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Lateral interference, effects of flankers and reference bar configuration on foveal depth discrimination thresholds

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1. Introduction

The human binocular visual system has the ability to accurately discriminate extremely small differences in the relative depth of targets in visual space (Berry, 1948; Stigmar, 1970). As a result of the horizontal positioning of the eyes, two objects located in front of an observer but at slightly different fixation distances (i.e. at different depths) will form images with slightly different retinal positions in each eye resulting in a horizontal retinal disparity, which is the fundamental cue to stereoscopic depth perception (Ogle, 1952, 1953; Wheatstone, 1838). Stereoscopic depth discrimination is most acute for stimuli located on or near the fixation plane and can be on the order of a few arc seconds of disparity (Berry, 1948; Blakemore, 1970; Westheimer & McKee, 1979). Similar to other spatial acuity tasks (e.g. visual acuity, Vernier acuity and judgment of tilt of short lines) (Bouma, 1970; Flom, Heathm & Takahashi, 1963; Flom, Weymouth & Kahneman, 1963; Levi, 2008; Pelli, 2008; Toet & Levi, 1992), stereoscopic acuity is also adversely affected by the presence of flanking targets ostensibly through a form of lateral interaction or visual crowding. Generally, visual crowding refers to the deleterious impairment of nearby contours (or targets) on the spatial discrimination of objects in the central and peripheral visual field (Bouma, 1970; Flom, Heathm et al., 1963; Flom, Weymouth et al., 1963; Toet & Levi, 1992). 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, Heath, et al., 1963; Tripathy & Levi, 1994), suggesting signals bypass early stages of visual processing to arise in the visual cortex. Visual crowding therefore provides an investigative tool to understand the mechanism by which the visual system collates visual information from the environment, by studying factors that influence depth discrimination thresholds (Butler & Westheimer, 1978; Mitchison & Westheimer, 1984; Westheimer & McKee, 1980; Westheimer & Truong, 1988).

The crowding effect on 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). They reported that crowding was evident for a small range of test-flanker line separations of less than 6 min arc. They observed that the relatively shorter flanking lines produced less crowding when closest to or farthest from the test target, resulting in a tuning function. 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 putative mechanisms that would induce crowding (Flom, Weymouth, et al., 1963; Shim, Alvarez, & Jiang, 2000). However, for small flanker–test separations the explanation is less obvious and valid questions may be asked as to whether the flanking lines themselves acted as reference targets in these circumstances. Other works have shown that unequal lengths of test and flankers such as those used by Butler and Westheimer (1978) (Kumar & Glaser, 1992a) and the number and position of flankers (Felisberti, Solomon, & Morgan, 2005; Kumar & Glaser, 1992b) in a stereoscopic task may be used to aid depth discrimination when flankers are close to the test. Westheimer and McKee (1980) examined the crowding effect in stereo by varying the distance between the nearest sides of stereoscopically presented test squares. Consistent with other results (e.g. Hirsch & Weymouth, 1948; Butler & 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 from 10 to 20 min arc. When they crowded their test square within a 3 × 3 matrix, the presence of extra reference square targets degraded the stereo acuity at small separations, less than 10 min arc, as thresholds rose quite considerably. Significantly, they found that, consistent with results using the isolated stereo square pair, the separation required for best performance was about 10 min arc. However, contrary to previous results of Butler and Westheimer (1978), Westheimer and McKee (1980) found that thresholds progressively increased for test –

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reference separations less than about 10 min arc, albeit not as dramatically and also when the separation was widened outside the range for best performance. Although crowding may explain the threshold elevation for small test – reference separations, it may be that at the wider separations, the flanking square became a non-effective reference target, and hence the relatively higher thresholds represented a near absolute depth discrimination of the test square. These assumptions about the effect of flanker and reference configuration on depth discrimination thresholds are subjected to further testing in this study. Two alternative basic neural mechanisms have been proposed to explain crowding in depth; an active lateral inhibition and a passive spatial pooling. In inhibition, flankers activate the inhibitory regions of neurons dedicated to the depth signals of the test within a small area of the visual space and thereby decrease the neural activity of the test (Badcock & Westheimer, 1985; Blakemore & Hague, 1972; Butler & Westheimer, 1978; Freeman & Ohzawa, 1990; Poggio & Fischer, 1977). In spatial pooling, depth signals related to the test and flankers are pooled and averaged within some integrative area in visual cortex (e.g. Badcock & Westheimer, 1985). However, there is evidence through psychophysical means that contour interaction between a test and nearby flankers does not only hinge on spatial separation, but also on other factors including stimulus size (McKee, 1983; Westheimer, 1979), contrast (Chung & Mansfield, 2009; Kooi, Toet, Tripathy, & Levi, 1994; O'Shea, Blackburn, & Ono, 1994), relative orientation (Andrews, Glennerster, & Parker, 2001) and feature properties such as colour (chromaticity) (Kennedy & Whitaker, 2010), texture (Frisby & Mayhew, 1978; Gantz & Bedell, 2011), spatial frequency composition (Siderov & Harwerth, 1993), direction of movement (Westheimer & McKee, 1978), shape (Kooi et al., 1994), as well as the visual status of the observer (Fricke & Siderov, 1997; Momeni-Moghadam, Kundart, Ehsani, & Gholami, 2011). Experiments examining the effects of contextual modulation on crowding have revealed that perceptual grouping of test and flankers plays an important role in threshold elevation, highlighting the importance of Gestalt factors in contextual interactions (Livne & Sagi, 2007; Malania, Herzog, & Westheimer, 2007; Sayim et al., 2008, 2010). More recently, Astle, McGovern, and McGraw (2014) examined how changing the disparity of the flankers relative to the test stimulus affected crowding. They found a systematic decrease in crowding as the relative disparity of the test and flankers increased and that there was a greater release from crowding when the target was perceived to be in front of the flankers rather than behind. Astle et al. (2014) suggested that such flanker effects are unlikely to be attributed to grouping, but are consistent with a disparity pooling mechanism. Flanker effects can be observed in studies that presented flanking lines at depths in front of (Butler & Westheimer, 1978; Felisberti et al., 2005; Sayim, Westheimer, & Herzog, 2008), or behind (Felisberti et al., 2005; Kooi et al., 1994; Sayim et al., 2008) a test target that either caused a decrease or increase in threshold. In the aforementioned studies, the dimensions of the interacting features and their influence on the depth discrimination thresholds were not well elucidated. The reason for carrying out this study was to investigate the nature and characteristics of stereo crowding in a test – flanker stimulus configuration that allows for optimum crowding effect. We were interested in the nature of the local interaction between the dimensions of the flanking bars and the depth perception of the test target. It will seem that an edge-to-edge mechanism will serve as a vital cue for depth discrimination in this instance, but the mechanism may shift to one which relies on centre-to-centre interactions due to the pooling of depth information when the flankers are widened (Badcock & Westheimer, 1985; Mitchell & O'Hagan, 1972; Richards, 1972). We are not aware of any study that combines the manipulation of stimuli configuration, reference and flankers when attempting to delineate the spatial extent and characteristics of crowding in depth in the fixation plane. If the magnitude of crowding depends on the relationship between the features in the stimuli, the present investigation, which investigates the influence of stimulus configuration on depth discrimination thresholds, is worthwhile.

2. Materials and methods

2.1. Apparatus

Stimuli were generated and displayed on a single high resolution, visually flat single, gamma corrected monochromatic 21″ Sony Trinitron colour graphic video monitor display (Model: GDM-F520), and were loaded using a frame store memory of the Cambridge Research Systems (CRS) Visual Stimulus Generator (VSG 2/5). Stimuli were presented to each eye separately using a liquid crystal shutter goggle (Cambridge Research Systems FE) synchronized to the video display unit. The refresh rate for the monitor display was 120 Hz while the shutter for each eye operated at 60 Hz.

2.2. Stimuli

The stereoscopic stimuli for the experiments were two relatively thin, luminous vertical targets (test and reference bars) displayed with the test bar directly below the reference and separated by a small gap that varied slightly between observers. Flanking bars were symmetrically placed around the test bar only. The dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. When present, for the initial experiments, the flanking bars were the same dimensions. In later experiments, the width of the flanking bars was systematically varied from 0.5, 1, 2, 4 to 6 min arc. The stimuli were positioned at equal vertical and horizontal distances from the middle of the monitor display, with a small vertical separation between them. Both the reference and the test bars were shifted vertically by equal distances from the centre of the display in the opposite direction. The separation between their endpoints used in the experiments depended on the observer's pre-determined optimum vertical separation. The test bar appeared at 51, 25.6, 17.0 and 8.5 sec arc in front or behind the reference bar or at the fixation plane i.e. at the same depth as the reference bar (zero disparity). Trials were randomly interleaved to prevent subjects making anticipatory eye movements. 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 (l) and the background (I_b), respectively. The luminance of the target and reference was the same and measured 52 cd/m^2 in dim illumination while the mean luminance of the display measured 4 cd/m^2 with a transmission rate of 15% for the shutter goggle. The luminance of the display was calibrated using a Pritchard Spectrophotometer (PR-650 Spectrascan Colorimeter).

Binocular disparity was produced by a programmed presentation of alternate, non-interlaced video frames to each eye viewed through shutter goggles, synchronized 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 test stimuli. Binocular fixation at the plane of the reference element was maintained between trials by observing the relative position of Nonius stimuli comprising a pair of luminous bars vertically aligned and separated by a fixation point all displayed at the centre of the monitor display. The diameter of the fixation point was 30 sec arc and the vertical bars were 1.4 min arc wide and 7 min arc long. They were surrounded by a thin square frame with a side length of 28 min arc. The Nonius stimuli 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. Stimuli for the experiments were created and controlled using a custom written programme in Matlab (version 10). Parameters for the stimuli and the required configuration for each experiment were specified in a programme condition file. The ambient laboratory room lighting conditions were kept low, to avoid glare from the computer screen and ensure that the stereoscopic stimuli and Nonius lines were clearly visible to observers.

2.3. Subjects and visual condition

In all, six observers (AC, JO, MC, MR, SO and VO) took part in the study, with at least three participating in each experiment. Three were naive subjects. Observers were either staff or students, including one of the authors. Subjects had normal binocular vision (no significant heterophoria) and stereo acuity better than 30 sec arc which was assessed clinically with the TNO (Lameris Ootech) stereo acuity test (Fricke & Siderov, 1997). All observers were emmetropic or conventionally corrected with glasses or contact lens to 6/6 Snellen acuity or better. They viewed the stimuli through their natural pupils and the shutter goggles were appropriately positioned on the face. This work was approved by the institutional research ethics committee, informed consents were obtained and adhered to the Helsinki Declaration on Research regarding Human Subjects.

2.4. Procedure

Conditions required for each experiment and presentation times were controlled precisely by setting the parameters in a condition file. All experiments were performed at a distance of 13.5 m measured from the centre of the monitor display to the spectacle plane of the observer (created using an optical quality mirror). Observers positioned the shutter goggles as required and viewed the monitor display, while maintaining their head position in primary gaze. The stimulus was presented for 300 ms at a self-timed rate. The psychophysical procedure of a single exposure, forced-choice paradigm was used to collect data. On any one trial, the observer's task was to indicate whether the 'test bar' (lower element) was in front of the 'reference bar' (upper element) or behind it. The observer indicated 'test in front' or 'test behind' by pressing an appropriate button of a response box (CRS CT-6) immediately following the presentation of the 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. Before each trial, observers were instructed to wait until the upper and lower Nonius bars appeared aligned before initiating a trial. Data collection was done in sessions, twice a week and each session lasted about one and half hours in duration. Before actual data collection commenced, observers were trained on the simple two bar stereoscopic stimulus to achieve stable thresholds.

2.4.1. Data analysis

For each experimental run, 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% to 75% of the fitted psychometric functions. Data points represent at least 500 responses. A one-way repeated measures Analysis of Variance (ANOVA) was performed to examine the 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 Tukey’s Honest Significant Difference (HSD) test ($\alpha = 0.05$) was carried out to determine the effect of flankers on threshold at each test-flanker separation. When interpreting the results however, the *p value* must not be used in isolation. Limitations associated with the relatively few subjects used in the experiments, and subjective bias in performance, which are not unusual in psychophysical studies may hide the magnitude and variability of the observed effects if not jointly interpreted with alternative graphical presentation, ratios or main performances (Twa, 2016). Error bars indicate $\pm$ 1 standard error (SE) of the mean. The magnitude of crowding was determined by comparing the 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 unflanked threshold. The extent of crowding was defined as the smallest test-flanker separation at which the flanked stereo-threshold was not statistically significantly different, relative to the unflanked stereo-threshold.

2.4.2. Estimating depth bias

In the main crowding experiment, the flankers were always positioned in the fixation plane. We also determined any effects of the flanker that resulted in bias in discriminating the depth direction of the test relative to the reference as test-flanker separation was varied. 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) similar to the annulling method used by Westheimer (1986). Therefore, it can be regarded as estimation of the point of subjective equality (PSE).

2.5. Experiments

2.5.1. Experiment 1

In Expt. 1A, the effect of the vertical distance between the nearest edges of the unflanked test and the reference target configuration on stereo acuity was studied. The dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. For each observer, the vertical separation was varied from abutting through to 21 min arc to determine the separation(s) that resulted in best stereo acuity. Observers were required to make a forced-choice response as to whether the test bar appeared in front of or behind the reference bar in the fixation plane. The individual optimum separation was defined as the separation which produced the best stereo acuity, derived from the probit fitting of the psychometric functions for each individual. This unflanked stereo acuity served as baseline condition, and was used to monitor the stability of each observer’s stereo acuity during the course of the other experiments.

In Expt. 1B, we investigated the spatial interactions in depth between the test target and flanking bars around the plane of fixation. Five subjects participated in this experiment. For each subject, the vertical separation between the reference bar and test bar was set at optimum values obtained in Expt. 1A, that is AC, 7; JO, 7; MC, 14; MR, 7 and SO, 14 min arc. Two vertical flanking bars of the same length, width and contrast as the test bar were used to induce crowding. The flanking bars were positioned symmetrically on either side of the lower test bar only. The dimensions of the test and reference bars were fixed at 14 min arc long and 2.8 min arc wide. The stereoscopic stimuli together with the flanking bars were presented simultaneously for 300 ms. The lateral edge-to-edge distance from the test bar to either flanker was systematically varied from 1 to 8 min arc to determine the separation that resulted in maximal crowding. The lower test bar appeared at one of the eight positions in depth – 51, 25.6, 17.0 and 8.5 sec arc in front or behind the reference bar. “Catch trials” where both test and reference lines were at the fixation plane (zero disparity) were introduced to assess each subject’s depth direction bias. The two flanking bars and reference bar always appeared in the plane of fixation (fronto-parallel plane). Observers were instructed to respond to the direction of the perceived depth of the test target (either in front of or behind) relative to the upper reference bar.

2.5.2. Experiment 2

In Expt.1B, the reference and flanking bars were displayed in the fixation plane. Although observers were instructed to only use the reference bar for relative depth discrimination of the test, it is possible that observers used other components of the configuration as an *ad hoc* reference in the fronto-parallel plane. For example, as the edge-to-edge distance between the flanking bars and the target was reduced in Expt. 1B, the flankers may have been used inadvertently as the reference bar, resulting in the dip in threshold at close separations (Butler & Westheimer, 1978). Expt. 2 was therefore conducted to determine if, at the close test-flanker distance, the flanking bars did become default reference targets for the stereoscopic task. The stimulus configuration used was identical to Expt. 1, with the exception that the reference bar was omitted. The dimensions of the test and reference bars were fixed at 14 min arc long and 2.8 min arc wide. The edge-to-edge separation of the flanking bars from the test bar was systematically varied from 1 to 8 min arc and observers were required to report the depth position of the test target relative to the flanking bars. Four observers (AC, SO, JO, MR) participated in this experiment.

2.5.3. Experiments 3

The next experiments investigated whether the width of the flanking and reference bars had an influence on the stereo thresholds at the optimal crowding distances. The size of the test was fixed as in the original conditions (i.e. 14 min arc long and 2.8 min wide). The width of the flanking and reference bars were then varied, in separate conditions, from 0.5, 1.0, 2.0, 4.0 and 6 min arc (i.e. normalised widths of 0.18, 0.36, 0.71, 1.43, 2.14, relative to the original test/reference bar size), while the edge-to-edge separation of the flanking bars to the test bar was kept at each observer's determined maximum crowding distance which was for SO, 1; MR, 2; JO, 2; AC, 1; and VO, 2 min arc. In Expt. 3A the dimensions of the reference and test target were kept the same while the width of the flankers was varied. In Expt. 3B the dimensions of the flanking bars and test target were kept the same while the width of the reference bar was varied. As the width of the flankers was varied, care was taken to ensure that the edge-to-edge separation for each observer remained the same. The observers were required to report the depth position of the test target relative to the reference bar. Five observers (AC, JO, MR, SO and VO) participated in this experiment.

3. Results

3.1. Experiment 1

All thresholds reported in this study were subsequent to subjects achieving consistently stable baseline thresholds after 1500–2000 training trials. Baseline thresholds were monitored throughout the experiment and they remained stable during several months of data collection. Fig. 1 shows a plot of each subject's stereo-threshold (sec arc) and their average as a function of the vertical test – reference separation (min arc) in the simple two-bar unflanked stimulus (Expt. 1A). Consistent with previous reports (Fendick & Westheimer, 1983; Westheimer & McKee, 1980), stereo acuity was keenest (13–21 sec arc) for non-abutting separations between 7 and 14 min arc depending on the observer. On average, stereo acuity showed a relatively sharp decline from when the test and reference bars were abutting to a more gradual decline when the bar separation extended beyond the optimum range (Fig. 1).

Fig. 2 depicts the results of Expt. 1B, investigating the effect of bar crowding on depth discrimination, and shows the individual stereo-thresholds (broken lines) together with the average (solid line) across

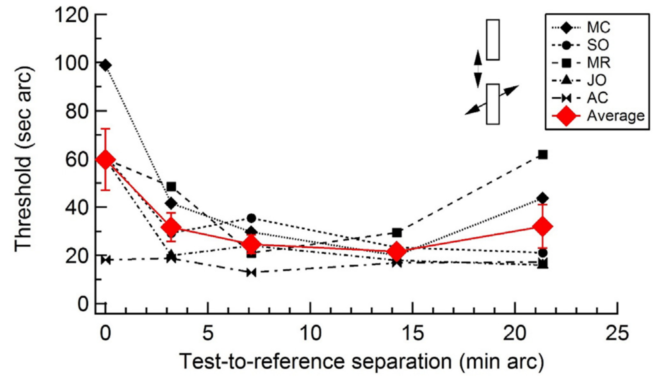

Fig. 1. Expt. 1A. Depth discrimination thresholds (sec arc) are plotted for each observer (and the average), as a function of the edge-to-edge vertical separation (min arc) of the test and reference bars in the two-bar baseline condition (inset). Individual results are shown by the different broken lines while the red solid line and large diamond symbols represents the average result. For clarity, error bars (± 1 standard error) are shown only for the average data. The dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

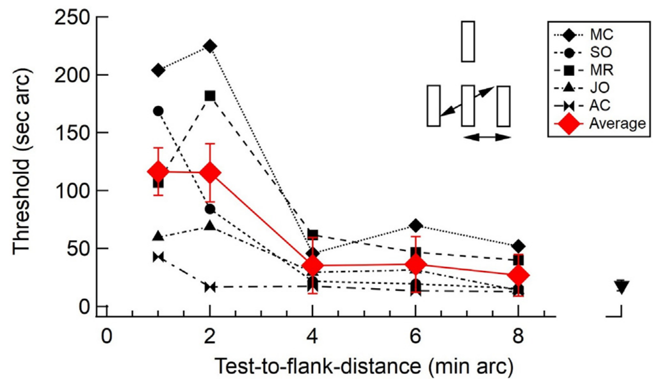

Fig. 2. Expt. 1B. Effect of bar crowding on depth discrimination. Depth discrimination thresholds (sec arc) are plotted as a function of the edge-to-edge separation between the test (stimulus) and the surrounding flankers (min arc) (inset). Individual results are shown by the different broken lines while the red solid line and large diamond symbols represents the average result. The inverted triangle represents the average unflanked condition from Expt. 1A. For clarity, error bars (± 1 standard error) are shown only for the average data. The dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. Optimum vertical edge-to-edge separation between the test and reference for AC, JO, MC, MR and SO were 7, 7, 14, 7, and 14 min arc respectively. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

the 5 subjects (sec arc), plotted as function of the test-to-flank distance (min arc). 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. For all observers, maximum crowding occurred at a test-to-flanker distance of around 1–2 min arc. At this separation, a three to eightfold elevation in threshold was observed across subjects over their respective unflanked values. The crowding effect decreased steeply for greater test-to-flanker distances up to about 4 min arc and then dissipated to values equalling the average unflanked condition. A one-way ANOVA was used to analyse the effect of test-flanker separation (including the unflanked condition) on crowding. There was a statistically significant effect of separation on discrimination [(F (5, 24) = 4.654, p = 0.004)]. Tukey post-hoc testing revealed that the effect of separation was statistically significant only when the flankers were 1 min arc [(116.6 ± 30.8 sec arc, p = 0.030)] or 2 min arc [(115.5 ± 38.2 sec arc, p = 0.033)] away

Table 1
Observers' Bias (Expt. 1): Negative and positive numbers represent 'in-front' and 'behind' bias respectively when the flanking bars were positioned at the plane of fixation and ± indicate standard deviations.

Bias (sec arc)					
Test-flanker distance (min arc)	SO	AC	JO	MR	MC
1	−20 ± 12.4	5.1 ± 2.6	−32 ± 28.4	−19 ± 4.0	−18 ± 8.5
2	−28 ± 20.4	10 ± 2.3	−4.2 ± 0.6	−34 ± 11.0	−81 ± 54.5
4	4 ± 11.6	15 ± 7.3	12.8 ± 15.6	−14 ± 9.2	−11.5 ± 15.0
6	−3.3 ± 4.3	9 ± 1.3	2.3 ± 5.9	−30 ± 7.0	−40 ± 13.5
8	−3.1 ± 4.5	12 ± 4.3	2.3 ± 5.9	−29 ± 6.0	−6 ± 20.5
INF*	5 ± 12.6	−4.8 ± 12.5	−2.9 ± 0.7	−12 ± 11.0	−2.4 ± 24.1

* INF = represents bias measured for unflanked test-flanker condition.

from the test.

In the unflanked (INF*) condition, all subjects except SO demonstrated crossed disparity bias, thus they judged the test target to be 'in-front' of the reference bar (Table 1). However, the presence of the flankers at optimum crowding distance (1 and 2 min arc) seem to enhance this apparent bias. That is, positional shifts in the test depth direction were induced. This resulted in subjects often judging the test to be further in front of the reference. Subject AC displayed 'behind' bias under crowding although the shift appeared to be less at optimum crowding distances. In general, the propensity of the flankers to enhance an apparent 'in-front' bias in target depth position was reduced (except for MR and MC) at farther test-flanker distances.

3.2. Experiment 2

Expt. 2 was performed to determine whether relative depth discrimination shifts from using the reference bar to using the flanking bars at smaller test-to-flank distances, suggesting that the flanking bars become relatively more useful depth cues than the reference bar. The stimulus configuration used was the same as that used in Expt. 1B, except that the upper reference bar was omitted. The distance from the test bar to the flankers was systematically varied as in Expt. 1B. The results are shown in Fig. 3 where, in each panel, stereo-threshold (sec arc) is plotted against test-to-flank distance (min arc) for each of the 4 individual subjects (broken lines and open symbols). For comparison, data from Expt. 1B, which included the reference bar, are also shown (solid lines and closed symbols). The results show that, in general, removal of the reference bar (E2) aids depth discrimination (i.e. thresholds were lower in Expt. 2 than in Expt. 1B). Similar to the results obtained in Expt. 1B, thresholds varied as a function of the test-to-flanker distance.

Maximum stereo-threshold occurred at a test-to-flanker distance of 1 min arc while the effect of crowding dissipated at test-to-flanker distances of about 4 min arc. However, except for observer MR, the stimulus configuration in Expt. 2 did not result in crowding effects as robust as those seen in Expt.1B. For example at 1 min arc separation, stereo-thresholds for AC, SO and JO were 31, 87, and 50 sec arc compared to 43, 169 and 60 sec arc respectively in Expt.1B. Atypically, subject MR demonstrated more crowding under this condition (281 sec arc) than when the reference bar was present (107 sec arc) for the same separation. A one-way ANOVA showed no statistically significant effect of separation on discrimination [(F (5, 18) = 2.137, p = 0.107)]. However, mean threshold appreciably decreased from the close separation of 1 min arc (112.2 ± 57.5 sec arc) to the wider separation of 6 min arc (23.5 ± 3.5 sec arc), corresponding to a 6.6X to 1.4X increase over baseline values.

3.3. Experiment 3

Fig. 4 depicts the effect of relative flanker width (inset) on depth discrimination and shows the individual stereo-thresholds (broken lines) together with the average (solid line) across the 5 subjects (sec arc), plotted as function of the relative (normalised) width of the flanking bars (min arc). Stereo-thresholds decrease for thinner flanker widths, approaching thresholds obtained in the unflanked condition, followed by an elevation in thresholds as flanking bar widths increased to match the original flanker width (depicted by the vertical arrow in the figure), and then a reduction in thresholds for wider flanker widths. Individual differences were noted as observer AC recorded better stereo thresholds and displayed relatively flatter functions, while observers SO, JO and VO displayed a steeper function indicating greater crowding for similar test and flanker widths. Despite individual differences, consistent among all observers, crowding was optimum when test and flanking bar widths were the same or similar. In addition, when the width of the flanks was less than a quarter of the width of the test, crowding reduced such that stereo thresholds were similar to the unflanked condition (AC, 13; JO, 22; MR, 13.8; SO, 24; and VO, 34 sec arc), and only marginally increased when the flanker width was increased to about one third of the test bar width (AC, 18; JO, 49; MR 14.7 SO, 42; VO, 67 sec arc). When the flanker width was a little over half the size of the test, the flankers induced about half of the maximum crowding compared to when the flanking bars and test were the same width. Optimum crowding occurred when the width of the flankers was similar to the size of the test (see Fig. 1) with thresholds reaching 36, 69, 75, 100 and 110 sec arc for AC, JO, VO, MR and SO, respectively. For all observers, increasing the width of the flankers reduced the crowding effect, evidenced by the improvement in stereo thresholds. One way ANOVA revealed no statistically significant main effect of width of flankers on discrimination thresholds [(F (4, 20) = 2.243, p = 0.101)]. However, mean threshold from the thinnest width was 21.4 ± 3.8 sec arc, increased at near the original test bar width to 68.1 ± 22.4 sec arc and reduced at the widest width to 30.4 ± 5.4 sec arc.

The results of Expt. 3B, which varied the width of the reference bar, are shown in Fig. 5. Stereo threshold (sec arc) for each individual observer (broken lines) is plotted as a function of the relative (normalised) reference bar width (min arc) together with the average across the 3 subjects (solid line). Varying the width of the reference bar from the original condition (depicted by the vertical arrow in the figure) saw average thresholds increase from about a 2 min width and were almost double at the thinnest width (< 0.5 min arc).

One-way ANOVA revealed no statistically significant effect of width of reference bar on discrimination [(F (4, 10) = 0.945, p = 0.477)]. Nevertheless, mean threshold at the thinnest reference bar width 0.5 arc min was 56.7 ± 14.7 sec arc and reduced to 32.7 ± 8.7 sec arc at the thickest width.

4. Discussion

Consistent with previous results (e.g. Butler & Westheimer, 1978), stereoscopic depth discrimination using a simple 2-bar test-reference configuration is impeded by the introduction of flanking bars in close

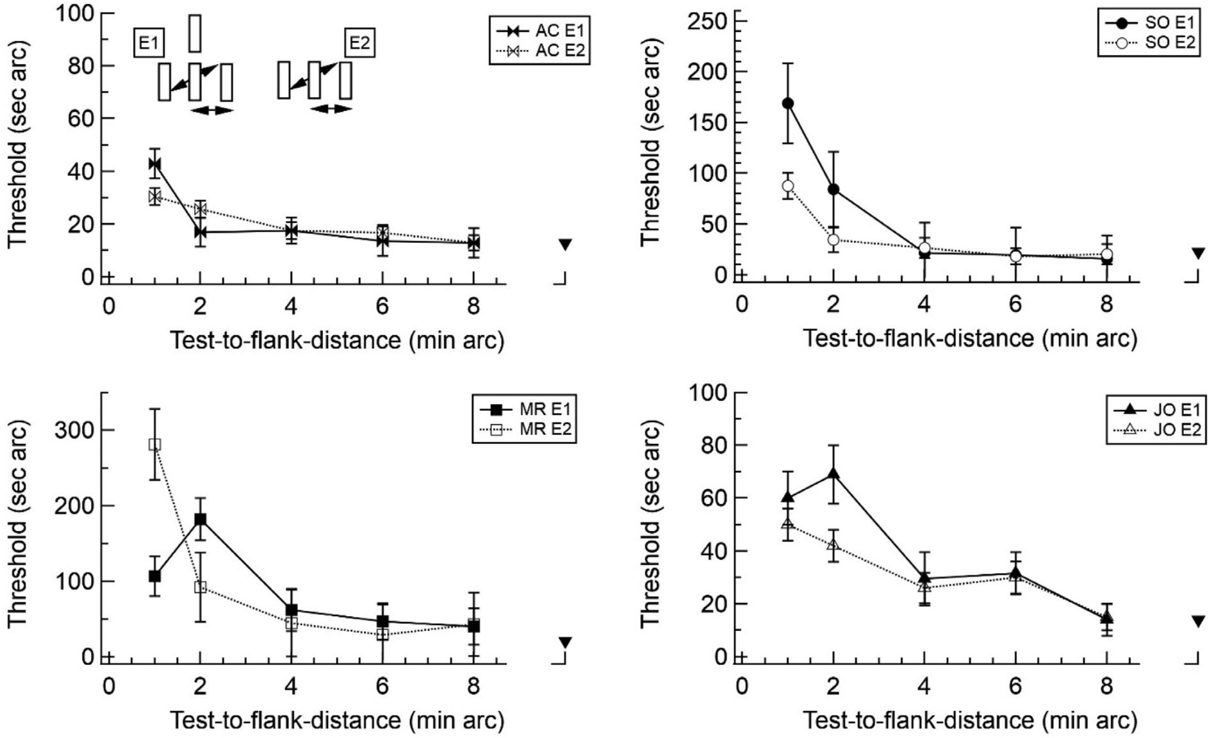

Fig. 3. Expt. 2 Comparative influence of configuration on depth discrimination. Each panel shows for each individual observer, the depth discrimination thresholds (sec arc) plotted as a function of the edge-to-edge separation between the test and the surrounding flankers (min arc) without the reference bar (E2) (broken lines and open symbols). Included are data from Expt. 1B where the reference bar was included (E1) (solid line and closed symbols) (see text for more details). Error bars represent ± 1 standard error. The inverted triangles in each panel represent results from the unflanked condition from Expt. 1A. The dimensions of the test and reference bars were fixed for each eye at 14 min arc long and 2.8 min arc wide. Vertical edge-to-edge separation between the test and reference for AC, JO, MR and SO were 7, 7, 7, and 14 min arc respectively. Note that the ordinate scales are different to clearly show individual data points.

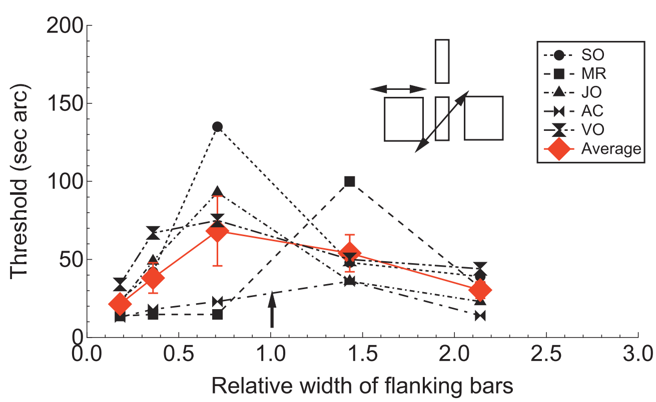

Fig. 4. Expt. 3A. Effects of varying the width of flanking bars on crowding at the test-flanker distance where crowding was maximal. Depth discrimination thresholds (sec arc) are plotted as a function of the relative (normalised) width of the flanking bars (inset). See text for more details. Individual results are shown by the different broken lines while the red solid line and large diamond symbols represents the average result. For clarity, error bars (± 1 standard error) are shown only for the average data. Width of the flanker used in Expt.1B is normalised to 1.0 as shown by the vertical arrow. The dimensions of the test and reference bars were fixed at 14 min arc long and 2.8 min arc wide, while the width of flankers varied from 0.5 to 6 min arc. Optimum vertical edge-to-edge separation between the test and reference was maintained for AC, 7; JO, 7; MC, 14; MR, 7 and SO, 14 min arc. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

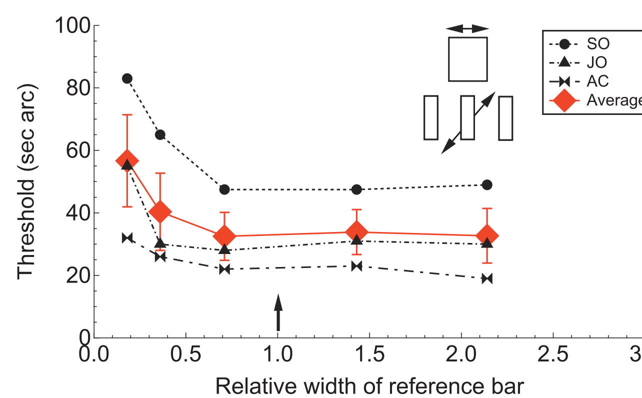

Fig. 5. Expt. 3B. Effects of varying the width of reference bar to crowding at the test-flanker distance where crowding was maximal. Depth discrimination thresholds (sec arc) are plotted as a function of the relative (normalised) width of the reference bar (inset). See text for more details. Individual results are shown by the different broken lines while the red solid line and large diamond symbols represents the average result. For clarity, error bars (± 1 standard error) are shown only for the average data. Width of the reference used in Expt.1B is normalised to 1.0 as shown by the vertical arrow. The dimensions of the test and flanking bars were fixed at 14 min arc long and 2.8 min arc wide, while the width of reference varied from 0.5 to 6 min arc. Optimum vertical edge-to-edge separation between the test and reference was maintained for AC, 7; JO, 7; MC, 14; MR, 7 and SO, 14 min arc. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

proximity to a stereoscopic test bar (Figs. 1 and 2). The crowding effect was greatest when the flanking bars were in close proximity (around 1–2 min arc) to the test bar, for flankers located at the same fixation plane as the reference. This is similar to the findings of Butler and Westheimer (1978) who demonstrated that maximum crowding was obtained when the test-flanker separation was about 2.5 min arc, and Westheimer and McKee (1980) who reported that stereo-thresholds for small squares located in a matrix, progressively increased for smaller test-reference separations due to lateral interference. Westheimer and McKee (1979) 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 less than 3 min arc, depth judgment became difficult. Further, the interactions observed in the present study are consistent with other findings which revealed that lateral interactions increase with decreasing distance between test and flankers and are negligible at greater separations of 6–15 arc min (Astle et al., 2014; Butler & Westheimer, 1978; Gantz & Bedell, 2011; Westheimer & Levi, 1987).

We also investigated the crowding effect at very close test-flanker distances. We asked whether observers could use the flanking bars as default reference targets at such close distances (Kooi, 2011; Shim et al., 2000), thereby relieving some or all of the crowding effect. When the reference bar was omitted in Expt. 2, on average stereo-thresholds were not as affected compared to Expt. 1B, except for very close test-flanker distances. In Expt. 1B, observers were instructed to ignore the flankers and perform the relative test-reference depth discrimination. The higher thresholds recorded in Expt.1B especially at close test-flank distances indicate that the observers were really trying to compare the test to the reference rather than using the flankers as a new reference. Since thresholds were lower in Expt. 2, this suggests that subjects did not use the flankers as the disparity reference in Expt.1B. Indeed in Expt. 3B, where the width of the reference bar was varied, narrowing the reference bar increased thresholds, showing that observers were trying to use the reference as the reference, which got more difficult as it shrunk in width. In Expt. 2, the two flankers symmetrically placed around the test target in the fixation plane acted as both reference and flankers. Butler and Westheimer (1978) showed that if a single flanker is used, crowding is obviated, presumably either because the single flanker offers a stimulus that is too weak to cause crowding or perhaps because subjects were able to ignore it when performing the stereo task. Given such results, it may be argued that removal of the reference bar in Expt.2 may have effectively reduced the number of flankers around the test target, and hence resulted in reduced thresholds. However, such an outcome was minimized by maintaining the test-reference separation at the optimum for best stereo acuity for each observer in Expt.1B. Hence, the reduction in stereo-threshold observed in Expt. 2 cannot wholly be attributed to the removal of the reference bar (Fig. 3), but rather the flankers providing better depth cues for relative discrimination of the test at close test-flanker distance. Taken together, the results of Expts 1B and 2 show that when the designated reference is ignored (similar to the case when the reference bar was omitted in Expt. 2) and flankers are used as default reference targets, much less crowding is recorded. We therefore suggest that the reduction in crowding recorded at the closest (1 min arc) test-flanker distance reported by Butler and Westheimer (1978), and seen in some of the results of our Expt. 1 (e.g. subjects MC, MR and JO), cannot solely be explained by lateral interference of the flanker bars on the test. Rather, some observers could have relied on the flanking bars to judge the relative depth position of the test at close separations, even though they were asked to use the reference bar for the depth comparison. Since, in Butler and Westheimer (1978), the flankers were made shorter than the test, the flanker effect at close test-flanker distances may have been more enhanced than in the present study (Kumar & Glaser, 1992a; Malania et al., 2007).

Our results are, however, in agreement with the Butler and Westheimer (1978) assertion that the extent of crowding is maximal at a particular test-flanker distance, and we have shown here that the magnitude of the effect also depends on the configuration used. The similarity in the functions obtained with and without the reference (Fig. 3) suggests that the same processing mechanism was used for the conditions in Expts 1B and 2. The nature of the cortical mechanism that encodes for this crowding effect has not yet been agreed or clearly understood though crowding has been suggested to reveal integrative processes within the visual system (Butler & Westheimer, 1978; Levi, 2008; Sayim, Westheimer, & Herzog, 2010). Usually, local neural mechanisms of pooling or lateral inhibition mechanisms are put forward as explanations. In the pooling or 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 weakens 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. In the inhibitory model, nearby flanking bars actively mitigate against the elaboration of the depth signals of the test because of competing visual direction at small separations. Recounting the manner in which the models are operationalized, if the interactions described here were due to the former mechanism, one would expect that there would be a progressive increase in crowding with decreasing test – flanker distance and vice versa. Since different observers showed different peak effects for crowding (i.e. optimum test – flanker distances), it is more likely that the inhibition mechanisms could be ascribed to the lateral interference found in this study (Butler & Westheimer, 1978; Tyler & Likova, 2007; Westheimer & McKee, 1978). Perhaps, the magnitude of the effect is optimum at a certain test-flanker distance for each observer, and may be affected by stimulus configuration and the task involved as has been alluded to previously (Butler and Westheimer (1978; Kumar & Glaser, 1992a; Malania et al., 2007).

The depth direction bias exhibited (Table1) is often reported in depth discrimination tasks and generally skewed towards crossed disparity responses (Lehmkuhle & Fox, 1980; Mustillo, 1985; Richards & Foley, 1971). The increasing strength of the front bias at small test-flanker distances demonstrates an 'exertion or pull' on the test by the flankers towards the crossed disparity direction. The pulling effect reduced the extraction of signals about the depth location of the stereo test, with the strength of the effect being greater at small test-flanker distances. As observed in Expts.1B and 2, 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 bias induced by flankers have been reported using flankers that carried disparity (i.e. positioned at a different depth plane from the test) (e.gs. Fox & Patterson, 1981; Westheimer, 1986). Such disparate flankers may distract the position of the assigned reference plane(s) in the stimulus (Westheimer, 1986). When that happens, positional bias is seen as a mechanism used 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 the preferential attention hypothesis, spatial features nearer to the observer receive proximal attention, and therefore their location is resolved first by the visual system (Fox & Patterson, 1981). Such a mechanism is suggested to have developed as an adaptive response to proximal stimulation (Mitchison & Westheimer, 1984; Westheimer, 1986). 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 (i.e. in-front) of the ground, and hence, closer in depth to the observer (Fox, 1981; Lehmkuhle & Fox, 1980). The effect is greatest near the fixation plane due to competing visual directions from the features in the stimuli (Fox, 1985). In our study, we attribute the front depth bias observed to the 'front effect' since the effect was greatest at the flanker-test separations where crowding was maximal.

Expt. 3A revealed that depth discrimination thresholds under crowded conditions depended on the extent to which the test and the flanking bars matched in width (Fig. 4). Thinner flankers produced less crowding resulting in better stereo acuity. As flanker width increased to the same size as the test, stereo acuity declined due to the increase in crowding and then subsequently improved as the flanker width increased further. These results suggest that the underlying depth discrimination processes are subject to interactions from other neural mechanisms, and thus crowding may be sensitive to images of a particular size (Richards & Kaye, 1974). Crowding has been shown to be stronger with increasing similarity of features between test and flankers including in the same depth plane (Kooi et al., 1994). Size effects can also be inferred from the study of Mitchell and O'Hagan (1972) who reported that neurons involved in the detection of retinal disparity are most sensitive to optimum size and precise orientation, and vary from cell to cell, and from the results here, perhaps among individuals depending on their stereo sensitivity. The results of our study are consistent with the explanation that the strength to which crowding impairs perception is generally modulated by the degree of similarity between a test target and its adjoining flankers (Astle et al., 2014; Bernard & Chung, 2011; Kooi et al., 1994; Malania et al., 2007; Sayim et al., 2008). Under conditions of maximal crowding, reducing or increasing the widths of the flanking bars relieves crowding and results in improved thresholds. When the local interaction mechanisms are considered, it will seem that depth information related to test and flankers are pooled across the width of flankers to produce improved performance (Astle et al., 2014; Mitchell & O'Hagan, 1972; Richards, 1972). Such interactions are consistent with depth discrimination in the central part of the fovea (10–20 min arc) where test-flankers are laterally separated by a few minutes of arc (Badcock & Westheimer, 1985). On the other hand, it has recently been suggested that contextual modulation of the stimuli plays a crucial role in local interactions, that may be attributed to "grouping" (e.gs. Malania et al., 2007, Sayim et al., 2008; 2010). Grouping proponents posit the involvement of a mid-level processing of signals based on Gestalt group factors (e.g. Sayim et al., 2010; Deas & Wilcox, 2012). As a result, widening the flanking bars to appear distinct from the stereoscopic test may have perceptually ungrouped the test and flankers and thereby led to improved performance. As suggested by Kooi and colleagues, the visual system may be responding to some compulsory grouping due to dissimilarity in the shape of the test and flankers (Kooi et al., 1994).

Alternatively, our results may be viewed as due to the difference in luminance energy of the test and flanking bars (Kumar & Glaser, 1995; Kumar, 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. In our configuration, wider flanker widths would potentially have more luminance energy across the stimulus relative to the test, thus appear potentially brighter than the test. The differences in the luminance of the test and flankers can be argued to have aided test-flanker 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 relatively higher contrast of the test which would have greater salience (pop out), and therefore evade crowding (Felisberti et al., 2005; Richards, 1972).

The final experimental condition, where the width of the reference bar was varied (Fig. 5), is consistent with the previous results (Figs. 2 and 3) and demonstrates the importance of the stereo-depth mechanism on the reference bar for discrimination (Kumar & Glaser, 1992a; Westheimer, 1979). Changing the width of the reference bar produced less elevation in threshold, except at thinner widths. Presumably, the relatively thinner reference bar than the test bar makes it less effective to be used as a reference target. We argue that the information provided by the bordering edge to the test bar is the more important cue for depth discrimination. 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. This may also be explained by the relative lack of a reference which effectively reduced the contrast of the reference bar making the task more of an 'absolute' threshold. 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 processes selectively tuned to different bar widths, but these mechanisms operate in parallel (possible matching or coupling) as suggested by Wilson and Bergen (1978).

5. Conclusion

Our findings suggest that apart from the effect of flanker-test distance, the stimulus configuration is important in 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 either thinner or thicker at the crowding distance reduced or removed the crowding effect. The behavior of the interaction described in this study can be attributed to local processing mechanisms of inhibition, but the crowding strength may be modulated by test and flanker similarity due to spatial pooling of their depth information across the widths. The differences in performance among observers could stem from the specialization required for depth discrimination, their depth discrimination experience and their subjective sensitivity to depth thresholds.

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