



Orientation and luminance polarity tuning of the transient-vergence system

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

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

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Abstract

Previously, Edwards, Pope & Schor, *Vision Research*, 38, 705–717, demonstrated that transient disparity vergence appears to be mediated by a system that employs a single low-pass sensitive spatial channel whose performance is not reduced by dichoptic mixed contrasts (no contrast paradox) or dichoptic mixed spatial frequencies. This broadband tuning to both contrast and spatial frequency may be indicative of a second-order or non-linear envelope extraction system. The current study tests for lack of tuning to orientation and luminance polarity which are typically taken as evidence of a second-order system.

We found that when the transient vergence system was simultaneously presented with both convergent and divergent disparities, there was a small but distinct bias in favor of responding in the direction defined by matched orientations or luminance polarities over unmatched pairs. Although less frequent, responses to orthogonal carriers or opposite luminance polarities were possible. The vergence system could match a horizontal with a vertical carrier, or a light gaussian with a dark gaussian. The degree of orientation or luminance polarity tuning varied inversely with the disparity magnitude over the range of 2.5–5°, and the orientation tuning peaked at a spatial frequency about 2 cpd. At all disparities tested, however, the tuning was very broad, and other candidate features for mediating transient-vergence need to be investigated. © 1998 Elsevier Science Ltd. All rights reserved.

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1. 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 stimulated by binocular parallax and they appear to be comprised of 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 maintains a vergence lock on the stimulus. It appears that these two components are mediated by separate systems, with the systems differentiating early in the sensory processing (Jones & Kerr, 1971; Semmlow, Hung & Ciuffreda, 1986; Edwards, Pope & Schor, 1997a).

The general aim of the present paper is to determine the extent to which the images in the two eyes have to be similar in order to initiate a disparity-vergence response with brief, transient disparities. Studies by Westheimer & Mitchell (1969), Mitchell (1969) and Jones & Kerr (1971) have addressed this issue. These authors investigated the ability of observers to make transient-vergence movements to various 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 magnitudes of these responses were the same as those elicited by similar stimuli in each eye. It is 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, unlike the sustained-vergence system, the transient-vergence system is not at all form selective. However, in all three of the studies, small stimuli, which were broadband in their spatial frequency con-

* Corresponding author. Fax: +1 510 6435109; e-mail: schor@socrates.berkeley.com.

tent were used. It is possible that the transient vergence system was responding to the common low frequency content in the stimuli.

More recently, Edwards, Pope & Schor (1997a), using a competition paradigm (Jones & Kerr, 1971), found that increasing the contrast of one or both of the images that stimulate one response direction (e.g. convergent disparity) relative to the contrast of the image/s that constitute the opposite stimulus direction (e.g. divergent) increases the likelihood that the observer will make a response in that (convergent) direction. Vergence responses are more likely to be made in the direction defined by a low-spatial-frequency stimulus, even when paired with a high spatial-frequency gabor, rather than the direction defined by two high spatial-frequency gabors; and when presented with a monocular stimulus, the transient-vergence system makes random responses in either direction, confirming the necessity of binocular input. They concluded that the transient-vergence system appears to employ a single low-pass sensitive channel whose performance is not reduced by dichoptic mixed contrasts.

Based on our previous findings (Edwards, Pope & Schor, 1997a) it seems likely that the spatially low-pass sensitivity of the transient vergence system is achieved by pooling many narrow band spatial frequency channels, with a heavier weighting being given to the lower frequencies. The question to be investigated in this paper is whether or not the system pools across orientations or luminance polarities as well. Specifically, does the transient-vergence system extract the disparity signal using orientation or contrast-polarity tuned filters, and does the orientation or contrast-polarity in each eye have to match to initiate a vergence response? We will again use the competition paradigm (Jones & Kerr, 1971; Edwards, Pope & Schor, 1997a) to answer this question.

It is possible that the low pass tuning of the transient vergence system is achieved by pooling across spatial frequencies but not across orientations or On and Off channels (Perry & Silveira, 1988; Schiller, 1992). This would lead to all responses being in the direction of stimuli with matching orientations or luminance polarity when in competition with orthogonal pairings. It is also possible that the transient vergence system pools across both spatial frequency and orientation, or pools both luminance increments and decrements. If this is the case, then the transient-vergence system will demonstrate no response bias in favor of like pairings of orientation or luminance polarity compared to orthogonal pairings.

Several investigators have studied this question in the stereo system (Wilcox & Hess, 1994; Simmons & Kingdom, 1995; Wilcox & Hess, 1996; Edwards, Pope & Schor, 1997b; Wells & Simmons, 1997). While there is disagreement between the studies as to whether or not

stereopsis is possible with orthogonal stimuli, all of the studies found that performance was at least impaired for orthogonal carriers compared to paired vertical carriers.

In order to test for orientation or luminance polarity tuning in the transient vergence system, the experiments presented in this paper use two types of stimuli. The first stimulus is a spatial-frequency band-limited gabor in which the sine wave carrier can be oriented either horizontally or vertically. The second stimulus is a spatially localized luminance change with a gaussian spatial profile, where the luminance change can either be an increment or a decrement.

2. General methods

2.1. Observers

The observers for each study were drawn from four male observers, including the three authors and one observer (EG) who was naive with respect to the aims of the study. All observers had normal (EG) or corrected to normal (CS, DP & ME) visual acuity with no history of any visual disorders.

2.2. 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 left half of the screen was presented to the left eye, and the right half of the screen to the right eye. Non-fusible apertures were placed in front of each eye, which also ensured that no region of the screen was visible to both eyes. The viewing distance was 70 cm. The observer initiated each trial via a button press and eye movements were recorded via an SRI dual-Purkinje eye-tracker. To stabilize the observer's head, a bite bar and forehead rest were used.

2.3. Stimuli and procedure

The stimuli used were either gabors, which are defined by the following equation:

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

or gaussians, defined by the following equation:

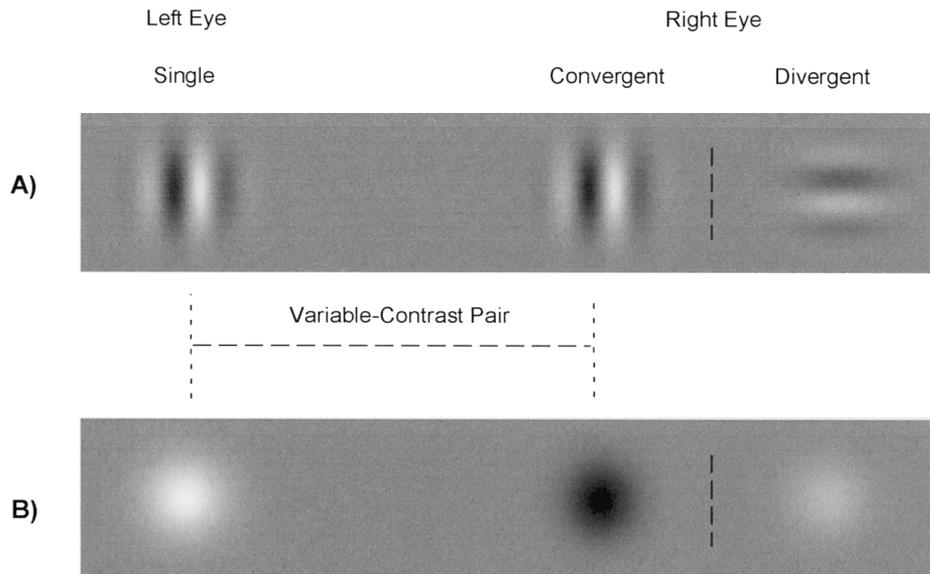


Fig. 1. Examples of the stimuli presented. An example showing gabor stimuli is presented in (A), while an example showing gaussian stimuli is presented in (B). Note that the variable contrast pair has a higher contrast than the remaining gabor or gaussian. In (A) the carrier orientation of the single stimulus and the convergent stimulus match (vertical), while the carrier orientation of the divergent stimulus is orthogonal (horizontal). In (B) the other case is shown. The luminance polarity of the single and divergent gaussians match (light), while the luminance polarity of the convergent gaussian is the opposite (dark).

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

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 gaussian or gabor and sf is the spatial frequency of the gabor.

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 (Green, 1986; Kooi, De Valois & Switkes, 1991; Hess & Wilcox, 1994). All gabors presented for this paper were presented in sine phase.

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 ms 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 (see Fig. 1). The image presented to one eye contained a single gabor (or gaussian), and will be referred to as the single-stimulus gabor, while the other eye's image 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 either 2.5 or 5° horizontally from 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. The disparity offset was either 2.5 or 5°, making the difference between the convergent and divergent disparities either 5 or 10°. Thus on each trial either a convergent or divergent pairing was possible. The eye that was presented with the single-stimulus image was randomized from trial to trial. The duration of the test stimulus was 500 ms and the standard deviation of the envelope was 0.5°. Examples of the stimuli used, one with gabors and one with gaussians, are shown in Fig. 1.

The experimental procedure consisted of several steps. The first was to use three identical gabors to find the observer's initial response bias, either convergent or divergent. All observers tested had a strong bias to respond in one direction when all three gabors were of equal contrast. Three observers diverged (DP, EG & ME), and one converged (CS). The contrast of the twin-stimulus gabor that corresponded to that bias direction was held constant at a low base-contrast level. This level was chosen to enable us to alter the response

direction away from the original bias direction by raising the contrast of the variable contrast pair over the range of contrasts from the base contrast level to 100% contrast. The base contrast level varied between subjects from 6 to 23%. The contrasts 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 in 20% steps. With the correct base-level contrast, observers' responses go from their innate bias (e.g. divergent) when the contrast of the variable-contrast pair is near the base-level contrast to the opposite response (e.g. convergent) at higher contrast levels. The contrast at which responses are equally likely to go in either direction varies with the relative strength of the divergent and convergent stimuli.

Each block of trials consisted of four trials 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.

2.4. Analysis of the eye-movements traces

The binocular Dual Purkinje eye tracker was first calibrated over a 2° range (1° either side of the fixation point). Eye position was recorded for 1 s 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 was 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 were shown in our previous paper (Edwards, Pope & Schor, 1997a). Given that there was 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 ms moving window. If the calculated slope was greater than 3 °/s then a further slope was calculated over a 90 ms window. If this second slope was greater than 0.225 °/s 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 ms time period was then calculated, starting at the first point used in the slope calculation, and using the average of the preceding 100 ms as the base vergence state of the eyes. If this integral, divided by the 250 ms observation time was larger than the threshold value (0.02°) 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 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 algorithm (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 corresponded to was not identified until after the decision to reject or accept the trial had been made. Also all of the observers took turns at running the other observers.

3. Experiment 1: effect of carrier orientation

Electrophysiological studies have shown that the responses of binocular cells in the visual system are tuned to the same carrier orientation in both eyes (Ohzawa, DeAngelis & Freeman, 1996; Anzai, Ohzawa & Freeman, 1997). Consistent with such findings, studies have shown that altering the stimulus orientation between the two eyes prevents the sustained vergence system from functioning (Mitchell, 1969; Westheimer & Mitchell, 1969; Jones & Kerr, 1971). In a related system, the stereo system, orthogonal orientations impair performance compared to vertically oriented stimuli (Wilcox & Hess, 1994; Simmons & Kingdom, 1995; Wilcox & Hess, 1996; Edwards, Pope & Schor, 1997b, Wells & Simmons, 1997), with one study finding the impairment rising with spatial frequency (Wells & Simmons, 1997). The aim of the present study was to determine whether altering the relative carrier orientation of the divergent and convergent stimuli would also affect performance for transient vergence; specifically, whether the carrier orientations (vertical, horizontal or orthogonal) in our competition paradigm would influence the direction of the response of the transient vergence system.

3.1. Stimuli

The binocular stimuli for this experiment consisted of gabors with a spatial frequency of 2 cpd, oriented either horizontally or vertically, and presented at a disparity

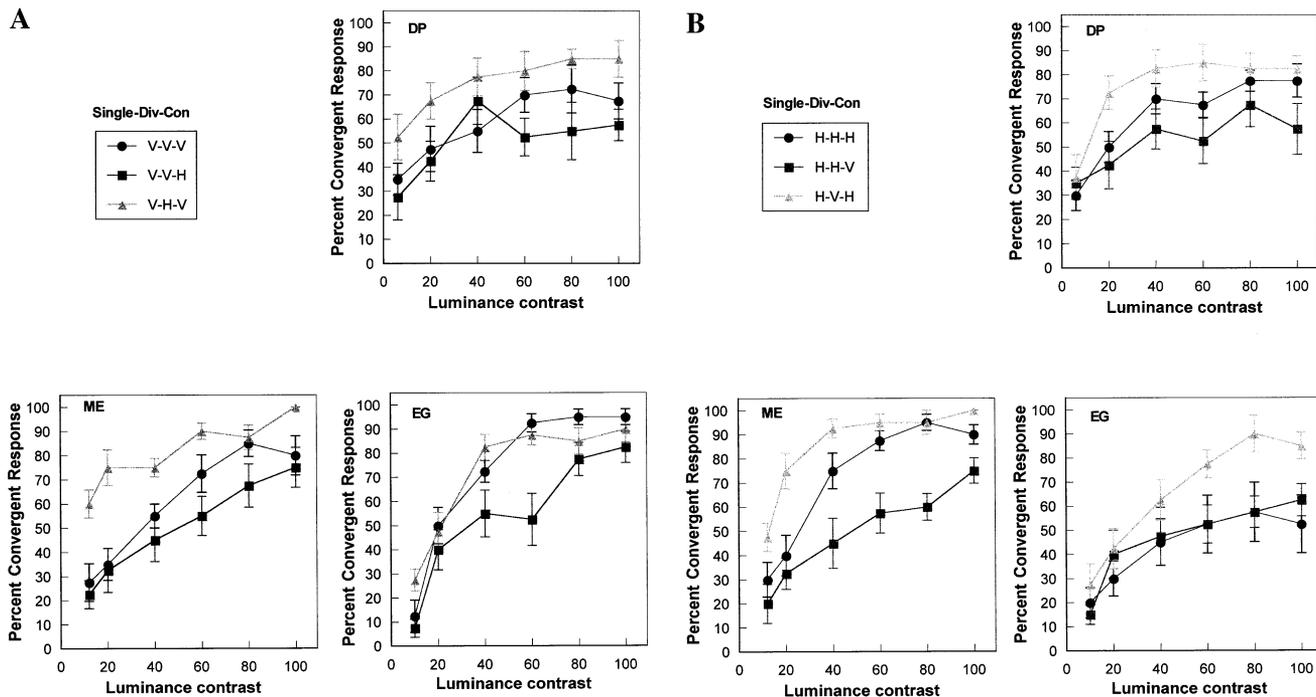


Fig. 2. Results for Experiment 1. Performance, percent responses opposite to the original bias direction, is plotted against the contrast of the variable-contrast pair. Error bars represent ± 1 S.E.M. The order of gabors in the legend is single gabor, divergent gabor, convergent gabor and V stands for vertical, H stands for horizontal. The three conditions shown in (A) are: all three gabors have parallel carriers (V V V), an orthogonal carrier in the convergent gabor with the other two carriers parallel (V V H), and an orthogonal carrier in the divergent gabor with the other two carriers oriented parallel (V H V). (B) shows the same three conditions with a horizontal carrier in the single gabor. In both (A) and (B) all three subjects demonstrate a small bias towards responding to stimulus pairs with parallel carriers.

of 2.5°. A total of six conditions were tested, which have been split into two groups of three. Each group consisted of: one condition in which all three gabors had parallel carriers, one in which the convergent gabor's carrier was orthogonal to the other two (see Fig. 1A), and one in which the divergent gabor's carrier was orthogonal to the other two. The groups differed in the orientation of the carrier in the single gabor, one was vertical and one was horizontal.

3.2. Results and discussion

The results for the three observers are shown in Fig. 2. Fig. 2A presents the results for the single gabor with a vertical carrier orientation, while (B) presents the data for the single gabor with a horizontal carrier orientation. The observer's response, the percentage of vergence responses made in the direction opposite to their original bias direction, is plotted against the contrast of the variable-contrast pair. All observers used in this experiment showed an original bias to respond in the divergent direction; that is the observers responded in the divergent direction when all gabors had the same contrast. The measure of performance used was therefore the percentage of responses in the convergent direction. Error bars indicate ± 1 S.E.M.

The pattern of results is the same for all observers. When the divergent gabor was orthogonal to the other two, the observer responded in the convergent direction more often than when the convergent gabor was orthogonal to the other two. The curve representing the condition when all three gabors were parallel tends to lie between the other two curves.

The same pattern was found when the single gabor carrier orientation was either horizontal or vertical. This indicates that the transient vergence system does not exhibit a preference for either horizontal or vertical, but rather any tuning it does have is for the same orientation. It was possible that, like it's bias to respond to low spatial frequency stimuli, the transient vergence system would respond more often to either vertically or horizontally oriented gabors. Instead the specific orientation does not matter, just the relative orientations of the images in the two eyes.

While the transient vergence system exhibits a bias towards stimuli of similar orientation, it is, however, capable of responding to gabors with orthogonal carrier orientations. This is in marked contrast to the sustained vergence system. The sustained vergence system is unable to track stimuli when the orientations do not match (Westheimer & Mitchell, 1969; Mitchell, 1970; Jones & Kerr, 1971). The response of the transient vergence system is more similar to that of the

transient stereo system, where studies have found that stereopsis is possible but impaired with orthogonal carriers (Wilcox & Hess, 1994; Simmons & Kingdom, 1995; Wilcox & Hess, 1996; Edwards, Pope & Schor, 1997b; Wells & Simmons, 1997).

4. Experiment 2: effect of luminance polarity

Mitchell (1970) has previously investigated the response of the transient vergence system to small lines ($40'$) of opposite contrast sign, and found that responses could be initiated by lines of opposite contrast. However, he did not use a competition paradigm so his results may have been confounded by volitional components. Since only one dichoptic pair of stimuli were presented, the observer may have initiated a volitional eye movement to that stimulus. Additionally a competition paradigm is a more sensitive method than that used by Mitchell since, while the system might be able to respond to opposite contrast stimuli, it may respond more frequently towards a matched polarity stimulus when matched and opposite contrast stimuli are presented simultaneously.

More insight comes from the work on opposite contrast stimuli in the sustained stereo system. Reversed-contrast stereo stimuli have been studied by several researchers (Helmholtz, 1925; Treisman, 1962; Kaufman & Pitblado, 1969; Anstis & Rogers, 1975; Rogers & Anstis, 1975; Levy & Lawson, 1978; Cogan, Lomakin & Rossi, 1993; Cogan, Kontsevich, Lomakin, Halpern & Blake, 1995). The most recent of these papers is by Cogan, Kontsevich, Lomakin, Halpern & Blake (1995), who conclude that stereopsis is possible with opposite contrast images, and that the opposite contrast stereo mechanism remains unknown. The stereo-acuity found with opposite contrast stimuli, however, was approximately a log unit worse than for same contrast stimuli.

If the transient vergence system parallels the stereo system, it should respond to opposite contrast stimuli, but will have a strong bias to respond to same contrast stimuli. If, however, the transient vergence system's response to opposite contrast stimuli parallels its response to orthogonally oriented gabors, then the bias to respond to same contrast stimuli should be small.

4.1. Stimuli

The stimuli for Experiment 2 differ from those used in Experiment 1 only in that bright and dark gaussian blobs were substituted for the vertically and horizontally oriented gabors (see Fig. 1B).

4.2. Results and discussion

The results are shown in Fig. 3. Fig. 3A presents the results for a light single gaussian, while (B) presents the

data for a dark single gaussian. The observer's response, the percentage of vergence responses made in the direction opposite to their innate direction, is plotted against the contrast of the variable-contrast pair. Error bars indicate ± 1 S.E.M.

The pattern of results is the same for all observers, and is very similar to the results found in Experiment 1. When the divergent gaussian was the opposite contrast of the other two, the observer responded in the convergent direction more often than when the convergent gabor was the opposite contrast of the other two. The curve representing the condition when all three gaussians had the same contrast polarity tends to lie between the other two curves.

Once again, the same pattern was found when the single gaussian contrast was either positive or negative. This indicates that the transient vergence system does not exhibit a preference for either light or dark stimuli, but rather any tuning it does have is for the same luminance polarity.

As was the case with carrier orientation, the effect is not all or nothing. By increasing the contrast of the gabors with opposite luminance polarity, we were able to induce the transient vergence system to respond in that direction. The effect of opposite polarities was a relatively small increase in the transient vergence system's bias to respond in the direction of equal polarities. This differs from the sustained stereo system, where Cogan, Kontsevich, Lomakin, Halpern & Blake (1995) found that stereo acuity was about an order of magnitude worse for reversed-contrast than for matched stimuli: reversed-contrast pairs are not much weaker in driving the transient vergence system than are same-contrast pairs.

5. Experiment 3

The results of the above studies would seem to indicate that the transient vergence system at a disparity of 2.5° shows limited tuning to both orientation and contrast sign, while we know that the sustained vergence system, at small disparities, is tightly tuned to orientation and contrast sign. It is possible that there is a gradual falling off of the tuning for orientation and contrast polarity as the disparity is increased. This would be analogous to visual acuity falling off in the periphery. The acuity fall off is due both to increased receptor spacing, and to greater pooling of receptors. Likewise, the transient vergence system might pool across more orientation or luminance-polarity channels as the disparity is increased. It is also possible, if less likely, that the tuning of the low level inputs to the transient vergence system to orientation and luminance polarity varies with disparity magnitude.

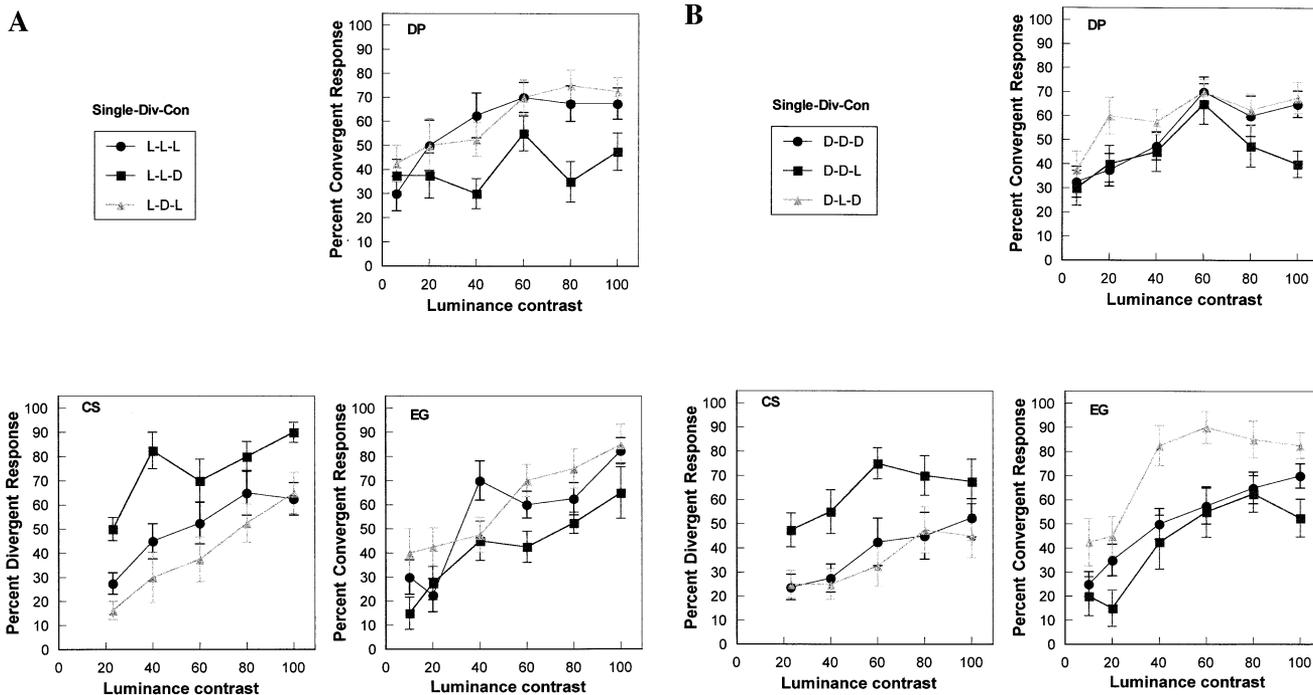


Fig. 3. Results for Experiment 2. In the legend, L stands for light, D for dark. The three conditions shown in (A) are: all three gaussians are the same luminance polarity (L L L), an opposite polarity convergent gaussian compared to the other two (L L D), and an opposite polarity divergent gaussian compared to the other two (L D L). (B) shows the same three conditions with a dark single gaussian. All three subjects demonstrate a small bias towards responding to stimulus pairs with like luminance polarities. Note that subject CS had an original bias in the opposite direction to the other subjects. His measure of performance is therefore percent divergent responses.

The results from Experiments 1 and 2 suggest that at 2.5° disparity, the transient vergence system is already using information from all orientations or luminance polarities, but is not doing so equally. The input from orthogonal orientations or opposite luminance polarities is attenuated compared to the input from like orientations or luminance polarities. The effect of increased pooling or more broadly tuned inputs at larger disparities would be to broaden the tuning of the transient vergence system to orientation or luminance polarity and thus lessen the attenuation of the signals from orthogonal stimuli.

To test the hypothesis that tuning varies with disparity, we have repeated Experiments 1 and 2 at 5° disparity. If the hypothesis of greater pooling or more broadly tuned inputs at larger disparities is correct, we would expect to see less or no tuning to carrier orientation or luminance polarity at 5° disparity. This would be seen in our data as the results for the three conditions becoming the same.

5.1. Stimuli

The stimuli and procedure for Experiment 3 were the same as for Experiments 1 and 2, except the size of the disparity was increased to 5°. Since the results in both Experiments 1 and 2 were the same for the

two types of single stimuli, only three conditions were tested for both the gabors and the gaussians. For the gabors, the three conditions with a vertically oriented single gabor from Experiment 1 were used, and for the gaussians, the three conditions with a bright single gaussian from Experiment 2 were used. This assumes that the transient vergence system does not develop a response bias towards either vertical or horizontal, or light or dark stimuli at disparities other than 2.5°, and that any change in response bias seen is due to the tuning varying with the disparity.

5.2. Results and discussion

The results for all observers are shown in Fig. 4. Fig. 4A presents the results using the gabor patches, while (B) presents the results using gaussian blobs.

There are now clear variations across observers in how the transient vergence system responds to our stimuli at 5° disparity. Three observers demonstrate weak tuning to either orientation or luminance-polarity, while one clearly does not. Observer EG shows no tuning to either orientation or luminance polarity at 5° disparity. One could claim a small orientation tuning effect for observer ME, but compared to his data at 2.5° disparity, it is much smaller, if it exists at all. The

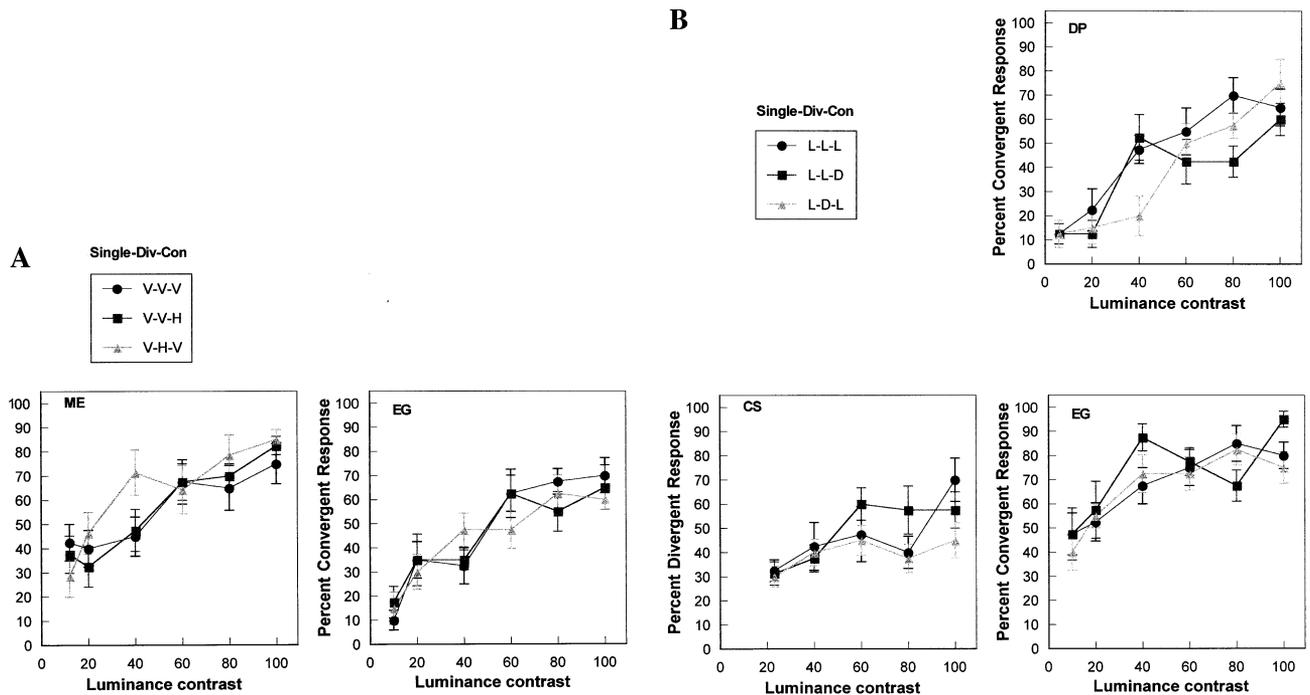


Fig. 4. Results for Experiment 3. (A) The bias of the transient vergence system to respond to the stimulus pair with parallel carrier orientation is clearly reduced. Observer EG shows no remaining bias, while for observer ME there is a possibility of some remaining, but clearly reduced, bias. (B) The bias of the transient vergence system to respond to the stimulus pair with like luminance polarity is clearly reduced. Again, observer EG shows no remaining bias, while for observers DP and CS there is a possibility of some remaining, but clearly reduced, bias.

same could be said for the luminance polarity tuning of observers CS and DP. One thing, however, is consistent across all the observers, if the data indicates tuning to either orientation or luminance polarity, the tuning is weaker than it was at 2.5° disparity (See Figs. 2 and 3.) These results indicate that the tuning of the transient vergence system to both orientation and contrast polarity does indeed fall off with increasing disparity.

6. Experiment 4

The results of Experiment 3 suggest that the tuning of the transient vergence system to orientation or luminance polarity falls off as disparity increases. A similar effect is possible with carrier spatial frequency. The 2 cpd stimulus used in Experiment 1 was very close to the frequency at which Wells & Simmons (1997) found the stereo system transitions from not being tuned to orientation at low spatial frequencies to being tuned to orientation at high spatial frequencies. If the vergence system is similar to the stereo system, we might find different amounts of tuning to both a lower and a higher spatial frequency.

We have repeated Experiment 1 using both 1 cpd and a 4 cpd carrier frequencies in the gabors. If the transient vergence system parallels the stereo system, we expect to see less or no bias for like orientations at 1 cpd, while at 4 cpd we expect to see the same or increased bias.

6.1. Stimuli

The stimuli and procedure for Experiment 4 were the same as for Experiment 1 (2.5° disparity) with the exception of the carrier frequencies used. Two carrier frequencies were used in Experiment 4, 1 cpd and 4 cpd. As in Experiment 3, only the conditions with the single gabor's carrier oriented vertically were tested.

6.2. Results and discussion

The results for all observers are shown in Fig. 5. Fig. 5A presents the results using the 1 cpd gabor patches, while (B) presents the results using the 4 cpd gabor patches.

Unlike Experiment 1, very little orientation tuning was found for either the 1 cpd or the 4 cpd stimuli. The predictions based on the stereo system were not borne out. While compared to the 2 cpd carrier there was clearly a reduction in the bias towards responding to the like oriented pair for the 1 cpd stimuli, there was no corresponding increase in the bias for the 4 cpd stimuli. Instead, there was also a reduction in the bias with the 4 cpd stimuli. It thus appears that in addition to the dependence of the tuning of the transient vergence system upon the disparity magnitude, it also depends upon the spatial frequency of the stimuli, and that the tuning is greatest around 2 cpd.

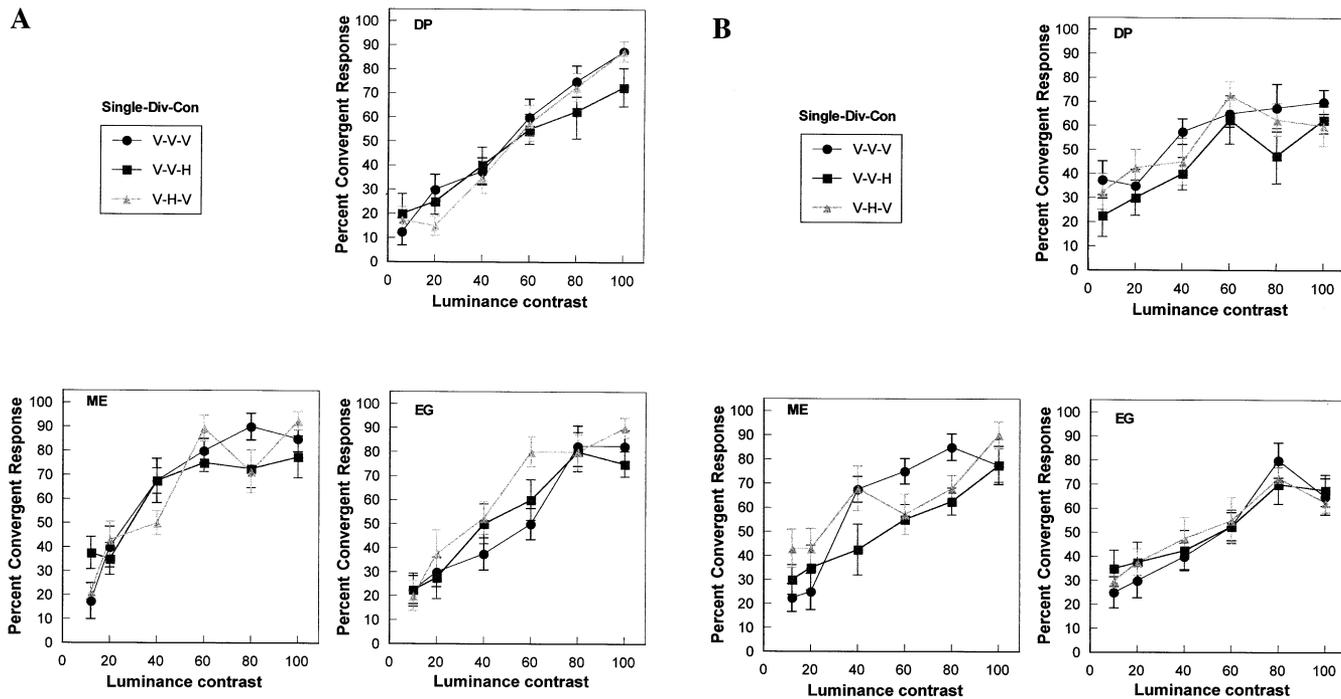


Fig. 5. Results for Experiment 4. The bias of the transient vergence system to respond to the stimulus pair with parallel carrier orientation is clearly reduced for a 1 cpd carrier (A) and a 4 cpd carrier (B) compared to the 2 cpd carrier shown in Fig. 2.

7. General discussion

The primary results from the present experiments are that while the transient vergence system does indeed show tuning to both orientation and luminance polarity, it is not tightly tuned and this tuning falls off as disparity is increased. We found that at 2.5° disparity the transient vergence system has a small bias towards stimuli with like orientations or luminance polarities, while at 5° disparity this bias either disappeared or was at least greatly reduced.

We also found that the tuning to orientation at 2.5° disparity was greater with a carrier frequency of 2 cpd than with either 1 or 4 cpd. This orientation tuning does not peak at the carrier frequency to which the transient vergence system is most sensitive. Edwards, Pope & Schor (1997a) found that the transient vergence system's peak sensitivity is less than 1 cpd. The tuning peak also does not appear to fall at the peak of the contrast sensitivity function. Schober & Hilz (1965) found the peak of the CSF for a 500 ms presentation to be 3 cpd. In octave space, which is how the visual system appears to be tuned (De Valois & De Valois, 1988), this is closer to 4 cpd than it is to 2 cpd, and were the tuning to be greatest at the peak of the CSF, we would expect to see greater tuning at 4 than 2 cpd. One remaining possibility is that the peak of orientation tuning is due to an interaction between spatial frequency and envelope size.

There are several possible explanations for the broad

orientation and luminance-polarity tuning we have found, and its variation with disparity magnitude. The first is that the inputs to the transient vergence system are tuned to orientation and luminance polarity, but the transient vergence system pools these inputs. If this is the case then there is comparatively less pooling across orientation or luminance polarity channels at small disparities than at large disparities. This pooling would constitute a second-order mechanism, since to obtain a non-zero net sum of the pooled inputs for the present stimuli would require a non-linear stage. Cortical cells effectively carry out one such non-linearity, half-wave rectification, since they have a low maintained-discharge rate (De Valois & De Valois, 1988). An alternate, if less likely, explanation for the lack of tuning is that the low level inputs to the transient vergence system themselves are broadly tuned to orientation or luminance polarity, with this tuning varying with the disparity magnitude. This would be a first-order system. A final possibility is that there is a separate transient vergence neuron that codes for every possible orientation pair at every disparity. At smaller disparities, there would be relatively more cells tuned to parallel orientations than to orthogonal orientations. Again, this would be a first order system. Our current experiments cannot differentiate between these models. Edwards, Pope & Schor (1997a) found that transient-vergence responses appear to be mediated by a system that employs a single low-pass sensitive channel whose

activity is not reduced by mixed dichoptic contrasts (no contrast paradox). Coupled with the current findings, this suggests a model of the transient-vergence system composed of a low-pass spatial-frequency tuned channel with a peak sensitivity in the range of 0–1 cpd. This channel either pools across orientation and luminance polarity channels or has broadly tuned low level inputs, with the amount of pooling/tuning dependent upon the magnitude of the disparity and the spatial frequency.

This finding leads to the question of what stimulus features the transient vergence system is tightly tuned for. It must be tuned in some way, because in complex visual scenes the visual system is able to correctly move the eyes to objects with large disparities most of the time. The system does not make random matches. Remaining possibilities for initiating correct responses include tuning to temporal characteristics or envelope shape and size. These possibilities are currently being investigated.

The pattern of results obtained supports the concept that, with respect to contrast, spatial frequency, luminance sign and orientation the transient-vergence system responds to the ‘energy’ in the pairing. The ‘energy’ of the pairing relates to the contrast of each stimulus component after compensating for the low-pass sensitivity and for the orientation or luminance polarity tuning of the transient vergence system. This means that the transient-vergence system will preferentially respond to the stimulus pairing that contains the highest combined ‘energy’, regardless of differences in spatial frequency, contrast, orientation or luminance polarity.

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