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Cyclopean Motion Perception Produced by Oscillations of Size, Disparity and Location*

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For cyclopean and monocularly-visible targets we measured psychophysical thresholds for perceptions produced by the following three stimuli: oscillations of disparity (DO), oscillations of size (SO) and oscillatory motion within the frontoparallel plane (FPO). *Results*: thresholds for motion in depth perception produced by DO were similar for cyclopean and non-cyclopean targets over the entire 0.25–8 Hz frequency range investigated. Thresholds for perceiving motion in depth produced by SO were considerably (up to 2.5 times) higher for cyclopean targets than for monocularly-visible targets, as were thresholds for perceiving size oscillations. For both cyclopean and monocularly-visible target the perception of motion in depth could be canceled by pitting DO vs SO. Thresholds for perceiving FPO were similar to DO thresholds for the monocularly-visible targets, but for the cyclopean targets FPO thresholds rose more steeply than DO thresholds for oscillation frequencies above 1 Hz. *Conclusions*: (1) for our subjects, the effective binocular stimulus for motion in depth perception is a rate of change of disparity; an interocular velocity difference is significant only to the extent that it produces a rate of change of disparity. (2) The sensations of motion in depth produced by DO and SO are qualitatively identical. (3) Neural signals produced by DO and SO converge onto a single neural mechanism that signals motion in depth.

Binocular vision Motion Motion in depth Looming Cyclopean vision Stereomotion

INTRODUCTION

It has long been known that changing an object's retinal image size can produce a compelling impression that the object is moving in depth, even though the object is, in fact, stationary (Wheatstone, 1852). A similarly compelling impression that a stationary object is moving in depth can also be produced by changing the binocular disparity of the object's retinal images (Wheatstone, 1852). In a previous study we compared the two effects by measuring detection thresholds for motion in depth perception caused by disparity changes alone and by size changes alone (Regan & Beverley, 1979). In that study, however, all moving stimuli were visible monocularly, so that processing that occurred before the signals from the left and right eyes converged was confounded with processing that took place after convergence. In the present study we separate these two stages of information processing by comparing psychophysical responses to size and disparity oscillations for a cyclopean target with corresponding data for monocularly-visible targets.

GENERAL METHODS

Apparatus

A pseudo-random dynamic pattern of bright dots was generated by shift registers in laboratory-designed and built hardware electronics (Regan & Beverley, 1984), and displayed on two electrostatically-controlled monitors (Tektronix model 608 with green P31 phosphor). During the display of any given frame, the hardware electronics generated two independent random-dot patterns RDP (1) and RDP (2). The two dot patterns were electronically superimposed on each monitor and the two monitors were viewed dichoptically. Each monitor displayed roughly 770 dots during each frame.

A high-speed switch selected whether pattern RDP (1) or pattern RDP (2) was displayed at any given instant. The effect of the switch was that, of pattern RDP (1), only a square area of side length 2 deg was ever displayed. We will refer to this square as the aperture. No dots from pattern RDP (2) were ever displayed within the aperture. Conversely, the area outside the aperture comprised pattern RDP (2) only.

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FIGURE 1. Subject's view of the stimulus. A circular, random pattern of small dots was displayed on two electrostatic monitors and viewed dichoptically. The pattern consisted of two parts: a square aperture of side length 2 deg and the dots surrounding this aperture. Nonious lines were superimposed on the dot displays 1 deg to the left of the aperture's left edge. The dichoptically-viewed monitor displays were surrounded by a plane of randomly-scattered large black dots. The nonious lines, pattern of large dots and the pattern of small dots surrounding the aperture were all in the same plane. The aperture had a mean near disparity of 15 min arc. Dashed lines were not present in actual stimulus. The small dots were much smaller and much more numerous than depicted here.

At the viewing distance of 50 cm, the dot pattern was a circular disk of diameter 8.5 deg. Each dot subtended roughly 5 min arc. Nonious lines were optically superimposed on the dot displays in the plane of the monitors. Each line subtended 50 (vertical) \times 10 (horizontal) min arc at the eye. The dichoptically-viewed monitor displays were surrounded by a binocularly-viewed, uniformlyilluminated plane of randomly-scattered large (34 min arc diameter) circular black dots that subtended 46 (horizontal) \times 57 (vertical) deg. This plane was the same distance as the monitors. Figure 1 gives an impression of what the subject saw.

Cyclopean stimuli were created using the dynamic random-dot technique (Julesz, 1971). Fifty new stereopairs were generated per sec, and the display looked like the 'snow' displayed on the screen of a detuned TV set. When the aperture was assigned a near disparity of 15 min arc, all subjects reported that they saw a small $(2 \times 2 \text{ deg})$ square area at the center of the dot pattern and floating in front of the surrounding dot pattern. When instructed to close one eye, subjects reported that the central region of the dot pattern reverted to the same plane as the remainder of the dot pattern, and could not be distinguished visually from the remainder of the dot pattern. In that sense the 2×2 deg square was perfectly camouflaged to monocular viewing, and could only be seen binocularly. As well, the 2×2 deg square remained perfectly camouflaged to monocular viewing when its disparity, size or location were modulated; these stimulus modulations were not quite visible at any modulation amplitude when viewing was monocular, though they were quite clear binocularly when modulation amplitude was sufficiently above threshold.

The design of a monocularly-visible target presented a problem. Since the location and nature of reference marks have a large effect on the perception of motion in depth produced by modulating a target's disparity (Tyler, 1975; Erkelens & Collewijn, 1985a,b; Regan, Erkelens & Collewijn, 1986), it was important to ensure that reference marks for the cyclopean and monocularlyvisible targets were matched as closely as possible. In all cases the dots displayed on the monitors in the region immediately outside the 2 deg aperture provided the major contribution to the reference. In the cyclopean and all monocularly-visible cases these dots extended right up to the edges of the aperture, and the aperture was filled with dynamic dots presented at a rate of 50 new stereopairs/sec. In the cyclopean case, the dots outside the aperture were presented at a rate of 50 new stereopairs/sec. We used four different kinds of monocularly-visible targets. In one case, monocular visibility was created by presenting 25 rather than 50 new stereopairs/sec in the region outside the aperture while continuing to run the aperture at 50 new stereopairs/sec. This was the closest to the cyclopean case. We also recorded data while presenting 18.75 and 12.5 new stereopairs/sec in the region outside the aperture, but most data were collected with static dots in the region outside the aperture. In all cases, each monitor ran at 50 frames/sec.

The following two manipulations were possible. First, the location of the aperture could be displaced horizontally across the two monitors by equal distances that were either in the same or in the opposite directions. The amplitude of these displacements could be indefinitely small. Second, the side length of the aperture could be varied.

The following three stimulus dimensions were varied. First, the disparity of the square was modulated sinusoidally about a near disparity of 15 min arc with frontoparallel plane location held constant and square size held constant at 2 deg. Second, the frontoparallel plane location of the square was modulated sinusoidally with disparity held constant at 15 min arc and square size held constant at 2 deg. Third, the side length of the square was modulated sinusoidally about a mean value of 2 deg with disparity and frontoparallel plane location held constant.

Psychophysical methods

Method of constant stimuli: presentations contain a constant number of oscillation periods. All presentations had a total of five oscillation periods windowed by a Gaussian waveform. The starting phase of the sine wave was zero. The reason for using five periods was to ensure

that the bandwidth of the stimulus was tolerably narrow, the reason for using a constant number of periods was to ensure that the frequency bandwidth of the stimulus was independent of frequency, and the reason for using a Gaussian window was to restrict the spread of energy along the temporal frequency axis (these technical considerations are reviewed in Regan, 1989, pp. 76– 80). Each trial comprised a test and a reference presentation whose durations were equal. Test and reference were in random order. The test presentation had one of five oscillation amplitudes whose values were spaced to give approx. 80% correct button presses (for best efficiency, see Levitt, 1971). The reference presentation had zero oscillation amplitude.

Subjects were instructed to fixate the nonious lines and ensure that they were collinear. They were also instructed to press button 1 if the designated percept (motion in depth, or size oscillation, or motion in the frontoparallel plane) was present during the first presentation, and button 2 if the designated percept was present during the second presentation. Auditory feedback was provided.

Method of constant stimuli: presentations of constant duration. A problem with the psychophysical procedure just described was that each presentation was so long at the lowest frequency used (20 sec at 0.25 Hz) that the attention of some subjects tended to flag during a presentation. The second procedure addressed this problem. The second psychophysical procedure was the same as the first, except that, rather than using five complete oscillation periods, any given trial had a duration of approx. 5 sec. We ensured that the peak of the Gaussian window coincided with a peak of the sinusoidal oscillation. The result of coupling this requirement with the requirement that the oscillation started and ended at a positive zero crossing was that the waveform duration could not be completely independent of oscillation frequency (the maximum duration was 6.0 and the minimum 5.0 sec).

Method of adjustment. Subjects were provided with a round knob that turned a potentiometer that varied the amplitude of oscillation of the designated variable. The gain of the potentiometer was varied randomly from setting to setting so that there was no consistent relationship between the setting of the knob and the amplitude of the stimulus oscillation it controlled. Subjects were allowed up to 30 sec to make a setting, though most settings were made more rapidly. Subjects were instructed to press a button when satisfied with the setting. The stimulus was then switched off and the setting recorded. The stimulus was switched on again after a delay of 5 sec.

Subjects

Five subjects were used. Subjects 1 (author RG), 3 and 5 (author DR) were males aged 24, 22 and 59 yr respectively. Subjects 2 and 4 were females aged 22

and 27 yr respectively. All subjects had monocular visual acuity of 6/6 or better in both eyes.

CONTROL EXPERIMENT

Methods

Purpose

The purpose of this experiment was to respond to the criticism that comparisons between psychophysical responses to cyclopean and monocularly-visible stimuli are valid only when the two kinds of stimuli have been equated for stimulus strength.*

Procedure

We measured the effect of luminance contrast on thresholds for the perception of disparity oscillations (DO), on thresholds for motion in depth produced by size oscillations (SO), on thresholds for the perception of size oscillations produced by SO and on thresholds for the perception of oscillations of location within the frontoparallel plane (FPO).

The method of adjustment was used to estimate oscillation thresholds. Oscillation frequency was 2.0 Hz throughout. Each data point in Fig. 2 is the mean of 12 settings.

Square detection threshold was measured by temporal two-alternative forced choice (2AFC). Each trial consisted of two presentations, each of which had a duration of 1.0 sec. The inter-trial interval was 0.5 sec. The test presentation was a monocularly visible square of fixed contrast. The square's contrast was zero during the reference presentation and the sequence of presentations was random. The subject was instructed to press one of two buttons depending on whether the test square was in the first or second presentation. The percent correct responses was calculated on the basis of 60 responses. Then the contrast of the test square was altered and the measurement repeated. Data were collected for five test contrasts, and a square detection threshold was estimated from the resulting 300-response psychometric function by using probit analysis (Finney, 1971).

Subjects

Subject 1 carried out this experiment.

Results

Figure 2(A–D) plots data for a monocularly-visible square. In Fig. 2(A), DO threshold is plotted vs the contrast of the square. The vertical arrow indicates that contrast detection threshold for the square was 2.5%. Figure 2(A) shows that DO threshold fell sharply from just over square detection threshold up to roughly 4 times square detection threshold, then leveled out and was approximately constant up to 100% contrast. Figure 2(B–D) show that the same behavior was shown by thresholds for the perception of FPO, by thresholds for the perception of motion in depth caused by SO and for thresholds for the perception.

^{*}We thank Dr R. Patterson for pointing out this problem.



FIGURE 2. Detection thresholds for oscillations (ordinates) vs the luminance contrast of the stimulus square (abscissae) for subject 1. (A) Motion in depth perception produced by oscillations of the square's disparity. (B) Frontal plane motion perception produced by oscillations of the square's location. (C) Perception of motion in depth produced by oscillations of the square's size. (D) Perception of size oscillations produced by oscillations of the square's size. The square was visible monocularly and the oscillation frequency was 2.0 Hz. The vertical arrows indicate contrast detection threshold for the square which was approx. 2.5%.

Discussion

Subjects reported that the visibilities of the cyclopean square and the monocularly-visible square used in the rest of this study were both less than that of the 100% contrast monocularly-visible squares and higher than the visibility of the square at the contrast for which the curves of Fig. 2(A–D) leveled out. We conclude that, so far as the four thresholds plotted in Fig. 2(A–D) are concerned, differences reported below between thresholds for cyclopean and monocularly-visible squares are not due to any mismatch between the visibilities of the cyclopean and monocularly-visible squares.

EXPERIMENT 1

Methods

Purpose

The aim of Expt 1 was to compare the effectiveness of DO as a stimulus for the perception of motion in depth for cyclopean and monocularly-visible targets.

Psychophysical procedure

All three psychophysical methods described in the General Methods section were used.

Analysis of data

Psychometric functions were fitted with cumulative Gaussian curves using Probit analysis (Finney, 1971). Threshold was defined as $(A_{75} - A_{25})/2$ where A_{75} and A_{25} were the peak-to-peak amplitudes of disparity

oscillation for 75% and 25% presses of button 1 respectively.

Subjects

Subjects 1, 2 and 3 carried out Expt 1.

Results

In Fig. 3(A-C), the peak-to-peak amplitude of the DO stimulus at the threshold for perceiving motion in depth is plotted as ordinate vs oscillation frequency over a frequency range of 0.25-8.0 Hz. The method of constant stimuli was used with a fixed number of oscillation periods. \bullet are for the cyclopean square and \Box are for the monocularly-visible square. The vertical bars indicate \pm 1 SE. Threshold fell to a minimum at approx. 2 Hz for all three subjects. The minimum peak-to-peak thresholds were 1.8, 0.87 and 2.1 min arc respectively for subjects 1, 2 and 3. Thresholds for the cyclopean and monocularly-visible squares were not significantly different except for a small (3.7 compared with 2.6 min arc) difference for subject 2 [Fig. 3(B)] at 0.25 Hz (P < 0.05, d.f. = 4). Similar results were obtained using the other two psychophysical procedures described in the General Methods section.

In Fig. 3(A-C) the non-cyclopean square was filled with a dynamic random-dot pattern presented at a rate of



FIGURE 3. Peak-to-peak amplitude of disparity oscillation at threshold for perceiving motion in depth is plotted as ordinate vs the oscillation frequency. ● are for the cyclopean target. □ are for the monocularly-visible target. (A), (B) and (C) are for subjects 1, 2 and 3 respectively. These data were collected using the method of constant stimuli with a constant number of oscillation periods.

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50 new stereopairs/sec while the dots outside the square were static. We also collected data for two subjects, at an oscillation frequency of 1.0 Hz, for targets whose monocular visibility was created by presenting the dots outside the aperture at rates of 25, 18.75 and 12.5 new stereopairs/sec. Thresholds were not significantly different for the four kinds of monocularly visible target. Thresholds for subject 1 were as follows: static background, 2.03 (SE = 0.07) min arc; 25 new stereopairs/sec, 1.96 (SE = 0.06) min arc; 18.75 new stereopairs/sec, 2.2 (SE = 0.1) min arc; 12.5 new stereopairs/sec, 2.0 (SE = 0.2) min arc. The threshold for each dynamic non-cyclopean target was compared with the threshold for the non-cyclopean target with a static background using two-tailed *t*-tests giving P > 0.5, d.f. = 34 for 25 new stereopairs/sec; P > 0.5, d.f. = 34 for 18.75 new stereopairs/sec; P > 0.5, d.f. = 34 for 12.5 new stereopairs/sec. Similar results were obtained for subject 3. Thresholds were 1.9 (SE = 0.1) min arc for static background; 2.0 (SE = 0.03) min arc for 25 new stereopairs/sec; 1.9 (SE = 0.1) min arc for 18.75new stereopairs/sec; 1.82 (SE = 0.05) min arc for 12.5 new stereopairs/sec. *t*-Test results were P > 0.5, d.f. = 34 for 25 new stereopairs/sec; P > 0.5, d.f. = 34 for 18.75 new stereopairs/sec, P > 0.2, d.f. = 34 for 12.5 new stereopairs/sec. Similar results were obtained when the method of constant stimuli with a constant duration was used.

It is known that, for a monocularly-visible target, exposure to disparity oscillations of high amplitude can elevate threshold for perceiving motion in depth, and that this threshold elevation has largely died away within 1 min after the adapting stimulus is removed (Beverley & Regan, 1973). We considered the possibility that such adaptation might be different for monocularly-visible and cyclopean stimuli, and this might have affected our results.* Our evidence that any effect is negligible are as follows. (A) When the method of adjustment was used, six settings were made for each condition before changing to the next condition. Then the subject would take time to change the oscillator setting, switch to cyclopean vs monocularly-visible and type in new settings into the computer. All this took roughly 1-2 min, during which time recovery from any adaptation to disparity or size oscillation would have been largely completed according to the results of Beverley and Regan (1973) and Regan and Beverley (1978b). Thus, if adaptation had been appreciable we would have expected that the first two threshold settings in any given block of six would have been significantly lower than the last two settings. This was not the case for either cyclopean or monocularly-visible targets. In particular, we calculated the ratio $(\Delta \delta)_{\rm L}/(\Delta \delta)_{\rm F}$ for 12 sets of six settings of threshold for the monocularly-visible stimulus and 12 sets of six settings for the cyclopean stimulus where $(\Delta \delta)_{\rm L}$ and $(\Delta \delta)_{\rm R}$ were the mean of the first two settings

and the mean of the last two settings in a block of six respectively. The ratio was averaged over all six oscillation frequencies and compared with 1.00 using a 2-tailed t-test. Results were as follows (SEs in parentheses). Subject 1: monocularly-visible stimulus, 1.00 (0.03), t = 0.08, P > 0.5, d.f. = 1; cyclopean stimulus, 1.01 (0.02), t = 0.5, P > 0.5, d.f. = 11. Corresponding figures for subject 2 were 0.98 (0.05), t = 0.5, P > 0.5, d.f. = 11 and 0.99 (0.02), t = 0.5, P > 0.5, d.f. = 11. Corresponding figures for subject 3 were 0.97 (0.02), t = 1.5, P > 0.1, d.f. = 11 and 0.98 (0.03), t = 0.67, P > 0.05, d.f. = 11. (B) When the method of adjustment was used, depth oscillations were below or only a little above threshold for most of the time, so the adapting effect would have been small because threshold elevation depends on the amplitude of the adapting oscillation of disparity (Beverley & Regan, 1973). (C) Similar results were obtained using the method of constant stimuli when the presentation duration was 5-6 sec for all test frequencies, and when presentation duration varied widely from 20 to 0.625 sec.

Discussion

Suppose that an observer views a rigid array of nearby objects O_1, O_2, \ldots, O_n , all of which are stationary except for object O_1 which is moving towards the observer. The left and right retinal images of object O₁ will have different translational velocities with respect to the retinal images of the stationary objects. In addition, the retinal image size of object O₁ will expand continuously. In the situation just described the rate of change of binocular disparity is an effective stimulus for motion in depth perception, as is the expansion of the object's retinal image size, and a normally-sighted observer will see object O_1 moving in depth with respect to the stationary objects. It is known, however, that the binocular correlate of object motion is an ineffective stimulus for motion in depth sensation when there are no reference marks visible within the visual field (Erkelens & Collewijn, 1985 a,b; Regan et al., 1986). Nevertheless, even if all stationary objects are removed from the visual field, the observer will still see object O_1 moving in depth, but now only the expansion of retinal image size will be an effective stimulus for motion in depth sensation (Regan et al., 1986).

In the everyday situation just described, objects are visible monocularly, and this gives rise to a problem when interpreting binocular psychophysical data. It is not self-evident whether the binocular stimulus for motion in depth should be described as $[(d\phi/dt)_R - (d\phi/dt)_L]$ where $(d\phi/dt)_R$ and $(d\phi/dt)_L$ are the angular speeds with respect to the retinal images of a stationary object of the right and left retinal images of object O₁ respectively, or whether the binocular stimulus should be described as $d\delta/dt$, where δ is the disparity of object O₁ relative to a stationary object (Beverley & Regan, 1973, 1975; Regan *et al.*, 1986; Collewijn & Erkelens, 1990; Cummings & Parker, 1994). The uncertainty arises because $[(d\phi/dt)_R - (d\phi/dt)_L]$ and $d\delta/dt$ are quantitatively the

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FIGURE 4. (A)–(C): Peak-to-peak amplitude of size oscillation at threshold for perceiving motion in depth is plotted as ordinate vs oscillation frequency. (D)–(F): Peak-to-peak amplitude of size oscillation at threshold for perceiving size oscillation is plotted as ordinate vs oscillation frequency. \bullet are for the cyclopean target. \Box are for the monocularly-visible target. (A, D) Subject 1, (B, E) subject 2 and (C, F) subject 3.

same and completely confounded for monocularlyvisible objects. On the other hand, in cyclopean vision neither $(d\phi/dt)_R$ nor $(d\phi/dt)_L$ exists, because objects are invisible monocularly. Only the $d\delta/dt$ correlate of object motion in depth remains. Our finding that thresholds for motion in depth perception produced by DO were similar for cyclopean and monocularly-visible targets over the entire 0.25–8 Hz range of frequencies investigated [Fig. 3(A–C)] is consistent with the hypothesis that, for the subjects tested, the rate of change of disparity is sufficient to explain the data on the monocularly-visible target.*

Our finding that DO threshold for cyclopean targets falls to a minimum of 1–2 min arc at approx. 2 Hz is in line with the report of Cummings and Parker (1994). On the other hand, their finding that thresholds were higher when motion was visible monocularly conflicts with our data. Our finding that motion in depth perception for a cyclopean target is restricted to a frequency range that does not extend much above 8.0 Hz compares with the finding of Norcia and Tyler (1984) that apparent motion in depth for a cyclopean target is limited to alternation frequencies below roughly 6.0 Hz.

*This is not to deny the possibility that, in other subjects, the interocular velocity difference might be an effective binocular stimulus for motion in depth perception for motion within the plane that contains the eyes. If visual responses to the two cues show no mutual facilitation, and we assume that their effects sum according to a 'winner takes all' rule, then our present data tell us only that, for our particular subjects, the rate of change of disparity is a more effective stimulus than the interocular velocity difference.

EXPERIMENT 2

Methods

Purpose

The aims of Expt 2 were as follows. (1) To compare, for cyclopean and non-cyclopean targets, the effectiveness of SO as a stimulus for the perception of motion in depth. (2) To compare, for cyclopean and non-cyclopean targets, the effectiveness of SO as a stimulus for the perception of size oscillations.

Psychophysical procedure

In Expt 2 we required subjects to attend selectively to two different sensations produced by the same stimulus, and to judge when one or the other of these two sensations were at threshold. As in a previous study we found that this is considerably easier to achieve when using the method of adjustment than when using the method of temporal 2AFC, and in addition subjects are considerably more confident as to which of the two thresholds is being measured (Regan & Beverley, 1979).

Subjects

Subjects 1, 2 and 3 carried out Expt 2.

Results

The amplitudes of the SO stimulus that produced a just-detectable sensation of motion in depth for cyclopean (\bigcirc) and noncyclopean (\Box) targets are plotted as the ordinate in Fig. 4(A-C) vs oscillation frequency. The two curves were approximately the same shape, but thresholds for the cyclopean target were roughly 2.5, 1.5 and 1.6 times higher than for the non-cyclopean target in Fig. 4(A,B,C) respectively. A comparison of Figs. 4(A-

C) and 3(A-C) shows that the SO curve was less Ushaped than the DO curve. The lowest threshold for the cyclopean target in Fig. 4(A) was 6.3 (SE = 0.7) min arc compared with a lowest value of 1.8 (SE = 0.1) min arc in Fig. 3(A). In Fig. 4(B, C) (subjects 2 and 3) the lowest motion in depth thresholds for the cyclopean target were 3.1 (SE = 0.1) and 4.5 (SE = 0.2) min arc compared with the lowest values of 1.0 (SE = 0.1) and 2.2 (SE = 0.2) min arc respectively in Fig. 3(B,C).

Differences in absolute values of threshold in Figs 4(A-C) and 3(A-C) were less marked for the non-cyclopean target. The lowest value of SO threshold for the non-cyclopean target in Fig. 4(A) was 3.3 (SE = 0.3) min arc compared with a DO threshold of 1.9 (SE = 0.1) min arc in Fig. 3(A). Corresponding non-cyclopean thresholds were 1.7 (SE = 0.1) min arc for SO [Fig. 4(B)] compared with 0.87 (SE = 0.11) min arc for DO [Fig. 3(B)] for subject 2 and 2.8 (SE = 0.1) min arc for SO [Fig. 4(C)] compared with 2.1 (SE = 0.4) min arc for DO [Fig. 3(C)] for subject 3.

We also collected data for two subjects using monocularly-visible targets with rates of 25, 18.75 and 12.5 new stereopairs/sec in the surround. Oscillation frequency was 1.0 Hz. Thresholds were not significantly different for the four kinds of monocularly-visible target. For subject 1 thresholds for motion in depth produced by SO were as follows. Static background: 3.7 (SE = 0.1), 25new stereopairs/sec; 4.0 (SE = 0.2), 18.75 new stereopairs/sec; 3.7 (SE = 0.2), 12.5 new stereopairs/sec; 3.6(SE = 0.2). Thresholds for the three non-cyclopean targets with dynamic dots in the surround were all not statistically different from the threshold for the noncyclopean target with a static surround (two-tailed *t*-test, d.f. = 34). Similar results were obtained for subject 3. The four thresholds were 3.1 (SE = 0.1), 3.3 (SE = 0.2), 3.2 (SE = 0.1) and 3.0 (SE = 0.1). Thresholds for the noncyclopean targets with dynamic dots in the surround were not statistically different from the threshold obtained with static dots in the surround (two-tailed *t*-test, d.f. = 34). We also compared the non-cyclopean stimulus that was the closest approximation to the cyclopean stimulus (25 new stereopairs/sec) with the cyclopean stimulus (50 new stereopairs/sec). For subject 1, thresholds were 4.3 (SE = 0.2) and 8.1 (SE = 0.5) min arc for the 25 new stereopairs/sec and cyclopean target respectively. These thresholds were compared with a two-tailed *t*-test giving P < 0.001, d.f. = 34. For subject 3, the two thresholds were 3.5 (SE = 0.1) and 4.8 (SE = 0.1) giving P < 0.001, d.f. = 34. We conclude that cyclopean thresholds for the perception of motion in depth produced by SO were significantly greater than thresholds for our closest monocularly-visible approximation to a cyclopean stimulus.

The amplitudes of the SO stimulus that produced a just-detectable perception of SO for cyclopean (\bigcirc) and non-cyclopean (\Box) targets are plotted as ordinate in Fig. 4(D-F) vs oscillation frequency. As in Fig. 4(A-C) the two curves were approximately the same shape and their vertical separation was roughly the same as in

Fig. 4(A–C). Vertical separations were roughly 1.8:1 [Fig. 4(D)], 1.6:1 [Fig. 4(E)] and 1.5:1 [Fig. 4(F)].

Thresholds for the perception of size oscillation were again similar for the four different kinds of noncyclopean targets. Subject 1: 2.3 (SE = 0.1) min arc for static background; 2.4 (SE = 0.1) min arc for 25 new/ stereopairs/sec; 2.3 (SE = 0.12) min arc for 18.75 new stereopairs/sec; 2.6 (SE = 0.16) min arc for 12.5 new stereopairs/sec. The four thresholds for subject 3 were 2.4 (SE = 0.1), 2.5 (SE = 0.1), 2.3 (SE = 0.1) and 2.3 (SE = 0.1) min arc. For both subjects, *t*-tests comparing each dynamic non-cyclopean stimulus with the noncyclopean stimulus with static dots in the background all gave P > 0.5, d.f. = 34. The story was different for the cyclopean target. Size oscillation thresholds were significantly greater for the cyclopean target than the non-cyclopean target with a rate of 25 new stereopairs/ sec. Thresholds were as follows. Subject 1: 2.3 (SE = 0.1) min arc for the 25 new stereopairs/sec target and 4.7 (SE = 0.1) min arc for the cyclopean target, giving P < 0.001, d.f. = 34 (t-test). Subject 3: 2.3 (SE = 0.1) and 3.3 (SE = 0.3) min arc, giving P < 0.01, d.f. = 34. A comparison of Fig. 4(A-C) and Fig. 4(D-F) shows that thresholds for the perception of motion in depth were considerably higher than for the perception of size oscillations for both cyclopean and non-cyclopean targets, roughly 2.7:1 [Fig. 4(A,D)], 1.7:1 [Fig. 4(B,E)] and 1.8:1 [Fig. 4(C,F)].

It is known that, for a monocularly-visible target, prolonged exposure to repetitive high-amplitude modulations of size can elevate threshold for perceiving size modulation, and that these threshold elevations have largely died away within 1 min after the adapting stimulus is removed (Regan & Beverley, 1978a,b). Our arguments that a difference in this adaptation effect for monocularly-visible and cyclopean targets did not affect the results in Expt 2 are similar to our arguments in Expt 1. We carried out similar statistical calculations. Results for the perception of motion in depth produced by size oscillations were as follows. Subject 1: 1.02 (0.05), t = 0.4, P > 0.5, d.f. = 11 and 0.98 (0.03), t = 0.67, P > 0.5, d.f. = 11. Subject 2: 0.97 (0.02), t = 1.5, P > 0.1, d.f. = 11 and 1.00 (0.04), t = 0.07, P > 0.5, d.f. = 11. Subject 3: 1.04 (0.03), t = 1.33, P > 0.2, d.f. = 11 and 1.03 (0.04), t = 0.75, P > 0.2, d.f. = 11. Results for the perception of size oscillations produced by size oscillations were as follows. Subject 1: 1.03 (0.04), t = 0.53, P > 0.5, d.f. = 11 and 1.06 (0.06),t = 0.94, P > 0.2, d.f. = 11. Subject 2: 0.95 (0.03), t = 0.85, P > 0.05, d.f. = 11 and 1.03 (0.04), t = 0.75, P > 0.2, d.f. = 11. Subject 3: 0.99 (0.04), t = 0.25, P > 0.5, d.f. = 11 and 0.94 (0.03), t = 2.0, P > 0.05, d.f. = 11.

Discussion

We report that oscillating the size of a cyclopean target produces a sensation, not only of changing size but also of motion in depth. However, even large-amplitude (15 min arc peak-to-peak) oscillations of the size of a cyclopean target produce only a weak sensation of motion in depth. So far as motion in depth perception is concerned, Fig. 4(A-C) shows that cyclopean thresholds are considerably higher than for a monocularly-visible target. In this respect, the SO data differ from the DO data shown in Fig. 3(A-C).

Thresholds for perceiving SO are also higher for cyclopean targets than for monocularly-visible targets, and by roughly the same amount as the motion in depth thresholds. This suggests that poor cyclopean sensitivity to SO is the major reason why oscillations in the size of a cyclopean target produce only a weak sensation of motion in depth. Our proposed explanation is that only the edges of the stimulus square are important for processing changes in size: the dots within the square convey no information about the square's size. The cyclopean square's edges are comparatively ill-defined, and furthermore their movement is partially masked by apparent movement of groups of dots within the square and the surround. On the other hand, the edges of the monocularly-visible square are defined by texture contrast and luminance contrast as well as by disparity contrast, and thus are more visible.

The DO stimulus is a different story. Every single dot within the square conveys information about motion in depth rather than only dots near the edges, so that the cyclopean square is not at such a disadvantage compared with the monocularly-visible square.

A further possible reason why oscillations in the size of a cyclopean square produce only a weak sensation of motion in depth is that, while the size of the square was modulated, the size of the dots within the square remained constant. There is evidence that the motion in depth system is disrupted when the rate of change of a textured square's size is not matched to the rate of change of size of the texture elements (Beverley & Regan, 1983).

EXPERIMENT 3

Methods

Purpose

The aims of Expt 3 were as follows. (1) To find out whether the sensation of motion in depth produced by DO and by SO were qualitatively identical. (2) To compare quantitatively the effectiveness of suprathreshold oscillations of disparity and of size as stimuli for motion in depth perception.

Psychophysical procedure

The amplitude of SO was held constant at 15 min arc peak-to-peak. This large value was selected in order to create a clearly-visible impression of motion in depth when using the cyclopean target (Expt 2 showed that oscillating the size of a cyclopean target is a comparatively ineffective stimulus for motion in depth perception). Oscillations of disparity were pitted against oscillations of size, and subjects were provided with a circular knob that controlled the amplitude of the DO stimulus. Subjects were instructed to set the knob on the



FIGURE 5. Amplitude of disparity oscillation that canceled the impression of motion in depth produced by a 15 min arc peak-to-peak size oscillation is plotted as ordinate vs oscillation frequency for three subjects. \bullet are for the cyclopean target. \Box are for the monocularly-visible target. (A), (B) and (C) are for subjects 1, 2 and 3 respectively.

point of zero perceived motion in depth. Each data point in Fig. 5(A-C) is the mean of 18 settings.

Subjects

Subjects 1, 2 and 3 carried out Expt 3.

Results

All subjects reported that the perception of motion in depth was clear when the knob was turned fully down, and that as the knob was slowly turned up the oscillations of perceived depth first fell to zero then became progressively larger. Our procedure was slightly biased in favor of disparity oscillations since subjects were instructed to turn the knob up to the point that the perception of motion in depth was just canceled. This point would presumably correspond to the threshold for the perception of motion in depth caused by SO for the particular oscillation frequency.

The amplitude of DO that canceled the impression of motion in depth produced by a 15 min arc size oscillation for cyclopean (\bigcirc) and non-cyclopean (\square) targets were plotted as ordinate vs oscillation frequency in Fig. 5(A-C) for three subjects. In Fig. 5(A) the two curves had roughly the same shape, but were displaced along the ordinate. The amplitude of the DO required to cancel the impression of motion in depth produced by the fixed SO

was approx. 3.2 times greater for the non-cyclopean target than for the cyclopean target. Corresponding ratios for the other two subjects were 1.7:1 [Fig. 5(B)] and 1.6:1 [Fig. 5(C)].

Discussion

We conclude that qualitatively-identical sensations of motion in depth are produced by oscillations of size and by oscillations of disparity for cyclopean and monocularly-visible targets. These findings provide further support for the proposal that the neural signals produced by changing-size and by changing-disparity converge onto a single mechanism that signals motion in depth (Regan & Beverley, 1979).

Our finding that a small amplitude of DO cancels the impression of motion in depth produced by a large amplitude SO for cyclopean targets while a considerably larger amplitude is required for monocularly-visible targets, would be expected at a qualitative level from the data on the comparative effectiveness of SO alone and DO alone shown in Figs 3 and 4.

EXPERIMENT 4

Methods

Purpose

The aim of Expt 4 was to compare, for cyclopean and non-cyclopean targets, visual sensitivity to oscillatory motion within the frontoparallel plane (FPO) and at right angles to the frontoparallel plane. Our approach was to compare detection thresholds for oscillations of location within the frontoparallel plane with detection thresholds for DO. The only difference between the two stimuli was the 0 vs 180 deg phase difference between oscillations of the 2 deg square in the left and the right eyes.

Psychophysical procedure

The amplitude of oscillation of the square's location was always equal in the left and right eyes. Subjects were provided with a knob that controlled oscillation amplitude. When setting thresholds for frontal plane motion, subjects were instructed to set the knob so that the entire square was clearly oscillating from side to side, and then reduce the setting until this bodily oscillation was just detectable. Instructions for setting depth oscillations were analogous. Each data point in Fig. 6(A-F) is the mean of 12 settings except for frequencies of 1.0 and 3.0 Hz for which data points were the mean of 18 settings.

Subjects

Subjects 1, 4 and 5 carried out Expt 4.

Results

Thresholds for monocularly-visible targets are plotted in Fig. 6(A-C). • indicate thresholds for inphase oscillations of the target (i.e. FPO), and \Box indicate thresholds for antiphase oscillations of the target (i.e. DO). Thresholds for FPO and DO were similar at all oscillation frequencies tested. Consequently, when we set the amplitude of the antiphase oscillation to just above threshold and switched the relation between oscillations presented to the two eyes from antiphase to inphase motion perception was abolished, even though the input to the left eye and to the right eye remained unchanged. (Switching from inphase to antiphase oscillation converts a FPO of amplitude θ deg to a DO of amplitude 2θ deg.) Again, with the amplitude of the antiphase oscillation set to produce just detectable motion in depth oscillations, no oscillations were visible when one eye was occluded.

Cyclopean thresholds for FPO and DO are represented by \bullet and \Box respectively in Fig. 6(D–F). Thresholds for the two kinds of oscillation were similar at low oscillation



FIGURE 6. Detection thresholds for motion within the frontoparallel plane (●) and motion in depth thresholds (□) are plotted as ordinate vs oscillation frequency. Motion in depth perception was generated by disparity oscillations. (A)–(C) Monocularlyvisible targets. (D)–(F) Cyclopean targets. (A, D) Subject 1, (B, E) subject 4 and (C, F) subject 5.

frequencies but, for frequencies above about 1.0 Hz, thresholds for FPO were considerably higher than thresholds for DO. In Fig. 6(D) FPO and DO thresholds were not significantly different at 1.0 Hz (P > 0.7, d.f. = 34), but at 3.0 Hz the two thresholds differed at a highly significant level (P < 0.001, d.f. = 34). Corresponding statistics for Fig. 6E were P > 0.2, d.f. = 34 at 1.0 Hz and P < 0.001, d.f. = 34 at 3.0 Hz. Corresponding statistics for Fig. 6(F) were P > 0.2, d.f. = 34 at 1.0 Hz and P < 0.001, d.f. = 34 at 3.0 Hz. Corresponding statistics for Fig. 6(F) were P > 0.2, d.f. = 34 at 1.0 Hz and P < 0.001, d.f. = 34 at 3.0 Hz. In contrast, in Fig. 6(A), thresholds were not significantly different at either 1.0 Hz (P > 0.8, d.f. = 34) nor at 3.0 Hz (P > 0.2, d.f. = 34). Corresponding statistics for Fig. 6(B) were P > 0.5, d.f. = 34 and P > 0.7, d.f. = 34 and, for Fig. 6(C), P > 0.5, d.f. = 34 and P > 0.2, d.f. = 34.

It is known that, for a monocularly-visible target, prolonged exposure to high-amplitude oscillations in the frontoparallel plane elevate threshold for FPO and that prolonged exposure to high-amplitude oscillations of disparity elevate thresholds for DO, and that threshold elevations have largely died away within one minute after the adapting stimulus is removed (Sekular & Ganz, 1963; Beverley & Regan, 1973). Our arguments that a difference in these adaptation effects for monocularlyvisible and cyclopean targets did not affect the results of Expt 4 are similar to our arguments in Expts 1 and 2. We carried out similar statistical calculations. Results for detection thresholds for FPO were as follows. Subject 1: 1.06 (0.06), t = 1.0, P > 0.2, d.f. = 9 and 1.01 (0.06), t = 0.17, P > 0.5, d.f. = 9. Subject 4: 0.98 (0.07), t = 0.29, P > 0.5, d.f. = 9. Subject 5: 1.02 (0.04), t = 0.53, P > 0.5, d.f. = 9 and 1.03 (0.04), t = 0.75, P > 0.2, d.f. = 7.

Discussion

There is substantial literature comparing the perception of oscillatory motion in the frontoparallel plane and in depth (Richards, 1972; Tyler, 1972, 1975; Tyler & Torres, 1972; Regan & Beverley, 1973; reviewed in Regan, 1991). All these studies, however, were restricted to monocularly-visible targets. Although several studies have been published on the cyclopean processing of motion within the frontoparallel plane (Julesz & Payne, 1968; Patterson, Ricker, McGary & Rose, 1992; Patterson, Bowd, Phinney, Pohndorf, Barton-Howard & Angilletta, 1994), a comparison of cyclopean thresholds for motion in depth and motion within the frontoparallel plane has been lacking.

Our finding that, for a cyclopean target, frontal plane motion detection is restricted to a frequency range that does not extend above 7 Hz is in line with an earlier report that frontal plane motion cannot be detected for cyclopean gratings at frequencies above 8 Hz (Patterson *et al.*, 1992).

One possible explanation for our finding that thresholds for motion in depth are lower than thresholds for oscillatory motion in the frontoparallel plane is the same as that suggested to explain the results of Expts 2 and 3 every single dot within the square conveys information about motion in depth, but only the dots near the edge of the square convey information about motion in the frontoparallel plane.

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