



Stereoacuity thresholds in the presence of a reference surface

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Abstract

With isolated binocular targets, the best depth discrimination is found in the fixation plane (Blakemore, C., *Journal of Physiology* 211 (1970) 599). More recent studies have suggested that stereoscopic thresholds are not always a simple function of absolute disparity, but depend on the relative disparities in the stimulus. Here, we explored the effects of relative disparity in more detail, taking particular care to control for the possibility that subjects might change their binocular eye position or exploit monocular information provided by additional reference cues. Subjects judged the depth of a vertical target line presented above a comparison line in a blank window within a fronto-parallel reference surface composed of randomly positioned dots. On individual trials, the reference surface was presented at one of three disparities (-10 , 0 and $+10$ arc min). To control for changes in binocular eye position, exposure duration was 150 ms, and experimental conditions with different disparities of the reference surface and comparison line were randomly interleaved. To control for monocular cues, changes in threshold were determined with respect to a disparity noise condition that was in all ways identical to the reference plane condition, except that the disparities of the dots were randomly assigned between -10 and $+10$ arc min. Stereo-thresholds were lowered by a factor of about 2 when the surface was at the same depth as the comparison line. Thresholds were also lowered when the comparison disparity was close to the same depth as the reference surface, but were often raised when the comparison disparity had the opposite disparity sign. These results provide unequivocal evidence that the fundamental sensitivity of the disparity detecting system can be influenced by relative disparity cues that are not related to the task. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Relative disparity; Binocular stereopsis; Stereoacuity; Reference plane

1. Introduction

As we move about in the 3-D world, our perception of depth is compelling, immediate and highly reliable. An important contributor to this perception is our binocular stereoscopic system. The binocular system extracts depth from the left and right retinal images by exploiting the small geometric difference between these images (absolute disparity). With isolated targets, stereoacuity thresholds are lowest in the fixation plane and increase rapidly with pedestal disparity (Ogle, 1953; Blakemore, 1970; McKee, Levi, & Bowne, 1990). This decline in stereo-thresholds has been related to the proportion of neurons in primary visual cortex selective for different absolute disparities (Barlow, Blakemore, & Pettigrew, 1967; Lehky & Sejnowski, 1990).

Stereoscopic depth is not, however, a simple function of absolute disparity. Rather, it appears that our perception of stereo-depth depends on the *relative* disparities in a stimulus—relative disparity between two points being the difference between their respective absolute disparities. For example, stereoacuity thresholds in the fixation plane are lowered by an order of magnitude when subjects can use a reference line against which to judge the depth of a target (Westheimer, 1979; McKee et al., 1990; Kumar & Glaser, 1991). Indeed, Erkelens and Collewijn (1985) and Regan, Erkelens, and Collewijn (1986) found that large changes in the absolute disparity of a large field of random dots may drive a continuous change in vergence without giving rise to any perceptual sensation of motion-in-depth, whereas the introduction of relative disparities into the same display does yield the perception of motion-in-depth. Similarly, Steinman, Levinson, Collewijn, and van der Steen (1985) showed that dynamic changes in absolute

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disparity caused by head movements do not affect stereo-thresholds. The advantage of basing stereo-depth judgements on a relative disparity signal is that it is independent of eye position. When the eyes rotate, most relevantly with a small fluctuation of vergence angle, the retinal correspondences (i.e. absolute disparities) change, but the relative disparity between two visible features does not. Westheimer and McKee (1979) and Westheimer (1979) suggested that this relative disparity signal could be generated by a simple subtraction of the disparities of two features.

The demonstration of the involvement of relative disparity goes further than just showing that the best stereo-thresholds are obtained with targets that allow for relative disparity judgments. Relative disparity cues have also been shown to influence various aspects of stereo-processing such as binocular correspondence, perceived depth and threshold, even when the relative disparity information is in a formal sense irrelevant to the task assigned to the psychophysical observer. Mitchison and McKee (1985, 1987) generated stereograms to show that a reference plane at an unambiguous disparity can help resolve ambiguous disparity matches elsewhere in the stimulus. Interestingly, this reference plane need not be in the fixation plane, but can apply to fronto-parallel planes at different depths or even slanted in depth. The perceived depth of an object can also be affected by the presence of nearby objects (Helmholtz, 1909; Gogel, 1963). For example, Mitchison and Westheimer (1984, 1990) showed that perceived depth between two lines can be dramatically influenced by the presence of a background reference plane with a horizontal disparity gradient. Glennerster and McKee (1999) also used a slanted reference plane to investigate whether its presence could 'reset' the plane of best stereoacuity thresholds to one that was slanted in the direction of the reference plane. They found some evidence in favour of this hypothesis. Unlike many other experiments showing the effect of a reference plane on stereoacuity, their results could not be explained simply in terms of a 'subtraction' hypothesis as originally proposed by Westheimer (1979).

We wished to examine in more detail how the relative disparity between a reference plane of dots and the binocular depth targets adjusts the threshold sensitivity of the stereo system towards or away from a different binocular depth plane. We used a relative disparity stimulus in which subjects always saw a target line with a comparison line immediately beneath it, against which they had to judge the target's disparity. The disparity of the reference plane that surrounded the target and comparison lines was selected randomly from trial to trial so that it could not be used as an additional comparison stimulus and improve performance in that way. The design of our experiment was such that we could investigate whether the reference

surface had any effect on 'resetting' the stereo system, such that relative disparity thresholds were best in the plane of the reference surface and climbed either side of this plane.

It is clearly important when testing this hypothesis to establish some important controls. First, we needed to ensure that the subjects maintained their vergence during a trial and that they did not begin a trial with any knowledge about what state of vergence might be most effective in dealing with the information to be presented on that trial. Second, we needed to be sure that the presence of the relative disparity surface did not affect the subject's performance through a purely monocular effect: such effects can be quite subtle, so that when the disparity of an irrelevant line target is altered, then the monocular adjacency of that line to the depth probe is also altered. Third, we needed to manipulate the relative disparity between the reference plane and the test and comparison targets and show that any changes of threshold are under the control of relative disparity. A careful analysis of the literature suggests that these criteria have never been fully met in any previous study.

For example, in a previous experiment, Kumar and Glaser (1992) showed that stereo-thresholds at different pedestal disparities are lowered when relative disparity cues are placed at, or close to, the same pedestal disparity as their target. For much of their data, they used exposure durations of one second (their fig. 8). Because this duration is well above the latency for vergence eye movements (Rashbass & Westheimer, 1961; Masson, Busetini, & Miles, 1997), it is possible that changes in vergence could account for the lowering of thresholds. Kumar and Glaser addressed this possibility by collecting further data with brief presentations of 150 ms duration. To control further for changes in vergence, psychometric functions measuring different conditions were interleaved to prevent subjects making anticipatory eye movements. However, for these additional data, the experimental design only manipulated the absolute disparity of the entire binocular display (i.e. its fixation disparity) without specifically manipulating the relative disparity between the test and reference stimuli. Thus, there is no unambiguous demonstration of a specific effect of relative disparity on stereoacuity thresholds, when careful controls for vergence are applied.

It is also important to control for the monocular effect of the reference surface, such as any change in the spatial location of a stimulus feature that covaries with the change in disparity. The line stimuli that have been used in many previous experiments are at a particular disadvantage here. For these experiments, we added the additional relative disparity information in the form of a random dot pattern surrounding the two lines whose depth was to be judged. With this stimulus, we generated an important control, in which thresholds were

also compared with a disparity noise condition, which has the same monocular spatial distribution of dots as the reference surface except that the disparities of the dots were randomly distributed. With adequate controls over vergence and monocular cues, our aim was to determine whether the plane of maximal stereoacuity was altered by the relative disparity of an irrelevant surrounding surface. We found that the disparity of the reference surface relative to the test and comparison lines changes the pattern of thresholds in a systematic way. Thresholds were decreased at, or close to, the disparity of the reference surface, but were raised at more distant disparities.

2. Methods

2.1. Apparatus and stimuli

Stimuli were generated on a Sun Ultra-10 Workstation and displayed on two high-resolution colour monitors (Flexscan T961, Eizo). Stereo images were viewed via a modified Wheatstone stereoscope at a viewing distance of 2.65 m. The display was 1152×900 pixels, and each pixel subtended 0.42 min of arc. Anti-aliasing was used to generate sub-pixel resolution. Stimuli were viewed in a dimly lit room. The background luminance was low (0.4 cd/m^2), and the stimuli were bright (55 cd/m^2). All three observers had normal monocular visual acuity: two were authors (TA, AG), and the third (JVD) was an experienced stereo observer, who was not informed about the hypotheses being tested.

The screen was first filled with a black background and five white dots forming a 4° square and a central fixation dot, which was flanked vertically by a pair of

Nonius lines (24 arc min long separated vertically by 1°). Once the Nonius lines appeared aligned, the subject pressed a mouse button to initiate a trial. The fixation cross and Nonius lines were replaced by two lines (target and comparison), 40 arc min long and 2 arc min thick, 15 arc min above and below the fixation point. The target and comparison lines were presented for 150 ms, after which the fixation cross and Nonius lines reappeared. Horizontal jitter (± 5 arc min) of spatial position was applied independently to the target and comparison lines. On some trials, a reference plane was presented simultaneously with the target and comparison lines. The reference plane was a field of random dots 6° wide and 4° high with a blank central window 60 arc min wide and 180 arc min high (Fig. 1). The dots subtended 2×2 arc min and were presented at a density of 10 dots/deg^2 . The disparity of the dots within the reference plane was either $+10$, 0 or -10 arc min. In a disparity noise condition, the dots had the same spatial configuration, but each dot was randomly assigned a disparity between $+10$ and -10 arc min.

2.2. Psychometric procedure

Stereo-thresholds were measured in the presence of a reference plane and were compared to those obtained in the absence of a reference surface and in the disparity noise condition. The subject's task was to judge whether the depth of the target line was in front of, or behind, the comparison line. No feedback was given. For each psychometric function, the target line was presented at one of seven disparity values about the fixed pedestal disparity of the comparison line (0 , ± 1 , ± 2 and ± 3 times the step size), and each combination was repeated five times. In each run, psychometric

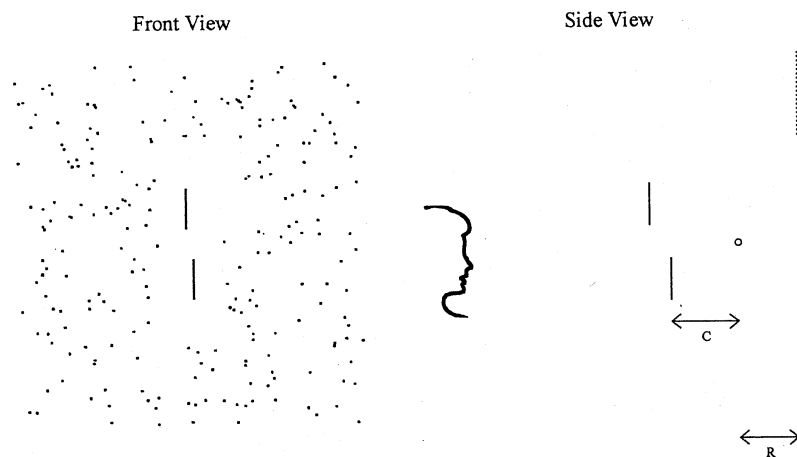


Fig. 1. Front and side views of the stimulus. The reference plane was a grid of dots that subtended $6^\circ \times 4^\circ$. The dots are shown as dark on a bright background in the figure, but were bright on a dark background on the display monitor. The target and comparison lines were presented within a blank window that was 1° wide and 3° high and were separated vertically by 1° . The viewing distance (not shown to scale) was 2.65 m. The fixation point is indicated to show the pedestal disparities of the reference plane (R) and the comparison line (C) in this example, but was shown only in the interval preceding the trial.

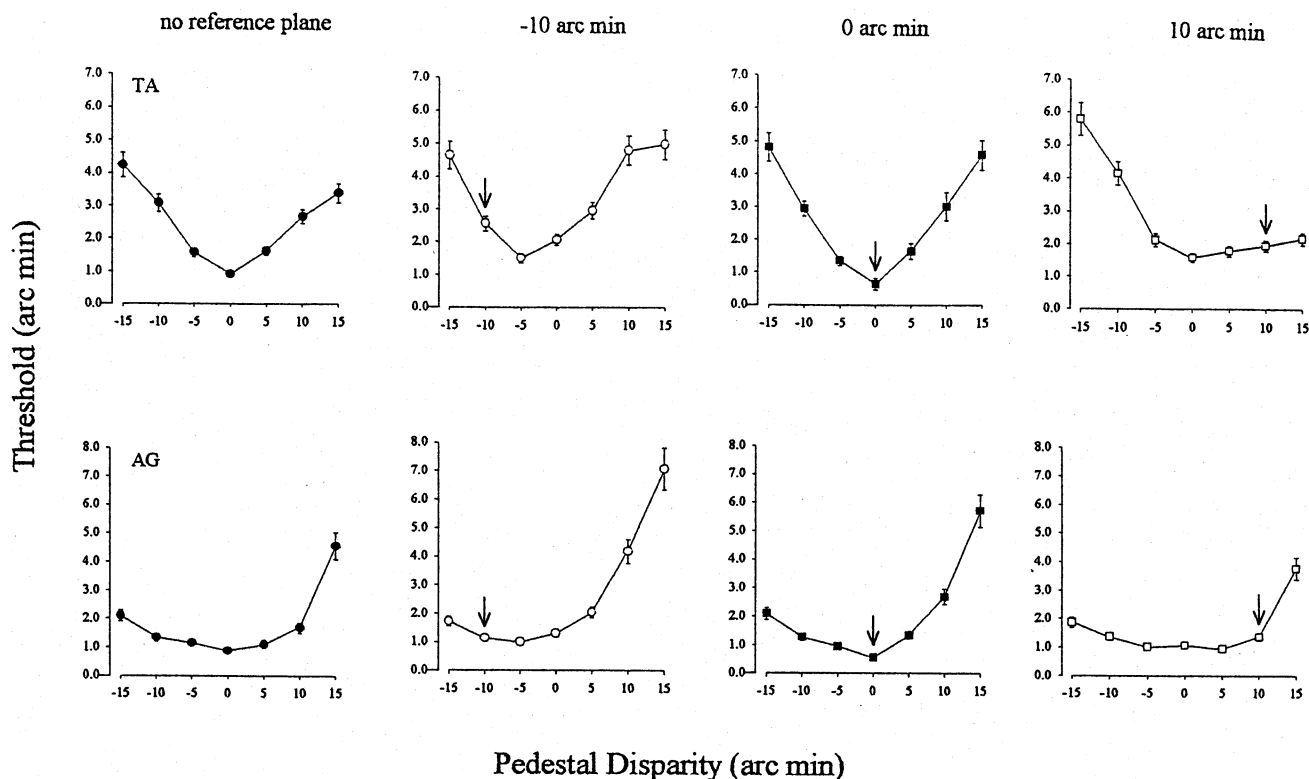


Fig. 2. Stereoacuity thresholds for two subjects for different pedestal disparities of the comparison line in the presence of a reference plane at different disparities (-10 , 0 , $+10$ arc min) and in the absence of the reference plane. The pedestal disparity of the reference surface, in this and following figures, is indicated by an arrow.

functions with different pedestal disparities and grid configurations were interleaved. To avoid inducing a bias in the initial vergence state of the eyes, the disparities of the reference plane and the comparison line were balanced about the fixation plane. Cumulative-Gaussian curves were fitted to the forced-choice data by using a maximum-likelihood estimator, and an iterative procedure was used to determine the 95% confidence limits for the fitted parameters (Watson and Pelli, 1983). The standard deviation of the fitted Gaussian was taken as the threshold. For the first four runs, the disparity values of the target line were fixed at steps of 2 min of arc. A temporary estimate of threshold was then calculated for each psychometric function and the step sizes of the target line were changed to $2/3$ of the threshold estimate. After four additional runs, this procedure was repeated, and the step size was changed to $1/3$ of the threshold estimate. Thresholds were determined by fitting a single cumulative Gaussian to all the data collected for a given condition. In total, 420 trials were used to measure the threshold for each psychometric function. The relative effect of the reference plane was determined by the ratio of thresholds in the presence and absence of a grid for different pedestal disparities. The variance of these ratios was calculated by the following equation:

$$V_R = V_1/T_2^2 + V_2*(T_1^2/T_2^4)$$

where T_1 , V_1 are the threshold and its estimated variance in condition 1, T_2 , V_2 are the same for condition 2, and V_R is the estimated variance of the ratio (see Armitage & Berry, 1994, page 91).

3. Results

3.1. Experiment 1

In accordance with previous studies (cf. Blakemore, 1970), thresholds in the absence of a reference surface increased as the target and comparison were moved away from the horopter (Fig. 2). This increase in thresholds is usually reported to be symmetrical about the fixation plane, as is the case for subject TA. However, subject AG showed an asymmetrical pattern of thresholds in the absence of a reference surface, with a bias toward convergent disparities. This bias could reflect an asymmetry in the underlying neural circuitry, or it could represent a systematic change in vergence position prior to stimulus presentation. However, because individual psychometric functions were interleaved, subjects had no prior knowledge of the relative disparity between the reference plane and the compari-

son line. Moreover, the Nonius lines were estimated as aligned before each trial was initiated. Thus, if there were any bias in vergence position for this observer, it was presumably the same across all stimulus presentations. The brevity of the presentations did, however, have the effect of raising the thresholds found here in comparison with those from previous studies. Another possible reason for the increased thresholds could be the large vertical separation (30 arc min) between the target and comparison lines.

Despite the fact that subjects reported that they were unaware of the depth of the surrounding reference surface and its presence was not relevant to the task, it significantly changed the pattern of thresholds (see Fig. 2). For both subjects, the reference surface biased the pattern of thresholds, lowering the threshold in the neighbourhood of its own disparity and raising it elsewhere. For subject *TA*, reference planes with convergent or divergent disparities resulted in patterns of thresholds that were no longer symmetrical about the

fixation plane. We quantified the effect of the reference plane by calculating the ratio of thresholds in the presence of a reference surface with those measured for isolated targets (Fig. 3). This ratio is below 1 when the test and comparison lines were at the disparity of the reference plane. This pattern was observed for both subjects in each of the three reference plane configurations. When the reference plane was in the plane of the comparison line, average thresholds were lowered to 0.76 ± 0.03 (mean \pm S.E.M.) of their values when no reference surface was present; thresholds were reduced by a similar factor at all three disparities tested (-10 , 0 and $+10$ arc min). The effect of the reference plane was not only to lower thresholds. It also resulted in relatively higher thresholds at other pedestal disparities. For example, when the test and comparison lines had disparities of 10 arc min but of the opposite sign to the reference surface, thresholds were raised by a factor of 1.66 ± 0.22 (mean \pm S.E.M.) compared with their value in the absence of a reference surface (see Fig. 3).

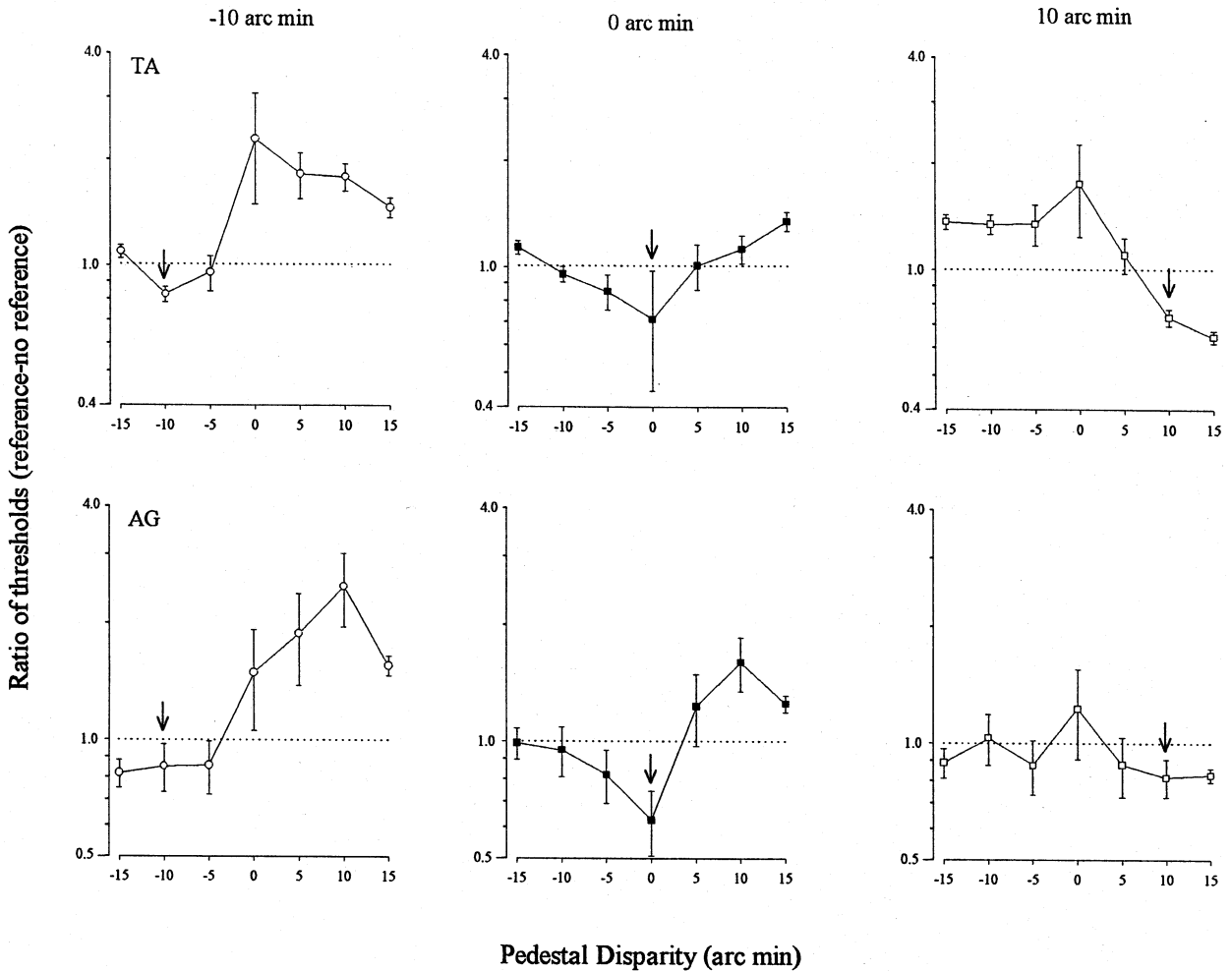


Fig. 3. Stereoacuity thresholds measured in the presence of a reference plane (-10 , 0 , $+10$ arc min) plotted as a ratio of thresholds measured for the target and comparison presented alone. The presence of a surrounding reference surface significantly lowered stereo-thresholds when the comparison line was at the same depth, but resulted in relatively higher thresholds at other pedestal disparities.

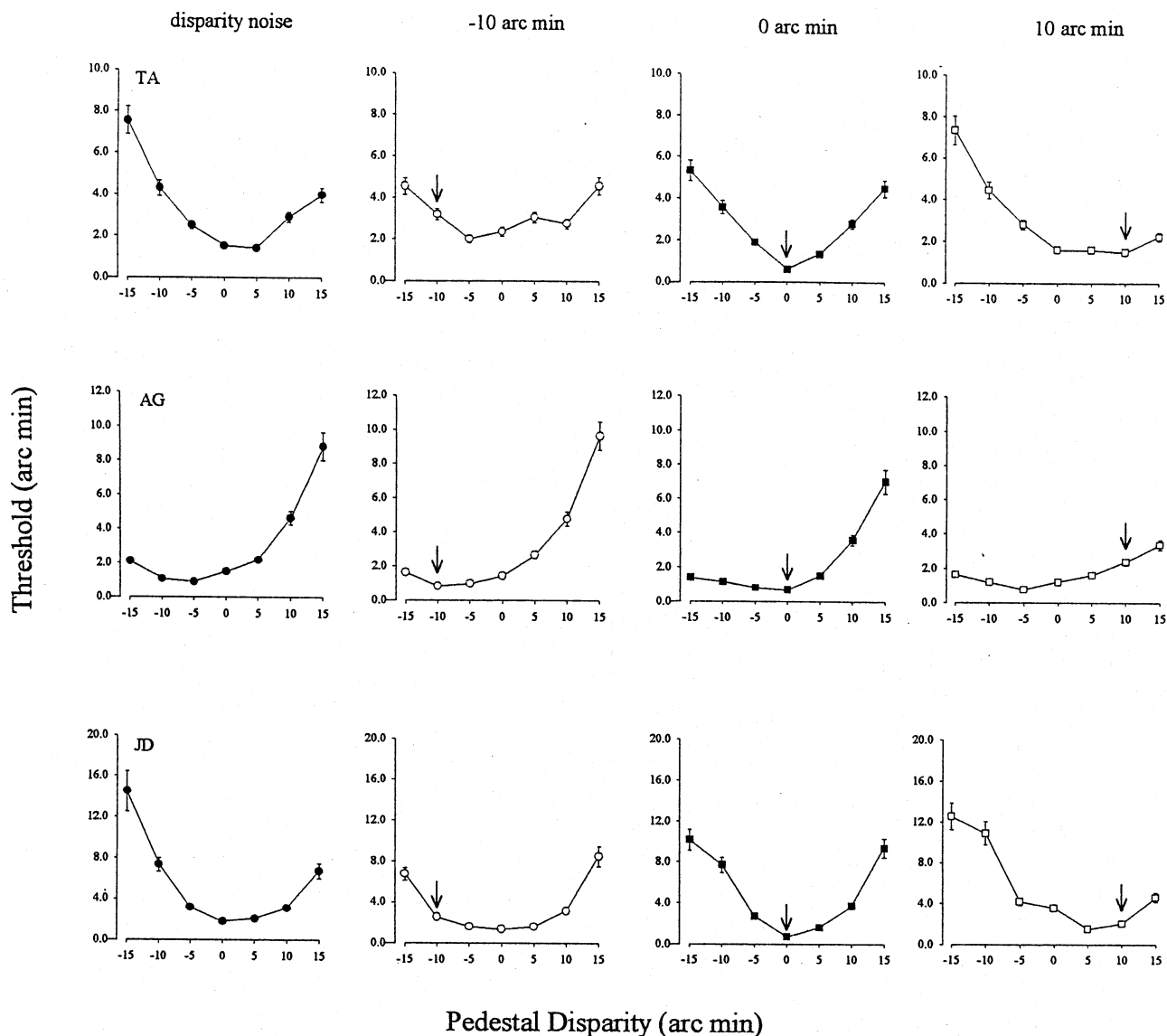


Fig. 4. Stereoacuity thresholds for three subjects at different pedestal disparities of the comparison line in the presence of a reference plane at different pedestal disparities (-10 , 0 , $+10$ arc min) and in the presence of disparity noise.

3.2. Experiment 2

The dots in the reference plane could have had a number of monocular effects that were unrelated to their disparities. To control for these factors, we used a stimulus that was identical to the reference plane condition in all respects, except that the dots had randomly assigned disparities—the disparity noise condition. The disparities of the dots were drawn randomly from a uniform distribution between $+10$ and -10 arc min.

Thresholds in the presence of disparity noise increased as the target and comparison were moved away from the horopter (Fig. 4). However, this increase in thresholds was not always symmetrical. For example, subject *AG* again tended to have lower thresholds at

convergent disparities, whereas subjects *JD* and *TA* showed slightly lower thresholds at divergent disparities. Fig. 4 shows that the presence of a reference plane with a single disparity affected this underlying pattern in all subjects in a way that depended upon the value of the surface's disparity. As before, we quantified this by taking the ratio of thresholds in the presence of a reference surface with those in the disparity noise condition. Stereo-thresholds were again lowered when the pedestal disparity of the comparison line was at the same depth as the reference surface (Fig. 5). This was apparent for each of the three subjects and for all reference plane disparities. On average, thresholds were reduced to 0.53 ± 0.05 (mean \pm S.E.M.) of their values in the disparity noise condition. Thresholds were also lowered at disparities that were close to, but not at, the

depth of the reference surface. For example, average thresholds at disparities ± 5 arc min from the reference surface were lowered to 0.74 ± 0.04 (mean \pm S.E.M.) of their value in the disparity noise condition. Thresholds for pedestal disparities with an opposite sign to the reference surface were raised on average (1.11 ± 0.07 ;

mean \pm S.E.M.) but this difference was not statistically significantly ($P = 0.32$; t -test).

In these experiments, subjects were given no feedback as to the correctness of their stereo-judgements. It is possible that the different patterns of stereo-thresholds for different grid configurations could be explained by

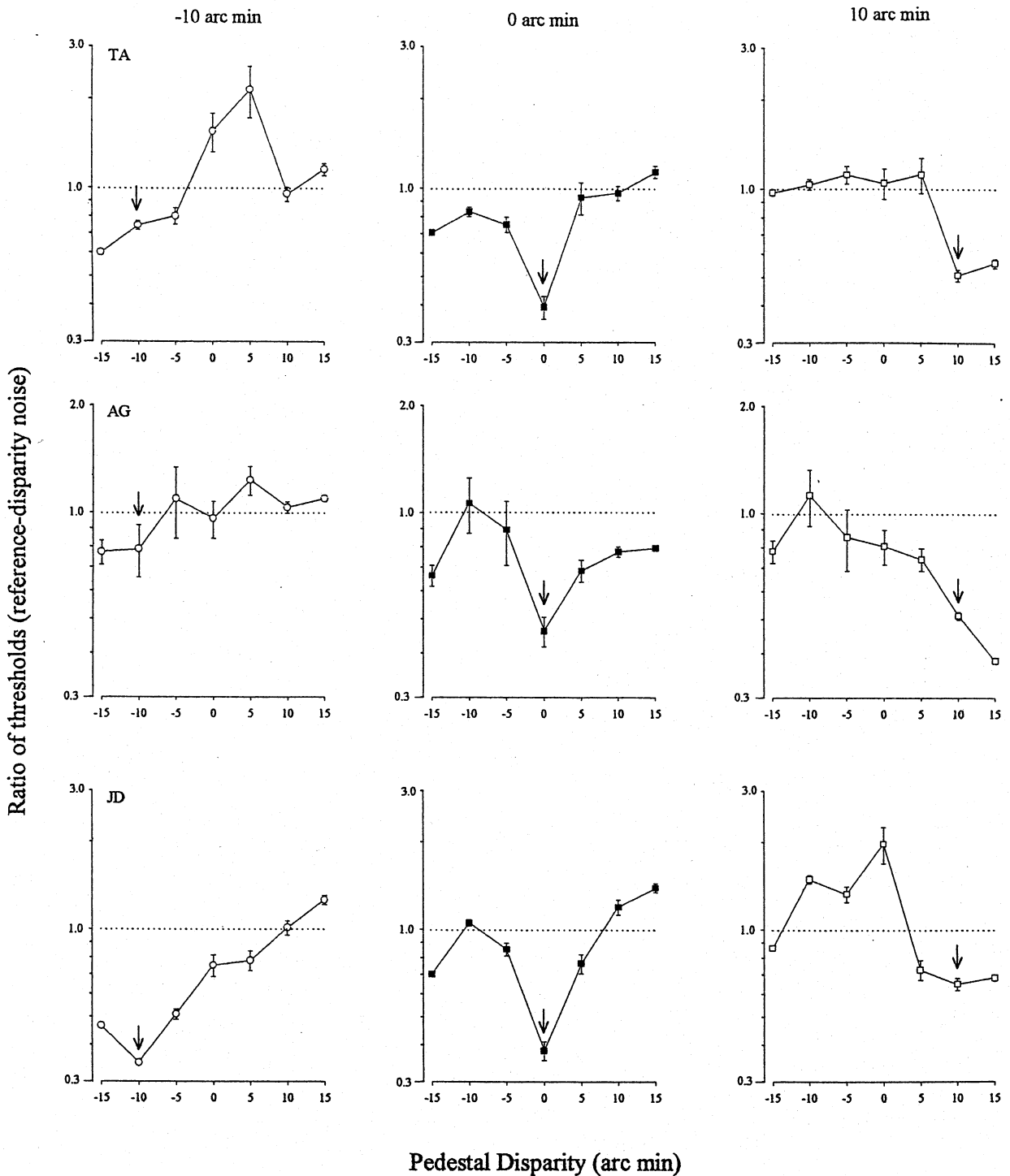


Fig. 5. Stereoacuity thresholds measured in the presence of a reference surface at different pedestal disparities plotted as a ratio of thresholds measured in the disparity noise condition for three subjects. The presence of a surrounding reference surface significantly lowered stereo-thresholds when the comparison line was at, or close to, the same depth of the reference surface.

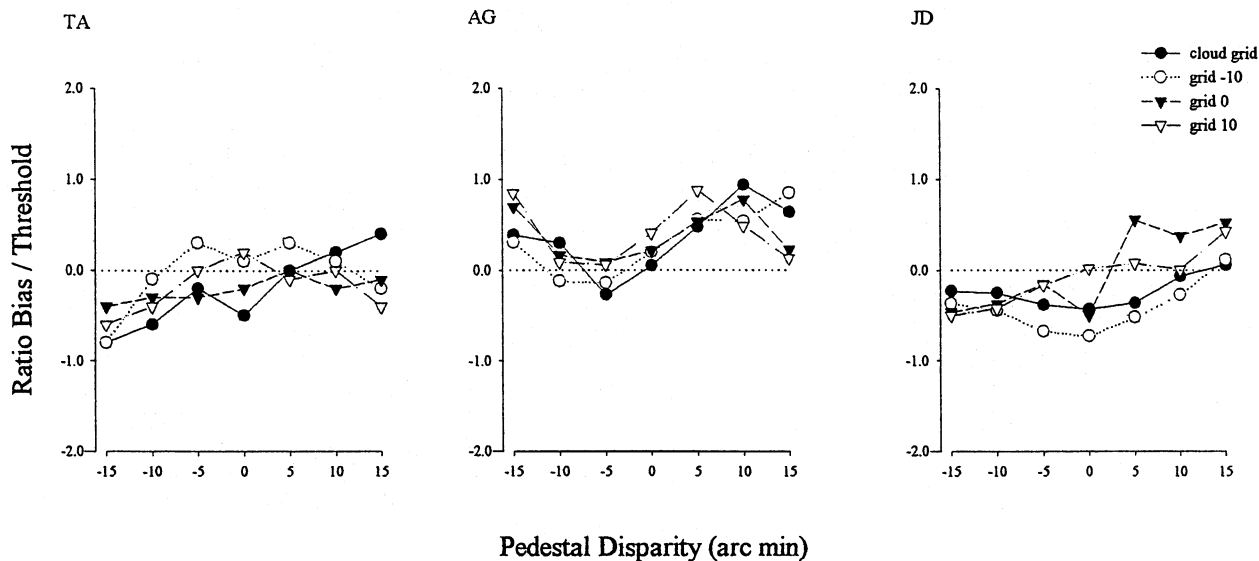


Fig. 6. Ratio of the bias in the 50% point of the psychometric function and stereoacuity thresholds shown for three subjects. Subjects were given no feedback as to the correctness of their responses, so it is possible that the different patterns of stereo-thresholds for different grid configurations could be explained by the undersampling of a psychometric function due to a non-zero 50% point. Accordingly, we calculated a value (threshold/bias) that could be compared across conditions in which the absolute values of thresholds are known to change. The graph shows that although biases in the 50% point were apparent, these did not appear to be systematic across conditions or subjects.

changes in the mean (50% point) of the psychometric function. Thus, an increase in threshold might be due to the undersampling of a psychometric function as a result of a shift in the location of the 50% point. To generate a value that can be compared across conditions in which the absolute values of thresholds may change, we calculated the ratio of threshold/bias. Although biases in the 50% point were apparent, these did not appear to be systematic across subjects (Fig. 6). Indeed, it seems unlikely that the magnitude of the effect that we found could have resulted from these differences in the mean of the psychometric curve.

3.3. Experiment 3

We were also interested to know if thresholds could be lowered still further when subjects knew that the grid would always be presented at the same disparity as the comparison line so that they could exploit it as an additional comparison cue. We compared thresholds in this situation with those gathered exclusively (a) in the absence of a reference surface or (b) in the presence of disparity noise. We also carried out runs that interleaved all these conditions so that subjects had no way of knowing whether or not any particular trial would contain a reference surface that could be used as an additional disparity cue.

Stereo-thresholds were always lowered by the presence of a reference surface in the plane of the comparison line (Fig. 7), as we found in Experiments 1 and 2. However, with the exception of subject TA in Fig. 7B, the results for blocked conditions were no better than for the

interleaved conditions. Compared with the disparity noise condition, thresholds with a reference surface were reduced by a factor of 0.40 ± 0.10 , (mean \pm S.E.M.) when trials were interleaved and 0.49 ± 0.06 when they were blocked. Compared with the absence of a reference surface, the equivalent comparison reveals that thresholds were reduced by 0.64 ± 0.04 and 0.60 ± 0.04 .

As a further control for changes in vergence after stimulus presentation, we repeated Experiment 3 with 90 ms exposures in one subject (TA). These results show that, for stimulus presentations shorter than the minimum latency for the initiation of a vergence eye movement, the presence of a reference surface at the same depth as the comparison line still lowered stereo-thresholds. Note that the ultra-short latencies for vergence only occur when large stimuli are presented immediately after a saccade has landed on a new target (Masson et al., 1997). Longer latencies are more typical for the type of stimulus that we have used here, and thus 150 ms is probably a more relevant figure (Rashbass & Westheimer, 1961; Stevenson, Cormack, & Schor, 1994). Values of less than 90 ms for exposure duration raised thresholds considerably and increased variability. In this context, 90 ms appears as an adequate compromise between eliminating adaptive vergence movements and measuring stable thresholds.

4. Discussion

We measured the influence of a fronto-parallel reference surface on stereoacuity thresholds. The main find-

ing is that the thresholds for relative depth judgements between two lines were consistently improved when one line had a disparity that was at the same depth as the reference surface or nearby (i.e. a relative disparity of zero). Stereo-thresholds were, however, often raised when the comparison line had the opposite disparity sign to the reference surface.

These results show that the additional disparity information provided by the reference surface has lowered thresholds. One interpretation is that the lower thresholds could be explained by changes in vergence eye position. We used brief presentations *and* interleaved different psychometric functions, so that subjects could not predict the relative disparity between the comparison lines and the reference surface on consecutive trials. In addition, the pedestal disparities of the comparison line and the reference plane were balanced

about the fixation point on each run. When the reference plane was in the plane of the comparison line, thresholds were reduced by a similar factor at each of the three disparities tested. This argues against the hypothesis that changes in binocular eye position explain these results. It is also unlikely that the reference plane somehow stabilises the control of vergence and reduces any fluctuations in vergence, since the exposure duration is too brief for the eyes to move far from their initial positions.

We also controlled for the additional monocular cues provided by the reference surface. For example, the reference dots both raise the mean luminance compared to the stimulus without a reference plane and provide potentially useful monocular cues about the location of the target. We used a ‘disparity noise’ condition, in which the dots had the same spatial configuration in

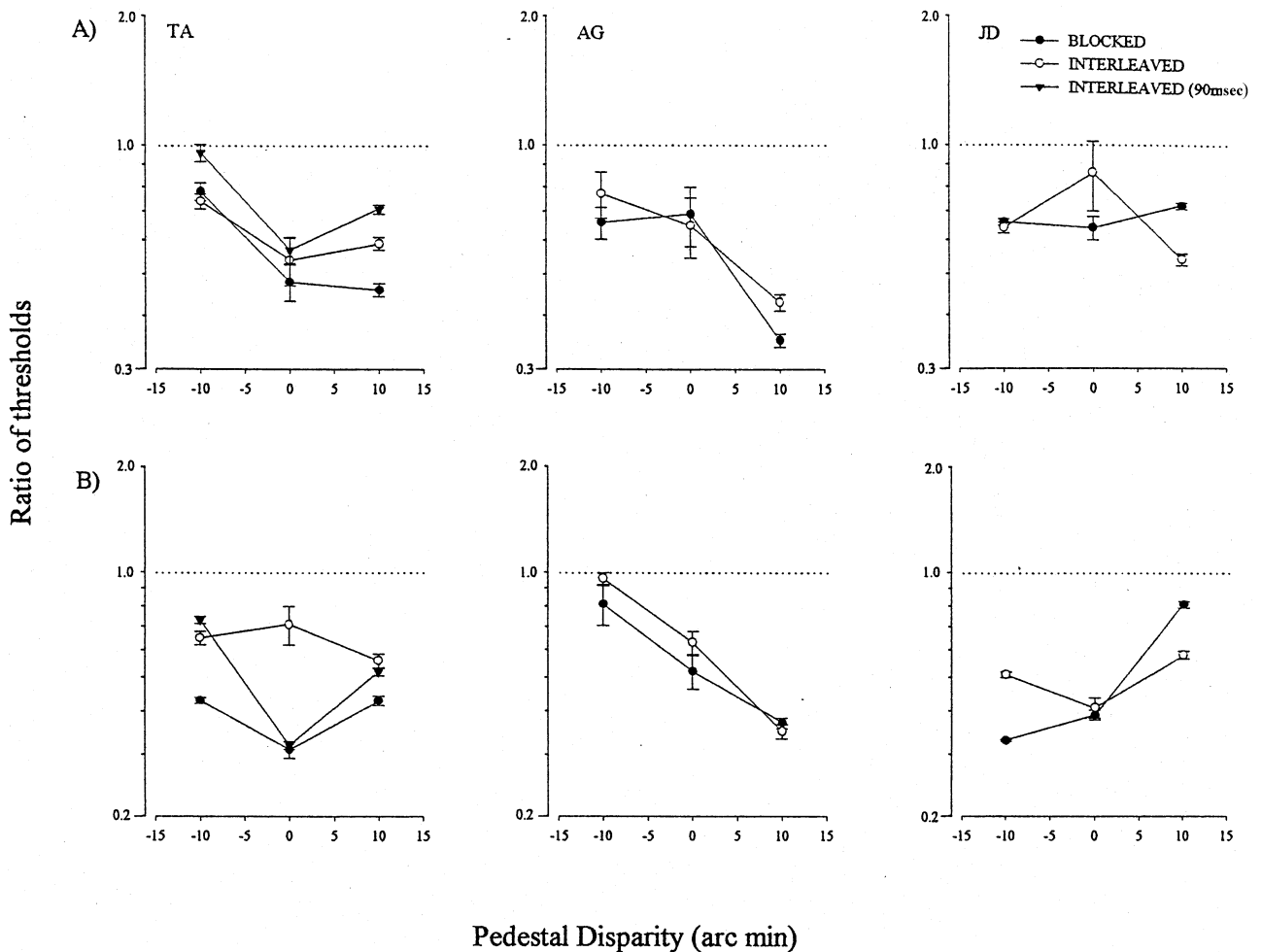


Fig. 7. Thresholds for conditions in which the subjects knew that the grid was always at the same disparity as the comparison line and thus could use it as an additional comparison cue compared with thresholds gathered when two different conditions were interleaved: one in which the comparison line was at the same disparity as the reference surface and one in which the stimuli were presented in the absence of reference surface or in the presence of disparity noise. Thresholds are plotted here as a ratio of (A) thresholds with no reference surface and (B) thresholds in the disparity-noise condition. In each case, the presence of a surrounding reference surface at the same depth as the comparison line significantly lowered stereo-thresholds. In addition, data are shown for subject TA gathered with a presentation time of 90 ms as an additional control against the intrusion of vergence movements (see Section 3).

each eye, but each dot was randomly assigned a disparity. Thus, within a single stimulus, the dots occupied a zone in depth of a range equal to the extremes of the disparities explored with the planar stimuli. An additional control was the application of horizontal jitter to the target and comparison lines. With all of these controls in place, stereo-thresholds were still lower by a factor of about 2 when the comparison line had the same disparity as the reference surface.

Our results suggest that stereoacuity thresholds are likely to be determined by a more complex interaction between features than Westheimer (1979) supposed because in all of our experiments, at least one relative disparity cue was always available due to the presence of both a test *and* a comparison line. Thus, the information required by a simple subtractive mechanism is always available *in every stimulus* presented to the observer. Yet, performance varied markedly, depending on the disparity of the reference plane. This suggests that the processing of binocular depth involves more than a simple subtraction of disparity values between a pair of neighbouring points in the visual field (Westheimer, 1979), even if that subtraction is afforded by a weighting principle to generate a measure of 'salience' in the disparity domain (Mitchison & Westheimer, 1984). Specifically, although subtraction mechanisms may be able to account for the perceived depth of stereoscopic features, there are problems in accounting for improvements in stereoacuity because even with a subtractive mechanism, the variance of statistical estimates is additive. Any sources of uncorrelated noise between the disparity of neighbouring features are enhanced by a subtractive mechanism. The types of noise that are reduced by subtraction are those that are highly correlated, which, in the case of disparity, is most likely to be unknown fluctuations in convergence. We therefore constructed our experiments to measure how threshold stereoacuity for a relative depth judgment is affected by the presence of a field of other relative disparity information that is irrelevant to the task assigned to the subject. By basing the entire comparison on a baseline of relative disparity judgments, we ensured that a simple subtraction process would already be supplied with adequate information.

In fact, it is difficult at first sight to see what the reference plane adds that could help the subject, since in terms of the formal definition of information, it is irrelevant to the task. One possibility, discussed by Glennerster and McKee (1999), is that the disparities of *both* the target and the comparison lines are computed relative to other features in the scene (i.e. the dots in the reference plane). If each of these computations comprises an independent measurement that is then combined optimally, the estimate of relative disparity between the target and comparison would have a lower variance than if it were based on a single difference

measurement of the two lines alone. Also, if the errors on the relative disparity measures varied according to Weber's law (i.e. were proportional to the relative disparity), thresholds should be lowest when the lines are at the same disparity as the reference plane and rise symmetrically away from this plane. However, although thresholds were always lower when the comparison line had the same pedestal disparity as the reference surface, this did not always represent the plane of maximal stereoacuity (see Figs. 2 and 4). Presumably, this reflects the fact that the eccentricity of the monocular features in each eye increases with the pedestal disparity of the target (McKee et al., 1990). This is reflected in the differential sensitivity to different absolute disparities of the population of neurons in primary visual cortex from which the relative disparity signal is presumably derived (Barlow et al., 1967; Prince, Pointon, Cumming, & Parker, 2000). In other words, the patterns of thresholds we observed also reflect limitations imposed by the absolute disparity of the target, in addition to its disparity relative to the reference surface.

The effect of the reference surface was not restricted to its influence on thresholds when the comparison line was at the same depth. Thresholds were also lowered at pedestal disparities that were close to, but not at, the same depth as the reference surface. This argues against the idea that subjects adopted a cognitive strategy that uses the grid as an additional comparison cue. Rather, it suggests that the processing involved in relative disparity judgements occurs at a low level in the visual system. Interestingly, thresholds were raised at pedestal disparities that were distant from the depth of the reference surface. A similar type of disparity tuning function was reported by Cormack, Stevenson, and Schor (1993) and is consistent with a recent report (Neri, Parker, & Blakemore, 1999) that determined sensitivity in a stereo-detection task, when noise dots were presented at random disparities with respect to the target. Neri et al. (1999) reported that sensitivity for the task was increased if the noise had the same disparity as the target, but was decreased when it was presented at flanking pedestal disparities. This pattern of psychophysical responses was found to be remarkably similar to that of individual neurons in monkey primary visual cortex (Cumming & Parker, 1997).

If the perception of stereo-depth is based on relative disparity, where might the underlying neuronal processes take place? It is established that the representation of stereo-depth in V1 is based on absolute disparity. Cumming and Parker (1999) controlled vergence movements in a feedback loop to manipulate absolute disparities independent of relative disparities. The results showed clearly that neurons in V1 signalled absolute, not relative, disparity. Relative disparity signals are evident in the responses of neurons in extrastr-

ate visual areas such as V2 (Thomas, Cumming, & Parker, 1999). The response of neurons to different absolute disparities in their classical receptive field was compared for different surround disparities. If a neuron encodes relative disparity, its preferred central patch disparity should shift when the disparity of the surround is changed, and by the same amount. For some neurons in V2, this is exactly the response that was found. It is possible that the responses of neurons like these may underlie the threshold judgements probed in this paper, but it is unclear whether these neurons actually perform more than a simple subtractive difference between the depth signals in the centre and surround regions of their receptive fields. This would be necessary to give a complete account of the data obtained here.

In summary, we provide unequivocal evidence that the processing of relative disparity does not simply reflect a subtraction of two absolute disparity signals. We find that judgements on the relative depth of two lines were consistently improved by adding a reference surface at the same depth or close to the same depth as the comparison line. This is despite the fact that the disparity of the reference plane was varied from trial to trial and therefore could not be used directly in the depth judgement. The implication is that the reference surface has influenced the stereoscopic system at a level that is often considered to be 'hard-wired' in the circuitry of primary visual cortex (Barlow et al., 1967; Lehky & Sejnowski, 1990).

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