



Envelope size-tuning for transient disparity vergence

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Abstract

Our prior studies have demonstrated that the transient-vergence system responds preferably to dichoptic stimulus pairs that contain the highest combined energy, regardless of dichoptic differences in spatial frequency, contrast, orientation, or luminance polarity (Edwards, M., Pope, D. R., & Schor, C. M. (1998), *Vision Research* 38, 705; Pope, D. R., Edwards, M., & Schor, C. M. (1999) *Vision Research* 39, 575). This broadband tuning for spatial frequency, orientation and contrast is indicative of a second order (non-linear) extraction system. The current study examined the potential size-tuning of binocular channels to the contrast envelope that is extracted by a non-linear process. Stimuli were size-scaled Gabor patches with parallel and orthogonal carrier orientations that subtended a large (3.8°) disparity. Results indicate that the transient-vergence system exhibits broad band-pass tuning to overall size of dichoptic targets, independent of interocular differences in carrier orientation, spatial frequency or contrast. Equal sizes elicited a higher proportion of vergence responses than unequal sizes, however responses to unequal size still occurred over a 2-octave range, illustrating broad band-pass tuning. Size tuning was found to be broader for small than large envelope sizes. The broad tuning for envelope size is likely to result from the overlapping extracted low-pass frequency spectra of the contrast envelopes. However, the transient-vergence system also responds to monocular, hemi-retinal stimuli over a larger (3-octave) range. Thus some of the observed ‘binocular tuning’ may be due to these monocular responses. © 2001 Elsevier Science Ltd. All rights reserved.

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1. Introduction

Two components of binocular-vergence eye-movements respond to sudden or transient changes in viewing distance. The vergence response is initiated by a transient mechanism that responds to a large disparity range in excess of 10° (Jones, 1980; Erkelens, 1987; Jones & Stevens, 1989; Semmlow, Hung, Horng, & Ciuffreda, 1993; Bussetini, Miles, & Krauzlis, 1996). Once the response is triggered, it is guided with disparity feedback and maintained at its destination point by a sustained system that is sensitive to the small disparities within Panum’s fusional-limit (Riggs & Niehl, 1960; Mitchell, 1970). These two phases of vergence appear to be mediated by different systems that are differentiated early in sensory processing. The transient-vergence system can respond to non-fusible targets of different shape, spatial-frequency content, and contrast polarity

(Winkelman, 1953; Westheimer & Mitchell, 1969; Mitchell, 1970; Jones & Kerr, 1971; Edwards, Pope, & Schor, 1998; Pope, Edwards, & Schor, 1999). The sustained-vergence system requires similar images with matched features (Mitchell, 1970) to provide disparity feedback for fine vergence control.

To be effective in coding disparity, the vergence system needs to be selective in matching images that correspond to the same object in space when several targets are visible at a given time. This selective matching process would be facilitated if disparity detectors were also tuned to spatial features such as spatial frequency, orientation and contrast polarity. In our prior studies of transient vergence, we have observed very broad tuning to these features, i.e. limited dichoptic selectivity to spatial frequency, orientation, contrast equality and contrast polarity (Edwards et al., 1998; Pope et al., 1999). Based on those results, transient-vergence responses appears to be mediated by a single low-pass-sensitive spatial channel whose performance is not reduced by dichoptic mixed contrasts of unequal

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amplitude or polarity, unequal spatial frequencies, or orthogonal orientations.

Given the broadband tuning to stimulus carrier, could binocular matching be assisted by a sharper tuning to the size of the stimulus-contrast envelope that might be extracted by a non-linear process? The ability of the transient-vergence system to binocularly match stimuli that are markedly different is indicative of performance being mediated by a second-order system (Cavanagh & Mather, 1989). In such a system, a non-linearity, such as full-wave rectification, transforms the activity of initial (first-order) filters into a lower frequency range defined by the contrast envelope of the stimulus. A second filtering stage extracts the contrast envelope. Because the stimulus envelope is localized and the negative component is eliminated by the non-linear extraction, the resulting frequency spectrum will have D.C., or luminance, offset and low-spatial-frequency components. The upper-frequency limit of the extracted frequency-spectrum will increase as target size decreases. Frequency spectra of dichoptically-unmatched target-sizes will overlap in the low-frequency range. However, the energy in the overlapping range may be unequal, depending upon a number of factors, including the relative strength of the initial filters tuned to the specific carrier-frequencies and the physical power-spectrum of the carrier. Matched low-frequency information extracted from contrast envelopes could activate disparity detectors that initiate transient-vergence responses. In this way the transient-disparity system might utilize contrast-energy information to guide binocular matches based upon the overall size of the target stimuli. Thus the general aim of this paper is to investigate size tuning, or how similar the size of contrast defined envelopes presented to the two eyes must be to form disparities that elicit transient-vergence response.

2. General methods

2.1. Observers

Subjects were three young-adult observers, one of the authors (MS) and two observers who were naive with respect to the aims of the experiment. All observers had either normal or corrected to normal visual acuity, normal stereopsis (as measured by a Randot Stereotest) and no history of any visual disorder.

2.2. Apparatus

Stimuli were generated using a Cambridge Research System 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 through a telestereo-scope. Non-fusible apertures were placed in front of each eye to ensure that no region of the screen border was visible to both eyes. The viewing distance was 57 cm. Eye position was recorded with a SRI dual-Purkinje eye tracker. A bite bar and a forehead rest were used to stabilize the observer's head position.

2.3. Stimuli and procedure

The luminance profile of the test stimulus was a Gabor function defined by the following equation:

$$L(x, y) = A \sin\{2\pi f(-x \sin \theta + y \cos \theta)\} \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) + M,$$

where A is the amplitude of the function, f is the spatial frequency of the carrier grating, θ is the orientation of the grating, σ is the standard deviation of the Gaussian envelope and M is the mean luminance of the background field. The contrast of the stimulus was defined by the ratio of the amplitude of the carrier to the mean luminance level. Sinewave carriers were presented in sine phase and the standard deviation of the Gaussian envelope varied from 0.3 to 2.4°. Carrier frequency (cyc deg⁻¹) was 0.6 times the reciprocal of the space constant (σ) in units of degrees such that carrier size was scaled with envelope size producing three cycles of the carrier in each envelope and a constant full-bandwidth of 0.93 octaves at half height. The narrow bandwidth reduced the luminance spatial-frequency overlap of unequal size left and right images as the difference in their size increased. We used an overall rather than meridional size differences to produce size disparity in all meridians in order to find the most sensitive indicator of reduced performance. Based on the dimensions of Panum's fusional-limit (Schor & Tyler, 1981) if either the vertical or horizontal meridians had matched sizes, performance would have been less impaired by size difference of the orthogonal meridian.

Fig. 1 shows the configuration of the stimulus. Initially the observer's vergence angle during monocular fixation (resting vergence) was determined. Fixation crosses and nonius lines were presented to hold the initial vergence at the resting status, as shown in Fig. 1 (A). The luminance-contrast polarity of the fixation crosses and nonius lines was reversed following each trial in order to minimize the effect of luminance adaptation over the time course of trials. Once the observer established binocular fixation on the cross and confirmed that the nonius lines were aligned, he/she pressed a button to initiate the presentation of the test stimulus. A random delay of between 100 ms and 1 s was included prior to the disappearance of the fixation target and simultaneous presentation of the test stimu-

lus in order to prevent the observer from making an anticipatory eye movement. The duration of the test stimulus was 500 ms and the initial-fixation patterns followed the test stimulus. The observer was instructed not to make volitional eye movements to the test stimulus. The likelihood of volitional eye movements was further reduced by the short 500 ms stimulus duration.

The test stimulus consisted of two different images, as shown in Fig. 1 (B) that were presented dichoptically. Both images contained a Gabor patch presented in crossed disparity and two small Gaussian blobs presented above and below the test Gabor in uncrossed disparity. The Gaussian blobs stimulated a baseline, or reference, divergent response that was in competition with the crossed-disparity Gabor stimulus. They had 3.8° uncrossed disparity and were separated vertically by 12.4° . The crossed-disparity test stimulus was composed of a fixed-size Gabor that was presented to one eye and a variable-size Gabor that was presented to the other eye. The Gaussian blobs and Gabor stimuli both subtended 3.8° of disparity, which is beyond the range of the sustained-disparity vergence system but well within the range of the transient-disparity vergence system. The left and right image components of the Gabor stimulus had different orientations. One was at 45° and the other was at 135° . The orientation disparity of the orthogonal stimulus was beyond the useful range for sustained-stereo processing (Blakemore, Fiorentini, & Maffei, 1972; Von der Heydt, Adorjani, & Hanny,

1977; Ohzawa, DeAngelis, & Freeman, 1996; Anzai, Ohzawa, & Freeman, 1997). Thus, the large orientation difference precluded any contribution to stereo performance by the sustained first-order system that is sensitive to the carrier (luminance sinewave) information.

We used a competition paradigm to measure how effectively the crossed-disparate Gabor patches elicited disparity-vergence responses when their diameters or standard deviations (sigmas) were unequal. The competition paradigm consisted of presenting both an uncrossed (Gaussian blob) and a crossed disparity (Gabor patch) stimulus and varying the contrast of the crossed disparity to bias the observer's response in that direction. The size and contrast of the uncrossed-disparity Gaussian-blob stimuli were fixed (standard deviation was 0.2° and contrast was 75%). These targets stimulated a divergence response that had a constant magnitude. The contrast of the crossed disparity Gabors was co-varied from 0 to 100% in steps of 20%. When contrast was low, subjects diverged and when contrast of the Gabor patch was increased, subjects converged. In order to investigate envelope-size tuning for transient vergence, the sigma of the Gaussian envelope of the Gabor patch presented to one of the eyes was varied over a three-octave range while the envelope size of other eye's Gabor image remained constant. Previously Edwards, Pope, and Schor (1998) have shown that as a dichoptic combination of unequal Gabors became more efficient at stimulating the vergence system, less contrast was required to overcome the diver-

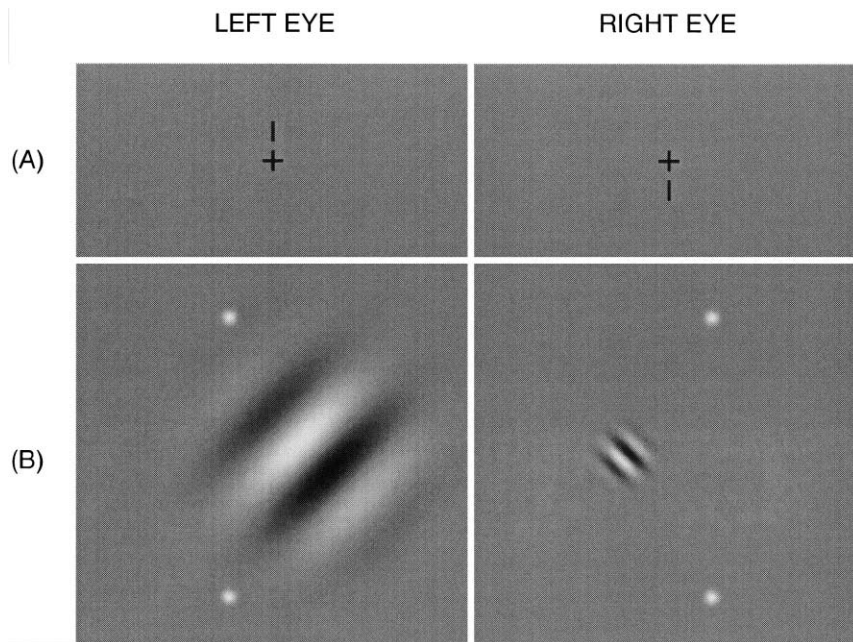


Fig. 1. (A) Fixation cross and nonius line; (B) An example of the test stimulus. The fixation pattern was replaced by the test stimulus for 500 ms. Each dichoptic image contained a Gabor patch presented in crossed disparity and two Gaussian blobs presented in uncrossed disparity. Envelope size (Experiment 1), orientation (Experiment 2), spatial frequency (Experiment 3), and contrast (Experiment 4) of the Gabor stimulus were manipulated to examine the tuning of the transient-vergence system.

gence response and initiate a transient convergence response. The direction of the reference disparity depended on the direction of a vergence response bias exhibited by all of our subjects. Pilot testing showed that all three observers had a convergence response bias. Accordingly, the reference Gaussian stimuli were always presented at a fixed contrast with uncrossed disparity. The contrast of the crossed-disparity Gabor patch was increased until the convergence response could overcome the baseline divergence response.

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, as 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 response was calculated by taking the difference of these two values. Typical eye-movement responses were illustrated in our previous paper (Edwards, Pope, & Schor, 1998). Given that there was noise in this recorded signal, a moving average over a 15-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. Classifying a vergence response as being either convergent or divergent was a multistage process. First the slope of the vergence data was analyzed over a 30 ms moving window. If the calculated slope was greater than $0.5^\circ/\text{s}$ then a further slope was calculated over a 90 ms window. Note that the two temporal windows had the same temporal starting-point. If this second slope was both greater than $0.375^\circ/\text{s}$ and in the same direction as the original slope then the magnitude of the vergence response was calculated. The magnitude of the response was calculated by taking the difference between the average vergence-state during the 250 following temporal starting-point and the average vergence-state during the preceding 100 ms. If the magnitude of the vergence response was larger than the threshold value (0.02°) and the direction agreed with the original slope, then the eye movements were labeled as a vergence response in the appropriate direction. A typical amplitude of vergence response was about 0.2° although observer MS showed much larger responses (e.g. 2°). A relatively low threshold value was used to label the responses so that in the competition paradigm most responses could be labeled as either divergent or convergent, even when there was a weak response to a closely balanced stimulus pair.

While this algorithm proved to be reasonably effective in identifying the vergence responses made by the observers, occasionally responses would be labeled incorrectly. For example, the algorithm could miss the initial vergence response in one direction and then label it in the opposite direction when returned to the starting position. To eliminate this erroneous labeling, at the end of each presentation the experimenter viewed a plot of eye positions, vergence trace and the averaging regions used in the calculation on a computer monitor. If an obvious error had been made by the algorithm, the experimenter rejected 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 corresponding to the plotted response was not identified until after the decision had been made to reject or accept the trial.

3. Experiment 1: envelope size tuning for orthogonally oriented patterns with unequal (scaled) carriers

3.1. Stimuli

Envelope size tuning for transient-vergence responses was investigated with band-limited (0.93 octaves) dichoptic Gabor targets of unequal size, whose carriers were non-fusible (orthogonal). The 3.8° crossed-disparity stimulus for this experiment consisted of Gabors with sigmas fixed at 0.3 or 2.4° for one eye and varied for the other eye ($0.3, 0.6, 1.2,$ or 2.4°). Four variable-sigma conditions were interleaved in the same block of data collection in order to reduce the influence of a day-to-day variance we noticed in a pilot experiment. Ninety-six trials were executed in random order (6 [contrast values] $\times 4$ [variable sigmas] $\times 2$ [fixed sigma presented to the right eye or left eye] $\times 2$ [repetitions]). Each observer repeated five sessions for each fixed sigma.

3.2. Results and discussion

The performance measure was the percentage of convergence responses made above baseline responses to the fixed uncrossed disparity (divergence stimulus) when it was presented in isolation. Fig. 2 shows the probability of convergent responses as a function of the contrast of the crossed-disparity Gabor stimulus. Because responses to conditions in which the fixed-size Gabor was presented to the right or left eye did not differ, they were combined. Thus, the each data point was calculated from twenty trials. The error bars indicate ± 1 standard error of the mean calculated from five repeated sessions. The right and left columns of

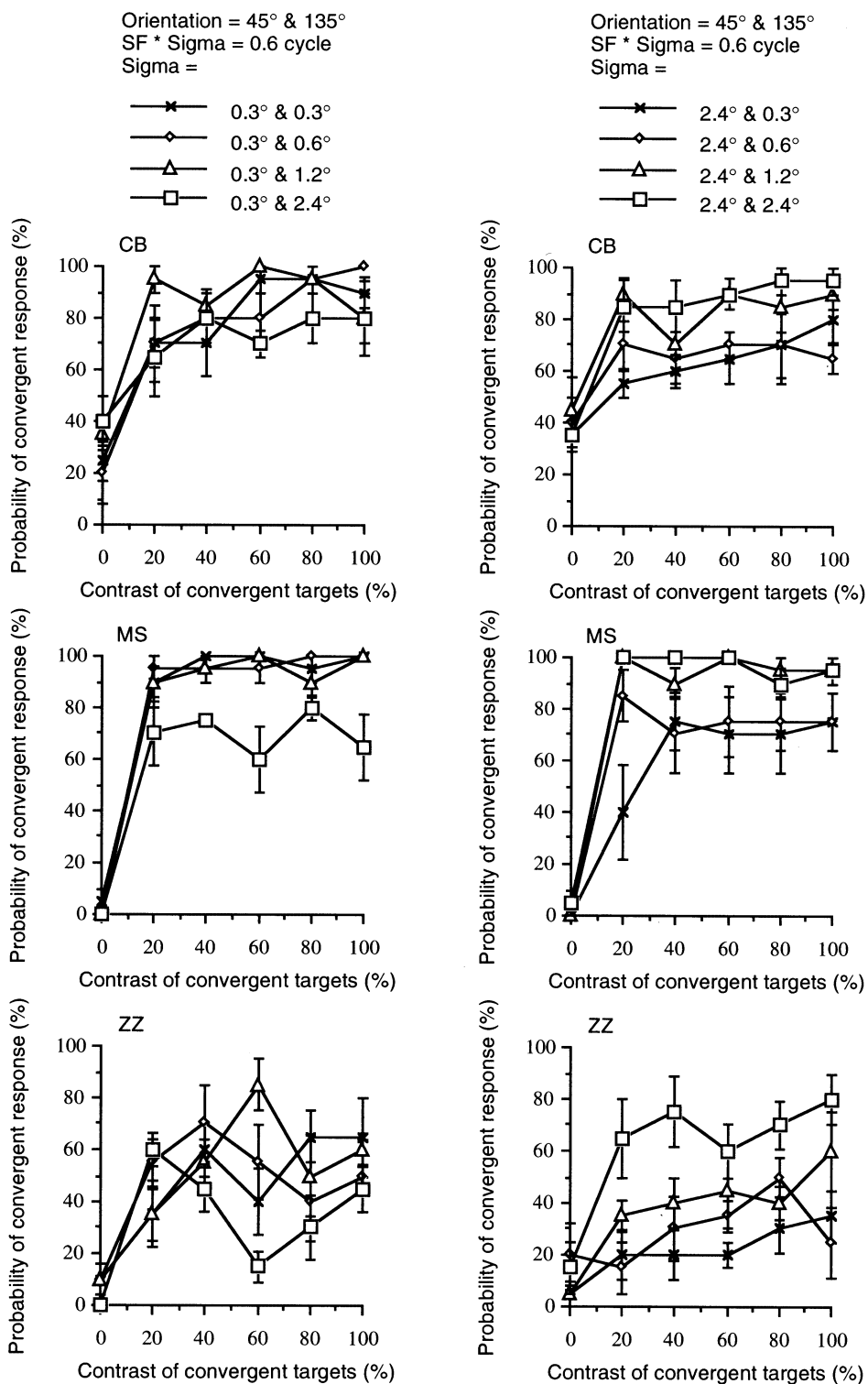


Fig. 2. Results of Experiment 1. Probability of convergent response is plotted against the contrast of the crossed-disparity Gabor stimulus. Performance was highest when sigmas were equal in size and it declined as the difference between sigmas increased, demonstrating a band-pass tuning for contrast envelope-size in the transient-vergence system.

Fig. 2 illustrate results for the large and small fixed Gabors (σ 2.4 and 0.3°, respectively) paired with sigmas ranging from 0.3 to 2.4°. The response at the origin

(zero contrast) represents the baseline percentage of convergence responses when the uncrossed-disparity Gaussian stimulus was presented in isolation. This

baseline was in the convergence direction for one subject (CB) because of her strong convergence-bias. The other subjects had a divergence response to the isolated uncrossed-disparity stimulus. Note that since vergence responses in the convergent direction were stimulated by dichoptic Gabors of unequal size, the proportion of responses in the convergent direction indicated how effectively these stimuli could drive the vergence system. Variations of convergence-response frequency with size difference were used to estimate dichoptic-size tuning.

The pattern of results with the crossed-disparity stimulus present was the same for all observers. The probability of a convergence response increased as the contrast of the crossed-disparity stimulus was increased, until a plateau was reached. The probability of a convergence response depended upon the size similarity of the left and right eye components of the Gabor stimulus. Probability of a convergence response was highest when sigmas were equal in size and it declined as the size of the variable Gabor was reduced (right column) or increased (left column). Even when the largest and smallest Gabors were paired, probability of a convergence response for all subjects was still above the baseline level, demonstrating that the transient-disparity vergence system could respond to size differences over at least a 3-octave range. The tuning varied between the three subjects. It was broadest for CB who only showed a small 10% reduction of performance when size differences were three octaves. Subject ZZ showed the largest (40%) reduction of performance with the 3-octave difference in size.

This experiment demonstrates that while the transient-vergence system exhibits a bias towards stimuli of similar size, it is capable of responding to Gabors whose size differ by at least 3 octaves. As can be observed by un-cross fusing the lower half of Fig. 1, the sustained-vergence system is unable to respond to these large size-discrepancies. The response of the transient-vergence system is more similar to that of the transient-stereo system, where we have observed a similar broad bandwidth for contrast-envelope size tuning (Schor, Edwards, & Sato, 2001).

4. Experiment 2: envelope sizetuning for parallel oriented patterns with unequal carriers

It is possible that the transient-disparity vergence system might be tuned more sharply to envelope size for patterns with parallel carriers. Such finer tuning may occur if a first order system could binocularly match carrier features and contribute to the vergence response. This experiment compared performance with mixed small (0.3°) and large (2.4°) dichoptic Gabor patterns with either parallel (both vertical) or orthogonal (45 and 135°) carrier-orientations. If size tuning were narrowed

by an association with carrier orientation, then the performance with contrast envelopes of unequal size would be greater with orthogonal than parallel carriers.

4.1. Stimuli

The 3.8° crossed-disparity stimulus for this experiment consisted of Gabors with sigmas fixed at 0.3 or 2.4° for one eye and varied for the other eye (0.3 or 2.4°). Parallel and orthogonal conditions were interleaved in the same block of data collection. Ninety-six trials were executed in random order (6 [contrast values] $\times 2$ [variable sigmas] $\times 2$ [parallel or orthogonal] $\times 2$ [fixed sigma presented to the right eye or left eye] $\times 2$ [repetitions]). Each observer repeated five sessions for each fixed sigma.

4.2. Results and discussion

The right and left columns of Fig. 3 illustrate results for the large- and small-fixed Gabors (σ 2.4 and 0.3° , respectively) paired with Gabors having sigmas ranging from 0.3 to 2.4° . Triangle and square symbols correspond to orthogonal- and parallel-carrier conditions. As in the prior experiment, the response at the origin (zero contrast) represents the baseline percentage of convergence responses when the uncrossed-disparity Gaussian stimulus was presented in isolation. The pattern of results is the same for all three observers. Performance was independent of carrier orientation; parallel or orthogonal orientations yielded similar results. As in Experiment 1, performance was higher with matched than mixed size envelopes, particularly, as shown in the right column, when the fixed Gabor was large ($2.4^\circ \sigma$). When the fixed Gabor was small ($0.3^\circ \sigma$) performance was similar for all size combinations, indicating broader size tuning.

The similarity of results for parallel and orthogonal carrier-orientations demonstrates that envelope size, independent of carrier orientation, determined performance. Furthermore, since the lack of orientation selectivity is indicative of performance being mediated by a second-order system, the results show that strength of the second-order system is at least as strong as any putative first-order transient-vergence system. Note that while the (spatially-localized) Gabors used in the parallel-orientation condition constitute a first-order stimulus, they could also be processed by a second-order system (Edwards & Badcock, 1995). Hence the strong vergence responses in the parallel condition do not necessarily indicate the presence of a first-order system. The present results also verify our prior observations, that used a slightly different competition paradigm, of weak orientation tuning of the transient-vergence system at large disparity magnitudes (Pope, Edwards, & Schor, 1999).

5. Experiment 3: envelope sizetuning for orthogonally oriented patterns with equal carriers

It is possible that the transient-disparity vergence system might be tuned more sharply to envelope size for patterns with equal than unequal spatial frequency

carriers. This experiment compared performance with mixed small (0.3°) and large (2.4°) dichoptic Gabor patterns with either equal (2 cpd) or size scaled (2 and 0.25 cpd) carrier spatial frequencies. Carrier orientations were orthogonal (45° and 135°). If size tuning were narrowed by an association with carrier spatial

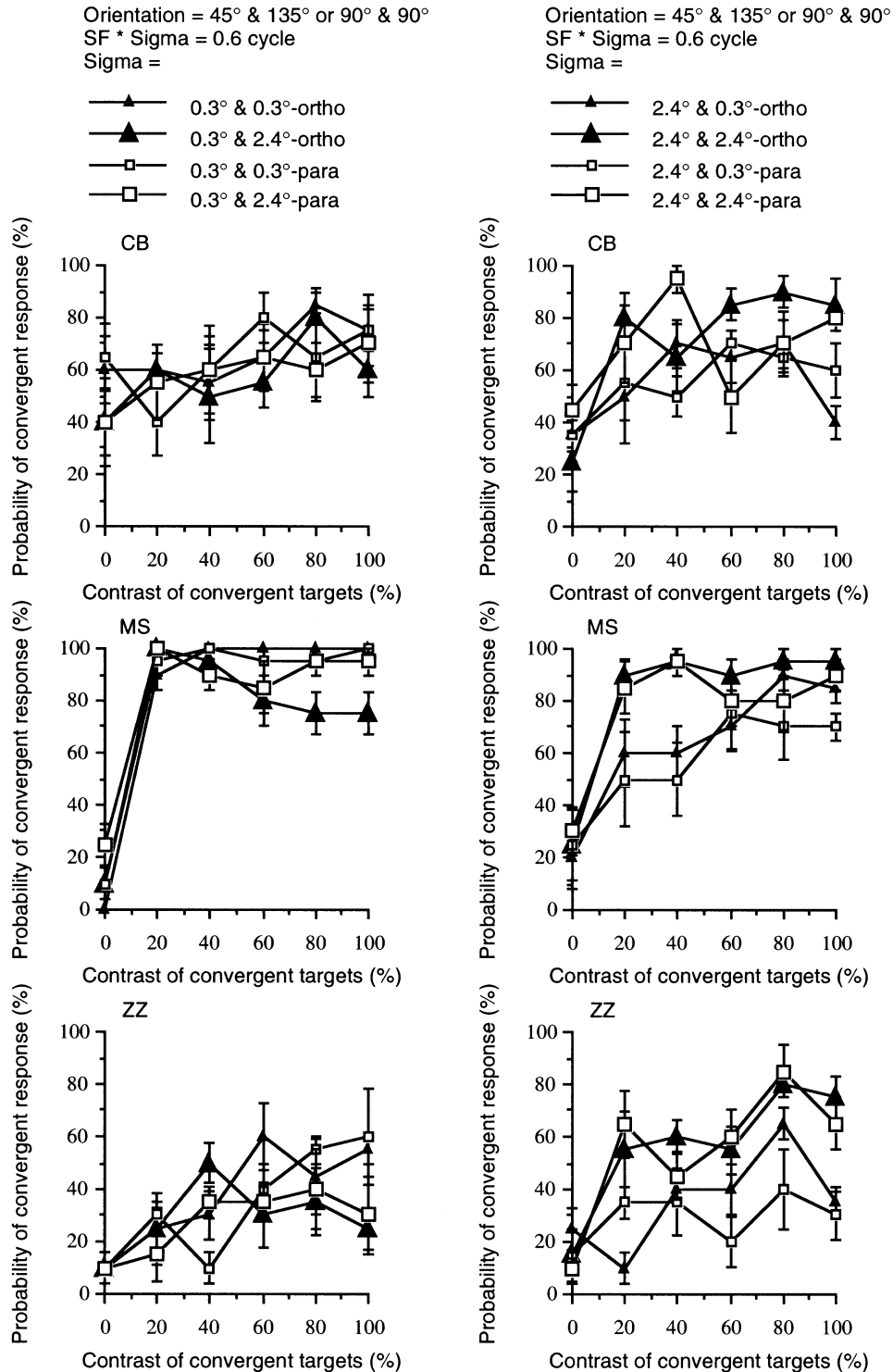


Fig. 3. Results of Experiment 2. Effects of carrier orientation. Parallel (both 90°) and orthogonal (45 and 135°) carriers were compared. Performance was independent of carrier orientation, demonstrating a second-order envelope extraction.

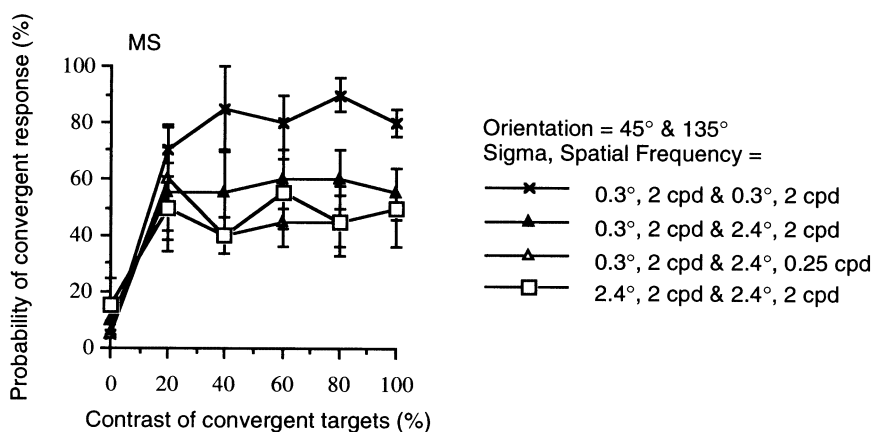


Fig. 4. Results of Experiment 3. Effects of carrier spatial-frequency. Envelope size determined performance independent of carrier spatial-frequency.

frequency, then the performance with equal (2 cpd) spatial frequency would be reduced with contrast envelopes of unequal size compared to performance with size-scaled spatial frequency carriers. The present experiment investigated this possibility.

5.1. Stimuli

The envelope sizes of Gabor stimuli and procedure for Experiment 3 were the same as for Experiment 2 (0.3 and 2.4° σ). Carrier orientations were always orthogonal, and their spatial frequency was either equal at 2 cpd, or unequal with a scaled (0.25 cpd) spatial frequency in the large (2.4° σ) Gabor. The two envelope-sizes were either matched or mixed, yielding two matched sizes of equal spatial frequency, and two mixed-sizes with either matched or mixed spatial-frequencies. This experiment was performed on one subject (MS) who had participated in the prior two experiments.

5.2. Results and discussion

Probability of convergence is plotted in Fig. 4 as a function of the contrast of the crossed-disparity Gabor stimulus. The main observation is that performance with mixed size envelopes (0.3° and 2.4° σ) was independent of whether the carrier spatial-frequencies were equal (2 cpd) or scaled with envelope size (2 and 0.25 cpd, respectively). Thus envelope size determined performance independent of spatial frequency similarity of the carrier. It is interesting to note that performance with the large 2.4° matched stimulus was reduced when the equal carrier frequency was high (2 cpd) compared to performance with an equal scaled carrier frequency (0.25 cpd) shown in the right column of Fig. 2. This

observation confirms our prior report of the low-pass spatial-frequency tuning of the transient-vergence system when tested with a different competition paradigm (Edwards, Pope, & Schor, 1998).

6. Experiment 4: contrast tuning

The results of the first three experiments demonstrate a broadband-size tuning for binocular matches of the contrast envelope that defines the overall size of the disparity stimulus. If the tuning to envelope size results from interocular inhibition stimulated by unequal signal-strength (Kontsevich & Tyler, 1994) then it may be possible to broaden the apparent envelope-size tuning by varying the stimuli along another dimension to equate their relative signal strengths. One possible dimension is stimulus contrast (Schor, Edwards, & Pope, 1998).

The spatial-frequency content of the extracted localized-contrast envelope will be low-pass in nature and contain a D.C. component. Unequal size envelopes have different extracted low-pass spatial frequency spectra such that the smaller stimulus has less power in the low frequency range and more power in the high frequency range near its cut-off. Even though both large and small envelopes have overlapping extracted low-frequency spectra, the power or activity levels in the overlapping range are not equal, except at intermediate frequency, and this could stimulate interocular inhibition (Kontsevich & Tyler, 1994). To equate signal strength at low frequency, the physical contrast of the larger size envelope would need to be reduced. Previously Edwards, Pope, and Schor (1998) observed that transient-vergence responses were not reduced by mixed contrasts of Gabor patches with equal-size envelopes

containing equal or unequal spatial-frequency carriers (i.e. no contrast-paradox effect) (Legge & Gu, 1989; Schor & Heckmann, 1989). However, it is possible that there is contrast tuning for binocular channels that process the extracted contrast envelope for Gabor patches. This experiment determined if performance with unequal size envelopes can be improved by adjusting the relative contrast of dichoptic Gabor targets of unequal size and orthogonal orientation. As a control, we also determined if performance with orthogonal-orientation stimuli with matched envelope-size and carrier frequency could be reduced by increasing the contrast of one ocular image to produce a mismatch in signal strength.

6.1. Stimuli

The envelope sizes of Gabor stimuli and procedure for Experiment 3 were the same as for Experiment 4 (0.3 and $2.4^\circ \sigma$). The two envelope-sizes were either unequal or matched. The carriers had orthogonal orientations and their spatial frequency was scaled with envelope size (2.0 and 0.25 cpd, respectively). In both the unequal and equal size Gabor conditions, contrast of one envelope size was fixed at 100% while the contrast of the other envelope size was varied from 0 to 100% (0, 5, 10, 20, 40 and 100%) in approximately 1 octave steps. In addition, when Gabors were equal in size, the contrast of both images was varied together from 0 to 100%. The various stimulus combinations were mixed in a given run to avoid contamination of the data with day-to-day performance shifts.

6.2. Results and discussion

Probability of convergence is plotted in Fig. 5 as a function of the contrast of the crossed-disparity Gabor stimulus. The graphs in the three rows describe performance with large matched Gabors (top), small matched Gabors (middle) and mixed size Gabors (bottom).

For the matched-size conditions, contrast of the patterns was varied together (open symbols) or fixed at 100% in one eye and varied in the other eye (filled symbols). The 100% contrast point on the abscissa represents the condition in which the two Gabors had the same contrast. If there were contrast tuning, performance would be higher when both Gabors had equal low-contrast, compared to when contrast was high in only one of the stimuli. For large Gabors, as shown in the top graphs, performance increased and reached plateau when the contrast of one or both convergent targets was increased for observers CB and ZZ. For MS, performance with the large matched sigmas (2.4°) was unaffected by contrast variation. For the all three observers, difference between the two contrast conditions was not significant (i.e. most data points for the

two conditions lie within two standard errors of one another). The middle plots show the results for small Gabors. Performance was reduced when contrast of both Gabors was reduced (open symbols). Performance for the mixed contrast condition (filled symbols) was the same as the matched contrast condition for CB and ZZ and it was even higher than the matched contrast condition for MS. These results do not support the notion of contrast tuning (i.e. the contrast-paradox effect) for the transient-vergence system. The bottom graphs describe performance with unmatched-size envelopes, when the contrast was reduced for the smaller Gabor (solid triangle) or for the larger Gabor (open triangle) while the contrast of the other Gabor was fixed at 100%. Performance was independent of whether contrast of either Gabors was reduced.

The lack of contrast tuning for the extracted envelope that was observed in this experiment confirms our prior report that transient-vergence responses were not reduced by mixed contrasts of dichoptic Gabor patches (Edwards, Pope, & Schor, 1998). Even though the two studies used different competition paradigms, an absence of contrast tuning was observed with equal-size envelopes containing equal or unequal spatial-frequency carriers (i.e. no contrast-paradox effect). The current study used separate dichoptic image pairs to stimulate convergence and while the former study presented a single target to one eye and two parafoveal targets to the other eye producing a stimulus similar to Panum's limiting case. The latter condition required the vergence system to make a forced choice between the two possible stimulus combinations. In spite of these differences, both studies observe no contrast tuning for transient vergence. This observation is surprising, given that both the transient and sustained stereo systems show marked contrast tuning (Schor, Edwards, & Pope, 1998; Schor, Edwards, & Sato, 2001), and one would assume contrast tuning occurred at an early stage where common disparity signals were used by the stereo and vergence system.

Prior studies (Schor & Heckmann, 1989) illustrate that like disparity vergence, binocular sensory fusion, measured as Panum's fusional area, is unaffected by contrast differences. Both sensory fusion and disparity vergence respond to absolute disparity, whereas stereopsis responds to small relative disparities (differences in two large absolute disparities). The contrast paradox is described as a reduction of signal strength, resulting from interocular inhibition followed by the addition of noise (Schor & Heckmann, 1989; Kontsevich & Tyler, 1994). The reduction of signal-to-noise ratio caused by contrast tuning is small for large absolute disparities utilized by binocular sensory fusion and disparity vergence, but the reduction is larger for the small relative disparity stimuli used for stereopsis. Consequently, tasks using relative judgements such as

stereopsis appear to be more sensitive to reductions of signal strength resulting from unequal contrast of dichoptic images than tasks that use absolute disparity such as fusion and disparity vergence.

6.3. Monocular vergence stimuli

The symbols on the ordinate of Fig. 5, corresponding to contrast of zero, indicate performance with the isolated Gaussian divergence stimulus for the matched-contrast conditions, or for a monocular Gabor at 100%

contrast for the mixed-contrast conditions. The top and middle graphs show that the probability of a convergence response to the monocular condition (filled symbols) was higher than that to the isolated divergence condition (open symbols), indicating that the monocular stimulus evoked convergence responses. The data points on the ordinate of the bottom graphs act as a monocular control for the mixed-size condition. The bottom graphs show that performance to the binocular mixed size stimulus was not significantly higher than the monocular baseline performance. This indicates

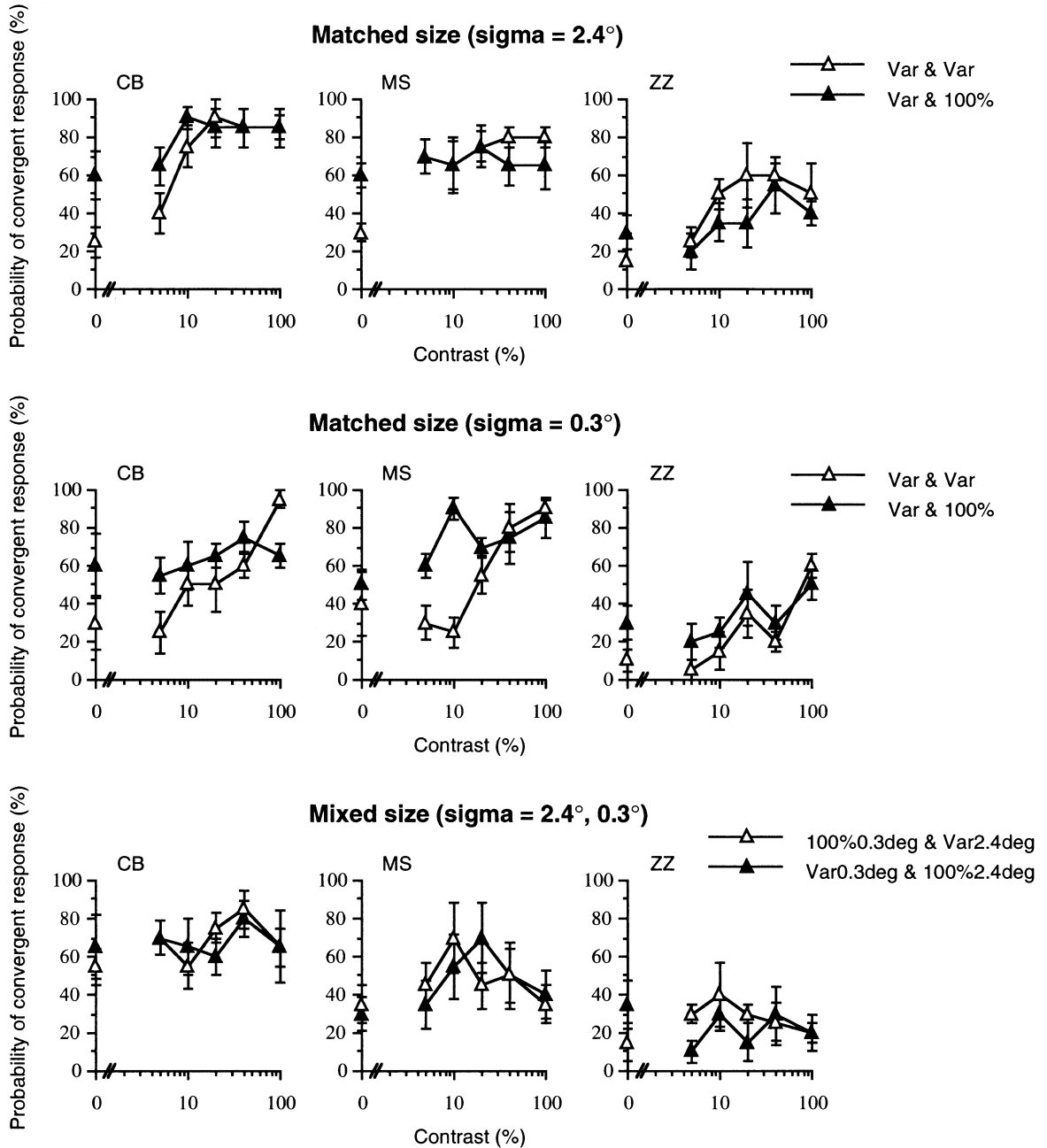


Fig. 5. Results of Experiment 4 show a lack of contrast tuning in transient vergence. The contrast of one Gabor was kept 100% and that of the other stimulus was manipulated. Performance was not reduced for mixed-contrast stimulus.

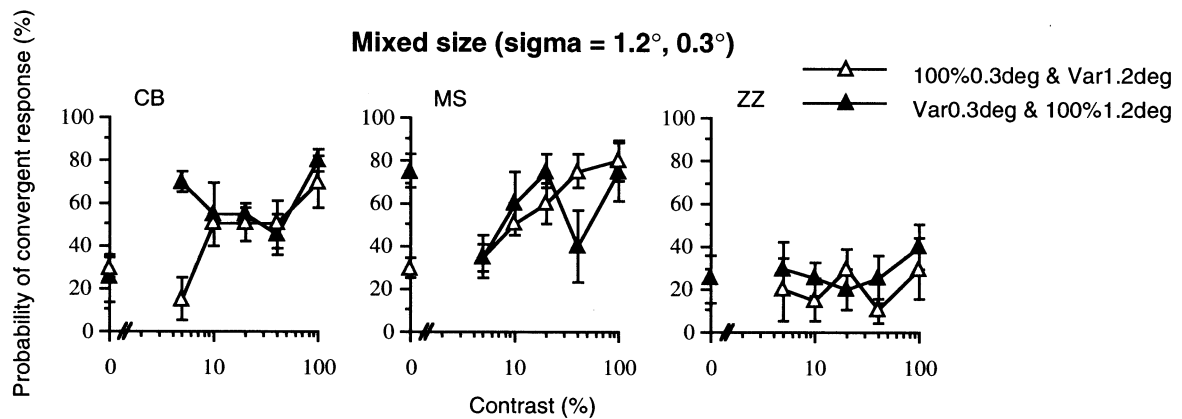


Fig. 6. Supplemental results for Experiment 4. Mixed size stimulus with smaller size difference ($\sigma = 1.2$ and 0.3°) was tested. One of three observers (CB) made clear convergent responses to the binocular targets with 2-octave size difference. Performance for the other two observers did not exceed the monocular control performance.

that vergence responses made to large (up to 3 octaves) size difference observed in the present study had both monocular and binocular components.

In order to determine a binocular size-difference range to evoke vergence response, the mixed size condition was repeated, using a pair of Gabors with a smaller size difference (0.3 and $1.2^\circ \sigma$). The standard deviation of the Gaussian target that stimulated divergence was increased to 0.5° for CB and MS to reduce the monocular performance level. For ZZ, it was held at 0.2° since the probability of him making a convergent response to the monocular target was not as high as for the other two observers. The results are shown in Fig. 6. For CB, the probability of convergence was clearly higher for the binocular stimulus than for the monocular stimulus; except for the condition in which the contrast of the large Gabor was very low (5%). The probability of a convergence response to the monocular Gabor with 0.3 and $1.2^\circ \sigma$ was 30 and 25%, respectively. If the vergence system did not receive binocular input from this stimulus combination, the performance to the binocular stimulus would have been 47.5%, assuming probability summation as described by $1 - \prod(1 - P_i)$. However, actual performance to the binocular stimulus presented at 100% contrast was greater than expected by probability summation (i.e. 70 and 80%). This result demonstrates that the transient-vergence system receives binocular inputs from orthogonal Gabors whose envelope size differ by 2 octaves. For MS, probability of a convergence response to the large monocular ($1.2^\circ \sigma$) target was high (filled symbol on the ordinate) and performance to the binocular targets did not exceed the monocular performance level. This suggests his convergence responses to large size difference were monocular based and the size tuning function of transient-vergence system could have been sharper than it appears. His strong response-bias in the convergent direction may be related to his strong exophoria

(14 prism diopter). Since initial vergence status was adjusted to the subject's resting-vergence state, a reasonable strategy could be to make a convergence responses to seek a binocular match when an unusual monocular target was seen. For ZZ, performance to binocular targets did not exceed monocular-control performance, indicating that his convergence response to large size-differences was elicited by monocular stimulation.

These results demonstrated that monocular stimuli evoke binocular vergence responses. However, vergence responses can not be totally attributed to monocular input because the responses were strengthened when the binocular input were similar in size (Experiment 1). It is difficult to quantify the monocular and binocular contribution from these results. However, it appears that the transient-vergence system receives binocular input over a range up to 2 octaves and monocular contribution makes tuning appear broader. Monocular-based depth discrimination was also previously reported (Kaye, 1978; Harris & McKee, 1996). Kaye suggested that inadequate monocular stimulation to the binocular depth mechanism produces a weak qualitative depth percept, possibly interpreting it as an occlusion cue (Nakayama & Shimojo, 1990). The monocular target could stimulate the binocular-vergence system in a similar way.

7. General discussion

The present study is an extension of our previous work that has investigated the tuning of the transient-vergence system to the spatial properties of the stimulus. In other words, the question addressed by these studies was, what does the transient-vergence system use as matching cues when solving the correspondence problem? Our prior studies have demonstrated minimal

tuning to spatial frequency, orientation and contrast polarity (Edwards, Pope, & Schor, 1998; Pope, Edwards, & Schor, 1999). Spatial-frequency tuning for the transient-vergence system can be described as low-pass for the first-order luminance information contained in the carrier (Edwards et al.). For example, transient-vergence responses are preferentially made to lower luminance-spatial-frequencies compared with high spatial-frequencies at high contrasts, even when a low spatial-frequency is paired with a higher one. Similarly, with stimulus orientation and contrast polarity, transient-vergence responses are equal with both parallel and orthogonal carrier orientations and matched and opposite contrast-polarities, when presented at large disparities (3.8° in this study and 5° in our prior study) (Pope et al.). It is worth noting, however, that there is a small, but distinct bias in favor of responding to matched orientations at smaller-disparity values (2.5°) (Pope et al.). The transient-vergence system responds preferentially to the stimulus pairing that contains the highest combined-energy, regardless of differences in spatial frequency, contrast, orientation, or luminance polarity.

This lack of tuning to carrier information in the stimulus is indicative of performance being mediated by a second-order system. Hence we expected the system to show at least some tuning to envelope size. The present results confirm that expectation. Experiment 1 demonstrates that the transient-vergence system exhibits band-pass tuning to overall size of dichoptic targets. Equal sizes elicit a higher proportion of vergence responses than unequal size, however responses to size difference still occur over a 3-octave range. Size tuning, specified in octaves, was found to be broader for small envelope-sizes than for larger ones. Monocular-control conditions in Experiment 4 indicate that vergence responses can be evoked by monocular stimulation, however, one of the three observers clearly demonstrates that the transient-vergence system receives binocular inputs from 2 octave size-differences for orthogonal dichoptic Gabors, illustrating broad size tuning. Also, the presence of a response to monocular stimuli does not rule out a similar amplitude response to a binocular stimulus since the dichoptic Gabor has both monocular and binocular stimulus components. Experiments 2 to 4 demonstrate that envelope-size tuning was independent of carrier orientation, spatial frequency, or contrast. Thus carrier spatial frequency and orientation do not contribute to the band-pass envelope size-tuning exhibited by the transient vergence in its solution of the matching problem for large disparities.

This apparently broad tuning for envelope size is likely to result from the overlapping extracted low-pass frequency spectra of the contrast envelopes. Broader size-tuning with small envelopes might have resulted because the extracted frequency spectrum is broader for

small than for large envelopes. Binocular combinations of unequal size envelopes could be based upon the intermediate frequency region where energy levels for the small and large envelopes are equal. However, because the vergence system does not exhibit contrast tuning, matches do not require equal energy and information could be combined at any frequency where the two spectra overlap.

The fact that the transient-vergence system essentially shows no (or at most, low-pass) tuning to the carrier information (orientation, spatial frequency and contrast polarity) of the stimulus indicates that the system does not require these features to be matched when it solves the correspondence problem. The band-pass tuning exhibited to envelope size indicates that envelope size is used as a matching cue. However, the band-pass tuning observed in Experiment 1 was relatively broad. This finding may indicate that while envelope size is a matching cue, it is not an overly strong one. However, it is likely that the tuning to envelope size is actually tighter than the results of Experiment 1 indicate. This is due to the potential effect of probability summation of vergence responses made to monocular stimulus components (Experiment 4). That is, the summation of monocular responses may give the impression that binocular-tuning to envelope size is broader than it actually is. This was demonstrated by subjects MS and ZZ whose performance to binocular stimuli of 2 octave size-difference did not exceed probability summation to monocular stimuli. It is likely that the dominant matching cue for all subjects was stimulus onset synchrony, since targets must be presented with onsets within approximately 100 ms of each other in order to initiate transient vergence (Mitchell, 1970). Thus, it would appear that in solving the correspondence problem, the transient vergence uses matching cues of both stimulus size and onset synchrony.

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References

- Anzai, A., Ohzawa, I., & Freeman, R. D. (1997). Neural mechanisms underlying binocular fusion and stereopsis: position vs. phase. *Proceedings of the National Academy of Sciences of the USA*, *94*, 5438–5443.
- Blakemore, C., Fiorentini, A., & Maffei, L. (1972). A second neural mechanism of binocular depth discrimination. *Journal of Physiology*, *226*, 725–749.
- Bussettini, C., Miles, F. A., & Krauzlis, R. J. (1996). Short latency disparity vergence responses and their dependence upon a prior saccadic eye movement. *Journal of Neurophysiology*, *75*, 1392–1410.

- Cavanagh, P., & Mather, G. (1989). Motion: The long and the short of it. *Spatial Vision*, 4, 103–129.
- Edwards, M., & Badcock, D. R. (1995). Global motion perception: no interaction between the first- and second-order motion pathways. *Vision Research*, 35, 2589–2602.
- Edwards, M., Pope, D. R., & Schor, C. M. (1998). Luminance contrast and spatial-frequency tuning of the transient-vergence system. *Vision Research*, 38, 705–717.
- Erkelens, C. J. (1987). Adaptation of ocular vergence to stimulation with large disparities. *Experimental Brain Research*, 66, 507–516.
- Harris, J. M., & McKee, S. P. (1996). Monocular location provides a signed 'depth signal' for discriminating the sign of large disparities. *Investigative Ophthalmology and Visual Science*, 37, S283.
- Jones, R., & Kerr, K. E. (1971). Motor responses to conflicting asymmetrical vergence stimulus information. *American Journal of Optometry and Archives of the American Academy of Optometry*, 48, 989–1000.
- Jones, R. (1980). Fusional vergence: sustained and transient components. *American Journal of Optometry and Physiological Optics*, 57, 640–644.
- Jones, R., & Stevens, G. L. (1989). Horizontal fusional amplitudes. *Investigative Ophthalmology and Visual Science*, 30, 1638–1642.
- Kaye, M. (1978). Stereopsis without binocular correlation. *Vision Research*, 18, 1013–1022.
- Kontsevich, L. L., & Tyler, C. W. (1994). Analysis of stereothresholds for stimuli below 2.5 c/deg. *Vision Research*, 34, 2317–2329.
- Legge, G. E., & Gu, Y. (1989). Stereopsis and contrast. *Vision Research*, 29, 989–1004.
- Mitchell, D. E. (1970). Properties of stimuli eliciting vergence eye movements and stereopsis. *Vision Research*, 10, 145–161.
- Nakayama, K., & Shimojo, S. (1990). Da Vinci stereopsis: depth and subjective occluding contours from unpaired image points. *Vision Research*, 30, 1811–1825.
- Ohzawa, I., DeAngelis, G. C., & Freeman, R. D. (1996). Encoding of binocular disparity by simple cells in the cat's visual cortex. *Journal of Neurophysiology*, 75, 1779–1805.
- Pope, D. R., Edwards, M., & Schor, C. M. (1999). Orientation and luminance polarity tuning of the transient-vergence system. *Vision Research*, 39, 575–584.
- Riggs, L. A., & Niehl, E. W. (1960). Eye movements recorded during convergence and divergence. *Journal of Optical Society of America*, 50, 913–920.
- Schor, C. M., & Tyler, C. W. (1981). Spatio-temporal properties of Panum's fusional area. *Vision Research*, 21, 683–692.
- Schor, C. M., & Heckmann, T. (1989). Interocular differences in contrast and spatial frequency: effects on stereopsis and fusion. *Vision Research*, 29, 837–847.
- Schor, C. M., Edwards, M., & Pope, D. R. (1998). Spatial-frequency tuning of the transient-stereopsis system. *Vision Research*, 38, 3057–3068.
- Schor, C. M., Edwards, M., & Sato, M. (2001). Envelope size-tuning for stereo-depth perception of small and large disparities. *Vision Research*, submitted.
- Semmlow, J. L., Hung, G. K., Horng, J. L., & Ciuffreda, K. (1993). Initial control component in disparity vergence eye movements. *Ophthalmic and Physiological Optics*, 13, 48–55.
- Von der Heydt, R., Adorjani, C., & Hanny, P. (1977). Neural mechanisms of stereopsis: Sensitivity to orientational disparity. *Experientia*, 33, 786.
- Westheimer, G., & Mitchell, D. E. (1969). The sensory stimulus for disjunctive eye movements. *Vision Research*, 9, 749–754.
- Winkelman, J. E. (1953). Central and peripheral fusion. *AMA Archives of Ophthalmology*, 50, 179–183.