

Illusory contrast-induced shifts in binocular visual direction bias saccadic eye movements toward the perceived target position

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The perceived binocular visual direction of a fused disparity stimulus with an interocular contrast difference is biased toward the direction signaled by the eye presented with the higher contrast image (J. S. Mansfield & G. E. Legge, 1996). Does the amplitude of binocular saccadic eye movements have a similar bias? We examined saccades to fused disparate Gabor patches with interocular contrast differences. The effect of these contrast differences on saccadic amplitudes was compared to the perceptual biases in binocular direction obtained in a vernier acuity task. Saccades to unequal contrast targets landed between the end points for equal contrast and monocular targets. For three of our eight subjects, the saccadic bias equaled the perceptual effect. For the other subjects, however, saccades were affected to a lesser extent. Three models for binocular combination were used to evaluate these responses: A maximum-likelihood model failed to predict our results, whereas a model with contrast-dependent weighting of direction estimates by two monocular channels and a gain control model of binocular contrast summation gave a better approximation to our data. Both models showed that for the perceptual system, the influence of the eye that was presented with the higher contrast image was more dominant in the binocular combination than expected from the stimulus contrast ratio. The oculomotor system, however, was close to following linear summation.

Keywords: saccades, visual direction, contrast, binocular combination

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Introduction

Objects that subtend small binocular disparities appear fused if they lie within Panum's fusional limit (Mitchell, 1966; Panum, 1858) and are assigned a single binocular visual direction. Objects with disparities exceeding Panum's fusional limit appear diplopic and the two eyes' images are perceived in different directions for the same object. Various studies have found that the head-centric direction of fused objects is judged from a point midway between the two eyes, often referred to as the cyclopean eye (Ono & Barbeito, 1982; Porac & Coren, 1986). Figure 1 illustrates the binocular visual direction (blue line) as the average of the two eyes' monocular directions (green) as originally proposed by Hering (1942). However, Hering's law of visual directions does not hold in certain situations. For example, biases of ocular dominance can lead to a shift of the binocular visual direction away from the average toward the dominant eye (Charnwood, 1949; Francis & Harwood, 1951; Porac & Coren, 1986; Sheedy & Fry, 1979). Similar effects can be caused by interocular differ-

ences in image quality, such as blur (Charnwood, 1949) or luminance (Charnwood, 1949; Francis & Harwood, 1951; Verhoeff, 1933). More recently, it was reported that an interocular contrast difference biased the position judgments for disparate objects toward the position of the higher contrast image (Mansfield & Legge, 1996). The authors concluded that the computation of binocular visual directions is based on weighted averaging of visual directions for the left and right eyes' images.

In the present study, we investigated whether contrast-dependent weighting of direction estimates, similar to that described above for the perceptual system, also occurs with binocular stimuli for the oculomotor system. We measured responses of binocular saccades to disparate (yet fused) stimuli with interocular contrast differences. Motor response biases were compared to biases of perceptual estimates for the cyclopean direction of the same targets. Binocular saccades are normally conjugate. If they occur after a vergence movement nulls the disparity, then the stimulus has equal retinal eccentricities in the two eyes. However, if the saccades occur before vergence nulls the disparity, then they are stimulated by two different retinal

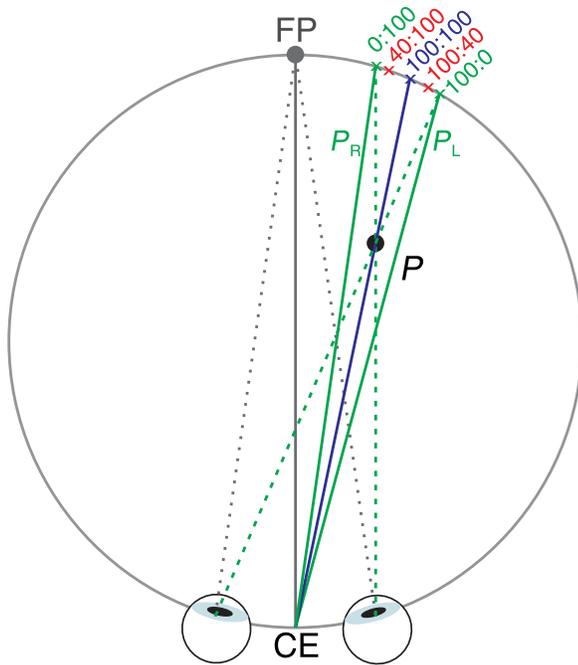


Figure 1. The binocular visual direction of a disparate object (P) is approximately the average (blue) of the two monocular directions (P_L , P_R , green), if the contrast is equal in the two eyes. If the contrast is unequal (40:100% and 100:40%, red), then the binocular direction is biased toward the direction of the higher contrast image. Solid lines represent head-centric visual directions from the cyclopean eye (CE), and dashed lines represent visual directions from each eye. FP: fixation point. Numbers give interocular contrast ratios (left:right).

eccentricities. Ideally, the saccade would aim at the averaged retinal eccentricity that would correspond to the eccentricity of the fused target. Does the oculomotor system direct saccades to the perceived binocular position or rely on retinal or some other source of information? To investigate the strategy of the saccadic system, we applied a disparity to a stimulus that elicited a sizable ambiguity between left and right eyes' direction signals combined with a large interocular contrast difference to influence the weights assigned to the two eyes. The resulting contrast-induced biases (CIBs) for perception and saccades were found to be unequal for some subjects, and this result will be interpreted with three different models for binocular combination.

Experiment 1: Interocular contrast differences and binocular perceived direction

Methods

The influence of interocular contrast differences on binocular perceived direction was quantified using a psychophysical vernier acuity task.

Subjects

Six female and two male human subjects (age range 22–26 years) with normal or corrected-to-normal vision participated in the experiment. Except JW, all were naïve to the aims of the study. The subjects were screened on binocular fusion abilities before the start of the experiment. They were asked to view several trials of the experiment during which the disparity of the stimulus was randomized between 0° and 5° . After each trial, the subject was instructed to report whether the stimulus had appeared single or double. Only those subjects who consistently reported a fused percept for disparities of up to 3° were used for the experiment. There were no obvious abnormalities in binocular eye alignment or stereopsis.

Stimuli and apparatus

The stimulus used for all experiments was a vertically oriented Gabor patch with the luminance profile

$$L(x, y) = A \sin[2\pi f(-x \sin \theta + y \cos \theta)] \exp\left(-\frac{x^2 + y^2}{2\sigma^2}\right) + M, \quad (1)$$

where A is the amplitude, f the spatial frequency, θ the orientation of the sinusoidal grating, σ the standard deviation of the Gaussian envelope, and M the mean luminance of the background. The contrast of the stimulus was defined by the ratio of the amplitude of the grating to the mean luminance level. The Gabor carrier was in cosine phase to center a dark bar in the Gaussian envelope. Binocular disparity was produced with position shifts of the entire Gabor patch.

To elicit a large bias of binocular perceived direction, we combined a crossed disparity of 2.5° with an interocular contrast ratio of 100% in one eye to 40% in the other eye (henceforth 100:40). A large standard deviation of the Gaussian envelope (3°) and a low spatial frequency (0.17 cpd) was within Panum's fusional area (Schor, Wood, & Ogawa, 1984) so that the subjects always perceived a single fused Gabor patch.

Stimuli were presented on a Sony Trinitron Multiscan 20SE-color monitor and viewed dichoptically through a Wheatstone mirror haploscope. Nonfusible peripheral apertures (square and circle, 20° in diameter) in front of each eye ensured that the edges of the mirrors and the monitor screen were hidden from the observers' view. The viewing distance was 50 cm. Head movements were minimized using a bite bar and a forehead rest.

Procedure

Perceived direction of the Gabor was measured with a vernier task (Figure 2). The horizontal position of a small black line (reference line) that contained zero disparity

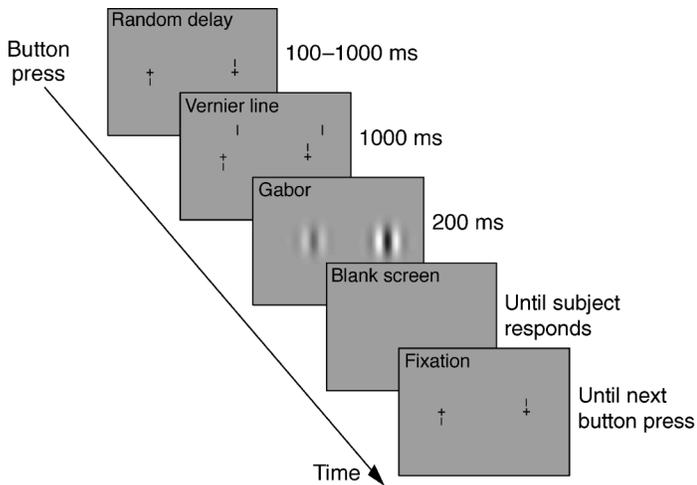


Figure 2. Stimulus presentation for the vernier task. Right eye targets are shown on the right, left eye targets are shown on the left. All stimuli were fused during the trials. Subjects had to judge the position of a thin line with respect to a Gabor patch that could have different interocular contrast ratios.

was compared to the position of the central black bar of the Gabor patch. The method of constant stimuli, i.e., testing the subject's response at a number of fixed stimulus levels (reference line positions), was used to obtain psychometric functions for five different interocular contrast ratios. Each psychometric function was based on 192 trials. The measurements were conducted in blocks of 24 trials requiring a total of 40 blocks for the five stimulus conditions. All trials in a certain block had the same interocular contrast ratio, which could belong to one of three categories. The positions of the Gabor patches on the monitor screen were constant but the perceived binocular direction (position) was influenced by the interocular contrast ratio. The three conditions are given below.

Equal contrast condition

An interocular contrast ratio of 100:100 should let the Gabor appear at or close to its average position (Figure 1, blue).

Unequal contrast conditions

Interocular contrast ratios of 40:100 (i.e., higher contrast in right eye's image) or 100:40 should lead to apparent shifts toward the higher contrast image, respectively (Figure 1, red).

Monocular conditions

The visible half-images for stimuli with interocular contrast ratios of 0:100 and 100:0 were presented at the same screen locations as in the binocular stimulus with crossed disparity. The monocular condition was a control to make sure that subjects were not simply suppressing the input from one eye during the unequal contrast condition because psychophysical and neurophysiological studies showed that a high contrast grating presented to one eye

can suppress the percept of and the neural response to a lower contrast grating presented to the contralateral eye (Abadi, 1976; Berardi, Galli, Maffei, & Siliprandi, 1986). Monocular suppression would result in the perceived directions shown in Figure 1 (green).

At the beginning of each experimental session, the mirrors of the haploscope were adjusted so that the binocular parallax of the fixation cross equaled the subject's horizontal phoria. For this purpose, the participant viewed a black screen with a white L-shape in front of one eye (permanently on the screen) and a flashing white L-shape, flipped vertically and horizontally, in front of the other eye. The subject was instructed to adjust the horizontal and vertical position of the permanent L-shape until the two shapes appeared to form a cross. This eliminated a disparity vergence stimulus by the fixation target. As illustrated in Figure 2, subjects initially fixated a zero disparity black cross that was positioned near the center of the screen with nonius lines above and below it. Once the nonius lines appeared in vertical alignment, the subject initiated a trial by pressing a button. After a random delay (100–1000 ms), a thin black reference line with zero disparity was presented for 1 s up and to the right of the fixation cross at one of several randomly selected horizontal positions within the range of constant stimuli. Immediately afterward, a Gabor patch with 2.5° crossed disparity was presented below the position of the reference line for 200 ms. The fixation cross and reference line were extinguished before the Gabor was presented to eliminate a disparity gradient between them and the Gabor that would have reduced Panum's fusional limit and produced diplopia (Burt & Julesz, 1980). The reference line could be displayed at six different horizontal positions with respect to the Gabor (method of constant stimuli). Ideally, three of the line positions would be perceived on either side of the Gabor center. To accomplish this, the set of reference lines had to be displayed in a different range of eccentricities for each interocular contrast ratio because changes in the contrast ratio led to changes in the perceived position of the Gabor. Estimates of the perceived Gabor position were obtained for each subject and for each interocular contrast ratio in preliminary experiments. The so-obtained perceived positions were then used as the center points around which the six different reference line positions were equally distributed. The separation between the line positions was adjusted to each subject's performance (small separations for subjects with low vernier thresholds) but was constant across the conditions within one subject. The distance between two of the line positions ranged from 0.15° to 0.24° . The positions of the Gabor and the reference line were covaried over a range of 0.5° to prevent subjects from relying on the eccentricity of the line for their position judgments. Therefore, the Gabor center could be presented in a range of $2.5\text{--}3.0^\circ$ eccentricity. The peripheral target presentation was chosen to match the conditions in the subsequent eye movement experiment

(Experiment 2). The six reference line positions were randomized over the trials of a block and interocular contrast ratios were randomized over the blocks.

The subject was instructed to maintain fixation in the center of the screen for the duration of the trial. After the stimulus was presented, the monitor remained blank (gray) until the subject indicated with a button press whether the reference line was seen displaced to the left or to the right of the center of the Gabor patch. All trials in which a subject reported moving his or her eyes, a loss of attention, blinking, or accidentally giving the wrong response were repeated.

Data analysis

Psychometric functions were obtained using Probit analysis performed with MatLab 6.5. For each function, the point of subjective equality (PSE) and the just noticeable difference were determined. The PSE was defined as the stimulus level at which the answers “left” and “right” occurred with equal probability. The just noticeable difference was equal to the standard deviation of the underlying probability density function. The perceptual CIB was quantified using Equation 2:

$$\text{CIB} = \frac{\text{PSE}_{\text{eq}} - \text{PSE}_{\text{ueq}}}{\text{PSE}_{\text{eq}} - \text{PSE}_{\text{mon}}}, \quad (2)$$

where eq represents the equal contrast condition, ueq represents one of the unequal contrast conditions (e.g.,

40:100), and mon represents the associated monocular condition (e.g., 0:100). The CIB value ranges between 0 and 1 regardless of direction. A value of 1 represents monocular suppression ($\text{PSE}_{\text{ueq}} = \text{PSE}_{\text{mon}}$), whereas a value of 0 would be obtained if unequal contrast targets were seen at the same position as equal contrast targets ($\text{PSE}_{\text{ueq}} = \text{PSE}_{\text{eq}}$). A CIB between 0 and 1 occurs if unequal contrast targets were perceived at a location in between the extreme positions of equal contrast and monocular targets ($|\text{PSE}_{\text{eq}}| < |\text{PSE}_{\text{ueq}}| < |\text{PSE}_{\text{mon}}|$).

Results

Results are shown in Figure 3. Negative PSE values signify a perceived direction to the left of the average screen position of the two Gabor patches. The PSE for the equal contrast condition matched the average position well, whereas the PSEs for unequal contrast stimuli were shifted toward the monocular directions of the higher contrast image. All subjects exhibited this qualitative pattern. The PSEs for the different contrast conditions within each subject were significantly different (t tests), except for the right shifts of subject AS. For most subjects, the perceived directions of the monocular stimuli were biased toward the center point between the two monocular stimulus positions. Additionally, two subjects showed large biases that could not be explained by their ocular dominance: For AS, most PSEs (including 100:0)

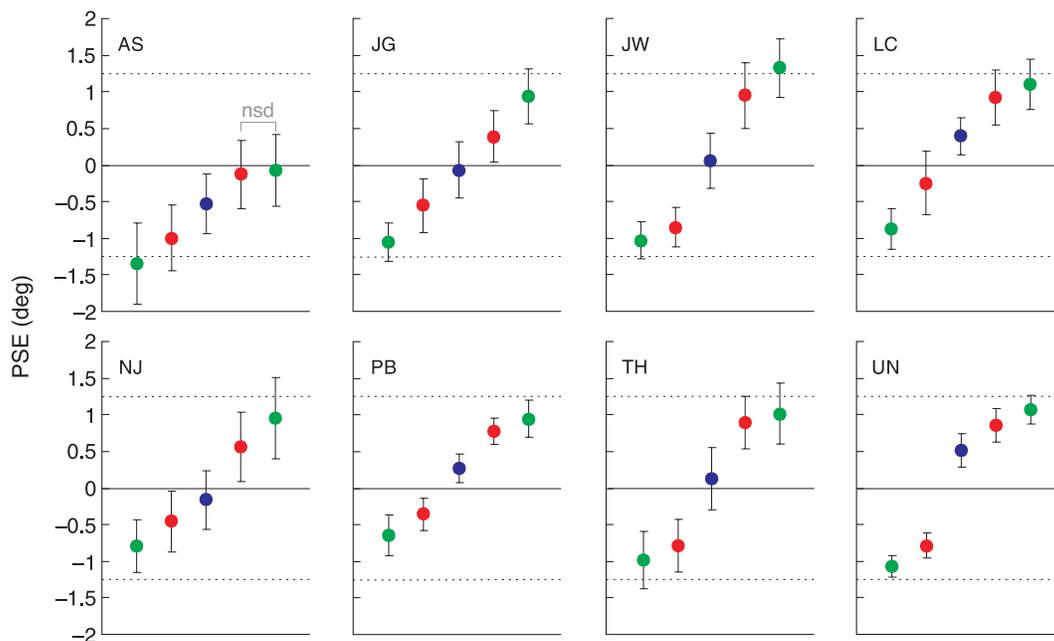


Figure 3. PSEs and thresholds for all subjects. For each subject, PSEs for monocular (green), unequal contrast (red), and equal contrast (blue) targets are plotted for the five different interocular contrast ratios: 0:100, 40:100, 100:100, 100:40, and 100:0 (from left to right). Error bars represent the just noticeable difference. The dotted lines mark the real positions of the monocular targets; nsd: not significantly different.

Subject	Left shift (40:100)	Right shift (100:40)
AS	0.58	0.88*
JG	0.49	0.45
JW	0.83	0.70
LC	0.50	0.75
NJ	0.47	0.64
PB	0.68	0.76
TH	0.82	0.87
UN	0.82	0.62

Table 1. Perceptual CIBs (Equation 2) for all subjects. Asterisk indicates a nonsignificant difference between monocular and unequal contrast PSEs.

were shifted to the left. Subject UN only exhibited an obvious bias for the equal contrast condition. The thresholds were relatively high in all conditions and for all subjects (just noticeable differences between 0.15° and 0.56°).

The perceptual CIBs were calculated from the PSE data using Equation 2 and they are summarized in Table 1. PSEs varied between subjects and also for the two directions (right/left shifts) within one subject. The mean CIB over all subjects was 0.65 ± 0.05 ($\pm SE$) for perceived left shifts and 0.70 ± 0.05 for perceived right shifts. The difference between these means was not significant (t test: $p = .44$; Wilcoxon rank sum test for medians: $p = .5$).

Discussion

The vernier acuity task confirmed earlier findings (Mansfield & Legge, 1996) that the position judgments for unequal contrast targets are biased toward the position of the higher contrast image. However, the magnitude of the effect varied between the subjects. Sources for this variation will be discussed in relation with the saccade task in Experiment 2. Consistent biases in the monocular conditions could have been due to a shift in the reference position used for the vernier judgments. Instead of comparing the position of the reference line with the center of the black bar in the Gabor patch, subjects might have used the outer edge of this bar (width approximately 1°) for trials close to the fovea and the inner edge for trials in the periphery. The strong additional biases of subjects AS and UN cannot be explained easily. If biases were mainly due to ocular dominance, then they should have occurred in all binocular conditions (not true for subject UN), but not in the monocular conditions (not true for subject AS).

Vernier thresholds for all conditions were high compared to the thresholds for foveal line stimuli, which are on the order of several arcsec (Westheimer & McKee, 1977). These elevated thresholds can be attributed to the

nonfoveal target presentation (Schor & Badcock, 1985; Westheimer, 1982), the low spatial frequency of the stimulus (Bradley & Skottun, 1987; Schor & Badcock, 1985), the large disparity (Heinrich, Kromeier, Bach, & Kommerell, 2005), and the sequential target presentation (Beard, Levi, & Klein, 1997).

Experiment 2: Interocular contrast differences and binocular saccades

Binocular saccades were measured in response to the same stimuli used in Experiment 1 to determine if the same binocular estimates of direction are used for both perception and the programming of saccade metrics. Saccade amplitudes were examined to obtain an estimate of the CIB of the saccadic system.

Methods

Subjects, apparatus, and stimuli were the same as in Experiment 1. Eye movements were recorded with the Stanford Research Institute dual Purkinje eyetracker at a sampling rate of 500 Hz. For some subjects, it was necessary to dilate the pupils using 2.5% phenylephrine hydrochloride to avoid artefactual changes in the recorded eye position signal due to a change in pupil size.

Procedure

The binocular parallax of the fixation cross was adjusted with the Stanford Research Institute visual stimulator to equal the subject's phoria. All further disparity stimuli and measurements of binocular eye position were relative to this phoria position. During this procedure, mirrors were positioned to image each eye's monitor screen normal to the visual axis when fixating the screen center. Therefore, all purely translational movements of the stimulus were on the isovergence circle. Before each eye movement session, the eyetracker was calibrated over an 8° range (4° on either side of the fixation cross).

The experiment was conducted in blocks of 24 trials and required a total of 37 blocks. Unless otherwise stated, 32 trials per target position were collected. The stimulus sequence for a single trial is shown in Figure 4. Each trial started with a fixation cross in the screen center surrounded by a pair of nonius lines. Once the observer had established stable fixation, he or she initiated the trial by a button press. After a random delay (100–1000 ms), a zero disparity Gabor with equal (100%) contrast in both eyes replaced the fixation cross in the center of the visible

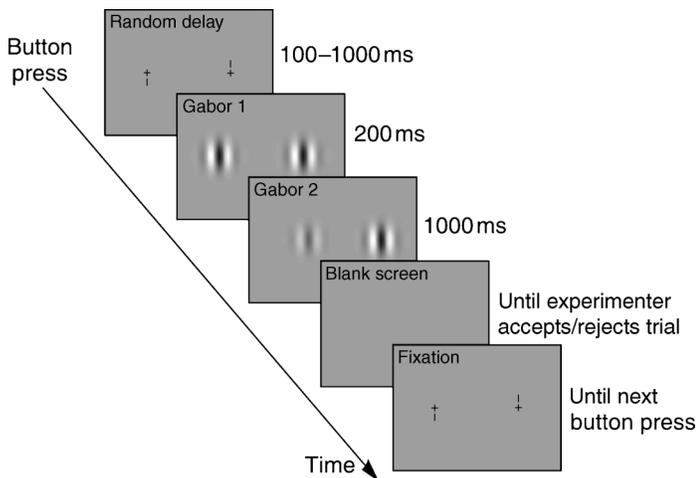


Figure 4. Stimulus presentation for the eye movement experiment. Right eye targets are shown on the right, left eye targets are shown on the left. All stimuli were fused during the trials. The subject was instructed to keep the center of the Gabor patch fixated.

field. The subject was instructed to maintain fixation in the center of the Gabor as stably as possible. After 200 ms, the Gabor was substituted for a second Gabor (duration: 1000 ms) that was displaced to the right or to the left with respect to the position of the (now extinguished) fixation cross and the first Gabor. The two sequentially presented Gabors appeared to be the same target that jumped horizontally, making it more likely that subjects would saccade to the same position on the Gabor carrier (the central black bar) than if the fixation cross had been used as the starting point of the saccade. Additionally, this sequence facilitated the occurrence of early saccades, before vergence movements had a chance to null out the stimulus disparity and, with it, the contrast-induced effect. Contrast and lateral eccentricities of the second Gabor were condition dependent and are described in the following sections. The long stimulus duration (1000 ms) was chosen because subjects reported difficulties with making accurate saccades to stimuli with shorter presentation times (200 ms) used in the vernier task. After the stimulus presentation, the screen remained blank until the experimenter had examined the recorded eye position signal. Trials were repeated if blinks, anticipatory saccades, or no eye movements occurred.

Influence of interocular contrast differences on saccades

The different trial types used for the saccade tasks are shown in Figure 5. Red crosses mark the binocular target positions that would be perceived if both eyes' images were weighted equally (in binocular trials) whereas filled circles indicate the corresponding hypothetically perceived positions if contrast-dependent weighting was employed. To investigate whether interocular contrast differences affect the amplitude of saccadic eye movements or not, we compared the amplitudes of saccades to

equal and unequal contrast Gabors. Two different paradigms were conducted, in which the Gabor was always presented with a 2.5° crossed disparity. In the first (long-jump paradigm), the Gabor appeared at a lateral eccentricity of 3.5° , and in the second (short-jump paradigm) it appeared at a lateral eccentricity of 2.5° . In the long-jump, the four trial types shown in Figures 5a and b were randomized: The Gabor could be presented either in the left or in the right visual hemifield and the contrast could be either equal (Figure 5a, both 100%) or unequal (Figure 5b, 100% and 40%). Target jumps to the right were associated with higher contrast in the right eye (40:100, perceived as shifted to the left), and target jumps to the left with higher contrast in the left eye (100:40, perceived as shifted to the right). Therefore, the perceived shift was always centripetal for the long-jump. In the short-jump paradigm, the opposite contrast/direction assignment (Figures 5d and e) would cause the target to appear shifted centrifugally. Field size limitations of the Stanford Research Institute visual stimulator made it necessary to have unequal jump sizes for these two types of bias.

Monocular control

As with the vernier task, a monocular control mimicked the monocular suppression response by presenting a 100% monocular target in the position it would have had in a binocular trial. The trial types of Figures 5a, c and d, f were randomized.

Zero disparity control

A second control condition examined the possibility that interocular contrast differences systematically influ-

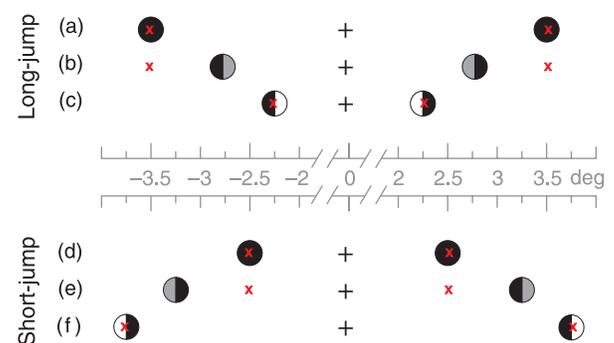


Figure 5. Hypothetical perceived positions for the long- and short-jump paradigms of the eye movement experiment. The black plus sign represents the fixation cross in the screen center, eccentricities of targets are given in degrees. Red crosses mark apparent target positions that would result if the saccadic system gave equal weight to the left and right eyes' images in binocular trials (a, b, d, e) and to only the viewing eye in monocular trials (c, f). Filled circles indicate hypothetical binocularly perceived target positions. The left half represents the contrast of the left eye, the right half represents the contrast of the right eye. Contrasts assigned to colors are as follows: white: 0%; gray: 40%; black: 100%.

ence saccadic amplitudes in the absence of disparities. The Gabor was presented with zero disparity and at a lateral eccentricity of 2.5° either to the left or to the right of the fixation cross. For both directions, interocular contrast ratios of 40:100 and 100:40 were tested. Thirty saccades per direction and interocular contrast ratio were collected.

Data analysis

Eye movements were recorded for 1 s beginning at the onset of the second Gabor patch. Analysis of the recorded data was performed offline using Matlab 6.5 and Microsoft Excel 2000. The recorded eye movement signal was smoothed with a moving average over a 5-point range. The version component was calculated as the average of the two eyes' positions, and vergence was calculated as the difference between the positions (left eye – right eye). Saccade onset was defined as the point where version velocity first exceeded $20^\circ/\text{s}$. Saccade offset was taken at the time immediately following the well-known saccadic artifact elicited by the Purkinje eyetracker (Deubel & Bridgeman, 1995), see Figure 6. For the analysis of saccade amplitudes, only primary saccades were taken into account. The amplitudes were normalized by calculating the saccadic CIB, with the following equation:

$$\text{CIB} = \frac{\text{mean}_{\text{eq}} - \text{trial}_{\text{ueq}}}{\text{mean}_{\text{eq}} - \text{mean}_{\text{mon}}}, \quad (3)$$

where the amplitude value for the unequal contrast condition (ueq) was derived from single trials; the other amplitude values were derived from the means (mon: monocular; eq: equal). Therefore, all normalized data

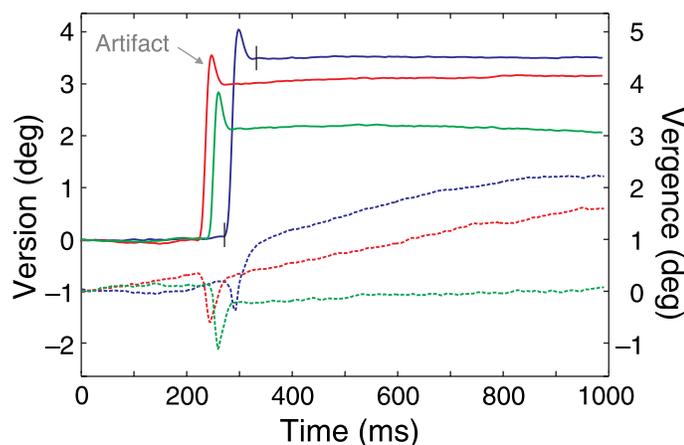


Figure 6. Version (solid) and vergence (dashed) traces for three single trials. Blue: equal contrast; red: unequal contrast; green: monocular. Saccade onset and offset are marked by black lines. Saccade offset was defined following the saccadic artifact elicited by the Purkinje eyetracker.

except those for the zero disparity control were combined. Data were represented independent of direction or jump size such that interindividual differences in saccadic behavior (e.g., hypometria) were canceled out. Ideally, the CIB should range between 0 and 1, but it could also be lower or higher due to variance.

The criterion for statistical significance was set at $p < .05$ for all tests. Differences in means were analyzed using t tests for independent samples when we could verify that the underlying data were described by a normal distribution. Normality was tested using the Kolmogorov–Smirnov and Lilliefors test with further inspection of normal probability plots. If normality was in doubt, additionally differences in medians were tested with the Wilcoxon rank sum test.

Curve fitting

To get a veridical estimate for the saccadic CIB (Equation 3), we further processed the normalized data to avoid a possible confounding response. If the subjects had made a saccade to the equal contrast target position in some of the unequal contrast trials and to the high contrast target position (suppression) in the remainder of the trials, then the average CIB for unequal contrast targets would lie between 0 and 1, although the saccadic system was unaffected by the interocular contrast difference. To avoid this misinterpretation, we excluded suppression trials from the analysis of CIB. This was done for each stimulus condition and each subject separately. Histograms of the CIB values were created and fitted with both a single Gaussian and a mixture of two Gaussians with a least squares curve fitting algorithm (Figure 7). F tests were used to determine the significantly better fit. In most cases, a single Gaussian was sufficient to describe the underlying distribution (Figure 7a). For some data sets, however, the CIB histograms showed bimodality with one distribution consisting of suppression trials that clustered around 1 and another distribution with lower mean (Figure 7b). Trials in the suppression distribution were rejected. In addition, all unimodal distributions with a CIB above 0.9 were excluded from further data analysis because they most likely were composed of suppression responses. A limit of 0.9 was chosen because perceptual CIBs never exceeded that value. Ideally, suppression distributions should have a mean of 1, but it could also be higher or lower due to variance.

Results

Zero disparity control

No subject exhibited significant differences between the mean amplitudes to zero disparity stimuli with interocular contrast ratios of 100:40 and 40:100 (t tests). Thus, it can be ruled out that interocular contrast differences influenced the oculomotor behavior in the absence of disparities.

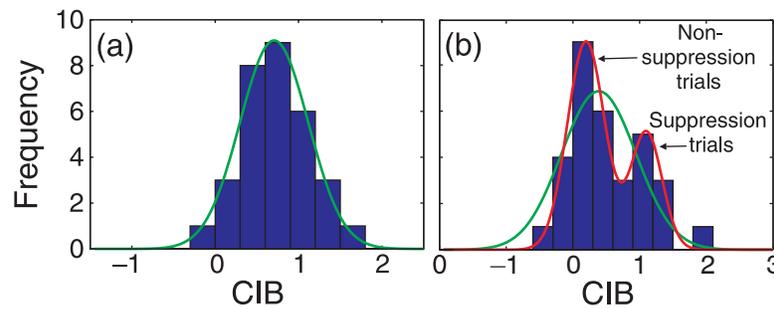


Figure 7. Examples for a unimodal (a) and a bimodal (b) CIB histogram. The histogram in panel a is sufficiently described by a single Gaussian distribution (green), whereas the data in panel b require a fit with a mixture of two Gaussians (red). Trials under the Gaussian component centered at a CIB of 1 result from suppression.

Influence of interocular contrast differences on saccades

Means of the raw amplitudes for equal and unequal contrast and for monocular and unequal contrast conditions were significantly different (t tests) for almost all data sets of all subjects. The standard deviations of saccadic end points were on average 0.45° , varying between subjects but not systematically between conditions. For a more detailed analysis, the raw amplitude values were normalized by calculating the saccadic CIB (Equation 3). Mean saccadic CIBs, after exclusion of suppression trials (see curve fitting section), were compared between the four stimulus conditions (short- vs. long-jump, leftward vs. rightward saccades) using the pooled data of all subjects. Because no significant differences between these conditions were found, the data were combined (Figure 8). The dotted lines mark the hypothetical CIB limits of 0 (equal contrast position) and 1 (monocular suppression). A substantial fraction of trials lies outside this range due to variance, but the peak of the distribution is centered between 0 and 1. This means that saccadic amplitudes were influenced by the interocular contrast difference. The mean CIB values ($\pm SD$) for each

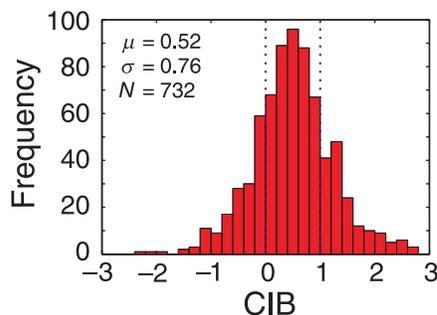


Figure 8. Histogram of all subjects' CIB values (excluding suppression trials). The dotted lines represent the theoretical CIB limits of 0 (equal contrast target position) and 1 (monocular target position). The peak of the distribution (mean, μ) lies in between these limits. Frequency units are number of occurrences. σ : standard deviation; N : number of observations.

subject are shown in Figure 9 together with the means for the equal and monocular contrast condition, which were always 0 and 1 due to the normalization process. Differences between the means for equal and unequal contrast condition and between the means for monocular and unequal contrast condition were always significant. The CIB varied between the subjects.

Saccades in all contrast conditions were usually hypometric, as is commonly reported in the literature (Aitsebaomo & Bedell, 1992; Becker & Fuchs, 1969; Henson, 1978). However, some subjects had slightly hypermetric saccades for the monocular targets in the long-jump condition (smallest eccentricity of all targets) or at least smaller undershoots to those targets than for the monocular targets located further in the periphery (short-jump). This saccadic behavior is consistent with the data from the perceptual task in which monocular targets close to the fixation cross were seen shifted outward (centrifugally) with respect to their real positions, and monocular targets in the periphery appeared displaced inward (centripetally).

Vergence and CIB

Initiation of vergence before saccade start was examined as a possible source of CIB variation. Because the CIB is disparity dependent, vergence movements that lower the disparity will also lower the perceived CIB. Although all saccades occurred early in the eye movement responses (latencies between 200 and 300 ms, see Figure 6), most subjects completed a small amount of vergence before the saccade started. Correlations between the CIB values for all trials (including suppression trials) with the associated vergence amplitudes were analyzed at the onset of the saccade and at a time equal to half the saccadic latency. Saccade amplitude can be influenced by information during the latency period until approximately 80 ms before saccade onset (Becker & Jürgens, 1979) so that the vergence amplitude at saccade onset is a very conservative measure of any reduction in disparity that would influence saccade amplitude. However, in both cases, no correlation between the CIB and vergence could be found (Pearson's correlation coefficient below 6%).

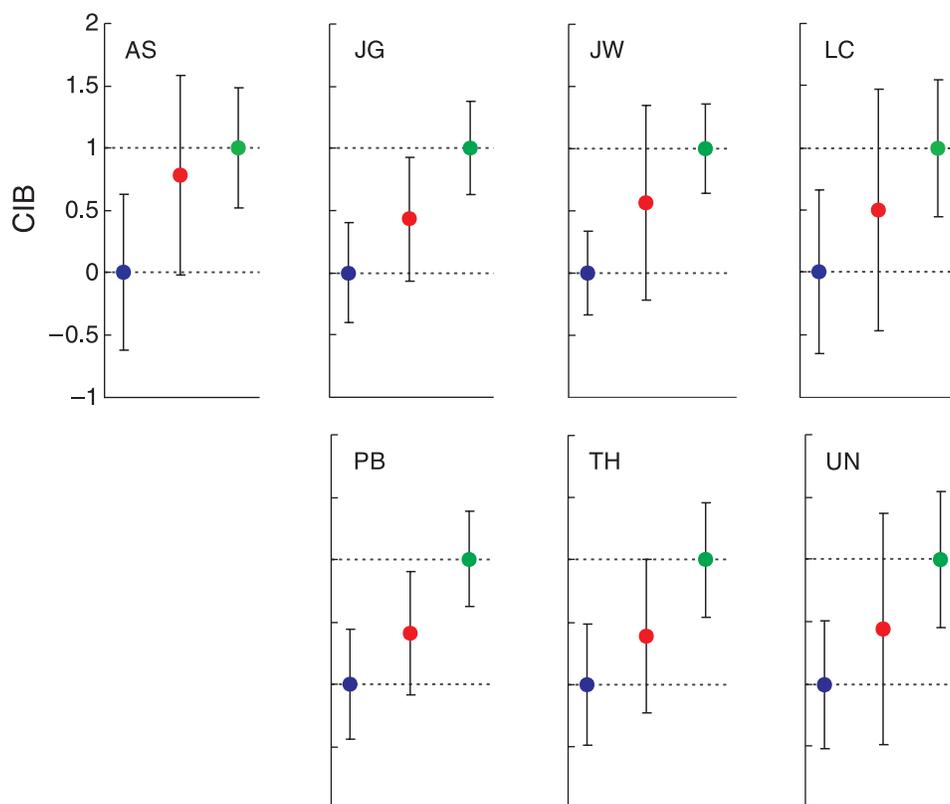


Figure 9. Saccadic CIBs for all subjects. Mean CIBs (red) together with the results of the equal contrast (blue) and monocular (green) condition. The means for the latter were always 0 and 1 due to the normalization process. Data of NJ were excluded from the analysis because of large variance (no significant differences between equal contrast and monocular conditions). Each data point for the unequal contrast data is on average based on 99 trials (128 max, 64 min). Error bars are ± 1 SD. Differences between means for the unequal contrast condition and the corresponding monocular or equal contrast condition were always significant with $p < .001$.

Comparison of perceptual and saccadic CIB

To compare the magnitude of interactions of interocular contrast differences with perception and saccades, we expressed CIBs for saccades as a percentage of the associated perceptual CIBs (comparison CIB) and plotted the comparison CIBs in Figure 10 for each subject. If perceptual and saccadic CIBs were equal, the comparison CIB would have a value of 100% (solid horizontal line). Shorter bars indicate that the saccadic CIB was smaller than the perceptual CIB. The mean comparison CIB (right blue bar) was significantly smaller (marked by asterisk) than 100% (one sample *t* test, sign test for nonnormally distributed data sets). This was, however, only true for the data after the exclusion of suppression trials (blue bars). Because suppression can only be detected for the saccade data, a difference between perceptual and saccadic CIBs could result from an unbalanced exclusion of suppression trials. Because of this, data containing suppression trials are plotted for comparison (blue and red bars together). The group mean for data including suppression trials is not different from 100%. However, three individual subjects still show a significantly smaller saccadic than perceptual CIB, including JW, who did not exhibit suppression at all. Thus, the relation between perceptual

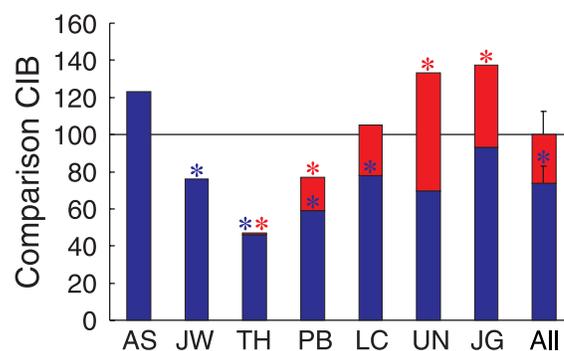


Figure 10. Saccadic CIBs expressed as percentage of the perceptual CIBs (comparison CIB) for each subject and average (mean + SE). Data are plotted after (blue bars) and before exclusion of suppression trials (blue + red bars). A value of 100% represents equality of perceptual and saccadic CIBs. Lower values denote saccadic CIB < perceptual CIB. Significant deviations from 100% (*t* test or sign test) for the data excluding suppression trials are indicated by blue asterisks. Significant deviations of the data including suppression trials are marked by red asterisks. Error bars for the single subjects are omitted for clarity. Estimates of each subject’s variance can be obtained from Figure 9.

and saccadic CIB seemed to be different for individual subjects whether suppression was accounted for.

Discussion

Our results illustrate that saccade amplitudes of all subjects showed a CIB in all tested conditions ($0 < \text{CIB} < 1$), meaning that saccades are influenced by interocular contrast differences. The contrast dependence of binocular saccade amplitude could not be explained by a less-effort strategy. The latter would predict that when forced to choose between two target positions (i.e., contrast-biased position vs. average position), the eye would always move to the least eccentric target. To the contrary, amplitudes were biased toward the higher contrast targets whether this required a smaller (long-jump) or a larger (short-jump) movement than to an equal contrast target.

For several subjects, the saccadic CIB was significantly smaller than the perceptual CIB and the magnitude of that difference varied across the subjects. Both effects could not be explained by an unbalanced exclusion of suppression trials (exclusion only in the saccade task) as shown by a comparison between perceptual and saccade data including suppression trials (Figure 10). If there were more suppression in the vernier than in the saccade task, this would result in a higher CIB for the perceptual task. Two observations argue against this: Thresholds in the vernier task did not increase as contrast became unequal, suggesting that not many suppression trials were added, which would increase the variance of the results (assuming that suppression is more likely for unequal than for equal contrast targets). Secondly, suppression trials were more prevalent in the saccade condition with the large than the small target eccentricities and small eccentricities were used for the vernier task. In addition, the effective exposure duration was the same for vernier and saccade task (200 ms) since primary saccades started usually with a latency of approximately 200 ms. Therefore, the timing was about equivalent for the two tasks. These observations suggest that suppression does not account for the larger CIB for perception than for saccades.

Besides suppression, the vergence amplitude before saccade onset was tested as a possible source of the CIB variance, but no correlation between vergence and CIB magnitude was found. As a consequence, some other inherent factor has to account for the CIB variance and the difference between perception and saccades.

Three models of binocular combination

Experiment 2 did not provide a clear answer to whether perception and saccades use the same contrast weighting

during the computation of binocular visual direction; the results suggested, however, that the integration of the sensory inputs from the two eyes was handled differently by different subjects. We attempted to account for these individual differences with three models of binocular combination: a maximum-likelihood model; a contrast-dependent monocular combination model, based on Mansfield and Legge (1996); and a modified linear summation model recently proposed by Ding and Sperling (2006).

Model 1: Maximum-likelihood estimation

Mansfield and Legge (1996) first showed that position estimates of disparate contrast-mismatched Gabor patches were biased toward the position of the higher contrast image and that these data were well described by a modified version of the maximum-likelihood estimation (MLE) model. However, it was argued later that the data were most likely confounded by vergence changes that altered stimulus disparity (Banks, van Ee, & Backus, 1997). MLE is commonly used to predict a signal estimate for combined cues (for instance, a binocular visual direction) based on the variances of the individual cue signals (direction estimates of each eye alone) and assumes that the more reliable (lower variance) cues are more heavily weighted. We compared our observed vernier and saccade data for unequal contrast targets with predictions by the MLE model based on the variances in the monocular stimulus conditions. Differences in the variance in monocular conditions might account for the variation of the CIBs between the subjects and between the vernier and saccade data.

Methods

To predict the position of a binocular unequal contrast stimulus, we needed data for both single cues (monocular high contrast and monocular low contrast). Thus, additional data in a monocular 40% condition were collected on four subjects that had participated in the former experiments (JG, JW, PB, and TH). Stimuli and apparatus were the same as in Experiments 1 and 2.

Procedure

Data of both the psychophysical vernier task and the saccadic eye movement experiment were complemented by a monocular 40% contrast condition. The procedure was in each case the same as described for Experiments 1 and 2. For the vernier experiment, the stimulus locations

were the same as in the two 100% monocular conditions, only with a monocular 40% contrast image. Target eccentricities for the saccade task were 4.75° for the long-jump and 1.25° for the short-jump paradigm. The short-jump paradigm was conducted in the left and right directions, and the long-jump paradigm was conducted only in the right direction. The three conditions were randomized over the trials. The monocular stimulus was presented to the eye that did not receive the monocular stimulus in [Experiment 2](#). For example, in [Experiment 2](#) for the long-jump to the right (interocular contrast ratio of 40:100) the right eye saw a 100% contrast target during the monocular condition. In the present experiment, therefore, the left eye was presented with a 40% contrast monocular stimulus. Thus, for all tested conditions in the vernier and saccade task, data were available for a particular binocular unequal contrast stimulus and for the two monocular targets constituting this binocular stimulus.

Data analysis

The MLE model describes a strategy for integrating two (or more) cues into a combined estimate (for instance a binocular visual direction \hat{B}) of the lowest possible variance by computing a weighted average of the single cues (here left and right eyes' direction estimates \hat{L} and \hat{R}):

$$\hat{B} = w_L \hat{L} + w_R \hat{R}, \quad (4)$$

where w_L and w_R are the left (L) and right (R) eye weights that are normalized to sum up to 1. The weights represent reliabilities and are dependent on the variances (standard deviations σ) of the single cue estimates as defined by:

$$w_L = \frac{1/\sigma_L^2}{1/\sigma_L^2 + 1/\sigma_R^2} \quad \text{and} \quad w_R = \frac{1/\sigma_R^2}{1/\sigma_L^2 + 1/\sigma_R^2}. \quad (5)$$

If the estimate of one of the cues is very noisy, the reliability of that cue is weak and the assigned weight will be low. Because vernier acuity is known to deteriorate with decreasing contrast (Banton & Levi, 1991; Bradley & Skottun, 1987; Hess & Holliday, 1992; Krauskopf & Farell, 1991; Whitaker, 1993), the eye seeing the lower contrast image is expected to be weighted less in the computation of binocular visual direction. Given [Equation 5](#), we predicted the single cue weights for the vernier and saccade data based on the variances measured in the monocular conditions with 40% and 100% contrast. We then compared the predicted weights with the experimen-

tally observed weights derived from incorporating the normalization assumption $w_L + w_R = 1$ into [Equation 4](#) to achieve

$$\hat{B} = w_L \hat{L} + (1 - w_L) \hat{R} \Rightarrow w_L = \frac{\hat{B} - \hat{R}}{\hat{L} - \hat{R}}. \quad (6)$$

If the estimate of a binocular visual direction is obtained by combining the single cues, dependent on their variances, observed and predicted weights should be the same.

Results

The results of the comparison between the weights predicted by the MLE model (calculated from [Equation 5](#)) and the experimentally observed weights (calculated from [Equation 6](#)) are plotted in [Figure 11](#). The data excluding suppression trials were used for the saccade task, which led to exclusion of one condition for subject JG and adjustment of one data point for PB (0.25° lower amplitude than with suppression). If the MLE model were to describe the data correctly, all points should lie close to the 1:1 line (gray). [Figure 11](#) shows that this is neither the case for the vernier (left) nor for the saccade data (right). However, the data points do not randomly scatter. Instead, data of a certain interocular contrast ratio cluster together, showing that the MLE model systematically underestimates the influence of contrast for the determination of the weights. Variances were not determined by contrast, as we expected, but possibly by stimulus eccentricity or different acuities in the two eyes. In the 100:40 case, the observed weights for the left eye were higher than predicted by the model. Accordingly, the observed left eye weights for the 40:100 case were lower than predicted. The data illustrate that monocular visual directions are not simply combined by weighting left and right eyes' inputs dependent on the variances of the signals.

Discussion

Contrary to the combination of single cues from different sensory modalities into a unified percept (Ernst & Banks, 2002; Hillis, Watt, Landy, & Banks, 2004; Oruç, Maloney, & Landy, 2003), binocular combination does not seem to obey the MLE model. There was no correlation between observed weights and weights predicted by the MLE model for the vernier and saccade data because the model underestimated the influence of contrast on the weights. The deviations of the results from the predictions cannot be due to ocular dominance effects: To bring the observed and predicted weights

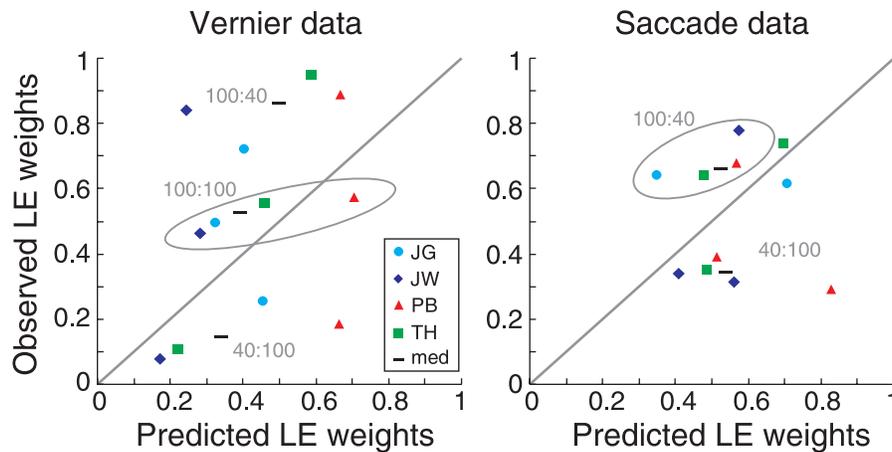


Figure 11. Comparison of observed and MLE predicted left eye (LE) weights for vernier (left) and saccade data (right). Black bars mark the median values (med) for the different interocular contrast ratios. Data for three contrast ratios are plotted for the vernier task. However, only data for the two unequal contrast conditions were available for the saccade task (100:40, short right; 40:100, short left and long right). Ellipses group data points of the same interocular contrast ratio. For both experiments, none of the data points fall on the 1:1 line (gray) as would be expected, if MLE were to predict the results.

closer together, we would need a lower weight to be assigned to the left eye for an interocular contrast ratio of 40:100, but a higher weight for a ratio of 100:40.

Model 2: Contrast-dependent monocular combination

The MLE model of Mansfield and Legge (1996) attempted to describe the binocular visual direction with a model that sums weighted estimates of direction from two monocular channels. Because the variance-dependent weighting of the MLE model obviously failed to describe our data by underestimating the influence of contrast on the weights, we applied a model in which the weights are solely determined by the contrasts. In this model, the direction estimates of the monocular channels (\hat{L} , \hat{R}) are weighted by the normalized contrasts (C_L^n , C_R^n) of left and right eyes' images and then summed to obtain the estimate of the binocular visual direction (\hat{B} , see Figure 12a):

$$\hat{B} = C_L^n \hat{L} + C_R^n \hat{R}. \quad (7)$$

The left and right eye weights C_L^n and C_R^n are required to sum up to 1 and are defined by the following equations:

$$C_L^n = \frac{C_L}{C_L + C_R} \quad \text{and} \quad C_R^n = \frac{C_R}{C_L + C_R}, \quad (8)$$

where C_L and C_R are the absolute contrasts of the left and right eyes' images. Because the contrasts of both images are scaled by the same factor, the contrast ratio (C_L/C_R) stays constant. For contrasts of 40% and 100%, the predicted weights were approximately 0.286 and 0.714 and (unlike the weights for MLE) were constant across subjects. The same data as for Model 1 were used (because Equation 7 is analogous to Equation 4), where the observed weights were derived from Equation 6.

The monocular combination model has been used previously in the context of binocular brightness and contrast perception (de Weert & Levelt, 1974; Legge & Rubin, 1981).

Results

The results of the comparison between observed weights and weights predicted by the monocular combination model are plotted in Figure 12b. This model provides a better approximation to the data than the MLE model. For the vernier task (Figure 12b, left), all data points show a systematic distribution with respect to the 1:1 line (solid). However, except for subject JG the data still deviate from the model predictions in that the weight for the eye presented with the lower contrast is too high with respect to the weight of the eye presented with the higher contrast. The opposite is the case for the saccade data (Figure 12b, right). Here, the influence of the eye presented with the higher contrast stimulus is on average slightly overestimated (compare the slopes of the linear fits (dashed lines) to the median values). Two of the data points for an interocular contrast ratio of 40:100 largely deviate from the model predictions.

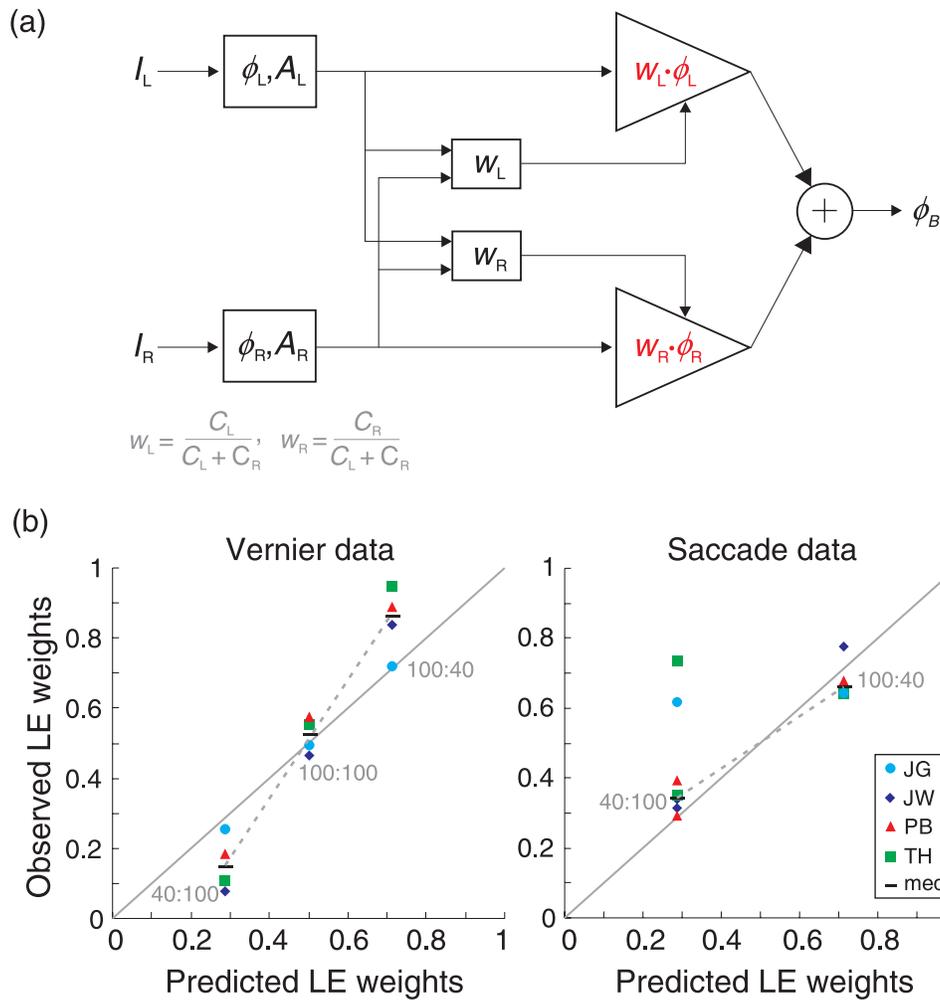


Figure 12. (a) Monocular combination model for computation of binocular visual direction. I_L and I_R are two input sine waves presented to left and right eyes that differ in amplitudes (A_L, A_R) and phases (ϕ_L, ϕ_R). Each channel (left, right) computes its own monocular phase (direction) estimate, which is weighted by the contrast (red) before binocular combination to derive the resulting phase (ϕ_B). The weights for left (w_L) and right eye (w_R) are simply given by the normalized contrasts calculated from the absolute contrasts C_L and C_R . (b) Comparison of observed and predicted left eye (LE) weights for vernier (left) and saccade data (right). Data for three interocular contrast ratios are plotted for the vernier task. Only data for the two unequal contrast conditions were available for the saccade task (100:40 short right; 40:100 short left and long right). For both experiments, the data points show a systematic relation to the 1:1 line (solid) on which all data points would lie if the model were to predict the results. Black bars mark the median values (med).

Discussion

The monocular combination model, in which each channel estimates the position of one eye’s image and weights it by its normalized contrast, provided a better description of our data than the maximum-likelihood model (Model 1). However, the influence of the eye presented with the higher contrast was on average underestimated for the perceptual data and slightly overestimated for the saccade data. Hence, the model reflected the observed difference between the saccadic and perceptual systems in the computation of binocular visual direction. The saccadic system might be described better by the monocular combination model than is the perceptual system. However, to evaluate this hypothesis, more data

on saccades are needed to verify whether the two outliers observed in our data set (see Figure 12b, right) were simply caused by variance or indicate a systematic deviation from linear summation for some subjects.

Model 3: Contrast-dependent binocular summation

Because both Models 1 and 2 were *linear* models that could not sufficiently predict our results, we also applied our data to a recently proposed nonlinear binocular summation model (Ding & Sperling, 2006). Models 1

and 2 failed to describe the data by either under- or overestimating the influence of the eye presented with the higher contrast image. In the third model, the strength of the influence of the eye seeing the higher contrast image is an adjustable parameter (γ). We determined this parameter γ from our observed data and compared the results for vernier and saccade task.

In Models 1 and 2, the *positions* (phases) of the two eyes' images were weighted by their respective contrasts and then the left and right eyes' position estimates were summed (Figure 12a). In Model 3, the *amplitude* of each eye's Gabor sine wave carrier is weighted by its contrast (Figure 13a). Then, the weighted sine waves of left and right eyes are summed, which results in another sine wave with an intermediate amplitude and phase (position). Assuming that the carrier frequency is the same for left and right eyes, the phase of the combined sine wave is given by

$$\theta_C = \frac{A \sin \theta_A + B \sin \theta_B}{A \cos \theta_A + B \cos \theta_B}, \quad (9)$$

where A and B are the amplitudes and θ_A , θ_B , and θ_C are the phases of the sine waves. For example, when sine waves A and B have phases of 0° and 90° and equal contrast, their combined phase (θ_C) would be 45° . For the same phases of 0° and 90° , but unequal contrasts of 40% for sine wave A and 100% for sine wave B , the phase of the combined sine wave would be approximately 68° . This illustrates that weighting each eye's sine wave amplitude will bias the phase of the combined sine wave resulting from linear summation. Hence, in contrast to the monocular combination model (Model 2), here the phase of the fused percept is derived in a binocular channel that sums the two weighted sine waves.

The binocular summation model of Ding and Sperling (2006) is based on this summation of sine waves; however, it incorporates a subject-dependent parameter (γ) that causes the model to be nonlinear. The model is described by the following equation:

$$\hat{\theta} = 2 \tan^{-1} \left(\frac{1 - \delta^{\gamma+1}}{1 + \delta^{\gamma+1}} \tan \left(\frac{\theta}{2} \right) \right), \quad (10)$$

where $\hat{\theta}$ is the contrast-induced perceived phase shift of the binocular percept (equivalent to the contrast-induced shift in binocular direction), θ the real phase difference between left and right eyes' sine waves, δ the contrast ratio ($0 \leq \delta \leq 1$), and γ a subject-dependent parameter. The term $\gamma + 1$ scales the contrast ratio. If $\gamma = 0$, the model reduces to the simple linear summation of two sine waves described in Equation 9. As γ increases ($\gamma > 0$), the eye seeing the higher contrast image gains more and more influence in the binocular combination process, i.e., the contrast ratio becomes exaggerated. If γ decreases below 0, the eye seeing the lower contrast image gains more and more weight in the binocular combination process (the

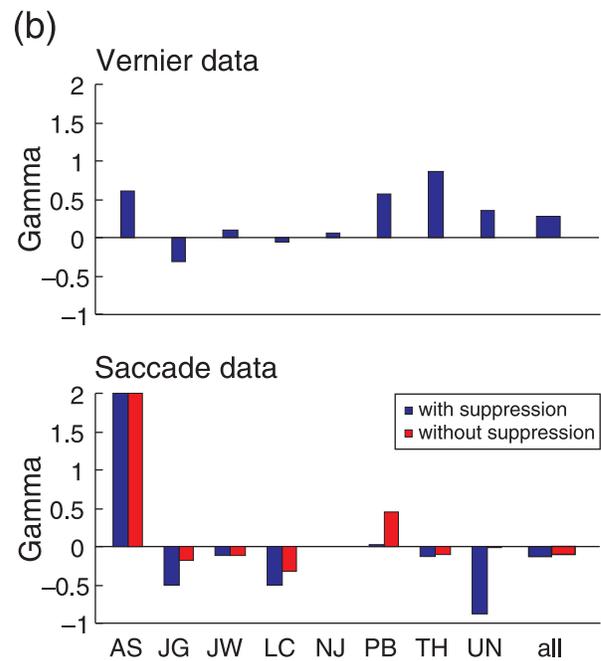
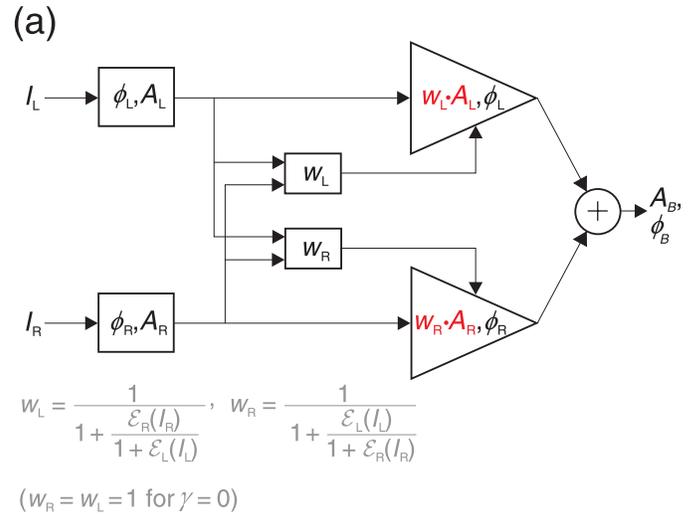


Figure 13. (a) Binocular summation model of Ding and Sperling (2006). The input sine waves presented to left and right eyes (I_L , I_R) differ in amplitudes (A_L , A_R) and phases (ϕ_L , ϕ_R). Each sine wave's amplitude is weighted by the contrast (red). A phase estimate is first derived after binocular combination. The weights are determined by the total visually weighted contrast energies of both eyes ($\epsilon_L(I_L)$, $\epsilon_R(I_R)$). For $\gamma = 0$, the model reduces to the simple linear summation of two sine waves and $w_L = w_R = 1$. (b) The subject-dependent parameter gamma of the binocular summation model for each participant. Results are shown for the perceptual data (top), the saccade data including suppression trials (bottom, blue), and the saccade data excluding suppression trials (bottom, red). Wide bars represent the median.

contrast-induced perceived phase shift decreases), until both eyes' images are weighted equally ($\gamma = -1$). For further details of the model, see Ding and Sperling.

We converted the data of all our eight subjects into degrees of phase angle. The phase difference between the stimuli of left and right eyes (θ) originated from the disparity (2.5° of visual angle = 153° of phase angle). However, because the perceived separation between left and right eyes' images was smaller than the physical separation (**Experiment 1, Figure 3**), we used the perceived separation obtained from the vernier data as input value for θ for each subject. In doing so, we have to assume that the perceived phase of the stimuli changed without being accompanied by a change in perceived spatial frequency. $\hat{\theta}$ was derived from the differences in points of subjective equality between equal and unequal contrast conditions for the vernier task, and from the differences in amplitudes between equal and unequal contrast conditions for the saccade task. (The model required doubling of these values, see Ding & Sperling, 2006.) All saccade data were corrected with an estimate of the normal hypometric motor error (Aitsebaomo & Bedell, 1992; Becker & Fuchs, 1969; Henson, 1978).

For each subject, γ was determined graphically: Model predictions were plotted ($\hat{\theta}$ against δ) for a substantial number of γ values together with our observed data. Each γ plot resulted in a separate prediction curve. The γ for a particular data point was determined by finding the curve, on which that data point fell. This curve corresponded to a certain γ value.

Results

The values for γ are plotted for each subject in **Figure 13b**. For the vernier data (**Figure 13b, top**), the γ values are positive or close to 0 (median: 0.27). This means that the subjects either linearly summed the two sine waves ($\gamma = 0$) or scaled the contrast ratio so that it became larger ($\gamma > 0$). The latter means that the eye presented with the higher contrast image dominated the binocular combination more than expected simply from the contrast ratio. A γ of .27 indicates that the physical contrast ratio of 40:100 was treated by the system as a ratio of approximately 31:100.

For the saccade data (**Figure 13b, bottom**), most γ values were negative. However, subject AS had a much higher γ than all other subjects. Most likely, the data analysis did not exclude all of his suppression trials so that his data were still confounded by suppression. To avoid overemphasis of AS' anomalous behavior, we used median values. The group average resulted in a value close to 0. This was true for data including (blue bars, median: -0.11) and excluding suppression trials (red bars, median: -0.13). The negative γ value indicates that the system effectively treats the physical contrast ratio (40:100) as a contrast ratio of approximately 44:100. Hence, the results resemble the differences between perception and saccades found with the monocular

combination model (although differences in medians did not reach significance due to the small sample size).

Discussion

The binocular summation model proposed by Ding and Sperling (2006) could describe our results in a similar way as the monocular combination model (Model 2), showing that saccades on average obeyed an almost linear summation of the sine wave carriers presented to the two eyes (γ close to zero). For perception, however, the binocular combination was on average dominated more by the eye presented with the higher contrast than expected from the contrast ratio ($\gamma = .27$). Thus, differential contrast scaling is required in the two systems. Psychophysical measurements revealed that some scaling for contrast perception takes place in the visual system. This results in a reduction of apparent contrast with respect to the physically presented contrast (Gottesman, Rubin, & Legge, 1981; Kulikowski, 1976). The contrast threshold determines the difference between perceived and physical contrast (Kulikowski, 1976). However, because thresholds for high contrast stimuli similar to those used in the present study increase approximately linearly with pedestal contrast (Bird, Henning, & Wichmann, 2002), this effect cannot account for the scaling required for the model.

General discussion

Our study confirmed earlier findings (Mansfield & Legge, 1996) that the computation of binocular visual directions is influenced by interocular contrast differences and furthermore showed that the same is true for saccadic eye movements. For some subjects, the contrast-induced response bias was the same for perception and saccades, for others saccades were affected to a lesser extent. To accurately estimate target direction and make saccades to the position where a disparate target will appear after a vergence movement eliminates the disparity, saccades and perception should use a contrast-independent direction computation. Interocular contrast differences do not usually occur in natural viewing conditions. Also, objects belonging to the natural environment are broadband stimuli that contain high spatial frequencies. Because Panum's area decreases with increasing spatial frequency (Schor et al., 1984), only objects containing small disparities can be fused and consequently CIBs for these objects would be extremely small. Hence, the sensory and motor errors described in the present experiments are only relevant under laboratory conditions where they can provide insight into how the information from the two eyes is combined to estimate direction. Given that the effect of interocular contrast differences on perception and

saccades can be different, two possible explanations for our results can be considered: First, the perceptual and saccadic systems could be independent and obey different contrast weighting rules in early bottom-up processing. Alternatively, higher level information about the perceived stimulus position in combination with an unbiased (i.e., contrast-independent) position estimate from the retinal signals could be used by the saccadic system.

Different contrast weighting for perception and saccades

Different weighting mechanisms that could underlie the saccadic and perceptual systems were tested by implementing our data in three models for binocular combination. A maximum-likelihood model failed to predict our results by underestimating the role of contrast for assigning the weights. Two other models, a combination of weighted monocular directions and a binocular summation of sine waves with weighted amplitudes (Ding & Sperling, 2006) for phase computation, gave a better approximation to the data. Both models demonstrated that perceptual position judgments of contrast-mismatched stimuli were on average dominated more by the eye seeing the higher contrast stimulus than expected from the contrast ratio. Such disproportionate weighting can also be found in binocular contrast perception (Legge & Rubin, 1981). In the model by Ding and Sperling (2006), the subject-dependent parameter γ accounts for this dominance by amplifying the contrast ratio. To fully describe our data with the monocular phase combination model, we would need to incorporate a comparable parameter that scales left and right eyes' contrasts in addition to the normalization.

Both models are similar in that they require a primary stage with interacting monocular cells whose information is later converged onto binocular cells to derive the resulting phase (and contrast) of the fused percept. Neurophysiological studies have shown that contrast variation between the two eyes has only little or no influence on the binocular tuning of simple cells in the striate cortex (Freeman & Ohzawa, 1990; Truchard, Ohzawa, & Freeman, 2000). Hence, interactions between the left and right eyes for normalizing or scaling of contrasts must take place at a later cortical stage. The oculomotor system seems to bypass these interactions to a certain degree. Exaggeration of the contrast ratio was nearly absent in the saccade data. The results were close to being described by linear summation, either by the simple monocular combination model or by the binocular summation model with a γ close to zero. We would need to test additional contrast ratios and disparities to verify whether saccades really follow linear summation and can be described by both the monocular combination and the binocular summation model.

Combination of perceived and center-of-gravity position

There is evidence in the current literature that action and perception might be based on different visual representations in the brain and hence be affected differently by ambiguous visual information (Goodale & Milner, 1992). In agreement with this theory, motor behavior was found to be unaffected by a variety of visual illusions (Aglioti, DeSouza, & Goodale, 1995; Otto-de Haart, Carey, & Milne, 1999; Wong & Mack, 1981). Other studies, however, have shown that a complete separation of the two subsystems might not hold when carefully choosing the experimental design. Similar to our results, these studies reported either no difference between action and perception (Brenner & Smeets, 1996; Franz, Fahle, Bühlhoff, & Gegenfurtner, 2001; Franz, Gegenfurtner, Bühlhoff, & Fahle, 2000; Pavani, Boscagli, Benvenuti, Rabuffetti, & Farnè, 1999) or that both are affected but to different extents (Aglioti et al. 1995; Daprati & Gentilucci, 1997). Our results could be explained by assuming a summing junction that receives input about the perceived position of an object and combines this information with an unbiased (i.e., contrast-independent) representation of the retinal signals. For large targets, the latter is likely to be the center-of-gravity position (He & Kowler, 1991; Melcher & Kowler, 1999), which would be the average between the monocular positions for a disparate stimulus. The weighting of these two cues, perceptual and center-of-gravity, could differ between the subjects. Hence, the data presented here would require crosstalk between the two cue sources whether they lie within the hypothesized visual pathways or beyond them. In contrast to this hypothesis, Vishwanath, Kowler, and Feldman (2000) showed that in certain situations (occlusion of selected stimulus features) saccades rely on the visible information rather than on higher level perceptual cues from which the whole target shape can be inferred, even if instructed to saccade to the whole shape. This could indicate that saccades in our experiment were biased toward the perceived stimulus position because of the contrast influence during early bottom-up processing and not due to higher level influences. However, occlusion and binocular visual direction are different and could hence be treated differently by the saccadic system.

Conclusions

When the perceived binocular direction of an object is made disparate from the direction that would result from simple averaging of the two monocular directions due to an interocular contrast difference, saccadic end points are biased toward the perceived position of the stimulus. This oculomotor bias was significantly smaller than the

perceptual bias for some subjects. The result could be explained by either a different contrast weighting rule for perceptual and saccadic systems or by an integration of the perceived target position with the average target position.

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