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Luminance Contrast and Spatial-frequency Tuning of the Transient-vergence System

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Vergence has transient components that are stimulated by brief presentations of stimuli at large disparities (up to several degrees). The question that we have addressed is what stimulus features are encoded by this system. A competition paradigm [Jones & Kerr, (1972). *Vision Research, 12,* 1425–1430) was used in which three gabors were presented. A single Gabor was presented to the fovea of one eye and two gabors, 2.5 deg to either side of the fovea, to the other; one of which, when paired with the single Gabor defined a convergent direction, the other a divergent direction. When these Gabors are identical, observers have a tendency to respond in one particular direction. First we determined if increasing the luminance contrast of the Gabor pair whose disparity was opposite to the observer's response-bias direction (variable-contrast pair) relative to the remaining Gabor (reference) could alter the observer's response direction. Secondly, we determined if the contrast required for such a change in response was affected by the relative spatial frequency of the convergent and divergent Gabors. The reference Gabor was held at 2 cpd and the variable Gabor pair was varied between 5.6 and 0 (a gaussian) cpd. Results demonstrated that increasing the luminance contrast of the variable pair relative to the reference Gabor could alter the observer's response direction, even when the contrast of only one of the variable-pair Gabors was increased. The luminance contrast required for this change to occur was directly related to the spatial frequency of the variable pair over the entire frequency range tested. Vergence responses were preferentially made to lower spatial frequencies, even when a low spatial frequency was paired with a high one. We conclude that transient-vergence responses are not reduced by mixed contrasts (i.e. no contrast-paradox effect) and appear to be mediated by a system that employs a single lowpass sensitive channel.

Spatial frequency Contrast Vergence Stereopsis Transient

INTRODUCTION

In order to change the alignment distance of the eyes, it is necessary for the two eyes to move in opposite horizontal directions. Such eye movements are called disparity-vergence eye movements when elicited by binocular parallax and they appear to comprise two components. The first is a transient component which initiates the movement and the second is a sustained component which controls fine vergence movements as the two eyes converge onto a target and maintain a vergence lock on the stimulus. It is possible that these two components are mediated by separate systems (Erkelens, 1987; Jones & Kerr, 1971; Semmlow, Hung, Horng, & Ciuffreda, 1993). Prior studies have isolated transient, as opposed to the sustained, vergence responses by using either briefly flashed stimuli (Jones & Kerr, 1971; Mitchell, 1970; Bussettini, Miles, & Krauzlis, 1996) or disparities substantially in excess of Panum's fusional range; up to 10 deg (Erkelens, 1987). In the present study we combined these two stimulus features, short stimulus-duration (500 msec) and large disparities (2.5 deg) in an attempt to tap the transient-vergence system. It should be stressed here that we are investigating the transient mode of the vergence system, which is a separate issue from saccade-facilitated vergence (Maxwell & King, 1992; Enright, 1984).

Since vergence eye movements involve the co-ordinated movements of the two eyes, which generally follow Hering's Laws, it is reasonable to assume that the system that controls such movements relies upon binocular input—though as we shall discuss (and dismiss) later, an argument could be made for the possibility that the transient-vergence system could use purely monocular input. The general aim of the present paper is to determine what stimulus features are encoded by the transient-vergence system.

Studies by Westheimer and Mitchell (1969), Mitchell (1970) and Jones and Kerr (1971) have addressed this

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issue. These authors investigated the ability of observers to make vergence movements to various transient stimuli. They concluded that the transient-vergence system is not selective to stimulus form, since they found that vergence responses were initiated when dissimilar-shaped stimuli were presented to each eye. Additionally, the magnitude of these responses were the same as those elicited by similar stimuli. It is also worth noting that while these authors found that vergence responses could be initiated by dissimilar stimuli, such stimuli did not allow sensory-motor fusion to occur. This finding suggests that the sustained-vergence system is more form-selective than the transient system.

A consideration of the dissimilar stimuli used in these studies leads to one possible explanation for their failure to find any degree of form selectivity. Westheimer and Mitchell (1969) employed circles and crosses (which were also used by Mitchell, 1970) or short lines of various lengths (up to 40 arc min) and orientation. Jones and Kerr (1971) used curved line segments with the stimulus presented to each eye having either the same or opposite curvature. The lines were 3.5 by 0.5 deg and were slightly curved (the actual degree of curvature is not given in the paper). It is important to note that the spatial-frequency representations of these "dissimilar" stimuli are not dissimilar across the entire frequency spectrum. In the case of the stimuli used by Westheimer and Mitchell (1969) and by Mitchell (1970) there is substantial common low-spatial-frequency information. Similarly with the Jones and Kerr stimuli, an oriented spatial-frequency-tuned filter, tuned to the appropriate spatial frequency (which would be at a lower spatial frequency than the one optimally tuned to straight versions of the lines) would give a strong response to the lines, regardless of the direction of curvature of the lines. It is therefore possible that the transient-vergence system matched the various "dissimilar" stimuli, based upon this common low spatial-frequency information.

In order to test this possibility the present paper uses stimuli that have a band-limited spatial-frequency composition which can be arranged so that there is minimal overlap in their spatial-frequency content. That a different pattern of results might be obtained for stimuli that do not contain significant overlap in their spatial-frequency content is suggested by similar studies of the motion system. It was initially thought that low-level motion units were not selective for spatial frequency since it had been shown that apparent motion could be perceived between dissimilar geometrical shapes like circles and squares (Kolers & Pomerantz, 1971; Navon, 1976). However, Green (1986) was able to show differential sensitivity to different spatial frequencies when he used band-limited Gabor stimuli (see also Werkhoven, Sperling, & Chubb, 1993; Nishida, Ledgeway, & Edwards, 1997). Gabors are the product of a gaussian and a sinewave grating. These stimuli have proved to be effective in investigating the spatial-frequency tuning in various types of visual processing (e.g. Green, 1986; Hess & Wilcox, 1994; Kooi, DeValois, & Switkes, 1991) and will be used in the present study.

Volitional eye movements

In addition to the spatial composition of the stimuli, another important consideration is their spatial layout. For example, the studies by Westheimer and Mitchell (1969) and Mitchell (1970) used isolated targets, with a single image being presented to each eye. However, it is not entirely clear that such a spatial arrangement taps the low-level, or involuntary, vergence system; as opposed to the attention-based or volitional system (McLin & Schor, 1988). That is, since only a single target was presented, it is possible that the observers made a voluntary decision to verge to the only stimulus that was visible to them—though the short stimulus duration of 200 msec used in those studies would have minimized the likelihood of a volitional response. Such isolated targets are thus not ideal stimuli for investigating the spatial-tuning characteristics of the involuntary transient-vergence system.

The study by Jones and Kerr (1971) overcame this problem by employing a competition paradigm. One eye was presented with a single stimulus at the point of fixation, while the other eye was presented with two stimuli, one on either side of the fixation point. Thus, on any given stimulus presentation the observer was confronted with both a potential convergent and a divergent stimulus pairing. Whether the transient-vergence system is tuned to a particular stimulus property can be determined by varying that stimulus dimension in the two stimuli presented to one eye, so that for one stimulus pairing (e.g. divergent) the stimuli presented to both eyes are the same, while for the other pairing (convergent) they differ. Observers' responses should be biased towards the stimulus pairing for which the feature is matched if the transient-vergence system is tuned to that particular feature. If the system is not tuned to the stimulus feature, then varying it should have no effect upon the observers' response.

Observer's response bias

We used a modification of the Jones and Kerr competition paradigm in the present paper. An important point to consider when using this paradigm is that most people have a bias to respond in a particular direction, either to converge or diverge, when the potential divergent and convergent stimuli pairs are composed of identical stimuli. Jones and Kerr (1971) altered the "magnitude" of the competing stimuli pairs by varying the relative disparity of the two stimuli presented to the one eye. They found that if a particular observer had a specific response bias, e.g. to diverge, then a convergent response could be elicited by decreasing the disparity offset of the convergent stimulus relative to the divergent one. That is, the transient-vergence systems appears to be biased towards initiating responses to the nearest stimulus. In altering the observer's response, we attempted to vary a stimulus feature that did not alter the spatial relationship of the stimuli and also one that

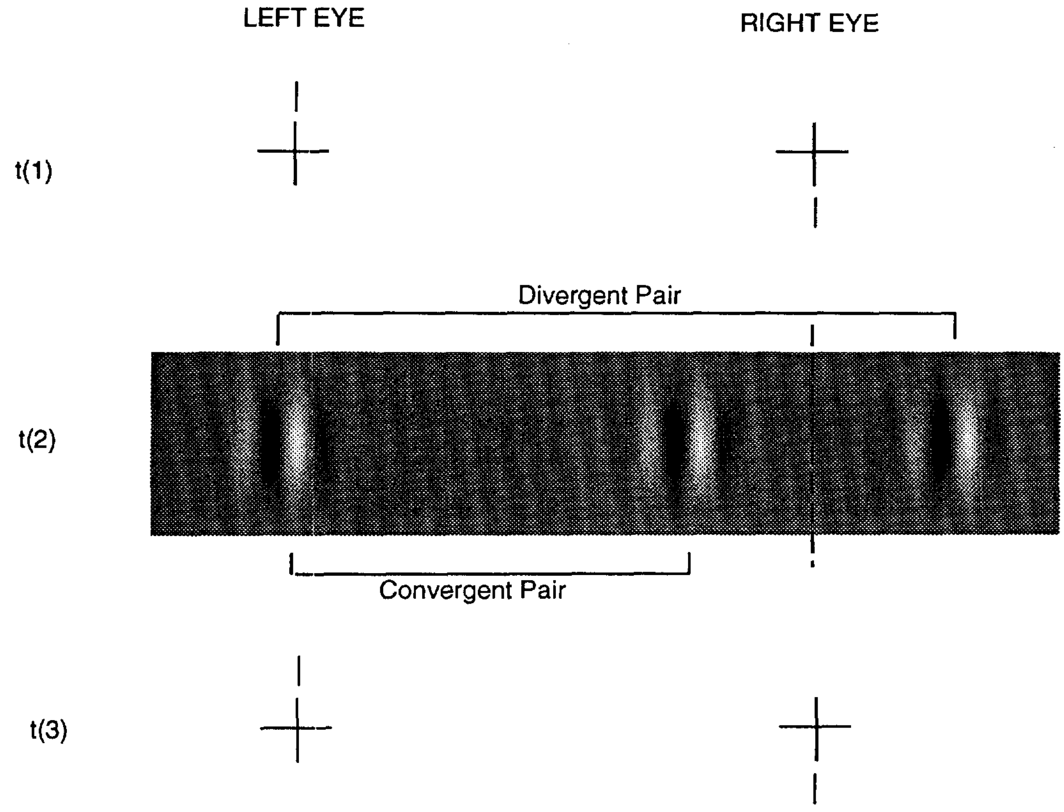

FIGURE 1. Procedure used to present the stimuli. Observers initially fused fixation crosses and nonius lines (t1). Once the nonius lines where aligned, the observer initiated the presentation of the test stimuli. The test stimuli (t2) appeared following a random delay of between 100 and 1000 msec. In order to minimize the effect of adaptation over the course of a block of trials, the luminance-contrast polarity of the fixation crosses and nonius lines was reversed following each presentation. The test image consisted of two different images which were dichoptically presented. One image contained a single Gabor (single-stimulus Gabor) while the other contained two Gabors (twin-stimulus image). The single-stimulus Gabor was placed at the former location of the fixation cross in one eye and the two Gabors in the twin-stimulus image were placed symmetrically about the fixation position in the other eye; one at a crossed disparity (twin-stimulus convergent Gabor) and the other at an uncrossed disparity (twin-stimulus divergent Gabor) when paired with the single-stimulus Gabor. Thus, on each trial either a convergent or divergent pairing was possible.

would provide a useful metric in gauging the effect of spatial frequency on vergence responses. One obvious candidate for such a parameter is luminance contrast.

EXPERIMENT 1: EFFECT OF LUMINANCE CONTRAST

A number of electrophysiological studies have shown that the response of cells in the visual system increases as the luminance contrast of the stimulus is raised (up to a saturation level). Consistent with such findings, psychophysical studies have shown that for various visual tasks, increasing the luminance contrast of a stimulus above its threshold level increases its salience to the visual system (Edwards, Badcock, & Nishida, 1996; Raymond & Darcangelo, 1990; Cormack, Stevenson, & Schor, 1991). The aim of the present study was to determine whether altering the relative contrasts of the divergent and convergent stimuli in the Jones and Kerr competition paradigm could alter the response bias of observers.

Method

Observers. Four male observers were used, the three authors and one observer (MC) who was naive with respect to the aims of the study. All observers had either normal (ME) or corrected to normal (CS, DP & MC) visual acuity, with no history of any visual disorders.

Apparatus. Stimuli were generated using a Cambridge Research Systems VSG 2/3 graphics card in a host Pentium computer and were displayed on a Sony Trinitron Multiscan 20SE color monitor. The monitor screen was divided in half vertically and the images were selectively presented to each eye via a telestereo scope. The observer initiated each trial via a button box and eye movements were recorded via a SRI dual-Purkinje eye-tracker. To stabilize the observer's head, a bite bar and forehead rest were used.

Stimuli and procedure. The stimuli used were Gabors which are defined by the following equation:

$$L = \left[\frac{1}{\sqrt{2 \cdot \pi} \cdot \sigma_x} \cdot e^{-\frac{1}{2 \cdot \sigma_x^2}(x-\mu_x)^2}\right] \cdot \left[\frac{1}{\sqrt{2 \cdot \pi} \cdot \sigma_y} \cdot e^{-\frac{1}{2 \cdot \sigma_y^2}(y-\mu_y)^2}\right] \cdot \cos(2 \cdot \pi \cdot x \cdot SF),$$

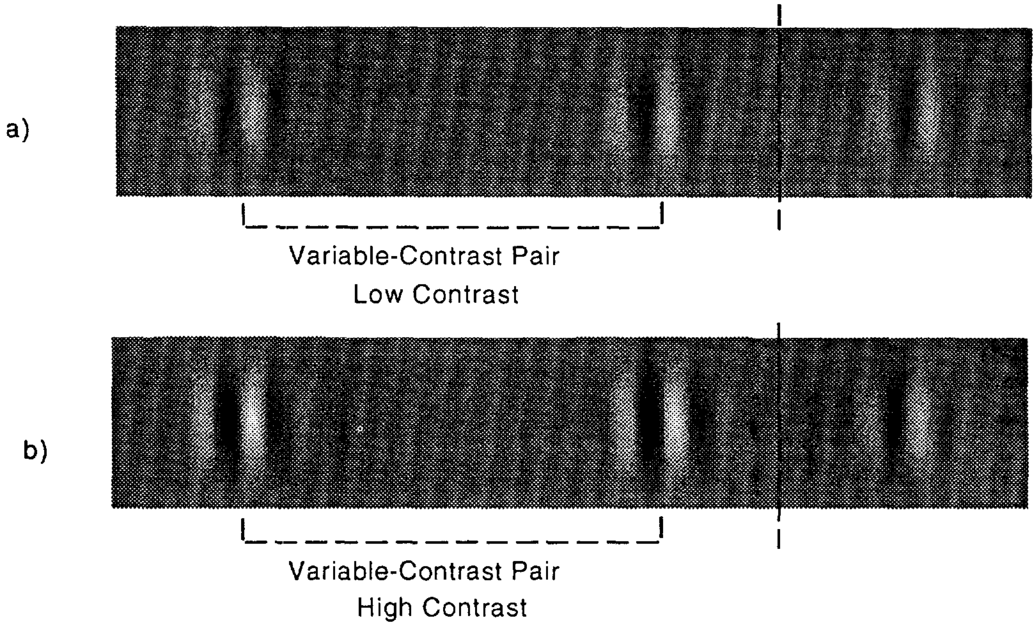

FIGURE 2. Contrast manipulations used in the present studies. The two Gabors that defined the response direction that was opposite the observers response-bias direction (variable-contrast pair) were varied while the contrast of the remaining Gabor was held contrast. Depicted are the contrast manipulations for an observer with a divergence bias. (a) Contrast of all three Gabors the same. (b) High contrast on the variable-contrast pair.

where L represents luminance contrast; σ_x and σ_y are the standard deviations in the x and y directions, respectively; μ_x and μ_y are center x and y values, respectively, of the Gabor and SF is the spatial frequency. The stimuli were presented as shown in Fig. 1. The observer first maintained fixation on a pair of crosses and nonius lines. Once the observer had established fixation he initiated the presentation of each test stimulus. A random delay of between 100 and 1000 msec was included prior to the disappearance of the fixation stimuli and simultaneous presentation of the test stimuli in order to prevent the observer from making anticipatory eye movements. Additionally, in order to minimize the effect of adaptation over the course of a block of trials, the luminance-contrast polarity of the fixation crosses and nonius lines was reversed following each presentation. The test image consisted of two different images which were dichoptically presented. One image contained a single Gabor, and will be referred to as the single-stimulus Gabor, while the other contained two Gabors; the twin-stimulus image. The single-stimulus Gabor was placed at the former location of the fixation cross in one eye and the two Gabors in the twin-stimulus image were placed symmetrically about the fixation position in the other eye; one at a crossed disparity (twin-stimulus convergent Gabor) and the other at an uncrossed disparity (twin-stimulus divergent Gabor) when paired with the single-stimulus Gabor. Thus, on each trial either a convergent or divergent pairing was possible. Two disparity offsets were used. All observers were tested at an offset of 2.5 deg (that is, total separation between the two Gabors of 5 deg) and two observers were additionally tested at an offset of 5 deg. The eye that was presented with the single-stimulus image was randomized from trial to trial. The duration of the test stimulus was 500 msec and the standard deviation of each Gabor was 0.5 deg with a carrier frequency of 2 cpd.

The experimental procedure consisted of several steps. The first was to use three identical Gabors to find the observer's response-bias direction, either convergent or divergent. Then the contrast of the twin-stimulus Gabor that corresponded to that bias was held constant at a base-contrast level* and the contrast of the other two Gabors, the other Gabor in the twin-stimulus image and the single-stimulus Gabor (these two stimuli will be called the variable-contrast pair) were varied in unison over the range defined by the base-level contrast and 100% contrast, in 20% steps (see Fig. 2). If the contrast of a stimulus affects the likelihood of a vergence response being made to it, then it may be possible to change the observer's response from their bias direction as the luminance contrast of the variable-contrast pair is increased. That is observers' responses may go from their bias direction (e.g. divergent) when the contrast of the variable-contrast pair is near the base-contrast level to the opposite response (e.g. convergent) at higher contrast

*For each observer, the base-contrast level was set so that it was high enough to elicit consistent responses in the observer's bias direction when the contrast of all three Gabors was at that level (if it was too low, the observer would not respond to the stimuli) but low enough so that increasing the contrast of the Gabors in the variable-contrast pair to their maximum contrast (100%) would bias the observer's response in the opposite direction. That is, if the base-contrast level was set too low, then the stimuli would not effectively drive the vergence system, and if it was set too high then we could not generate complete psychometric curves.

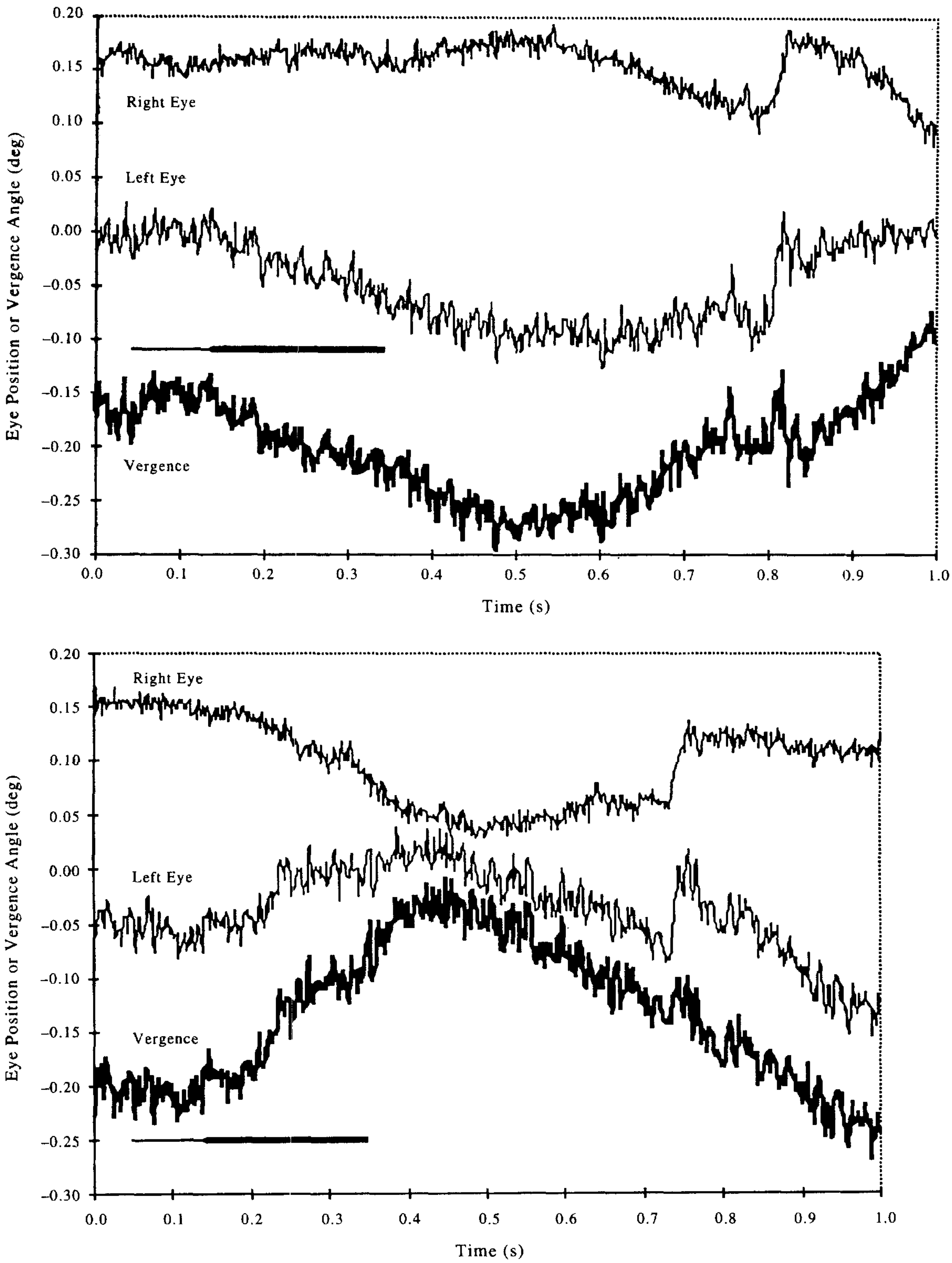

FIGURE 3. Two examples of typical non-averaged eye traces. Plotted are the responses for the left and right eyes and the combined vergence (left eye minus right eye) responses. The disparity stimulus that elicited these responses was composed of a single Gabor presented to the right eye and two Gabors to the left eye. The disparity onset was at time zero on the graphs. The top graph shows an divergent asymmetric response, in which the majority of movement was observed in the left eye (recall that the right eye was presented with the single stimulus that was at the point of fixation), while the lower graph shows a convergent, substantially symmetrical response. For both responses, the latency of the vergence response was in the order of 120 msec, the amplitude of response was 10 min of arc and the duration of the response, to peak amplitude, was about 300 msec. The peak vergence response coincides with the time that the disparity stimulus disappeared and the zero-disparity fixation cross reappeared. Note that in both responses a conjugate horizontal saccade occurs 250 msec following the reappearance of the binocular fixation cross. The horizontal line in both plots indicates both where the response was calculated (thick line) and the preceding 100 msec region that was used as the base-vergence state (thin line).

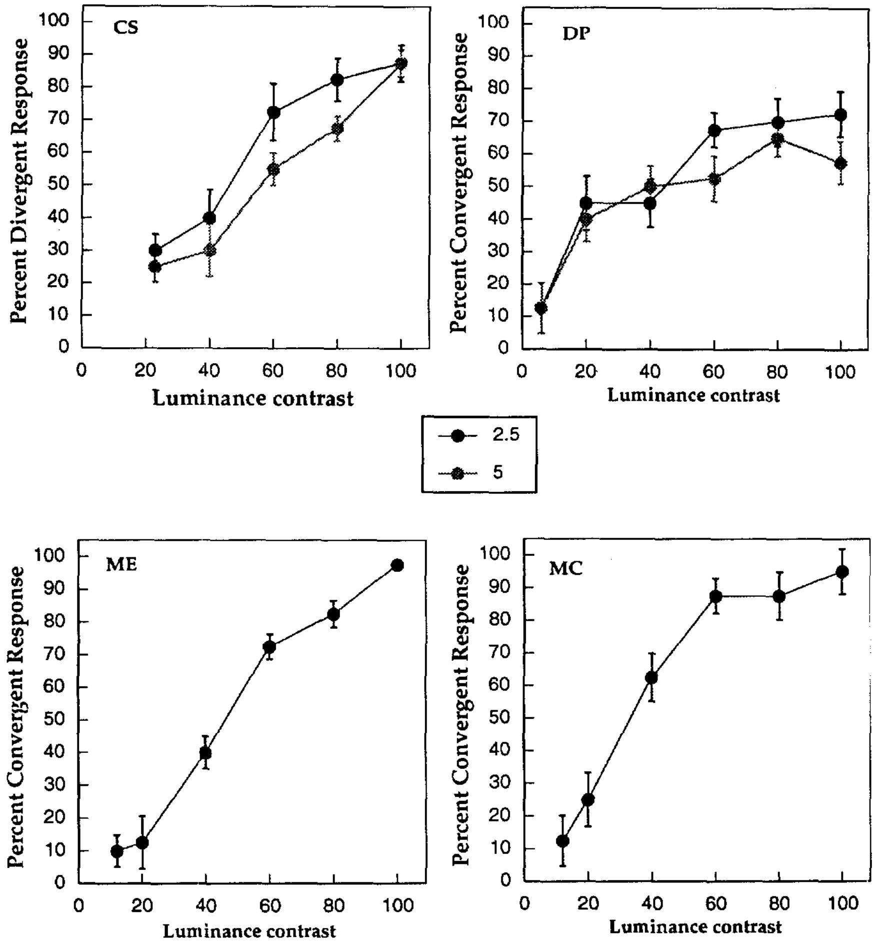

FIGURE 4. Results of Experiment 1. Observer's response (percentage of vergence responses made in the direction opposite to their bias direction) is plotted against the contrast of the variable-contrast pair. Error bars indicate ±1 SEM. All observers were tested at 2.5 deg disparity and two of them (DP and CS) were also tested at 5 deg disparity. All four observers show the same pattern of results. When the contrast of the three Gabors was the same (left-most data point) observers responded predominantly in one direction, their bias direction; convergent for CS and divergent for DP, ME and MC. As the contrast of the variable-contrast pair was increased, the response of the observers progressively moved away from their bias direction, such that at the highest-contrast level all observers were making vergence responses that were predominantly in the opposite direction. DP and CS show substantially the same pattern of performance for the two disparity conditions.

levels. Each block of trials consisted of four conditions at each contrast level; two with the single-stimulus Gabor presented to the left eye and two to the right. The presentation order of stimuli was randomized and reported values represent the mean of ten blocks of trials.

Analysis of the eye-movement traces. The binocular Dual-Purkinje eye tracker was first calibrated over a 2-deg range (1 deg either side of the fixation point). Eye position was recorded for 1 sec following the presentation of the stimulus. The sampling rate was 500 Hz. If the observer made an eye blink during that time period, which was determined by monitoring the SRI's Track Blink signal, the trial was rejected. The calibration data were used to determine the left and right eye's position and the vergence state was calculated by taking the difference of these two values. Typical eye-movement responses are shown in Fig. 3. Given that there was intrinsic noise in this signal, a moving average over a 17-point range was calculated. All further analysis was performed on this averaged data. This analysis was performed on-line following each stimulus presentation and before the presentation of the next stimulus. The slope of the vergence data was first analyzed over a 30-msec moving window. If the calculated slope was greater than 0.3 deg/sec then a further slope was calculated over a 90-msec window. If this second slope was greater than 0.225 deg/sec and was in the same direction as the original slope then a vergence response was deemed to have been made. An integral over a 250-msec time period was then calculated, starting at the point where the original calculation of the slope was made, and the average of the 100 msec preceding this point was used as the base-vergence state of the eyes. If this integral, divided by the 250-msec sampling period was larger than the threshold value (0.02 deg) and the sign (direction) agreed with the original slope, then this was labeled as a vergence response in the appropriate direction.

While this algorithm proved to be reasonably effective in identifying the vergence responses made by the observers, it would occasionally incorrectly label the

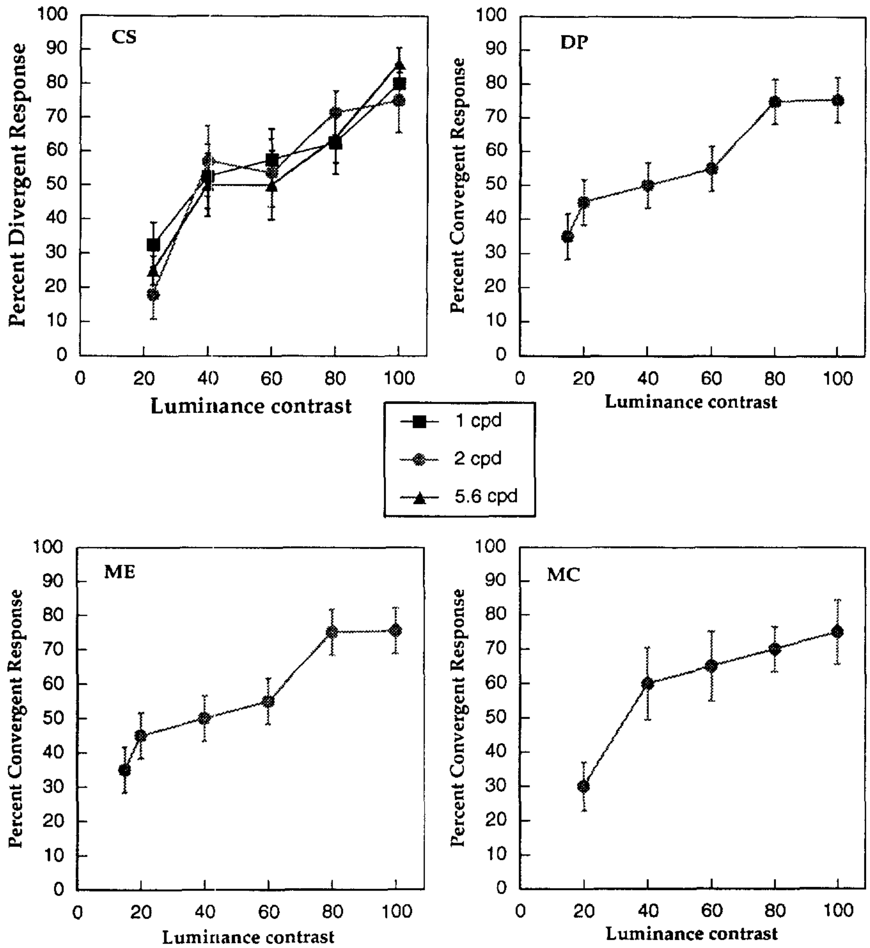

FIGURE 5. Results of the control study in which the contrast of the single-stimulus Gabor was kept constant at the base-contrast level; only the contrast of the twin-stimulus Gabor that corresponded to the direction opposite to the observer's innate-response direction was increased. The pattern of results is the same as that obtained in Fig. 3.

response e.g. when the observer's eyes made a slow drift in one direction, as opposed to clean vergence response, or when it missed the initial vergence response in one direction and then labeled the opposite response back to the starting position as the response. To eliminate these erroneously labeled responses, at the end of each presentation the experimenter was presented with a plot on the computer's monitor of the eye positions, vergence trace and the averaging and integration regions used in the calculation. If an obvious error had been made by the algorithim (as described above) then the experimenter could reject that trial and the particular stimulus condition was returned to the pool of remaining conditions that were presented to the observer in a random sequence. In order to minimize the potential for the experimenter to bias the results, the actual stimulus condition that the plotted response corresponds to was not identified until after the decision to reject or accept the trial had been made. In addition, all observers took turns at running the other observers.

Results and discussion

The results for the four observers are shown in Fig. 4. The observer's response, the percentage of vergence responses made in the direction opposite to their bias direction, is plotted against the contrast of the variable-contrast pair. Error bars indicate ±1 SEM. The pattern of results is the same for all observers. When the contrast of the three Gabors was the same (left-most point in the graphs), the observers responded predominantly in their bias direction; convergent for CS and divergent for DP, ME and MC. As the contrast of the variable-contrast pair was increased, the response of the observers progressively became biased away from their bias direction, such that at the highest-contrast level, all observers were making vergence responses that were predominantly in the direction opposite to their bias direction. This pattern of results occurred for both disparities used, 2.5 and 5 deg.

Control study

The results of the above study would seem to indicate that increasing the contrast of a stimulus results in that stimulus driving the transient-vergence system more strongly. However, another interpretation is possible. A number of studies have shown that the ability of observers to extract stereoscopic depth information is markedly impaired when the images presented to the two eyes are of unequal contrast. That is, when the contrast is reduced in one eye, stereo-thresholds are elevated to a greater extent than when contrast is equally reduced in both eyes; the contrast-paradox effect (Legge & Gu, 1989; Schor & Heckman, 1989). Thus, it could be argued that the contrast manipulation in the above experiment had an affect due to the weakening of the vergence response to the mixed-contrast Gabors (which corresponded to the observer's response-bias direction), as opposed to the strengthening of the response to the matched variable-contrast pair at high contrast levels.

To test for this possibility, we ran a control study in which the contrast of the single-stimulus Gabor was kept constant at the same base-contrast level as that of the twin-stimulus Gabor that corresponded to the observers response-bias direction; only the contrast of the twin-stimulus Gabor that corresponded to the direction opposite to the observer's response-bias direction was increased. If the factor that affected the observers' responses in the above experiment was the mismatch in the contrasts of the two Gabors that corresponded to their response-bias direction, then increasing the contrast of the Gabor in this experiment should have no effect on the observer's response; they should continue to respond in the direction of their bias, since the two Gabors that provide the input to that response have the same contrast. However, if the strength of the vergence signal depends upon the product of the contrasts of the two stimuli that comprise a particular response direction, then increasing the contrast of one of the Gabors while keeping the Gabor in the single-stimulus image constant should bias the observers' responses in that direction so that the pattern of results in the present experiment should be similar to those obtained above.

The impairment of stereo-thresholds due to contrast differences appears to be spatial-frequency dependent; being strong at low (0.8 cpd) but relatively weak at higher (3.2 cpd) spatial frequencies (Halpern & Blake, 1988; Schor & Heckman, 1989). Thus, for observer CS we ran the control experiment at three spatial frequencies (1, 2 and 5.6 cpd), while the other three observers were run at 2 cpd. For ease of comparison, we used the same size gaussian envelope (0.5 deg) for all carrier frequencies. In this experiment and all subsequent experiments, a disparity of 2.5 deg was used.

Results and discussion

The results are shown in Fig. 5. The basic pattern of the results is the same as that observed in Fig. 4. Regardless of the spatial frequency of the Gabors, as the contrast of the twin-stimulus Gabor that corresponded to the direction opposite to the observers response-bias direction was increased, the observers' responses were progressively biased towards that direction, even though the Gabor pair that defined that direction had mismatched contrasts.

The results of the above two experiments show that increasing the contrast of one or both of the Gabors that comprise a vergence stimulus increases the salience of

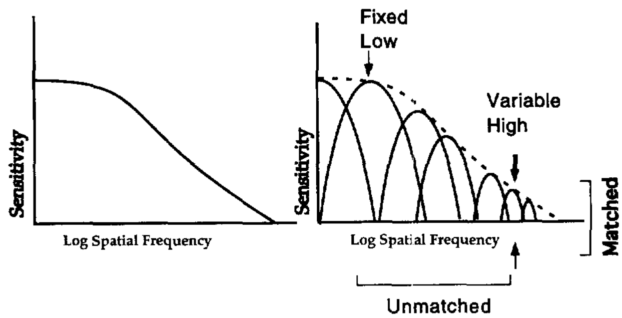

FIGURE 6. The two main ways in which the transient-vergence system could be tuned to spatial frequency. (a) A single lowpass tuned spatial-frequency channel. (b) Multiple narrow-band spatial-frequency tuned channels.

that stimulus to the transient-vergence system. Thus, it would appear that the transient-vergence system performs a form of luminance-energy calculation. In this regard the transient-vergence system differs from the sustained-stereopsis system which, as previously noted, is impaired when differential contrasts are used; this finding suggests that the sustained-stereopsis system performs more of a feature matching process. We are currently determining how the transient-stereopsis system processes such stimuli.

EXPERIMENT 2: SPATIAL-FREQUENCY SELECTIVITY

The aim of the present study was to determine the spatial-frequency tuning of the transient-vergence system. There are essentially two main ways that the system can be selective for spatial frequency: the system can either be narrowly or broadly tuned for spatial frequency.

It has been well established that the human visual system contains a number of channels that are tuned for spatial frequency (Blakemore & Campbell, 1969; Shapley, 1985). It is, therefore, possible that transient-vergence responses are mediated by a system that is composed of multiple-bandpass channels, as appears to be the case for pattern perception (Blakemore & Campbell, 1969) and sustained stereopsis (Schor, Wood, & Ogawa, 1984). Such a system would show a high degree of spatial-frequency selectivity in that the stimuli presented to the two eyes would have to be matched in terms of their spatial-frequency content in order to elicit a vergence response. Another possibility is that responses are mediated by a system that contains a single channel with broadband sensitivity. Given that it is a transient mechanism, any single broadband mechanism would be likely to have lowpass sensitivity—see Fig. 6. To determine which of these two possibilities is correct, a multiple-bandpass or single-lowpass system, we employed an experimental technique similar to that used in Experiment 1.

Methods

Stimuli and procedure. The stimuli used were Gabors with sinewave carriers of different spatial-frequency. The

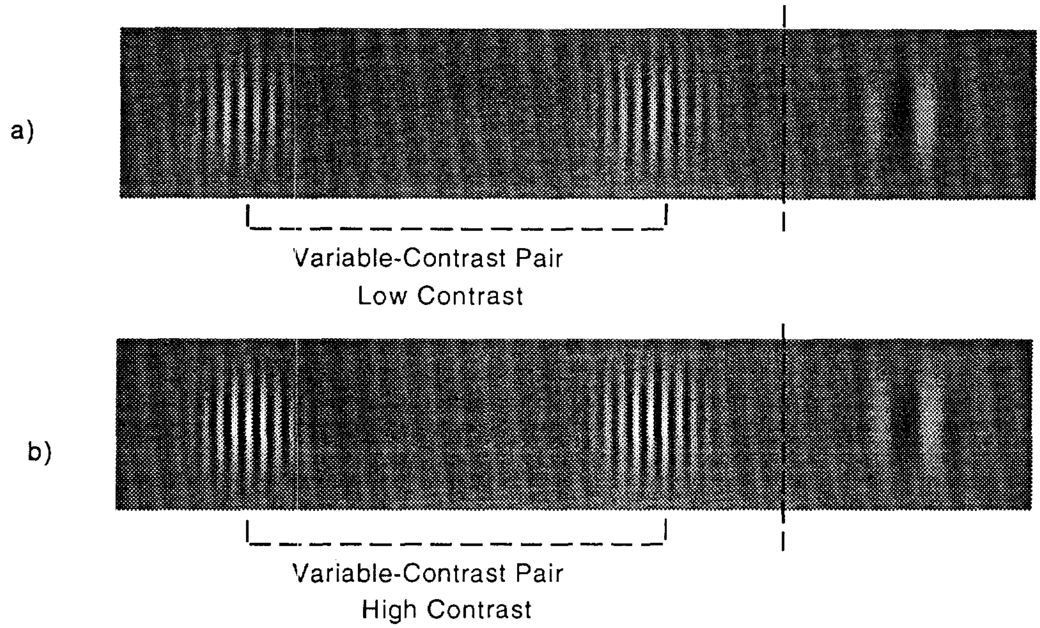

FIGURE 7. Contrast and spatial-frequency manipulations used in Experiment 2. As in Experiment 1, the two Gabors that defined the response direction opposite the observer's bias direction (variable-contrast pair) were varied, this time in both spatial frequency and contrast, while the contrast and the spatial frequency of the remaining Gabor were held contrast. Depicted are the manipulations used in Experiment 2 for an observer with a divergence bias. High spatial-frequency variable-contrast Gabors are paired with the low spatial-frequency reference Gabor. (a) Contrast of all three Gabors the same. (b) High contrast on the variable-contrast pair.

Gabor in the twin-stimulus image that corresponded to the observer's response bias (the reference Gabor) was held at a constant contrast and spatial frequency (2 cpd) and the contrast of the other two Gabors (the variable-contrast pair) was varied from the observer's reference contrast to 100% contrast in 20% contrast steps. This procedure was carried out for a number of variable-contrast pair spatial-frequency settings (1, 4 and 5.6 cpd—observers CS and MC were also tested at 3.2 cpd and CS, DP and ME were tested at 0 cpd; a gaussian—see Fig. 7. For ease of comparison, we used the same size gaussian envelope (0.5 deg) for all of the carrier frequencies used. We are currently conducting experiments to determine whether there is any link between carrier frequency, envelope frequency and the disparity offset of the Gabors. The measure of interest in this analysis is how the luminance cross-over point (that is, the luminance contrast of the variable Gabor-pair at which the observer's response switches from their response-bias direction to the opposite direction) varies as the spatial frequency of the variable Gabor-pairs is changed. Depending upon which model is correct (multiple-bandpass channels or a single-lowpass channel) the cross-over point will either increase or decrease as the spatial frequencies of the Gabors are varied.

The expected pattern of results for the two models depicted in Fig. 6 can be estimated by considering the manner in which the stimuli were presented in Fig. 7. With multiple bandpass channels, as the spatial frequencies of the reference Gabor and the variable Gabor-pair become more disparate, they will not drive the same channel strongly. Since the two Gabors that elicit the vergence response in the observer's response-bias direction are of dissimilar spatial frequency, while those that elicit the opposite response always have matched spatial frequencies, increasing the spatial frequency of the variable Gabor-pair would weaken the strength of the response in the bias direction relative to the opposite response. Thus, the luminance contrast of the variable Gabor-pair required to achieve the switch in response from the observer's bias direction to the opposite direction should decrease as the spatial frequencies of the reference Gabor and variable Gabor-pair become more disparate. Indeed, if the spatial frequencies become sufficiently disparate so that the Gabors would no longer drive the same channel, then it should be impossible to elicit a vergence response in the observer's bias direction so that even when the contrast of the three Gabors is the same, the observer should respond in predominantly the direction opposite to their bias direction. Hence if the transient-vergence system is composed of multiple bandpass channels, then the luminance cross-over point should decrease as the spatial frequency of the variable Gabor-pair is increased, relative to the reference Gabor.

The opposite pattern of results should be obtained for a single-lowpass channel. As the spatial-frequency of the variable Gabor-pair is increased relative to the (lower) reference Gabor, the stimulus pairing driving the response in the observer's bias direction (a low plus a high spatial frequency) would drive the transient-vergence system more strongly than the pair driving the opposite response (high plus a high spatial frequency). Hence, a higher luminance contrast would be needed for the variable Gabor-pair to elicit a vergence response in

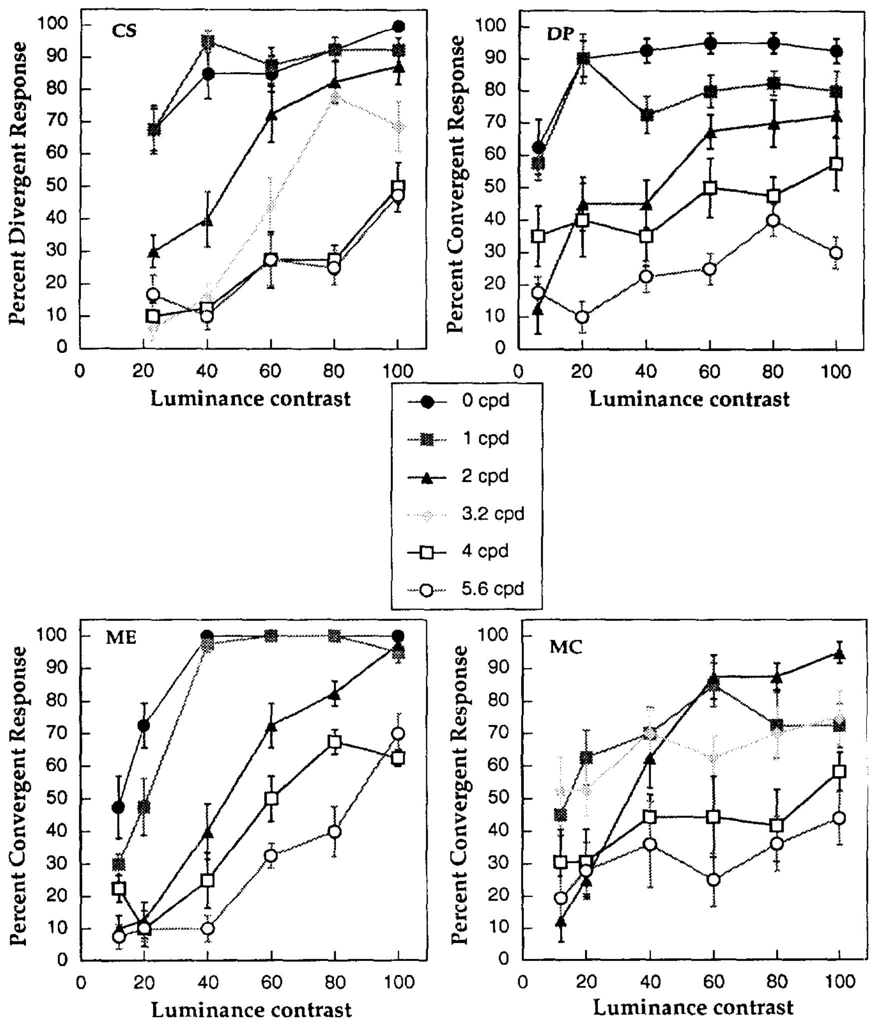

FIGURE 8. The results for Experiment 2 in which different variable-contrast-pair spatial frequencies were paired with the reference Gabor (2 cpd). The percentage of the observers' responses in the direction opposite to their bias direction is plotted against the contrast of the variable Gabor-pair. The results are the same for all observers. As the spatial frequency of the variable Gabor-pair was raised above that of the reference Gabor, a higher contrast cross-over point was obtained, as compared with the condition where the spatial frequency of all three Gabors was the same (2 cpd). Additionally when the spatial frequency of the variable Gabor-pair was lowered to 1 and 0 cpd, a lower cross-over contrast was obtained.

the direction opposite to the observer's bias direction. Thus, if the transient-vergence system is composed of a single-lowpass channel then the luminance cross-over point should increase as the spatial frequency of the variable Gabor-pair is increased relative to the reference Gabor.

Results and discussion

The results for the four observers are shown in Fig. 8. For the various variable Gabor-pair spatial frequencies, the percentage of the observers' responses in the direction opposite to their bias direction is plotted against the contrast of the variable Gabor-pair. The basic pattern of the results is the same for all observers. As the spatial frequency of the variable Gabor-pair was raised above that of the reference Gabor, a higher contrast was required to bias the observer's response away from their bias direction, as compared with the condition where the spatial frequency of all three Gabors was the same (2 cpd). Additionally, when the spatial frequency of the variable Gabor-pair was lowered to 1 and 0 cpd, a lower cross-over contrast was obtained. Indeed, at the lowest spatial frequency (0 cpd) all observers failed to show their standard response bias when the contrast of all three Gabors (the 0 cpd variable pair and the 2 cpd standard) were the same.

These results provide strong evidence for a single lowpass channel that has a peak sensitivity at or below 1 cpd. Furthermore, the results suggest that the upper-frequency cutoff in sensitivity is relatively low. The latter finding may, however, be merely due to the competition paradigm used. That is while, for example, observer CS appears to exhibit limited sensitivity to frequencies equal to or above 4 cpd in Fig. 8, the results in Fig. 5 clearly demonstrate that he is sensitive to spatial frequencies at least up to 5.6 cpd. Thus, the results in Fig. 8 indicate that compared with CS's response to a 2 cpd Gabor, his response to a 4 cpd or higher spatial-frequency Gabor

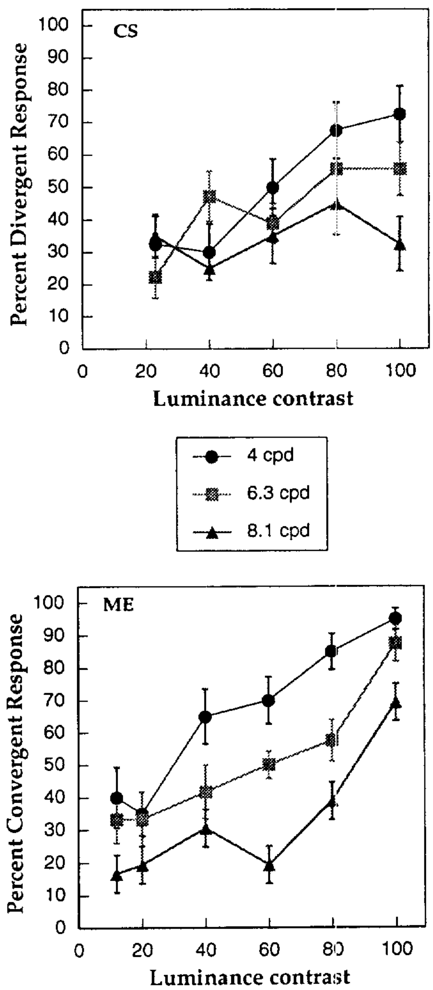

FIGURE 9. Extension of results shown in Fig. 8. For two observers a reference Gabor with a spatial frequency of 4 cpd was used and variable-contrast-pair spatial frequencies of 4, 6.3 and 8.1 cpd. Both observers show differential effects for all frequencies used.

was substantially weaker, not that he is unable to respond to a 4 cpd or higher stimulus. To further confirm this point, we ran two observers, CS and ME, on three additional conditions in which the reference spatial frequency was 4 cpd and that of the variable Gabor-pair was either 4, 6.3 or 8.1 cpd—these spatial frequencies were obtained by doubling the viewing distance and scaling the stimulus parameters accordingly to obtain the same envelope standard deviation of 0.5 deg. As can be seen from Fig. 9, CS (and ME) now shows differential sensitivity to spatial frequencies at least up to 8.1 cpd.

EXPERIMENT 3: MONOCULAR- OR BINOCULAR-BASED RESPONSE

A number of authors have shown that it is possible to elicit a strong impression of depth from a transient monocular hemi-retinal stimulus (Kaye, 1978; Harris & McKee, 1996). It is therefore possible to argue that the responses observed in Experiment 1 and Experiment 2 were monocular based. That is, it is possible that a monocular-based vergence response was made to whichever of the twin-stimulus Gabors was the most visible. Thus, the results obtained in the above experiments may not reflect how two monocular stimuli are binocularly integrated by the transient-vergence system but merely reflect monocular sensitivity to hemi-retinal stimuli at short durations. That is, in the competition paradigm used in the present study, the most salient hemi-retinal stimulus may elicit the vergence response—though such a possibility is unlikely since even at short stimulus durations (100–200 msec), the peak of the contrast-sensitivity function is about 3 cpd (Schober & Hilz, 1965), while the sensitivity of the transient-vergence system, as determined in Experiment 2 does not fall away at low spatial frequencies.

Stimuli and procedure

To test this possibility we ran a control condition in which the stimuli were the same as those used in Experiment 1, except that the single-Gabor stimulus was replaced by a blank field; only the twin-stimulus image was presented. If the responses observed above are the result of a monocular-based response then the same pattern of results should be obtained in the present experiment. If, however, the transient-vergence system cannot make responses to a monocular stimulus, requiring instead a binocular stimulus, then an essentially random pattern of results should be obtained. That is, observers should make equal numbers of divergent and convergent responses regardless of the relative contrast of the twin-stimulus Gabors.

Results and discussion

The results for four observers are shown in Fig. 10. For purposes of comparison the results from Experiment 1 (Fig. 4) are also included. As can be seen, while the pattern of responses for the earlier binocular condition show a marked dependence upon luminance contrast (going from responses that were predominantly in the observer's bias direction at low contrast to predominantly the opposite direction at high contrasts), responses for the monocular condition do not vary with contrast. At all contrast levels tested, the percentage of responses in a given direction are around the 50% mark. Such a finding indicates that observers cannot make consistent transient-vergence responses to monocular targets and, more importantly for the present paper, that the data presented in the previous experiments reflect the sensitivity of the (binocular) transient-vergence system and not merely monocular sensitivity at short durations.

GENERAL DISCUSSION

The results from the present experiments are that: increasing the contrast of one or both Gabors that stimulate one response direction (e.g. convergent disparity) relative to the contrast of the Gabor/s that constitute the opposite stimulus direction (e.g. divergent) increases the likelihood that the observer will make a response in that (convergent) direction (Experiment 1); vergence responses are more likely to be made in the

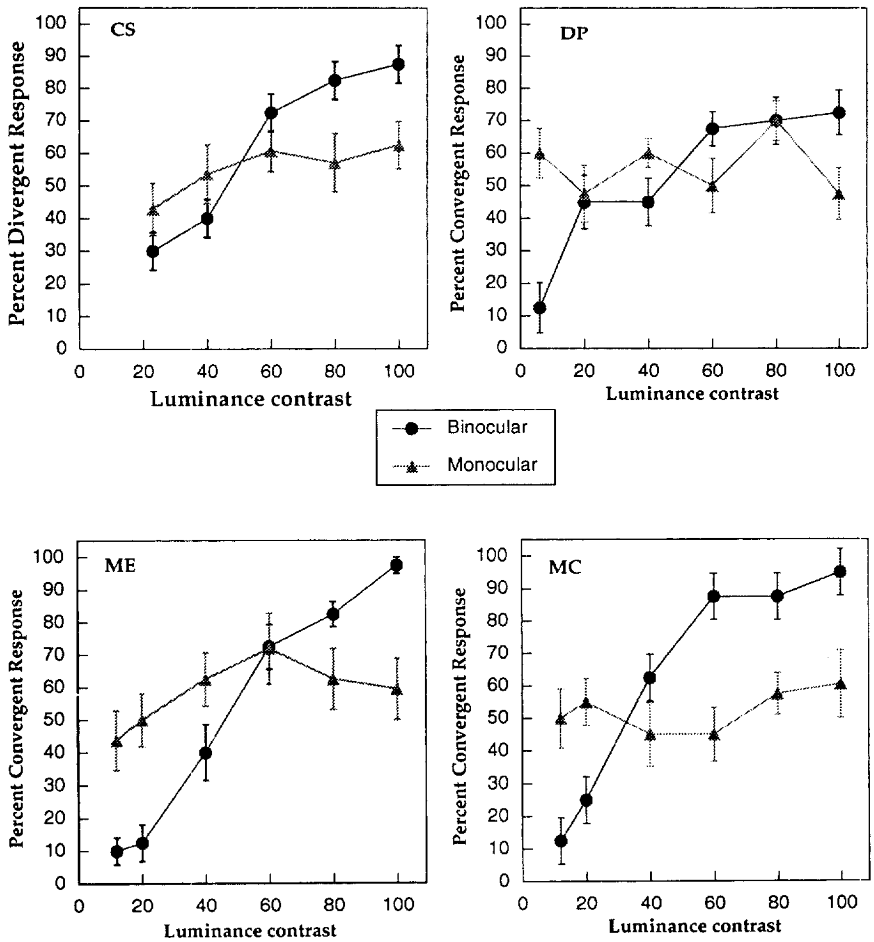

FIGURE 10. Results of the monocular-control experiment in which the single-Gabor stimulus was replaced by a blank field. That is, only the twin-stimulus image was presented. For purposes of comparison the results from Experiment 1 (Fig. 4) are also included. While increasing the contrast of the variable-contrast Gabors leads to a systematic change in the response of the observers, increasing the contrast in the monocular condition leads to random responses.

direction defined by a low spatial-frequency Gabor, even when paired with a high spatial-frequency Gabor, rather than the direction defined by two high spatial-frequency Gabors (Experiment 2) and when presented with a monocular stimulus, the vergence system makes random responses in either direction (Experiment 3).

Luminance sensitivity

The results of the present study show that when the vergence system is presented with two competing stimuli of the same spatial frequency, it is more likely to respond to the stimulus pair that has the higher contrast. This preference for higher contrast stimuli occurs even if the Gabors that constitute the stimulus have dissimilar contrasts. That is, the vergence response is determined by the combined contrast of the stimuli. Such a situation is different to that obtained with both the sustained-stereopsis system (Legge & Gu, 1989; Schor & Heckman, 1989) and the transient-stereopsis system (Edwards *et al.*, 1997), which give weaker responses to dichoptic stimuli that have mismatched contrasts—the so-called contrast-paradox effect. The lack of a contrast-paradox effect for the transient-vergence system holds at both low (1 cpd) and high (5.6 cpd) frequencies.

Lowpass spatial-frequency sensitivity

As can be seen from Fig. 8, a vergence response is more likely to be made to a low spatial-frequency stimulus than to a high spatial-frequency one. Like the situation found with the response to luminance contrast, this low-frequency bias is maintained even when the low frequency Gabor is paired with a high frequency one (2 and 5.6 cpd vs two 5.6 cpd Gabors). These two results suggest that the transient-vergence system is composed of a single lowpass spatial-frequency tuned channel and that the peak sensitivity of this channel is in the range of 0–1 cpd. This broad tuning to spatial frequency is different to that observed for the sustained-vergence system (Westheimer & Mitchell, 1969; Schor *et al.*, 1984—though also see Kontsevich & Tyler, 1994).

It is also interesting to note that the observed peak in the spatial-frequency sensitivity of the transient-vergence system of 1 cpd or less is lower than the peak sensitivity in the monocular contrast-sensitivity function for short-duration stimuli (500 msec), which peaks at about 3 cpd

(Schober & Hilz, 1965). This difference between the two peak sensitivities suggests that either additional filtering occurs prior to transience vergence processing or that transient-vergence responses are mediated by a system that is distinct from the one that mediates the contrast-sensitivity response.

The pattern of results obtained in the present experiments supports the concept that, with respect to both luminance contrast and spatial frequency, the transient-vergence system responds to the "energy" in the stimulus. In terms of its response to contrast, this means that it will preferentially respond to the stimulus pairing that contains the highest combined contrast. Similarly, with regard to spatial frequency, transient-vergence responses appear to be mediated by a system that employs a single lowpass sensitive channel. This pattern of response is different to that obtained for both the sustained-stereopsis and sustained-vergence systems, both of which exhibit a high degree of spatial-frequency selectivity.

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