PERGAMON

Vision Research 39 (1999) 2717–2727

Vision Research

Orientation tuning of the transient-stereopsis system

Mark Edwards *, David R. Pope, Clifton M. Schor

School of Optometry, University of California, Berkeley, California, CA 94720, USA

Received 17 October 1997; received in revised form 5 October 1998

Abstract

Stereo-perception appears to be mediated by at least two systems: a transient system that processes stimuli presented briefly and a sustained one that processes stimuli presented for longer durations. In this paper we investigated the tuning of the transient-stereopsis system to stimulus orientation. Narrowband-gabor targets with a constant envelope size (Gaussian standard deviation of 1°) were presented for brief (140 ms) durations at large (from 4 to 8°) disparities. The results were as follows: (1) while observers could extract depth from orthogonally-oriented gabors at above chance levels, their performance was worse than that with gabors of matched orientation; (2) varying the relative contrasts of the two orthogonally oriented gabors of the same spatial frequency resulted in a reduction in performance; (3) varying the relative spatial frequencies of the orthogonally-oriented gabors impaired performance, relative to that for matched frequencies; and (4) varying the relative contrasts of orthogonal gabors that were at different spatial frequencies could improve performance. These results indicate that transient stereo-performance in the orthogonal condition was not mediated by the channels that extracted depth in either the horizontal- or vertically-matched gabor conditions. This apparent lack of orientation tuning is indicative of a second-order pathway. That this performance was mediated by a binocular, as opposed to a monocular channel, is supported by the finding that performance decreased as the contrast of one of the gabors was reduced. The finding that performance with orthogonal gabors of unmatched spatial frequency (0.5 and 4 cpd) could be improved by varying their relative contrasts suggests that the binocular spatial-frequency tuning exhibited by this channel is broadband in nature. Finally, the observation that lowering the contrast of either the high or low spatial-frequency gabor improved performance suggests the presence of at least two broadband channels: one with its peak sensitivity at a low and the other at a high spatial-frequency. © 1999 Elsevier Science Ltd. All rights reserved.

Keywords: Orientation; Spatial frequency; Contrast; Stereopsis; Transient

1. Introduction

Stereoscopic-depth perception appears to be mediated by at least two mechanisms that differ in terms of their temporal and disparity tuning, as well as in the nature and the pattern of sensitivities of the perceived depth they generate. One system can process diplopic images and requires briefly presented stimuli. The percept of depth generated by this system fades with long presentations, (Ogle, 1952; Westheimer & Tanzman, 1956). The other system (mainly) processes dichoptic stimuli that are fused and requires longer stimulus durations. The percept of depth generated by this system can be sustained in nature (Ogle, 1952). Additionally, observers can show asymmetries in their sensitivity to crossed and uncrossed depths with briefly presented stimuli that they do not show for long duration stimuli (Richards & Foley, 1971; Richards, 1973). Ogle has labeled these systems qualitative and quantitative, respectively, due to his observation that the perceived depth mediated by the quantitative system varies with the magnitude of the disparity, while the qualitative system merely gives the sign of the depth. However, in a number of pilot studies, we have observed that the qualitative system can process stimuli that are within Panums area. We have also found that the magnitude of the perceived depth mediated by the qualitative system can be varied (by changing the spatial-frequency content of the stimuli) though this effect may be monocular in nature. Based upon our observations, it would appear that the defining difference between these two systems is their respective temporal sensitivities. Accordingly, we describe them in a way analogous to

* Corresponding author. Fax: +1-510-643-5109.
E-mail address: mark@hering.berkeley.edu (M. Edwards)

PII: S0042-6989(98)00277-6

the description of the transient and sustained components of the disparity-vergence system (Jones, 1980).

We have conducted a number of studies to determine the degree to which the transient-stereoscopic system is dichoptically tuned to various physical parameters of the stimulus, e.g. spatial frequency, orientation and contrast polarity. Given that the transient system responds only to briefly-presented stimuli and can process highly diplopic images, our expectation was that it would be less tuned than the sustained system to these stimulus parameters. That is, the transient system would be able to handle greater dichoptic differences in these stimulus parameters than the sustained system could. We have previously shown this to be the case with spatial-frequency tuning. While the sustained system exhibits fairly tight, or at most broad bandpass tuning to spatial frequency (Schor, Wood & Ogawa, 1984; Kontsevich & Tyler, 1994) the transient system shows broad-lowpass tuning (Schor, Edwards & Pope, 1998). It is quite likely that this broad-lowpass tuning to spatial frequency is due to the pooling of the output of more tightly tuned initial filters prior to stereoscopic processing. The question addressed in the present study is that of orientation tuning. Specifically, whether the transient stereo-system, unlike the sustained system (Mitchell & O'Hagen, 1972) can extract depth from orthogonally oriented stimuli. In other words, in pooling across different spatial frequencies, does the transient stereo-system also pool across different orientations?

A number of previous studies have investigated the ability of observers to extract depth with orthogonally-oriented stimuli. Wilcox and Hess (1996) found that in a stereo-acuity task, observers could not extract the depth of orthogonally-oriented uncorrelated noise-elements whose contrast was modulated within a Gaussian envelope. Since the stimuli used in their study were presented in a temporal-raised-cosine envelope, that had a total duration of 1 s, it is likely that this experiment tapped the sustained-stereopsis system. Note that the precise difference in the temporal properties of the stimulus that defines the transition between the transient and sustained processing still needs to be established. However, based upon the work of Ogle (1952) and our pilot studies, it would appear that the sustained system starts to become active with stimulus durations of 0.5 s (also see Pope, Edwards & Schor, 1998a,b). Mitchell (1969) and Simmons and Kingdom (1995) found that observers could extract depth from dichoptically-orthogonal stimuli. These studies used stimuli that were within the temporal range of the transient system (100 and 200 ms, respectively) and disparities that were, at least in part, beyond the upper disparity limit of the sustained system (0.5–4 and 2°, respectively). It is therefore possible that results of these two studies reflect the properties of the transient stereo-system. Thus the results of these two studies suggest that the transient-stereopsis system is insensitive to stimulus orientation. However, this conclusion is not necessarily valid. It is possible that performance may have been mediated by a different system. The response latency for vergence eye-movements is in the order of 160 ms (Rashbass & Westheimer, 1961) which means that it is likely that the 200 ms duration stimuli used by Simmons and Kingdom elicited a vergence response. Even the 100 ms duration used by Mitchell would still have been sufficient to initiate a vergence eye-movement. It is therefore possible that observers were able to use this motor response, elicited by the single dichoptic pair of stimuli used in the two studies, to determine the depth sign of the stimuli (Howard & Rogers, 1995). That is, performance may have been mediated by the second-order component of the transient-vergence system (a system that shows limited tuning to stimulus orientation Pope et al., 1998a,b) rather than by the transient stereo-system. Thus whether the transient stereo-system shows dichoptic tuning to stimulus orientation is still an open question.

The basic aim of the present paper is to determine whether the transient stereo-system is sensitive to the relative orientation of dichoptic stimuli. This will be achieved by using an experimental design that precludes the possibility of observers performing the task by monitoring any vergence responses elicited by the stimuli.

2. Experiment 1

2.1. Effects of relative orientation on transient-stereopsis performance

The aim of the this experiment was to determine whether the transient stereo-system exhibits dichoptic tuning to stimulus orientation. The technique employed in this analysis was to establish whether performance was better when each dichoptic half-image had the same orientation (either vertical or horizontal) as compared to when the orientations were orthogonal.

2.1.1. Method

2.1.1.1. Observers. Three male observers were used. All had either normal or corrected to normal visual acuity, normal stereopsis (as measured by a Randot Stereotest) and no history of any binocular visual disorders.

2.1.1.2. Stimuli and procedure. The stimuli used were gabors with carriers presented in sine phase within a circular Gaussian envelope with a 1° sigma (see Edwards, Pope & Schor, 1998 for further details). The observer first maintained fixation on a pair of crosses and vertical nonius lines. Once the observer had established fixation, while perceiving the nonius lines aligned, he initiated the presentation of the test stimulus. The test stimulus replaced the fixation cross and nonius lines and consisted of two pairs of dichoptic gabors. The centers of one pair was presented 2.8° above and the other pair 2.8° below the former center location of the fixation point. One of these pairs was presented at a crossed and the other at an uncrossed horizontal disparity relative to the depth that had been defined by the fixation point. The observers task was to indicate which gabor pair (upper or lower) was perceived to be nearest in depth to them.

A large (highly-diplopic) disparity and brief (140 ms) temporal duration (with rapid onset and offset of the stimulus) were used. This combination of disparity and temporal duration was used in order to tap the performance of the transient stereo-system to the exclusion of the sustained system. The performance measure used was the percentage of correct responses made by the observer. In order for this performance measure to be effective, observers must have been able to extract the depth of matched-orientation gabors at a relatively high level of performance. For each observer it was decided to use the largest disparity for which this was possible. Like D_{max} values, this value depended upon the particular observer. A mean disparity of 6° was used for observers CS and DP and 4° for ME. The magnitude of the disparity used was jittered from trial to trial in an anti-correlated manner, i.e. if the uncrossed gabor-pairs disparity was increased, the crossed pairs was decreased by the same amount. This was done to ensure that differences in perceived horizontal separation of the diplopic gabors could not be used as a cue to their depth. The magnitude of the jitter added to any given trial was randomly chosen from a set of three values. For DP and CS these values were 0.3, 0.15 and 0° and ME used half of these values, since he was less sensitive to this cue. Both crossed and uncrossed disparities were presented for two reasons. Firstly, it ensured that observers with a transient near or far depth bias (Richards, 1973) would be sensitive to at least one of the two dichoptic pairs of stimuli, and that this sensitivity would not vary significantly from trial to trial. Secondly, since the observers were fixating midway between the two pairs of gabors, they would be unable to use any vergence eye movements to determine which pair of gabors was at the near depth. In other words, the obtained results would not be confounded by any vergence responses elicited by the stimuli.

Three basic conditions were used. Two matched-orientation conditions and an orthogonal-orientation condition. In the matched conditions, the orientation of the carriers in the two dichoptic half-images were the same, either vertical or horizontal. In the orthogonal condition, vertical and horizontally oriented gabors were paired dichoptically. These three conditions were tested at four spatial frequencies: 0.5, 1, 2 and 4 cpd. For ease of comparison we used the same size Gaussian envelope (a standard deviation of 1°) for all of the carrier frequencies used. The contrast of all gabors was 100% and the mean luminance of the display was 25 cpd m^{-2}. A range of spatial frequencies were used since it has been previously shown that the dichoptic tuning of stereopsis to visual parameters can depend upon the spatial frequency of the stimulus. For example, contrast tuning, as indicated by the presence of a contrast-paradox effect (performance being worse for dichoptically-mixed as opposed to matched contrasts) depends upon the spatial frequency of the stimulus (Halpern & Blake, 1988; Legge & Gu, 1989; Schor & Heckman, 1989). A vertical gap of 1.35° was maintained between the two pairs of gabors to ensure that stimulus crowding did not occur (Westheimer & McKee, 1979). This was achieved by clipping the top vertical extent of the lower gabors and the bottom vertical extent of the upper ones. The centres of the gabors were separated vertically by 5.6°. Feedback was given to the observers, indicating whether their response was correct or not. The viewing distance was 1.0 m. Stimuli were presented in blocks of 20, within which the spatial frequency and orientation(s) used in each trial were kept constant. Each data point reported represents the mean of ten blocks of trials.

2.1.1.3. Apparatus. Stimuli were generated using a Cambridge Research Systems VSG 2/3 graphics card in a host Pentium computer and were displayed on a custom Model 3 Vision Research Graphics monitor. The dichoptic half-images were selectively presented to each eye via the use of Vision Research Graphics ferro-electric shutters. The fast decay rate of the monitors P46 phosphor (0.1 μs to 10% of the phosphors initial luminance value) ensured that there was no interocular cross-talk via the shutters. The frame rate of the monitor was 120 Hz so that the effective frame rate to each eye was 60 Hz. At this frame rate there was no noticeable flicker of the images. The observer initiated each trial and responded via a button box. A chin rest was used to stabilise the observers head.

2.1.2. Results and discussion

The results for the three observers are shown in Fig. 1. Performance (percent-correct responses) is plotted against the spatial frequency of the gabors. Error bars represent plus and minus one standard error of the mean. The basic pattern of results is substantially the same for all observers. Performance for the orthogonal condition, while still above chance, is worse than that obtained for the two matched-orientation conditions. For two of the observers, CS and ME, the degree of impairment for the orthogonal condition was substan-

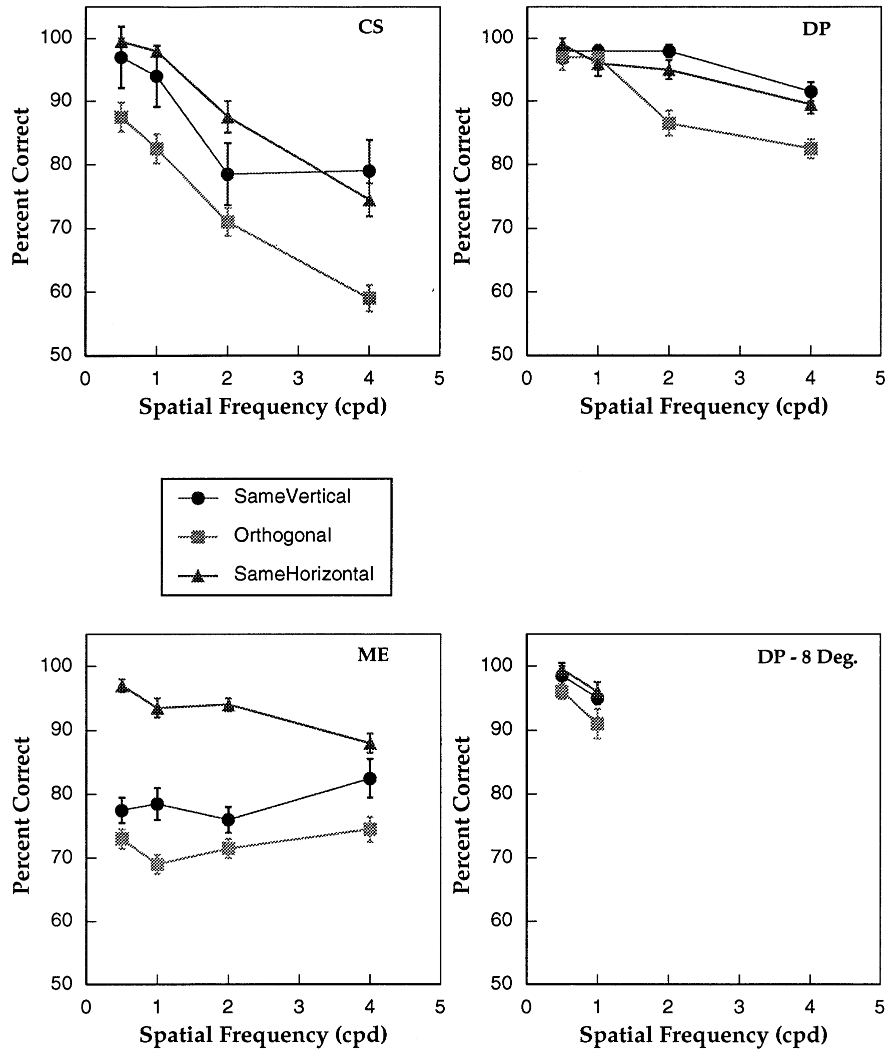

Fig. 1. Results for Experiment 1. Performance, percent correct response, is plotted against spatial frequency. Error bars represent ± 1 S.E.M. Three conditions were used: two in which the gabors had the same orientation, either vertical (SameVertical) or horizontal (SameHorizontal) and an orthogonal condition (Orthogonal). DP was fully tested at his standard disparity (6°) and also retested at the two lowest spatial frequencies at 8° disparity. All observers showed worse performance for the orthogonal condition, compared to the two other conditions.

tially independent of the spatial frequency of the stimuli, while for the third observer, DP, performance for the orthogonal condition at the two lowest frequencies (0.5 and 1 cpd) was the same as that for the matched conditions. Impaired performance for the orthogonal condition was obtained only at the higher two spatial frequencies. Wells and Simmons (1997) have also investigated the dichoptic-orientation tuning of stereo-depth perception using gabor patches with carrier spatial frequencies of 0.5–4 cpd. They found the same pattern of results that we obtained for observer DP. There was no difference in performance between the matched and orthogonal conditions at low (0.5 and 1 cpd) frequencies and performance was worse for the orthogonal condition at high (2 and 4 cpd) frequencies. To determine whether the matched performance for DP at the two lowest spatial-frequencies was due to a floor effect, we retested him on a more difficult version of the task. Task difficulty was increased by raising the disparity of the gabors to 8°. As can be seen from Fig. 1, DP now showed slightly differential performance at low spatial frequencies.

3. Experiment 2

3.1. The effect of differential contrast on transient stereo-performance

The above experiment showed that transient stereo-performance was typically better for matched, rather than for different (orthogonal) orientations. We have previously shown that a similar situation occurs with spatial frequency. Performance is better for matched rather than for mixed spatial frequencies (Schor et al., 1998). However, following Kontsevich and Tyler's

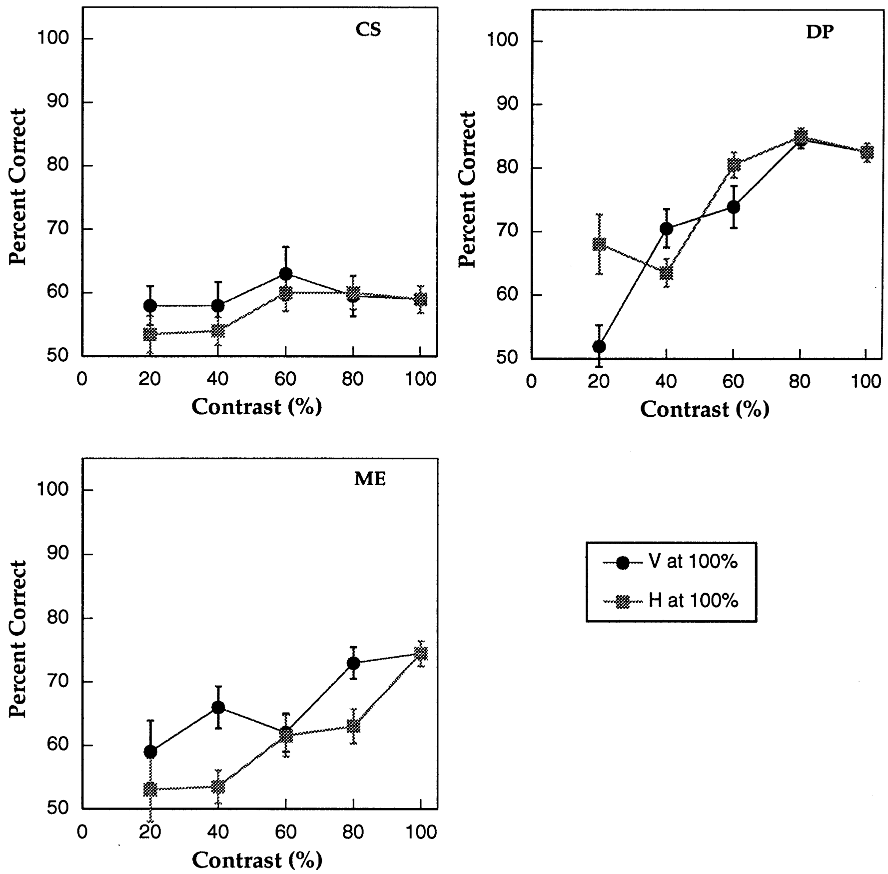

Fig. 2. Results for Experiment 2 which investigated the effect on performance of manipulating the relative contrasts of orthogonal gabors. In one condition, the contrast of the vertical gabor was held constant at 100% and that of the horizontal one was reduced in 20% steps (V at 100%) and in the other the opposite manipulation occurred (H at 100%). Neither manipulation resulted in an improvement in performance.

(1994) finding for the sustained stereo-system, we have also shown that transient-stereoscopic performance with mixed spatial frequencies can be improved by varying the relative contrasts of the different spatial frequencies. Specifically, transient stereo-performance can be improved by decreasing the contrast of the low spatial-frequency gabor relative to that of the high-frequency gabor (Schor et al., 1998). In the present experiment, we investigated whether a similar contrast manipulation would enhance transient stereo-performance with stimuli that had dichoptically-different orientations.

3.1.1. Method

3.1.1.1. Stimuli and procedure. The spatial arrangement of the stimuli was the same as that used in Experiment 1. Two conditions were used. In the first condition, the contrast of the vertically-oriented gabor was kept constant at 100% and that of the horizontally-aligned gabor was reduced in 20% steps. The second condition was the opposite of the first. The spatial frequency of the gabors was 4 cpd. This frequency was used since all observers showed impairment for the orthogonal-orientation condition, relative to the matched-orientation conditions, with this frequency in Experiment 1.

3.1.2. Results and discussion

The results for the three observers are shown in Fig. 2. Performance is plotted against contrast for both conditions. Note that the contrast value on the x-axis refers only to the contrast of one of the gabors in each dichoptic pair. The contrast of the other gabor was kept at 100%. The basic pattern of results is the same for all observers. Rather than improving performance, varying the relative contrasts of the horizontal and vertical gabors impaired performance.

To account for our previous finding that performance with mixed-spatial-frequencies improved when the relative contrasts of the gabors were varied, it was proposed that transient stereopsis is processed by a single broad-lowpass spatial-frequency-tuned channel whose two ocular-based signals interact in an inhibitory manner prior to binocular combination (Schor et al., 1998, see also Kontsevich & Tyler, 1994). The outcome of this interaction is that the subsequent binocular activity will be lowered if the two ocular-based signals are of different strengths. The activity in each ocular channel can be altered by varying either the contrast or the spatial frequency presented to that eye. This alteration in activity is possible since the transient stereo-system is tuned to both of these parameters. Thus performance for the mixed spatial-frequency condition could be improved by reducing the contrast of the gabor with the carrier frequency to which the system had greater sensitivity (Kontsevich & Tyler, 1994; Schor et al., 1998). The present finding that varying the relative contrasts of the orthogonal gabors did not improve performance thus suggests that reduced performance for the orthogonal condition is not caused by unequal sensitivity to the vertical and horizontal orientations.

4. Experiment 3

4.1. Mixing spatial frequencies for the orthogonal condition

While performance for the orthogonal-orientation condition was typically worse than that obtained for the matched conditions, it was above chance-level, indicating that the orthogonal stimulus was being processed by some channel. That this is a binocular, as opposed to a monocular channel (Kaye, 1978; Harris & McKee, 1996) is supported by the finding that performance decreased as the contrast of one of the gabors was reduced (see Fig. 2). Our inability to improve performance by varying the relative contrasts of the dichoptic gabors suggests that this channel is not involved in the processing of either the matched vertical or horizontal gabors. The question addressed in this experiment is whether the system that processes the orthogonal gabors exhibits dichoptic tuning to spatial frequency. That is, is performance with orthogonal gabors better for matched as opposed to mixed spatial frequencies?

4.1.1. Method

4.1.1.1. Stimuli and procedure. The spatial arrangement of the stimuli were the same as that used in Experiment 1. Three conditions were used. A 0.5 cpd vertically oriented gabor was paired with either a 1, 2 or 4 cpd horizontally oriented gabor.

4.1.2. Results and discussion

The results for the three observers are shown in Fig. 3. Results for the mixed spatial-frequency condition (Mixed SFs (0.5+)) are shown plus, for purposes of comparison, results for the conditions in which the spatial frequency of the gabors were matched (Matched SFs-data from the orthogonal condition in Experiment 1). Two observers (ME and DP) showed evidence of spatial-frequency tuning, i.e. their performance was better for the matched condition than it was for the mixed condition. The third observer (CS) showed no evidence of spatial-frequency tuning with orthogonal gabors. His performance for the two conditions was the same.

5. Experiment 4

5.1. Orthogonal condition, mixing contrasts and spatial frequencies

Results from the previous experiment suggest that the system involved in processing stereo-depth from orthogonal gabors is binocularly tuned to spatial frequency. Given the apparent broadband nature of this system (Fig. 1) there are two main ways that this tuning could be implemented. The first is by a number of narrowband channels that remain functionally independent up to and including the stage where binocular depth is extracted (Schor et al., 1998). The second possibility is that performance could be mediated by a single broadband channel that has two characteristics. The first is that the channel shows differential sensitivity to the various spatial-frequencies. The second characteristic is that the channel has dichoptic contrast-tuning (Kontsevich & Tyler, 1994). This contrast tuning could be implemented by an ocular-based inhibitory link prior to binocular combination. This putative broadband spatial-frequency channel could be formed by the pooling of several narrowband channels and such a channel appears to mediate performance for gabors of matched orientations (Schor et al., 1998). The aim of this experiment was to determine which of these two models (if either) are consistent with stereo-responses to transient-orthogonal stimuli. This aim was achieved by varying the relative contrasts of the dichoptically mixed-spatial-frequency gabors. If independent-narrowband channels are employed, then transient-stereoscopic performance should be impaired as the relative contrasts are varied. However, if a broadband channel is mediating performance on the task, performance should improve as the relative contrast is manipulated.

5.1.1. Method

5.1.1.1. Stimuli and procedure. The spatial arrangement of the stimuli was the same as that used in Experiment 1. Two conditions were used. In both conditions, a

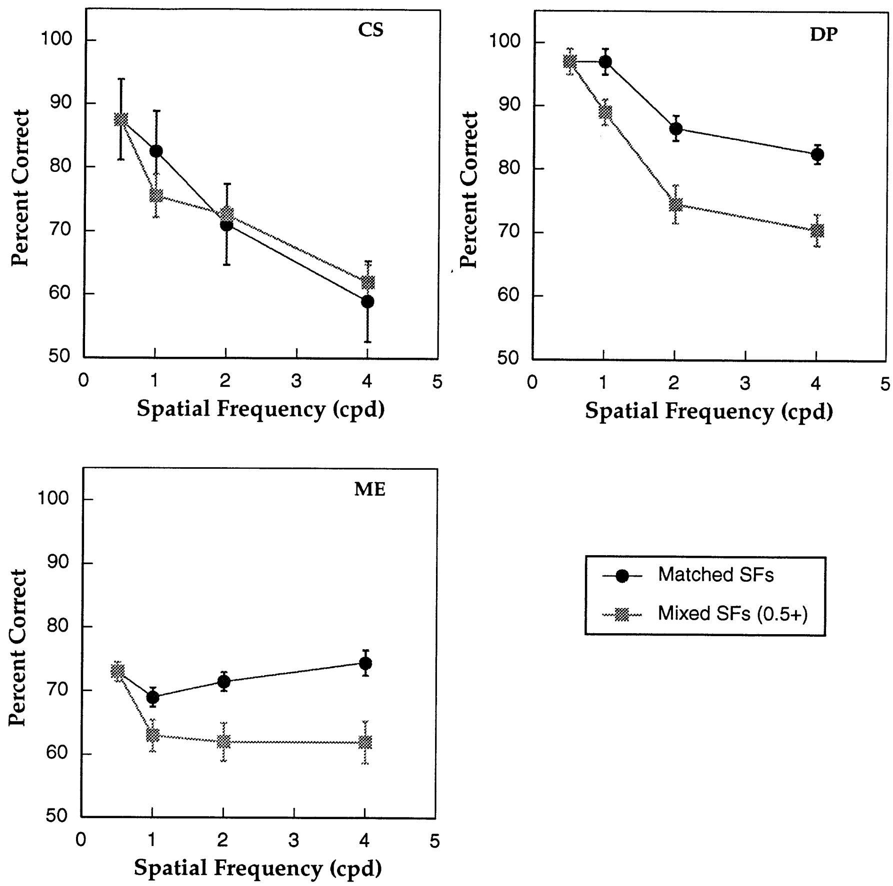

Fig. 3. Results for Experiment 3. For the orthogonal condition, performance with gabors of matched spatial frequencies (Matched SFs) is compared to that for a mixed frequency condition in which a 0.5 cpd gabor was with a 1, 2 or 3 cpd one (Mixed SFs (0.5 +)). Two of the observers (DP and ME) show best performance for the matched SFs condition while CS shows the same performance for both.

vertical 0.5 cpd gabor was paired with a horizontal 4 cpd gabor. In one condition, the contrast of the 0.5 cpd gabor was kept at 100% and the contrast of the 4 cpd gabor was reduced in 20% steps. In the other condition, the opposite manipulation occurred (i.e. the contrast of the horizontal 4 cpd gabor was kept at 100%).

5.1.2. Results and discussion

The results for the three observers are shown in Fig. 4. Performance is plotted against contrast for both conditions. All three observers showed an improvement in performance as the contrast of either of the gabors in the dichoptic pair was reduced relative to that of the other. However the actual contrast value at which the improved performance occurred was different for the three observers. ME showed improved performance as the contrast of either the 0.5 or 4 cpd gabor was reduced to 80 or 60%. DP showed improvement at these contrasts when the contrast of the 0.5 cpd gabor was reduced, while the contrast of the 4 cpd gabor had to be reduced to 20% before a marked improvement in performance was observed. The pattern of results for CS were the mirror image of those of DP.

The present finding is that performance with orthogonally-orientated gabors, of dichoptically-mixed spatial-frequencies, was improved by decreasing the relative contrast of either the low or high spatial-frequency gabor in the dichoptic pair. We previously obtained a different pattern of results with matched carrier-orientations. With matched carrier-orientations, performance could be increased only by decreasing the contrast of the low-spatial-frequency gabor (Schor et al., 1998). These different findings suggest that while transient stereo-performance with gabors of matched-vertical orientations is mediated by a single broad-band-lowpass channel (Schor et al., 1998) transient stereo-performance with orthogonal gabors is mediated by multiple (at least two) spatial-frequency-tuned channels. At least two channels are necessary to account for the results with the orthogonal stimuli since with a single lowpass spatial-frequency-tuned channel, it is possible to match the responses in the two ocular-based channels only by decreasing the contrast of the

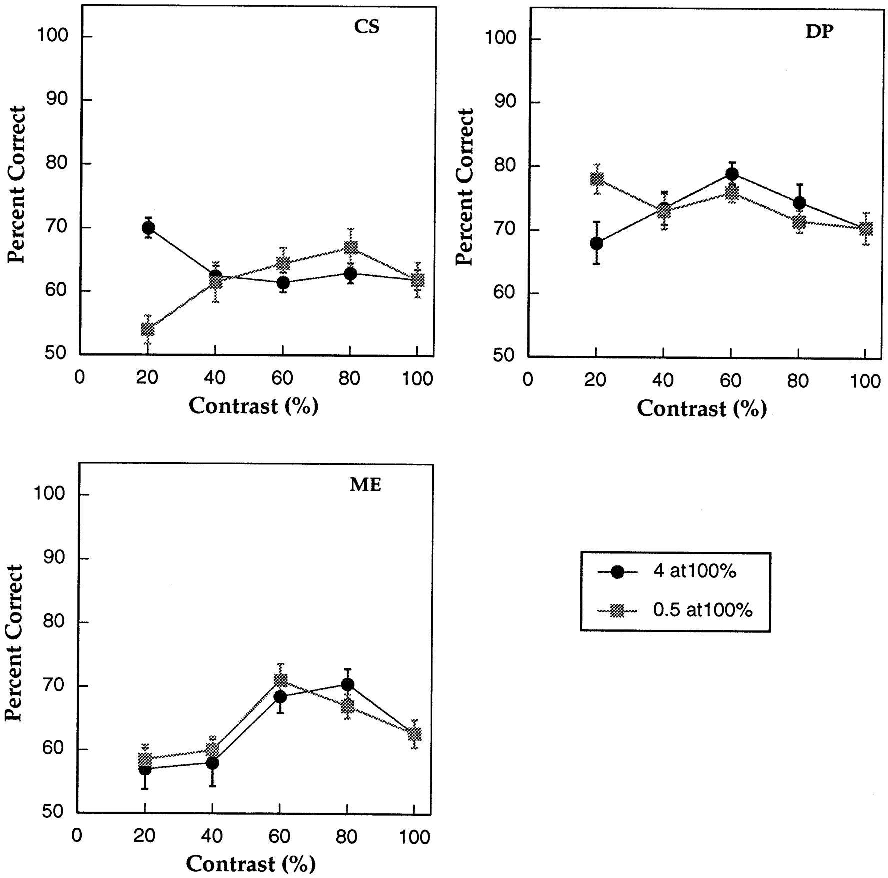

Fig. 4. Results for Experiment 4. For the orthogonal condition with mixed spatial frequencies (0.5 and 4 cpd) the effect of manipulating the relative contrasts of the gabors was investigated. For all observers, both keeping the contrast of the 4 cpd gabor and reducing that of the 0.5 cpd one (4 at 100%) and holding the contrast of the 0.5 constant and reducing that of the 4 cpd gabor (0.5 at 100%) resulted in improved performance.

lower spatial frequency relative to the other. Performance of a lowpass system would be impaired by lowering the contrast of the high-spatial-frequency gabor relative to the low-frequency gabor. However, the performance of a highpass system would be improved by lowering the contrast of the high-spatial-frequency gabor relative to the low-frequency gabor. Thus a system which incorporates both lowpass and highpass spatial-frequency-tuned channels could account for the present results with the orthogonal condition. See Schor et al. (1998) for a full discussion.

While the results in Fig. 4 suggest such a multi-channel model, the observed change in performance is relatively slight. To further test this model, and in particular the presence of a lowpass channel, the three observers were retested on a new spatial-frequency pairing. Observers DP and ME were tested with a pairing of 0.25 and 4 cpd while CS was tested with 1 and 4 cpd. Selection of these frequency pairings was based upon the pattern of results obtained for the condition in which the contrast of the 0.5 cpd gabor was reduced relative to that of the 4 cpd gabor (Fig. 4). For this condition, both DP and ME showed optimal performance at a relatively high contrast for the 0.5 cpd gabor. Thus if performance is being mediated by a lowpass channel, optimal performance with the 0.25 cpd gabor should be obtained at a lower, though still measurable contrast as compared to the optimal-contrast obtained for the 0.5 cpd condition. For CS, however, optimal performance with the 0.5 cpd gabor was obtained at the lowest contrast used (20%). Thus for him the higher (1 cpd) spatial-frequency gabor was paired with the 4 cpd gabor. For CS a lowpass channel would be indicated if his optimal performance with the 1 cpd gabor was obtained at a higher contrast than that obtained with the 0.5 cpd gabor.

Results for these conditions are shown in Fig. 5. For the purposes of comparison, the results for the 4 and 0.5 cpd condition are also presented. For all observers the pattern of results obtained is consistent with performance being mediated by a lowpass system in which the strength of the two ocular-based signals need to be matched (dichoptic contrast-tuning). For the new conditions, all observers showed optimal performance when the contrast of the low-frequency stimulus was

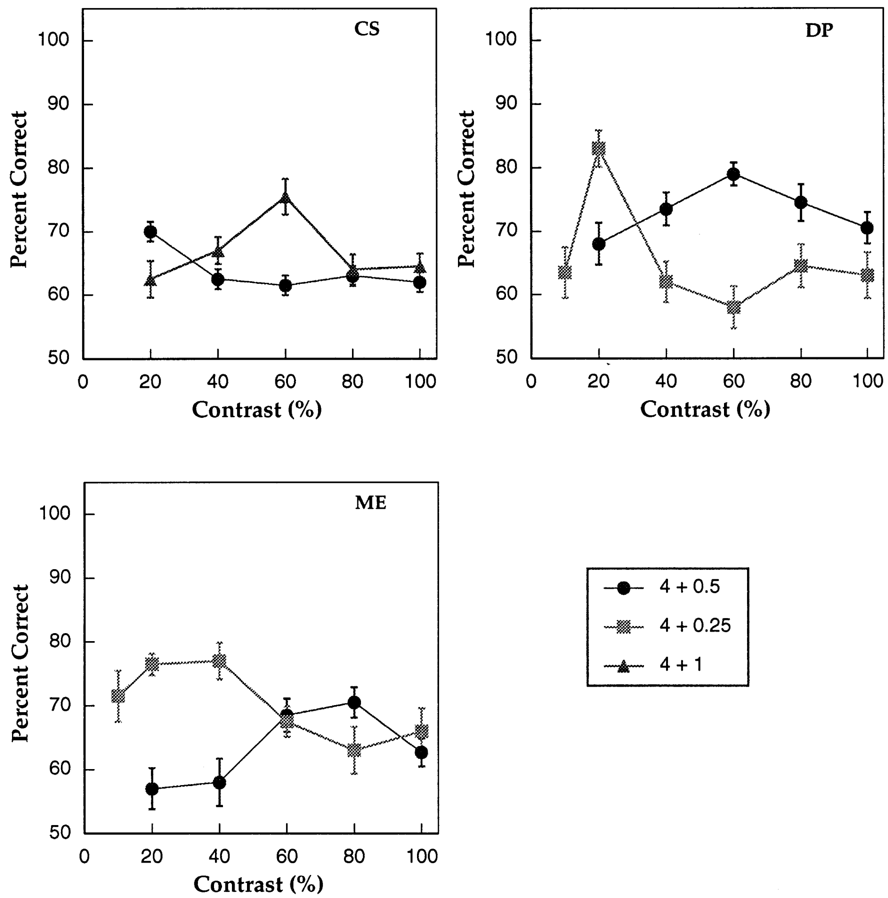

Fig. 5. Results for the additional spatial-frequency pairings. Observers DP and ME were tested with 4 and 0.25 cpd and CS with 4 and 1 cpd. For purposes of comparison, results for the 4 and 0.5 cpd pairing is also shown. In all conditions, the contrast of the 4 cpd gabor was kept at 100% contrast and the contrast of the other gabor is indicated by the x-axis value.

below 100% and the offset of this contrast, relative to that obtained for the original condition (4 plus 0.5 cpd) was in the predicted direction. For DP and ME, optimal performance with the 0.25 cpd gabor was at a lower contrast than that obtained with the 0.5 cpd gabor while for CS, the optimal performance with the 1 cpd gabor was obtained at a higher contrast than that for the 0.5 cpd gabor.

Since optimal performance in the above conditions were obtained at low contrasts, it is unlikely that performance was being mediated by a first-order system that responded to any luminance artifacts in the stimulus. The use of gabors in sinewave phase balances the luminance energy in the stimulus i.e. luminance increments and decrements are the same. Though perceptually, this is true only if there are no asymmetries or compressive non-linearities in the response of the initial detectors to light increments and decrements (Cornsweet, 1970). Such compressive non-linearities are unlikely to exist at the low-contrast levels used here. Obtaining optimal performance at low contrasts also makes it unlikely that performance was being based upon cues from the vergence system. That is, it is unlikely that observers were making vergence eye-movements to one of the gabor pairs and determining the sign of the depth of that pair based upon that vergence response (Howard & Rogers, 1995). If such a process was occurring, optimal performance should have been obtained at the highest, rather than the lowest contrasts used (Edwards et al., 1998).

6. General discussion

The results from the present study show that: (1) while observers could extract depth from orthogonally oriented gabors at above chance levels, their performance was worse than that with gabors of matched orientation; (2) varying the relative contrasts of the two orthogonally oriented gabors of the same spatial frequency resulted in a reduction in performance; (3) varying the relative spatial frequencies of the orthogonally oriented gabors impaired performance, relative to that for matched frequencies; and (4) varying the relative contrasts of orthogonal gabors that were at different spatial frequencies could improve performance.

The fact that the reduced performance for the orthogonal condition could not be improved by varying the relative contrasts of the mixed vertical and horizontal gabors is interpreted as indicating that performance for the orthogonal condition is not mediated by either of the channels involved in the extraction of depth from the horizontal or vertically matched gabors. The logic for this assertion is as follows. According to the Kontsevich and Tyler (1994) contrast-tuning model, non-optimal performance occurs when the two ocular-based signals have different signal intensities. Performance can be improved by balancing the two signal intensities. Thus if the system is dichoptically presented with two stimuli to which it shows differential sensitivity (e.g. two gabors with different spatial frequencies) reducing the contrast of the stimulus to which the system is more sensitive will reveal a balance point where both ocular responses to the two spatial frequency and contrast combinations are equal. Thus performance will be improved relative to the condition in which the different frequency gabors have the same contrast. We have shown this to be the case for performance with gabors of matched (Schor et al., 1998) and orthogonal (present Experiment 4) orientations. Such a finding supports the proposed model and shows that the system is broadly tuned to spatial frequency and contrast over the ranges used in the experiments. A similar situation should occur for a channel tuned to orientation. That is, the response of a orientation-tuned channel would be reduced as the orientation of the stimulus is varied from the channels preferred orientation, just as the response of a spatially-tuned channel varies with spatial frequency. Hence the finding that varying the relative contrast of the two orthogonal gabors of the same spatial frequency did not improve performance indicates that the channel(s) mediating performance does not have peak-tuning sensitivity for either vertical or horizontal orientations. That is, performance for the orthogonal condition is not mediated by either of the binocular channels processing matched vertical or horizontal gabors. This apparent lack of binocular tuning to stimulus orientation is indicative of a second-order pathway.

That the channel mediating performance for the orthogonal gabors is actually a binocular, as opposed to a monocular channel (Kaye, 1978; Harris & McKee, 1996) is supported by the additional finding that performance for two of the observers decreased as the contrast of one of the gabors was reduced (Fig. 2). Interestingly, while this channel appears to be largely insensitive to stimulus orientation, it does exhibit binocular spatial-frequency tuning. Performance was better for orthogonal gabors of matched spatial frequency than for mixed frequencies. Such spatial-frequency tuning could result from pooling of a number of independent narrowband spatial-frequency-tuned channels. However, given the broadband tuning to stimulus orientation, this situation is unlikely. The finding that performance with orthogonal gabors of unmatched spatial frequency (0.5 and 4 cpd) could be improved by varying the relative contrasts of the gabors suggests that performance is mediated by a broadband system that has dichoptic spatial-frequency tuning. Furthermore, the fact that lowering the contrast of either the high or low spatial-frequency gabor could improve performance suggests the presence of at least two broadband channels; one with its peak sensitivity at a low and the other at a high frequency. Thus the present results suggest that transient-stereopsis performance is mediated by at least two types of channels. One that is tuned to stimulus orientation, and is possibly a first-order mechanism, and another that is largely insensitive to stimulus orientation and is likely to be a second-order (envelope-extraction) mechanism (Cavanagh & Mather, 1989; Sato & Nishida, 1993; Hess & Wilcox, 1994). It is also possible that both transient-stereoscopic channels are second-order, differing only in terms of the range of orientations that their initial input filters are tuned to. Whether such a pattern of results is also obtained at small (non-diplopic) disparities still needs to be determined, though pilot studies have indicated that observers can extract depth from briefly-presented orthogonal stimuli at small (0.5°) disparity. Note that this preliminary finding further supports the notion that the defining difference between the transient- and sustained-stereoscopic systems resides in their respective temporal sensitivities, and not in the range of disparities to which they are sensitive.

Acknowledgements

This research was supported by NEI grant EYO-8882.

References

Cavanagh, P., & Mather, G. (1989). Motion: the long and the short of it. *Spatial Vision*, *4*(2/3), 103–129.

Cornsweet, T. N. (1970). *Visual perception*. New York: Academic Press.

Edwards, M., Pope, D. R., & Schor, C. M. (1998). Luminance contrast and spatial-frequency tuning of the transient-vergence system. *Vision Research*, *38*(5), 705–717.

Halpern, D. L., & Blake, R. (1988). How contrast affects stereoacuity. *Perception*, *17*, 3–13.

Harris, J. M., & McKee, S. P. (1996). Monocular location provides a signed 'depth signal' for discriminating the sign of large disparities. *Investigative Ophthalmology & Visual Science*, 37 (3), pS283.

Hess, R. F., & Wilcox, L. M. (1994). Linear and non-linear filtering in stereopsis. *Vision Research*, *34*, 2431–2438.

Howard, I. P., & Rogers, B. J. (1995). *Binocular vision and stereopsis*. Oxford: Oxford University Press.

Jones, R. (1980). Fusional vergence: sustained and transient components. *American Journal of Optometry and Physiological Optics*, *57*(9), 640–644.

Kaye, M. (1978). Stereopsis without binocular correlation. *Vision Research*, *28*, 1013–1022.

Kontsevich, L. L., & Tyler, C. W. (1994). Analysis of stereo thresholds for stimuli below 2.5 cpd. *Vision Research*, *34*(17), 2317–2329.

Legge, G. E., & Gu, Y. (1989). Stereopsis and contrast. *Vision Research*, *29*(8), 989–1004.

Mitchell, D. E. (1969). Qualitative depth localization with diplopic images of dissimilar shape. *Vision Research*, *9*, 991–994.

Mitchell, D. E., & O'Hagan, S. (1972). Accuracy of stereoscopic localization of small line segments that differ in size or orientation for the two eyes. *Vision Research*, *12*, 437–454.

Ogle, K. (1952). On the limits of stereoscopic vision. *Journal of Experimental Psychology*, *44*, 253–259.

Pope, D. R, Edwards, M., & Schor, C. M. (1998a). Orientation and contrast tuning of the transient-vergence system. *Vision Research*, *39*(3), 575–584.

Pope, D. R., Edwards, M., & Schor, C. M. (1998b). Extraction of depth from opposite-contrast stimuli: Transient system can, sustained system cant. *Vision Research* (submitted).

Rashbass, C., & Westheimer, G. (1961). Disjunctive eye movements. *Journal of Physiology* (*London*), *159*, 339–360.

Richards, W. (1973). Reversal in stereo discrimination by contrast reversal. *American Journal of Optometry and Archives of American Academy of Optometry*, *50*(11), 853–862.

Richards, W., & Foley, J. M. (1971). Interhemispheric processing of binocular disparity. *Journal of the Optical Society of America*, *61*, 419–421.

Sato, T., & Nishida, S. (1993). Second-order depth perception with texture-defined random-dot stereograms. *Investigative Ophthalmology and Visual Science*, *34*, 1438.

Schor, C. M., Edwards, M., & Pope, D. R. (1998). Spatial-frequency tuning of the transient-stereopsis system. *Vision Research*, *38*(20), 3057–3068.

Schor, C. M., & Heckman, T. (1989). Interocular differences in contrast and spatial frequency: effects on stereopsis and fusion. *Vision Research*, *29*, 837–847.

Schor, C. M., Wood, I., & Ogawa, J. (1984). Spatial tuning of static and dynamic local stereopsis. *Vision Research*, *24*, 573–578.

Simmons, D. R., & Kingdom, F. A. A. (1995). Differences between stereopsis with isoluminant and isochromatic stimuli. *Journal of the Optical Society of America A*, *10*, 2094–2104.

Wells, A. T., & Simmons, D. R. (1997). The influence of first-order orientation information on second-order stereopsis. *Investigative Ophthalmology & Visual Science*, *38*(4), 906.

Westheimer, G., & McKee, S. P. (1979). What prior processing is necessary for stereopsis. *Investigative Ophthalmology and Visual Science*, *18*(6), 614–621.

Westheimer, G., & Tanzman, I. J. (1956). Qualitative depth localization with diplopic images. *Journal of the Optical Society of America*, *46*(2), 116–117.

Wilcox, L. M., & Hess, R. F. (1996). Is the site of non-linear filtering in stereopsis before or after binocular combination. *Vision Research*, *36*, 391–399.