A specialization for vertical disparity discontinuities

Ignacio Serrano-Pedraza Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, UK

Graeme P. Phillipson Institute of Adaptive and Neural Computation, School of Informatics, Edinburgh University, Edinburgh, UK

Jenny C. A. Read Institute of Neuroscience, Newcastle University, Newcastle upon Tyne, UK

Because our eyes are set apart horizontally in our head, most disparities between the retinal images are horizontal. However, vertical disparities also occur, and can influence depth perception. The classic example is Ogle's induced effect (K. N. Ogle, 1938), in which applying a uniform vertical magnification to one eye's image produces the illusion that the surface has been rotated around a vertical axis. This is thought to be because uniform vertical magnifications can be produced in natural viewing when the eyes are in eccentric gaze (J. E. Mayhew, 1982; J. E. Mayhew & H. C. Longuet-Higgins, 1982). Thus, vertical magnification is taken by the visual system as indicating that the viewed surface is slanted away from the line of sight. Here, we demonstrate that the induced effect becomes stronger when the sign of the magnification alternates across the visual field. That is, as one moves horizontally across the screen, the left eye's image is alternately stretched and squashed vertically relative to the right eye's image, producing the illusion of a surface folded into triangular corrugations (H. Kaneko & I. P. Howard, 1997). For most subjects, slant judgments in this folded surface have lower thresholds and greater reliability than the classic induced effect, where magnification is applied uniformly across the whole visual field. This is remarkable, given that the disparity pattern of the classic induced effect can be produced by real surfaces with the eyes in eccentric gaze, whereas it is not clear that stripes of alternating vertical disparity could be produced by any physically realizable situation. The analogous improvement for alternating horizontal magnification is attributed to neuronal mechanisms which detect the jumps in horizontal disparity that occur at object boundaries. Our results suggest that a similar, previously unreported system may exist for vertical disparity. Jumps in vertical disparity do occur at object boundaries, and we suggest that our surprising results may reflect the activation of neuronal mechanisms designed to detect these.

Keywords: binocular vision, stereo-resolution, vertical disparity, relative disparity, induced effect

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Introduction

Light rays from a given object may strike the retina at different vertical positions in the two eyes; Figure 1 shows an example. We define the vertical disparity to be the difference between the elevation coordinates of the two images, where elevation is measured as longitude, as in the coordinate system marked on each retina in Figure 1. In general, the size of any such retinal vertical disparity depends on how the eyes are oriented and where the object is located. There is increasing evidence that the visual system detects and uses vertical disparities in order to calibrate depth perception (Howard & Rogers, 2002). This is most strikingly demonstrated in the induced effect (Ogle, 1938), in which one eye's image is magnified vertically relative to the other. This produces the illusion that the surface has been rotated about a vertical axis, so the side of the surface nearer to the eye in which its image has been expanded looks closer. The same rotation is produced in the geometric effect, in which a horizontal magnification of one eye's image produces the impression that the surface has rotated about a vertical axis. However, in the geometric effect the rotation is in the opposite direction: the side of the surface nearer to the eye in which the image has been expanded looks further away. The geometric effect can be understood straightforwardly from the geometry, since a physical surface rotated in this way really does subtend a larger horizontal angle in the magnified eye. The induced effect, in contrast, appears to arise from the way in which the pattern of vertical disparities across the visual field is used to calibrate information from horizontal disparity (Backus & Banks, 1999; Banks & Backus, 1998; Gårding, Porrill, Mayhew, & Frisby, 1995; Gillam & Lawergren, 1983; Rogers & Bradshaw, 1993, 1995; Rogers & Cagenello, 1989). Regardless of exactly how this occurs, the induced effect is strong evidence that the visual system detects vertical disparity and uses it to influence depth perception.

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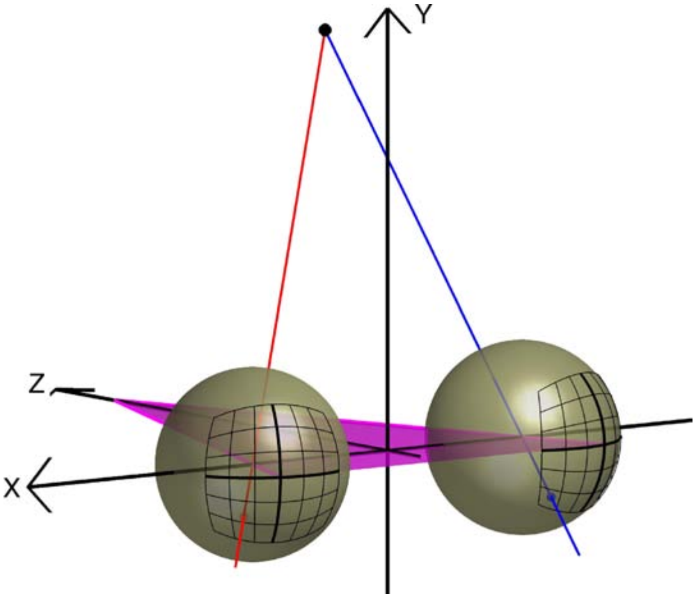

Figure 1. How vertical disparity arises. The eyes are shown fixating a point on the midline, (X,Y,Z) = (0,0,8). An azimuth-longitude/elevation-longitude coordinate system is marked on each retina, with the fovea at its origin. Heavy black lines mark the horizontal and vertical retinal meridians; lighter lines mark lines of longitude drawn every 15°. The pink lines show the optic axes, i.e. the line linking the fixation point to each fovea. Colored rays show the retinal projections of an object at (−6,6,10). Comparing where the red and blue rays intersect each retinal coordinate system, it is clear that the object projects lower down in the right retina than the left.

It is often stated that retinal vertical disparity mainly reflects binocular eye posture, varies only slowly across the visual field, and is largely independent of object distance (Gårding et al., 1995; Read & Cumming, 2006; Rogers & Bradshaw, 1993; Stenton, Frisby, & Mayhew, 1984). Figure 2 exemplifies this. Here, the eyes fixate one surface, with an adjacent surface at a different depth. The horizontal disparity reflects the distance to each surface, with a clear discontinuity at the depth boundary. In contrast, the vertical disparity varies smoothly across the visual field, in a pattern which depends primarily on the particular eye posture, rather than the details of the surface viewed. This has led to the suggestion that the visual system needs only a relatively coarse representation of vertical disparity, in contrast to the much finer map required to capture variations in horizontal disparity produced by depth structure within a visual scene (Backus & Banks, 1999; Gårding et al., 1995; Rogers & Bradshaw, 1993; Stenton et al., 1984). In principle, the pattern of vertical disparity across the entire visual field could be used to extract a single estimate of eye position (Longuet-Higgins, 1981; Mayhew, 1982; Mayhew & Longuet-Higgins, 1982). In fact, this is not what happens. When opposite vertical magnifications are applied to the two halves of the visual field, viewers perceive slant in opposite directions in the two halves (Kaneko & Howard, 1996; Rogers & Koenderink, 1986). Such observations have led to the idea that vertical disparity is extracted over local regions, and used directly to calibrate how horizontal disparity is mapped onto estimates of surface slant and curvature, without necessarily being combined into an explicit estimate of eye position (Backus & Banks, 1999; Backus, Banks, van Ee, & Crowell, 1999; Gårding et al., 1995).

This raises the question of how wide the regions are over which vertical disparity is "pooled." The results of Rogers and Koenderink (1986) show that these regions are less than the entire visual field, but leave open the possibility that they are still very large. Stenton et al. (1984) examined slant perception in a stimulus containing different vertical magnifications in different regions, and found that the perceived slant reflected the average vertical disparity. They argued that this shows vertical disparity is pooled across at least the 7.2° × 7.2° extent of their stimulus. However, in their experiments subjects were asked to adjust the horizontal magnification until the entire array appeared as close to frontoparallel as possible; they were not given an opportunity to report any variations in surface slant they perceived within the stimulus. Consistent with this, Adams et al. (1996), Kaneko and Howard (1996) and Pierce & Howard (1997) intermingled elements with different vertical disparities. They all found that the percept corresponded to an average of the different vertical disparities present, whereas when they intermingled different horizontal disparities, the percept was of two transparent surfaces. Both labs concluded that vertical disparity is represented on a coarser scale than horizontal disparity, and came up with broadly similar estimates of the size of the regions across which vertical disparity is pooled: around 14° (Adams et al., 1996) or 20–30° (Kaneko & Howard, 1996).

Kaneko and Howard (1997) examined the issue in more detail. In their Experiment 2, they used stimuli in which vertical magnification changed sign many times across the visual field, and examined the highest frequencies at which this variation in vertical-disparity-induced slant could be detected.

The rationale behind such experiments is sketched in Figure 3, assuming for convenience that vertical disparities are pooled over a Gaussian region with standard deviation σ. Then, strips of alternating vertical magnification on the screen will be blurred by this Gaussian, reducing the effective amplitude of the magnification (insets in Figure 3). The main curve in Figure 3 plots how the effective amplitude falls as a function of frequency. Assuming that sensitivity reflects the effective amplitude of the magnification signal, we could estimate the effective width of pooling by fitting the observed sensitivity/frequency function with this theoretical curve. Kaneko and Howard (1997) found that the illusory corrugations could be detected up to a maximum spatial

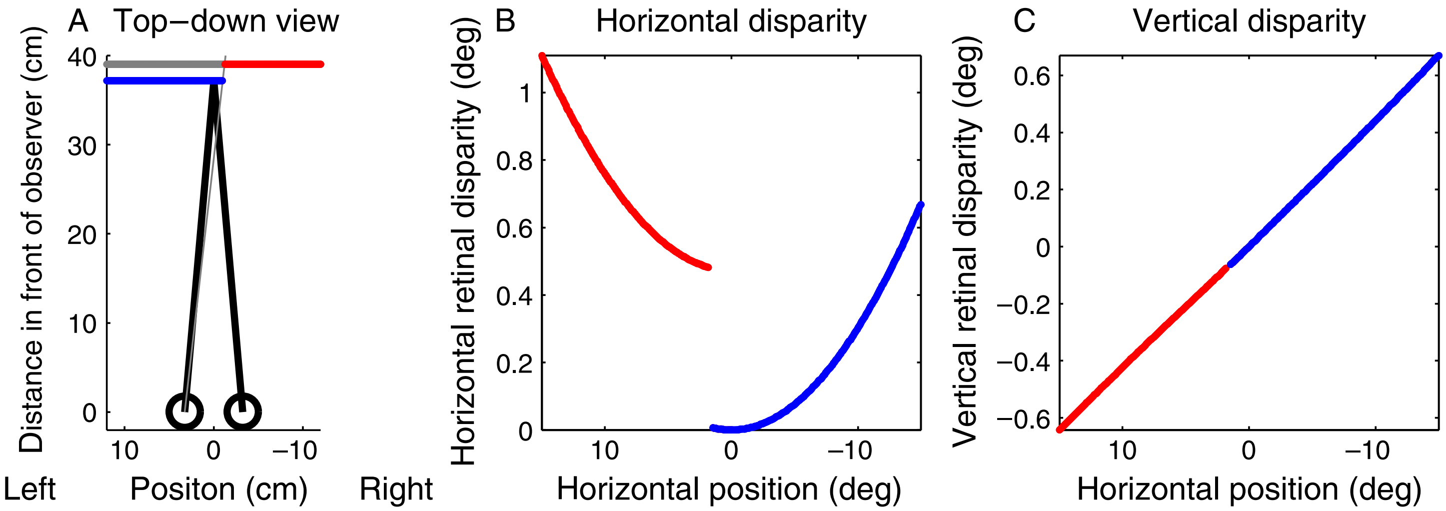

Figure 2. Depth boundary, showing discontinuities in horizontal but not vertical disparity. A: The eyes are fixating the blue surface 37 cm in front of the observer. This surface partially occludes a more distant surface at 39 cm, shown in red where visible to both eyes, gray where occluded from one or both eyes. The thin gray line is drawn from the nodal point of the left eye past the edge of the blue surface, to show where the more distant surface disappears from the left eye's view. B shows the horizontal, and C the vertical, retinal disparity of points on the red and blue surfaces, at a constant 10 cm above the plane of fixation (points in the plane of fixation have no vertical disparity). Because the retinas are behind the nodal point, directions are reversed so the blue surface is on the right. The depth boundary is marked by a discontinuity in horizontal disparity, but vertical disparity varies smoothly across the whole visual field, with a pattern determined almost entirely by the eye position. In this figure, horizontal disparity is defined as the difference in azimuth-longitude coordinates, α_Δ in the notation of Read et al. (2009), and vertical disparity as the difference in elevation-longitude, η_Δ. Horizontal retinal position is defined as the azimuth-longitude coordinate on the cyclopean eye, α_c, i.e. the mean of the azimuth-longitude coordinates of the point's projections onto the left and right retinas. See Read et al. (2009) for detailed definitions.

frequency of 0.04 c/deg, and deduced that vertical disparities are averaged over an area about 20° in extent, far coarser than the representation of horizontal disparity.

However, Experiment 2 of Kaneko & Howard has a number of features which may have affected the results. It included only 2 subjects, although as we show here, there is considerable variation between subjects. The stimuli used very large, sparse dots, 2° in diameter. Subjects viewed the stimuli for 1s, in principle allowing vertical vergence movements. Vertical magnification varied across the image with a sinusoidal profile. While most studies of frequency limits have used sinewaves, this has a clear theoretical motivation only in the luminance or contrast domain (Campbell & Robson, 1968). In the case of the induced effect, a vertical disparity gradient with respect to vertical position in the image is expected to produce an illusion of surface slant, ultimately based on a misestimate of gaze azimuth (Backus & Banks, 1999; Backus et al., 1999; Mayhew, 1982; Mayhew & Longuet-Higgins, 1982). However, a sinusoidal variation of vertical magnification introduces a gradient of vertical disparity with respect to horizontal position as well as to vertical position. Theoretically, such a gradient would be expected to produce a complicated change in surface slant, tilt and curvature, reflecting a misestimate of vergence as well as gaze azimuth (Cumming, Johnston, & Parker, 1991; Frisby et al., 1999; Rogers & Cagenello, 1989). It is not

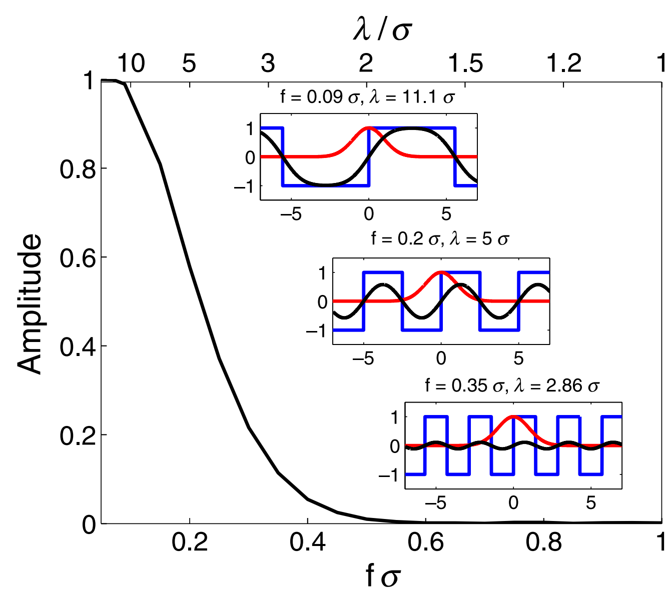

Figure 3. Results of convolving a square wave with a Gaussian. Square-waves of different fundamental frequency f (inset, blue) are convolved with a Gaussian of standard deviation σ (insets, red), resulting in the waveform shown (insets, black). The main plot shows the amplitude of this waveform as a function of the square-wave frequency.

	Presentation duration (ms)	Waveform	Screen size W × H, cm (degrees)	Distance (cm)	Dot diameter (deg)	Dot density dots/m^2 (dots/deg^2)	Nyquist limit (c/deg)	Number of subjects
Kaneko & Howard, 1997, Their Experiment 2	1000	Sinusoidal	98 × 98 (55° × 55°)	94	2	703 (0.223)	0.236	2
Present study	200	Square-wave	127 × 95 (42° × 32°)	165	0.12	13540 (12.15)	1.74	9

Table 1. Summary of differences between the experiments of Kaneko & Howard and the present paper. The Nyquist limit refers to the frequency limit imposed by the discrete dot sampling, $0.5\sqrt{\rho}$, where ρ is the dot density, in dots/deg^2 (Banks et al., 2004).

clear what effect this would have on the visibility of illusory corrugations.

We therefore decided to readdress the issue of the spatial scale of vertical disparity pooling. We used dense, small dot patterns to be sure we would not approach the Nyquist limit (Banks, Gepshtein, & Landy, 2004; Table 1). Subjects viewed the stimuli for 200 ms. We used square-wave modulations of vertical magnification. That is, we applied uniform vertical magnification to either the left eye or the right eye, alternating which eye was magnified as a function of horizontal position across the image, effectively dividing the image up into vertical strips of induced-effect stimuli with alternating sign. To make a direct comparison between the resolution of horizontal and vertical disparity encoding in the same subject, we also performed the experiment with horizontal magnification varying as a function of vertical position.

Methods

Subjects

We show data from a total of 10 human subjects: the 3 authors, 2 further lab members, plus 5 observers unaware of the purpose of the study, most of them with experience in psychophysical observation (in total, 8 male, 2 female, all aged between 17 and 36 years). All subjects had normal or corrected-to-normal refraction, normal visual acuity, and viewed the screen with natural pupils through polarizing filters. Experimental procedures were approved by Newcastle University's Human Psychology Ethics Committee.

Stimulus presentation

The experiments were carried out in a dark laboratory. A head and chin rest (UHCOTech HeadSpot) was used to stabilize the subject's head and to control the observation distance. Stimuli were presented on a rear projection screen, frontoparallel to the observers, who viewed it from a distance of 165 cm (except where stated in the Control Experiments). Each eye's image was presented using a separate F20 Sx+ DLP™ projector (Projection Design, Norway) driven by a NVIDIA GeForce 8600 GT graphics card, with a resolution of 1400 × 1050 pixels (horizontal × vertical). Both displays were carefully linearized (gamma corrected). Polarizing filters ensured that each eye saw only one projector's image; the interocular cross-talk was less than 1%. White on our display had a luminance of 4 cd/m^2, reduced to 2.8 cd/m^2 when viewed through the polarizing glasses; the black background had a luminance of 0.07 cd/m^2, reduced to 0.05 cd/m^2. All luminance measurements were carried out with a Minolta LS-100 photometer.

The images were carefully aligned to within a pixel everywhere within the central 30°, to ensure that as far as possible the only disparities were those introduced by the experimenter (Serrano-Pedraza & Read, 2009). The projected image was 127 × 95 cm subtending 42° × 32°. Each pixel thus subtended 1.8 arcmin. In all experiments, stimuli were generated by a DELL workstation running MATLAB with the Psychophysics Toolbox extensions ((Brainard, 1997; Pelli, 1997), www.psychtoolbox.org). Subpixel disparities were achieved using anti-aliasing built into the Psychophysics Toolbox "DrawDots" function.

Stimuli

To minimize eye movements, the subjects were instructed to maintain fixation on a small cross (0.3° × 0.3°) in the center of the screen, flanked by vertical and horizontal Nonius lines of length 0.6°, presented in between stimuli. Stimuli consisted of circular white dots, 0.12° in diameter, distributed uniformly and randomly across a black background with a density of 12 dots/deg^2. The same dot pattern was displayed to both eyes, except for the disparity manipulations described now. Experiment 1 used a version of the geometric effect, in which the horizontal coordinates of the dots in one eye's image are multiplied by a constant factor and the horizontal coordinates of the other eyes' dots are divided by the same factor. Thus, one eye's image is expanded horizontally relative to the other, although the sizes of individual dots are unchanged. The magnitude of this expansion was constant across the whole image, but its sign, i.e. which eye's image was expanded and which was compressed, alternated in a square-wave pattern as a function of vertical position. This produces the illusion of a surface split into horizontal slats slanted in alternating directions, as illustrated in Figure 4B. Experiment 2 applied the analogous manipulation in the vertical dimension, creating a version of the induced effect. The sign of the vertical magnification again alternated in a square-wave pattern (Figure 5). Since the induced effect produces an illusion that the surface is slanted about a vertical axis, this manipulation produced an impression of a surface whose slant alternated as a function of horizontal position, as if it were folded into vertical triangle-wave corrugations. This illusion is much less compelling than the "slats" produced in Experiment 1, and looks visibly "wrong" if subjects are given the opportunity to view it for more than a few hundred milliseconds.

A transformation was applied to all stimuli in order to simulate screens orthogonal to each eye's optic axis (for details see Serrano-Pedraza and Read (2009), where this transformation is described as "geometric correction"). This means that there were no disparities on the retina due to the viewing geometry: the only vertical disparities on the retina were those explicitly introduced by the vertical magnification in the induced-effect stimuli, and the only horizontal disparities were those introduced by the horizontal magnification in the geometric-effect stimuli. Because of the long viewing distance (165 cm), the shifts due to this orthogonality transformation were small, and control experiments on a subgroup of subjects indicated that it had no significant effect (Control Experiment 2).

We defined the stimuli by their spatial frequency f. The width of each strip of constant magnification is $\lambda/2$, where $\lambda = 1/f$. The lowest frequency possible was one where a constant magnification was applied to the entire screen, full-width W. We defined this stimulus as having $f = 1/2W$, although clearly any lower f would produce the same image.

Procedure

Subjects were introduced to the experiments by being shown long-duration stimuli with horizontal corrugations (Experiment 1) and with vertical corrugations (Experiment 2) and asked to report the direction of perceived slant of the central part by indicating whether the left or right side of the stimulus central part was closer to them. After they had learnt to report the direction of perceived

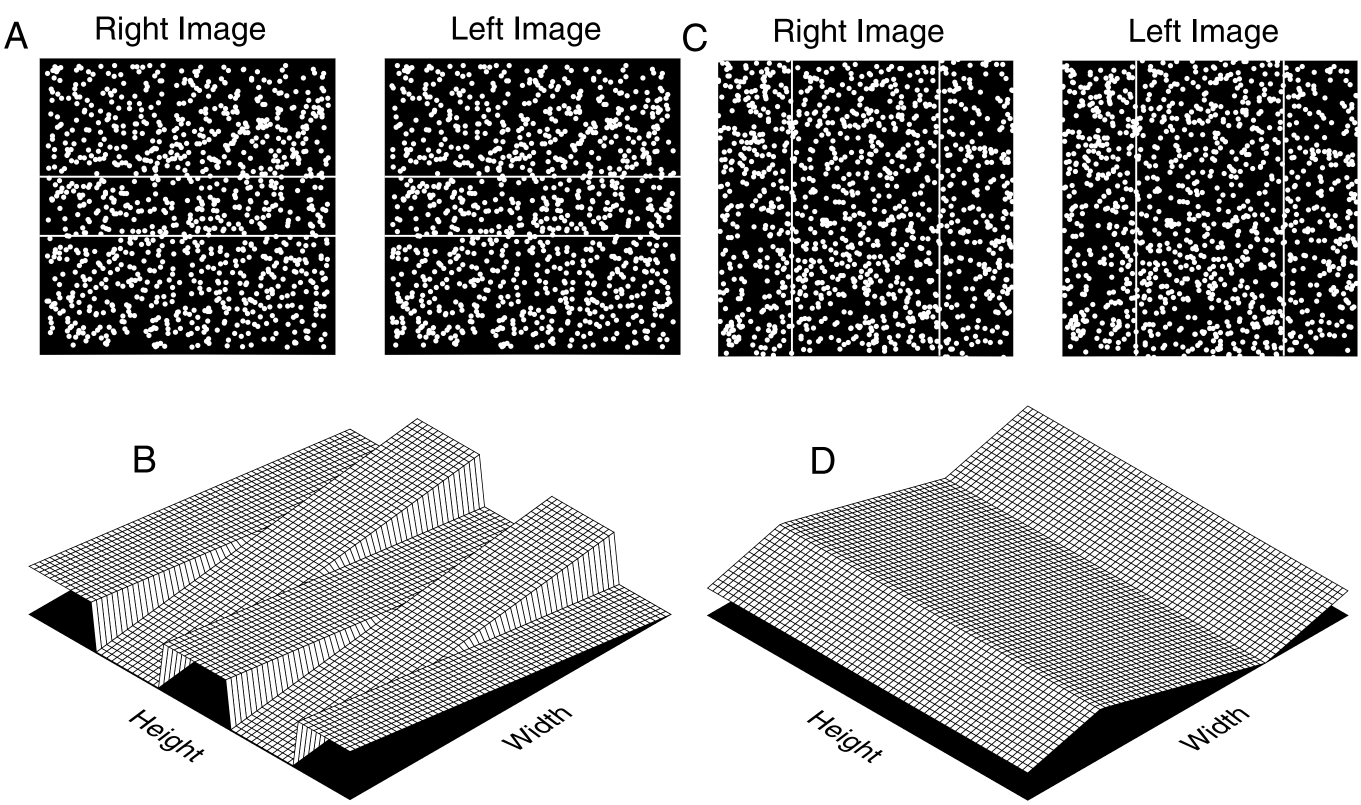

Figure 4. Example stimuli, shown for cross-fusion (top) and as sketches representing the 3D percept produced (bottom). The task of the subjects was to indicate whether the left or right side of the horizontal or vertical strip demarcated by white lines appeared closer to them. AB) Experiment 1. Horizontal square-wave magnification of spatial frequency of 2.5 cycles per image. CD) Experiment 2. Vertical square-wave magnification of 1 cycle per image.

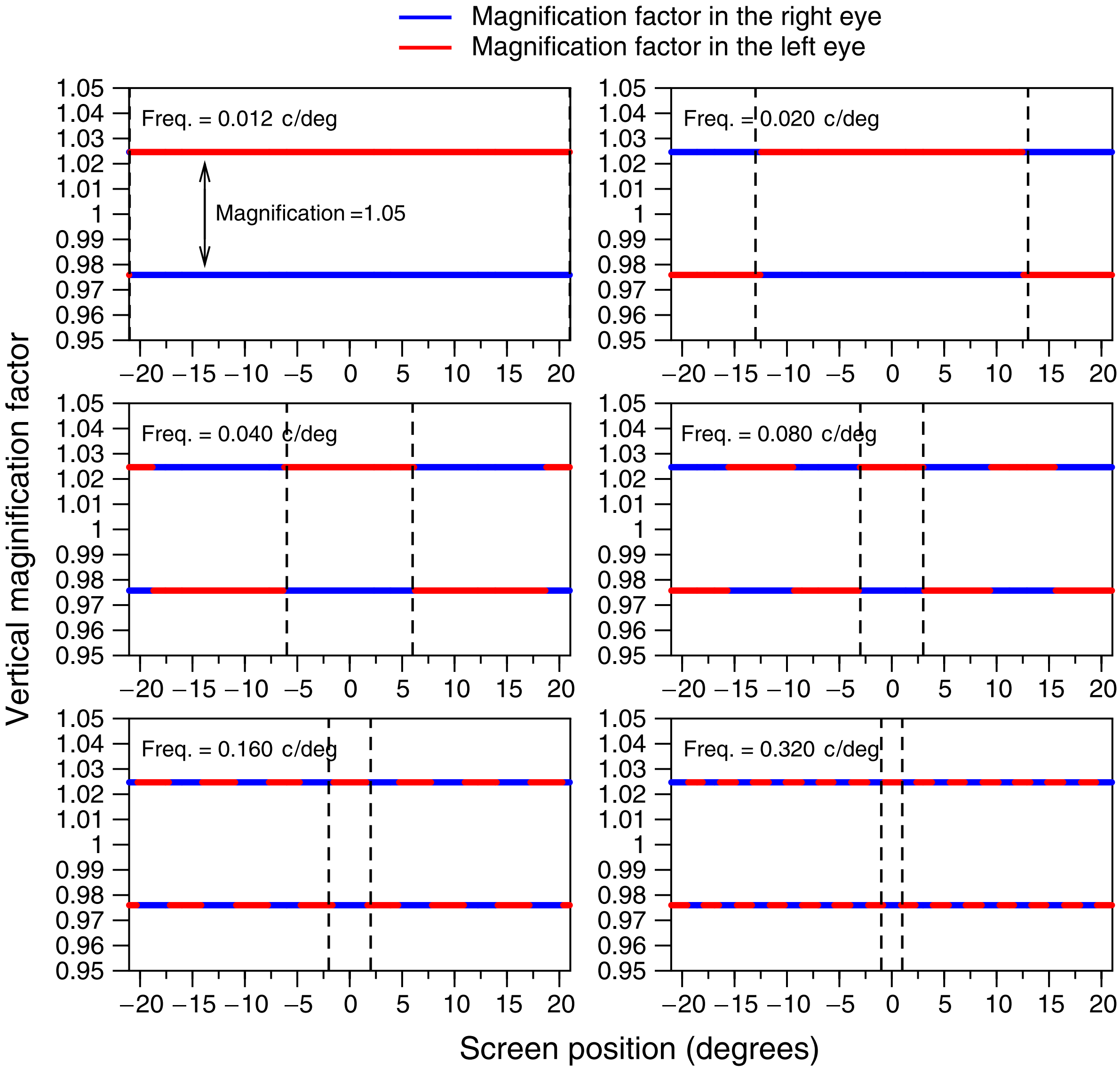

Figure 5. Distribution of vertical square-wave magnifications across the screen used in Experiment 2. Blue line represents the position on the screen where the vertical magnification was applied to the dots presented in the left eye (values higher than 1 expand the image's dots and values lower than 1 compress the image's dots). Red line represents the vertical magnification applied to the right eye. Each panel shows the square-wave magnifications for different spatial frequencies. In all panels, the total magnification is 1.05. The vertical dashed lines enclose half cycle in the central part of the screen where the subject had to attend in the experiment.

slant in these stimuli, stimulus duration was reduced to 200 ms. In Experiment 1, the spatial frequencies of the horizontal disparity modulation were 0.02, 0.04, 0.08, 0.16, 0.32, 0.64, 1.28 cycles/deg. In Experiment 2, the spatial frequencies of the vertical disparity modulation were 0.012, 0.02, 0.04, 0.08, 0.16, 0.32 cycles/deg (for some subjects not all frequencies were used because they could do the task only at the lowest spatial frequencies). A strip of constant magnification, either positive or negative, was always centered on the middle of the screen (Figure 5). To obtain the sensitivity to horizontal and vertical disparity modulations, we used the method of constant stimuli. In each experimental session, the frequency of disparity modulation was kept constant and 10 magnifications were presented a minimum of 20 times each in random order. The magnification sign of the central strip was chosen at random, corresponding to opposite slants. The observer's task was to indicate, by pressing a mouse button, whether the left or right side of the central strip appeared closer to them. In order to make it clear which part of the stimulus they were meant to be reporting, the central strip was demarcated by zero-disparity white lines extending across the whole screen, horizontally in Experiment 1 and vertically in Experiment 2 (Figure 4). A new trial was initiated only after the observer's response, thus the experiment proceeded at a pace determined by the observer. No feedback about the correctness of responses was provided.

Data analysis

In Experiment 1, the geometric-effect stimulus, observers typically rose from chance at small horizontal magnifications, to 100% accuracy as the horizontal magnifications increased. In the induced-effect stimulus of Experiment 2, several observers were unable to approach 100% accuracy at any vertical magnification. Their performance increased to a maximum as vertical magnification was initially increased, and thereafter fell back to chance at still larger vertical magnifications. An example of the two types of performance is shown in Figure 5 (open circles and error-bars).

Due to the different type of data obtained in each experiment, two different psychometric functions were fitted to the data by maximum likelihood, shown by black curves in Figure 6. The first one is the cumulative Gaussian function (see Figure 6A), which has two parameters, the mean A and standard deviation D, reflecting the bias and threshold respectively. The second function has three parameters and was chosen as an economical and accurate empirical description of the data obtained in Experiment 2 (black curve in Figure 6B). This function has the equation

$$\Psi(M) = 0.5 + \frac{B \times (M - A)}{1 + (M - A)^2 / C^2}; \quad (1)$$

where A (bias), B (maximum gradient) and C (position of best performance) are the parameters of the function and M is the magnification factor. Because we did not want to use one function or the other *a priori,* we fitted both functions to all data in both experiments and then the function with the highest likelihood was taken as the best description of the data.

Sensitivity S was defined as $\sqrt{2\pi}$ times the maximum gradient of the fitted psychometric function. This gives the commonly used value of $\underline{S} = 1/D$ for the cumulative Gaussian, and $S = B \times \sqrt{2\pi}$ for the other function. The units of S are therefore the reciprocal of magnification-factor. Thus a sensitivity of S = 100 means (for a cumulative Gaussian) that performance reaches the 84% threshold at 1% magnification, M = 1.01.

Results

Experiment 1: Horizontal magnification

In this experiment, the horizontal magnification relating left and right images alternated in sign as a function of vertical position in the image. This caused a vivid percept of horizontal "slats" side-on to the observer, slanting alternately either left or right (Figure 4A). Subjects had to discriminate the direction of slant of the middle slat. Their

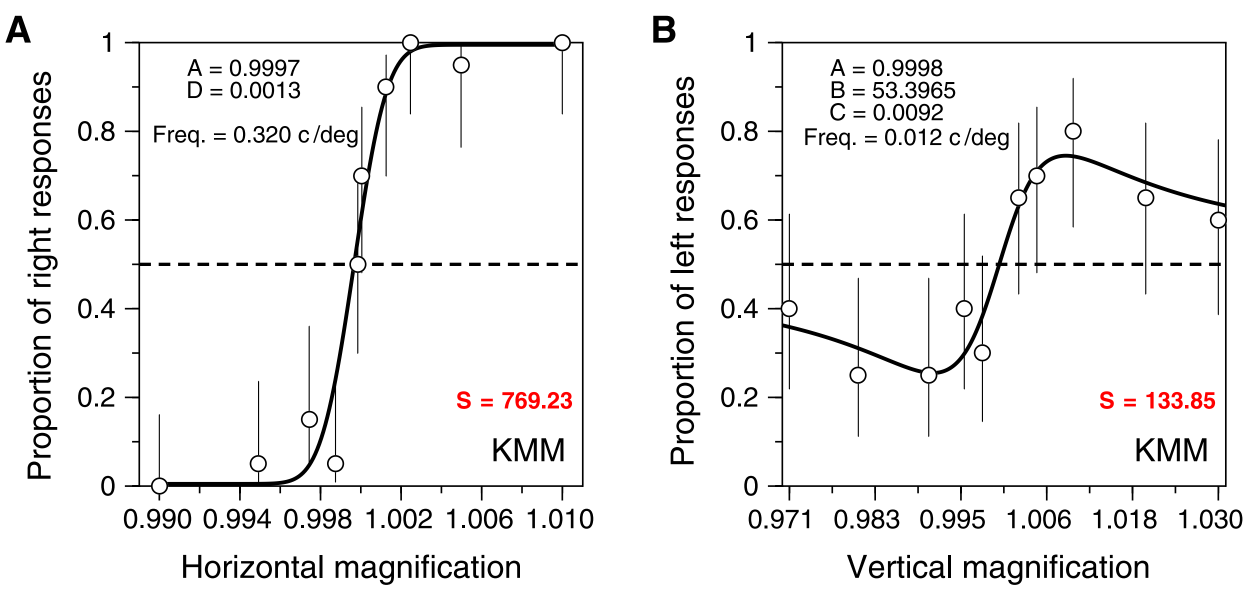

Figure 6. Example results for subject KMM. A) Experiment 1: geometric effect with a magnification modulation of spatial frequency 0.32 cycles/deg. Open circles show the proportion of "right side closer" judgments as a function of horizontal magnification amplitude. Error bars show the 95% confidence limits assuming binomial variability; the limits were obtained using the score confidence interval. Solid black line is the Gaussian psychometric function with two parameters (A and D, upper-left) fitted to the experimental data by maximum likelihood. B) Experiment 2: induced effect with spatial frequency 0.012 cycles/deg. Circles show the proportion of "left side closer" judgments as a function of vertical magnification amplitude. Solid black line is the function of Equation 1 with fit parameters A, B, C given in the upper left. Sensitivity S (in red), proportional to the maximum gradient, is given for both functions in the bottom-right.

sensitivity was defined as described in the Methods (Data analysis section), to reflect how rapidly performance improved as the amplitude of magnification was increased. Figure 7 shows sensitivity as a function of frequency for 9 subjects. For all subjects, sensitivity has a marked band-pass pattern. At the very lowest frequency, where the same magnification was applied to the entire screen, subjects needed relatively large magnifications before they could accurately say whether the screen appeared slanted to the left or right. At higher frequencies, where

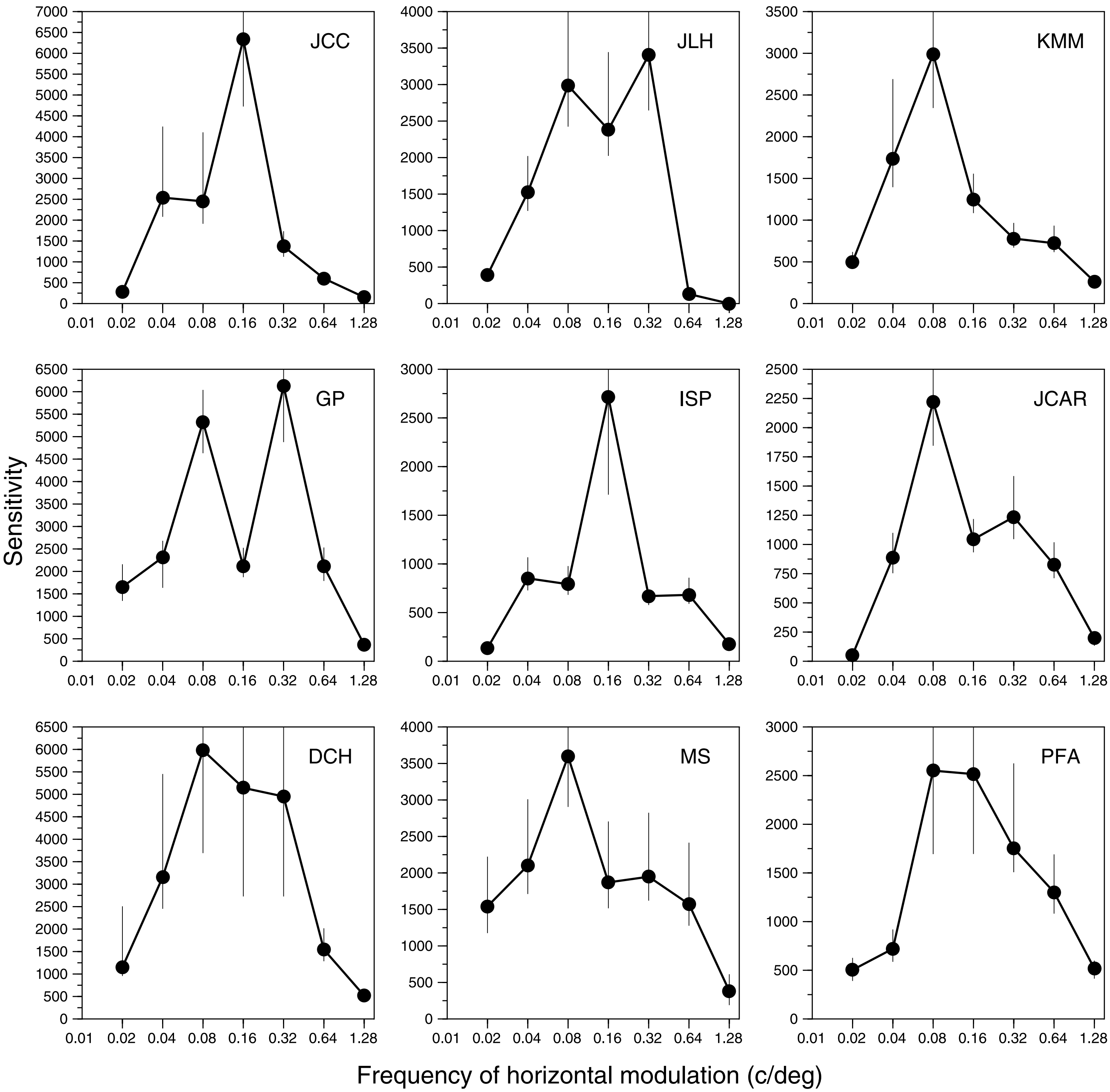

Figure 7. Results of horizontal magnification experiment (Experiment 1, Figure 4A). Sensitivity for square-wave corrugations as a function of the spatial frequency of the horizontal disparity modulation for nine subjects. Because individual subjects varied greatly in their sensitivity, note that different vertical axes are used for each subject. Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling. The viewing distance was 165 cm, and a orthogonality transformation was applied such that there were no vertical disparities on the retina, and the only horizontal disparities were those introduced by the magnification.

the stimulus contained several slats slanted in opposite directions, performance improved, before finally declining at still higher frequencies. Most subjects reach their peak sensitivity around 0.08–0.16 cycles/deg. For comparison, on a different but related task, Rogers and colleagues (Bradshaw & Rogers, 1999; Rogers &

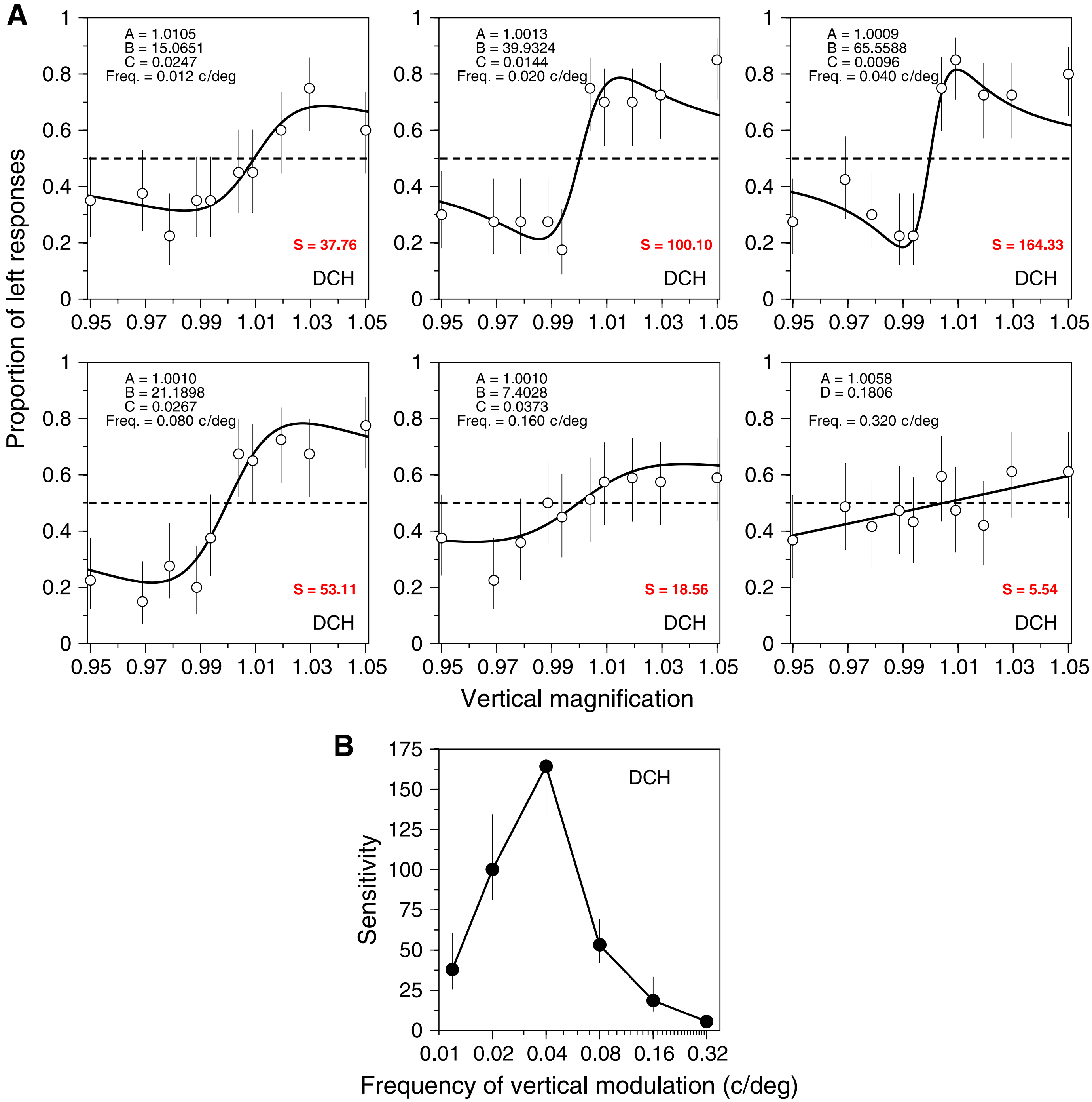

Figure 8. Results of Experiment 2 for the subject DCH. A) Each panel shows the proportion of left responses as a function of the vertical magnification and shows the results for a single spatial frequency (0.012, 0.02, 0.04, 0.08, 0.16, 0.36 cycles/degree) of the square-wave modulation of the vertical magnification. Two psychometric functions (one with two parameters and the other with three) were fitted to the data; only the best-fitted function (see text for details) is shown (black line). The value of the fitted sensitivity is printed in red on the lower right. B) Sensitivity of the subject for the square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation (black dots). Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling. The viewing distance was 165 cm, and a orthogonality transformation was applied such that there were no horizontal disparities on the retina, and the only vertical disparities were those introduced by the magnification.

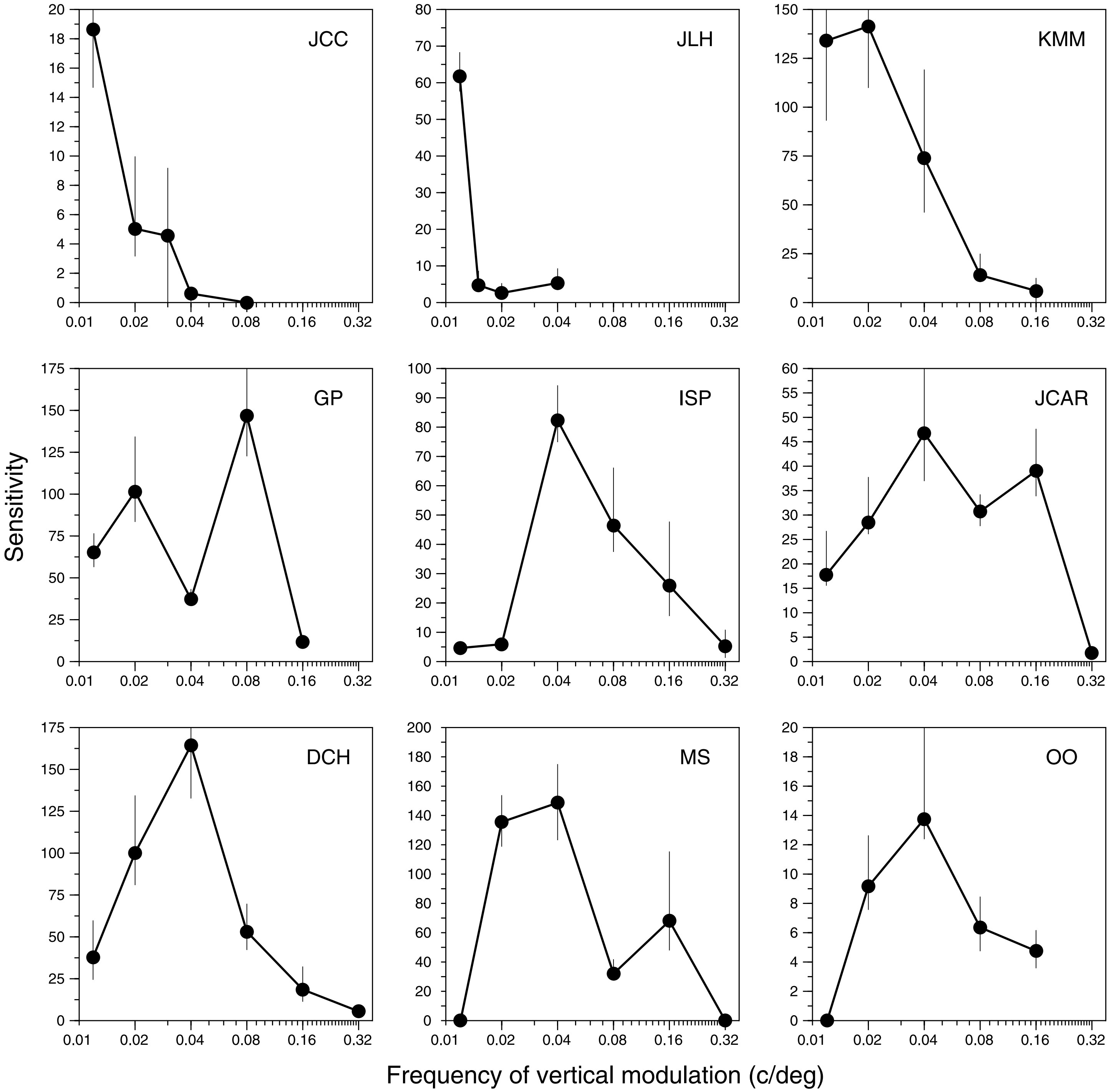

Figure 9. Results of vertical magnification experiment (Experiment 2). Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for nine subjects. Other details as for Figure 7.

Graham, 1982) found that sensitivity to horizontally oriented horizontal-disparity sine gratings peaked at around 0.2–0.5 cycles/deg.

A plausible explanation for this pattern is that it reflects the brain's specialization for relative horizontal disparities (Gillam, Blackburn, & Brooks, 2007; Gillam, Flagg, & Finlay, 1984; Hirsch & Weymouth, 1948; McKee, Welch, Taylor, & Bowne, 1990; Westheimer, 1979). Stereo vision is exquisitely sensitive to relative disparities between adjacent surfaces, but much less sensitive to absolute disparities (Erkelens & Collewijn, 1985; Regan, Erkelens, & Collewijn, 1986). In the same way, the percept of slant becomes much stronger when it is contrasted with opposite slant at a disparity boundary, than when disparity changes only gradually across the whole screen (Gillam et al., 2007). In our experiment, subjects were fixating at

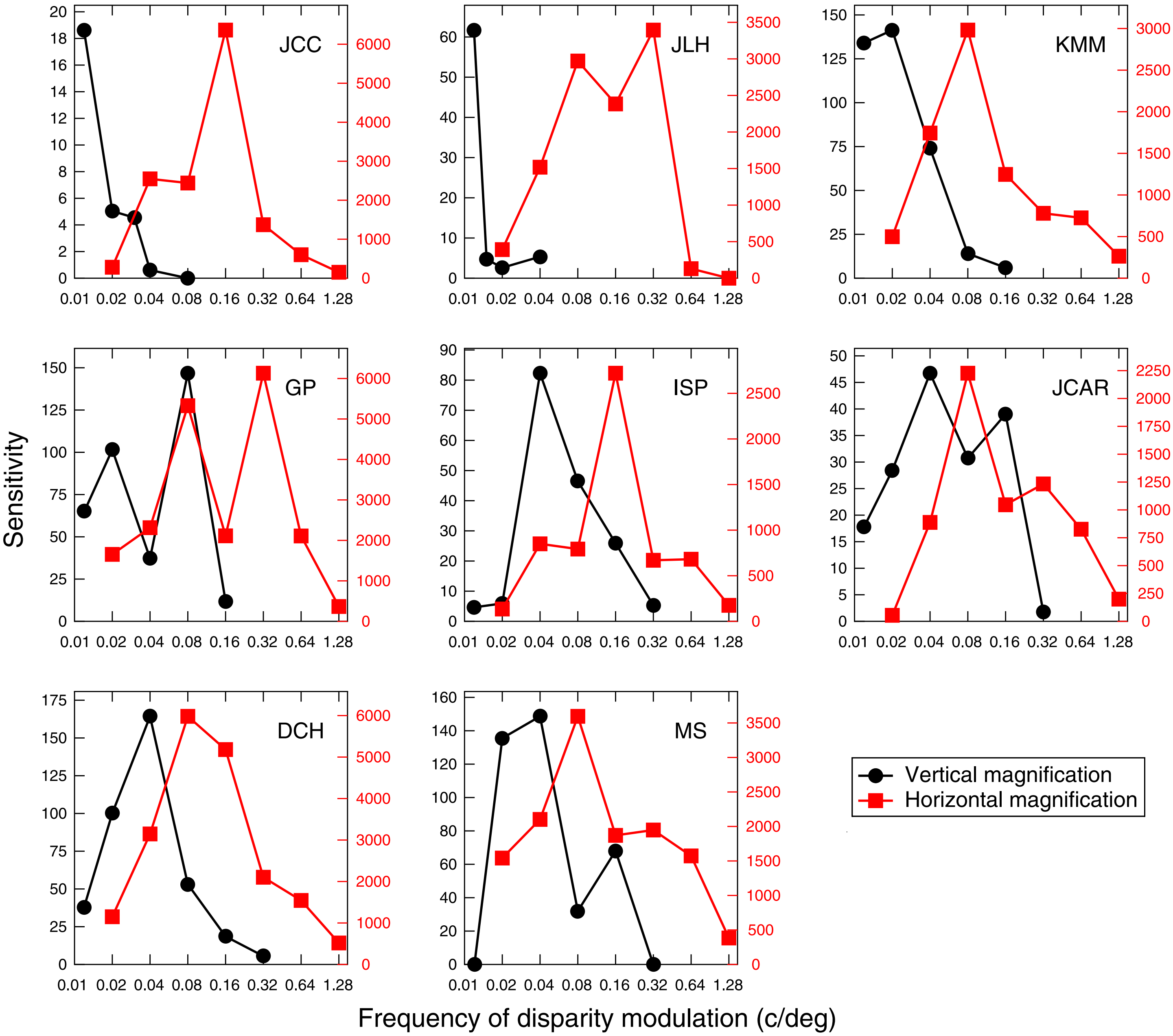

Figure 10. Results of Experiments 1 and 2 for all 8 subjects who could do the induced-effect task and who performed the horizontal disparity task. Performance is expressed as normalized sensitivity as a function of the spatial frequency of the vertical (black lines and circles) and horizontal (red lines and squares) disparity modulation. Note that the values of the ordinate axis are different for each condition (left values, vertical magnification; right values, horizontal magnification).

the center of the middle slat, so that as frequency was increased, the depth boundaries at the edges of this slat moved in from the periphery and thus aided perception. Performance began to decline only when the frequency was high enough that the width of a slat became comparable to the resolution with which horizontal disparity was encoded (Bradshaw & Rogers, 1999; Tyler, 1974, 1977). In other words, we interpret the high-frequency fall-off in Figure 7 as being due to the mechanism sketched in Figure 3 (signal being blurred by convolution with a finite-size sensor), whereas the low-frequency fall-off reflects the loss of specialized relative-disparity mechanisms which boost performance at intermediate frequencies.

Experiment 2: vertical magnification

We now move onto the analogous experiment in the vertical disparity domain. Here, vertical magnification alternated sign as a function of horizontal position on the screen, Figure 4B. Figure 8 shows complete results for

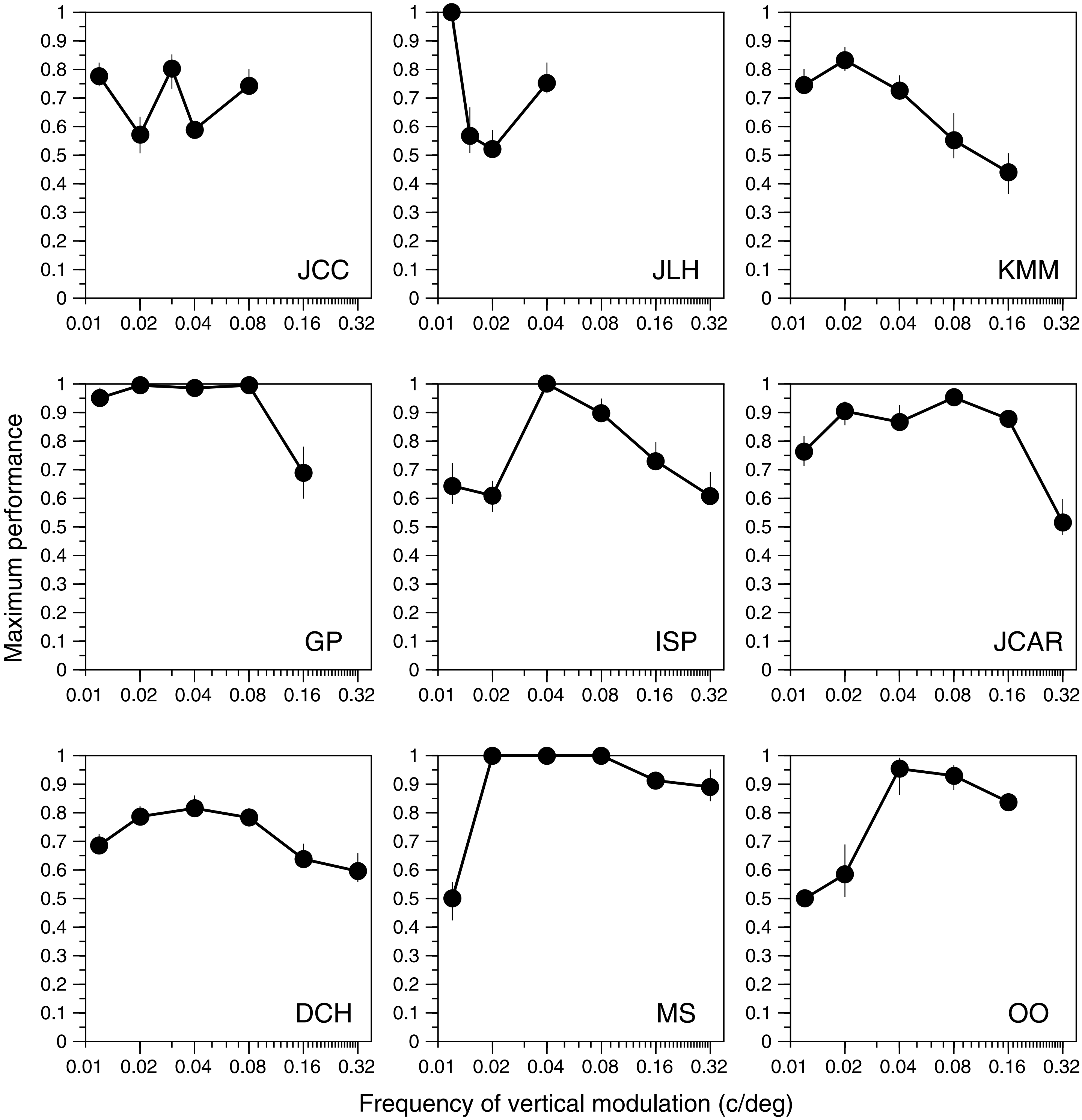

Figure 11. Results of Experiment 2 for 9 subjects who could do the induced-effect task, expressed as maximum performance reached for any magnification, as a function of the spatial frequency of the disparity modulation. For each frequency of the square-wave modulation, we plot the peak of the fitted function, i.e. our estimate of the best performance reached. 1 = 100% accuracy, i.e. the subject could always correctly detect the sign of magnification applied to the central strip; 0.5 = chance. Error-bars show the 70% confidence interval for maximum performance, estimated by bootstrap resampling.

one subject on this stimulus. The 6 panels in Figure 8A show the psychometric functions obtained for successively higher-frequency modulations of vertical disparity. Figure 8B shows fitted sensitivity as a function of spatial frequency.

Based on the published literature, we had expected this fitted sensitivity to resemble the function plotted in Figure 3. Performance would be best at the lowest frequency, where the vertical magnification was constant across the whole screen, simulating the effect of eccentric gaze. As frequency was increased, the finite resolution of vertical disparity encoding would start to impair performance, and sensitivity would fall. Thus, in contrast to the band-pass pattern with horizontal magnification (Figure 7), sensitivity to vertical magnification would have a low-pass function. Yet subject DCH does not show this pattern at all. It is very clear from Figure 8 that subject DCH performs better at intermediate frequencies than at low ones. At the lowest frequency used, the same magnification was applied to the entire screen, i.e. this was the classic induced effect. Here, the subject requires a magnification of some 3% to reach his best performance, and even then reaches only 80% correct. This poor performance is probably due to several factors, including (1) The short duration of the stimuli, only 200 ms, given that many authors have reported that the induced effect takes time to develop (Allison, Howard, Rogers, & Bridge, 1998; Kaneko & Howard, 1997; Ogle, 1938; Westheimer, 1984); (2) The long viewing distance, causing a greater cue-conflict with sensed vergence, since in natural viewing, large vertical disparities can occur only for converged eye positions (Backus & Banks, 1999; Read, Phillipson, & Glennerster, 2009); and (3) the large screen size, since as we show below, performance is better for narrower stimuli. However, what is striking is how, for the same viewing distance and stimulus duration, performance is improved as frequency increases. At the third frequency used, 0.04 cycles/deg, each “strip” of constant vertical magnification was just 12.5° across, so the central strip was flanked by two complete strips of the opposite magnification (Figure 5). Such a pattern of vertical disparities is, we believe, impossible under natural viewing conditions. Yet the subject’s sensitivity is improved. Now, he needs only 1% magnification to reach his maximum performance, although for the full-screen induced effect, this magnification was not enough to raise his performance above chance.

Several of our subjects showed the same band-pass pattern as DCH. Figure 9 summarizes the results of Experiment 2 for 9 subjects. Subject PFA was unable to perceive slant in the induced-effect stimulus at any spatial frequency, despite being a lab member with considerable experience of stereo psychophysics. His panel in Figure 9 is therefore replaced with data from subject OO, who had no previous experience of psychophysical experiments. 3 of our subjects (JCC, JLH, KMM) showed the low-pass pattern reported by Kaneko and Howard (1997). In these subjects, vertical magnification produced a percept of slant at low spatial frequencies, but as the frequency increased, either the level of performance fell, or the magnification required to maintain a given level of performance increased, so that the sensitivity to vertical magnification decreased. However, 6 of our 9 subjects showed a band-pass effect similar to that observed with horizontal disparity. Like DCH, they showed substantially greater sensitivity to vertical magnification when this alternated in sign across the screen than when it was constant, as in the classic induced effect. Figure 10 compares results on Experiments 1 and 2, by plotting sensitivity normalized so that 1 is the maximum sensitivity obtained for that direction of magnification. For all subjects, the frequency where maximum sensitivity occurs is less for vertical magnification than for horizontal magnification. For the 6 band-pass subjects, sensitivity to vertical magnification generally peaks near 0.04 cycles/deg, about half that observed for horizontal magnification.

Is the band-pass performance an artifact of how we have defined sensitivity?

As noted above, the psychometric functions for the induced effect often failed to reach 100% performance for any magnification. Thus, changing the frequency could improve performance in two ways. It might leave the best performance unchanged but reduce the magnification needed to achieve this. This would show up as an increase in the sensitivity plotted in Figures 7, 9 and 10. Alternatively, it might improve the peak performance achievable at any magnitude. An improvement of this kind would not necessarily show up as an increase in sensitivity. In the data of subject DCH (Figure 8), it is clear that changing the frequency from 0.012 cpd to 0.02 cpd produces both an increase in sensitivity and an increase in peak performance. Thus, for vertical magnifications, it is important to examine peak performance as well as sensitivity. In contrast, for horizontal magnifications, 100% performance was always reached (except for a few subjects at the very highest frequencies examined), so changing frequency affected only the sensitivity, i.e. the smallest magnification necessary to achieve 100% performance. Figure 11 shows how peak performance on Experiment 2 varies as a function of spatial frequency. Overall these functions show the same broad pattern as the sensitivity measure. The “low-pass” subjects who showed most sensitivity at the lowest frequencies (JCC, JLH, KMM) also tend to achieve the highest performance at low frequencies, while “band-pass” subjects who were most sensitive at intermediate frequencies (JCAR, DCH, ISP, GP, MS, OO) also reach their highest level of performance at these same frequencies. Thus, both sensitivity and maximum performance lead to the same conclusion: many subjects perform better on the vertical magnification task at intermediate than at high or low

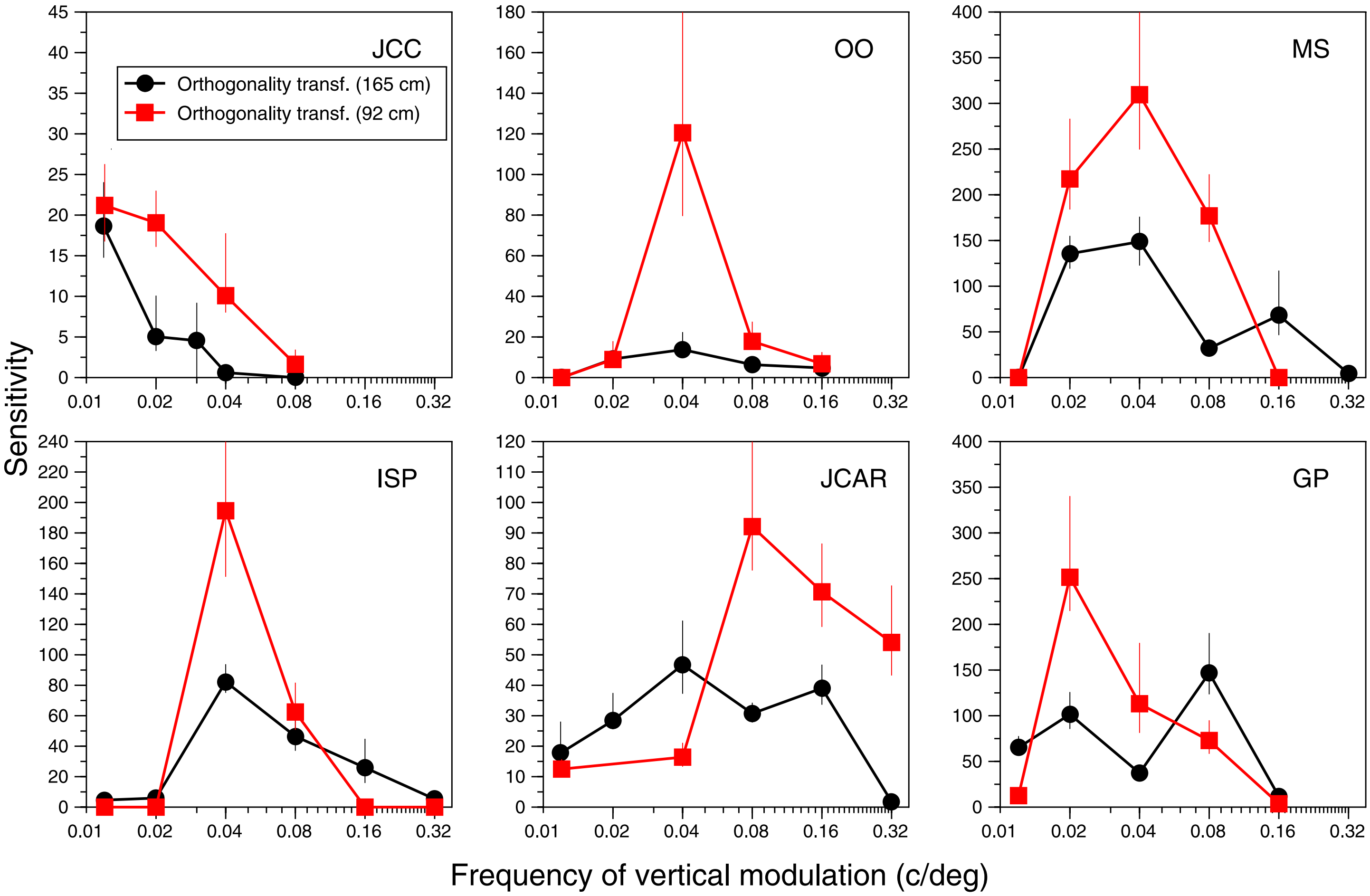

Figure 12. Results of Control Experiment 1. Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for 5 subjects in two conditions: with orthogonality transformation at 165 cm (simulating infinite viewing, black circles, data from Figure 9, Experiment 2). With orthogonality transformation at 92 cm (red squares, the width of the projected image was 71 cm). The angular size of screen, pixels, dots, and spatial periods were exactly the same in both viewing distances. The angle between the line of sight from each eye and its simulated screen was 90° in both experiments. Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling.

frequencies. This is a surprising result, given that uniform vertical magnification can occur in natural viewing, whereas we are not aware of any situation which could produce the uniform-magnitude, alternating-sign vertical magnification of our stimuli. For this reason, we carried out several tests to investigate whether the band-pass pattern observed in Figure 9 was genuine, or reflected some artifact of our original experiment.

Some possible artifacts and simple controls

An obvious concern is whether subjects are using some other cue than vertical disparity, e.g. dot density. This is unlikely, since subjects were not given feedback, and so had no opportunity to learn to use cues other than those which produce a sensation of slant. For two subjects, we verified that they could not perform better than chance when viewing the stimuli monocularly. Another concern was whether misalignment between the two projected images could somehow be responsible. The alignment between our images is not perfect; in particular there are gradients of disparity which convert perfect alignment at the center of the screen to mismatches of up to 2 pixels at the edges. However, it is not clear how these could artifactually produce a bandpass pattern of results. A disparity gradient due to misalignment simply adds on a small artifactual slant to the screen. This could produce a small shift in the point of subjective equivalence, but could not boost performance at high frequencies relative to low ones. Nevertheless, as an additional control two subjects performed the task using a single projector with red/blue anaglyph. We use single-chip Digital Light

Processing projectors, in which each pixel corresponds to one mirror in the array, and its color is determined by which filter on the colorwheel is currently in the path of the light-beam. Thus, different colors are presented at very slightly different times, but in exactly the same position on the screen. The use of anaglyph therefore removes any misalignment between the two images. For the two subjects tested, the band-pass pattern persisted exactly as before.

Because our experiments used short durations, it is unlikely that vertical vergence movements are involved, and none were apparent with the nonius lines.

As shown in Figure 4, we used vertical lines to demarcate the central strip about which subjects were asked to make a slant judgment. This was necessary to avoid the subject accidentally reporting slant in the wrong region of the screen, but obviously meant that as spatial frequency varied, our stimuli differed not only in the vertical magnification pattern, but also in the position of the white lines. The lines always had zero horizontal disparity on the screen, so it seems unlikely that they could aid in making a depth judgment. However, in order to check, we examined performance for two band-pass subjects on the full-screen stimulus (0.012 cycles/deg), while displaying the white lines in the position they would normally have for 0.04 cycles/deg, where these subjects performed much better. The presence of the lines made no significant difference to performance; if anything, the lines slightly impaired accuracy, presumably because their zero disparity weakened the slant percept introduced by the uniform vertical magnification. This confirms that the line position is not responsible for the improved performance at intermediate frequencies.

These checks gave us confidence that our results are not due to some unintended property of our stimulus resulting from an artifact of our experimental apparatus. In the following control experiments, we probed how the known properties of our stimulus might contribute to this novel band-pass pattern.

Control Experiment 1: Shorter viewing distance, same image angular size

Backus and Banks (1999) have shown that estimates of surface slant from vertical magnification become less reliable as viewing distance increases. Our experiments used a long viewing distance, 165 cm, which we suggested is a likely reason for the poor performance of our subjects on the classic induced effect stimulus. This raises the question of whether substantially different results would have been obtained at a shorter viewing distance. We thus repeated Experiment 2 with 6 subjects at a viewing distance of 92 cm, similar to the 94 cm used by Kaneko and Howard (1997). As well as moving the observer closer to the projection screen, we also moved the projectors closer on the other side, so as to maintain the angular size of the image at 42° × 32°. The angular size of pixels, dots, spatial periods, etc, were thus all exactly the same in both viewing distances. Due to the finite zoom range of the projectors, 92 cm was the shortest viewing distance for which this could be achieved. The results are shown in Figure 12, red squares. The black circles replot the results at 165 cm, previously shown in Figure 9.

As expected, the shorter viewing distance has increased sensitivity at almost all frequencies. Since the angular size of the image, the dot density, etc are all exactly the same, we attribute this strengthening of the induced effect to the change in sensed vergence. Backus and Banks (1999) suggest that this occurs because at short distances, vertical magnification becomes a more reliable cue to surface slant than sensed vergence.

However, the change in vergence has not altered whether subjects show a low-pass or band-pass pattern of results. Intriguingly, for all subjects, the increase in sensitivity is strongest at intermediate frequencies, meaning that the band-pass pattern of results is actually enhanced at a viewing distance of 92 cm.

Control Experiment 2: No orthogonality transformation

It is important to distinguish between vertical disparity experienced on the retina, and vertical disparity applied to the screen (Read et al., 2009). Vertical disparities on the retina were defined in Figure 1. As that figure shows, such disparities occur naturally in normal viewing (Longuet-Higgins, 1982; Rogers & Bradshaw, 1993). However, in the literature the term "vertical disparity" is often used to refer to shifting left and right image-points vertically on a screen frontoparallel to the observer (head-centered vertical disparity in Helmholtz coordinates; see (Read et al., 2009) for further discussion). These disparities are "unnatural" in that they could not be produced by any physical object, given the current eye position. Such disparities are referred to in the literature as *non-epipolar*.

In Experiments 1 and 2, we minimized the distinction between retinal and on-screen vertical disparity by using a large viewing distance. Objects at infinity viewed with zero convergence never produce vertical disparity on the retina under natural viewing conditions, so any vertical component of their retinal disparity is non-epipolar. Under these conditions, applying vertical disparity to the stimulus on the screen automatically produces the same vertical disparity on the retina, without introducing any horizontal component. In our lab, we could not arrange for viewing at infinity, but the orthogonality transformation we applied ensured that the stimuli produced purely vertical disparities on the retina (in elevation-longitude coordinates (Read et al., 2009)), as in Backus and Banks (1999) and other studies from the Banks lab. However, the orthogonality transformation did not change the actual,

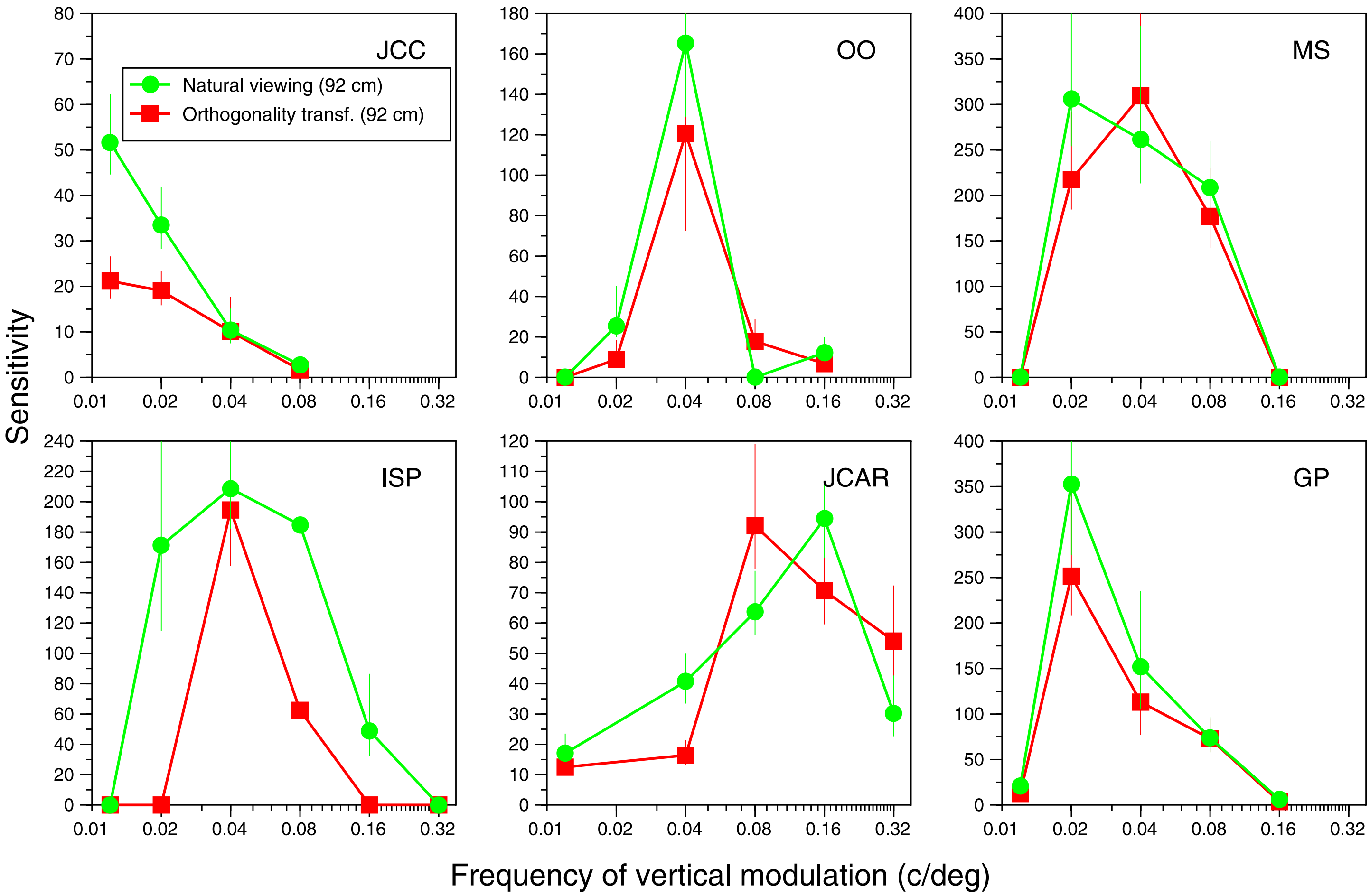

Figure 13. Results of Control Experiment 2. Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for 6 subjects in two conditions: With orthogonality transformation (red squares, data from Figure 12, Control Experiment 1); without orthogonality transformation (green circles). The width of the projected image was 71 cm for both experiments and the viewing distance was 92 cm. The angle between the line of sight from each eye and its simulated screen was 90° with the geometrical correction, and 88° without it. Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling.

physical convergence. Since the eyes are (slightly) converged, (small) vertical retinal disparities occur in natural viewing. The purely vertical retinal disparities produced by our stimulus thus have some small epipolar component. We deliberately made the viewing distance large in order to minimize this.

For the shorter viewing distance used in Control Experiment 1, this epipolar component becomes more important. In natural viewing at 92 cm, retinal disparities can have a measurable vertical component. Thus, the vertical retinal disparities we introduced by our magnification contained a non-zero epipolar component. Conceivably, if the visual system encodes disparity in epipolar coordinates, this small epipolar component could have been driving the band-pass response. That is, the visual system may be sensitive to discontinuities in epipolar disparity, not to discontinuities in vertical disparity per se.

To address this, in Control Experiment 2, 6 subjects repeated the experiment at 92 cm without the orthogonality transformation. That is, corresponding dots were at the same horizontal position on the screen in each eye, and differed only in their vertical position, as in (Kaneko & Howard, 1997; Ogle, 1938). This manipulation produces both horizontal and vertical disparities on the retina, but importantly, all disparities will be non-epipolar: This stimulus contains no epipolar components of disparity. The results are shown in Figure 13, green circles; the red squares reproduce the results with the orthogonality transformation from Figure 12. Clearly, the presence or absence of the orthogonality transformation makes no difference to our results. This is in agreement with our previous study of the standard induced effect (Serrano-Pedraza & Read, 2009), which showed that the orthogonality transformation made no difference at a viewing distance of 165 cm. We conclude that the slant percept is driven by vertical disparities on the retina, and does not depend critically on the presence or absence of a small horizontal or epipolar component.

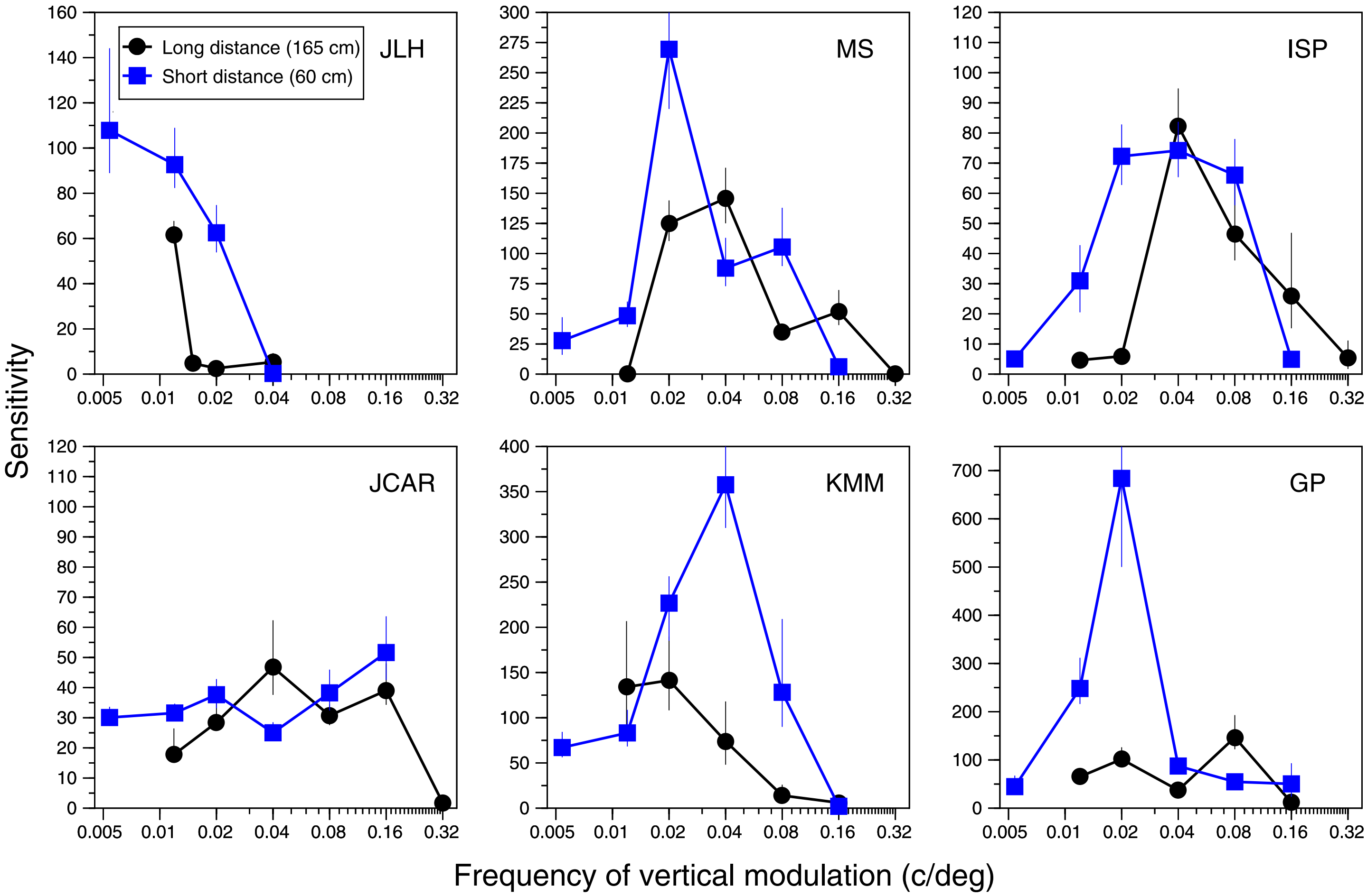

Figure 14. Results of Control Experiment 3. Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for 6 subjects in two conditions: with orthogonality transformation at 165 cm (black circles, data from Figure 9, Experiment 2); with orthogonality transformation at 60 cm (blue squares). The width of the screen was 127 cm for both experiments. The angle between the line of sight from each eye and its simulated screen was 90° in all experiments. Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling.

Control Experiment 3: Extending to lower frequencies

Bradshaw and Rogers (1999) discussed a potential artifact which might produce a fall-off in measured sensitivity at low frequencies. For sinusoidal horizontal disparity corrugations at low frequencies, there may be less than a cycle present on the screen. This presents obvious problems, since it reduces the total peak-to-trough amplitude of the variation in horizontal disparity. There are a number of reasons for believing that this artifact is not a concern in our experiment. We used square-wave magnification profiles, so the magnification is constant across half a cycle. The full amplitude from positive to negative magnifications is thus present in the second-lowest frequency we used, while the performance of all band-pass subjects continues to rise. Second, vertical disparity per se (as opposed to vertical magnification) does not produce any depth percept (Read & Cumming, 2006). Thus, although for a given vertical magnification, a larger stimulus will reach larger vertical disparities at the top and bottom of the stimulus, it is not clear why this should improve perception. This is different from slant produced by horizontal magnification, since there, the horizontal disparities necessarily introduce a depth which grows steadily as one moves away from the center of the stimulus. Thus, a horizontal magnification which is subthreshold for small stimuli might become suprathreshold for large stimuli, as the left and right edges of the stimuli acquire a perceptible horizontal disparity.

However, to make sure, 6 subjects re-ran Experiment 2 at a shorter viewing distance, 60 cm. This time we did not move the projectors closer, meaning that while the physical size of the projected image remained constant (127 cm full-width), it now subtended a larger angular size, 93°, allowing us to investigate lower frequencies

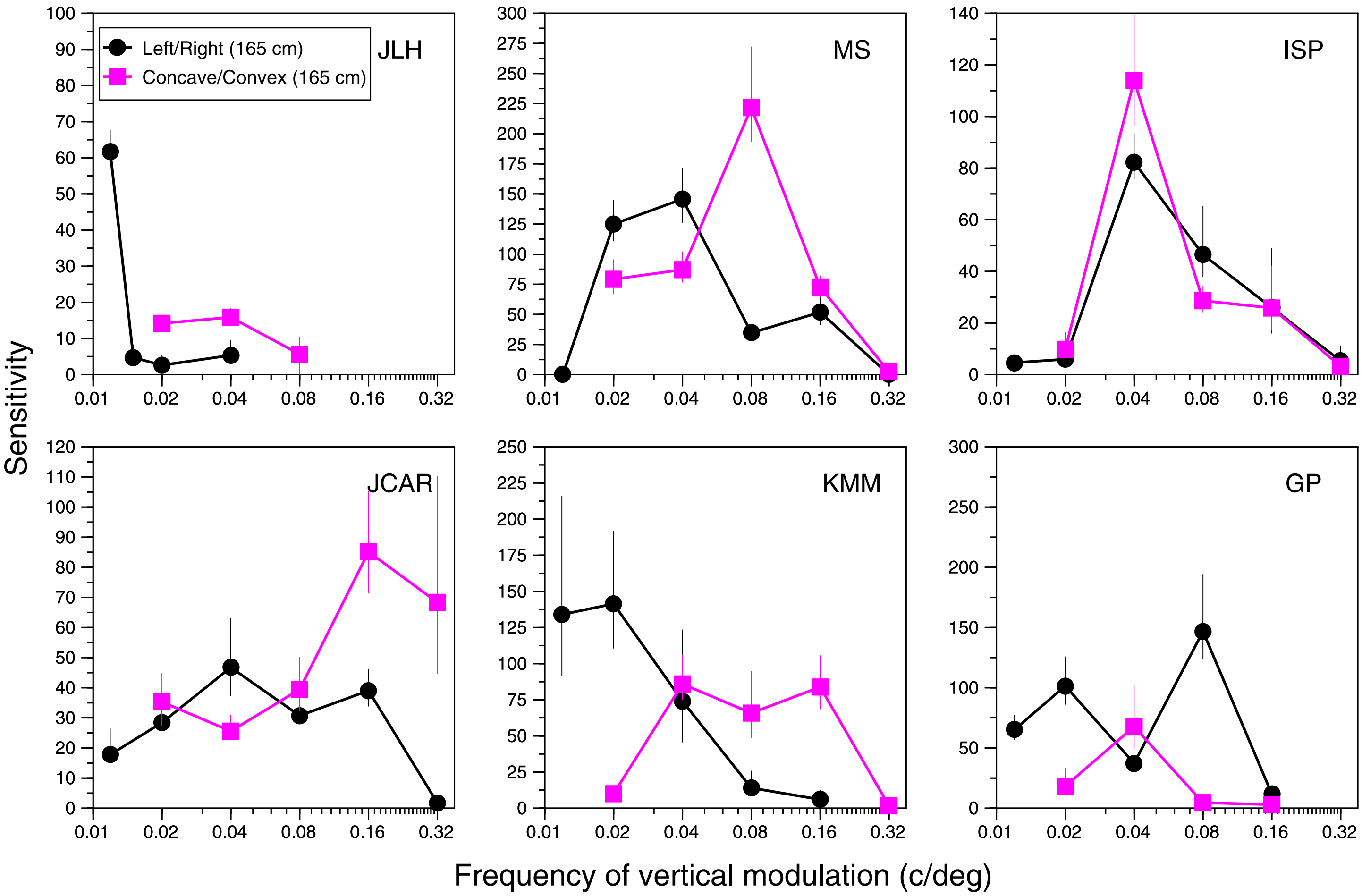

Figure 15. Results of Control Experiment 4. Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for 6 subjects in two conditions: with orthogonality transformation at 165 cm (black circles, data from Figure 9, Experiment 2, Left/Right task); Concave/Convex task at 165 cm (purple squares), The angle between the line of sight from each eye and its simulated screen was 90° in all experiments. Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling.

(0.0054 c/deg). The same stimulus code was used, meaning that the stimulus was the same in pixels; thus, the dots were larger in degrees.

Figure 14 shows the results (blue squares) superimposed on those for Experiment 2 (black circles). Once again, performance is generally slightly better at the shorter viewing distance, although this effect is less marked than in Control Experiment 1 (Figure 12), presumably reflecting the other changes in the stimulus (dot size, density, larger angular extent, greater number of cycles etc). However, critically, the band-pass pattern persists. The sole low-pass subject who performed this experiment, JLH, remains low-pass. At a frequency of 0.012 cycles/deg, he performs slightly better at 60 cm than at 165 cm in Experiment 2, even though the central 42°-wide strip of constant magnification is now flanked by two strips of opposite magnification. But when the central strip is extended to cover the entire 93° extent of the screen (frequency 0.0054 cycles/deg), his performance rises still further. This confirms the previous results that, for JLH, changes in vertical magnification sign impair performance.

However, most subjects show an even clearer band-pass pattern with this stimulus than in the original experiment. Subject KMM, who showed a low-pass pattern in the initial Experiment 2, now shows very pronounced band-pass performance. Subject JCAR now has a rather flat pattern of performance, but all the other subjects show a clear drop in sensitivity moving from 0.012 cycles/deg down to 0.0054 cycles/deg. Thus, this control experiment rules out the possibility that the band-pass pattern in the original experiment was due to an artifact connected to the reduced number of cycles at low frequencies.

Control Experiment 4: Discontinuity on midline

Kaneko and Howard (1997) performed their experiment for two phases of the sine-wave pattern of magnification.

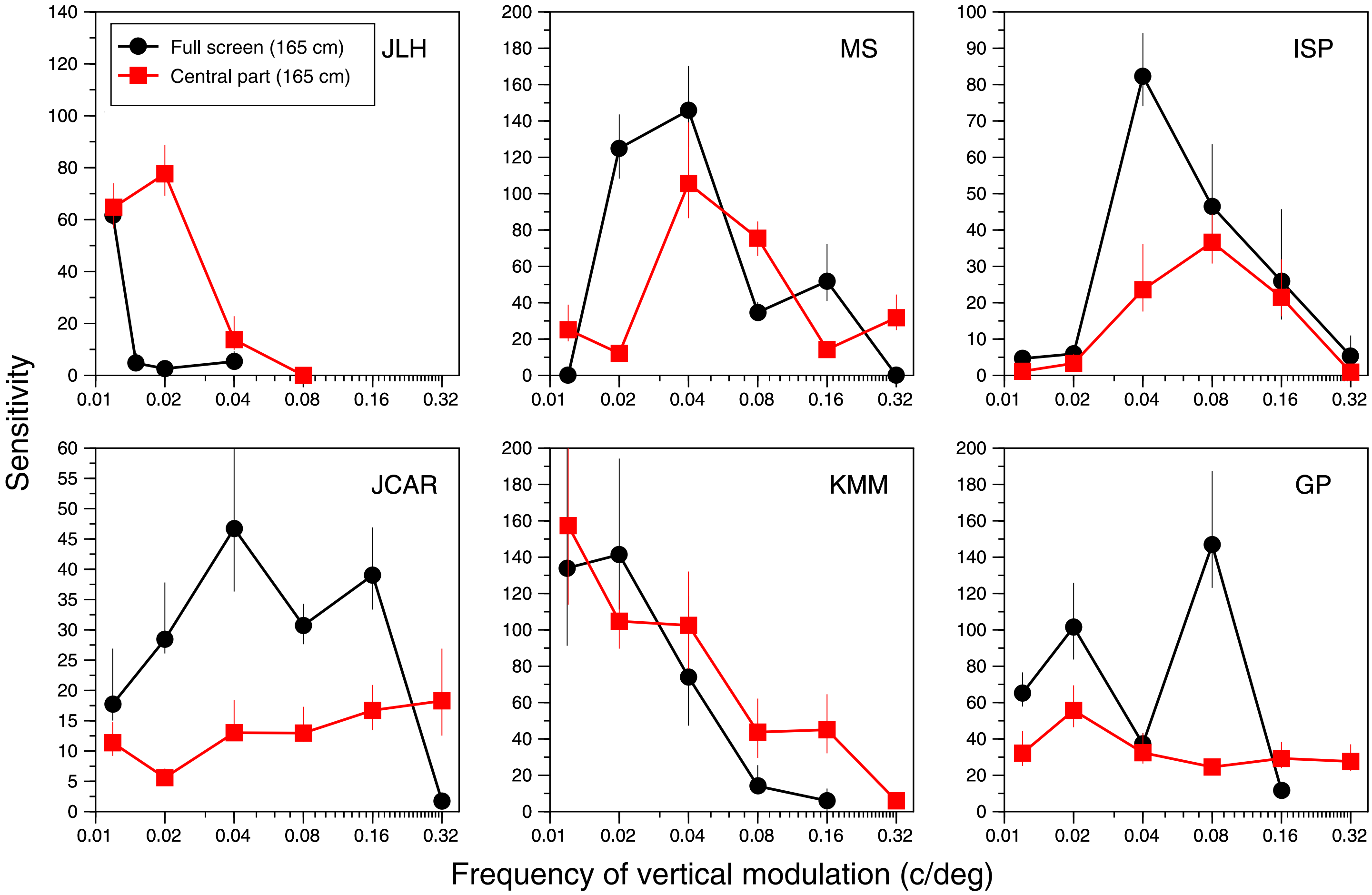

Figure 16. Results of Control Experiment 5: central-strip only (red). Sensitivity for square-wave corrugations as a function of the spatial frequency of the vertical disparity modulation for six subjects in two conditions: Corrugations covering the whole screen (black circles, data from Figure 9, Experiment 2); same corrugations but only the central part of the stimulus was presented (red squares). Error-bars show the 70% confidence interval for sensitivity, estimated by bootstrap resampling.

In one version, the changes in vertical disparity sign occurred on either side of the midline, as in our Experiment 2. They also show results for when the sign-change occurred on the midline, through fixation. In this case, subjects were asked to report whether the center of the stimulus appeared convex or concave. (A puzzling aspect of their results is that they report thresholds for frequency zero, "uniform vertical size-disparity," for both phases of the sine-wave. It is not clear how these differed). We wondered whether the band-pass pattern was dependent on the particular task we used. We therefore repeated Experiment 2, this time placing a vertical-magnification sign-change on the midline. The lowest effective frequency was when the magnification was constant in each half of the screen (Rogers & Koenderink, 1986). Following our practice of labeling each stimulus by the highest notional frequency which could produce that image (see Stimuli), we defined this as being $f = 1/W$, twice the lowest frequency in Experiment 2.

Results are shown in Figure 15, pink squares; the black circles, as usual, reproduce the original results from Experiment 2. The only change is that subject KMM, who was low-pass in Experiment 2, now displays a band-pass pattern of results. Subject JLH remains low-pass, and all other subjects remain band-pass. Thus, Control Experiment 4 shows that the band-pass pattern observed in most subjects does not depend on the precise details of the perceptual judgment required.

Control Experiment 5: Only central strip present

The experiments presented so far suggested to us that discontinuities in vertical magnification aid slant discrimination. As a test of this, we compared performance on a stimulus which lacked such discontinuities. The stimulus in this experiment was identical to Experiment 2 in between the white lines marking the central strip, but beyond this, the screen was black. This is therefore a standard induced effect stimulus, with stimulus full-height constant at 32°, and stimulus full-width varying from a maximum of 42° down to a minimum of just 1.6°. Figure 16 compares the results of the 6 subjects who performed this experiment (red squares) with their results on Experiment 2 (black circles), in which the central strip was flanked by alternating regions of opposite magnification. At the lowest frequency (0.012 cycles/deg), the central strip covered the whole screen, and thus the two experiments were identical. Any differences here thus reflect fluctuations in performance over time/practice effects etc. For most subjects, these differences were small.

For the low-pass subject JLH, removing the flanking regions improved performance at all frequencies. This confirms our previous conclusion that, for this subject, vertical magnification discontinuities impair slant perception. For subject KMM, who was low-pass in the original Experiment 2 but band-pass in Control Experiments 3 and 4, the manipulation made little difference to performance. For the remaining subjects, all of whom were band-pass in Experiment 2, removing the flanking regions impairs performance. That is, these subjects' performance on a standard induced-effect stimulus can be improved by adding flanking regions of alternating vertical magnification, even though such a pattern of vertical disparity cannot be produced by any natural stimulus we are aware of.

Discussion

The original motivation for this work was the desire to establish the resolution with which vertical disparity is encoded. Following in the footsteps of Kaneko and Howard (1997), we examined subjects' ability to discriminate the sign of slant due to vertical magnification, in stimuli divided into strips of alternating vertical magnification sign. Performance will fall to chance once the width of each strip becomes small compared to the spatial resolution with which the visual system extracts vertical disparities. Consistent with previous reports (Gårding et al., 1995; Kaneko & Howard, 1997; Rogers & Koenderink, 1986; Stenton et al., 1984), we found that this high-frequency limit was much lower for vertical magnification than for horizontal. We did not rigorously pursue the high-frequency limit on the horizontal-magnification task, but most of our subjects were still able to do the task at 1.28 cycles/deg, whereas only a few were above chance at 0.32 cycles/deg for vertical magnification. Other workers have found that sinusoidal disparity gratings can be perceived up to ~4 cycles/deg (Banks et al., 2004; Harris, McKee, & Smallman, 1997; Rogers & Graham, 1982; Tyler, 1974). Thus, we confirm previous reports that spatial stereoresolution is considerably worse for vertical than for horizontal disparity.

To quantify this, we assume that the vertical magnification signal is blurred by convolution with a Gaussian of standard deviation σ (Figure 3), and define the width of the regions across which vertical disparity is pooled as $w = 2\sigma$. According to this model, the signal falls to 10% of its maximum value at a frequency $f_{10} = 0.35/\sigma$. For the performance measure used by Kaneko and Howard (1997), the threshold magnification required to reach 75% correct, f_{10} would be where threshold rises to 10 times its smallest value. For Kaneko and Howard's two subjects, f_{10} is about 0.04 cycles/deg, resulting in their estimate of ~20° for the width of vertical disparity pooling. For our 3 low-pass subjects, very rough estimates are $f_{10} = 0.03, 0.012, 0.08$ cycles/deg respectively (top row in Figure 9), resulting in the following estimates of pooling width: $w = 0.7/f_{10}$: 23°, 58°, 9°. These are broadly in line with previous estimates of ~14° (Adams et al., 1996) or 20~30° (Kaneko & Howard, 1996).

However, our remaining six subjects (bottom two rows in Figure 9) show a clear band-pass pattern of performance: their sensitivity on this slant discrimination task is greater at intermediate frequencies than at low or high. This means that they perform better on a stimulus which contains alternating regions of opposite vertical magnification than on the classic induced-effect stimulus where magnification is constant across the screen. We assume that the high-frequency fall-off is set by spatial pooling, as in Figure 3, but now there is some additional effect either impairing their performance at low-frequencies, and/or boosting their performance at intermediate frequencies. This is puzzling, because uniform vertical magnification occurs naturally for eccentric gaze (Gårding et al., 1995; Gillam, Chambers, & Lawergren, 1988; Longuet-Higgins, 1982; Mayhew & Longuet-Higgins, 1982; Read & Cumming, 2006; Rogers & Bradshaw, 1993), whereas we are not aware of any stimulus which could produce the alternating pattern in our higher-frequency stimuli. It is therefore remarkable that, for most subjects, performance should be better for the latter.

Given, this, we have been at pains to establish that this band-pass pattern is not due to some peculiarities of our experimental apparatus or task. The use of naïve subjects who were simply asked to report perceived slant and not given any feedback makes it unlikely that subjects could have used some cue unrelated to disparity. We have verified that subjects cannot perform the task monocularly, and that the band-pass pattern persists when the stimulus is presented in anaglyph. We have conducted a range of control experiments varying the viewing distance, stimulus geometry and task. None of these have abolished the band-pass pattern; several have strengthened it.

Our results suggest that discontinuities in vertical disparity actively improve performance. That is, the visual system appears to benefit from relative vertical disparities as well as from horizontal ones (Gillam et al., 2007; Westheimer, 1979). Previous workers have suggested that the visual system simply pools vertical magnification over finite regions, and uses the average vertical magnification

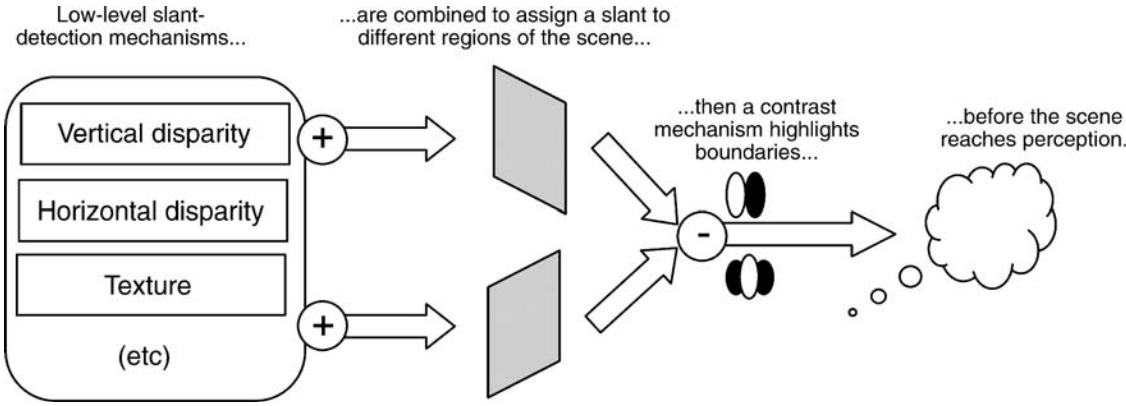

Figure 17. Cartoon of a possible set of computations which could produce the observed band-pass pattern. Vertical disparity is just one of several cues which can cause a surface to be assigned a local slant. Before this low-level signal reaches perceptual awareness, it is subject to a subtractive "contrast" operation which boosts the signal at slant boundaries.

within this region to calibrate the depth percept produced by horizontal disparity (Adams et al., 1996; Gårding et al., 1995; Stenton et al., 1984). In this picture, the "receptive field" for vertical magnification is a Gaussian or other low-pass function (Figure 3). Our results, in contrast, suggest that at least some vertical-magnification receptive fields must be band-pass, e.g. with two regions of opposite sign, or a central region flanked by side-lobes of opposite sign. This is a surprising conclusion. We can only sketch a few possible interpretations.

First, these "receptive fields" may not encode vertical magnification per se, but slant more generally. The mechanisms underlying slant perception may include a form of "slant contrast" which operates independently on the source of the signal indicating the slant. Several workers have found evidence for such mechanisms (Allison, Rogers, & Bradshaw, 2003; Gillam et al., 2007; Gillam et al., 1984). This idea is sketched in Figure 17. On the left, several possible low-level signals are shown, which are used to assign a slant to each region in the scene. However, before this slant signal reaches the level of conscious awareness, it is subject to a "contrast" mechanism which computes differences between the slant of adjacent regions and thus highlights object edges. This would correspond to the band-pass "receptive fields" implied by our results. However, in this picture they would be receptive fields for surface slant irrespective of cue, rather than specifically for vertical disparity. By hypothesis, this mechanism would tend to enhance performance when slant boundaries are present. Such a model might be able to explain our band-pass pattern of results, even if vertical magnification is simply pooled over a finite region at the low-level slant-assignment stage (Adams et al., 1996; Gårding et al., 1995; Stenton et al., 1984). A potential challenge is that, under this hypothesis, the low-level slant signal from vertical magnification would grow weaker as spatial frequency increased. To explain the band-pass results, the enhancement provided by the high-level slant-discontinuity detectors would have to more than compensate for this reduction in the low-level signal.

If it exists, this high-level subtractive mechanism would also contribute to the band-pass pattern observed with horizontal magnification (Experiment 1, Figure 7). However, in the case of horizontal disparity it seems clear that low-level, cue-specific mechanisms make an additional contribution. Early visual cortical areas contain neurons which are selective for discontinuities in horizontal disparity (Bredfeldt & Cumming, 2006; von der Heydt, Zhou, & Friedman, 2000), in that they respond better to step changes in horizontal disparity than to any uniform horizontal disparity. Their response can be well modeled by a subtractive operation between V1 neurons which compute local absolute disparity (Bredfeldt, Read, & Cumming, 2009; Parker, 2007; Thomas, Cumming, & Parker, 2002). These mechanisms may explain why, for example, our subjects JCC, JLH and KLM show a band-pass pattern for horizontal magnification and not for vertical (Figure 10). Similarly, some of the 4 subjects in Allison et al.'s (2003) Experiment 2, examining relative slant between adjacent surfaces, perceived a greater difference for "twist" configurations involving a horizontal-disparity discontinuity, than for "hinge" configurations where there was no discontinuity. It is possible that some subjects possess an analogous mechanism for vertical disparity, e.g. neurons tuned to sharply different vertical disparities in different subregions of their receptive field.

This might seem unlikely, since most authors state that vertical disparity varies only slowly across the visual field (Gårding et al., 1995; Read & Cumming, 2006; Rogers & Bradshaw, 1993; Stenton et al., 1984). However, discontinuities in vertical disparity do occur in natural viewing. Figure 18 shows an example. This is the same situation shown in Figure 2, except for two changes designed to enhance vertical disparity discontinuity: the far surface is now at 50 cm, not 39 cm, and the eyes are looking 15° off

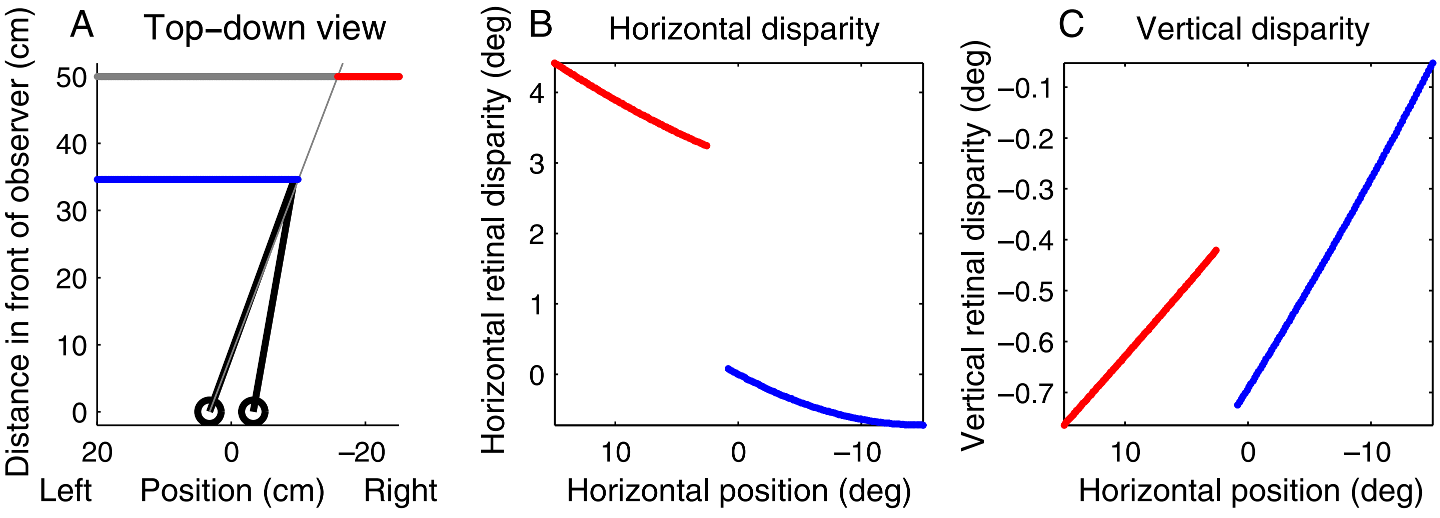

Figure 18. Depth boundaries cause discontinuities in vertical as well as horizontal disparity. As Figure 2, except the distant surface is further away, and the eyes are in eccentric gaze.

to the right. Now, at the boundary between the near and far surfaces, there is a step change in both horizontal and vertical disparity. The horizontal disparity jump is an order of magnitude larger than the vertical disparity jump (3° vs. 0.3°), but nevertheless, the scene structure is visible in the vertical disparity field as well as the horizontal disparity field. Previous authors have stressed the fact that vertical disparity is unaffected by small depth steps near fixation, such as that between the surfaces at 37 cm and 39 cm in Figure 2, but have not pointed out that vertical disparity does reflect larger steps such as the jump from 35 cm to 50 cm in Figure 18. If the visual system represents vertical disparity in the Fourier domain, as suggested for luminance (Campbell & Robson, 1968) and horizontal disparity (Brookes & Stevens, 1989; Lunn & Morgan, 1995; Rogers & Graham, 1982; Schumer &

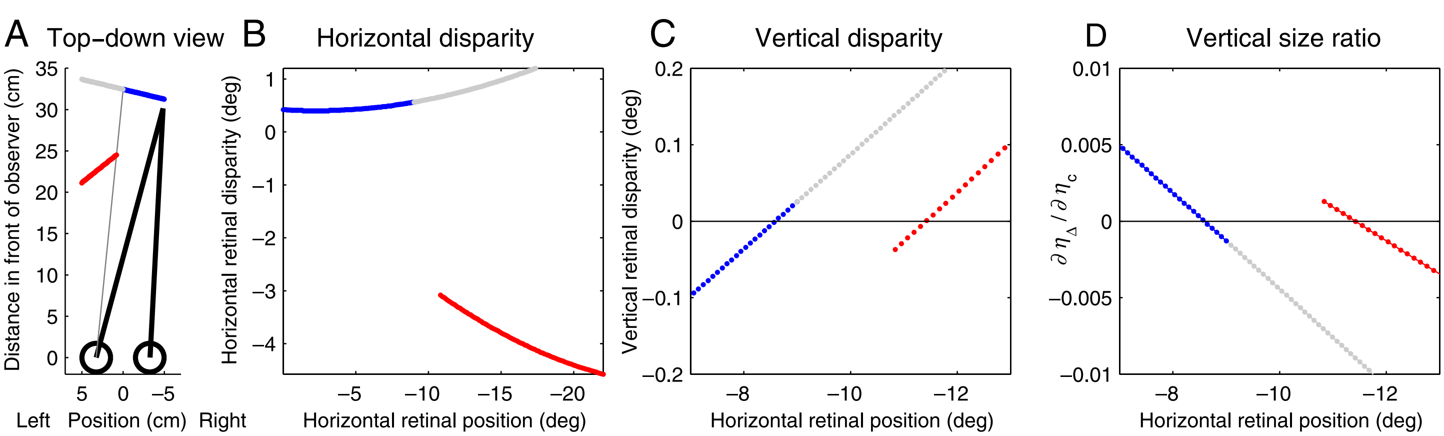

Figure 19. Depth boundaries can cause sign changes in vertical disparity and vertical size ratio. Here, a different stimulus and viewing geometry are shown. Panels A–C are as in Figure 2. Once again, colored regions represent points viewed binocularly; gray shows regions which are occluded from one eye. In B–D, gray points represent disparities which the blue surface would have at that position, if it were not occluded by the red surface. Panel C shows vertical retinal disparity η_Δ, defined in the notation of Read et al. (2009) as the difference in the elevation-longitude coordinates of the projections onto the two retinas. Panel D shows the first derivative of this with respect to vertical position on the retina. This panel was generated by considering two rows of points on the surface, one row 10 cm above the plane of fixation (as used in panels B and C), and one very slightly higher, at 10.02 cm. The difference in Y coordinate produced a slightly different vertical position on the retina, $\delta\eta_c$, and also very slightly different vertical disparities, $\delta\eta_\Delta$. The ratio of these differences was taken as an estimate of the first derivative, $\partial\eta_\Delta/\partial\eta_c$. This quantity, known as vertical size ratio in the literature (Backus et al., 1999; Brenner et al., 2001; Rogers & Bradshaw, 1993, 1995), was artificially manipulated in our experimental stimuli by applying a dichoptic vertical magnification.

Ganz, 1979), then sensors tuned to a range of frequencies would be needed to represent vertical disparity steps like that in Figure 18C.

Figure 19 shows the disparity pattern produced by another possible visual scene. This example is particularly relevant to our results, since here both vertical disparity (Figure 19C) and its first derivative with respect to vertical position (Figure 19D) change sign at the boundary between two surfaces. This derivative corresponds to the ratio of the vertical sizes of corresponding features in the two eyes' retinal images (Backus et al., 1999; Brenner, Smeets, & Landy, 2001; Read et al., 2009; Rogers & Bradshaw, 1993, 1995). Vertical size ratio (VSR) arises in natural viewing when surfaces are slanted relative to the gaze axis, and was introduced artificially in our stimuli by the vertical magnification. Figure 19 is of interest because it demonstrates that, even in natural viewing, it is possible for VSR to change in sign at a depth boundary. If some subjects have developed specialized neuronal mechanisms to detect these naturally occurring discontinuities in VSR, this could perhaps explain why they performed better when VSR discontinuities were introduced artificially by alternations in magnification.

Our results potentially have implications for physiologists using single-unit recording to probe disparity encoding. If spatial stereoresolution is ~0.1° for horizontal disparity but >10° for vertical, and a wider range of horizontal disparities can be perceived than vertical disparities, this would suggest that less than 1 neuron tuned to a non-zero vertical disparity could be expected for every 100 tuned to horizontal disparity. Even for those subjects who can detect vertical disparity fluctuations down to 3° or so, vertical disparity detectors would still be expected to be very sparse compared to horizontal detectors. Single-unit electrophysiology would then be a poor tool for probing the properties of vertical disparity encoding; for example, one could not conclude that vertical disparity detectors do not exist simply because they are not revealed by single-unit physiology (Cumming, 2002; Read & Cumming, 2006). Physiological studies of vertical disparity encoding may have to employ the modern imaging techniques which can examine hundreds of neurons simultaneously (Kara & Boyd, 2009).

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Corresponding author: Jenny Read.
Email: j.c.a.read@ncl.ac.uk.
Address: Henry Wellcome Building, Framlington Place, Newcastle upon Tyne, NE2 4HH, UK.

References

Adams, W., Frisby, J. P., Buckley, D., Gårding, J., Hippisley-Cox, S. D., & Porrill, J. (1996). Pooling of vertical disparities by the human visual system. *Perception, 25,* 165–176. [PubMed]

Allison, R. S., Howard, I. P., Rogers, B. J., & Bridge, H. (1998). Temporal aspects of slant and inclination perception. *Perception, 27,* 1287–1304. [PubMed]

Allison, R. S., Rogers, B. J., & Bradshaw, M. F. (2003). Geometric and induced effects in binocular stereopsis and motion parallax. *Vision Research, 43,* 1879–1893. [PubMed]

Backus, B. T., & Banks, M. S. (1999). Estimator reliability and distance scaling in stereoscopic slant perception. *Perception, 28,* 217–242. [PubMed]

Backus, B. T., Banks, M. S., van Ee, R., & Crowell, J. A. (1999). Horizontal and vertical disparity, eye position, and stereoscopic slant perception. *Vision Research, 39,* 1143–1170. [PubMed]

Banks, M. S., & Backus, B. T. (1998). Extra-retinal and perspective cues cause the small range of the induced effect. *Vision Research, 38,* 187–194. [PubMed]

Banks, M. S., Gepshtein, S., & Landy, M. S. (2004). Why is spatial stereoresolution so low? *Journal of Neuroscience, 24,* 2077–2089. [PubMed]

Bradshaw, M. F., & Rogers, B. J. (1999). Sensitivity to horizontal and vertical corrugations defined by binocular disparity. *Vision Research, 39,* 3049–3056. [PubMed]

Brainard, D. H. (1997). The Psychophysics Toolbox. *Spatial Vision, 10,* 433–436. [PubMed]

Bredfeldt, C. E., & Cumming, B. G. (2006). A simple account of cyclopean edge responses in macaque V2. *Journal of Neuroscience, 26,* 7581–7596. [PubMed]

Bredfeldt, C. E., Read, J. C., & Cumming, B. G. (2009). A quantitative explanation of responses to disparity defined edges in macaque V2. *Journal of Neurophysiology, 101,* 701–713. [PubMed]

Brenner, E., Smeets, J. B., & Landy, M. S. (2001). How vertical disparities assist judgements of distance. *Vision Research, 41,* 3455–3465. [PubMed] [Article]

Brookes, A., & Stevens, K. A. (1989). The analogy between stereo depth and brightness. *Perception, 18,* 601–614. [PubMed]

Campbell, F. W., & Robson, J. G. (1968). Application of Fourier analysis to the visibility of gratings. *The Journal of Physiology, 197,* 551–566. [PubMed] [Article]

Cumming, B. G. (2002). An unexpected specialization for horizontal disparity in primate primary visual cortex. *Nature, 418,* 633–636. [PubMed]

Cumming, B. G., Johnston, E. B., & Parker, A. J. (1991). Vertical disparities and perception of three-dimensional shape. *Nature, 349,* 411–413. [PubMed]

Erkelens, C. J., & Collewijn, H. (1985). Motion perception during dichoptic viewing of moving random-dot stereograms. *Vision Research, 25,* 583–588. [PubMed] [Article]

Frisby, J. P., Buckley, D., Grant, H., Gårding, J., Horsman, J. M., Hippisley-Cox, S. D., et al. (1999). An orientation anisotropy in the effects of scaling vertical disparities. *Vision Research, 39,* 481–492. [PubMed] [Article]

Gårding, J., Porrill, J., Mayhew, J. E., & Frisby, J. P. (1995). Stereopsis, vertical disparity and relief transformations. *Vision Research, 35,* 703–722. [PubMed] [Article]

Gillam, B., Blackburn, S., & Brooks, K. (2007). Hinge versus twist: The effects of 'reference surfaces' and discontinuities on stereoscopic slant perception. *Perception, 36,* 596–616. [PubMed]

Gillam, B., Chambers, D., & Lawergren, B. (1988). The role of vertical disparity in the scaling of stereoscopic depth perception: An empirical and theoretical study. *Perception & Psychophysics, 44,* 473–483. [PubMed]

Gillam, B., Flagg, T., & Finlay, D. (1984). Evidence for disparity change as the primary stimulus for stereoscopic processing. *Perception & Psychophysics, 36,* 559–564. [PubMed]

Gillam, B., & Lawergren, B. (1983). The induced effect, vertical disparity, and stereoscopic theory. *Perception & Psychophysics, 34,* 121–130. [PubMed]

Harris, J. M., McKee, S. P., & Smallman, H. S. (1997). Fine-scale processing in human binocular stereopsis. *Journal of the Optical Society of America A, Optics, Image Science, and Vision, 14,* 1673–1683. [PubMed]

Hirsch, M. J., & Weymouth, F. W. (1948). Distance discrimination; Effect on threshold of lateral separation of the test objects. *Archives of Ophthalmology, 39,* 224–231. [PubMed]

Howard, I. P., & Rogers, B. J. (2002). *Seeing in depth, volume 2: Depth perception*. Ontario, Canada: I. Porteous.

Kaneko, H., & Howard, I. P. (1996). Relative size disparities and the perception of surface slant. *Vision Research, 36,* 1919–1930. [PubMed]

Kaneko, H., & Howard, I. P. (1997). Spatial limitation of vertical-size disparity processing. *Vision Research, 37,* 2871–2878. [PubMed] [Article]

Kara, P., & Boyd, J. D. (2009). A micro-architecture for binocular disparity and ocular dominance in visual cortex. *Nature, 458,* 627–631. [PubMed] [Article]

Longuet-Higgins, H. C. (1981). A computer algorithm for reconstructing a scene from two projections. *Nature, 293,* 133–135.

Longuet-Higgins, H. C. (1982). The role of the vertical dimension in stereoscopic vision. *Perception, 11,* 377–386. [PubMed]

Lunn, P. D., & Morgan, M. J. (1995). "The analogy between stereo depth and brightness": A reexamination. *Perception, 24,* 901–904. [PubMed]

Mayhew, J. E. (1982). The interpretation of stereo-disparity information: The computation of surface orientation and depth. *Perception, 11,* 387–403. [PubMed]

Mayhew, J. E., & Longuet-Higgins, H. C. (1982). A computational model of binocular depth perception. *Nature, 297,* 376–378. [PubMed]

McKee, S. P., Welch, L., Taylor, D. G., & Bowne, S. F. (1990). Finding the common bond: Stereoacuity and the other hyperacuities. *Vision Research, 30,* 879–891. [PubMed] [Article]

Ogle, K. N. (1938). Induced size effect: I. A new phenomenon in binocular vision associated with the relative size of the images in the two eyes. *Archives of Ophthalmology, 20,* 604.

Parker, A. J. (2007). Binocular depth perception and the cerebral cortex. *Nature Reviews, Neuroscience, 8,* 379–391. [PubMed]

Pelli, D. G. (1997). The VideoToolbox software for visual psychophysics: Transforming numbers into movies. *Spatial Vision, 10,* 437–442. [PubMed]

Pierce, B. J., & Howard, I. P. (1997). Types of size disparity and the perception of surface slant. *Perception, 26,* 1503–1517. [PubMed]

Read, J. C. A., & Cumming, B. G. (2006). Does depth perception require vertical-disparity detectors? *Journal of Vision, 6*(12):1, 1323–1355, http://journalofvision.org/6/12/1/, doi:10.1167/6.12.1. [PubMed] [Article]

Read, J. C. A., Phillipson, G. P., & Glennerster, A. (2009). Latitude and longitude vertical disparities [Abstract]. *Journal of Vision, 9*(13):11, 1–37, http://journalofvision.org/9/13/11/, doi:10.1167/9.13.11.

Regan, D., Erkelens, C. J., & Collewijn, H. (1986). Necessary conditions for the perception of motion in depth. *Investigative Ophthalmology & Visual Science, 27,* 584–597. [PubMed]

Rogers, B. J., & Bradshaw, M. F. (1993). Vertical disparities, differential perspective and binocular stereopsis. *Nature, 361,* 253–255. [PubMed]

Rogers, B. J., & Bradshaw, M. F. (1995). Disparity scaling and the perception of frontoparallel surfaces. *Perception, 24,* 155–179. [PubMed]

Rogers, B. J., & Cagenello, R. (1989). Disparity curvature and the perception of three-dimensional surfaces. *Nature, 339,* 135–137. [PubMed]

Rogers, B. J., & Graham, M. (1982). Similarities between motion parallax and stereopsis in human depth perception. *Vision Research, 22,* 261–270. [PubMed] [Article]

Rogers, B. J., & Koenderink, J. (1986). Monocular aniseikonia: A motion parallax analogue of the disparity-induced effect. *Nature, 322,* 62–63. [PubMed]

Schumer, R., & Ganz, L. (1979). Independent stereoscopic channels for different extents of spatial pooling. *Vision Research, 19,* 1303–1314. [PubMed] [Article]

Serrano-Pedraza, I., Phillipson, G., & Read, J. C. A. (2009). Size of vertical disparity pooling and the induced effect [Abstract]. *Journal of Vision, 9*(8):280, 280a, http://journalofvision.org/9/8/280/, doi:10.1167/9.8.280.

Serrano-Pedraza, I., & Read, J. C. A. (2009). Stereo vision requires an explicit encoding of vertical disparity. *Journal of Vision, 9*(4):3, 1–13, http://journalofvision.org/9/4/3/, doi:10.1167/9.4.3. [PubMed] [Article]

Stenton, S. P., Frisby, J. P., & Mayhew, J. E. (1984). Vertical disparity pooling and the induced effect. *Nature, 309,* 622–623. [PubMed]

Thomas, O. M., Cumming, B. G., & Parker, A. J. (2002). A specialization for relative disparity in V2. *Nature Neuroscience, 5,* 472–478. [PubMed]

Tyler, C. W. (1974). Depth perception in disparity gratings. *Nature, 251,* 140–142. [PubMed]

Tyler, C. W. (1977). Spatial limitation of human stereoscopic vision. *SPIE Three-Dimensional Imaging, 120,* 36–42.

von der Heydt, R., Zhou, H., & Friedman, H. S. (2000). Representation of stereoscopic edges in monkey visual cortex. *Vision Research, 40,* 1955–1967. [PubMed] [Article]

Westheimer, G. (1979). Cooperative neural processes involved in stereoscopic acuity. *Experimental Brain Research, 36,* 585–597. [PubMed]

Westheimer, G. (1984). Sensitivity for vertical retinal image differences. *Nature, 307,* 632–634. [PubMed]