Long-distance interactions in Cyclopean vision

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We report on evidence for selective long-distance interactions in Cyclopean binocular vision. When presented with a pair of Cyclopean test bars observers could discriminate trial-to-trial uncorrelated variations in the mean orientation, orientation difference, separation and mean location of the test bars while ignoring random variations in the orientation, width and location of a third bar placed between the two test bars. We propose that the human visual system contains Cyclopean long-distance comparators (i) that compare the outputs of two narrow receptive fields some distance apart while being insensitive to stimuli located between those receptive fields, and (ii) the outputs of which carry orthogonally labelled indicators of orientation difference, mean orientation, separation and mean location. In the evolutionary context, one role for the proposed mechanisms might be to encode information about the silhouettes of animals whose camouflage is broken by the binocular vision of predators.

Keywords: stereopsis; Cyclopean vision; receptive fields; long-distance interactions; feature-based attention

1. INTRODUCTION

Although the vivid depth created by a stereoviewer was commonly attributed to binocular disparity in the years following Wheatstone's (1838) paper, the stereo line drawings that he used contained monocular as well as binocular cues to depth as do almost all stereo photographs. A demonstration that binocular disparity alone can support the perception of spatial form by breaking camouflage was not available until Julesz (1960) isolated the neural processing that occurs after signals from the left and right eyes have converged. He did this by creating patterns that contain no monocularly available cues to the camouflaged form (Julesz 1960). A Julesz random dot stereogram consists of randomly located texture elements such as dots. One eye views such a pattern, which is identical to the pattern viewed by the other eye except that one or more parts of the pattern are shifted bodily to the left or right. The resulting empty areas are filled in with more random dots. In monocular view the shifted area(s) are perfectly camouflaged: each pattern looks like a flat array of random dots. In binocularly fused vision, however, normally sighted individuals see the camouflaged form. Furthermore, the camouflaged form is perceived in vivid depth. Many dramatic illustrations are to be found in Julesz (1971). Julesz (1971) called this kind of vision Cyclopean and the kind of form seen in random dot stereograms Cyclopean form. The spatial properties of Cyclopean perception have been recently reviewed (Regan 2000, pp. 343–374). In this paper we used random dot stereograms, one of which is illustrated in figure 1.

Current models of the early processing of Cyclopean form are chiefly based on experimentally measured changes in the detection threshold caused by adaptation or masking. The stimuli used in these experiments were either Cyclopean gratings or more localized stimuli such as a Cyclopean difference of Gaussians. The resulting models are framed in terms of a parallel array of first-stage

Cyclopean spatial filters, each of which has a strictly local receptive field and is tuned to both spatial frequency and orientation. Each small area of the retina feeds a small number of filters that prefer different spatial frequencies and orientations (Julesz & Miller 1975; Schumier & Ganz 1979; Tyler 1983, 1991, 1995; Yang & Blake 1991; Cormack *et al.* 1993).

The contrast sensitivity curve for Cyclopean gratings falls off from 0.5 to 1.0 cycles deg⁻¹ to give a grating acuity of only *ca.* 4 cycles deg⁻¹ (Tyler 1974). If the Cyclopean visual system were linear, this low acuity would conflict with the findings that Cyclopean vernier acuity is 40 arcsec (Morgan 1986) and the aspect ratio discrimination threshold for a Cyclopean rectangle of mean area 1.0 deg² can be as low as 3% (Regan & Hamstra 1994). A proposed explanation for these findings and for the observation that a Cyclopean boundary can appear sharp (for a demonstration, see figure 2A in Regan & Hamstra (1994)) is that the subjective sharpness of a Cyclopean edge as well as the threshold for the relative position of the edge is determined by the pattern of activity among an array of Cyclopean filters that serve different locations along a line that straddles the edge (Regan 1991). This proposal can be reconciled with the finding that Cyclopean grating acuity is low if we assume that the Cyclopean visual system exhibits the following nonlinear behaviour: the second-stage, edge-sharpening, spatially integrative process that supports high sensitivity for the relative position of an isolated Cyclopean edge is disrupted when there is more than one disparity gradient within its summation field (Regan 1991).

Not only is the orientation discrimination threshold for a Cyclopean bar (0.6–1.5° according to Mustillo *et al.* (1988) and Hamstra & Regan (1995)) far lower than the orientation tuning bandwidth for Cyclopean filters, it is even lower than the orientation tuning bandwidth for the most sharply tuned striate cortical neurons that respond to luminance-defined gratings (DeValois *et al.* 1982). A proposed explanation for this conflict is that the orientation discrimination threshold is determined by the pattern of activation within a population of neurons that

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Figure 1. Photograph of a typical test stimulus. Place a pencil point above the page at such a height that it appears to be centred on the right half of the stereo pair when the right eye is closed and centred on the left half of the stereo pair when the left eye is closed. Now stare at the pencil point. The Cyclopean bars will slowly emerge. The faint dots in the plane of the background that can be seen within the bars in the photograph were not visible to the eye during the experiment and, therefore, provided no monocular cue to the bars.

are tuned to the orientation of Cyclopean targets, each of which prefers a different orientation.

So far, we have discussed models that seek to explain spatial discriminations in terms of the relative activity of first-stage Cyclopean filters, each of which is driven from a small area of the binocular visual field. Such models could be couched in a line element format analogous to the Wilson & Gelb (1984) line element model of spatial discriminations for luminance-defined form in which the outputs of Cyclopean filters would be represented in a multidimensional filter output space. Alternatively, an opponent process approach could be adopted in which, as already mentioned, discrimination thresholds are determined by the relative activation of Cyclopean filters driven from a small area of the binocular visual field (Regan 1991). (The so-called combinational objection to the opponent process approach is discussed in the Appendix to Kohly & Regan (2000).)

In this paper, we report on findings that do not fit within the framework of current models of Cyclopean vision. In particular, these new findings cannot be described fully in terms of the pattern of activity within the outputs of first-stage Cyclopean filters, each of which is driven from a small area of the visual field. These findings require a second stage of processing that involves long-distance Cyclopean interactions.

2. GENERAL METHODS

(a) *Stimulus and apparatus*

Cyclopean stimuli were generated by a PC that contained 16 bit D/A converters (Cambridge Instruments model D300) and were displayed on a large-screen, electrostatically driven monitor (Hewlett-Packard model 1321A) with green P31

phosphor. This arrangement gave a maximum of *ca.* $65\,000 \times 65\,000$ (i.e. 4×10^9) possible locations within the display. A complete stereo pair was displayed every 27.4 ms. The monitor was viewed through a pair of high-speed goggles (Cambridge Instruments model FE1) that were switched in synchrony with the presentations of the left and right eyes' components of a stereo pair. The pattern subtended $12 \times 12^\circ$. Each test bar had a constant width of 0.64° and the mean width of the noise bar was 0.80° . Each eye saw 3500 dots. Any given dot subtended 2.4 arcmin. Stimuli were presented in a darkened room and viewed from a distance of 143 cm.

Figure 2 explains the meaning of α_T , β_T , S_T , M_T , β_N , W_N and M_N and figure 1 allows the reader to experience a typical test stimulus.

In order to constrain the effective duration of the stimulus by curtailing neural persistence and abolishing iconic memory, a masker was presented for 112 ms immediately after each test presentation. The masker was eight Cyclopean bars, the orientation of each of which was selected randomly from within the range of test bar orientations. Masker bars were 0.64° wide. The location of any given masker bar was assigned randomly within a region 1.5 times wider than the widest three-bar test display. Ten different masker patterns were pre-computed and each masker presentation was a random selection from the ten. The disparities of the test bars, noise bar and masker bars were equal. The purpose of the masker was to allow us to test whether the early processing and encoding of the four relationships between the two test bars was carried out in parallel.

(b) *Observers*

Observer 1 (R.P.K.) was a female aged 26 years. Observers 2 and 3, who were both naive as to the aims of the study, were males aged 28 and 32 years, respectively. Observer 2 had no previous psychophysical experience.

Figure 2. The figure depicts two test bars with mean orientation β_T , orientation difference $2\alpha_T$, separation S_T and mean location M_T . Between the two test bars is a 'noise' bar of orientation β_N , width W_N and location M_N . Note that angles α_T , β_T and β_N are exaggerated for clarity.

(c) Experiment 1

The purpose of experiment 1 was to determine whether, following each single presentation, observers can discriminate trial-to-trial variations in the orientation difference, mean orientation, separation and mean location of a pair of Cyclopean test bars while ignoring all task-irrelevant variables, including trial-to-trial variations in the orientation, width and location of a central noise bar.

(i) Rationale

We varied α_T and β_T simultaneously and orthogonally, with the maximum variation of α_T exactly the same as the maximum variation of β_T . This ensured that neither bar alone provided a reliable cue as to either angle discrimination task. Our purpose was to force observers to base their responses on a comparison of the two test bars (see figure 2 for an explanation of the symbols).

We varied M_T and S_T simultaneously and orthogonally, with the maximum variation of M_T exactly half the maximum variation of S_T . This ensured that neither bar alone provided a reliable cue for discriminating either M_T or S_T . Our purpose was to force observers to base discriminations of M_T and S_T on a comparison of both lines.

We ensured that the output of any first-stage Cyclopean filter with a strictly local receptive field that responded to both test lines would be corrupted by randomly varying the orientation (β_N), width (W_N) and location (M_N) of the central noise bar on a trial-to-trial basis. The maximum variation of β_N was equal to the maximum variation of β_T . The maximum variation of M_N was equal to the maximum variation of M_T .

(ii) Stimulus organization

The mean value of β_T was vertical (0°). There were six values of α_T and six values of β_T in the set of 216 stimuli, all symmetrically placed about zero. The range of values for α_T and β_T was $\pm 9^\circ$. There were six values of M_T and six values of S_T in the set

of 216 stimuli. The range of values of M_T was ± 24 arcmin and the range of values of S_T was $5.7\text{--}7.3^\circ$ (i.e. ± 48 arcmin).

The test stimuli were divided into six subsets. Two of the variables α_T , β_T , M_T and S_T were orthogonal (i.e. had zero correlation) within any given subset. Having six subsets allowed every possible pair of these four variables to be rendered orthogonal within at least one subset. In any given subset the values of the non-orthogonal variables were randomly selected from the possible six values. This procedure ensured that an observer could not know from which subset any given stimulus was drawn and, therefore, could not vary his or her criterion according to subset.

(iii) Procedure

Each trial consisted of a single presentation of one of the 216 test stimuli. The presentation duration was 82.3 ms in most experiments for observer 1, but some data were collected with a 54.9 ms presentation duration. For technical reasons, only three variables were discriminated (α_T , β_T and S_T) when the shorter duration was used. The less practiced observers (observers 2 and 3) were unable to provide low-noise data when the presentation duration was 82.3 ms. The presentation duration was set at 192 ms for observer 2 and 247 ms for observer 3. The observer was required to make four different classifications after each trial. In particular, after each trial the observer's task was to signal whether (i) the test bars were configured like an inverted letter V (as in figure 2) or like a letter V, (ii) whether the mean orientation of the two test bars was clockwise or anticlockwise of vertical, (iii) whether the mean location of the two test bars was to the left or to the right of the mean of the stimulus set, and (iv) whether the separation of the test bars was larger or smaller than the mean of the stimulus set. Feedback was provided.

(d) Experiment 2

The purpose of experiment 2 was to determine how the four discrimination thresholds were affected by the relative disparity of the test bars.

In the first part of experiment 2 we used a one-interval, yes-no psychophysical design in order to measure the disparity required to just detect the Cyclopean test bars (Macmillan & Creelman 1991). Each trial consisted of a single presentation of the same duration as used in experiment 1. There were two classes of stimuli: the test bars were either presented or not presented. However, the noise bars and the masker bars were always presented. Equal numbers of the two classes were presented during any given run. The observer's task was to signal whether the test bars had been presented. In the second part of experiment 2 the stimuli set and procedures were the same as in experiment 1, but we varied the relative disparity of the bars over a wide range.

Observer 1 carried out experiment 2.

(e) Experiment 3

The purpose of experiment 3 was to compare the discrimination threshold for the Cyclopean bars used in experiment 1 with corresponding thresholds for luminance-defined bars.

The procedure was the same as in experiment 1 except that all dots outside the three bars were switched off.

Observer 1 carried out experiment 3.

3. RESULTS

(a) Experiment 1

Each run of the 216 trials produced 16 psychometric functions. We plotted the percentage of 'mean location of

Table 1. *Estimates obtained by probit analysis of half the distances (in degrees) between the 25 and 75% response points on the 16 psychometric functions derived from the four-task response data*

(Carried out by observer 1 (R.P.K.) with presentation duration 82 ms.)

variable	task			
	M_T	α_T	S_T	β_T
M_T	0.34	13	7.7	5.5
α_T	149	5.9	26	102
S_T	12.3	2.8	0.37	7.4
β_T	194	171	35	6.5

the two test bars to the right of the mean of the stimulus set' responses versus all four variables for the condition that M_T was the task-relevant variable, giving four psychometric functions. The 0–100% plot versus the task-relevant variable was steep, indicating that trial-to-trial variations in M_T strongly affected the observers' responses. In contrast, the plots of 'mean location of the two test bars to the right of the mean of the stimulus set' versus each of the three task-irrelevant variables (i.e. S_T , α_T , and β_T) were approximately flat, indicating that the observers ignored trial-to-trial variations in α_T , S_T and β_T when discriminating trial-to-trial variations in M_T .

Next we describe how we quantified this qualitative impression. First, by subjecting each of the four sets of response data to probit analysis (Finney 1971), we estimated the distance along each abscissa between the 25 and 75% response points. Then, following the standard procedure, each of the 16 distances was divided by two. These data (in degrees) are set out in the second column of table 1 for observer 1 using an 82 ms presentation duration.

Analogously, each observer's 0–100% plot of the percentage of 'mean orientation of the two test bars was clockwise' versus β_T was steep when β_T was the task-relevant variable, while the three plots of the same response data versus the three task-irrelevant variables (α_T , M_T and S_T) were approximately flat. We analysed these response data in the same way as the response data for M_T discriminations and the results are set out in the fifth column of table 1. The third and fourth columns of table 1 show corresponding data for discriminating trial-to-trial variations in α_T and S_T .

When the task was to discriminate M_T and the variable was M_T , the number given in table 1 is the discrimination threshold for M_T . Similarly, when the task was to discriminate α_T and the variable was α_T , the number given in table 1 is the discrimination threshold for α_T and so on for S_T and β_T .

In order to compare data on dimensionally dissimilar variables (orientation and distance) we normalized the numbers set out in table 1 by dividing all the numbers with M_T as variable by the number when M_T was both the task and the variable. Similarly, we divided all the numbers with α_T as variable by the number when α_T was both the task and the variable and so on for the remaining variables S_T and β_T . This converted all the

Table 2. *The data shown in table 1 normalized to dimensionless ratios*

(Carried out by observer 1 (R.P.K.).)

variable	task			
	M_T	α_T	S_T	β_T
M_T	1.0	38	23	16
α_T	25	1.0	4.4	17
S_T	33	8	1.0	20
β_T	30	26	5.0	1.0

Table 3. *Discrimination thresholds (in degrees) and confidence ratios for the four tasks*

(Results shown for three observers.)

observer	discrimination task	threshold (s.e.)	confidence ratio
1	mean location	0.34 (0.03)	25
	orientation difference	12 (1)	8
	separation	0.37 (0.03)	4.4
2	mean orientation	6.5 (0.6)	16
	mean location	0.26 (0.03)	5.7
	orientation difference	14 (2)	2.7
3	separation	0.63 (0.08)	2.9
	mean orientation	5.5 (0.5)	4.0
	mean location	0.25 (0.03)	3.8
	orientation difference	14 (2)	3.3
	separation	0.47 (0.04)	7.2
	mean orientation	7.0 (0.8)	4.2

numbers set out in table 1 to dimensionless ratios. Table 2 sets out these normalized data for observer 1. We used this table as follows. The smallest ratio for the three task-irrelevant variables in the second column of table 2 is 25. We take this number (the confidence ratio) as a measure of our confidence that, when instructed to discriminate M_T , observer 1 ignored all task-irrelevant variables. A similar argument applies when the task-relevant variable was α_T , S_T or β_T (columns 3–5 in table 2, respectively). We have used a closely related statistic in previous studies (Kohly & Regan 1999, 2000). When observer 1 used the 55 ms presentation duration her thresholds were a little higher than for the 82 ms condition, but she still based her responses on the task-relevant variables. Confidence ratios and discrimination thresholds for all three observers are listed in table 3. The thresholds listed in table 3 are higher than those that were obtained with presentation durations of 1 s or longer. We used the shortest presentation duration compatible with a tolerable signal-to-noise ratio in our data.

We repeated the experiment just described with the central noise bar removed and compared the four thresholds in the 'with noise bar' and 'without noise bar' conditions by subjecting each threshold to a two-tailed-dependent *t*-test. The pairs of thresholds for M_T , α_T , S_T and β_T gave the following results, respectively: observer 1 $p > 0.41$, $p > 0.43$, $p > 0.99$ and $p > 0.20$, observer 2 $p > 0.07$, $p > 0.68$, $p > 0.23$ and $p > 0.26$ and

Figure 3. Effect of the relative disparity of the bars (abscissae) on the four discrimination thresholds (a–d) (ordinates). Disparity is expressed as a multiple of the relative disparity at the bar detection threshold.

observer 3 $p > 0.54$, $p > 0.12$, $p > 0.14$ and $p > 0.04$. Thus, the presence of the noise bar had no significant effect on 11 out of the 12 thresholds for the three observers, while one out of the four thresholds showed a significant difference at the 0.05 level for observer 3.

(b) Experiment 2

Relative disparity is expressed in figure 3 as a multiple of the 1.4 arcmin test bar detection threshold. Figure 3 shows that all four discrimination thresholds were independent of relative disparity for relative disparities more than approximately two to five times above the bar detection threshold. The onset of diplopia was at *ca.* 20 arcmin relative disparity.

(c) Experiment 3

The thresholds for M_T , α_T , S_T and β_T were 0.41, 6.2, 0.24 and 4.6°, respectively. These thresholds were little different from those listed in table 1.

4. DISCUSSION

How did the observers compare the two Cyclopean test bars? In principle, one way would be to shift fixation (i.e. saccade) from one bar to the other. However, for observer 1 this would not be possible within an 82 ms presentation duration (tables 1 and 2) and certainly not within a 55 ms presentation duration: the shortest reported saccade latency is 100–150 ms (Kowler 1990). In any case, the location of one or other test bar varied unpredictably

over a range of 96 arcmin so that, in general, a successive fixation strategy would require a saccade to one test bar followed by a second saccade to the other test bar. We conclude that, for observer 1 at least, information about relationships between the two test lines was processed in parallel.

Our observers ignored trial-to-trial variations in the orientation, width and location of a third Cyclopean bar that was placed between the two test bars. First-stage Cyclopean filters with strictly local receptive fields that responded to both test bars must necessarily also have been stimulated by the third bar. Our findings can be understood in terms of the fact that the hypothesis that the visual system of at least some individuals contain long-distance, Cyclopean, second-stage mechanisms that can compare information about a pair of Cyclopean bars but are insensitive to Cyclopean stimuli located between the two bars.

Our finding that the four kinds of discrimination threshold did not change when the central noise bar was removed is consistent with the idea that the proposed long-distance comparators determine the discrimination threshold even when first-stage Cyclopean filters driven from a single area of the retina could, in principle, provide reliable task-relevant information.

Now we turn to the question of orthogonality. In order to distinguish between trial-to-trial variations in α_T and β_T it was necessary to compare the two test bars. With one test bar removed, the ratio between the slopes of the psychometric functions, the abscissae of which were α_T

and β_T , respectively, would not be affected by changing the task from discriminating α_T to discriminating β_T . However, with both test bars present, when the task was changed the ratio changed by factors of 448, 21 and 27 for observers 1–3, respectively. Again, in order to distinguish between trial-to-trial variations in M_T and S_T it was necessary to compare the two test bars. With one test bar removed, the ratio between the slopes of the psychometric functions, the abscissae of which were M_T and S_T , respectively, would not be affected by changing the task from discriminating M_T to discriminating S_T . However, with both bars present, when the task was changed the ratio changed by factors of 1680, 16, and 126 for observers 1–3, respectively. On these grounds and on the basis of the data in table 2, we conclude that the proposed long-distance Cyclopean comparator mechanisms encode, near orthogonally, the mean orientation, orientation difference, mean location and separation of a pair of bars: cross-talk can be considerably less than 1%.

There is a sizeable literature on the theoretical construct of focal spatial attention. Some authors have suggested that visual attention acts like a spotlight focused on some discrete location (Posner *et al.* 1980), while others have used the metaphor of a zoom lens (Eriksen & James 1986). Still other authors have proposed the concept of feature- or object-based attention (Treisman & Gelade 1980; Roelfsema *et al.* 1998).

It seems unlikely that our observers performed their four assigned tasks by simultaneously attending to two focal locations because it was not possible to predict the future location of either one of the two test bars accurately. Our proposed explanation is that our observers attended to the outputs of the population of Cyclopean long-distance comparator mechanisms that, out of the possible three pairings of bars, signalled the widest separation. The effect of this strategy would be to attend to the population of comparators that were driven by the two test bars. Although this strategy might give the impression of simultaneously attending to two remote locations some distance apart, it was in fact a quite different thing and is better described as attending to a stimulus feature (here the 'outermost pair').

Following the algebra set out in the Appendix of Morgan & Regan (1987) we can understand why the four discriminations measured were independent of relative disparity for relative disparities more than approximately two to five times above the bar detection threshold. We assume that (i) the two test bars activated a population of Cyclopean long-distance comparators, each of which preferred a different test bar separation, and (ii) that the discrimination threshold for the separation of the test bars was determined by the relationship between the 'separation'-labelled outputs of this population of comparators. We further assume that each of the long-distance comparators activated by the test bars preferred a different mean orientation of the test bars and that the discrimination threshold for the mean orientation of the test bars was determined by the relationship between the 'mean orientation'-labelled outputs of this population of comparators. We assume that the discrimination thresholds for the mean location and orientation difference were determined along analogous lines.

We have recently reported on evidence that the human visual system contains long-distance comparators that process luminance-defined form in a similar way to that in which the Cyclopean long-distance comparators proposed here process Cyclopean form (Kohly & Regan 2000). However, the discrimination thresholds obtained using our luminance-defined targets (sharp, narrow, bright lines) were considerably lower than those obtained using our dotted Cyclopean bars. However, this is not a fair comparison because the spatial sampling of the two kinds of target was not matched. The results of experiment 3 show that the discrimination thresholds for the two kinds of target were little different when the spatial sampling of the luminance-defined and Cyclopean targets was identical. We conclude that, in our experimental context, long-distance processing of spatial information is not inherently superior for luminance-defined form than for Cyclopean form. This issue is discussed more generally in Regan (2000, pp. 164–169).

What might be the role of the mechanisms proposed here? Suppose that the evolution of forward-facing eyes in predators was driven by a competitive advantage of binocular stereopsis over the greater security offered by the near-panoramic view offered by side-facing eyes. In this context, the role of the mechanisms proposed here might be to encode information about the boundaries of prey whose bodies are matched to their surroundings in luminance, colour, texture and motion and whose camouflage is broken by means of binocular stereopsis.

In view of the psychophysical findings reported here, it might be of interest to search for long-distance Cyclopean interactions at single-unit level.

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