addition, at low flanker contrast, crowding did not show a facilitatory region, unlike pattern masking. At high flanker contrasts, thresholds rose with contrast with an exponent of 0.13 to 0.3, lower than corresponding exponents for pattern masking. They found that crowding exhibits spatial-tuning functions like masking, but with broader bandwidths than those of masking and was independent of the spatial frequency of the test.

Chung et al. (2001) concluded that the properties of crowding with respect to letter spacing are qualitatively similar at the fovea and that crowding and masking may share a similar processing mechanism. Their findings though contradicted a prediction based on the grouping explanation for crowding (Kooi et al., 1994).

On the other hand, other authors have adduced contrary evidence that crowding is a form of masking. Kooi et al. (1994) examined the role of similarities and differences on the spatial extent of crowding. For most of the stimulus parameters they examined, including shape, colour and contrast polarity, they demonstrated that crowding is maximal when the target and flanking letters share identical stimulus parameters. However, for the parameter of contrast, they tested all four combinations of high (83%) and low (29%) contrast for the test and flanking letters, but failed to show that crowding is maximal when the target and the flanking letter contrast were the same. Their contrast data agreed with Chung et al (2001) that implied that crowding is not a grouping-by-contrast phenomenon. Danilova and Bondarko (2007) found that for foveal viewing, the extent of crowding did not increase with larger Landolt Cs when they were increased in size to about 2.5 fold, as would be expected under a masking mechanism. Their results also revealed that the magnitude and extent of crowding for a test C flanked by either bars or Gabors with spatial frequency composition beyond the resolution limit (77 cpd) is similar to when single bars were used, which is contrary to the expected spatial frequency response in a simple masking phenomenon. A simple spatial frequency based masking hypothesis would predict that if the size of the target is increased, the extent of the spatial interaction should proportionally increase. Pelli et al (2004) and Ehrt and Hess (2005) also measured contrast thresholds and made similar conclusions. Pelli et al (2014) found that contrast threshold for letters in the periphery increase with the contrast of surrounding flanking letters, but contrary to masking effects, crowding reached a saturation effect when the critical flanking letter contrast is 3 times visibility. Ehrt and Hess (2005) found a similar effect at the fovea and concluded that discriminability and not detection is affected by the flankers' contrast level. These findings

contradict an explanation of crowding based on simple masking predictions of scaling and spatial frequency selectivity.

There is also a reported depth bias in the perceived depth of test target due to differences in spatial frequency composition of flankers (e.g. Brown and Weisstein, 1988). Brown and Weisstein (1988) reported that regions filled with relatively high spatial frequency gratings (sine wave) appear closer in depth than adjacent regions filled with lower spatial frequency gratings. Though some authors argue that the differences may be attributed to monocular cues, such as enhanced high frequency features in a perceived 'figure' relative to perceived 'ground' regions (Brown and Weisstein, 1988). Others posit stereoscopic depth processing by independent spatial frequency tuned channels (Marr and Poggio, 1979; Yank and Blake, 1991). To them, bias on the basis of spatial frequency composition suggests information being used differently, depending on which spatial frequency channel is stimulated, with marked differences in the widths (size) of crossed and uncrossed channels.

Whereas monocular and masking studies demonstrate spatial frequency specificity, and suggest that masking and crowding by Gabor stimuli might share a number of important properties (and possibly mechanisms), the relationship for stereo based crowding is not clear (Frisby and Mayhew, 1978, Legge and Gu, 1989). The putative argument when extended to stereo based crowding will presumably be based on the relation between contrast sensitivity and disparity sensitivity. Therefore, the present investigation extends these discussions in the stereoscopic depth-crowding domain by directly examining the influence of the spatial frequency on depth discrimination of test in the presence of flankers. A strong advantage of using spatial frequency defined stimuli to investigate the mechanisms of disparity integration is that the properties of the stimuli (contrast, spatial frequency, and size) are easily manipulated. Therefore, we manipulated the spectral content of Gabor gratings to facilitate the investigation of the spatial frequency properties of crowding to suggest the possible underlying mechanisms. We measured depth discrimination thresholds for a test stimulus under conditions where we systematically varied the spatial frequency of

adjoining Gabor patches. The purpose was to examine whether observers use similar features and spatial frequencies of the test and flankers to make perceptual decisions about the test in the presence of crowding.

Effects of Spatial Frequency on Stereo-threshold off the Horopter

In spatial vision, it is generally known that thresholds for stereoscopic depth discrimination increase with distance from the horopter (Blakemore, 1970; Poggio and Fischer, 1977; Badcock and Schor, 1985), and crowding is extensive in the periphery (Levi et al., 1985, Toet et al., 1992). Ogle (1952, 1953) described a dichotomy in stereopsis based on what has subsequently been referred to as fine and coarse disparity discrimination relative to the horopter, each processed by sets of mechanisms tuned to a restricted range of disparity (Felton et al., 1972; Richards and Kaye, 1974; Marr and Poggio, 1979). There is the general belief that the mechanisms mediating stereopsis are tuned to specific spatial frequency channels which operate within a positional requirement due to early spatial filtering (Julesz, 1971, Mayhew and Frisby, 1976). Evidence of this was provided by Felton et al. (1972), who measured disparity displacements from the fixation plane of up to 1.25 deg., with a spatial frequency range between 0.2 to 7.6 cycles per degree (cpd). They described coarse stereopsis as being tuned to low spatial frequency channels and fine stereopsis tuned more to high spatial frequencies. Blakemore and Hague (1972) supported the idea of disparity-tuned mechanisms, which have optimum sensitivity around a narrow range around the horopter. The idea of narrow channels was in contrast to Richard's (1971) findings, who proposed a three-pool hypothesis. Richard found that certain stereo-anomalous individuals were unable to make accurate disparity discriminations over a relatively broad range of disparities, and suggested the existence of three pools of disparity detectors, a fine pool for small disparities and near and far pools for larger, crossed and uncrossed disparities, respectively.

Poggio and colleagues (1977) agreed with the dichotomy in stereopsis, but further distinguished responses based on disparity sensitivity on, and off the plane of fixation. Firstly, they described responses elicited by small disparity changes on or near the horopter tuned to high spatial frequencies which produce acute discrimination, and secondly, responses to large disparities outside the fixation plane tuned to low spatial frequencies. Because the proposed mechanisms are based on different receptive field sizes, and play different roles in spatial tasks, the outcome is often referred as the size-disparity correlation (Marr and Poggio, 1979; Schor and Wood, 1983; Harris et al., 1997). Richards and Kaye (1974) looked for evidence of the distinction between fine and coarse disparity processing based on a size-disparity correlation. They used a magnitude estimation task and a range of stimulus sizes. They found no transition in their disparity function, but observed that as the size of the stimulus increased, the peak of the depth estimation function also increased. Julesz (1971) proposed a size-disparity correlation (i.e. coarse and fine disparity interaction) as the means by which the visual system addresses the so-called correspondence problem in stereopsis, where there may be more than one possible match between corresponding points. Marr and Poggio (1979) also suggested that mechanisms tuned to low spatial frequency first detect the disparity, and then pull it to the matching range of mechanisms tuned to higher frequencies. However, till date, there is no clear cut view on how different putative spatial frequency tuned mechanisms interact when resolving disparities off the horopter, and how such interactions relate to stereo crowding when the test and pedestal flankers carry different spectral compositions. We examine these issues by measuring stereo-thresholds for spatial frequency defined stimuli whose disparities are spatially integrated in a series of depth crowding experiments. Integration of spatial frequency-defined test target and flanker off the horopter has the ability to probe different channels and pathways tuned to process disparities off the horopter by the visual system.

There are some previous studies that can be cited relating to the present investigation. Mayhew and Frisby (1979) investigated spatial-frequency-tuned mechanisms in stereopsis.

Their subjects discriminated depth corrugations of convergent disparity in narrow-band filtered random-dot stereograms. For a disparity range of 2.6 to 20.8 min arc and a spatial frequency range of 2.5 to 16.2 cpd, they found similar stereo-thresholds regardless of the spatial frequency compositions. Mayhew and Frisby (1979) concluded that depth information is processed the same way regardless of the spectral composition. Several other authors have some similar findings, i.e. thresholds increased proportionally with spatial frequency defined-disparity (Tyler, 1973; Schor, Wood and Ogawa, 1984; Heckmann and Schor, 1989). Poggio and Fischer (1977) found tuned excitatory and inhibitory neurons which showed peaks or troughs in their response at a small range of disparities, near fixation, and tended to give balanced responses to inputs from either eye. They also described near/far units which showed a very different pattern of response, elevation for large disparities. Marr and Poggio (1979) developed a computational theory of stereopsis premised on the findings the previous studies. Their model used size-disparity correlation to propose that disparity processing proceeds from a coarse scale to fine scale, and suggested that the disparity range over which depth is processed is proportional to the receptive field size of disparity coding mechanisms.

Schor and Wood (1983) investigated the range of disparity sensitivity as a function of spatial frequency/size. They used spatially defined difference-of-Gaussian functions (1-DoG patterns), with fixed height and variable width for reference and test stimuli. Their results indicated that as the reference disparity was increased, increasingly coarser scale stimuli provided the most precise matches. The range of disparities between a test and reference that produced depth percept increased with spatial frequency, the effect being greater for low spatial frequency than for high spatial frequency. The matching data for the lowest spatial frequency/widest test stimulus suggested that all stimuli appeared at the same, presumably indeterminate depth corresponding to a large reference disparity. This observation was consistent with Ogle's qualitative stereopsis. Both the lower and upper limits of disparity sensitivity increased proportionally with increase in DoG width. Further, the

results of their depth matching paradigm was most precise with relatively high frequency test stimuli at small reference disparities. They also investigated the magnitude of supra-threshold disparities subtended by various width patterns that were required to stimulate the perceived depth of a standard disparities subtended by a fixed standard narrow width pattern. Results showed depth inefficiencies for small supra-threshold disparities subtended by low spatial frequencies. Schor and Wood (1983) also used a DoG test stimulus and asked observers to discriminate the perceived depth of a test relative to the perceived depth of a thin line presented at fixed crossed and uncrossed disparities. He found that for stimuli of broad spatial periods (less than 0.5 cpd peak frequency), a larger disparity was required for the DoG stimulus than the standard thin line to match the perceived depth position of the test. He also found that the effect was greater for crossed than uncrossed disparities. Schor and Wood (1983) concluded that the disparity-depth relationship was not as effective for low spatial frequency as high spatial frequency for supra-threshold stimuli.

Other authors have also investigated the effect of spatial frequency/size on depth perception using pedestal disparities. Badcock and Schor (1985) used DOG stimuli to assess depth increment thresholds at a range of pedestal disparities. They found that thresholds scaled with stimulus width/frequency as spatial frequency increased from 0.15 to 0.5 to 2.4 cpd, but were similar for 2.4 cpd, 9.0 cpd and bar stimuli. They also found that thresholds increased rapidly with increase in pedestal disparity over a range of fine disparities (0-20 min arc), but much less so over a coarser disparities (20 to 80 min arc). They reported that the knee point in the data was not related to spatial frequency although the flattening of the disparity stereo-threshold function appears more pronounced at higher special frequencies. They suggested that the occurrence of the knee point represented the occurrence of diplopia or loss of depth precepts for spatial frequencies above 2.4, compared to fusion that occurred at pedestals with low spatial frequencies. Badcock and Schor's (1985) assertion is in contrast to Ogle (1952; 1953), who found no reflection in the transition from patent to qualitative discrimination. Siderov and Harwerth, (1993) have pointed out that the depth increment

threshold function will follow the function reported by Ogle (1953) and Blakemore (1970) when the depth offset is randomised between trials. Badcock and Schor (1985) did not interleave crossed and uncrossed pedestal disparities, which could have allowed their subjects to base their judgement on the relative separation of the diplopic targets, rather than on their relative depth. In a later study, McKee et al (1990) used a different method (modified method of constants) to assess increment threshold as function of disparity. They made observations that support the transition in depth discrimination based on disparity and were consistent with Ogle's categorisation.

The afore-discussed studies provide credible support for disparity processing units that are tuned to spatial frequency channels that can separately be stimulated or adapted (Wilcox and Allison, 2009). Part of the present investigation extends previous studies by directly examining the effect of spatial frequency on stereo-thresholds off the horopter when there is crowding (i.e. as function of pedestal spatial frequency composition). By psychophysical means, we investigated the proposal that the range of disparities, when being integrated, maybe tuned to the putative spatial frequency channels around, and off the horopter. We achieved this by measuring test target depth discrimination thresholds for different crowding configurations using narrow-band stimuli varying in their spatial frequency composition. The aim is to investigate the influence of differences in the spatial frequency composition of stereoscopic test and flankers on the stereo-thresholds.

Rationale

Previous reports suggested a strong relationship between the spatial frequency composition of test stimuli and thresholds for perceived depth (Stigmar, 1971; Westheimer and McKee; 1980b; Ginsburg, 1982). Low spatial frequencies convey information about the existence of an object and its general form and high frequency information allows for identification and detailed inspection of the object (Brown and Weisstein (1988). Reviewed studies here on the influence of spatial frequency composition on perceived depth support this claim of the

effect of spectral composition on spatial discrimination. That is, mechanisms that depth-disparity relationship appears to show spatial frequency composition specificity. That is, depth perception is affected by spatial frequency composition and the stereo-threshold therefore varies with spatial frequency of the test (Julesz and Miller, 1975; Mayhew and Frisby, 1981; Schor and Wood, 1983; Siderov and Harwerth, 1995). These results imply that disparity is processed through channels tuned to different spatial frequencies. Evidence for such channels has been reported using different investigative approaches and spatial tasks (Blakemore and Campbell, 1969; Blakemore and Julesz, 1971; Felton, Richards and Smith, 1972; Beverley and Regan, 1975). Since crowding is thought to reflect integrative or inhibitory mechanisms, whose outcome depend on the placement of flankers from the test target (Fox, 1970; Butler and Westheimer, 1978; Kooi et al., 1994; Felisberti et al., 2005; Astle et al., 2014), the present investigation of crowding in stereopsis, with flankers whose spatial frequency can be varied from the spatial frequency of the test, has the potential to help further our understanding of spatial frequency tuned-channels relevant to depth discrimination of test stimuli.

In general, crowding in 2D task is most effective when the spatial frequency composition of the flanking stimuli is close to that of the test stimulus (e.g. s. Andriessen and Bouma, 1976; Schor and Wood, 1983; Polat and Sagi, 1993; Kooi et al., 1994; Chung et al., 2001; Farell, 2006). If such a relationship holds also for stereoscopic crowding, then it will be predicted that crowding will be greatest when the spatial frequency composition of test and flanking stimuli are similar and least or non-existent when the relative spatial frequency compositions differ. As a first step, we investigated whether or not stereoscopic crowding shows spatial-frequency specificity. Using a thin bar test target (relatively broad-band in spatial frequency composition), we measured the effectiveness of adjacent flankers, with varying spatial frequency composition, to cause crowding. Our rationale is that flanking elements with a relatively fixed range of spatial frequencies (i.e. spatially defined Gabor patches) may not be as effective in producing crowding when compared to flankers that are closer in spatial

content to the thin test bar stimulus. Hence, if stereoscopic crowding is spatial frequency specific, then stereo-thresholds should vary depending on the flankers' effectiveness, and perhaps also show different peak effects with test-flanker separation. We also performed similar investigations using Gabor stimuli as both the stereoscopic test and the flanking elements. We predicted that if stereoscopic crowding is spatial frequency dependent, the magnitude of crowding should be maximised when the test and flankers have the same or similar spatial frequency composition of the test stimulus. Contrast effects reveal inhibition at high flanker contrasts, and facilitation at low contrasts (e.g. Legge, 1979). A prediction based on simple spatial frequency masking would be that decreasing the contrast of the flankers will affect discrimination of the test to reduce stereo-thresholds (Chung et al., 2001). Further, the influence of flanker size, in terms of the Gabor stimulus spatial frequency and spread on the optimum crowding was also tested. If Gabor size is a factor in the lateral interactions, then we expect crowding to decrease as the size is varied to perceptually look different from the test target.

Stereo-thresholds increase with distance from the horopter as a result of a shift in the sensitivity of mechanisms that process disparity. There is psychophysical evidence that suggest that depth discrimination may be subserved by distinct populations of neurons tuned to fine and coarse disparities (Julesz, 1971; Mayhew and Frisby, 1976, Felton, Richards and Smith, 1972). According to the proposal by a number of authors, (Felton, Richards and Smith, 1972; Poggio and Fisher, 1977), putative high spatial frequency channels process disparities around the horopter, where depth information is more sharply tuned, and low spatial frequency channels process disparity at distances further from the horopter. In Chapter 4, we found bar flankers exhibited maximum crowding effect on the fixation but crowding decrease with small flanker disparity around the horopter, and subsequently increased at greater flanker disparity off the fixation (see Chapter 4, fig. 4.1A). The next set of experiments involved displacing the Gabor flankers off the horopter, where crowding was reduced to see what the effects would be. While the peak spatial frequency of the test

stimulus was fixed, the disparity of the flanking elements was varied in crossed depth directions, while their spatial frequency composition was also varied. We hypothesised that if the same finding with the bars in Chapter 4 (Fig. 4.1A) holds true for mechanisms sensitive to spatial frequency, high spatial frequency Gabors displaced off the horopter would decrease crowding as found with our bar stimuli, but the decrement may not extend if processed by channels tuned to process disparity at distances further away from the fixation plane (Felton et al., 1972; Westheimer and McKee, 1980b). On the other hand, stereo-thresholds for displaced low spatial frequency flankers may remain relatively invariant across the range used or show elevation for ranges tuned to process coarse disparity at distances away from the fixation plane.

The investigation here using a more spatially defined stimuli (containing a restricted range of spatial frequencies) with characteristics that match the receptive field properties of neurons in primary visual cortex (Felton et al., 1972; Maffei and Fiorentini, 1973; De Valois et al., 1982) is capable of probing the different pathways tuned to disparity in the visual cortex. We believe that differences in perceived depth as a result of differences in spatial frequency composition of both the test and flanking stimuli, premised on an integrative mechanism of stereoscopic crowding, should provide further insight into the underlying mechanisms for stereoscopic depth perception and crowding.

METHODS AND APPARATUS

Descriptions of the basic methods are found elsewhere, in Chapter Two. Here, only variations to the methods that are particular to the experiments described in this chapter are detailed.

Stimuli

Two different types of stimuli were employed in the experiments. Relatively thin, luminous bars (spatially broad-band) (see Chapter 2) and sinusoidal luminance modulated patches

(Gabor patches or gratings). Gabor test target peak spatial frequency was either a relatively low 0.5 cpd or a relatively high 4 cpd composition, and the peak spatial frequency of the flankers was varied from 0.5, 1.0, 2.0, 4.0 cpd with a Gaussian envelope of standard deviation (σ ; SD) 0.5 deg (0.6 and 0.3 deg were used when Gabor flanker size was tested). Selection of the type of spatial frequency composition and spread were based on the range allowed by the apparatus used, and on their visibility at the testing distance but were within the normal range for the type of experiments done (Polat and Sagi, 1993). Gabors test target and flankers were displayed with 90% Michelson contrast. Fig. 5.0 shows a representation of the Gabor stimuli used (not actual stimuli). Depending on the experiment, the stereoscopic test target was either the thin vertical bar or a Gabor patch. The reference target was always a bar which matched the size of the test target (but usually 28 arc min long and 10 arc min wide), and displayed with the test target directly below the reference target and separated by a small spacing that varied slightly between observers. In Chapter 3, it was determined that the vertical separation between the test and reference influenced depth discrimination (see Fig 3.1), therefore test-reference vertical separation was varied slightly for each observer's optimum vertical separation. Flankers were arranged symmetrically around the test only. To ensure that the Gabors did not overlap at small test-flanker separations, the edges of the Gabors were truncated slightly (in the written programme) to create an 'edge' in order to allow for the test-flanker separations used, and for the separations to be consistent with test-flanker separations used in Chapters 3 and 4. The Gabor test target were therefore displayed with edge-edge separation from the flankers. When a Gabor patches was used as the test target and flanker stimuli, the test viewing distance (visual angle) was varied by reducing the test distance between the screen of the monitor and the observer (see Fig 2.2), but care was taken to ensure that the spectral content of the stimuli remained the same.

Stimuli were generated and presented on a gamma corrected high resolution luminance-calibrated single, monochromatic video monitor using a stereoscopic video system. The

video system presents alternate, non-interlaced video frames to each eye, controlled by a shutter system synchronised to the monitor frame rate. The refresh rate of the monitor screen was 120 Hz while that of the shutter for each eye operated at 60 Hz. The stimuli were generated with a high resolution graphic VSG (2/5) graphic card. The resolution of the monitor was 1024 * 769 displayable pixels.

The contrast and luminance of the display were calibrated using a Pritchard Spectrophotometer and OptiCal photometer. The mean luminance of the screen was 55.5 cd/m². However, as the open state transmission of the shutters was 15%, the luminance of the targets and monitor display was reduced accordingly.

Binocular disparity of the test bar and Gabor patches were produced by introducing small lateral pixel offsets of the bar tests in opposite directions and presented, in an alternate non-interlaced fashion, to each eye through an electric shutter goggle system. Binocular disparity of flankers was produced by introducing shifts in image to each eye through a shutter goggle system (i.e. programmable delay of the horizontal sweep of the video image of one eye). The test stimulus was presented in randomly interleaved trials at one of 8 possible disparities (12.5, 25, 37.5 and 50) sec arc either in front of, or behind the fixation plane, and one on the fixation plane. Flanker disparities used were 0 (at the plane of fixation), 0.5, 1, 2 and 4 min arc in crossed depth directions and were quasi-randomly varied between runs, but not between trials.

Subjects maintained binocular fixation at the plane of the stimulus screen by monitoring the relative positions of a pair of vertically aligned Nonius bars which were displayed onto the center of the screen and separated by a 30 sec arc fixation spot. The Nonius bars measured 1.4 min arc wide and 7 min arc long. The bars which were flickered in synchrony with the shutter goggles, were seen one by each eye, presented just prior to a trial and disappeared when the test stimulus was presented. The ambient laboratory lighting was kept low, but the frame surrounding the Nonius targets was clearly visible and provided a binocular fusion lock.

A custom written Matlab (version 10) script was used to create the stimuli and control the display and presentation times.

Subjects

Five adult subjects (SO, AC, SB, PI, VO) in total participated in the experiments, including the author and at least 4 subjects were used in each condition examined. Four of the subjects (i.e. all except the author) were naive to the objectives of the experiments. Observers were students and staff of ARU. All Observers had normal or corrected to normal visual acuity of 6/6 using glasses and normal stereoacuity (< 30 sec arc) measured clinically using TNO (Lameris Ootech) (Fricke and Siderov, 1997) stereotest. All subjects were well practiced or trained to make relative depth discrimination judgements, some having been involved in experiments in the previous chapters.

Procedure

The procedure used here was similar to that described in previous chapters. The observers positioned the shutter goggles on the face by maintaining the head upright in the primary position of gaze, and viewed the display through their natural pupils. They viewed the stimuli at a distance of 6m when the test was a bar or 3m when all Gabor stimuli were used, measured from the plane of the monitor to the plane of the shutter goggle. The stimuli were presented for 300 msec at a self-timed rate by having the observers press a response button when they were ready to start a trial. Each stimulus display was preceded by the Nonius display, which the observer used to ensure that their binocular eye vergence was correctly aligned with the plan of the monitor. Observers were instructed to wait until the upper and lower Nonius bars appear aligned and then press the start button to initiate the trial. The psychophysical procedure used a single exposure, forced-choice paradigm. During a brief response period, immediately following the presentation of the stimulus, the observers

pressed the appropriate response button to indicate that the test stimulus appeared in front of or behind the reference target.

In each trial, the test could appear with either crossed or uncrossed disparity or no disparity, relative to the reference target. However, observers were instructed to choose only between crossed or uncrossed responses. Immediate feedback was provided by a high and low pitched sound for correct and incorrect responses, and no sound when the test had no disparity. If the run was not aborted, a data file which is a complete with summary statistics for the experimental session was stored. The spatial specifications and spatial frequency characteristics required for each experiment session was specified in a programme condition file.

Analysis

Data were analysed in a similar manner as employed in previous chapters. Stereoscopic depth discrimination thresholds were determined by first constructing a frequency of seeing curve from the percentage of correct in front responses. The data were then fitted using probit analysis (Finney, 1971) to compute the stereo-threshold by estimating the semi-interquartile range ($=0.675$). That is, the disparity for which the proportion of trials that occasioned between 50% - 75% of correct in front response from the psychometric function. When indicated, threshold-elevation was calculated as an increase over baseline values (i.e. threshold determined for the test relative to only the reference bar). Each of the data points represents at least 150 trials, but usually 300 trials. Error bars represent ± 1 standard error of the mean.

When appropriate, two-way ANOVA was done to examine differences in the strength of the main effect of separation (including test only condition) and flanker type and the interaction between both effects on depth discrimination thresholds. Results of statistical significance must however to be jointly interpreted with graphical representation of depth discrimination tuning functions, ratios or main performance plotted since observer bias and fewer number

of subjects used in the experiments may render the calculated p value statistically insignificant (Twa, 2016).

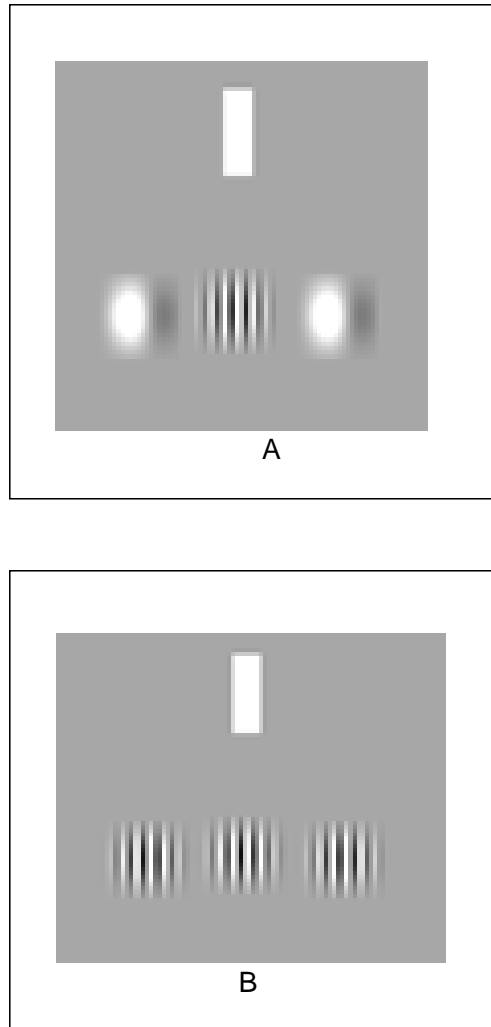


Fig. 5.0 Representation of the various stimuli in the Experiments (not actual stimuli used). In panels A and B, the central Gabor grating test is depicted with a 4cpd spatial frequency. In panel A, the outer flanking Gabors are depicted with the relatively low spatial frequency of 0.5 cpd, while the flanking Gabors shown in panel B depict the relatively high spatial frequency of 4 cpd. In both case, the Gabors have a standard deviation (SD) of 0.5 deg. In both panels, the upper reference is a relatively thin luminous bar (broadband). The stimuli were displayed with an edge-edge separation between test and flankers, and the test was slightly separated from the reference depending on the observer.

Crowding on the Horopter

Expt. 5.1A

Expt. 5.1A investigated the spatial frequency specificity to stereoscopic depth-crowding in the fixation plane. Crowding is known to be highest when test and flankers are similar in spatial frequency. To test this in an initial experiment, the magnitude and extent of crowding for a bar test (a relatively broadband frequency composition) in the presence of Gabor flankers that had their spatial frequency composition varied from 0.5 to 4.0 cpd was measured. Test-flankers appeared as edge-edge separation. The standard deviation (SD) of the Gabors was fixed at a σ of 0.5 deg. For comparison, crowding was also investigated for bar flankers 28 min arc long and 10 min arc wide. Because crowding diminishes with increasing test-flanker separation, and may demonstrate peak effects that vary for low and high frequency flanking Gabors, we also measured the effect across range of lateral separations up 6 min arc. The reference was a bar which appeared at the fixation plane, and vertically separated from the test by small spacing optimized for the observer's discrimination.

Control Experiments (Expt. 1B and 1C)

Expt. 5.1B

Expt. 5.1B was conducted as a control condition to determine if the observed interaction in Expt. 5.1A was spatial frequency dependant, and not due to other perceptual effects. The proposition was that, if crowding is spatial frequency dependent, then it will be most effective when the spatial frequency of the flankers is similar to that of the test. Therefore, in this experiment, only Gabor patches were employed as test and flanker stimuli. We examined this proposition within the small test-flanker separation that crowding is most effective. In one of two instances, first, the test spatial frequency was fixed at 0.5 cpd and flanker spatial frequency was quasi-randomly changed to 0.5 or 4 cpd between runs, but not between trials. In the second instance, the test spatial frequency was fixed at 4 cpd while the flanker spatial

frequency was quasi-randomly changed to 0.5 or 4 cpd between runs. The standard deviation of all the Gabors was fixed at a σ of 0.5 deg. Test-flankers were edge-edge separated up to 3 min arc. The reference was a bar and appeared at the fixation plane.

Expt. 5.1C

Expt. 5.1C investigated the effect of size (spread of the Gaussian envelope) of the Gabor flankers on stereoscopic depth-crowding. In the first part, the σ of the Gabor flankers was set at either 0.6 (selected to match the size of the bar test) or 0.3 degs SD (selected to match half the size of the initial spread) (for 1 cpd and 4 cpd) and experiments repeated across the test-flanker separations up to 6 min arc. In the second part, the test-flanker separation was fixed at 1 min arc (optimum crowding separation) and the spatial frequency of the Gabor flankers varied from 0.5 to 4 cpd. The comparative effect of size of the flankers (0.6 to 0.3 deg SD) on optimum crowding was then examined. For both experiments, the stereoscopic test and reference stimuli were vertical bars 14 min arc long and 2 min arc wide separated vertically as before. The experiment was conducted at 6m. The instruction to the observer remained unchanged, to respond to the relative depth direction of the test compared to the reference.

Expt. 5.1D

This additional control condition examined the perceptual effect of contrast of the Gabor flankers on crowding. If stereoscopic crowding is affected by contrast of the flankers, in a similar manner as spatial frequency based masking, variation in the contrast of the Gabor flankers would be expected to show a maximum effect when the flankers reached highest contrast, and decrease when the effective contrast is reduced. To test this, the spatial frequency of the test Gabor was fixed at 0.5 cpd and the contrast of 0.5 cpd Gabor flankers reduced from the maximum contrast available (i.e. reduced to 60% of the maximum contrast available (i.e. reduced by 40%) and then 40% (i.e. reduced by 60%). Further reduction on

contrast than those used made the targets harder to see. The effect was compared to the contrast for a 4 cpd spatial frequency flanker. In doing the task, the observer still indicated the depth direction of the test as either crossed or uncrossed relative to the reference. Stimuli dimensions were the same as in Expt 5.1A.

Crowding off the Horopter

Expt. 5.2A and 5.2B

Expts. 5.2A and 5.2B were conducted to investigate if disparity is modulated by spatial frequency-tuned mechanisms when Gabor flankers are displaced off the horopter. We measured depth discrimination thresholds for a condition when there is appreciable crowding (Expt. 5.2A), and one when there is less crowding (Expt. 5.2B).

In Expt. 5.2A, while keeping the edge-edge test-flanker separation fixed at 2 min arc (i.e. separation that produced appreciable crowding (i.e. optimum crowding distance (OCD))), the disparity of the flanking Gabors was varied in crossed depth directions up to 4 min arc. First, peak spatial frequency of the test was fixed at 0.5 cpd and the spatial frequency composition of the flankers changed from 0.5 or 4 cpd quasi-randomly between runs. Second, the peak frequency was fixed at 4 cpd and the flanker spatial frequency changed from 0.5 or 4 cpd.

In Expt. 5.2B, the edge-edge test-flanker separation was increased to 6 min arc (i.e. distance where crowding was less evident (i.e. least crowding distance (LCD))), and the same procedure as described repeated. It was important to do this as differences in depth discrimination due to variations in spatial frequency composition of the test and flankers displaced off the horopter have the potential to reveal mechanisms tuned to the integrative processing of disparities off the horopter. In both experiments, the standard deviation of the test and flankers Gabor's stimuli was fixed at a σ of 0.5 deg. The instruction to the observer remained unchanged, to respond to the relative depth direction of the test compared to the reference.

RESULTS

Expt. 5.1A Spatial Frequency Specificity of Crowding

Each panel of Fig. 5.1 shows the individual stereo-thresholds (sec arc) for the depth discrimination of a bar test stimulus, when surrounded by different flanking elements comprising flanking bars or flanking Gabor patches of varied spatial frequency content, plotted as a function of test to flanker edge-edge separation (min arc). Baseline performance measured for the test target alone relative to the reference target for each subjects is also shown and indicated by the dotted lines. Fig. 5.2 shows the threshold elevation, averaged across observers for the same conditions as Fig 5.1, and plotted against test to flanker edge-edge separation (min arc). The results suggests spatial-tuning, at least at small test-flanker separations. Crowding effect at the closest separation is quite appreciable, and differs among the observers (Fig 5.1), as also seen from the averaged threshold elevation (Fig 5.2). Consistent among the observers, at the smaller separations (Fig. 5.1), crowding reaches its peak when the spatial frequency of the flankers is close to that of the test stimulus, and reduces as the difference between their frequencies increases. On average, threshold elevation (Fig 5.2) at the peak crowding effect (optimum crowding) for a test stimulus surrounded by 0.5 cpd flankers (1.8) doubled when the flankers' spatial frequency was 4 cpd (3.9). For larger separations, thresholds elevation generally reduced, but did not show the same tuning as close separation regardless of spatial frequency. Generally, the crowding effect seems to drop of much quicker for the bar flankers (except for observer AC) compared to low spatial frequency flankers at large separation. Stereoscopic crowding with bar flankers appears to be comparable to the crowding observed with the 4cpd Gabor flankers. A two-way ANOVA (Fig 5.1) revealed that the interaction between main effect separation and flanker type on discrimination threshold was not statistically significant, [$F(12, 84) = 0.804$, $p = 0.645$]. There were however statistically significant differences in effect main effect separation [$F(4, 84) = 6.68$, $p = 0.000$] and flanker type [$F(4, 84) = 3.74$, $p = 0.008$]. A Tukey

post-hoc test revealed that compared to the no flanker condition, crowding was more evident at 1 min arc separation which was statistically significantly [$(57.8 \pm 84 \text{ min arc}, p = 0.009)$] compared to other separations which were not statistically significant [$(p > 0.05)$]. The results revealed that depth discrimination was significantly most difficult with 4 cpd [$(p = 0.009)$] and least with 0.5 cpd ($p = 0.997$) flanker types compared to the bar crowding.

A two-way ANOVA (fig. 5.2) revealed statistically significant main effect of separation, [$F(4, 84) = 15.81, p = 0.001$] and flanker type [$F(4, 84) = 5.61, p = 0.001$]. However, the interaction between test-flanker separation and flanker type on discrimination threshold was not statistically significant [$F(12, 84) = 1.74, p = 0.074$]. A Tukey post-hoc test revealed that crowding was more evident at 1 min arc separation [$(2.77 \pm 0.152, p = 0.000)$] and 2 min separation [$(2.016 \pm 0.152, p = 0.008)$] compared to the no flanker separation. The results revealed that depth discrimination was significantly most difficult with 4 cpd [$(p = 0.009)$] and least with 0.5 cpd [$(p = 0.997)$] flanker types compared to the bar crowding. Depth discrimination was significantly more difficult with 4 cpd compared to all other flanker types [post hoc, $p < 0.001$].

Expt. 5.1B Dependency of Crowding on Flanker Spatial Frequency Composition

The results averaged across all five observers are shown in Fig. 5.3, where mean stereo-threshold (sec arc) is plotted as a function of test-to-flanker separation for different flanking Gabor spatial frequencies. Consistent with previous results, crowding is optimum at the closest test-flanker separations for the separations tested. The crowding effect, as evidenced by the increase in threshold, was more pronounced when the spatial frequency of the test and the flankers matched. As shown in panel (A), when test target was a low 0.5 cpd spatial frequency composition crowding was pronounced, reaching its peak (127 sec arc (1.6X over baseline) for flankers of similar spatial frequency as the test target (i.e. 0.5 cpd). However, the crowding effect substantially reduced (to 79 sec arc) for the flankers which differed from the test target's spatial frequency (i.e. 4 cpd). In panel (B), when the test

target spatial frequency was changed to a high 4cpd spatial frequency composition, the crowding effect of the flankers was not as pronounced as described for the low 0.5 cpd spatial frequency test target described in panel A. Stereo-thresholds measured for the 4cpd test target were comparatively low, but demonstrated similar action as flankers of similar or opposite spatial frequency to the test, as was observed for the low spatial frequency test target. Individual data for each observer were generally similar and are shown in appendix A (Figs. A1 and A2).

A two-way ANOVA determined statistically significant main effect of separation, [$F(2, 53) = 3.34, p = 0.041$] and flanker type [$F(1, 53) = 7.03, p = 0.011$]. However, the interaction between main effect separation and flanker type on discrimination threshold was not statistically significant [$F(2, 53) = 0.295, p = 0.764$]. A Tukey post-hoc test revealed that crowding was more evident with the 0.5 cpd flanker type [$p = 0.011$] and varied with the type of test frequency used [$F(1, 53) = 43.90, p = 0.000$].

Expt. 5.1C Effects of Flanker Size on Crowding

Fig. 5.4 (A) shows stereo-thresholds, averaged across 4 observers for a bar test plotted as function of test-flanker separation for different flanker sizes (and spatial frequencies). Reducing the size of the flanking Gabor stimuli to half their original spread (i.e. from 0.6 to 0.3 deg) reduced the stereo-thresholds across all test-flanker separations. The effect was similar for both low and high spatial frequencies. At the closest separation, where crowding is optimum, the effect was more pronounced. For the 4 cpd flanker, thresholds decreased from 110 to 66 sec arc and from 55 to 45 sec arc for the 1 cpd flanker. Individual data are shown in appendix A (Fig. A3). A two-way ANOVA revealed statistically significant main effect of separation, [$F(3, 55) = 10.02, p = 0.000$], size of Gabor flanker used [$F(1, 55) = 13.70, p = 0.000$] and the flanker type [$F(1, 55) = 5.32, p = 0.025$]. The results however revealed that the interaction between main effect separation and size on flankers was not statistically significant [$F(3, 55) = 2.38, p = 0.080$].

Fig. 5.4 (B) plots the stereo-thresholds, averaged across the same 4 observers, as a function of flanking Gabor spatial frequency for the 2 different Gabor sizes used (0.3 and 0.6 deg spread) and when the test-flanker edge-edge separation was fixed at the OCD. The data were consistent with previous results, and show that crowding progressively increased with increasing flanker spatial frequency (i.e. increasing frequency closer to that of the test). The crowding effect was stronger with a wider spread (i.e. 0.6 deg wider Gaussian envelope) of Gabor flankers compared to the 0.3 deg spread. Data for each observer were generally similar and are shown in appendix A (Fig A4). At the OCD, two-way ANOVA revealed statistically significant main effect of type of flanker frequency, [$F(3, 24) = 6.45, p = 0.002$] and size of Gabor flanker used [$F(1, 24) = 9.20, p = 0.006$]. Discrimination was most difficult with the wider Gabor patch size compared to the smaller Gabor patch [$p = .006$] for the 4 cpd flanker type compared to other frequency types [post hoc, $p = 0.002$].

Expt. 5.1D Effect of Flanker Contrast on the Interaction

In a further control condition, stereo-thresholds for identifying the depth direction of a low spatial frequency test (0.5 cpd) target in the presence of the relatively low contrast flanker stimuli was investigated. The results, shown in Fig. 5.5, depict a reduction in depth discrimination thresholds as the contrast of the 0.5 cpd flanking Gabors was reduced. As observed in Expt.1B (Fig. 5.3), crowding was more substantial with 0.5 cpd flankers which was similar to test target frequency relative to the 4cpd flanker. However, contrast reduction for 0.5 cpd effectively reduced the crowding effect when the original contrast was decreased by about 40% (threshold reduced from 225 to 63 sec arc), and then by 60% (i.e. to 40% from original contrast) (threshold reduced to 56 sec arc).

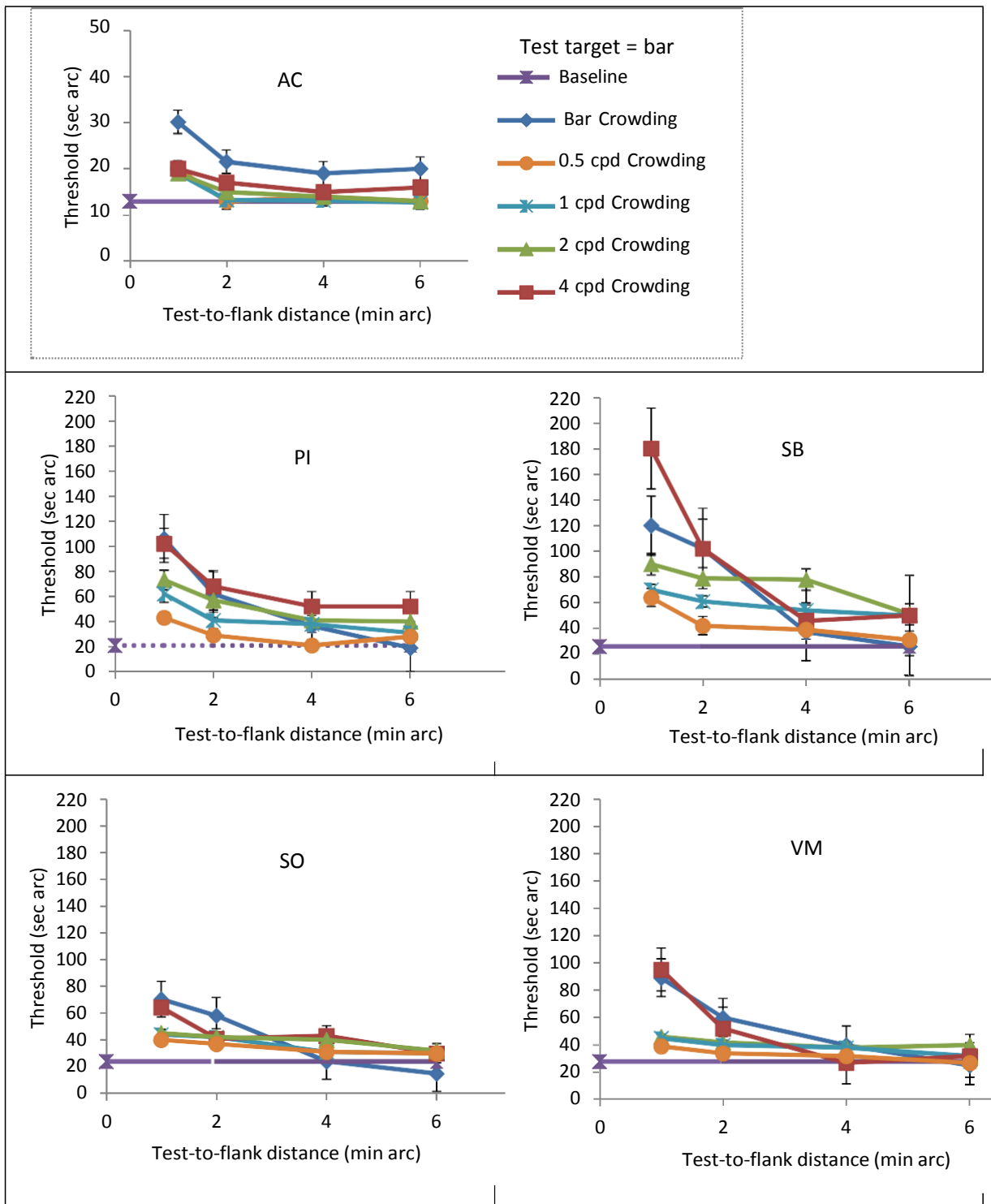


Fig. 5. 1 Expt. 5.1A Test Bar Crowding for a Range of Flanker Spatial Frequencies.

Each panel shows, for each individual observer, performance for test bar stereo-thresholds (y-axis) plotted as a function of separation for a range flanking stimuli spatial frequency composition (x-axis) (AC is plotted on a different scale because of his comparatively low thresholds). The colours represent bar (blue closed diamond symbols), 0.5 cpd (yellow closed circle symbols), 1 cpd (sea blue asterisk symbols), 2 cpd (green closed triangle symbols) or 4.0 cpd (red closed square symbols) different spatial frequencies, and baseline threshold (violet crossed dashed lines symbols). Error bars represent +/- 1 standard errors.

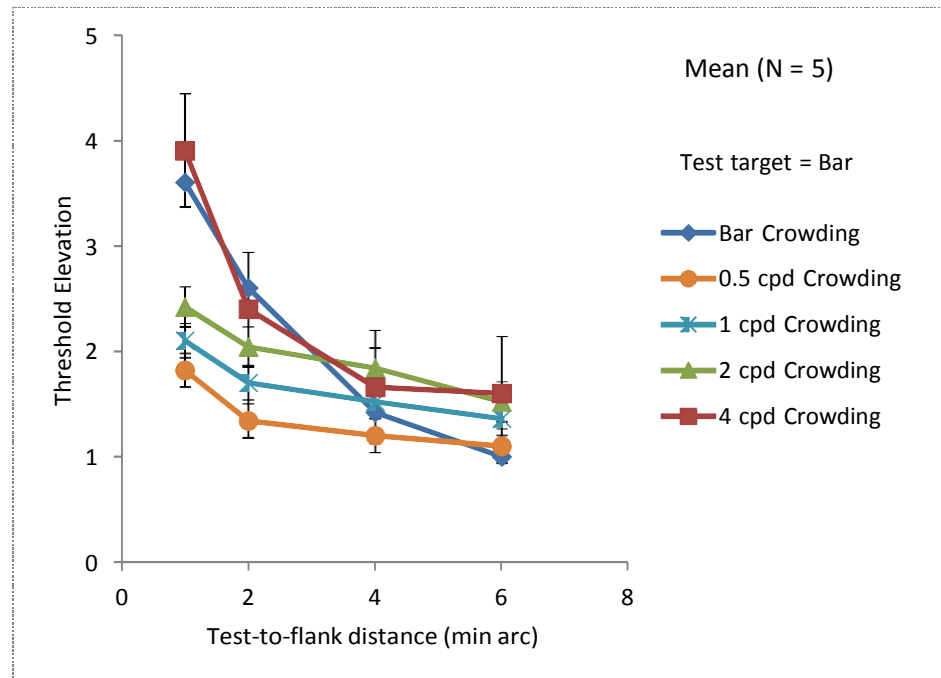


Fig. 5. 2 Expt. 5.1A Mean Performance for Test Bar Crowding for Range of Flanker Spatial Frequencies. Graph shows mean threshold elevation (y-axis) averaged across the 5 observers, plotted as a function of flanking stimuli spatial frequency across test-flanker separations. The colours represent bar (blue closed diamond symbols), 0.5 cpd (yellow closed circle symbols), 1 cpd (sea blue asterisk symbols), 2 cpd (green closed triangle symbols) or 4.0 cpd (red closed square symbols) different spatial frequencies and error bars represent ± 1 standard errors.

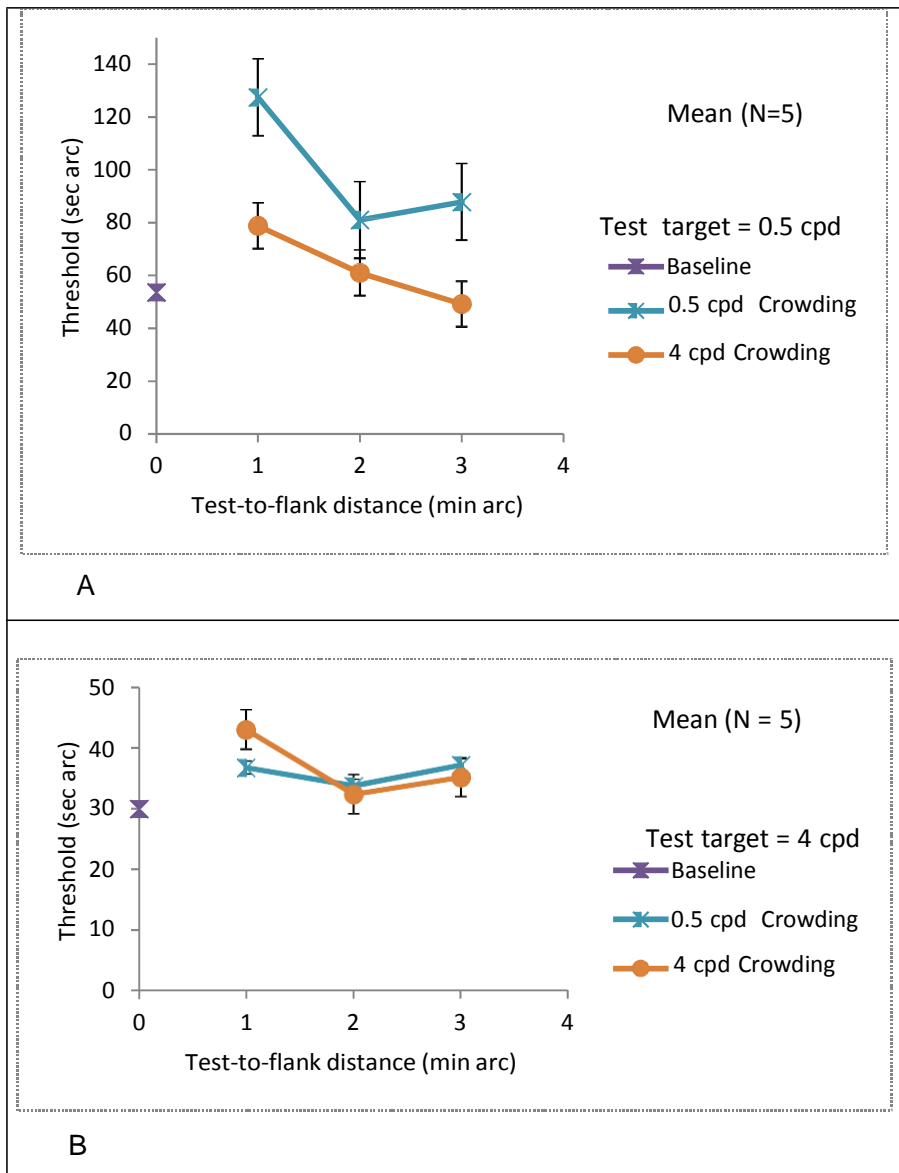


Fig. 5. 3 Expt.5.1B. Dependent of Crowding on Spatial Frequency. *Graphs shows mean stereo-threshold (y-axis) averaged across the 5 observers, plotted as a function of flanker spatial frequency for small separations (different scales are used due to marked differences in effect). In Panel A, the test spatial frequency was fixed at 0.5 cpd and in Panel B, the test spatial frequency was fixed at 4cpd while the flankers' spatial frequency was changed to either 0.5 cpd or 4 cpd. The colours are 0.5 cpd (sea blue asterisk symbols), 4 cpd (yellow closed circle symbols) different spatial frequencies flankers and baseline threshold (violet crossed symbols) and error bars indicate. +/- 1 standard errors.*

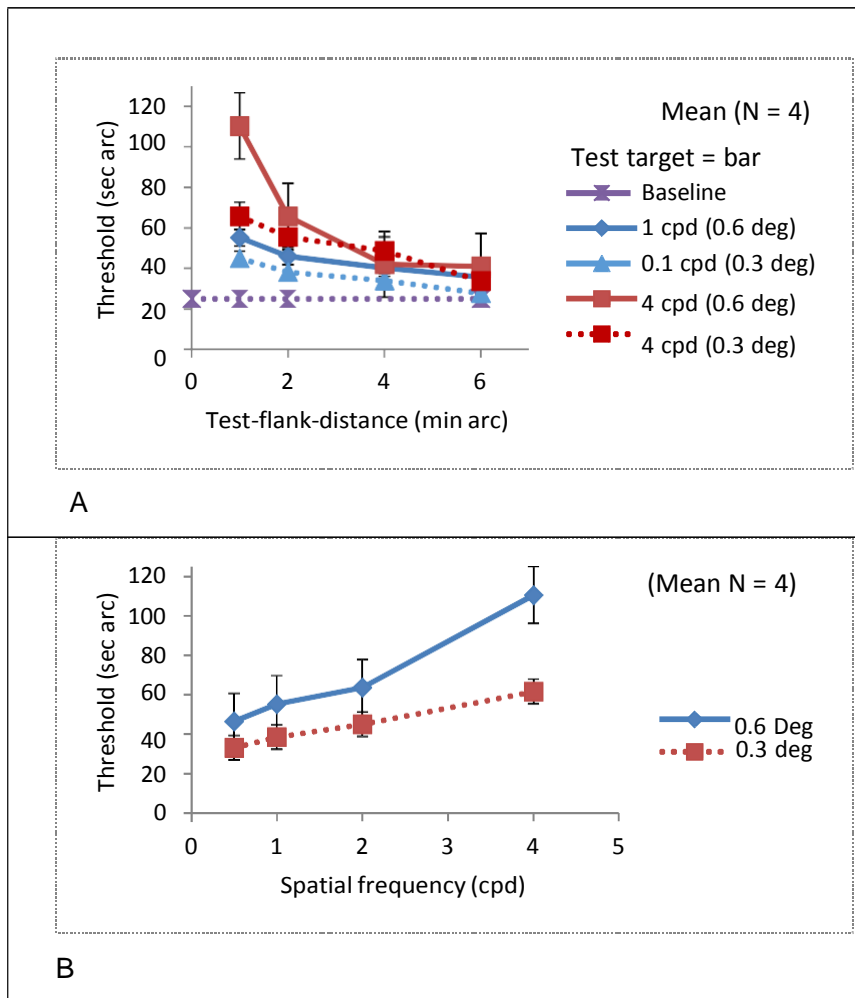


Fig. 5. 4 Expt.5.1C. Effect of Flanker Size on Crowding. Each panel depicts mean stereo-threshold (y-axis) averaged across the 4 observers plotted as a function of test-flanker separation (Panel A) and range of spatial frequency (panel B) for 2 flanker sizes. In the graphs, the comparative effect of 0.3 and 0.6 degs standard deviation of a low (1 cpd) and a high (4 cpd) spatial frequencies flankers on bar test are made. In Panel A, the colours represent Gabor flanker spreads of 0.6 deg of 1 cpd frequency (solid blue closed diamond symbols), 0.3 deg of 1cpd (dashed blue closed triangle symbols), 0.6 deg of 4 cpd (solid red closed square symbols), or 0.3 deg of 4 cpd (dashed red closed square symbols)and baseline threshold (violet crossed symbols). In Panel B, colours are 0.6 cpd (solid blue closed diamond symbols) and 0.3 cpd (dashed red closed square symbols) Gabors flanker spreads and error bars represent ± 1 standard errors.

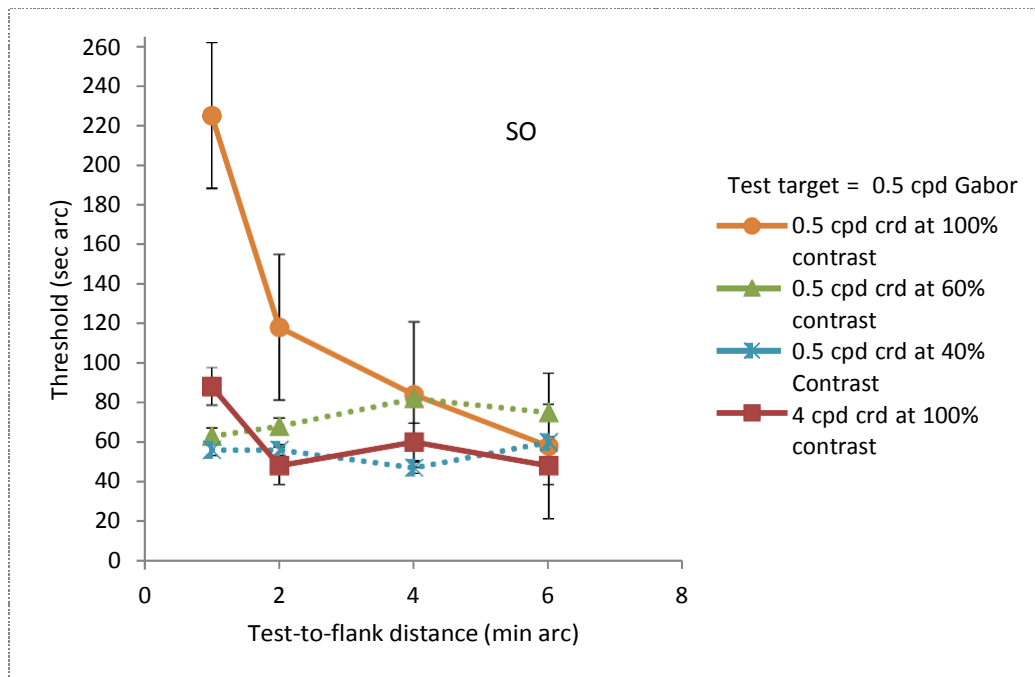


Fig. 5. 5 Expt.5.1D. Effect of Flanker Contrast on Crowding.

Stereo-threshold (y-axis for a single observer) is plotted as a function of flanker contrast across test-flanker separation (x-axis). The test target spatial frequency was fixed at 0.5 cpd and the effect of crowding measured for 0.5 and 4 cpd flanker composition. The contrast for 0.5 cpd flankers which produced most crowding (compared to the 4 cpd flanker) was reduced to assess the effect of contrast reduction on crowding. The colours represent the original (100%) (yellow closed circle symbol), 60% (i.e 40% reduction of original contrast) (dashed green triangle symbol), 40% (60% reduction of original contrast) (dashed sea blue asterisk symbol) contrast of the 0.5 cpd spatial frequency composition flanker, and 4 cpd flanker (red closed square symbol) and error bars represent ± 1 standard errors.

Expt. 5.3A and 5.3B: Tuning Crowding to the Flankers Disparity

Each panel in Fig. 5.6 shows the mean stereo-thresholds, averaged across 5 observers, for a fixed test stimulus, either a low spatial frequency Gabor (0.5 cpd shown in Panel A) or a relatively high spatial frequency Gabor (4 cpd shown in Panel B) as a function of flanker disparity off the horopter. In each condition, the test Gabors were surrounded by flanking Gabor stimuli of either low (0.5cpd closed diamond symbols) or high (4.0 cpd closed square symbols) spatial frequency separated from the test at the optimum crowding distance (OCD). Consistent with previous results (Figs 5.1 and 5.3), stereo-thresholds were higher when the test target comprised a low spatial frequency Gabor. However, for the 0.5 and 4 cpd flanker frequency composition used, the performance with both stimuli were similar, which revealed a reduction in threshold from the fixation with increasing crossed flanker disparity, until the flankers were sufficiently displaced (usually 0.5 min arc for high 4cpd and 1 min arc for low 0.5 cpd frequency compositions), then thresholds elevated again. In Panel A, when the test was of low frequency (0.5 cpd), the results indicate that crowding is produced on the horopter for both the low and high spatial frequency flankers. However, displaced 4 cpd flankers enhanced performance across all depth positions than the 0.5 cpd frequency flankers. However, improvement in performance for the 4 cpd flanker frequency composition does extended for all depth separations as the crowding effect was restored at greater depth separations. A two-way ANOVA did not reveal statistically significant main effect of relative depth separation, [$F(4, 40) = 2.43, p = 0.063$], though pairwise comparison revealed main effect at 2 min arc depth separation relative to the fixation condition [$p = 0.030$], compared to other depth separations which were statistically not significant. There was statistically significant main effect of flanker type used [$F(1, 40) = 11.21, p = 0.002$]. The interaction between main effect depth separation and flanker type on discrimination threshold was not statistically significant [$F(4, 40) = 0.382, p = 0.820$]. A Tukey post-hoc test revealed that the effect of depth separation of depth discrimination was statistically not significant all levels of flanker depth position [$p < 0.05$].

In Panel B, when the test was a high frequency (4 cpd), stereo-thresholds were generally low for all flankers, but recorded an appreciated rise when the flankers were well displaced off the horopter. The crowding effect of low spatial frequency flankers was generally slightly higher at greater flanker disparities. A two-way ANOVA did not reveal statistically significant main effect of relative depth separation, [$F(4, 40) = 2.43, p = 0.071$], and flanker type [$F(1, 40) = 0.64, p = 0.801$]. Pairwise comparison revealed main effect at 1 min arc depth separation relative to the fixation condition [$p = 0.026$], compared to other depth separations which were statistically not significant. The interaction between main effect depth separation and flanker type on discrimination threshold was not statistically significant [$F(4, 40) = 1.03, p = 0.404$]. A Tukey post-hoc test revealed that the effect of depth separation on depth discrimination was statistically not significant at all levels of flanker depth position [$p < 0.05$].

The results for the concurrent experiment conducted with the test flanker separation fixed at the least crowding separation (LCD) are shown in Fig. 5.7. Here, stereo-thresholds did not reduce from the fixation plane, but rather revealed a systematic rise as disparity of the flankers increased away from the horopter (i.e. crowding was strengthened). The crowding effect was also more pronounced when the test Gabor comprised the relatively low spatial frequency. Generally, low spatial frequency flankers produced worse performance than that produced by high spatial frequency at greater relative depth separations off the horopter. Individual data were generally similar, albeit some slight differences which are shown in appendix A for the OCD (Figs. A5 and A6) and LCD (Figs. A7 and A8) separations respectively. For the 0.5 cpd frequency test target, a two-way ANOVA revealed statistically significant main effect of relative depth separation, [$F(4, 30) = 13.93, p = 0.001$] and flanker type used [$F(1, 30) = 6.85, p = 0.014$]. The interaction between main effect depth separation and flanker type on discrimination threshold was not statistically significant [$F(4, 30) = 1.214, p = 0.325$]. A Tukey post-hoc test revealed that the effect of separation on depth discrimination was statistically significant at 1 [$p = 0.047$], 2 [$p = 0.001$] and 4 [$p = 0.001$] min arc levels of flanker depth position relative to the fixation condition. When the test was a high

4 cpd frequency target, two-way ANOVA revealed statistically significant main effect of relative depth separation, [$F(4, 30) = 3.62, p = .013$], but not flanker type [$F(1, 30) = 1.19, p = 0.281$]. The interaction between main effect depth separation and flanker type was however not statistically significant [$F(4, 30) = 0.784, p = 0.542$]. A Tukey post-hoc test revealed that the effect of depth separation of depth discrimination was statistically significant at only 4 min arc [$p = 0.012$], level of flanker depth position relative to the fixation condition.

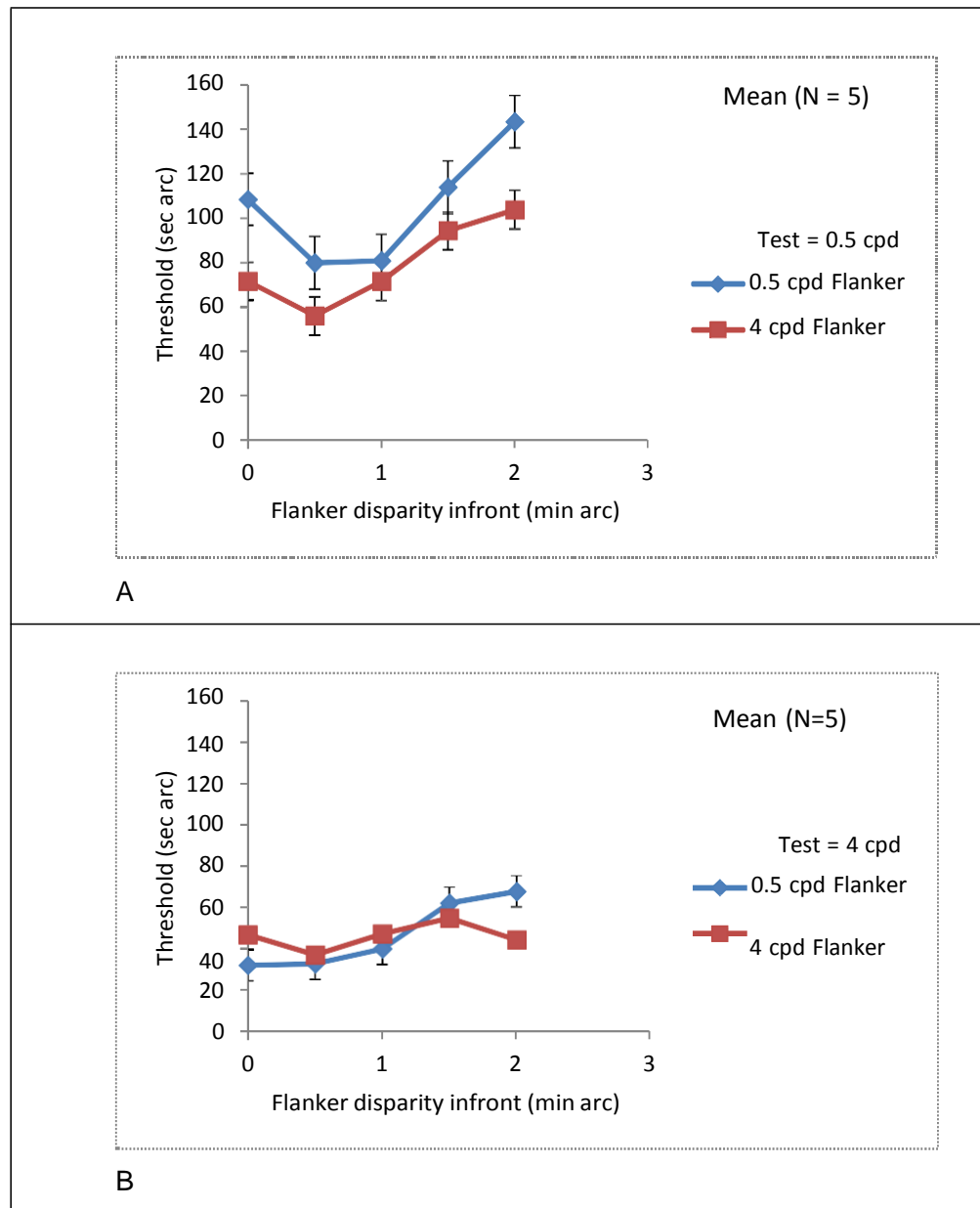


Fig. 5. 6. Expt.5.3A. Effect of Flanker Spatial Frequency for a fixed OCD Stimulus.

Each panel depicts mean stereo-threshold (y-axis) averaged across the 5 observers plotted as a function flanker disparity at OCD. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) flanker spatial frequency, for a fixed low (0.5 cpd) and high (4 cpd) test target in panel A and B respectively. All Gabors have the same SD of 0.5. The colours represent 0.5 cpd (blue closed diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies, and error bars represent ± 1 standard errors.

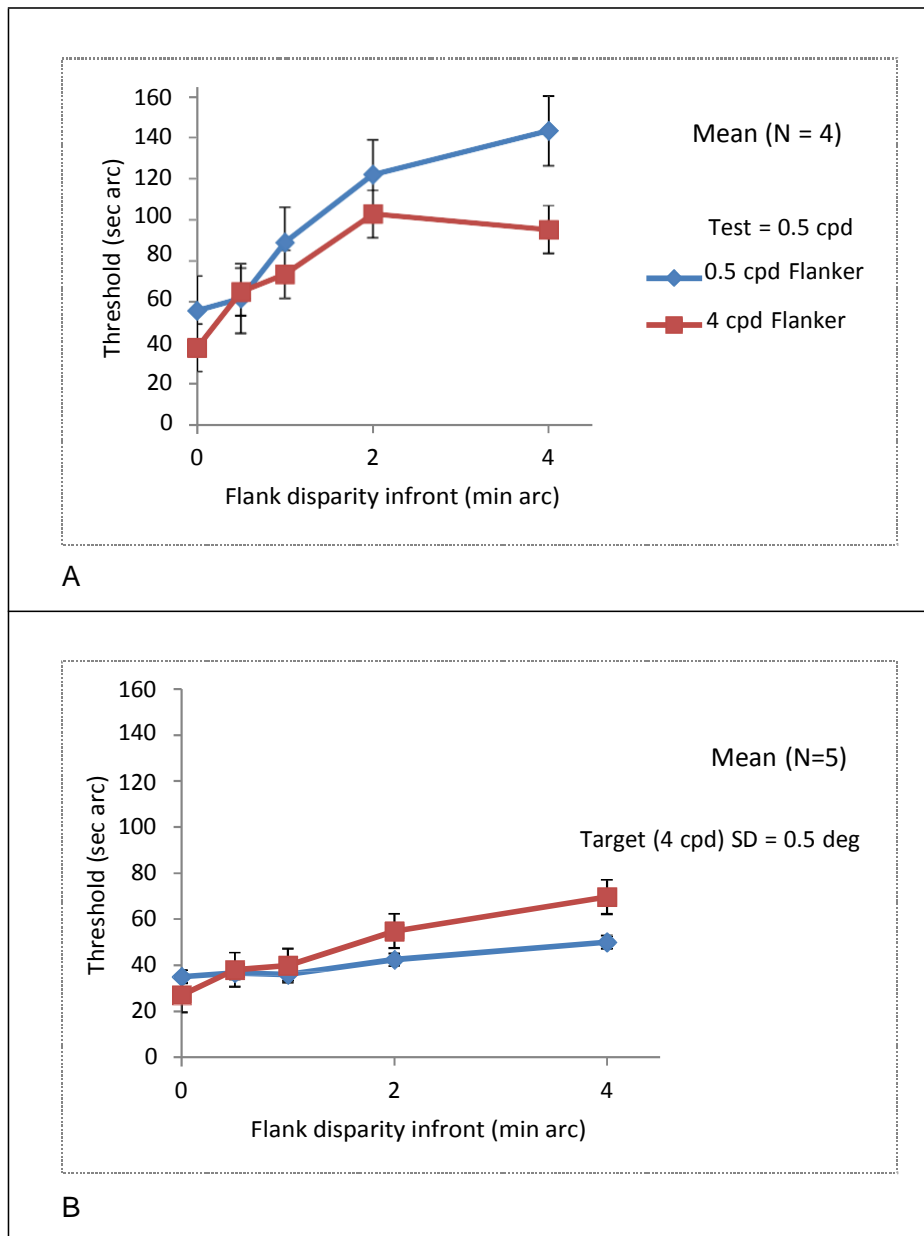


Fig. 5. 7. Expt.5.3B. Effect of Flanker Spatial Frequency for a fixed LCD Stimulus.

Each panel depicts mean stereo-threshold (y-axis) averaged across the 5 observers plotted as a function test-flanker depth separation. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) frequency flankers on a fixed low (0.5 cpd) and high (4 cpd) test frequency composition in panel A and B respectively. All Gabors have the same SD of 0.5. The colours represent 0.5 cpd (blue closed diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies, and error bars indicate ± 1 standard errors.

DISCUSSION OF RESULTS

We investigated the effects on stereoscopic depth discrimination, of differences in the spatial frequency composition of a test target and flanking stimuli. Our goal was to assess the effects of spatial frequency on the spatial properties of stereoscopic crowding on and off the horopter, in order to better understand the underlying psychophysical processing channels that encode for stereoscopic crowding. For test and flankers located on the horopter (i.e. at the plane of fixation) optimum crowding for both low and high spatial frequency flankers occurred at similar small test-flanker separation, and generally the threshold varied across separation, suggesting that the extents of crowding scaled with their receptive size of psychophysical mechanism that encode for crowding. For the range of spatial frequency and disparities used, the size of both the carrier (spatial frequency) and the envelope (spread), and contrast of the Gabor flankers had an influence on the measured crowding, suggesting the involvement of size-disparity mechanism. The effect of flanker contrast reduction also showed that crowding exhibits similar interaction as masking at the fovea. In the subsequent experiments, when the flankers were set with a pedestal disparity off the horopter, depth discrimination thresholds revealed a systematic reduction for small test-flanker depth separations, then elevation in thresholds at larger separated in depth. Both high and low spatial frequency flanker disparities demonstrated a similar tuning function, relative to fixation plane, but high spatial frequency flankers effectively reduced crowding outside the fixation plane, compared low spatial frequency flankers which showed pronounced elevation in crowding at farther distances off the horopter. These results support the idea of independent psychophysical channels, differently sized mechanisms that process spatial frequency disparities in a similar manner.

Spatial Properties and Dependency of Stereoscopic Crowding on Spatial Frequency

Previous results have suggested a strong relationship between the spatial frequency composition of test stimuli and spatial discrimination (Ginsburg, 1982; Campbell and Robson, 1968; Wilcox and Allison, 2009). The perceived depth of a spatially discrete test shows spatial frequency selectivity because of underlying processing of neural units tuned to those specific frequencies (Julesz and Miller, 1975; Marr and Poggio, 1979; Mayhew and Frisby, 1981). Psychophysical results also support the existence of multiple channels in the visual system, each tuned to a relatively narrow range of spatial frequencies (e.g. Campbell and Robson, 1968; Brown and Weisstein, 1988). There is also evidence that crowding is highest when test and flankers are similar in stimulus properties (e.g. Kooi et al., 1994), suggesting that stereoscopic crowding could also be spatial frequency dependent. Consequently, based on previous findings (e.g. Polat and Sagi, 1993; Chung et al., 2001) we predicted that for test and flanking targets that differed in their spatial frequency composition, depth discrimination thresholds would be influenced by a lateral interaction that is spatial frequency dependent.

We obtained results which showed that crowding differed with the spatial frequency of flanking stimuli and that optimum crowding occurred at a similar small test-flanker separation for all flanking stimuli (Fig 5.1). In addition, the optimum crowding effect occurred when the flanking spatial frequency composition was close to that of the test spatial frequency. Consistent with our prediction, high spatial frequency flanking Gabors were more effective in producing crowding, and exhibited a crowding pattern similar to that found when the flankers were bars. At peak (i.e. optimum) crowding, for the high (4cpd) spatial frequency Gabor flankers threshold elevation was about four times (4X) over baseline value, while that of the low (0.5cpd) spatial frequency Gabor flankers was twice (2X) over baseline (Fig 5.2). When the spatial extent of crowding is considered, generally the effect for high spatial frequency flankers appeared to drop off faster (except for observer AC) and was comparable to bar crowding presumably because it contained equivalent high spatial frequency

components as the test bar and facilitated discrimination at larger separations (Westheimer and McKee, 1980b). The effect could simply reflect differences in the visibility of the Gabor flankers since different spatial frequencies have different visibility levels. However, this did not manifest as different peak effects for the range of frequencies used. If crowding spatially scales with the spatial frequency of flankers across the psychophysical receptive size of the mechanism mediating it, then we expected similar increment or decrement in crowding to be found for each flanker's spatial frequency at each test-flanker separation. Indeed, that was the case at least at small separations (see Figs 5.1 and 5.2) where the flankers produced optimum crowding. Polat and Sagi (1993) employed Gabor-by-Gabor stimuli and similarly found that crowding scaled at small test-flanker separation for different spatial frequency-defined flankers. Wilson et al. (1983) who measured depth increment thresholds, found that lower spatial frequency sensitive mechanisms had larger bandwidths than higher spatial frequency sensitive mechanisms, though they did not find scaling of the crowding effect.

We asked the question: Could the difference in stereo-thresholds be due to other perceptual information available in the Gabor patches (related to their physical appearance)? We asked this question bearing in mind also, that the optimum crowding effect did not differ for low and high frequency flankers.

In a control condition (Expt. 5.1B), Gabor patches were used as test and flankers to investigate if crowding also depended on flanker spatial frequency. If different psychophysical channels are involved in the processing of stereoscopic depth perception, then the ability to discriminate the test spatial frequency would depend on the similarity of the flanker spatial frequency (i.e. stereo-thresholds should be reduced or crowding should be less or absent) (Schofield and Georgeson, 1999).

The results for this control condition (Fig 5.3) shows that the crowding is spatial frequency dependent as optimum crowding was achieved when the spatial frequency of the test and

flankers was similar. That is, optimum crowding occurs for test and flankers that had their spatial frequency similarly defined, but less when their spatial frequency composition differed. This result may also account for the crowding evident in the findings of Expt. 5.1A, when the bar test target was used and different spatial frequency flankers were used. The higher depth discrimination thresholds recorded for low spatial frequency test stimuli compared to the high spatial frequency test for this experiment is consistent with previous reports that stereo performance is generally better with higher spatial frequencies (Schor and Wood, 1983; Siderov and Harwerth, 1995). However, there was no appreciable difference between thresholds with different flanker spatial frequencies when the test target is 4cpd, but there is a difference at 0.5 cpd. This could reflect the nature of the different channels, but could simply reflect the wide inter-individual variation found (see figure A2).

Our findings can be reconciled with previous studies which showed a strong effect of spatial frequency on perceived depth (Blakemore and Julesz, 1971; Stigmar, 1971; Westheimer and McKee, 1980b; Schor and Wood, 1983; Polat and Sagi, 1993; Chung, Levi and Legge, 2001). Crowding here demonstrated spatial frequency dependence, being optimum for similar spatial frequency of test target and flankers, but also some crowding occurring when the test target and flankers spatial frequency differed (Fig 5.3). Scaling and dependence of crowding on flanker spatial frequency suggests physiological processing by the visual system, which does not support the suggestion by Bondarko and Danilova (1997) and Hess et al., (2000) that crowding is due to the analysis or 'physics' of the stimuli which occur prior to any neural processing. According to Hess et al., (2000) visual performance are degraded because nearby flankers interfere with detecting information about a test target in a manner that the energy in the frequency band most important to detection is increased at higher spatial frequencies for foveal tasks. The reduced depth discrimination threshold for high spatial frequency Gabor test agrees with Wood and colleagues, that the disparity-depth relationship is more effective (i.e. processed more efficiently) for high spatial frequency test target compared to low spatial frequency test target (Schor and Wood, 1983; Legge and Gu,

1989; Siderov and Harwerth, 1995). Legge and Gu (1989) found that stereo-thresholds were lowest near 3 cpd and rose in proportion to spatial period at lower frequencies. Crowding was more pronounced with high spatial frequency flankers and comparable to bar flanker crowding effect when the bar test target was used (Figs. 5.1 and 5.2) because they contained similar spatial frequency components as the test bar (Westheimer and McKee, 1980b; Schor and Wood, 1983; Howard and Rogers, 1995). Crowding for bar flankers and in some cases high spatial frequency diminished quicker at larger lateral separations compared to relative lower spatial frequency flankers because depth discrimination may have been enhanced by the edges of the bars or high spatial frequency flankers (Schor and Wood, 1983; Westheimer and McKee, 1980b). Westheimer and McKee (1980b) reported similar reduction in stereo-threshold for high spatial frequency flankers at wider separation relative for line tests. They employed several forms of spatial frequency filtering and observed that stereo-thresholds were elevated for the range of spatial frequencies used. The effect when high-pass filtering was used was more deleterious on stereo-thresholds than low-pass filtering. Schor and Wood (1983) found a similar deleterious effect of high spatial frequency on stereo-threshold for DOG and bar stimuli of equal size. Crowding effects found in configurations, where the crowding effect has been attributed to the separation between stereoscopic test target and surrounding flankers have suggested that flanker effect at small separations are mediated by short-range cortical connections whilst flanker effects at large separations been ascribed to long-range connections in the visual cortex (Wilson et al., 1983; Das and Gilbert, 1999).

The results here (Figs 5.1 and 5.3) suggest that crowding is spatial frequency selective, as demonstrated by the spatial scaling at least at the small separation, which suggest the crowding vary with the spatial frequency tuning of the mechanism. The finding supports the idea that the short range lateral interactions that mediate crowding varies with spatial frequency. The differences in crowding induced by the different spatial frequency flankers (Fig 5.1) and difference in depth discrimination thresholds found for the low and high spatial

frequency tests (Fig 5.3) reflect the processing by independent channels (Julesz and Miller, 1975), but possibly the interaction between the channels since test and flankers of different spatial frequency composition still produced some crowding.

Influence of Flanker spread on the Interaction

A competing grouping hypothesis for crowding predicts that crowding is greatest when the test and flankers have similar spatial properties (Kooi et al., 1994). In Chapters 3 and 4, we found graded influence of flanker width on stereo-thresholds. Here, using Gabor gratings we obtained results which indicate that differences in flanker size, in grating spatial frequency and Gaussian envelope (patch spread), influenced the measured depth discrimination of the test bar. The effect was consistent for the relatively low (1 cpd) and the relatively high (4cpd) flanker spatial frequencies tested. Smaller Gabor flankers decreased crowding across all test-flanker separations for most observers. At small test-flanker separations, the effect of the Gabor spread was substantial (Fig 5.4). There was apparent reduction in crowding effect for smaller patches (half size) and increment in crowding effect for wider patches. For large test-flanker separations, the effect of spread on crowding was not as pronounced for both the smaller and wider Gabor sizes. These results are consistent with those of Kooi et al. (1994), who showed that the magnitude of crowding is greater when the target and flankers were similar rather than different in terms of their spatial frequency. Felton et al (1972) found similar effect with flanker widths, and suggested that disparity selective neurons may be sensitive to particular sizes of flankers, and argued in support of a size-disparity correlation in human stereopsis. For the limited range of flanker widths and spatial range of spatial frequency used here, crowding was affected in a similar manner consistent with what would happen in masking (Polat and Sagi, 1993; Wood et al., 2002). Though difference in visibility of the flanker may have accounted for some of observed effects, it was apparent that increasing the spatial frequency and the spread (width) of the Gabors flankers resulted in

corresponding increase in crowding, a prediction also consistent with spatial frequency based masking.

Effect of Flanker Contrast on Stereoscopic Crowding

We asked the question: Does foveal stereoscopic crowding exhibit masking characteristics?

Decrease in stereo acuity caused by reduction in stimuli contrast are not uncommon in stereo tasks (e.g. Legge and Gu, 1989). One held view of foveal crowding is that is a form of masking (Legge and Gu, 1989; Polat and Sagi, 1993; Woods et al., 2002; Levi, Klein et al., 2002). Schor and Howarth (1886) contended that the effects of spatial frequency on depth discrimination could be due to differences in contrast of the stereoscopic stimuli. Liu (2001) and Danilova and Bondarko (2007) also asserted that perceptual information available from the amplitude difference spectra of Gabors may not be sufficient to explain differences in discrimination. In pattern masking, when the contrast of flankers is increased, the discrimination of the test becomes difficult, increasing the threshold, but when the contrast of the flankers is reduced discriminating the test becomes relatively easier, reducing the thresholds (Legge and Gu, 1989). In a similar manner, in lateral masking (i.e. where test and flankers do not overlap), the presence of the visible flankers affects the thresholds, increasing at close separations and decreasing (facilitation) at larger test-flanker separations (Polat and Sagi, 1993). If crowding is indeed a form of masking or has similar properties, then we expected that crowding would reduce when flanker contrast is reduced, but crowding would increase at higher flanker contrast.

The results of the control experiment (Expt. 5.1D) indicate that reducing the contrast of the 0.5 cpd flanker effectively decreased crowding. Crowding was optimum when the contrast between the test and the flankers was similar (condition in which the contrast of the flankers

was greater than that of the test target was not tested), but reducing contrast of the low 0.5 cpd spatial frequency flanker, which recorded greater crowding at the outset, effectively reduced crowding to levels below those seen in the presence of the high spatial frequency flankers (Fig 5.5). The typical decrement in crowding, where the low contrast flanker improved depth discrimination of the test at high contrast or vice versa is cognisant of a masking effect (Richards, 1972; Lehmkuhle and Fox, 1980). This relationship has been demonstrated for other experiments in sine-on-sine masking (e.g. Legge, 1979; Legge and Foley, 1980) and Gabor-by-Gabor lateral masking (Zenger and Sagi, 1996). The results supports the idea that relative effects of contrast are greater for low than for high spatial frequencies, and the link between crowding and masking. Moreover, in the classical stereoscopic crowding study by Butler and Westheimer (1978), due to the narrow spatial tuning of crowding that they found, and the fact that the crowding effect was greatest when there was a temporal delay between the test and flankers, the interference reported has been related to stereo-based masking (Whitney and Levi, 2011)

The flanker contrast reduction result (Fig. 5.5) here which demonstrated that crowding can be reduced by reducing contrast of Gabor flankers indicates that, under the conditions of our experiments, stereoscopic depth crowding at the fovea is affected by the difference in contrast between test and flankers, being optimum at similar contrast and reduced at low contrast flanker contrast. Such an effect of contrast supports the idea that stereoscopic crowding may share similar mechanisms as lateral masking (since the test-and flankers did not overlap). Unlike Kooi et al. (1994) and Chung et al (2001) whose results did not to show that crowding is optimum when the test and the flanking stimuli contrast were the same, our findings reveal a strong influence of contrast and flanker size on crowding, which is consistent with the postulation that posits a grouping hypothesis to explain crowding. With regards to the stimulus property of contrast, the grouping hypothesis predicts that crowding should be optimum when the contrast of the test and its flankers are the same, and reduces when the contrast of the flankers is either higher or lower than that of the test (e.g.

Andriessen and Bouma, 1976; Legge and Gu, 1989). The effect of contrast on the depth discrimination thresholds, is also consistent with the idea that disparity is computed from responses of size-tuned mechanisms characterised by compressive non-linearity transfer functions for contrast (Legge and Foley, 1980). It supports putative models that posit first-stage spatial-frequency linear filtering processes (linear band-pass spatial frequency channels), followed by divisive inhibitory channels.

These results on fixation which demonstrated the effect of different spatial frequency flankers on crowding, spatial frequency dependency of crowding, influence of Gabor flanker patch size on crowding, effects of flanker contrast on the crowding in stereoscopic depth perception, when taken together support the idea of differently sized independent channels that process depth information from spatial frequency defined test and flankers, which scale with their underlying psychophysical receptive size.

Effects Spatial Frequency on off the Horopter Disparity Processing

Previous reports have shown that increment threshold depth discrimination is most likely processed through depth information channels tuned to different and restricted ranges of disparities (Bouma, 1970; Marr and Poggio, 1979) underpinned by separate populations of neurons that encode for them. Due to spatial filtering, coarse stereopsis is associated with low spatial frequency channels, and fine stereopsis is associated with high spatial frequency channels with differences in their underlying psychophysical and physiological receptive field sizes (Richards and Smith, 1972; Poggio and Fischer, 1977; Richards, 1977; Marr and Poggio, 1979; Schor and Wood, 1983; Harris, McKee and Smallman, 1997). Based on these reports, we expected different depth discrimination tuning functions for low and high spatial frequencies test and flankers in experiments involving integrating test and flanker with different spatial frequency composition located off the horopter. Because the stimuli used here were relatively narrow-band in composition (i.e. Gabor patches), it is possible to assume that they stimulated putative channels tuned the respective centre spatial

frequencies of the stimuli. Therefore, when flankers are displaced from the horopter, it was expected that crowding should reduce around the horopter for high spatial frequency flankers, similar to what was found with the bar flankers in Chapter 4, but crowding should increase for low spatial frequency flankers at greater disparity off the horopter in response to coarse mechanism. Based on this, we predicted that, displaced high spatial frequency flankers will release crowding around the fixation plane (show improvement in thresholds) but will show distinctive fine and coarse ranges when sufficiently displaced. On the other hand, the effect low spatial frequency flankers on crowding was expected to be invariant regardless of changes to the depth position of displaced flankers.

When crowding was present at the onset (i.e. at the small lateral separation), we found results which indicate performance was relatively similar regardless of spatial frequency composition of the flanker stimuli (Fig. 5.6). However generally high spatial frequency flankers decreased crowding more when they displaced from the fixation plane compared to low spatial frequency flankers, though the decrement in crowding with the high spatial frequency flankers was generally faster. Displaced low spatial frequency flankers generally induced greater elevation in depth discrimination thresholds at greater test-flanker depth separations. Though low spatial frequency test target recorded greater threshold than high spatial frequency test target, their interaction with both low and high spatial frequency flankers similarly showed a decrement in crowding around the horopter, and subsequent increment in crowding or flanker effect with increasing flanker disparity. Threshold increase at greater flanker disparity off the horopter (restoration of crowding effect) perhaps reflect processing by a coarser mechanism. When test target and flanking stimuli were widely laterally separated, the results indicated (Fig. 5.7) that threshold demonstrated a systematic increase in stereo-threshold relative to the fixation plane with a similar effect of spatial frequency composition of test target and flankers as found for the small test-flanker depth separation.

Again, the thresholds recorded for different flanker spatial frequencies when the test target was 4cpd or 0.5 cpd (Fig. 5.6) is possibly due to the nature of the different channels, or simply reflect inter-observer variation in performance. The tuning functions found for displaced flankers are in accord with Ogle's (1952; 1953) distinction of quantitative and qualitative depth discrimination based on fine disparities around the horopter and coarse disparities off the horopter. Richards and colleagues (Felton, Richards and Smith, 1972; Richards and Kaye, 1974) also differentiated between fine and coarse disparity processing based on a size-disparity correlation. Marr and Poggio (1979), using the idea of a size-disparity correlation, predicted that the disparity range over which depth is processed is proportional to the receptive field size of disparity coding mechanisms and agreed with coarse to fine processing. Since then, Poggio and other authors (Poggio and Fischer, 1977; Schor and Wood, 1983; Badcock and Schor, 1985; Siderov and Harwerth, 1993) have adduced psychophysical evidence that supports a division in depth increment thresholds functions using different stimuli. These results with spatial frequency-defined flankers are also consistent with findings with bar test and flanker stimuli described in Chapter 4. In this study, the narrow range of disparities found compared to previously reported studies could be due to the integration of disparities in our stimuli (i.e. crowding), compared to the displacement of local test and reference only (e.g. Siderov and Harwerth, 1992), and the fact that the depth movements are less tolerated (compared to lateral movements) due to photoreceptor density which limits peripheral acuity (Westheimer and McKee, 1978, 1980b). The decrease in crowding effect around the fixation, followed by an elevation possibly reflect a transition between mechanisms tuned to process fine disparities around the horopter, mechanisms tuned to process large disparities outside the fixation plane (Blakemore, 1970; McKee, Levi, and Brown, 1990). While similar depth discrimination tuning for both low and high spatial frequency flankers raises tangible questions about hypothesis that posit that, high and low spatial frequencies are only respectively tuned to fine and coarse mechanisms, high spatial frequency effectively decreased more crowding effect, dropping off quicker

around the fixation plane (usually 0.5 min arc for observers), and low spatial frequency was less efficiently processed at greater flanker disparities, increasing the crowding effect at greater flanker disparities greater than 1 min arc. Differences in depth discrimination threshold for low and high spatial frequency test targets, coupled with different depth tuning function for low and high spatial frequency flankers (i.e. spatial differences in reduction crowding and elevation in the crowding effect) relative to the fixation plane support processing by independent channels (Julesz and Miller. 1975; Schor and Wood, 1983). In contrast to the findings of Mayhew and Frisby (1979), the results reported in this chapter provide support for the proposal by Felton and colleagues (1972) that low spatial frequency channels are tuned to relatively large disparity mechanisms and, high spatial frequency channels are tuned to relatively small disparity mechanisms. The present findings, in addition, suggest that channels respond to other spatial frequencies not tuned to their center frequency, in a similar manner but are not as efficient. These findings bear strongly on theories of disparity processing, and the perceptual role of different spatial frequency in depth discrimination. This study has extended these discussions to the stereoscopic depth-crowding domain.

CONCLUSIONS

Stereo-thresholds were measured for spatial frequency-defined flanker interactions on test stimuli in the fixation plane, and as test-flanker relative depth from the horopter. Several properties of stereoscopic crowding were investigated. In summary, the findings support theories linking the influence of spatial frequency composition on depth information integration and processing. Crowding spatially scaled for low and high spatial flankers at similar small separations, and the respective extent scaled with flanker sizes. For the range of flanker spatial frequencies used and separation examined, reduction in the size of flankers defined by the carrier spatial frequency and the envelope (spread) and contrast reduced the magnitude of the measured crowding, supporting the idea of size-disparity

correlation in discrimination. The effect of flanker contrast reduction also showed that, crowding exhibits similar interactions as masking at the fovea. The findings found here are consistent with current theories that posit that crowding and masking may share the same first stage linear filtering process, and perhaps a similar second-stage nonlinear (divisive inhibitory mechanism) process, with the additional property that crowding pools information over a spatial extent that varies with the size of the flankers (involvement of grouping factors).

Further, our findings may have revealed a distinction in fine and coarse disparities integration for on, and off the horopter crowding mechanisms, perhaps based on a size-disparity correlation. Our results, taken together do not support the notion of depth segregation based exclusively on differences in spatial frequency composition of stereoscopic stimuli (i.e. exclusive coding for each spatial frequency mechanism), but rather channels that respond to center frequencies when maximally stimulated. Thus, reduction in crowding reflect response to stimulation of the center frequencies to which the independent channels are tuned. This would be consistent with theories that posit independent spatial frequency selective channels in stereoscopic vision. It also suggest that stereoscopic disparity information is used in the same way regardless of the individual channel that is stimulated.

CHAPTER SIX

SUMMARY OF RESULTS, DISCUSSION AND CONCLUSION

The main objective of this research was to investigate stereoscopic crowding in order to advance our understanding of spatial interactions in the stereoscopic domain and better understand possible neural coding mechanisms behind such disparity interactions. A number of experiments were designed that measured depth discrimination in observers with normal vision, in the presence of flanking stimuli both on and off the horopter. The results of the first experiment, obtained using high contrast test, reference and flanking bar stimuli was consistent with previous results showing that stereopsis is subject to crowding when flanking targets are positioned at specific close lateral distances from test stimuli due to local inhibition. However, more global processes were also evident as the magnitude of the crowding effect reduced as the flanking bar width was increased beyond that of the test stimuli, suggesting a separation from a local to a more global process. When the test and reference bars were kept on the horopter but the flanking bars were moved in depth away from the horopter, the induced crowding effect varied as a function of both lateral separation of the flankers from the test and the relative depth separation between the test and flankers (i.e. the distance of the flankers from the horopter). For small test-flanker separations there was strong crowding evident when the flankers were on the same plane as the test (i.e. fixation), but crowding was less robust as the flankers were presented just off the horopter, thereby resulting in improved stereo-thresholds. However, as the flanker disparity was increased further, crowding returned and thresholds subsequently increased. For larger test-flanker separations, there was no crowding when all stimuli were located on the horopter; however, crowding returned and stereo-thresholds demonstrated a progressive increase, as the flankers were positioned away from the fixation plane (i.e. horopter), supporting the idea that disparity integration at small lateral separations off the horopter are occasioned by

action of a 'salience attraction' between then the test and flankers, but that discrimination was tuned to fine and coarse neural mechanisms that process disparity around and off the horopter. These results were repeated using Gabor flanking stimuli. On the horopter, crowding was maximum at similar close separation, but varied with the spatial frequency of Gabor flankers. The crowding effect was decreased by smaller Gabor flanker spread and contrast reduction of the Gabor patch, suggesting relationship between size and depth discrimination. Consistent with the results using bar stimuli, flanks disparity demonstrated systematic reduction in crowding from the fixation, until the stimuli are sufficiently displaced outside the fixation before the crowding effect is restored. High spatial frequency flanker generally improved threshold at close depth separation less than 1 min arc and low spatial frequency flankers revealed worse thresholds when flankers were positioned further off the horopter. Overall, the findings are consistent with independent channels for processing disparity, suggesting that crowding may occur through such independent channels. In addition, the results suggest that the independent channels respond to spatial frequency information not tuned to their center frequency a similar way but less efficiently. Since the spatial interaction reported is foveal, and possibly mediated entirely by a central mechanism, suggestions about probable underlying neural mechanisms were made. The sections below address the specific research aims developed at the beginning of the thesis that drove the experiments herein.

Extent and Degree of Crowding on the Horopter

Visual crowding has long been known to degrade the capacity of the visual system to resolve a test target through, presumably, a form of lateral interaction with neighbouring flankers both in the fovea and periphery (Flom et al. 1963a; Bouma, 1970; Toet and Levi, 1992). Crowding in observers with normal vision is strongest under binocular conditions (stereopsis) compared to other hyper acuities (Westheimer and Hauske, 1975). Flom and others have demonstrated that crowding still occurs under dichoptic conditions which is

evidence that crowding must have a cortical origin, requiring investigations to understand its neural coding mechanisms (Flom et al, 1963b; Tripathy and Levi, 1994). The degree and extent of crowding depends critically upon the distance between the test target and the neighbouring flankers (Hirsch and Weymouth, 1948; Butler and Westheimer, 1978; Westheimer and McKee, 1980a; Fendick and Westheimer, 1983). Foveal crowding in stereopsis has been found to be most detrimental at test flanker separations of less than 6 to 10 min arc (Butler and Westheimer, 1978; Westheimer and McKee, 1979b; Westheimer and McKee, 1980a). In order to confirm and then extend previous results, the investigations reported in this thesis measured the extent and degree of crowding between test and reference bars for a number of observers and stimuli configurations. The work also clarified a number of uncertainties present in previous work (Butler and Westheimer, 1978) in relation to stimuli properties (e.g. size of test and flankers) and other possible depth cues.

As reported in Chapter 3, crowding varied with the test-flanker (edge-to-edge) separation but the magnitude of crowding reached its peak when the flankers were in close spatial proximity, between 1 to 2 arc min, to the test (i.e. Optimum Crowding Distance, OCD). Depth discrimination thresholds returned to unflanked levels for separations around 4 arc min or greater (see Fig. 3.2A), revealing a reduction in crowding. The magnitude of crowding was evidenced as a 3 to 8 fold elevation in threshold over unflanked values depending on the observer. In a control condition, the reference bar was removed (see Fig 3.3A). Depth discrimination of the test stimulus in the presence of the flanking bars, but without the reference bar, generally improved depth discrimination of the test target, although crowding was still evident as a progressive decrease from the closest separation for that configuration. Quite unexpectedly, we found that the presence of the flankers on the plane of fixation increasingly induced 'in front bias' in the depth direction of the test target with decreasing test-flanker separation, with the greatest bias being at the optimum crowding distance (OCD) (Table 3.0).

The crowding effects may be explained on the basis of lateral interaction (interference), which was in accordance with the ideas of lateral inhibition within a single detector or inhibitory influences from distant neurones caused by interaction between features viewed foveally which fall within the inhibitory zone of neurons tuned to detecting disparities (Poggio and Fischer, 1977; Wilson and Bergen, 1979; Das and Gilbert, 1999). Here, it was argued that laterally placed flankers to the test target actively mitigated against detecting the depth direction of the test due to competing visual directions at small separations. While this result supported Butler and Westheimer's (1978) claim that the extent of inhibition is maximal at a particular test-flanker separation, in addition we showed that optimum crowding differed for different observers and depends on the stimulus configuration used. An explanation based on the inhibition of depth signals due to competing visual directions of test and flanking stimuli at the OCD (i.e. small test – flanker separations) also well accounted for the front bias effect reported (Fox, 1970; Richards and Foley, 1971; Lehmkuhle and Fox, 1980; Mustillo, 1985). In addition, the generally lower stereo-thresholds obtained when the reference bar was omitted discounted explanations based on shape effects (e.g. Kumar and Glaser, 1994b) explicated for the decreased crowding evident at the closest separation in the Butler and Westheimer (1978) study. Unlike the Butler and Westheimer (1978) study (also showed variation among the subjects used), which revealed that though some crowding occurred at the closest separation, optimum crowding occurred between 2 to 3 min arc, before decreasing as separation was widened. In this study, as described crowding was optimum at the closest separation between 1 to 2 min arc for different observers, and decreased monotonically as separations was widened (Fig. 6.1). In addition to the crowding effect being dependent on the configuration, the results from the present study suggest that the similarity in the resultant crowding either in the presence of absence of the reference (see Fig. 3.3B) was due to the use of either the same processing mechanism or different mechanisms that behave similarly.

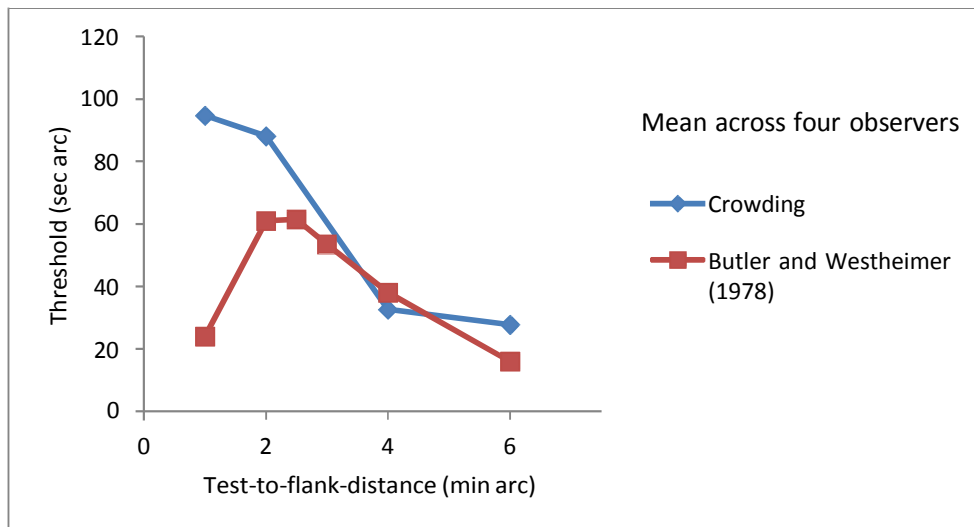


Fig. 6. 1. Replotted Mean Crowding for Bar Test and Flankers (Fig 3.2B). Depth discrimination thresholds (sec arc) are plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc) averaged across 4 observers (errors are not shown to aid in clarity). Also shown are the average data (redrawn) from the 2 observers in the Butler and Westheimer (1978) study. Error bars are not shown for clarity.

Effect of Flanker and Reference bar Configuration on Crowding on the Horopter

Most studies that have investigated the spatial extent and magnitude of crowding in stereopsis have employed test targets and flankers that had similar widths (Butler and Westheimer, 1978; Westheimer and McKee, 1980a, Fox and Patterson, 1981; Westheimer and Truong, 1988). However, a number of crowding studies in other hyperacuity tasks have shown that the extent and degree of the spatial interaction (i.e. crowding) is strongly influenced by targets of different dimensions (Kooi et al., 1994; Livene and Sagi, 2007; Westheimer, 1979a; 1979b). Researchers have largely come to agree that stereo precision is greatly influenced by size of the test stimulus (Richards, 1972; Mitchell and O'Hagan, 1972; Westheimer, 1979a; McKee, 1983; Kooi et al., 1994). However, to our knowledge no study had investigated effect of the differences in width between test target and flankers on

stereoscopic crowding. Therefore we carried out an investigation of the influence of flanker size by varying the width of the flankers and reference bars at the OCD. This helped assess if the interaction was based on an 'edge-to-edge' or 'center-to-center' metric based on the account of putative mechanisms of disparity that posit 'averaging' or 'pooling' (e. g. Kooi et al., 1994) as size is increased.

Results of the width tuning experiments (see Figs. 3.5A and 3.5B) supported the idea that the degree of crowding depended on the extent to which the test target and the flanking bars were similar in width. This suggests that the crowding effect is sensitive to dimensions of the flanking features in the configuration, which was in accord with evidence showing that disparity sensitive cortical cells are sensitive to size (Mitchell and O'Hagan, 1972; Richard and Kaye, 1974; Felton et al, 1972, Wood et al., 2002). Increasing the width of the flankers increased the amount of depth information available which was 'pooled' across the width of the flankers to subsequently decrease crowding. On the other hand, decreasing the width of the flankers, which also reduced the amount of crowding, was probably a result of the reduction in overall contrast of the flanker causing an increase in relative 'pop-out' of the test (due to reduced luminous flux) (Kumar and Glaser, 1995; Felisberti et al., 2005). The reduction in crowding with an increase in the width of the flankers is consistent with explanations based on the hypothesis of 'Gestalt grouping' in crowding, where component effects (i.e. flanking features with different depths or shape) help in ungrouping the test features to be discerned. (Kooi et al., 1994; Sayim et al., 2010; Deas and Wilcox, 2014). Similarity of the test target and the flanking bars made it most difficult to extract the relevant depth signals from the test with precision, resulting in optimum crowding (Kooi et al., 1994; Kumar and Glaser, 1992b; 1995). Results were mostly unaffected by increasing the width of reference bar (see Figs. 3.6A and 3.6B), thus also giving indirect support to the stated reason that crowding results from a lateral interaction between the test target and the flanking bars. Crowding only increased when the reference was made very thin (as if discriminating absolute disparity of the test target), which was attributed to the reference bar

becoming relatively less robust due to its relatively lower contrast energy (O'Shea et al, 1994).

We set out to determine if stereo based crowding is an edge-to-edge or center-to-center phenomenon (Richards, 1972). From the results reported, it was obvious that luminance flux between the test target and flankers enhanced edge detection between the test and the flankers. However, it seemed the particular kind of interaction reported was well-suited to the idea of integrating the depth signals in the center in order to extract an 'average' disparity for depth judgement, which supported the center-to-center interaction. This was in good agreement with the notion that similarity in the components of the features (i.e. shape and depth) was the primary factor that affected the degree of crowding at the OCD, where edge detection due to luminous flux had only a secondary effect.

In summary, the experiments in Chapter 3 which used broadband stimuli (bars) characterised the influence of lateral separation of flanking features on depth perception in the fixation plane and their integrative processes, and offered suggestions concerning the precision with which stereo-thresholds are established. In so doing, the study addressed some research gaps concerning the extent to which the test target, reference and flanking bars must be similar in size (width) in order to produce and relieve crowding. In light of these findings, this study has confirmed that stereo-thresholds can be degraded by crowding, while at the same time, demonstrated that flanker bar width is an important factor to consider in stereo configurations. These findings confirmed previous results which showed depth discrimination thresholds are reduced in the presence of flanking contours. The findings were explained as a consequence of local disparity interaction or inhibition, but with the involvement of Gestalt factors (for larger flanker widths) and contrast modulation (for thinner flanker widths) in the particular stimuli configurations used. These findings are therefore viewed as an extension of previous works which has helped clarify some aspects concerning the intellectual discourse of crowding in depth.

Spatial Characteristics of Crowding off the Horopter

Having determined the extent and degree of crowding, the next experimental Chapter (Chapter 4) focused on spatial interactions off the horopter, and examined if flanker component effects (depth and shape) would lead to a reduction or increase crowding. It followed on from the general idea that depth positioning (Butler and Westheimer, 1978; Astle et al., 2014) and spatial properties of flankers (e.g. Kooi et al., 1994) can influence the perceptibility of a stereoscopic test stimulus. This study offered a new perspective to study the putative mechanisms of crowding. The idea that perceived depth could be influenced by lateral separation (Butler and Westheimer, 1978), relative depth separation (Westheimer, 1986; Westheimer and Levi, 1987) and spatial dimension of flankers (Kooi et al., 1994) off the horopter has indirectly been reported. We studied the interaction by displacing crowding flankers from the fixation plane, by measuring the incremental (pedestal) depth threshold for a configuration that produced optimum crowding, and for a configuration that produced no or little crowding on the horopter. Evidence found in Chapter 3, that crowding is influenced by the width of the flankers based on the grouping hypothesis, was also investigated.

Effect of Depth and Lateral Separation on Crowding

Varied flanker component effects on perceived depth have been reported, depending on the depth plane the flanker is presented relative to the test target and observer (e.g.s. Fox, 1970, Butler and Westheimer, 1978; Westheimer and Levi, 1987; Felisberti et al., 2005). The general consensus has been that presenting a test target and adjacent flankers in the same depth plane on the horopter produces a robust crowding effect resulting in a pronounced increase in stereo thresholds. Flankers presented in depth behind a test target (i.e. uncrossed depth direction), such that the test target is relatively closer to the observer results in a decrease to the stereo threshold (Fox, 1970, Butler and Westheimer, 1978 Felisberti et al., 2005). On the other hand, displaying the flankers in front of a test (i.e. in crossed depth direction) results in comparatively higher thresholds than when presented at the same

perceived distance, but behind (Fox, 1970). Some studies have demonstrated that flankers positioned to appear in front of a test stimulus manifest two effects on perceived depth. First, there is a release of crowding and commensurate reduction in stereo threshold at small relative depth separations (Butler and Westheimer; 1978; Kooi et al., 1994), and second, a re-establishment of the crowding effect for flanker distances further from the fixation plane (Fox, 1970, Funke et al., 2015). Moreover, the findings of Butler and Westheimer (1978), Westheimer (1986) and Astle et al. (2014) revealed symmetric crowding effects for flankers positioned in front and behind depth positions relative to the test stimuli. An exception to this finding was the study by Felisberti et al. (2005) who found that displaying the flankers behind a test stimulus resulted in more crowding (i.e. worse thresholds) in 2 of the 3 subjects they used.

Explanations of how the relative depth positions of flankers influence crowding have been varied and are incomplete. One explanation has postulated that increases in stereo thresholds as a result of crowding, are due to activation of neurons tuned to the disparity of the test being inhibited as a result of the flankers falling in corresponding inhibitory neuronal regions (e.g. Butler and Westheimer, 1978). Another explanation has postulated mechanisms that integrate or average information from the test and the flankers (e.g. Badcock and Westheimer, 1985). Such pooling mechanisms could act to either interfere with thresholds or perhaps enhance them depending on how flanking elements interact (Levi and Carney, 2011). Other authors (Ogle, 1963; Mitchison and Westheimer, 1984; Westheimer, 1986) proposed the concept of 'saliency' in stereopsis, to explain the spatial interactions based on relative disparities or depth separation. Saliency describes a situation where the depth difference between a test and flanker creates a depth 'attraction' at small separations and a 'repulsion' at larger separation between test target and flankers (Westheimer and Levi, 1987; Westheimer, 1986). The asymmetric effect on depth discrimination threshold caused by flanker depth position relative to the test target has been

attributed to a so called 'front effect' (Fox, 1970). The explanation was that when flankers are displayed at depth positions in front of a test, they are regarded by the visual system as being spatially close to the observer due to a 'figure-ground' innate perception by the visual system and therefore making the test difficult to discriminate (Lehmkuhle and Fox, 1980; Fox and Patterson, 1981).

Results obtained in Chapter 4 indicated that in general crowding decreased and stereo thresholds improved when the flankers were positioned a small distance in front of the fixation plane and test target. For flankers positioned further from the fixation plane, beyond 1 min arc, crowding returned (see Fig. 4.1A). The reduction in crowding in the presence of flankers which are located just off the horopter and plane of the test is consistent with previous results of Fox (1970), Butler and Westheimer (1978), Kooi et al, 1994), Felisberti et al. (2005), Astle et al. (2014) and Funke (2015). The subsequent restoration of the crowding effect has been reported indirectly by Fox (1970) and Funke et al. (2015) but not in the detail as presented here. Accompanying control experiments revealed that although depth discrimination thresholds were slightly enhanced for uncrossed flanker depth separations, the effects were consistent for both flankers positioned with either crossed and uncrossed disparities. Trials where the flanker depths were randomised between crossed and uncrossed disparities confirmed that the flanker position was not used as a cue for discrimination (i.e., the disparity change was not used as a cue to the eye vergence system).

The relative reduction and subsequent elevation in threshold as a function of flanker disparity is interpreted as the response to two stereo mechanisms, coarse and fine, as previously proposed (e.g. Marr and Poggio, 1979), and a departure from a mechanism tuned only around the horopter as proposed by (Butler and Westheimer, 1978). Fig. 6.2 shows replotted data in this study (Fig 4.1A) compared to data averaged across the two observers used in the Butler and Westheimer (1978) study, showing averaged thresholds plotted as a function of flanker disparity in front of the fixation plane. For the range of flanker disparity

tested by Butler and Westheimer (1978), results for the depth discrimination tuning function are similar, that is, threshold symmetrically decreased from the horopter albeit lower threshold by Butler and Westheimer (1978), perhaps due to their use of louver flankers. Additionally, larger flanker disparity tested in this study than those tested by Butler and Westheimer (1978) show that the flanker effect were restored thereby increasing the threshold. These findings would also be consistent with the original proposals by Ogle (1952) of the operation of patent and qualitative disparity discrimination.

Quite interestingly, comparative experiments using a larger lateral test-flanker separation (separation of 6 min arc) which did not induce crowding when the stimuli were located on the horopter, revealed a crowding effect and progressive increase in the depth discrimination thresholds, as the flankers were moved in depth away from the horopter (see Fig 4.1B). For this test-flanker separation, as no crowding was evident when the flankers were on the fixation plane, the progressive elevation in thresholds when the flankers were positioned off the fixation plane must reflect the response of a more coarse mechanism engaged due to the disparity of the flankers.

The results obtained with flankers positioned off the horopter have been reported to operate only in the disparity domain (Butler and Westheimer, 1978; Stevenson et al., 1991). Westheimer (1986) (but see also Westheimer and Levi, 1987; Stevenson et al., 1991) who found that when adjacent targets (i.e. test and flankers) were laterally separated by between about 2 to 8 min arc disparity at the fovea, interactions between the targets had a character of 'salience attraction' which made depth discrimination more difficult, but for larger lateral separations a 'salience repulsion' effect occurred which improves the threshold. Previous studies (Westheimer, 1986; Westheimer and Levi, 1987) which used psychophysical 'annulling' methods revealed that the spatial interactions increased threshold monotonically with decreasing test-flanker lateral separation. In this thesis, using a similar psychophysical method, but employing the properties of crowding and coupling the influence of both lateral

and depth separation of test and flankers, Westheimer (1986) and Westheimer and Levi (1987) demonstrated that salience attraction is greatest when there is optimum crowding, and decreased (as if the test is being repelled) with less crowding. Therefore, the crowding effects observed in this study are ascribed to the action of a salience 'attraction' between the test and flanking bars. For the lateral separation tested, we did not find any evidence that the induction caused by the flankers had crossed into a 'repulsion' zone, probably because the lateral interactions examined were within the range of attraction as reported previously (Westheimer, 1986).

Within the range of disparities investigated, the 'attraction' depended on both lateral and depth separation of the flankers to the test, which is consistent with previous reports showing that spatial interactions in the disparity domain decrease monotonically with lateral separation (Westheimer, 1986; Westheimer and Levi, 1987). In addition, the present study revealed that when the test-flanker separation caused optimum crowding there is a release in crowding when flankers are off the horopter. Then crowding increases as the depth separation increases further. On the other hand, when there was no crowding from the flankers on the fixation plane, the crowding increased as thresholds got worsen from the fixation plane. The effects observed were not due to monocular localisation shifts in the interocular retinal images (i.e. shifts in the visual direction of targets before they are combined at a subsequent binocular stage), as previous studies have demonstrated that similar effects occurred for targets of opposite contrast presented separately to each eye (Westheimer and Levi, 1987). Furthermore, control conditions revealed similar results for both crossed and uncrossed flanker depth displacements which included trials where the disparity was randomised.

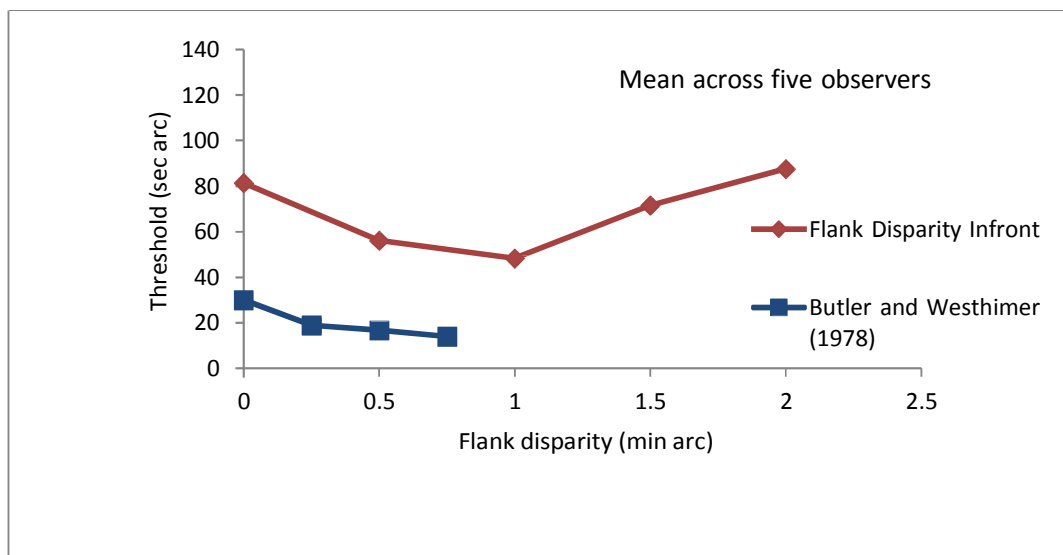


Fig. 6. 2. Comparison of Flanker Disparity Tuning to Butler and Westheimer (1978).

Replotted Mean Effect of Relative Depth Separation at Peak Crowding (Chapter 4, Fig. 4.1A), and redrawn averaged data for the two observes in Butler and Westheimer (1978), showing averaged threshold (sec arc) plotted as function of the test-flanker disparity (min arc). Peak crowding separation was 2 min arc in this study and 2.5 min arc Butler and Westheimer (1978). The test target appeared in the fixation plane, whiles the flanking bars were displaced in depth. Errors bars are not shown to aid in clarity.

Depth Bias effects by Flanker off the Horopter

Though ‘front effect’ (Fox, 1970; Lehmkuhle and Fox, 1980) and ‘salience’ (Westheimer, 1886) are different mechanisms, this study made a link between the two based on results adduced. Based on the bias finding in Chapter 3, where flankers placed at the OCD induced bias in the direction of the depth discrimination of the test stimulus, in Chapter 4 we investigated a link between front bias and salience by examining the proposition that the former mechanism is a physical outcome of the latter. If the proposal put forward was true, it was expected that the front bias effect observed in Chapter 3, when the flankers where positioned on the fixation plane, would increase and possibly scale with the depth position

of the flankers relative to fixation. Analysis of the lateral and depth separation data in Chapter 4 indicated that front bias increased relative to the test-flanker depth separation, but decreased with increasing lateral separation. The bias scaled by a factor of 2 for each 1 min arc increase in relative depth separation at the OCD, but progressively reduced at larger lateral separations where salience is absent or weak (see Fig 4.1D).

Previous studies by Westheimer (1986) and Westheimer and Levi (1987) avoided response bias induced by the flankers. For example, in the annulling method used by Westheimer (1986), flankers were displayed with one of two equal and opposite depth values. The difference in the mean of the two constructed psychometric curves for the two flanker depth conditions was used to calculate induced changes in the depth direction of the test target caused by the depth difference of the flankers. The annulling method had within it an inherent limitation of collecting hundreds of responses to calculate any induced effects. In the present study, induced effects were achieved by displacing the flankers in a single depth direction in front of the test. This allowed the determination of bias in the depth direction of the test induced by the actual change in the depth position of flankers. Crossed bias indicated a shift in the apparent disparity of the test target towards the disparity of the inducing flankers, indicative of an 'attraction' interaction. On the other hand, an opposite uncrossed bias between the test and flankers would have indicated a 'repulsion' interaction which we did not find. Results of the increasing bias caused by increasing flanker disparity made the previous crowding effect with separation which was attributed to salience attraction more definite. It also confirmed the prediction based on results on the fixation plane (Chapter 3) where interference from the flankers influenced perceived depth of the test.

Increment stereo-thresholds for both crowding and non-crowding configurations (test, reference and flankers) (see Figs 4.2A and 4.2B) demonstrated a similar pattern as described for the flanker disparity, which supported the earlier suggestion that disparity

integration relative to the fixation plane is subject to mechanisms tuned around the fixation plane and just off the fixation plane. Results showed that optimum crowding occurred in the fixation plane, then reduced when stimuli were removed slightly off the horopter, followed by an elevation in thresholds at greater depth distances. This observation of crowding with increment threshold depth discrimination was a new one, but is nevertheless consistent with the putative fine and coarse dichotomy in stereopsis (Ogle, 1952, Marr and Poggio, 1979).

Effect of Flanker Width Dimension of Crowding off the Fixation

When the flanking bars were positioned at 1 min arc off the horopter for the LCD configuration, results revealed that different sized flankers than test can enhance performance and thereby reduced crowding (see Fig. 4.4A). The results are consistent with earlier findings in Chapter 3, and previous explanations that differences in the width between test and flankers causes the test to 'pop out' (Felisberti et al., 2005, Kumar and Glaser, 1995), to reduce crowding. Similar flanker effects on crowding have been reported to occur for letter identification (Banks et al., 1979) and for Vernier tasks (Malania et al., 2007; Banks and White; 1984; Manassi et al., 2012; Herzog et al., 2015). The addition of a number of shorter, longer or bigger flanking lines relative to Vernier test decreased crowding in a Vernier discrimination task at the fovea and the periphery (i.e. improved performance compared to when the Vernier was presented alone). For flanking lines and Vernier of the same dimension, crowding did not change (Malania et al., 2007; Banks and White; 1984). However, we found that the width effect did not appear to scale with the depth position of the flankers. Consistent with the results reported in Chapter 3, crowding was maximum for near similar width, but thinner and thicker flanker widths reduced crowding. The observed influence of the width of the flankers on the interaction supports a pooling or averaging of depth signals assigned to individual features which fall within the disparity pooling or attraction zone of less than 8 min arc (Westheimer and Levi, 1987; Stevenson et al, 1991). This observation of crowding under conditions of an increment depth pedestal is also novel,

but is in support of the idea of disparity averaging and grouping hypothesis for crowding (Andriessen and Bouma, 1976; Westheimer and Levi, 1987; Kooi et al., 1994).

Discussion of Mechanisms of Disparity Interaction off the Horopter

There is physiological support for the disparity interactions reported in this study. The interactions bear semblance to the center-surround phenomenon described for monocular hyperacuity tasks (Badcock and Westheimer, 1985). Moreover, Stevenson et al., (1991) who used Random Dot Stereograms (RDS) (i.e. stimuli that allowed changes in test target depth without changes in the monocular stimulus) and studied interocular correlation, would suggest that the effects reported here are produced in the disparity domain. Subsequently, Lehky and Sejnowski (1990) using both psychophysical (Westheimer, 1986) and physiological data (e.g. Poggio and Fischer, 1977) proposed a computational model that could explain such interaction effects, based on overlapping depth tuning curves by populations of cells. In their model, the activity of a single cell was considered to give only a coarse indication of the test stimulus parameter and still maintained precise information about the test, but the interaction represented a distributed response of a group of neural cells. Lehky and Sejnowski (1990) (see also Lehky et al., 1990) proposed that the observation of disparity attraction and repulsion could be explained by the action of short-range excitatory (mutual excitatory) and long-range inhibitory connections between disparity-tuned units at neighbouring locations, a process first suggested by Ratliff (1965). Their model revealed that when a test target and flankers occupy 2 depth positions (and are laterally separated), units in the intermediate, unstimulated position develop a pattern of activity corresponding to the average of the 2 lateral disparities, and therefore become attracted to each other to increase crowding. When there is a large disparity gradient, units at the intermediate positions developed a pattern of activity corresponding to an independent superposition of the 2 lateral disparities, so that both disparities are represented simultaneously, therefore they repel each other to decrease crowding.

In a similar study, Mikaelian and Qian (2000) using psychophysical results of interactions in the disparity domain (Westheimer, 1986; Westheimer and Levi, 1987), modelled the interactions based on the known physiological organization of the binocular receptive fields (RFs) (Hubel and Wiesel (1962; Barlow et al., 1967; Poggio and Fischer, 1977). Mikaelian and Qian (2000) suggested that at small separations the apparent disparity of the test is shifted towards the disparity of the inducing flankers indicating an attractive interaction. At large separations, a transition from attraction to repulsion occurs due to the inducing flankers leaving the RF of neurons centered to decode the disparity of the test target. Intuitively, when both the lateral and depth separations are small, the images of the test target and flankers on each retina are close and consequently they fall in the same excitatory subregions of the vertically-oriented simple cell RFs and contribute equally to the responses. Then, the disparities of the two features are averaged at the complex cell stage which receives input from the simple cells (do not have separate excitatory and inhibitory subregions).

While the Lehky and Sejnowski (1990) and Mikaelian and Qian (2000) models, based on population tuning curves and binocular RFs respectively, correctly explain the observed disparity attraction and repulsion interactions, specifically, it is obvious that the physiological explanation related to disparity attraction (when targets are separated by small distances) at the fovea underline the results observed in this study. Westheimer and colleagues (Westheimer, 1986; Westheimer and Levi, 1987) suggested that individual subjects may have different transition separations (i.e. cross from attraction to repulsion) ranging from 3 to 8 min of arc.

Overall, off horopter interactions support the conclusion in Chapter 4, that salience attraction underpin stereoscopic crowding when flankers occupy different depth positions from the test target's depth plane. Additionally, this study made a link between salience attraction and front bias effects, with the latter suggested to be the physical attribute of the former

perceptual mechanism. This study also revealed that disparity integration relative to the horopter involved a dichotomy of fine and coarse integration, with disparities being pooled across the width of the flankers. This part of the study links earlier studies which detailed interactive aspects of disparity configurations on the fixation plane, and less exploited spatial interactions off the horopter concerning stereoscopic crowding to enhance our understanding of global disparity processing.

Tuning Crowding to Spatial Frequency

It is well known that many cells in V1 are responsive to sine-wave gratings, and that their responses are optimal to specific spatial frequencies positioned at specific spatial positions or orientations in their receptive fields (Maffei and Fiorentini, 1973; De Valois et al., 1982). This selective tuning of neural cells to different spatial frequencies creates a set of band-pass filters through which visual signals are processed, with a proportional increase in spatial scale as stimuli are located more towards the periphery (Julesz and Miller, 1975; Marr and Poggio, 1979; Siderov and Harwerth, 1993; 1995). Because of the selective sensitivity of visual neurons to spatial frequency composition of stimuli and the relationship with the receptive field, putative spatial frequency filters or mechanisms have long been hypothesised to play different roles in perception. Low spatial frequency filters act to provide initial quick background image segregation and high spatial frequency filters providing a slower mechanism to afford more detailed figural scrutiny of an image (Stigmar, 1971; Julesz, 1978; Westheimer and McKee; 1980b; Ginsburg 1982; Wong and Weisstein, 1982). In this context, the present study investigated the effect of spatial frequency on stereoscopic crowding for stimuli both on and off the horopter, in order to understand possible mechanisms mediating stereo based crowding. Because current models of depth discrimination posit multiple channels to explain neural processing of depth signals in the visual cortex, stereoscopic crowding, which involves integrating feature spatial properties,

offers a useful method to investigate these channels, through manipulations of stimuli properties.

Effect on Spatial Frequency on on-the Horopter Interactions

As reported (Fig. 6.3, see also Figs 5.1 and 5.2), the results of lateral interactions obtained using different spatial frequency flankers confirmed a strong relationship between spatial frequency of the flankers and perceived depth (Blakemore and Julesz; 1971; Stigmar, 1971; Westheimer and McKee, 1980b; Schor and Wood, 1983; Polat and Sagi, 1993; Chung, Levi and Legge, 2001). Crowding occurred when the test target was a bar for the range of Gabor (0.5 to 4 cpd) flankers used. Crowding also showed spatial frequency specificity, with an increasing degree of magnitude when the spatial frequency of the test was close to that of the flankers. Peak crowding demonstrated spatial scaling for small test-flanker separation for all frequencies, it but generally showed variation across larger separations. The higher spatial frequency flanker used (4 cpd) was most effective in producing crowding, and exhibited a crowding pattern similar to crowding with bar flankers. At the optimum crowding distance, threshold elevation was four times (4X) and two times (2X) for the relatively high (4cpd) and low (0.5cpd) spatial frequencies, respectively.

Based on the aforementioned results, a control experiment tested whether the channels involved were completely spatial frequency dependent, and therefore mediated by independent channels. The proposition was that, if different channels were involved in the processing, completely independent channels for spatial frequency composition of the test should be independent of flanker of opposite spatial frequency. Thus, crowding was expected to be most effective when the peak spatial frequency of the test was similar to the peak spatial frequency of the flankers and crowding would be less or absent when the peak spatial frequencies of the test and peak flankers were different. To test that proposition, Gabor stimuli were used as test and flankers. The results obtained (see Fig 5.3) revealed

that, as predicted, similar test and flankers spatial frequency produced more crowding, though some crowding also occurred when spatial frequency were most different.

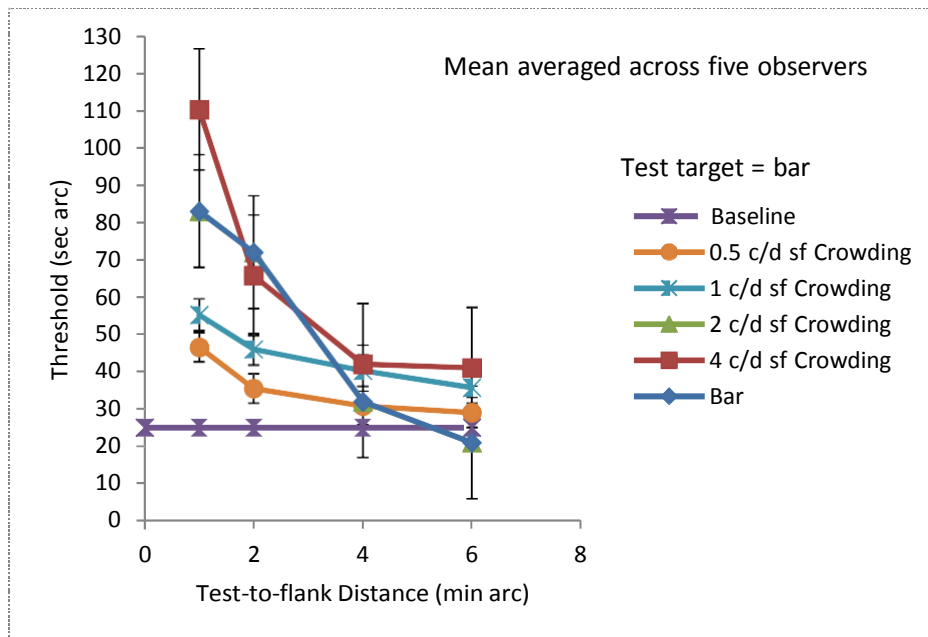


Fig. 6. 3. Averaged Crowding Effect for a Range of Flanker Spatial Frequencies. (Individual data plotted in Chapter 5 as Fig. 5.1). Stereo-thresholds (y-axis) averaged across five observers plotted as function test target-flanker separations (x-axis). The colours represent bar (blue closed diamond symbols), 0.5 cpd (yellow closed circle symbols), 1 cpd (sea blue asterisk symbols), 2 cpd (green closed triangle symbols) or 4.0 cpd (red closed square symbols) different flanker spatial frequencies, and baseline threshold (violet crossed dashed lines symbols). Error bars represent ± 1 standard errors.

Generally, higher stereo-thresholds were recorded for low spatial frequency test targets relative to high spatial frequency test targets, which was consistent with previous reports that stereo-acuity is generally better with higher spatial frequency stimuli (Schor and Wood, 1983; Badcock and Schor, 1985; Siderov and Harwerth, 1993). This finding is also in agreement with the suggestion that links between perceived depth and disparity (i.e. 'patent' stereopsis) is more effective for high spatial frequency to low spatial frequency (Ogle, 1952; 1962; Schor and Wood, 1983; Legge and Yuanchao, 1989). Crowding was more robust for test and flankers of similar spatial frequency (Figs 5.1 and 5.2). This result suggests that the spatial frequency composition of the bar test stimulus was biased more towards higher spatial frequencies as more robust crowding was obtained with the high spatial frequency flanking Gabors (4 cpd) relative to the lower spatial frequency flankers (0.5 cpd). The differences (Fig. 5.3) could reflect the nature of the different channels, but could simply also reflect the wide inter-individual variation in discrimination.

Control conditions showed that crowding effects were greatest when wider Gabor flanker spread and higher spatial frequency were used, which could reflect differences in visibility (see Fig. 5.4). In addition, reduction of flanker contrast exhibited a similar effect to foveal masking (see Fig 5.5) (e.g.s. Legge and Yuanchao, 1989; Zenger and Sagi, 1996), where optimum crowding occurred for similar high contrast of the low 0.5 cpd flanker. These effects of spread and contrast on crowding are consistent with our findings in Chapter 3 for bar stimuli on the fixation plane, where both increasing or decreasing flanker size reduced the crowding effect, but through different mechanisms as described. Further, the results support the idea that the crowding observed was not due to a monocular localisation of retinal images (Westheimer and Levi, 1987). These results provided further support of a size-disparity correlation in stereopsis, also consistent with the grouping hypothesis to explain crowding (Kooi et al., 1994).

The influence of flanking stimuli on stereo-thresholds on the horopter supports previous reported studies and is consistent with results using bar stimuli (Chapter 3), that the

observed crowding effect at small lateral target separations, can be attributed to an inhibitory action of short-range cortical connections in the visual cortex (e.g. Wilson and Bergen, 1979; Das and Gilbert, 1999; Chung et al., 2001). In addition, it is apparent that crowding depends on the spatial frequency composition of both the test and flanking stimuli and, in effect, the interactions reported provide support for independent channels. Although the fact that crowding was also seen with test and flankers composed of different spatial frequencies suggests an interaction between putative channels. The differences in peak crowding found with the different flanker spatial frequencies reflect separation in depth in information based on spatial frequency, and processing by independent channels (Julesz and Miller, 1975). The similarity of crowding to effects seen in masking studies, supports the idea that crowding and masking may share a similar mechanism of linear filtering. The results also supported the idea that disparity may be computed through size-tuned channels characterised by compressive non-linearity transfer functions for contrast (Legge and Foley, 1980). This is consistent with putative models of spatial localisation that posit first-stage spatial-frequency linear filtering process (linear band-pass spatial frequency channels), followed by divisive inhibitory channels which pools information over a spatial extent of crowding (Legge and Foley, 1980; Polat and Sagi, 1993). In summary, results on the fixation plane, support the idea of independent, differently sized mechanisms that are involved in the processing of spatial frequency-defined stereoscopic crowding.

Effect of Test and Flanker Spatial Frequency on off-the Horopter Crowding

When the spatial frequency defined flankers were separated at the OCD and displaced from the fixation plane, depth discrimination results (see Fig 5.6) were consistent with the findings with flanking bar stimuli reported in Chapter 4. Initially there was a systematic reduction in crowding relative to the fixation plane resulting in decreasing stereo-thresholds, then, for greater test-flanker depth separations crowding returned and thresholds got worse. Crowding was greater for test and flankers of similar spatial frequency composition.

Interestingly, the depth discrimination tuning profiles were similar for low and high frequency composition, but the relatively higher spatial frequency Gabor flankers (4 cpd) resulted in reduced crowding compared to the lower spatial frequency Gabor flankers (0.5 cpd). At the LCD, crowding was also evident for stimuli off the horopter (see Fig 5.7) and consistent with the results using bar stimuli reported in Chapter 4. Stereo-thresholds demonstrated a systematic rise as the flanking disparity were moved from the horopter with increasing crossed disparity. Consistent with results at OCD and with the crowding observed in the fixation plane, the crowding was more pronounced when the test was a low spatial frequency Gabor especially at greater depth separations and between test and flankers with similar spectral composition.

Discussion of Spatial frequency effects on Crowding

The findings with the Gabor flankers crowding effect on and off the horopter reiterated results obtained with bars flanking stimuli in the fixation plane in Chapter 3, and consistent with the results in Chapter 4, where flanking bars were displaced off the horopter. There was a reduction in threshold around the horopter for high spatial frequency but relatively worse threshold for low spatial frequency at greater depth separation (see Fig 5.6). The crowding effect observed was in accord with previous work which demonstrated a distinction in mechanisms that mediate stereopsis (Ogle (1952; 1953; Felton et al.,1972; Richards and Kaye, 1974; Marr and Poggio, 1979; Poggio and Fischer, 1977; Schor and Wood, 1983; Badcock and Schor, 1985; Siderov and Harwerth, 1993), and also provided support for the suggested idea that high spatial frequency channels are tuned to small disparity mechanisms around the horopter and low spatial frequency channels are tuned to larger disparity mechanism off the horopter (Felton et al.,1972). Because depth discrimination tuning functions for the low and high spatial frequency flankers were similar, the present findings suggest that underlying putative channels also respond to spatial frequencies not tuned to their center or peak frequency in a similar way regardless of spatial frequency. The

results obtained for the off horopter interaction (Figs. 5.6 and 5.7), which indicated a separation in the depth discrimination tuning profiles for the low and high frequency compositions of test and flankers was consistent with the findings on the fixation plane (Figs. 5.1, 5.3, and 6.4) where there was scaling in the magnitude of the crowding effect according to spatial frequency, but also suggested some cross interaction between channels.

The physiological bases that underpin the observed interactions have been alluded to above, but in addition, Mikaelian and Qian (2000) suggested that the transition between mechanisms that mediate stereopsis strongly depend on the orientation pooling distribution (i.e. stimuli configuration) and the spatial-frequency pooling distribution functions (i.e. the peak spatial frequency to which the cells are tuned) of the neurons that are stimulated. According to Mikaelian and Qian (2000) the dependence on the spatial-frequency distribution is particularly strong with the interaction when the distribution is shifted towards high frequency composition and when the transition separation becomes smaller (i.e. when there is crowding). The preference of the mechanism mediating stereopsis for spatial frequency could explain the observed differences in depth discrimination thresholds for the low and high spatial frequency flankers (that is, more reduction in crowding for the high spatial frequency flankers around the horopter compared to an elevation in crowding at greater disparities off the horopter). According to Mikaelian and Qian (2000) differences in depth discrimination among subjects could be due to individual differences in the preferred spatial frequency

Founded on previous physiological (Ohzawa et al., 1990; Qian, 1994; Zhu and Qian, 1996; Poggio and Fischer, 1977), psychophysical studies (Butler and Westheimer, 1878; Westheimer, 1986; Westheimer and Levi, 1987) and computation models (Lehky and Sejnowski, 1990; Lehky et al., 1990; Mikaelian and Qian 2000), and based on the results adduced in this study, the following proposals about stereoscopic crowding are made;

Disparity detection most likely begins from the simultaneous detection of disparity related test and nearby flankers in the excitatory and inhibitory subregions of simple cells but the

final responses come from complex cells, within their RFs in the primary visual cortex (V1) (Ohzawa et al., 1990; Qian, 1994; Zhu and Qian, 1996). Therefore, interactions between groups of neurons tuned to different frequencies related to the test target and flankers likely occurs in V1. Since crowding was found to depend on the configuration used, averaging or pooling of the relative disparity of the test and flankers could occur at a stage beyond the striate cortex such as V2 area MT (after feature and disparity detection in the V1) (see Fig. 1.3 for the loci of the projection). Moreover, disparity detection in the V2 and MT have qualitatively been found not be different (Lehky and Sejnowski, 1990, Pelli, 2008).

The results of this study, which were obtained by manipulating the spatial properties of stereoscopic crowding, bear strongly on theories of disparity processing, and the perceptual role of different tuned spatial frequency channels in depth discrimination. This study has extended previous discussions in the stereoscopic depth-crowding domain. The findings of this study are relevant because they have helped further our understanding of neural coding of stereoscopic crowding.

Limitations

There are a few inherent limitations. First, the relatively few subjects used and the inherent variability in stereo measurements such as those obtained, may have led to a reduction in the ability to apply traditional tests of statistical significance due to the inter-subject bias. However, to minimise the influence of both intra and inter-subject variability, stereo-thresholds were calculated by aggregating hundreds of responses after achieving practiced, stabilised thresholds.

Second, the separations between the stimuli features was on occasion quite small, which could have introduced a possibility of overlap of the stimuli at these close separations especially for the Gabor stimuli. However, the flanking stimuli were displayed with absolute disparities (not offsets) and the size of the flankers was accounted for in the stimuli programming so that test-flanker separations were measured from edge-to-edge. The edges

of the Gabor stimuli were truncated slightly in order to create an 'edge' in order to apply the correct separation distance.

Third, targets in the stimuli configurations were aligned vertically to prevent 'false matching', thus the specious association of a fellow eye's image with another which is common with horizontal arraying in stereoscopic experiments was avoided (Westheimer, 1986). Although there was a possibility that cues to depth could have resulted from eye movements during relative depth discrimination, such cues were minimised by brief and interleaved presentations of the test target (Stevenson et al., 1994).

Lastly, suppression of either eye due to fatigue was checked by allowing observers adequate rest times and spacing experimental conditions during a week. Subjects made sure their eyes were aligned, and therefore not suppressed, by keeping the two Nonius lines vertically aligned while fixating on the fixating spot at the center of the screen.

Conclusions

Crowding has long been known to have a cortical origin (Flom et al. 1963a; Bouma, 1970; Toet and Levi, 1992). However, the neural coding mechanisms behind stereoscopic crowding are still not clear (Butler and Westheimer, 1978; Levi, 2008), requiring further investigations into the underlying mechanisms of disparity processing. Based on the results adduced in this study which utilised stimuli manipulation to study several characteristics of stereoscopic crowding, the following conclusions are made;

1. Optimum or peak crowding is produced at specific test to flanker separation close to the plane of fixation between 1 to 2 min arc and decrease to unflank levels between 4 to 6 min arc,
2. The extent and degree of stereoscopic crowding depends on the observer and configuration used, but the crowding effect can be attributed to the action of the same processing mechanisms regardless of configuration,

3. Stereoscopic crowding is caused by local processing mechanisms of inhibition possibly within a single detector or inhibitory influences from distant neurones caused by interaction between the test and flankers which fall within the inhibitory zone of neurons tuned to detecting the test, being optimum at specific test to flanker separation depending on the configuration,
4. The degree of stereoscopic crowding does not depend exclusively on stimulus spatial separation, but on other spatial features such as the dimension (width) of the flankers, being optimum for similar test and flanker width demonstrating the possible involvement of spatial pooling, and Gestalt group factors (for thicker flanker widths) and luminance flux (for thinner flanker widths),
5. When crowding is present on the horopter, relative disparity of nearby flankers or pedestal disparity in front of the horopter decrease crowding relative to the horopter, but subsequently increase with greater flanker disparity, compared to a progressive increase in threshold from the horopter when no crowding is present at the onset, supporting the idea that disparity integration at small lateral separations off the horopter are occasioned by action of the 'salience attraction' between then the test and flanker, but discrimination was tuned to fine and coarse mechanisms,
6. 'Salience attraction' can be explained by 'front bias effect' induced by disparity of the flankers off the horopter, which increases with increasing relative test to flanker depth separation but decreases with increasing lateral separation.
7. The effect on crowding caused by the interaction of depth separation and lateral separation (i.e. salience attraction) of test and flanking stimuli is due to 'averaging of the disparities' assigned to the test and flankers due to the actions of short-range mutual excitatory tuned neurons,
8. On the horopter, optimum crowding varies with the spatial frequency of the test and flanker, and shows spatial frequency dependency.

9. High spatial frequency flanker disparity generally improves stereo-threshold at close depth separation less than 1 min arc around the horopter and low spatial frequency flankers reveal worse thresholds when flankers were positioned further off the horopter, consistent with findings of bar flankers which reveal dichotomy fine and coarse mechanisms.
10. Stereoscopic crowding is processed by independent channels, tuned to the center-frequency of test and flankers.

Case for future work

The findings of this thesis may have possible clinical applications by using tests designed for large data collection, which may be useful in developing new clinical tools to detect anomalies in the binocular signal processing. Because crowding places a sensory limit to visual resolution, future experiments to be conducted with observers who have binocular disruption, namely those who are clinically defined as amblyopic may help reveal patterns of stereoscopic crowding in them. For example, based on the results here, a designed hypothetical stereo test to measure stereo acuity based on different sized flanker widths as those shown in appendix B. The test in Fig. B1 may be easy to discriminate due to large separation between the square features, while a test embedded in Fig. B2 may be difficult to discriminate due to crowding. However, crowding may be released or reduced if the flanker of the middle test target in Fig. B3 are widened to look thicker or reduced to look thinner based on the results in this study. Further, because the empirical data adduced in the present investigations revealed that the mechanisms for crowding may be based on differentiation of fine and coarse stereopsis processing, and perhaps revealing the underlying receptive field properties of the neurons that code for those disparities, any future work could should consider measuring crowding across space at different eccentricities and with a longer range of disparity and spatial frequency composition which will compare fovea and peripheral stereoscopic crowding.

There are conflicting suggestions that coarse and fine stereopsis may be processed by different neural mechanisms (eg. Menz and Freeman, 2003) or the similar mechanisms (e.g. Gantz and Bedell, 2011). This thesis found that mechanisms that should process fine and coarse stereopsis respond differently to stimuli with different spatial frequency composition albeit in similar manner when crowding occurs. This reaffirms recent results from psychophysical studies that have suggested that fine (first order), and coarse stereopsis (second order) processes respond to different stimuli details (Wilcox and Allison, 2009). Therefore, further investigations that employ similar crowding configurations as used here but that employ luminance and contrast modulated stimuli may help in understanding putative mechanisms of patent (fine) and qualitative (coarse) disparity integration (i.e. crowding), interaction between mechanisms as well as the loci for stereoscopic crowding.

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APPENDICES

A. Individual Performance for Experiments in Chapter 5

Fig. A. 1 Individual Data for Expt.5.1B. Graphs show individual stereo-threshold (y-axis) plotted as a function of flanker spatial frequency for small separations. The test spatial frequency was fixed at 0.5 cpd and while the flankers spatial frequency was changed to either 0.5 cpd or 4 cpd. The colours are 0.5 cpd (sea blue asterisk symbols), 4 cpd (yellow closed circle symbols) different spatial frequencies flankers and baseline threshold (violet crossed symbols) and error bars indicate ± 1 standard errors.

Fig. A. 2 Individual Data for Expt.5.1B. Graphs show individual stereo-threshold (y-axis) plotted as a function of flanker spatial frequency for small separations. The test spatial frequency was fixed at 4 cpd and while the flankers spatial frequency was changed to either 0.5 cpd or 4 cpd. The colours are 0.5 cpd (sea blue asterisk symbols), 4 cpd (yellow closed circle symbols) different spatial frequencies flankers and baseline threshold (violet crossed symbols) and error bars indicate ± 1 standard errors.

Fig. A. 3 Individual Data for Expt.5.1C. Each panel depicts individual stereo-threshold (y-axis) plotted as a function of test-flanker separation for 2 flanker sizes. In the graphs, the comparative effect of 0.3 and 0.6 degs standard deviation of a low (0.5 cpd) and a high (4 cpd) spatial frequencies flankers on bar test are made. The colours represent Gabor flanker spreads of 0.6 deg of 1 cpd frequency (solid blue closed diamond symbols), 0.3 deg of 1cpd (dashed blue closed triangle symbols), 0.6 deg of 4 cpd (solid red closed square symbols), or 0.3 deg of 4 cpd (dashed red closed square symbols) and baseline threshold (violet crossed symbols).

Fig. A. 4 Individual Data Expt.5.1C. Each panel depicts individual stereo-threshold (y-axis) plotted as a function of range of spatial frequency for 2 flanker sizes. In the graphs, the comparative effect of 0.3 and 0.6 degs standard deviation Gabor flankers size on bar test are made. The colours represent Gabor flanker spreads of 0.6 cpd (blue solid closed diamond symbols) and 0.3 cpd (red dashed square symbols) for the range of frequencies used and error bars represent ± 1 standard errors.

Fig. A. 5 Individual Data for Expt.5.3A. Each panel depicts individual stereo-threshold (y-axis) plotted as a function of flanker disparity at OCD. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) flanker spatial frequency, for a fixed low (0.5 cpd) test target. All Gabors has the same SD of 0.5. The colours represent 0.5 cpd (blue closed

diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies, and error bars represent ± 1 standard errors.

Fig. A. 6 Individual Data for Expt.5.3A. Each panel depicts individual stereo-threshold (y-axis) plotted as a function flanker disparity at OCD. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) flanker spatial frequency, for a fixed high (4 cpd) test target. All Gabors have the same SD of 0.5. The colours represent 0.5 cpd (blue closed diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies, and error bars represent ± 1 standard errors.

Fig. A. 7 Individual Data for Expt.5.3B. Each panel depicts individual stereo-threshold (y-axis) plotted as a function test-flanker depth separation. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) frequency flankers on a fixed low (0.5 cpd) test target frequency composition. All Gabors have the same SD of 0.5. The colours represent 0.5 cpd (blue closed diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies and error bars indicate ± 1 standard errors.

Fig. A. 8 Individual Data for Expt.5.3B. Each panel depicts individual stereo-threshold (y-axis) plotted as a function test-flanker depth separation. The graphs show the comparative effect of low (0.5cpd) and high (4 cpd) frequency flankers on a fixed high (4 cpd) test target frequency composition. All Gabors have the same SD of 0.5. The colours represent 0.5 cpd (blue closed diamond symbols) and 4 cpd (red closed square symbols) flanker spatial frequencies, and error bars indicate ± 1 standard errors.

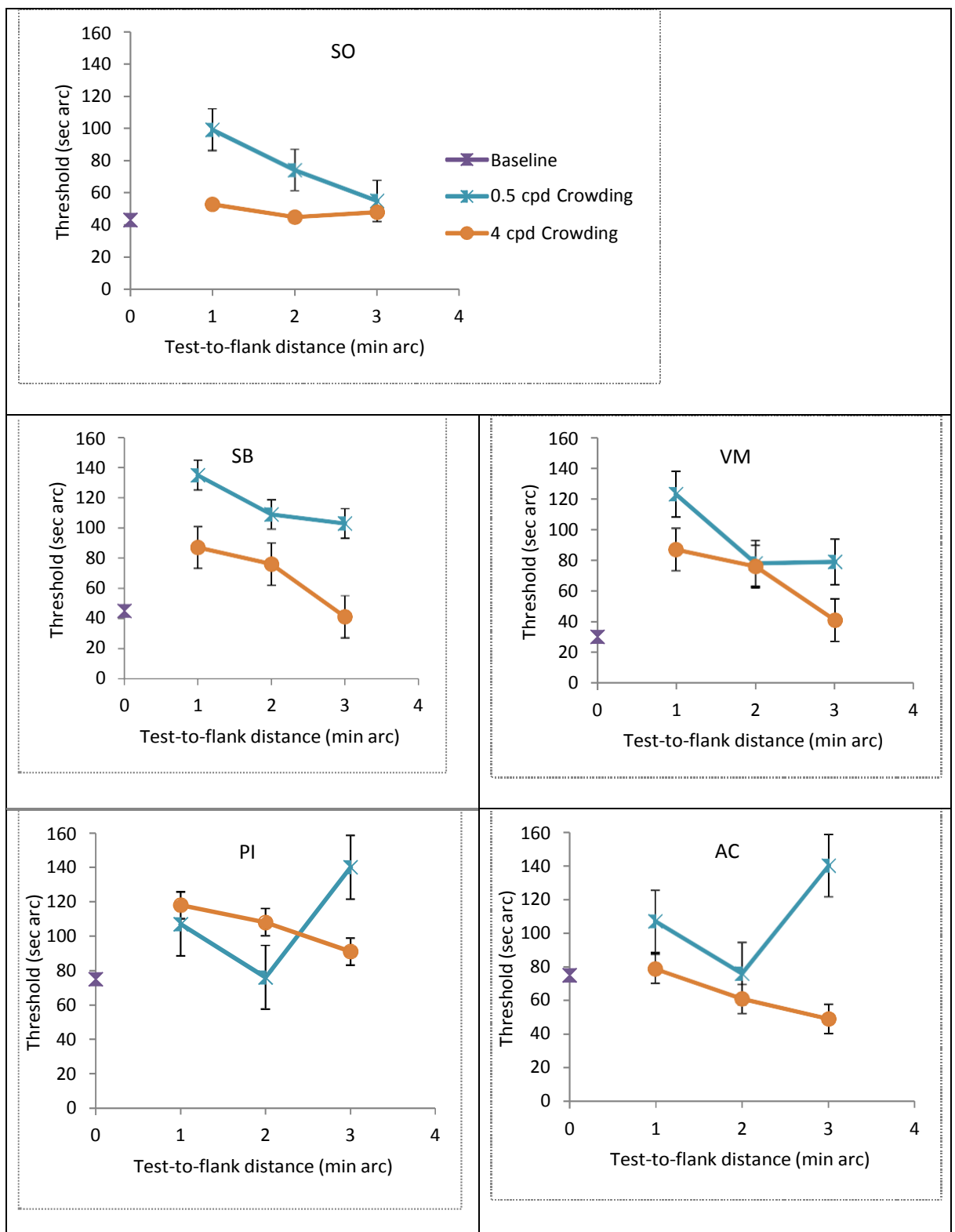


Fig. A1 for Expt.5.1B. Dependent of Crowding on Flanker Spatial Frequency measured for a low spatial frequency Gabor test target.

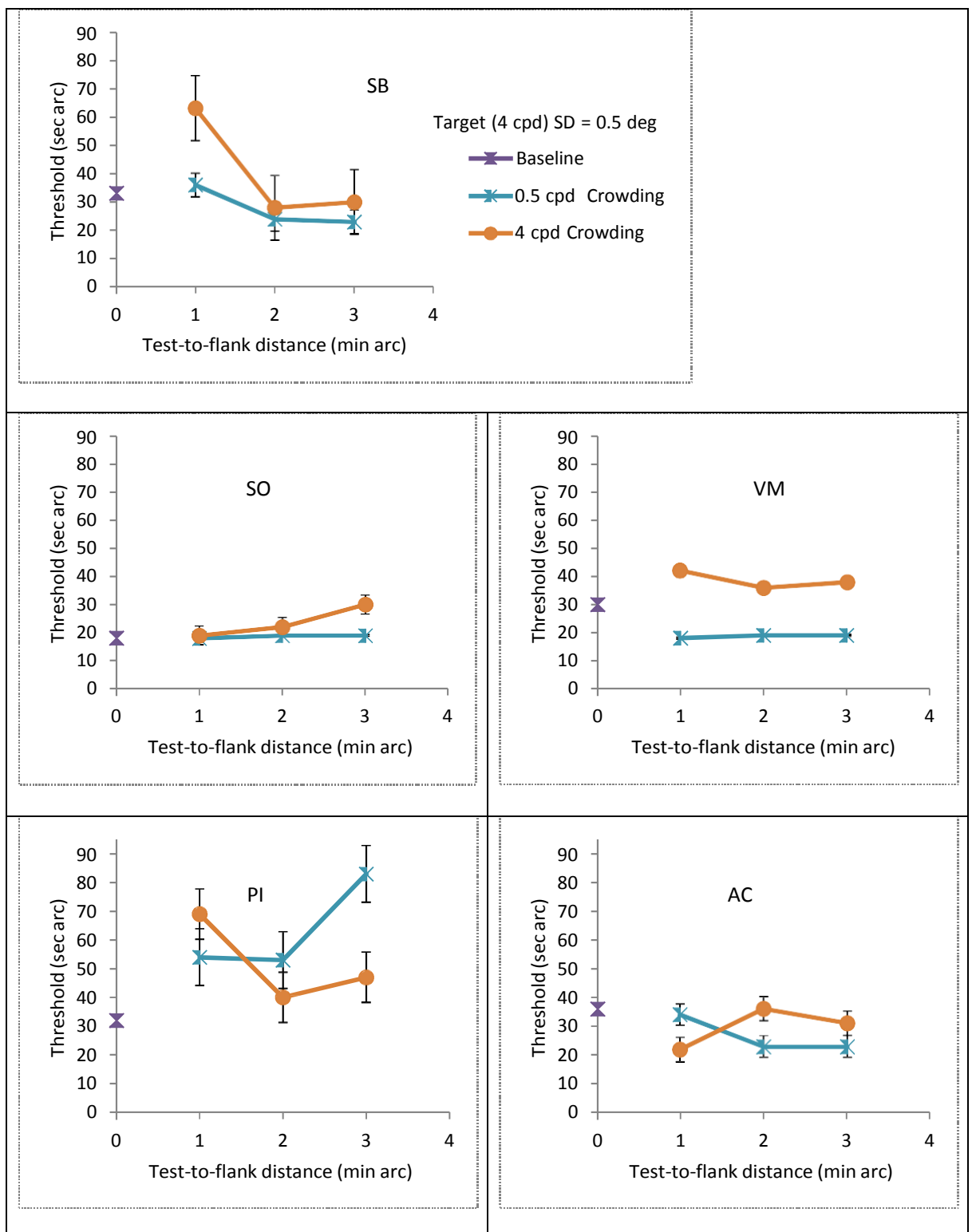


Fig. A2 for Expt.5.1B. Dependent of Crowding on Flanker Spatial Frequency measured for a high spatial frequency Gabor test target.

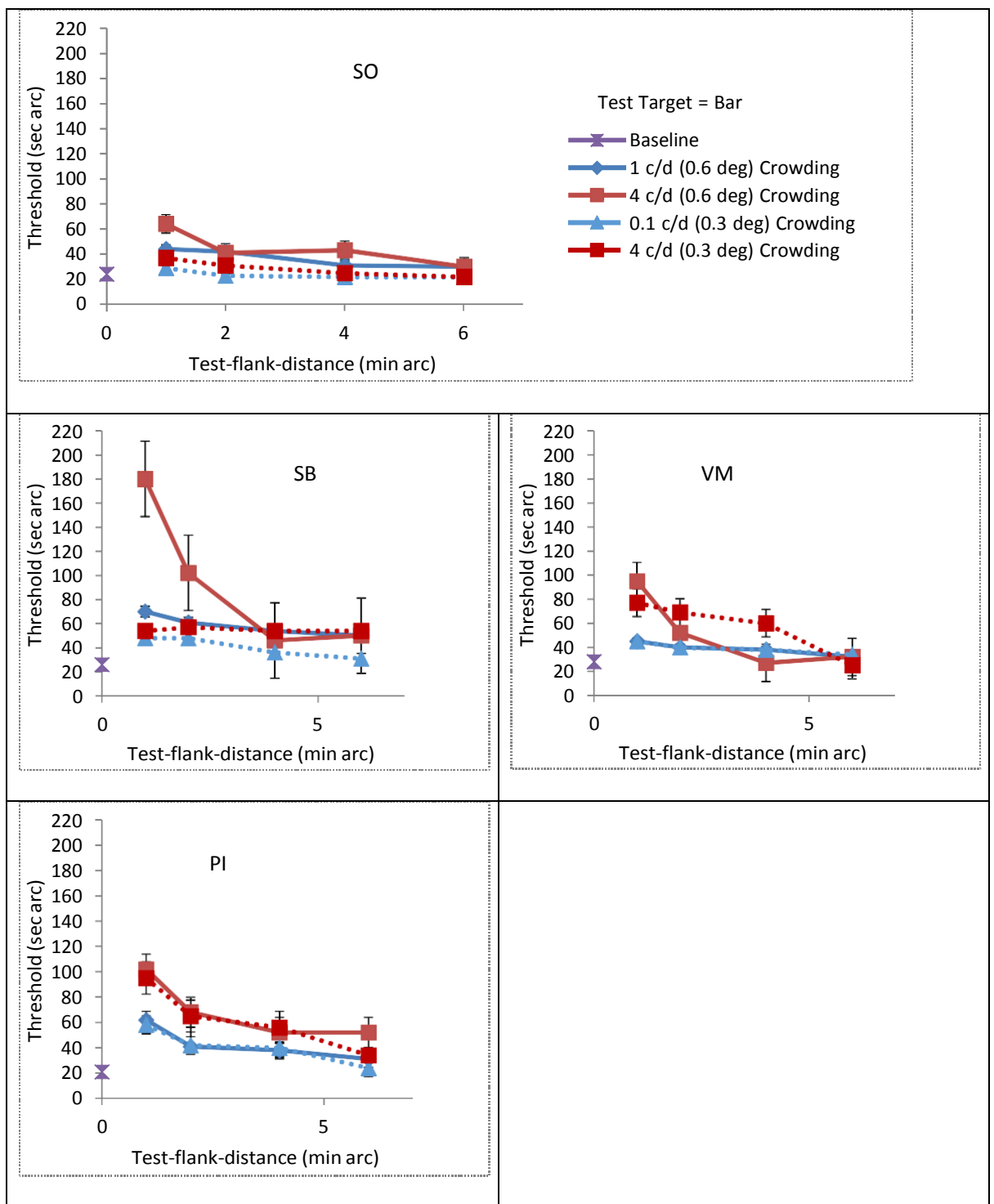


Fig. A3 for Expt.5.1C. Effect of Gabor Flanker Size on Crowding for a bar test target

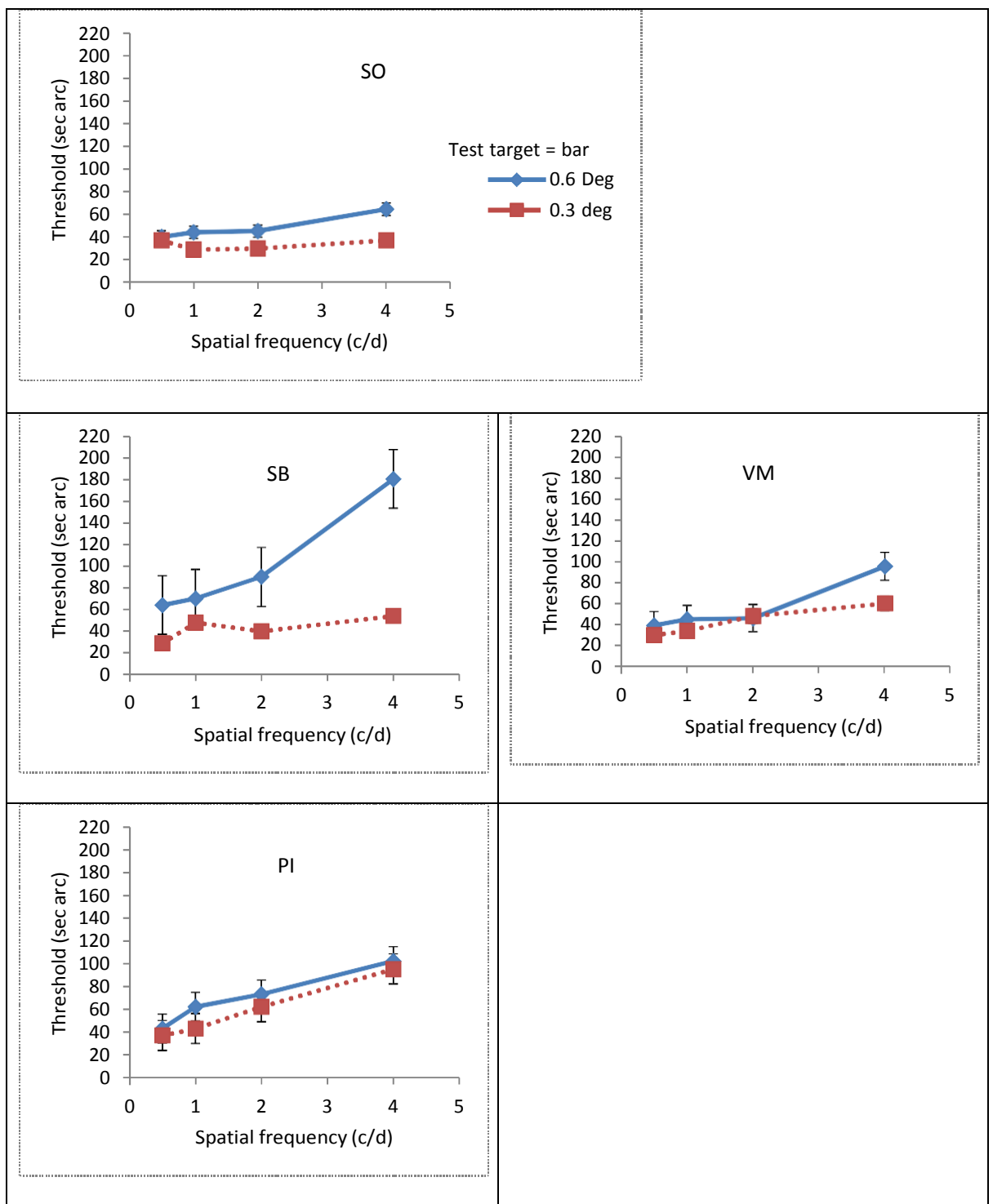


Fig. A4 for Expt.5.1C. Effect of Flanker spatial frequency at optimum crowding separation measured for a bar test target.

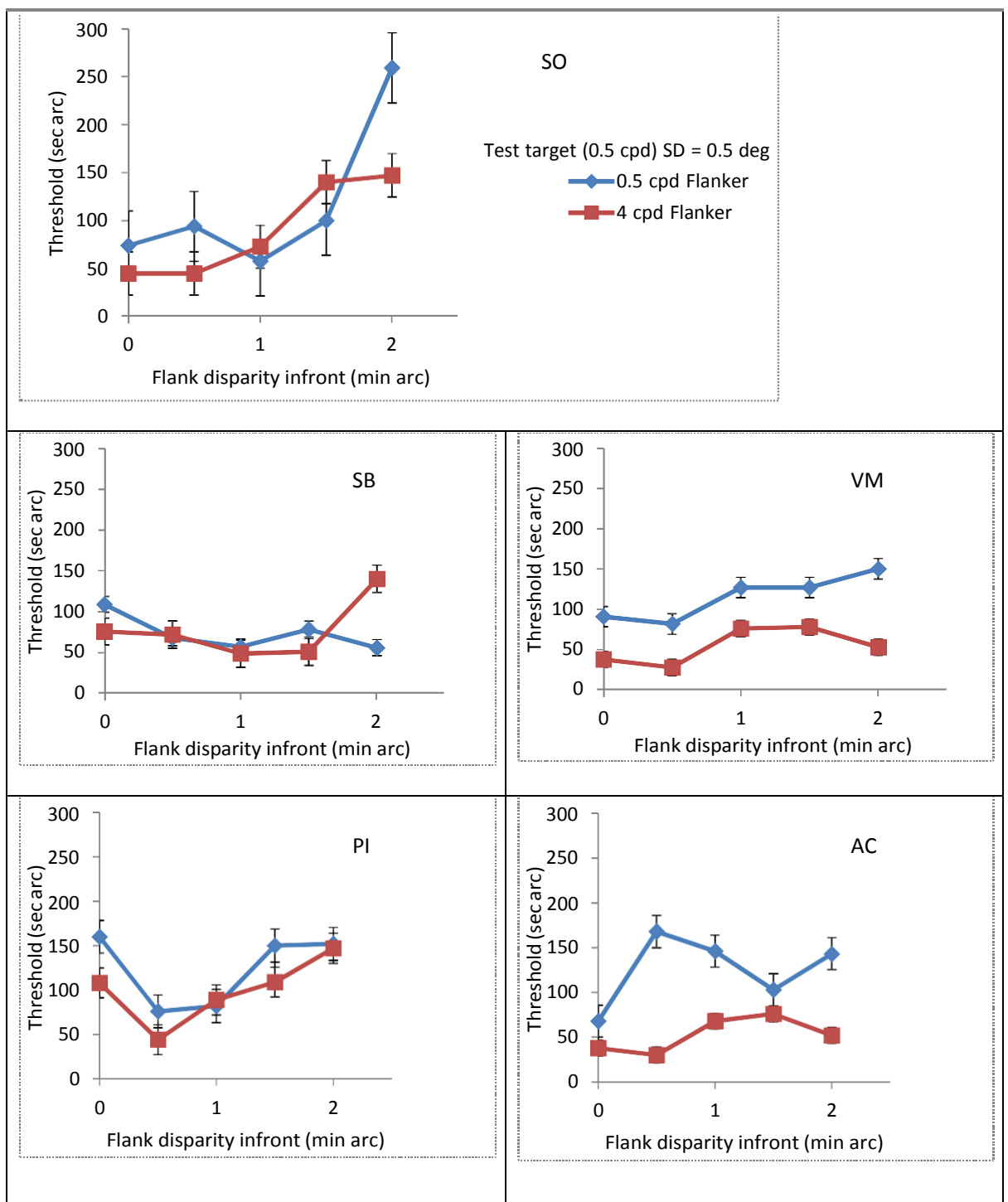


Fig. A5 for Expt.5.3A. *Effect of Flanker Spatial Frequency for a fixed OCD for low (0.5 cpd) spatial frequency Gabor test target. .*

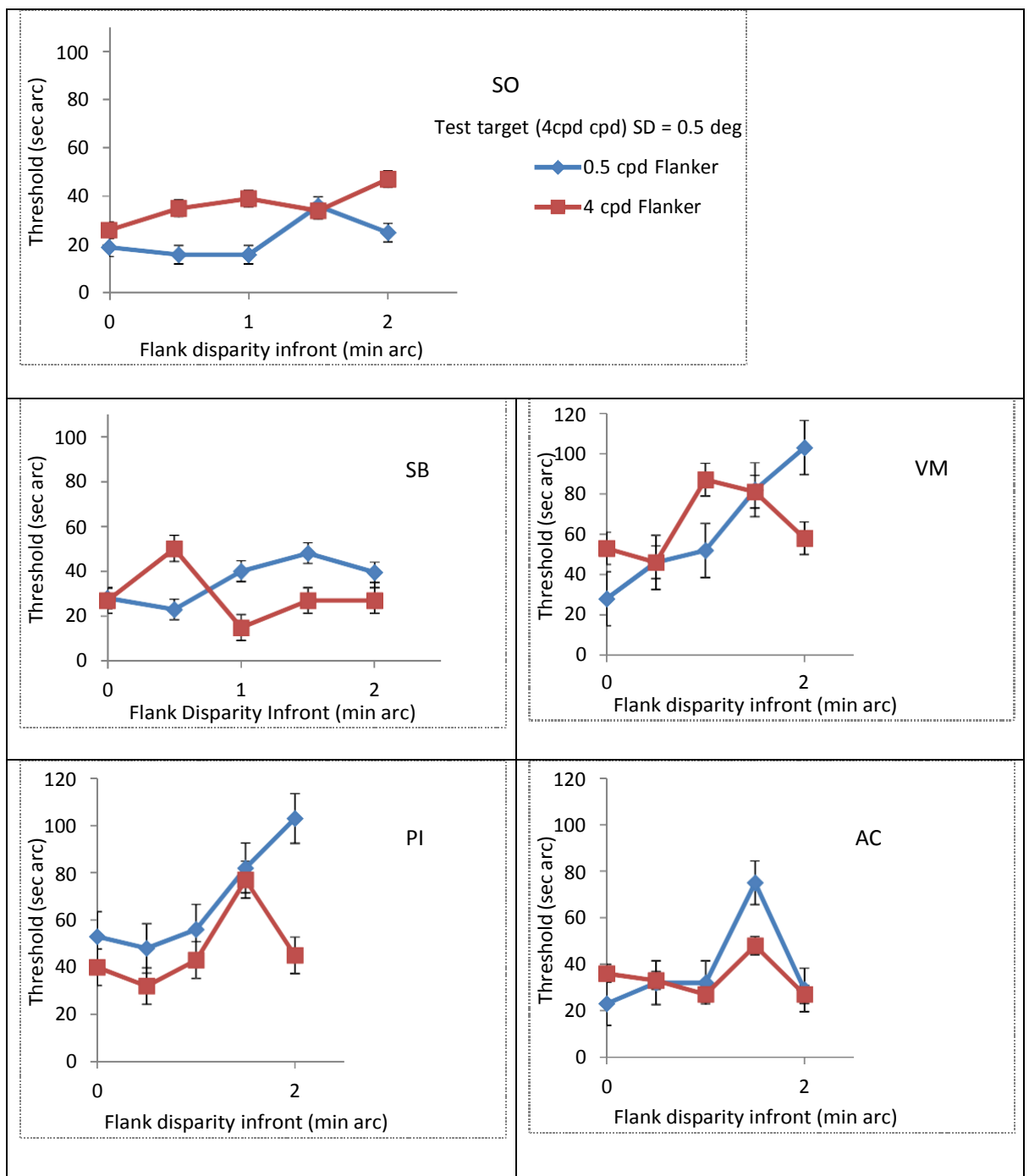


Fig. A6 for Expt.5.3A. *Effect of Flanker Spatial Frequency for a fixed OCD for high (4 cpd) spatial frequency Gabor test target. .*

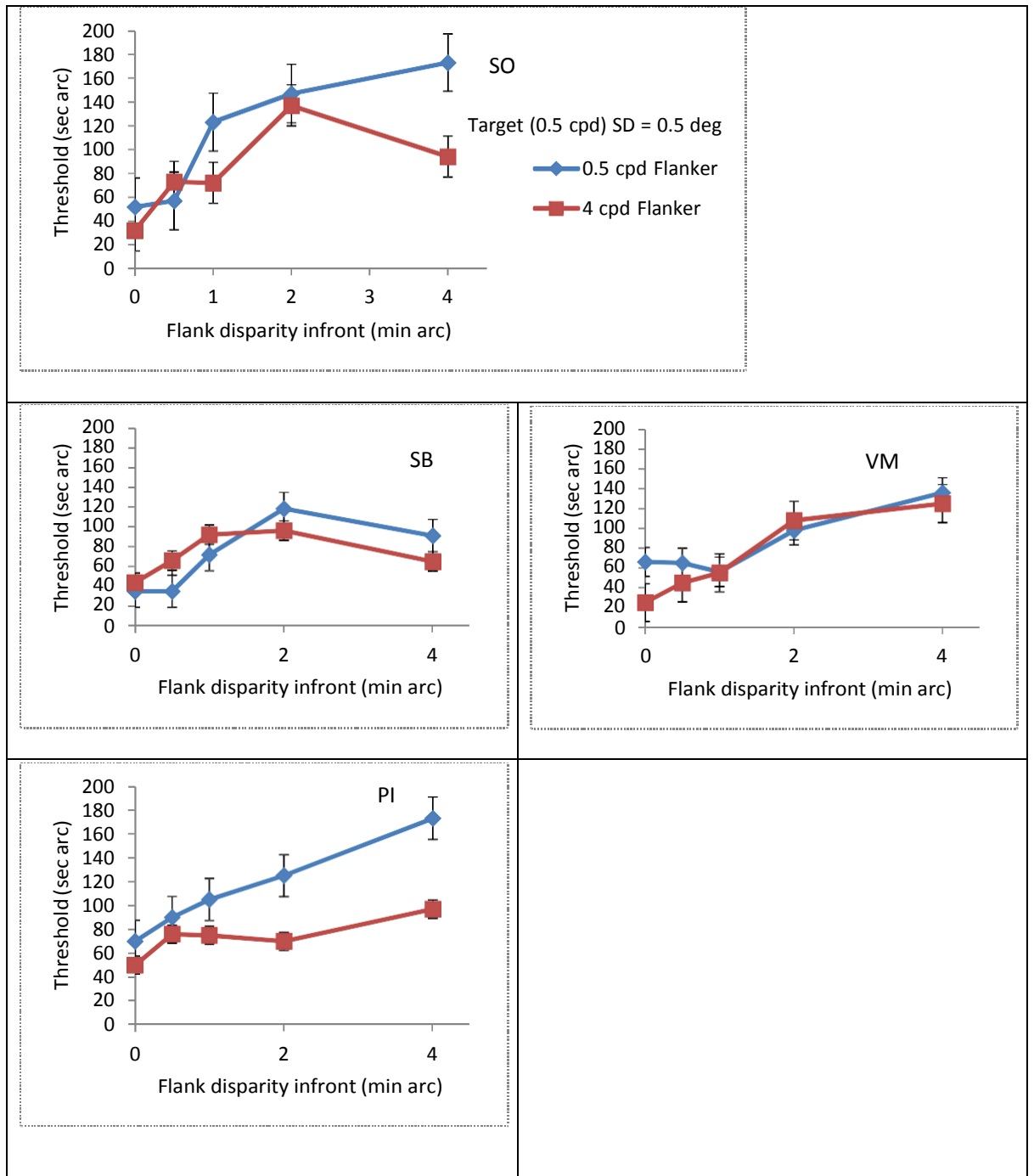


Fig. A7 for Expt.5.3B. Effect of Flanker Spatial Frequency for a fixed LCD for a low (0.5 cpd) Gabor test target

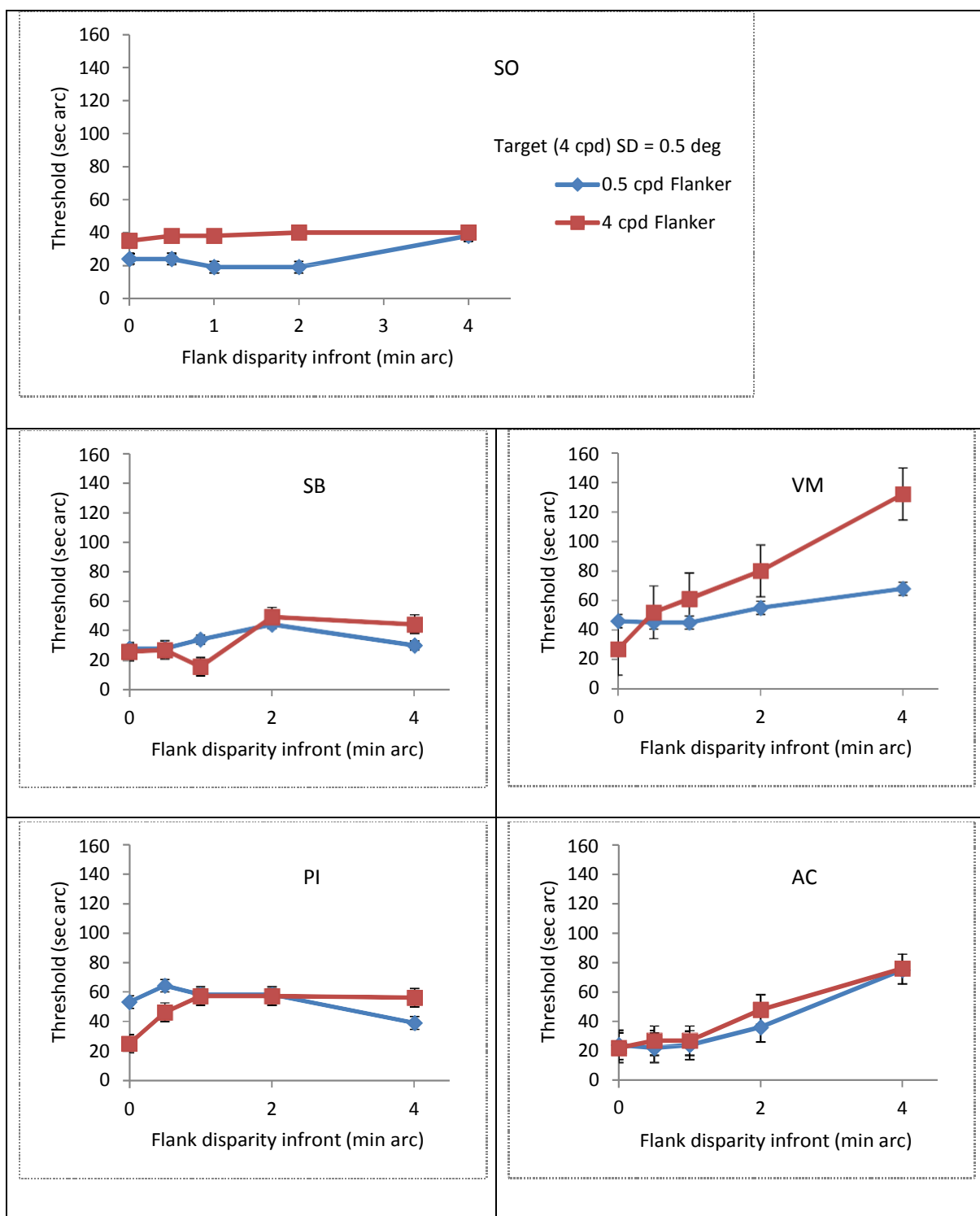


Fig. A8 for Expt.5.3B. Effect of Flanker Spatial Frequency for a fixed LCD for a low (4 cpd) Gabor test target.

B. Hypothetical Stereo Tests.

Diagrams of designed hypothetical stereo test made of 7 by 7 matrix of square features with horizontal separations between the features that can be fixed or varied. The test target consist of the middle 3 by 3 matrix, and outer flanker submatrices can be displaced with disparity between the two eyes. In Fig. B1, the matrix features is well separated with large distances between the square features, making it look uncrowded. In Fig B2, the matrix have small separation between their endpoints, making them appear crowded. In Fig B3, the middle test submatrix is surrounded by flankers that could have the width made thinner or widened and their length made shorter or longer. Based on the results of the experiments conducted in this study, one can hypothesis that depth discrimination of the test target in Fig B1 will relatively be easier based on the large separations between the features. However, depth discrimination in Fig B2 will relatively deteriorate due to crowding in the features. The crowding effect will however decrease if the size of the flankers are increased to make them appear perceptually different from the test target features due pop-out effect as result of ungroupping of the stimuli components. It may be interesting to examine the effect of the flanker and test pedestal disparity on the stereo-threshold.

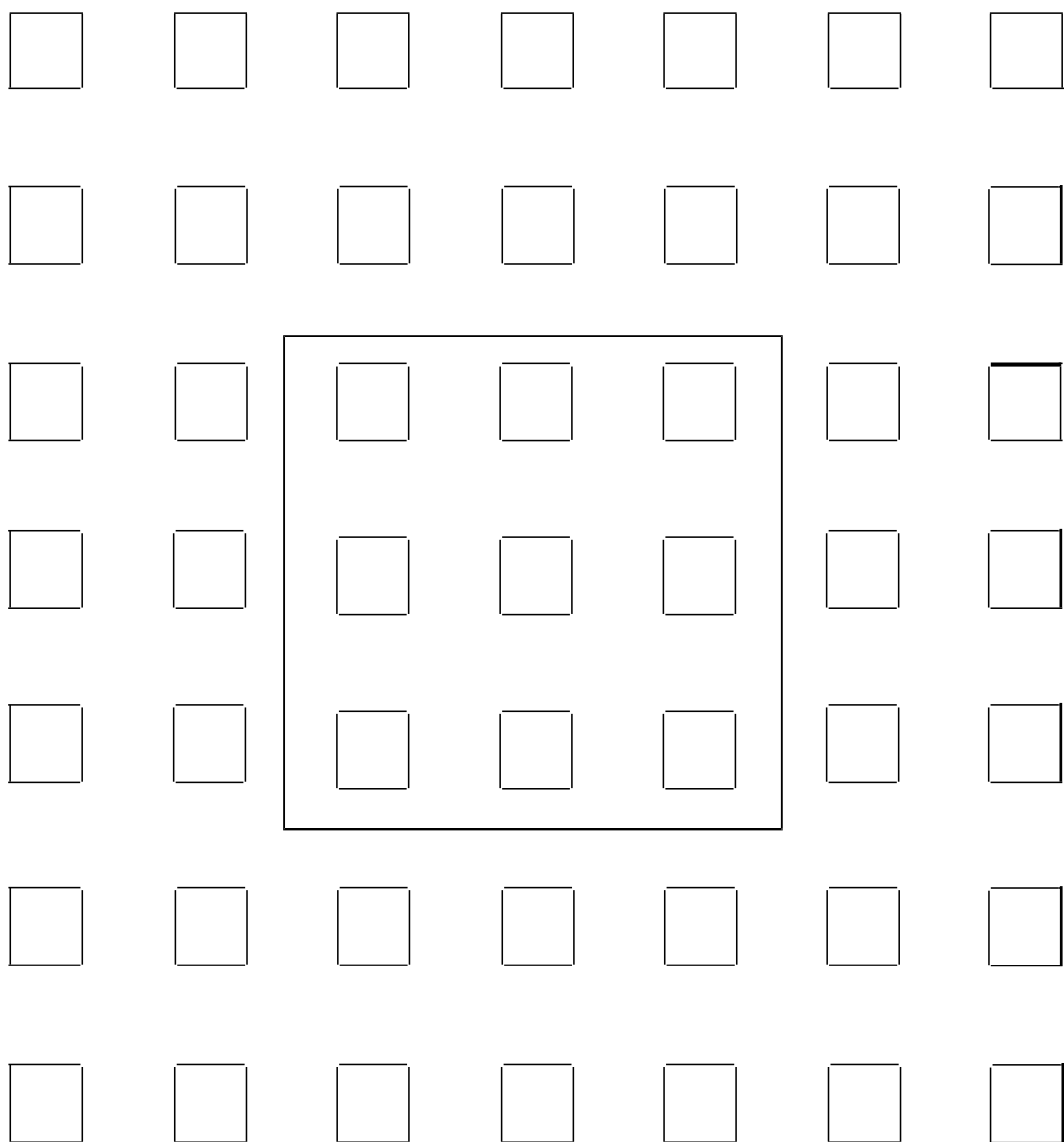


Fig. B. 1 Non-Crowded Stereo test.

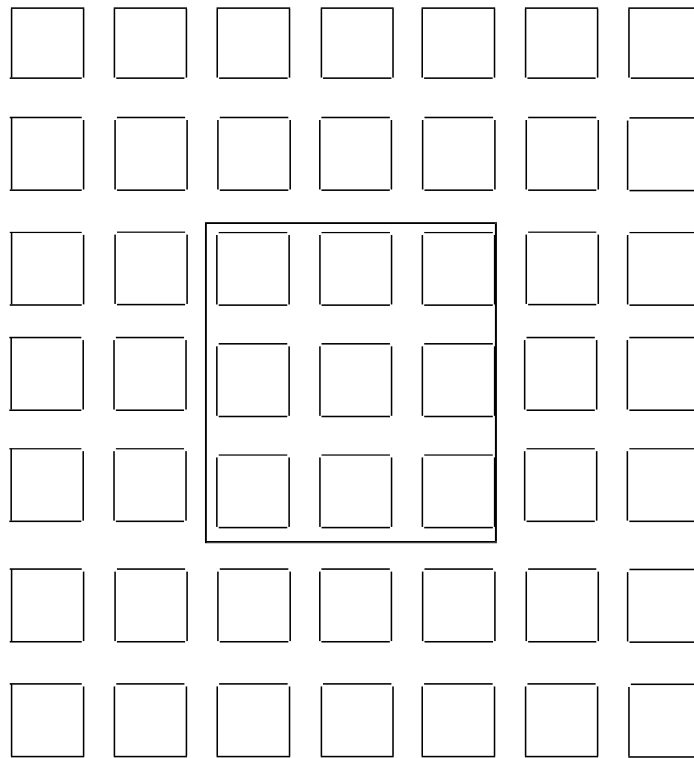


Fig. B. 2 Crowded Stereo test

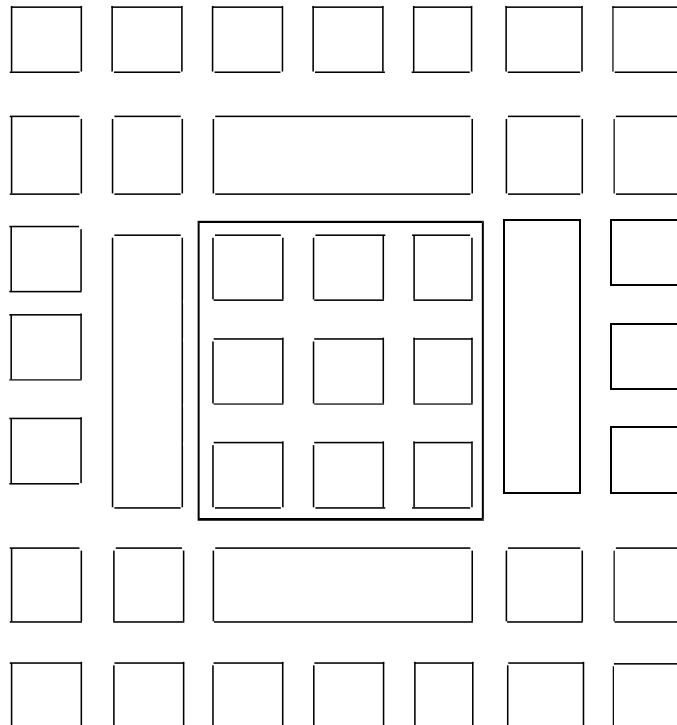


Fig. B. 3 Possible Effect of Flanker Dimension to Release Crowding

Table C. 1: Luminance Calibration for the Luminous Bars

Stimulus	Dim illumination				Bright illumination			
	(Cd/m²)				(Cd/m²)			
	Reading							
	1	Reading2	Reading3	Average	Reading1	Reading2	Reading3	Average
Reference	51.7	51.7	51.9	51.8	53.3	53.4	53.4	53.4
Target (RE)	27.0	27.0	27.0	27.0	29.5	29.3	29.5	29.4
Target (LE)	27.0	27.0	27.0	27.0	28.8	28.8	28.8	28.8
Nonius								
surround	47.2	47.1	47.1	47.1	49.2	49.0	49.0	49.1
Nonius bars	26.4	26.4	26.2	26.3	28.5	28.4	28.4	28.4
Fixation point	48.8	49.1	48.8	48.9	50.9	51.0	50.9	50.9
Display								
background	4.0	4.0	4.0	4.0	5.9	5.9	5.9	5.9

* Note: Transmission through Ferro-electric shutter goggle was 15%

Table C. 2: Clinical Details of Observers

Observer	Snellen VA on testing.	Stereoacuity (TNO test)(sec arc)	Corrected VA	Optical correction	Cover test
OS	RE 6/12	30	RE 6/5	RE -1.50/-0.25DC * 90	NMD
	LE 6/6		LE 6/5	LE -1.50/-0.25DC * 90	
AC	RE 6/5	15	RE 6/4	RE -0.50/-0.50DC * 135	NMD
	LE 6/9		LE 6/4	LE -0.75/-0.50DC * 45	
JO	RE 6/5	30	-	-	NMD
	LE 6/5		-	-	
MC	RE 6/5	30	-	-	NMD
	LE 6/5		-	-	
MR	RE 6/60	30	RE 6/5	RE -6.00DS*	NMD
	LE 6/60		LE 6/5	LE -6.00DS	
SB	RE 6/36	30	RE 6/5	RE +5.00/-0.50*15	NMD
	LE 6/18		LE 6/5	LE +5.00/-1.00*15	
PI	RE 6/9	30	RE 6/5	RE -1.00DS	NMD
	LE 6/9		LE 6/5	LE -1.00DS	
VO	RE 6/5	30	-	-	NMD
	LE 6/5		-	-	

**Rigid gas permeable contact lens. RE = Right Eye LE = Left Eye*