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Motion-stereo mechanisms sensitive to inter-ocular phase

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Abstract

We measured depth from interocular delay (The Pulfrich effect) using a dynamic random-dot pattern, consisting of a spatially-random noise field, the individual elements of which were sinusoidally-modulated in luminance over time. When an interocular phase difference in the flicker was introduced the display appeared to rotate in depth around a vertical axis like a transparent textured cylinder. The threshold phase lag was in the region of 5–10° in different observers, which translated into a non-constant, decreasing interocular delay (ms) as the flicker frequency was increased. We conclude that phase, not delay, is the critical parameter in determining the detection of depth. Threshold signal/noise ratios were measured at different delays to determine the optimum phase difference, which was found to be in the region 60–90°. However, delays centred around 180° were less detectable than those around zero, ruling out a quadrature input to the stereo-motion mechanisms. We show that depth-from-phase is a natural consequence of paired monocularly motion-direction sensitive neurones. Complex energy-detecting neurones are not required to explain the findings. © 2000 Elsevier Science Ltd. All rights reserved.

Keywords: Inter-ocular phase; The Pulfrich effect; Motion

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1. Introduction

Physiological evidence from the feline visual system (DeAngelis, Ohzawa & Freeman, 1991, 1995) agrees with psychophysical data (Schor, Wood & Ogawa, 1984; Morgan & Castet, 1997) in suggesting that stereoscopic disparities between the eyes are detected by mechanisms sensitive to the relative interocular phase of Fourier components, rather than the interocular point disparities. Using static grating stimuli, Morgan and Castet (1997) found that changes in depth detection thresholds with orientation were well predicted by phase differences measured at right-angles to the grating, but were not predicted by horizontal disparities. Similarly, with moving gratings Morgan and Castet (1995) reported that depth thresholds varied little with velocity up to 500 deg/s when expressed as interocular phase differences, but decreased to physiologically unrealistic values of 300 μs when expressed as delays. In the present paper, we report a powerful new method for investigating phase tuning of stereomechanisms with temporally-band limited noise, which could be easily adapted for physiological experiments. The technique is a variety of the Pulfrich stereo-phenomenon.

The Pulfrich effect is classically described as depending on an interocular delay. When a horizontally-swinging pendulum is viewed with a neutral density filter over one eye, it seems to move in an elliptical 3-D orbit. Carl von Pulfrich, after whom the effect is generally named, was not the first to report the phenomenon (Pulfrich, 1922). Neither did he ever see it, being blind in one eye. The accepted explanation, as Pulfrich makes clear in his 1922 paper, was put forward by the optical engineer Fertsch, working at Zeiss (Jena). Fertsch proposed that the neutral density filter introduced a temporal lag in the covered eye, thus converting the time-varying positional signal from the target into a disparity. The text books illustrate this explanation by showing the target as having a different instantaneous position in the two eyes, but this explanation is inadequate. The Pulfrich effect is seen even in a stroboscopic display where the interocular delay is too small to cause

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pairings of disparate positions in the two eyes (Lee, 1970; Morgan & Thompson, 1975). The motion-sampled version of the Pulfrich effect implies an early stage of spatio-temporal filtering (Morgan, 1979, 1980a,b; Fahle & Poggio, 1981). The Pulfrich effect is essentially a spatio-temporal phenomenon, requiring space–time rather than static disparity, a point recently re-emphasised by Qian and Anderson (1997), and by Pulfrich himself, who observed (quoting from *Parsifal*): "Du siehst mein Sohn, zum Raum wird hier die Zeit" – See, my son, how time is changed here to space: Richard Wagner, *Parsifal*, Act I, Scene I).

A Pulfrich-like effect is also seen when inspecting dynamic visual noise with an interocular delay (Ross, 1974; Burr & Ross, 1978; Morgan & Ward, 1980). The initially incoherent noise takes on a 3-D appearance, with some dots moving from left to right in front of the fixation plane and others moving from right to left. If the filter is front of the left eye, the nearer dots appear to move from left to right and the further dots appear to move from right to left. The direction of rotation is changed from clockwise (as if viewed from above) to anticlockwise if the filter is in front of the right eye. This dynamic visual noise version of the Pulfrich effect is not hard to understand in principle, since wide-spectrum noise contains by definition the horizontally-moving Fourier components which are known to be sufficient to cause the effect in isolation (Morgan & Tyler, 1995). Qian and Anderson (1997) have recently shown theoretically that quadrature-tuned pairs of left-eye and right-eye detectors, which detect both motion energy and disparity-energy, will produce Pulfrich-type phenomena from dynamic noise. There is thus a good general understanding of the class of Pulfrich effects, but the details of the implementation are still to be clarified.

Here we used a temporally band-limited stimulus designed to probe the temporal frequency response of the underlying motion-stereo mechanisms, and to determine whether inter-ocular delay or interocular phase is the critical variable to which the visual system responds. A spatially random noise field was constructed consisting of a grid of square elements with randomly-distributed luminance values (Fig. 1). The power spectrum of this stimulus is flat up to the frequency of the grid, and then declines linearly to zero at the display Nqyuist limit. Each element sinusoidally flickered so that the display as a whole had a wide range of spatial frequencies but only one temporal frequency (Fig. 1). This results in a set of elements that are all flickering at the same rate, but with a random phase with respect to each other. A delay could then be introduced as a phase difference in the flicker of corresponding elements between the eyes. An advantage of the technique is that it allows temporal lags that are limited only by the luminance resolution of the display, and not by the frame rate. We were thus able to introduce lags equivalent to 10 μs, represented by the instantaneous luminance difference between corresponding grid elements in the two eyes. There are no explicitly programmed movement signals in the display, but clearly they exist, as shown by the Fourier spectrum in Fig. 1. The spectrum shows that each spatial frequency is associated with a specific temporal frequency: in other words, it is a single velocity component. Unlike a broad-band pattern like a moving square-wave, however, the temporal frequency of a spatial component is not a function of its spatial frequency. All spatial frequencies have the same temporal frequency, namely the flicker rate of the display.

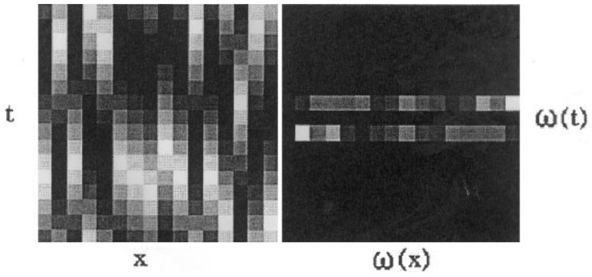

Fig. 1. The left-hand panel is an x–t plot of a single row of the random-noise stimulus used in the experiments. The figure shows how a single row of 2-D white noise changes over time (vertical axis). The right-hand panel shows the corresponding power spectrum, which contains temporal frequencies of $\pm\omega$ but a broad-band of spatial frequencies. Thus there are as many velocity components in the stimulus as spatial frequency components.

Using the display described in Fig. 1 we measured threshold interocular phase differences as a function of temporal frequency (experiment 1). Since there are two null phases for seeing depth (0 and 180°) we measured psychometric functions for delay around both null phases. In experiment 2 we varied the proportion of the grid elements carrying the signal: the remainder had a zero phase difference.

2. Methods

2.1. Apparatus and stimuli

Stimuli were generated on a Barco Calibrator II monitor under control of a Cambridge Research Systems VSG graphics board, with linear pseudo-12 bit luminance-calibrated look-up tables. The mean luminance of the display was 17 cd/m^2. The frame rate of the display was 200 Hz and the spatial resolution was 992×226 pixels. The non-square pixel geometry was compensated for when generating the stimuli. The stimulus consisted of a $10 \times 10°$ rectangle filled with $0.2 \times 0.2°$ elements which were placed in the centre of the Barco screen. The room was darkened, but reflected light from the display provided dim illumination, so that the borders of the monitor were visible. The borders were always visible through both eyes, and were sufficient to maintain vergence. Observers viewed the display foveally, and maintained fixation with the help of a small circular spot in the centre of the display.

The squares comprising the stimulus were re-computed on every trial so as to have randomly chosen look-up table values in the range 0–255, corresponding to a luminance range of 0–34 cd/m^2. Each element was then sinusoidally modulated over the whole luminance range at a pre-selected temporal frequency by loading a new look-up table every frame. The left and right eyes had separate sets of look-up tables, allowing the relative phase of the modulation to be determined.

Dichoptic separation was achieved by viewing the display through a pair of ferro-optical goggles (Cambridge Research Systems) switching between the two eyes at a rate of 200 Hz in synchrony with the frame rate of the display. Thus even numbered frames were presented to the left eye and odd numbered frames to the right eye. The look-up tables were also switched every frame to give the desired phase difference between the two eyes. We measured the attenuation of the signal by the goggles by placing them in turn between the screen and a photocell, and then alternating frames in the display between 20 and 0 cd/m^2. The goggles attenuated the luminance reaching the 'open' eye by 1 $\log_{10}$ unit, and the 'closed' eye by approximately 2 $\log_{10}$ units. The signal in the 'closed' eye was due mainly to phosphor persistence.

2.2. Psychophysics

To determine phase thresholds the stimulus was presented for 2 s (4 s for temporal frequencies less than 0.39 Hz) and the observer had to decide whether the apparently leftwards-moving dots were in front of or behind the plane of fixation (method of binary choice). The decision was indicated by pressing one of two keys on the computer keyboard (0 vs 2). There was no feedback, since it was not obvious what a 'correct' response should be nominated. The magnitude and sign of the lag was systematically changed over a series of 72 trials by the method of adaptive probit estimation (APE: Watt & Andrews, 1981) to determine a psychometric function spanning the range from $\sim 0\%$ clockwise decisions to $\sim 100\%$ clockwise decisions. The standard deviation of the function was calculated by probit analysis and taken as the threshold.

To determine signal/noise thresholds, APE was used to determine on each trial the percentage of elements that had the (fixed) phase lag. The remaining elements had a zero phase lag.

Five independent measures of threshold were taken for each temporal frequency/phase lag.

2.3. Observers

The observers were the two authors, and a variety of paid volunteer students, who were not informed about the aim of the experiment until they had finished their observations. Experienced colleagues passing through London were recruited to make additional observations which were aimed at making a preliminary survey of the range of sensitivities in the population.

3. Experiment 1

3.1. Phenomenology

With a null phase of 0° the display appeared like flickering noise, with no systematic depth. With a null phase of 180° the display appeared lustrous, again without depth. The appearance of the display with a phase difference of 90° was similar to that previously described for the dynamic random-noise Pulfrich effect (Ross, 1974). There was a distinct impression both of movement and of depth, as if the pattern had become solid and was rotating around a vertical axis. The appearance was somewhat paradoxical, like that of the movement after-effect (Wohlgemuth, 1911) in the sense that the individual flickering squares could also be seen to be stationary. The effect was seen both with the eyes stationary, and when the pattern was tracked. In the experiments the observer attempted to maintain fixation with the aid of a spot in the centre of the display. We did not measure the latency of the depth effect systematically, but we noticed that it took a perceptible time to appear, particularly in naive subjects. This was the reason for the relatively long (2 s) exposure duration. Around the null phase of 0°, increasing the magnitude of the left-eye lag made the display appear to rotate clockwise, as if viewed from the above, while increasing right-eye lag made it appear to rotate anticlockwise. Around a null phase of 180°, a left-eye lag made the display appear to rotate anticlockwise. In either case, it was possible to measure psychometric functions for the effects of delay, by requiring the observer to make a binary choice (clockwise vs anticlockwise) at different levels of lag.

3.2. Psychometric functions

Sample psychometric functions are shown in Fig. 2 to show how sensitivity to delay was measured. As the magnitude of lag increased, the probability of a clockwise response changed from near-zero to near-unity. The data were fitted to a cumulative gaussian error function by probit analysis and were then described by two parameters: the position of the inflexion point and the standard deviation of the error function. The first of

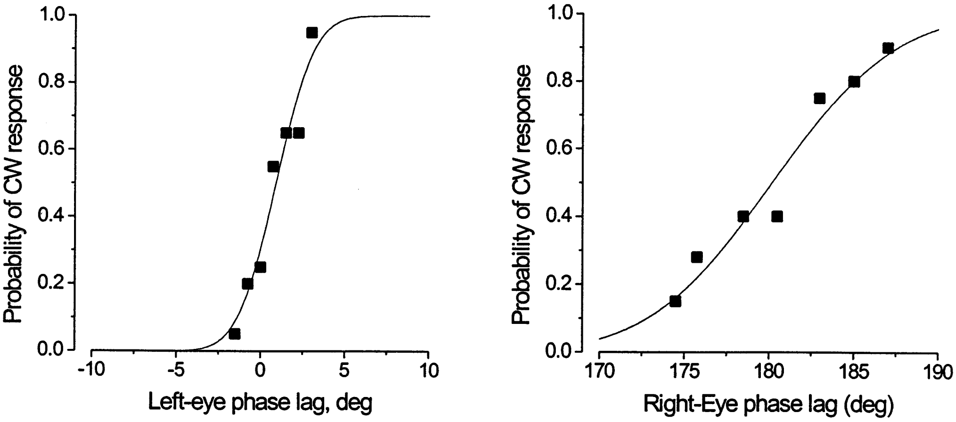

Fig. 2. Sample psychometric functions for observer MJM at 12.5 Hz flicker modulation. In the left-hand panel the base phase is 0, and the observer is highly sensitive to small phase changes around this value, as shown by the steep psychometric function. In the right-hand panel the base phase is 180° and the observer is much less sensitive to small phase changes around this base value, as shown by the relatively shallow psychometric function. For further details see text.

these corresponds to the 50% point of the function, and the second to difference between the 50 and 84% point correct point (Green & Swets, 1966; Watt & Andrews, 1981). In the absence of observer bias we would expect the 50% point to align with a zero phase lag. There was, however, an unavoidable artefact in the display which tended to shift the functions to the right, as is clear in the left-hand panel. At zero phase lag the eyes did not see the display simultaneously but with a slight (5 ms) right-eye lag due to the stereo goggles, which exposed the eye to alternate frames of the display. This meant that the theoretical 50% point was located not at a zero phase lag but at a left-eye lag in the temporal modulation sufficient to balance the right-eye lag in presentation. However, this bias did not affect the measure of threshold we used, which was the slope of the function. In the case of the left-hand function, the observer is highly sensitive to the phase lag and the slope is correspondingly steep. In the right-hand panel the observer is relatively insensitive to phase and the slope is shallow. The difference in sensitivity is described by the standard deviation of the error function, which is the measure we use of threshold.

3.3. Threshold measurements around the 0° null phase

Threshold inter-ocular delays and equivalent phase differences were measured over a range of temporal frequencies from 0.05 to 18.75 Hz. Two of the observers (MM & MF) were exposed to the whole of this range; the other two (KB & TM) experienced only the range 0.39–18.75 Hz. Data for four observers are shown in Fig. 3. For MM and MF threshold phase varied little across the range of temporal frequencies, while threshold delay decreased markedly as temporal frequency was raised. It is reasonable to conclude that these two observers detected the phase angle of the signal between the two eyes, and that the threshold phase angle was in the region of 5–15°. There was an upper temporal frequency above which depth could not be seen. This was 6.26 Hz for MF and 18.75 Hz for MJM. A lower temporal frequency limit was not determined, although it was obvious that at frequencies below 0.05 Hz the flicker, and thus the depth, was rapidly becoming imperceptible.

The data for the observer TM were similar, except for an overall lower sensitivity. The fourth observer (KB) showed a larger rise in threshold phase with frequency, but as in the other two observers this rise was less consistent than the decrease in threshold interocular delay.

To analyse these data statistically, and to determine whether the absolute slope of the phase versus frequency function is indeed smaller than that of the delay versus frequency function, the data were first transformed into relative values, as shown in Fig. 4. All thresholds were expressed relative to the value at 0.39 Hz, this being the lowest frequency tested on all four observers. The null hypothesis is that the absolute slopes of the delay and phase functions are the same. A two-way ANOVA was carried out with temporal frequency (X-axis) and delay versus phase as main factors, with observers as repeated measures. The effect of temporal frequency was highly significant ($F[4,30] = 7.99$, $P < 0.001$) as was that of delay versus phase ($F[1,30] = 52.8$, $P < 0.001$). The interaction term was also significant ($F[4,30] = 3.3$, $P = 0.0229$) indicating a significant difference in slope.

To analyse the data for each individual separately, over the whole range of temporal frequencies to which they were exposed, an analysis of covariance was carried out. This showed highly significant differences in slope for three of the four subjects ($P < 0.0001$, $P < 0.0001$, $P < 0.0073$) and a marginally significant one-

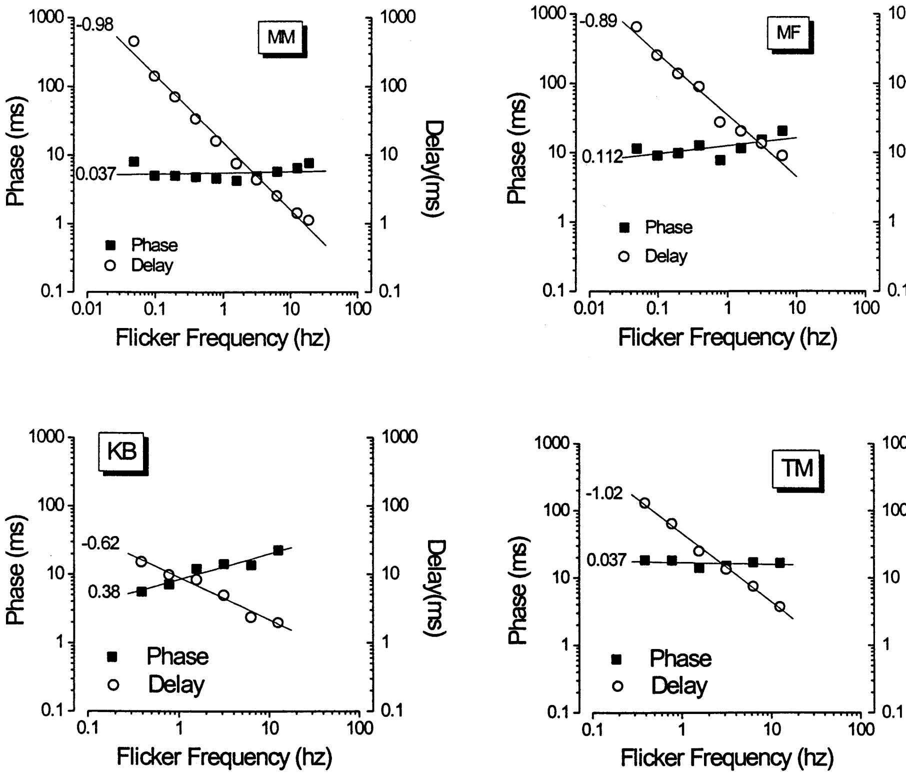

Fig. 3. The four panels show results separately for four observers in experiment 1, which measured threshold interocular delay and phase difference as a function of flicker frequency in patterns like those illustrated in Fig. 1. The solid lines are linear regressions, with the slopes shown by the figures near the left-hand axis.

tailed difference in subject KB ($P = 0.0878$). If the individual probabilities are combined into a single χ^2 by the formula $\chi^2 = -2\,\Sigma_k^{i=1}\ln(p_i)$ the resulting χ^2 (51.54, df $= k - 1 = 3$) is significant with $P < P < 0.005$.

Since threshold delay decreases in proportion to frequency, we conclude that it is not a useful independent measure of sensitivity. In particular, the apparently very small temporal thresholds of less than 5 ms simply represent a phase sensitivity of ~5°, consistent with apparently much larger delay thresholds at lower temporal frequencies. Thresholds for frequencies greater than ~20 Hz were impossible to measure, although the flicker was clearly seen.

Individual differences: It is clear from Fig. 3 that there are large overall differences in sensitivity between observers. Some observers that we have tested have great difficulties in seeing the effect at all, despite having normal static stereoacuity measured with the TNO random dot stereogram test.

To quantify differences between observers who could see the depth effect, and to see if age was a factor in determining performance, we compared data for seven observers tested at a temporal frequency of 3.125 Hz (see Fig. 5). There was an insignificant correlation (-0.44; $R^2 = 0.18$) with age. Practice does not seem to be the most important variable either. The most practised observer (MM) had the lowest thresholds but the next best observer (SB) had very little prior practice, and both TM and KB had extensive practice in the main experiment.

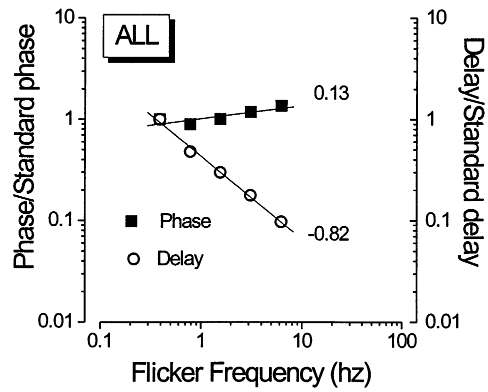

Fig. 4. The figure shows the mean data over observers from experiment 1 (Fig. 3) transformed into relative values. All thresholds were re-expressed as values relative to the reference value of 0.39 Hz. This was to allow a comparison between their absolute slopes, as explained in the text. Note that the slope for the phase data is considerably shallower than that for delay.

3.4. Threshold measurements around the 180° null phase

These observations were exactly like the foregoing, except that the flicker was 180° out of phase between

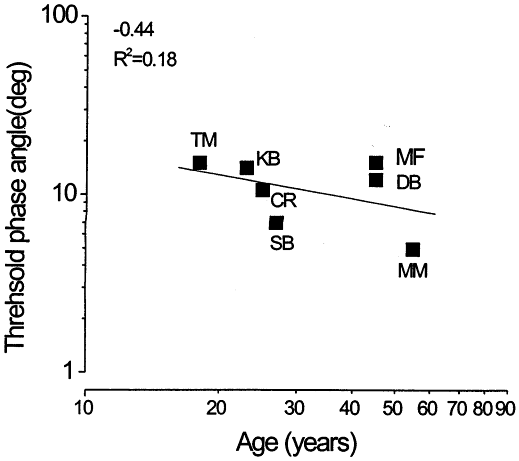

Fig. 5. The figure shows a scatterplot of individual phase thresholds for seeing depth in seven different observers (TM, KB, CR, SB, MF, DB, MM). The stimulus was the flickering random-dot pattern depicted in Fig. 1 with a temporal frequency of 3.125 Hz.

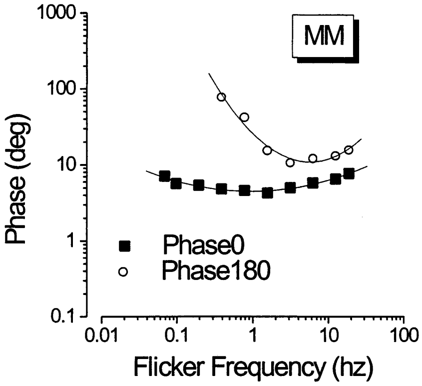

Fig. 6. The results of experiment 3, in which threshold interocular phase (vertical axis) was measured as a function of flicker frequency (horizontal axis). In the two different conditions the baseline phase difference between the eyes was wither 0 (■) or 180° (○). Thresholds were higher in the 180° condition, and the difference increased as temporal frequency decreased.

the eyes. To this baseline phase difference, a further phase difference was added, which the observer was required to detect as depth. The depth was difficult to see in this case, and only some observers were able to perform the task at all. For this reason, complete measurements were taken from one observer only (MM).The added phase difference could be either positive or negative, thus either increasing or decreasing the baseline 180° difference. The data were compared to those previously collected (experiment 1) for a 0° null phase. The data (Fig. 6) showed that phase differences around 0° are easier to detect than around 180°. The difference increased as the temporal frequency was lowered. The 180° condition was impossible below temporal frequency of ~0.5 Hz. The significance of this finding will be considered in Section 5, after the presentation of a model.

The technique used in this first experiment is unable to measure the detectability of different phase lags, except around null phases of 0 and 180°. To get a broader picture of detectability, we measured the signal:noise ratio required to reach criterion performance for a range of delays between 0 and 180°.

4. Experiment 2

Another way to measure sensitivity is by varying the proportion of the stimulus squares carrying the signal (Newsome, Britten & Movshon, 1989). We randomly selected a proportion of the squares as signal. These were given a fixed interocular phase difference, say ± 15°. The remaining squares had a zero interocular phase lag. The temporal frequency was 3.125 Hz. The proportion of signal was varied over trials by the adaptive probit method of estimation (Watt & Andrews, 1981) to determine the 82% point of discrimination between left-eye lag and right-eye lag. Otherwise the methods were identical to those in experiment 1.

4.1. Results

The results (Fig. 7a) once again showed large overall differences in sensitivity between observers. MM could detect depth with as few as 5% of the dots having a phase difference; KB required 50% signal. A scatterplot (Fig. 7b) of the best thresholds obtained for nine observers gives an idea of the range of variation.

Sensitivity was a broadly-tuned U-shaped function of phase with an optimum somewhere between 20 and 160°. Sensitivity to phase differences near to zero was greater than to phase differences nearer to 180°. Indeed, for two of the observers, threshold S/N ratios could not be measured for phase differences greater than 90°.

5. Discussion

The data show that phase rather than delay is the critical determinant of the dynamic visual noise stereophenomenon. We now show that a simple modification to static phase-sensitive disparity detectors (DeAngelis et al., 1991, 1995) explain these findings.

Consider two phases of a single, horizontally-moving Fourier component presented separately to either eye.

$$R(x,t) = \cos\,[2\pi(F_x x + F_t t) + \phi_r]$$

$$L(x,t) = \cos\,[2\pi(F_x x + F_t t) + \phi_l]$$

These stimulate separate left and right eye linear receptive fields which are sensitive to the same part of the visual field. For simplicity we define these receptive

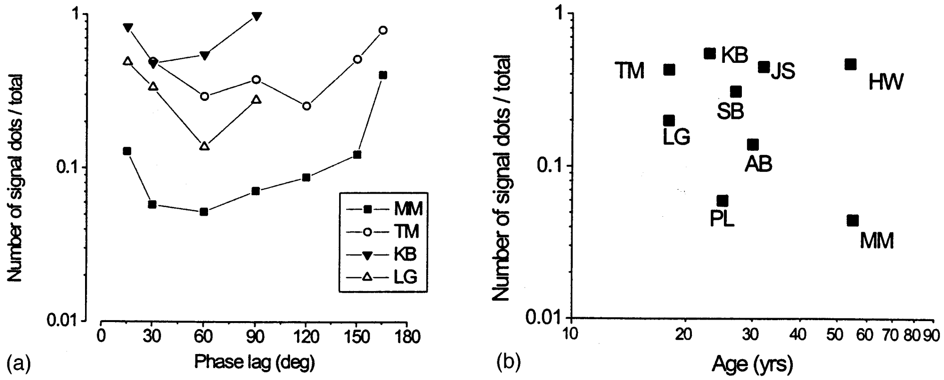

Fig. 7. Results of experiment 2, which measured the observer's sensitivity to interocular phase by determining the proportion of dots carrying the interocular phase signal required for the observer to detect depth. The non-signal dots were temporally in-phase between the eyes. (a) Shows thresholds in four different observers (MM, TM, KB, LG) as a function of the phase difference carried by the signal dots. (b) Shows a scatterplot of thresholds for nine observers at a fixed phase of 60°. The temporal frequency in all cases was 3.125 Hz.

fields as Gabor functions in quadrature phase, although any linear receptive field and non-zero phase difference will suffice. The summed response of the two receptive fields is given by the dot product:

$$F(t;x) = [G(x)\cos(2\pi(F_x x))] \cdot R(x,t) \\ + [G(x)\ \sin(2\pi(F_x x))] \cdot L(x,t)$$

where $G(x) = \exp(-x^2/2\sigma^2)$.

The response of this mechanism clearly reaches a maximum when the signal is 90° out of phase in the two eyes, whether because of a spatial phase shift between static gratings, or because of a temporal phase shift between moving gratings. The two kinds of phase shift are both theoretically and experimentally (Carney, Paradiso & Freeman, 1989) indistinguishable. A population of such detectors can encode the disparity either of stationary or of moving stimuli.

However, an additional step of directional selectivity is required to explain why depth is associated with direction of motion. We need only suppose that the receptive fields above are directionally selective, and that each sign of stereo-detector (near vs far) comes in two varieties: leftwards sensitive and rightwards sensitive. Fig. 8 shows that leftwards sensitive, near-tuned detectors are stimulated by a left-eye lag. They are not stimulated by rightwards motion because they are directionally-selective, and they are not stimulated by 'far' stimuli because of their disparity tuning. The same argument followed through for all four detector classes shows that left-eye lags stimulate rightwards detectors tuned to far stimuli and leftwards detectors tuned to near stimuli; while right eye lags stimulate leftwards detectors tuned to far stimuli and rightwards detectors tuned to near stimuli. The Pulfrich effect and its variants are thereby explained.

It is important to be clear that the model does not involve the computation of dichoptic motion. At first sight, the quadrature mechanism might seem compatible with the demonstration by Carney and Shadlen (1993) of motion when gratings are presented dichoptically in spatial and temporal quadrature. As in the present experiment, motion was only seen when the eyes are temporally out of phase. Doubts have been raised about whether the motion described by Carney and Shadlen (1993) is true low level motion sensing

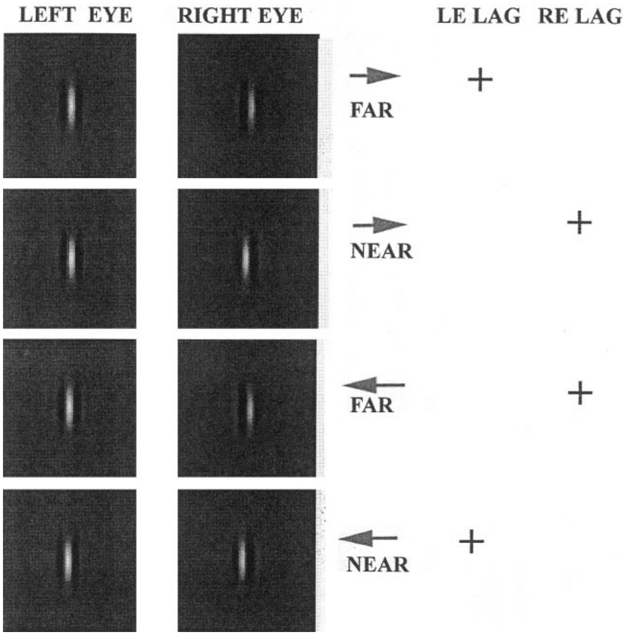

Fig. 8. A model for the detection of stereodisparity in moving objects or Fourier components. Each row represents the receptive field profiles (left and right eye shown separately) and the directional selectivity (arrow) of a single cortical simple cell. The receptive fields are in quadrature phase in the two eyes, which confers disparity selectivity on the cell. Each of the four classes of cell illustrated will respond optimally to a particular combination of eye delay and motion direction, as illustrated by the + signs. For example, a left eye lag will stimulate the receptive fields of 'near' units selective for leftwards retinal motion (rightwards object motion) and 'far' units selective for rightwards retinal motion.

rather than feature tracking (Georgeson & Shackleton, 1992; Lu & Sperling, 1995). However, the model we propose does not have dichoptic motion detectors. The directionally selective detectors are strictly monocular. The reason why coherent motion is not see without interocular delay is that the motion signals are balanced in the two directions by the random noise. Only when delay is introduced are the different directions associated with different stereo disparities, and thus become segregated.

The model we propose is the same as that of Qian and Anderson (1997), except that it does not involve energy computation. The main finding of our experiments is in agreement with eq. (10) in the Qain and Anderson model, which states that the product of temporal frequency and threshold interocular delay should be constant. In the Qian and Anderson model, complex cells compute both motion and disparity energies from quadrature-tuned simple cells. A problem with this model is that it does not predict the difficulty observers had in detecting phase differences around 180°. For quadrature pairs of detectors, phase differences centered at 0 and 180° should be similar in their detectability. This similarity is evident in the model quadrature-pair model implemented by Cumming and Parker (1997: see their Fig. 2) and in the responses that they report of complex cells to correlated and anticorrelated stereograms. On the other hand, it is well established that human (Cogan, Lomakin & Rossi, 1993) and monkey (Cumming & Parker, 1997) observers fail to detect depth in anticorrelated stereograms, in agreement with the findings we report here for what are, in essence, dynamic random stereograms. Cumming and Parker account for this discrepency between physiology and psychophysics by appealing to a further stage of processing beyond V1, in which the responses of complex cells to anticorrelated stimuli is somehow discounted. An alternative is that quadrature-pair complex neurones are not the basis for the fine stereopsis measured by threshold psychophysical techniques. The relevant population of cells could be tuned to near-zero disparities, rather than to 90° phase differences. The role of complex cells could be different, perhaps the control of vergence eye movements as suggested by Cumming and Parker (1997) and Masson, Busettini and Miles (1997).

In summary, we conclude that the mechanisms for dynamic stereopsis are tuned to spatiotemporal phase differences between the eyes, rather than to time differences per se. The astonishingly small threshold temporal delays that can be detected in the hundreds of microsconds region, are a reflection of quite modest phase differences in the region of 5° We have observed depth over a temporal frequency range between 0.05 and 18.75 Hz. Individual observers differ markedly in their overall sensitivity to phase, and in the temporal frequency range and phase angles over which they can see depth. All observers are less sensitive to anticorrelated temporal stimuli. We suggest, in agreement with Qian and Anderson (1997) that disparity and motion are encoded in the same population of cells. However, we think that any quadrature-pair model such as that of Qian and Anderson, must be modified to account for the insensitivity of observers to antiphase stimuli (see also Cumming and Parker, 1997). A possible alternative is that phase disparity is encoded primarily in a population of cells tuned to near-zero interocular phase differences.

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