
Disparity detection in anticorrelated stereograms

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Abstract. Recent physiological observations in which stimuli with opposite contrast signs in the two eyes have been used (anticorrelated stereograms) show that these stimuli evoke responses in primary visual cortex which are the reverse of responses to correlated stimuli. Psychophysical investigations reveal no such reversals: reversed-contrast bars with crossed disparities are seen in front of those with uncrossed disparities. For anticorrelated random-dot stereograms human subjects perceive no depth at all, except at low dot densities. However, these human studies were carried out with stimuli that differed in several ways from those used in physiological studies. We therefore reexamined psychophysical responses using stimuli similar to those used for physiological recordings. Our results confirm the previous findings: there is no evidence of a reversed depth sensation for bar stereograms (crossed disparities are never seen behind uncrossed disparities), and subjects are unable to detect depth in anticorrelated random-dot stereograms at the densities used for the physiological recordings. The discrepancy between the psychophysical data and the responses of single neurons in primary visual cortex suggests that further processing outside area V1 is necessary to provide the signals that produce the sensation of stereoscopic depth.

1 Introduction

Helmholtz (1909/1962) was the first to observe that binocular disparities can give rise to the sensation of depth even when the images presented to the two eyes are reversed in contrast with respect to each other. In such stereo pairs, features and contours that are white in one image are black in the other and vice versa. Julesz (1971) subsequently explored the perception of depth in random-dot stereograms (RDSs) that were constructed on the same principle: each bright dot in one eye's image is paired geometrically with a dark dot in the other eye's image. Such stereograms were termed anticorrelated by Julesz because the correlation between the left and the right eyes' images is -1 . (The terms anticorrelated and reversed contrast will be used interchangeably from here on.) Julesz demonstrated that human observers could not see depth in anticorrelated random-dot stereograms (A-RDSs).

Inversion of contrast thus has different effects according to whether a line stereogram (Helmholtz) or an RDS (Julesz) is considered (whereas depth perception for correlated RDSs is similar to that for bars). It is hard to reconcile these observations with a single stereo mechanism for both correlated and anticorrelated stimuli. There are difficulties with both of the obvious possibilities.

(i) Edges in one image are matched only with edges of the same contrast sign in the other image. The inversion of contrast leads to pairings between edges that are potentially unrelated by their geometry. In simple bar stereograms this can give rise to a systematic depth signal, because the left-hand edge of a vertical bright bar can be paired with the right-hand edge of the corresponding dark bar in the other eye's image. Any resulting perception of depth would clearly depend upon the bar width among other factors. In an A-RDS the number of false matches may defeat this matching strategy. One difficulty with this account is that one would expect small disparities to give rise to a reversed sensation of depth, but this is not observed (Cogan et al 1995).

Furthermore, this explanation gives no account of why the thresholds for detection of binocular disparity are much larger with reversed-contrast bars than same-contrast bars (Cogan et al 1995)—according to this hypothesis, all edges with matching sign of contrast should be processed for binocular disparity in the same way, so thresholds should be rather similar after taking into account the positions of matching edges.

(ii) An alternative view is that stereo matching may be performed after the image has been full-wave rectified in the contrast domain. This would make bright and dark features equivalent rather than possessing an opposite sign as they do with a linear mechanism. By itself this proposal does not offer a better explanation than previously of why thresholds are so much poorer for anticorrelated bars, nor does it explain the difference between perception of correlated and anticorrelated RDSs—after rectification these are equivalent. One proposal that could address these difficulties is to suppose that there is a separate mechanism that operates with rectified images and has a poorer acuity than the (linear) mechanism operating on unrectified images (Cogan et al 1995). When presented with anticorrelated stereograms, the linear mechanism fails to produce a consistent depth signal, so the thresholds then reflect the performance of the nonlinear mechanism.

1.1 *Comparison with physiology*

These complexities are in stark contrast to the physiological responses to anticorrelated stereograms. A single mechanism can explain the responses of binocular neurons in primary visual cortex to both correlated and anticorrelated stereograms, regardless of whether single isolated contours or dense random-dot patterns are employed (Ohzawa et al 1990, 1997; Cumming and Parker 1997).

Ohzawa et al measured the responses of binocular neurons in area V1 of anaesthetised cats both to bars whose contrast matched in the two eyes and to bars of opposite contrast in the two eyes. Neurons were equally selective for the disparity of both types of stimulus, but the tuning for the disparity of reversed-contrast bars resembled an inverted version of the tuning for same-contrast bars. A neuron maximally activated by a correlated bar at a crossed disparity is maximally activated by an anticorrelated bar at an uncrossed disparity. All this is predictable on the basis that cortical cells in cat V1 do indeed combine stimuli from the two eyes with a roughly linear type of mechanism. If neurons like these were directly responsible for the perception of depth, one would expect reversed-contrast bars to give rise to a reversed sensation of depth, but this is not found with human observers (Cogan et al 1995).

We previously examined the responses of neurons in V1 of alert monkeys to correlated and anticorrelated RDSs (Cumming and Parker 1997). We found that anticorrelation inverted the disparity-tuning function with RDS patterns. Here, the difference between the physiological responses in V1 and the psychophysical observations is particularly striking: neurons modulate their firing rate strongly and systematically to stimulus variations (the disparity of A-RDSs) that are psychophysically undetectable by either monkeys or humans.

These discrepancies between the properties of disparity-selective neurons in V1 and the psychophysical properties of stereopsis suggest that activity in these neurons is not directly responsible for the perception of stereoscopic depth. Since this is a strong claim that to some degree depends on a negative finding (lack of stereopsis), it is important to examine it critically. There are in fact some differences between the stimuli that have been used in human psychophysical studies and those used for the physiological studies, and one purpose of this paper is to address those differences with additional psychophysical studies.

Specifically, the bars used by Cogan et al (1995) had either a Gaussian or a difference-of-Gaussians profile, whereas the bars used by Ohzawa et al (1990, 1997) had a square-wave luminance profile. It may be, for example, that the spatial scale of the neuronal

receptive fields which show the inversion does not match that of the stimuli used for psychophysics. Similarly, the A-RDSs we used (Cumming and Parker 1997) were constructed differently from those used by Julesz (1971). Julesz used patterns consisting only of black and white pixels whereas we used stimuli constructed of black and white dots against a grey background. Also, dot density is a highly important factor. The dot density originally used by Julesz was 50%, while we used patterns with 25% dot density, and in neither study could depth perception be obtained with A-RDSs. By contrast, Cogan et al (1993) reported that human subjects can see depth in A-RDSs provided that they used low dot densities (5% or lower, with white dots on a black background). Moreover, the dots sizes used in all the studies were quite different, so it is unclear how to compare figures for dot density.

Last, no previous psychophysical study with anticorrelated stimuli has provided feedback to their observers. It is therefore possible that with feedback human observers could correctly identify depth in the anticorrelated stereograms used for our earlier physiological studies.

In order to establish whether there is a discrepancy between the response properties of neurons in primary visual cortex and the psychophysical responses of human observers, two new psychophysical experiments were performed: disparity-detection thresholds were measured for reversed-contrast bars with a square-wave luminance profile, and detection thresholds were determined for A-RDSs over a range of dot sizes and densities, with feedback in both cases. The effects of stimulus size, dot size, and dot density also provide some insights into the mechanism by which humans extract depth information from reversed-contrast bar stimuli and A-RDSs.

2 Methods

2.1 Apparatus and stimuli

Stimuli were generated on a Silicon Graphics Indigo Workstation and displayed on a Manitron VLR2044 monochrome monitor (P4 phosphor, mean luminance 66 cd m^{-2} , maximum contrast 92%). Stereo images were viewed via a modified Wheatstone stereoscope [as described by Johnston et al (1993)] at a viewing distance of 214 cm. The display was 1280×1024 pixels, and each pixel subtended 0.4 min of arc. Antialiasing was used to achieve subpixel resolution. The screen was first filled with a mid-grey background and a black binocular fixation cross. A single bar (width 1–12 min of arc) was shown binocularly beneath the fixation marker. For anticorrelated stimuli, the bar was white in one half image and black in the other, but which eye was shown the white bar was varied at random from trial to trial. In order to eliminate monocular cues, the horizontal location of the bar was varied randomly within ± 2 deg from trial to trial.

For the random-dot stimuli, each half image was constructed with both black and white dots, in equal proportions. This allowed dot density to be manipulated without changes in mean luminance. Dot width varied from 2.4–9.6 min of arc, and the stimulus consisted of a central rectangular patch (usually $2 \text{ deg} \times 4 \text{ deg}$) whose disparity was varied, surrounded by a background (usually $3.5 \text{ deg} \times 5 \text{ deg}$) which was always presented at zero disparity. We used the same method as previously (Cumming and Parker 1997) for constructing A-RDSs, although we previously used a fixed dot size of 4.8 min of arc. Example stereograms are shown in figure 1.

2.2 Procedure and analysis

On each trial, stimuli were viewed for up to 2 s. Subjects indicated by means of a mouse button whether the stimulus appeared in front of or behind the fixation marker. Each run usually consisted of seven different disparity values, repeated twenty times in pseudorandom order. Each block of 140 trials contained only one stimulus type, but one block of data was collected for each stimulus in an experiment before collecting a

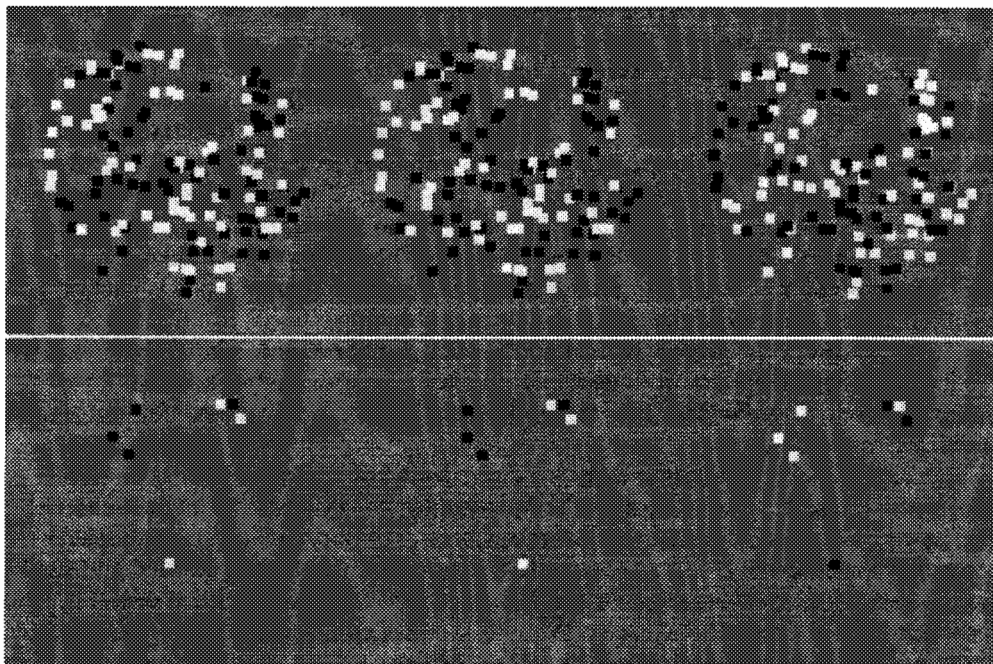


Figure 1. Example stereograms. The pair formed by the central image and the left image forms a correlated random-dot stereogram showing a central circular patch standing out in depth (shown for cross-eyed fusion). The pair formed by the central image and the right image is an anticorrelated random-dot stereogram. The top panel shows 25%-density RDS, identical to that used previously (Cumming and Parker 1997). The lower panel shows a stimulus of 2% density. Although this is a sufficiently low density that it supports depth discrimination in a forced-choice task, the impression of depth is much less robust than for the correlated pattern.

second block. Threshold measures were usually based on two blocks for each stimulus. Feedback was given on all trials, incorrect responses being followed by an audible beep and a brief bright flash on the visual display. 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 (Watson and Pelli 1983) for the fitted parameters. The standard deviation of the fitted Gaussian was taken as the threshold. All three observers had normal monocular visual acuity (after appropriate optical correction): two were authors, the third was naive.

3 Results

Figure 2 shows disparity thresholds for three observers. These data closely replicate the main features of the data reported by Cogan et al (1995): thresholds for reversed-contrast bars are approximately 10 times larger than for same-contrast bars, and the threshold is independent of bar width. (Cogan et al also found this result for Gaussian bars, although there was an effect of width for difference-of-Gaussians stimuli.)

One critical question is whether observers experience a reversed depth sensation that is related to the locations of individual edge features in each eye's image. If such a sensation is weak, then it is best studied by a careful analysis of the psychometric function for anticorrelated stimuli at small disparities. Figure 3 shows psychometric functions for two observers. The results show no evidence that the observers' psychometric functions are nonmonotonic—thus there is no indication that observers saw inverted depth at any disparity value, again confirming the findings of Cogan et al (1995).

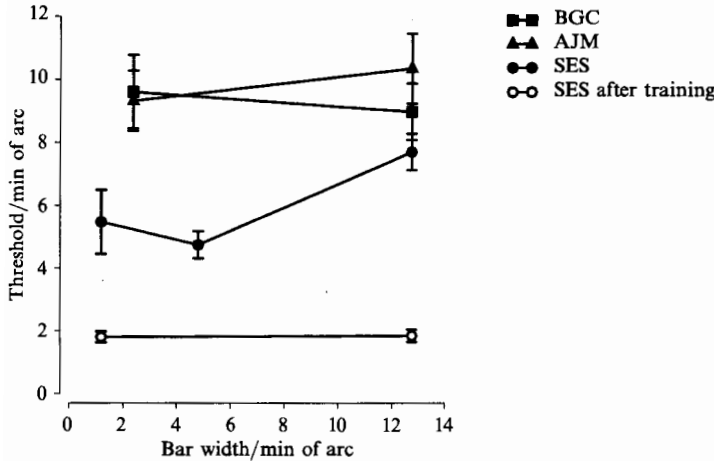


Figure 2. Stereoacuity measures for reversed-contrast bars (bars shown in white to one eye and black to the other) from three subjects. All three observers had stereoacuities less than 0.3 min of arc measured with correlated stimuli, so for all observers the thresholds for reversed-contrast bars were at least 10 times larger than for correlated stimuli. Subject SES showed a significant learning effect during the course of the study—open symbols show her thresholds for bars measured after all of the data with random-dot stimuli were collected. By the time these thresholds were measured, she had performed the discrimination on over 10 000 anticorrelated stimuli. Despite the twofold improvement, her thresholds are still larger by a factor of 6 than for same-contrast bars.

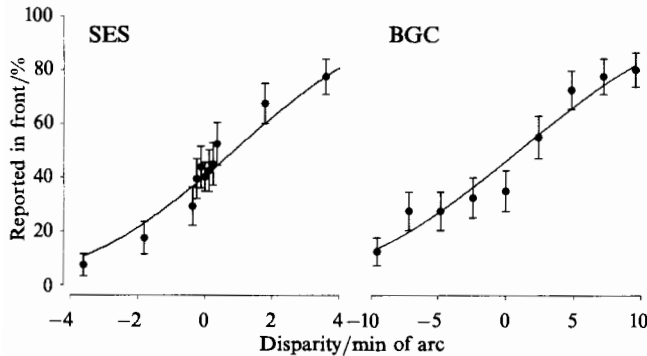


Figure 3. Psychometric functions (percentage reported in front) for reversed-contrast bars in two subjects. Data are shown for the narrowest bar used, width 1 min of arc for SES, 2 min of arc for subject BGC. Neither subject shows any evidence of a reversal in the psychometric function for small disparities.

If we turn now to A-RDSs, Cogan et al (1993) reported that subjects could perceive depth with these figures when the density of dots was low. However, in that paper, quantitative threshold measures were presented only for stimuli containing a single dot. When we initially attempted to make threshold measures by using A-RDSs, none of the subjects was able to judge the depth reliably, despite the use of feedback, even at the lowest dot density (1%). One subject (SES), after many trials with feedback, was able to perform above chance but, even for disparities as large as 24 min of arc, she never performed better than 70% correct. This was true even for a same/different task in which subjects were shown either two A-RDSs with zero disparity or one A-RDS at zero disparity and one A-RDS with a disparity. These initial attempts to measure thresholds were performed *before* the subjects were shown anticorrelated bar stimuli. After completing the measures with the bar stimuli, and a further period of training (with feedback) with A-RDSs with 1% density, all three subjects produced reliable psychometric

functions to these stimuli. All of the data presented in this section were collected after this extensive initial training.

Figure 4 shows the thresholds for all three subjects as a function of dot density. The dot size was fixed at the value we used previously (Cumming and Parker 1997) for physiological studies (4.8 min of arc), and the central part of the stimulus measured 1 deg \times 2 deg. The task gets increasingly difficult as density increases. At the highest densities used (16%–21%) none of the three subjects performed better than chance, despite the extensive training and the use of feedback. This result shows clearly that human observers are incapable of discriminating different disparities in exactly the same A-RDSs that produce disparity-selective modulations of the firing rates in neurons of primary visual cortex of monkeys (Cumming and Parker 1997).

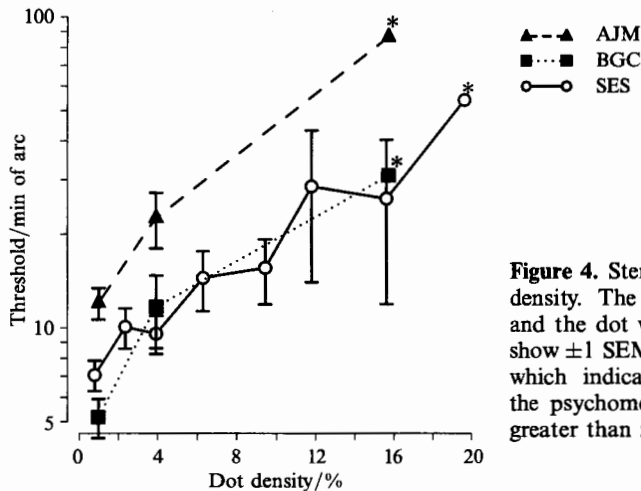


Figure 4. Stereo thresholds as a function of dot density. The stimulus size was 2 deg \times 4 deg, and the dot width was 4 min of arc. Error bars show ± 1 SEM, except for symbols marked with *, which indicate conditions where the slope of the psychometric function was not significantly greater than zero ($p < 0.05$).

Although subjects are unable to detect disparities in dense A-RDSs, the appearance of these stimuli is quite different from ordinary RDSs with zero disparity. The appearance of A-RDSs has a lustrous quality reminiscent of that described by Helmholtz (1909/1962) for other anticorrelated stimuli. We confirmed this by using a two-interval forced-choice identification task (with feedback), in which one interval contained an uncorrelated RDS and the other interval contained an A-RDS. Subjects indicated with a mouse button which interval contained the A-RDS. Even at dot densities of 25% subjects performed at 95% correct or better at this task, including the case where the A-RDS had zero disparity. A similar phenomenon was reported by Julesz and Tyler (1976).

Examination of individual psychometric functions for the A-RDS disparity-detection task (figure 5) reveals that the poor performance of the observers is not neatly summarised by a simple loss of sensitivity to disparity as the dot density increases. In this sense, the threshold measures presented in figure 4 are a little misleading. It can be seen from figure 5 that at low dot densities, the cumulative Gaussian provides a reasonable description of the forced-choice data. However, as the density increases, the data are not well described by a cumulative Gaussian with a larger standard deviation since the performance falls back down to chance levels at larger disparities. One consequence of this is that at densities greater than 2% we could find no disparity at which subjects performed better than 80% correct. For small disparities, subjects' performance can be fairly summarised by the cumulative-Gaussian curve so the estimates of threshold are not much affected, but at larger disparities the subjects' performance systematically deviates from the Gaussian fit.

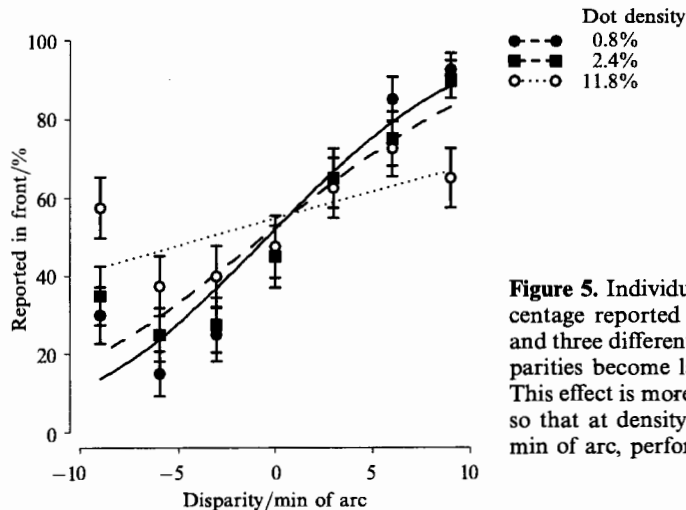


Figure 5. Individual psychometric functions (percentage reported in front) for one subject (SES) and three different dot densities. Note that, as disparities become large, performance deteriorates. This effect is more marked at higher dot densities, so that at density of 11.8% and disparities of ± 9 min of arc, performance is not above chance.

One interpretation of this pattern of results is that subjects are processing the low-density A-RDS in the same way that they had learnt via feedback to process reversed-contrast bar stimuli. By attending to one dot and matching it to the nearest dot in the other eye (regardless of whether that dot is black or white), subjects should be able to perform as accurately with sparse random-dot patterns as with a single bar. This hypothesis can account for the curious shape of psychometric discrimination functions as well as the changes in performance with dot density. Since subjects' thresholds are high even with bar stimuli, a large disparity is typically needed to support a reasonable level of performance. With A-RDSs at these disparities there is a good chance that the spatially nearest dot in the two eyes' images is not the geometrically corresponding one. As disparity becomes larger relative to the typical spacing of the dots, this problem gets worse. The problem is also accentuated by increases in dot density. As dot densities increase, the disparity at which these false matches become problematic gets smaller. The psychometric functions for subject SES show that with higher-density patterns *and* small disparities, subjects still behave much like they do for low-density patterns, but as disparity increases, there is no improvement or even a fall in performance.

If this interpretation is correct, we need to consider more carefully the relationships between dot size, number of dots per unit area, and what may be termed percentage coverage—the fraction of a given area that is occupied by dots rather than the space between them. The number of dots per unit area, rather than percentage coverage, would reflect more precisely the statistical incidence of nonmatching dots available in one eye for false matching with any particular dot in the other eye. We therefore examined thresholds as a function of percentage coverage for a variety of dot sizes and stimulus sizes. This allows the contributions of percentage coverage, number of dots per unit area, and total dot number to be examined independently. Figure 6 is a plot of the results as a function of percentage coverage. It is clear that dot size has a considerable effect on threshold when percentage coverage is held constant—as dot size increases thresholds decrease. Since any effect of bar width was in the opposite direction for single-bar stimuli, this is unlikely to be a direct reflection of changes in the dot size. In figure 7 the same data are replotted as a function of dots per unit area, and it is clear that all of the data fall close to a straight line, suggesting that the spacing between dots is the key factor in determining thresholds in A-RDSs.

The data in figures 6 and 7 show that stimulus size has little effect (if other factors are held constant), indicating that total dot number is not an important factor. Combined with the observation that threshold as a function of number of dots per square degree

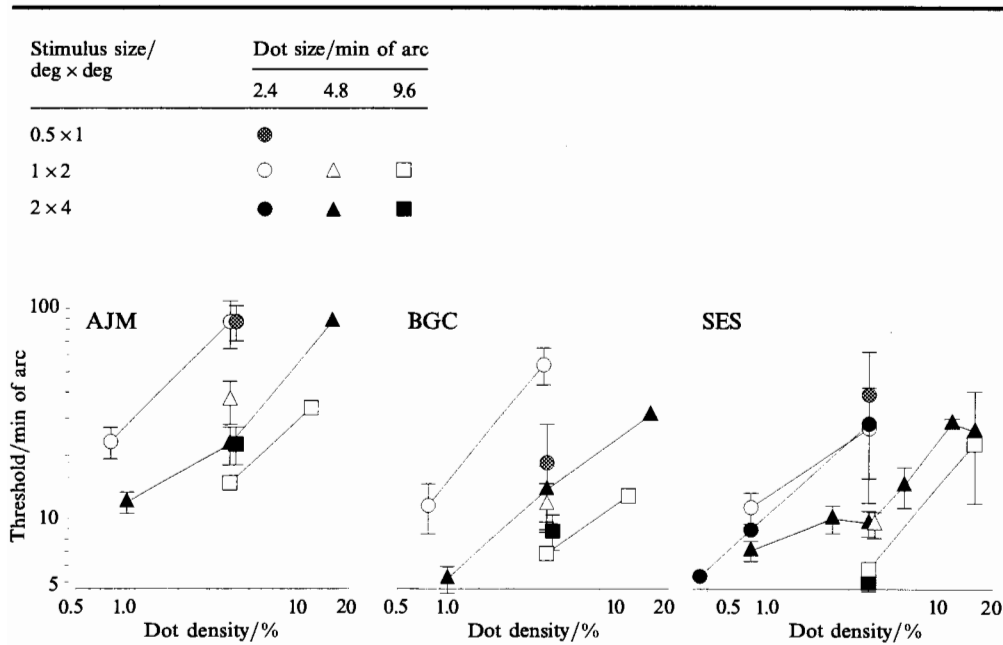


Figure 6. Stereo thresholds as a function of dot density and dot size for three subjects. Stimuli of the same dot size are shown with the same symbol shape. Stimuli of the same overall size are shown with the same fill style. It is clear that, for a given dot density, dot size has a considerable influence. The three symbols along the diagonal in the table of symbols indicate stimuli where dot size and stimulus size have the same ratio. These data are replotted as a function of stimulus size in figure 8.

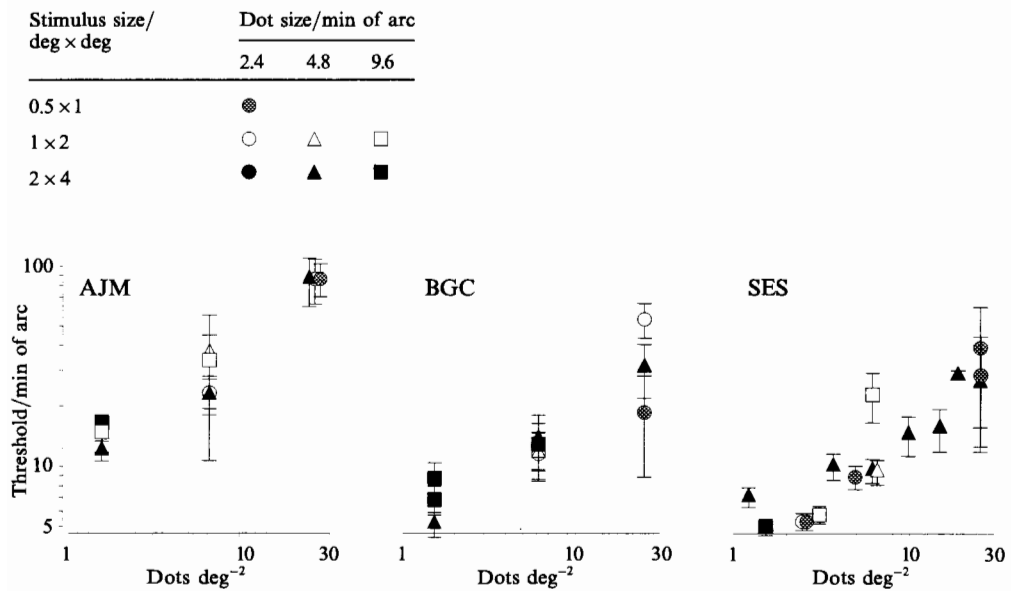


Figure 7. Data from figure 6 replotted as a function of number of dots per unit area for three subjects. Note that the relationship between this measure of density and percentage coverage depends upon dot size. All of the data are well described as a single function of dots per unit area, regardless of dot size.

shows little dependence upon dot size, this has an interesting consequence. If a stimulus is simply scaled up (dot size is increased parallel with stimulus size, so percentage coverage is constant) thresholds become lower, despite the coarser scale of the stimulus. For one of the densities tested (4%), three stimuli were used that were related by a simple scaling, and the scaling did have a substantial effect on thresholds (figure 8). Clearly the matches formed in these stimuli are not determined by the proximity of dots relative to their size, but by their absolute angular separation.

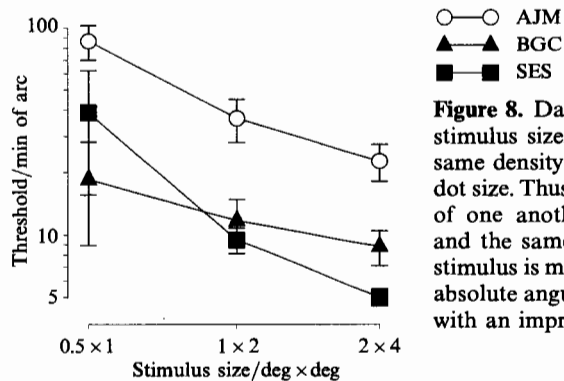


Figure 8. Data from figure 6 replotted as a function of stimulus size. The three stimulus configurations had the same density (4%), but the overall size is scaled with the dot size. Thus, the three stimuli are simply scaled versions of one another, with the same total number of dots, and the same relative spacing between the dots. As the stimulus is made larger the separation between the dots in absolute angular terms is increased, and this is associated with an improvement in performance.

4 Discussion

Single-unit-recording studies in both the anaesthetised cat and awake primates have demonstrated that the responses of disparity-selective neurons in area V1 to anticorrelated stereograms can be explained by the same mechanism that accounts for responses to correlated stereograms. This is not true for psychophysical responses. Using A-RDSs we found that, even with feedback, human observers were able to detect depth only at dot densities significantly lower than those used in the electrophysiological studies. This adds to the previous measurements on humans and monkeys and shows that even extensive feedback can raise performance with A-RDSs only to a limited degree. It is quite clear that stimuli that are psychophysically indistinguishable (eg a crossed and an uncrossed disparity in an A-RDS) give rise to completely different patterns of activity in primate area V1.

Furthermore, psychophysical responses to reversed-contrast bars do not correspond in a simple way with the properties of V1 neurons. The population of neurons activated by a given disparity in correlated bar stereograms will be inhibited by the same disparity in anticorrelated stereograms. No such inversion is evident in psychophysical responses—Cogan et al (1995) found no evidence of reversed depth responses, and the work here extends this observation to spatially broadband stimuli and a smaller range of disparities.

In order to be confident about this conclusion when using broadband stimuli, it is critically important to examine responses to small disparities, as illustrated in figure 3. Even with anticorrelated displays, the responses of filters like V1 neurons will signal a disparity of the correct sign when the disparity is greater than the spatial period implied by the peak spatial frequency of the filter (see figure 9). Only with small disparities does the entire population of V1 neurons normally activated by crossed disparities become activated by uncrossed disparities in anticorrelated bar displays, and vice versa.

The psychophysical results presented in this paper emphasise two ways in which the perception of stereoscopic depth requires considerable further processing to exploit the signals carried by disparity-selective neurons in V1. The psychophysical responses to both anticorrelated random-dot patterns and reversed-contrast bar stimuli are each qualitatively different from the signals in V1. It is important to note that merely pooling the outputs of many V1 neurons will not produce responses that account for

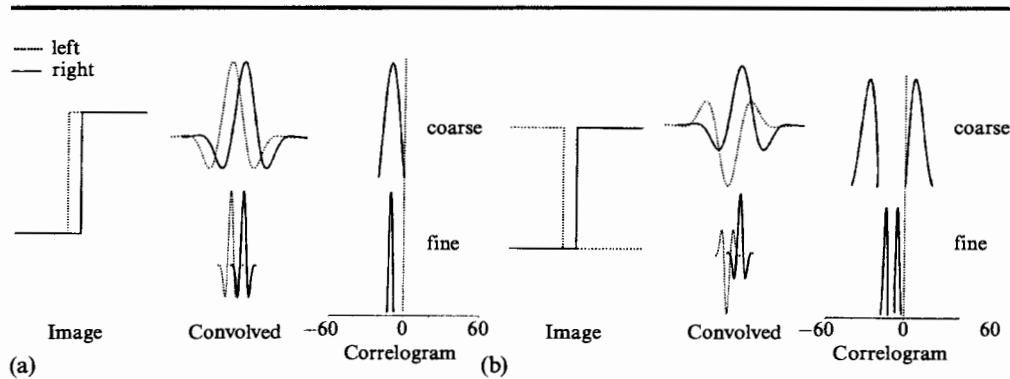


Figure 9. Effects of filter size on disparity signal (in arbitrary units) for (a) correlated and (b) anticorrelated displays. A simple step edge in luminance (image, left) is convolved with a spatially bandpass filter at two scales (centre). The binocular correlation is then calculated as a function of disparity and halfwave rectified (correlogram, right). For correlated stimuli, the peak correlation is at the same disparity at both spatial scales, and equals the stimulus disparity (10 units). For anticorrelated stimuli, there are two peaks in the correlogram, and their disparity depends on the scale of the filter. For the disparity illustrated, both peaks have the correct sign after filtering at the finer scale. However, at the coarse scale the nearest match (peak nearest zero disparity) has the opposite sign to the stimulus disparity.

the psychophysics—some more sophisticated combination is required. One possibility involves combining signals across spatial scales. For correlated stereograms the disparity signal is usually similar at different spatial scales, whereas this is not true for anticorrelated stereograms (figure 9). A mechanism activated only when neurons from V1 at different spatial scales signalled similar disparities might come close to matching psychophysical responses. This closely resembles the coarse-to-fine strategy exploited by stereo-correspondence algorithms (Marr and Poggio 1979; Grimson 1981). Thus, it is easy to see how the signals from neurons in V1 can contribute to stereopsis, but it is clear that further processing is required to make explicit the signals which are used for seeing depth.

In addition to demonstrating a discrepancy between psychophysical and neuronal responses, these experiments carry implications concerning the spatial primitives used for stereo matching. The threshold measures with reversed-contrast bars add further weight to the argument of Cogan et al (1995) that the responses to these patterns cannot be explained by assuming that subjects simply match up edges of the same contrast sign. Cogan et al point out that this explanation predicts some inverted-depth responses. It also predicts much better acuities for narrow bars than are actually found psychophysically. For the smallest bar used in this study (1 min of arc), disparities greater than 1.3 min of arc place both edge matches at a disparity that should be above threshold on the basis of the expectations from responses to correlated bar stimuli. Despite this, subjects performed at less than 65% correct with this stimulus.

The results with A-RDSs are also difficult to explain in terms of matching edges. Again, when the dot size is small, subjects fail to detect the depth reliably, even when all of the same-contrast edge matches are in the same direction with a suprathreshold disparity. Also, for larger dots one might expect performance to deteriorate, since larger disparities are required to ensure that all of the same-sign edge matches have the same disparity sign. But in fact, if density (expressed as percentage coverage) is held constant, performance *improves* as dot size is increased.

For these several reasons, it does not seem possible to explain psychophysical responses to anticorrelated patterns simply by assuming that all edges with appropriate contrast signs are matched. The other possibility is that there is a stereo mechanism that operates with rectified images. One would have to propose that this mechanism has a much poorer acuity than the (linear) mechanism that does not perform rectification.

Recently, in a number of studies with grating stimuli a nonlinear stereo mechanism has been characterised, and thresholds are indeed found to be substantially larger than for the linear mechanism (Wilcox and Hess 1996, 1997), typically in the range 3–15 min of arc. The similarity of these measured thresholds to those found here and elsewhere for anticorrelated stimuli suggest that these different psychophysical stimuli may be processed by a common nonlinear mechanism.

If this speculation is correct, then the experiments performed here with a variety of dot sizes and densities throw light upon the properties of this nonlinear mechanism. It appears to be rather crude in that it is not able to resolve matching ambiguities, rather dots in one image are matched with the spatially nearest dot in the other eye's image. Thus, as the spacing between dots gets smaller, performance deteriorates, as if dots are being matched incorrectly.

In conclusion, this study, combined with earlier studies on anticorrelated stereograms, makes it clear that the mechanisms that give rise to a sensation of depth in anticorrelated stereograms are different from those that give rise to depth in correlated stereograms. However, physiological evidence from both cats and monkeys suggests that the processing of these stimuli in area V1 is similar. What is most striking about this difference is that single neurons in V1 carry useful signals about the disparities in anticorrelated stimuli but these do not give rise to the sensation of depth. If the signals from V1 are exploited, then considerable further processing, presumably in extrastriate visual areas, is required to elaborate the signals. Alternatively, there may be a binocular pathway that evades V1 altogether and has characteristics better matched to the psychophysical phenomena arising with anticorrelated stimuli.

References

- Cogan A, Lomakin A, Rossi A, 1993 "Depth in anticorrelated stereograms" *Vision Research* **33** 1959–1975
- Cogan A, Kontsevich L L, Lomakin A J, Halpern D L, Blake R, 1995 "Binocular disparity processing with opposite-contrast stimuli" *Perception* **24** 33–47
- Cumming B, Parker A, 1997 "Responses of primary visual cortical neurons to binocular disparity without the perception of depth" *Nature (London)* **389** 280–283
- Grimson W, 1981 "A computer implementation of a theory of human stereo vision" *Philosophical Transactions of the Royal Society of London, Series B* **292** 217–253
- Helmholtz H L von, 1909/1962 *Treatise on Physiological Optics* volume 3 (New York: Dover, 1962); English translation by J P C Southall for the Optical Society of America (1925) from the 3rd German edition of *Handbuch der physiologischen Optik* (1909, Hamburg: Voss)
- Johnston E, Cumming B, Parker A, 1993 "Integration of depth modules: Stereo and texture" *Vision Research* **33** 813–882
- Julesz B, 1971 *Foundations of Cyclopean Perception* (Chicago, IL: University of Chicago Press)
- Julesz B, Tyler C, 1976 "Neurontropy, an entropy-like measure of neural correlation in binocular fusion and rivalry" *Biological Cybernetics* **23** 25–32
- Marr D, Poggio T, 1979 "A computational theory of human stereo vision" *Proceedings of the Royal Society of London, Series B* **204** 301–328
- Ohzawa I, DeAngelis G, Freeman R, 1990 "Stereoscopic depth discrimination in the visual cortex: Neurons ideally suited as disparity detectors" *Science* **249** 1037–1041
- Ohzawa I, DeAngelis G, Freeman R, 1997 "Encoding of binocular disparity by complex cells in the cat's visual cortex" *Journal of Neurophysiology* **77** 2879–2909
- Watson A, Pelli D, 1983 "QUEST: A Bayesian adaptive psychometric method" *Perception & Psychophysics* **33** 113–120
- Wilcox L, Hess R, 1996 "Is the site of non-linear filtering in stereopsis before or after binocular combination" *Vision Research* **36** 391–399
- Wilcox L, Hess R, 1997 "Scale selection for second-order (non-linear) stereopsis" *Vision Research* **37** 2981–2992

