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Binocular function during unequal monocular input

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Abstract

The fine task of stereoscopic depth discrimination in human subjects requires a functional binocular system. Behavioral investigations show that relatively small binocular abnormalities can diminish stereoscopic acuity. Clinical evaluations are consistent with this observation. Neurons in visual cortex represent the first stage of processing of the binocular system. Cells at this level are generally acutely sensitive to differences in relative depth. However, an apparent paradox in previous work demonstrates that tuning for binocular disparities remains relatively constant even when large contrast differences are imposed between left and right eye stimuli. This implies a range of neural binocular function that is at odds with behavioral findings. To explore this inconsistency, we have conducted psychophysical tests by which human subjects view vertical sinusoidal gratings drifting in opposite directions to left and right eyes. If the opposite drifting gratings are integrated in visual cortex, as wave theory and neurophysiological data predict, the subjects should perceive a fused stationary grating that is counter-phasing in place. However, this behavioral combination may not occur if there are differences in contrast and therefore signal strength between left and right eye stimuli. As expected for the control condition, our results show fused counter-phase perception for equal inter-ocular grating contrasts. Our experimental tests show a striking retention of counter-phase perception even for relatively large differences in inter-ocular contrast. This finding demonstrates that binocular integration, although relatively coarse, can occur during substantial differences in left and right eye signal strength.

Keywords

Binocular sensitivity; unequal monocular input; counter-phase gratings; contrast sensitivity; primary visual cortex; human binocular integration

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T.K., & R.D.F. contributed to conception and design of the experiments. T.K. collected data. T.K. analyzed data. T.K., and R.D.F wrote the manuscript. T.K., & R.D.F approved the final version.

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The authors declare no competing financial interests.

Introduction

Various factors can cause differences in left and right eye retinal image quality. Clinical conditions such as anisometropia, aniseikonia, strabismus, amblyopia, and disease or trauma in a monocular pathway can create differences in quality and therefore signal strength of left and right eye pathways. An obvious question concerns the effects that monocular imbalances have on binocular sensitivities. Various psychophysical tests with human subjects have been conducted in which binocular visual sensitivity has been measured during quality differences in left and right eye images (e.g., Blake & Fox, 1973; Anderson & Movshon, 1989). An example of this kind of study is the determination of binocular depth disparity thresholds for unequal monocular grating contrasts at different spatial frequencies (Legge & Gu, 1989; Schor & Heckmann, 1989; Cormack *et al.*, 1997). The experimental protocol and general findings for one of these investigations (Legge & Gu, 1989) are illustrated in Figure 1. Subjects viewed two horizontally arranged panels of vertically oriented sine-wave gratings as depicted in **A**. Left and right panels were seen separately by left and right eyes, respectively. A similar set of two additional panels was viewed below the first grating pair. The top pair could be viewed with relative inter-ocular binocular phase differences and in this case, there is an inward phase shift which causes crossed disparity that codes a "near" distance. A "far", uncrossed disparity stereo target may also be displayed. The bottom pair of grating panels forms a zero disparity reference target. For the data shown (Figure 1A, bottom), there is an equal stimulus contrast for left and right eyes, (in this case 25%), and subjects easily detected a target depth of minimal disparity. The threshold is raised for equal contrast targets when spatial frequency is lowered (gray curve). However, for both spatial frequencies, unequal left and right eye monocular contrasts yield clear deficits in depth perception and thresholds are raised in proportion to the interocular contrast differences.

For comparison, Figure 1B shows results from a neurophysiological study of single cells in the cat's visual cortex (Ohzawa & Freeman, 1994). The graph on the upper left illustrates a phase-tuning function for identical gratings with optimal parameters. Firing rates are shown (ordinate) for varying relative inter-ocular phases (abscissa). The resulting tuning curve shows both facilitation and suppression compared to the control monocular responses, and is typical for cortical cells (Ohzawa & Freeman, 1986a, 1986b, 1994; Freeman & Ohzawa, 1990; Smith *et al.*, 1997; Truchard *et al.*, 2000). Interleaved monocular controls for left or right eye stimulation are indicated by the filled arrows. The same protocol is used for the result shown in the bottom left of **B**, obtained from the same cell. However, in this case stimuli are no longer identical as there is a substantial difference (one log unit) between left and right eye contrasts (5% and 50%). Although overall response strength is reduced, there is a striking similarity in relative phase tuning to that of the upper graph where left and right eye stimuli are identical. A similar protocol was used during recordings of other cortical cells for which contrast differences between left and right eyes were varied. A constant contrast was used for one eye (50%) while that for the other was varied in octave steps (between 5%, 10%, 20%) and 50%. Summary results are shown in the lower right part of Figure 1B. Depth of modulation, as defined by the formula in the upper right panel, was computed for each run. The results (gray data points) show that depth of modulation is approximately constant over a wide range of contrast differences between left and right eye images (although overall signal-to-noise ratio is reduced since neuronal firing rate decreases with lowered contrast). For comparison, a contrast response function is also shown for the left eye alone (black symbols). In addition, response is shown of the right eye alone (black triangle) to a 50% contrast grating. These neurophysiological findings and more extensive data have been reported previously in a series of publications (e.g., Freeman & Ohzawa, 1990; Ohzawa & Freeman, 1994; Truchard *et al.*, 2000). Considered together, the psychophysical data noted above, show clear detriments in disparity sensitivity when contrast differences are imposed between left and right eyes. On the other hand, relatively large differences in inter-ocular contrast levels have minimal consequences for cortical cell tuning responses to relative phase-shifts of gratings. There thus appears to be a clear discrepancy between behavioral and neurophysiological consequences of contrast level differences between left and right eyes.

The study reported here is intended to explore this difference by use of a behavioral experimental protocol that is analogous to the cortical cell investigations. Specifically, we have designed a psychophysical test which requires integration of left and right eye stimuli consisting of gratings drifting to the left for one eye and to the right for the other. For gratings of equal contrast, the predicted wave theory result is a combination of the two gratings into a fused one which is perceived as a stationary grating flickering in a fixed position such that the counter-phasing component bars fluctuate between dark and light. This control condition is required to accompany the experimental one in which drifting grating stimuli of fixed contrast to one eye are combined with identical gratings presented to the other eye except in the latter case, mean contrast levels are varied and drift is in the opposite direction. For this case, the wave theory prediction is the same as that noted above but the binocular percept is in question. We ask here if the perceptual fluctuation of a counter-phased grating fixed in position persists when the two component gratings drifting in opposite directions have different signal strengths. By extrapolation, the answer provides insights regarding the perceptual range of binocular coordination in the visual system.

Materials and Methods

Participants

Three human subjects participated in the experiment (age range: 21–32; mean age: 25; 2 females, 1 male). All had clinically normal binocular vision and corrected Snellen acuity of 20/15 for each eye. Subjects provided written informed consent to participate prior to experimental tests. The study was approved by UC Berkeley's Committee for the Protection of Human Subjects and performed in accordance with the Code of Ethics of the World Medical Association (Declaration of Helsinki). The subjects were not previously trained observers and were given thorough instructions, demonstrations, and practice to be sure they were familiar with the visual conditions of the experimental tests (see below).

Apparatus

A standard mirror-based haploscope was used to present stimuli as illustrated in Figure 2. This is an optical instrument which allows controlled presentation to each eye separately or to both eyes together to enable binocular fusion. Precise adjustments are possible to provide clear control of optical conditions. In Figure 2A, two pairs of vertically mounted mirrors (gray filled bars) are depicted which allow adjustment of angular position as illustrated by the double arrow symbols. This allows vertical alignment of fixation targets. To prevent projection of stimuli to the contralateral eye, vertically positioned occluders (black filled bars) are adjusted laterally as indicated by the horizontal double arrow symbols. A subject is positioned in a chin rest and adjusts the angles of the two exterior mirrors along with the horizontal positions of the two occluders in order to achieve fusion of left and right eye images. This arrangement is similar to one used in our lab in a previous study in which binocular integration was achieved from two counter-phase gratings with a 90 degree phase difference in both spatial and temporal dimensions. In that case, it was possible to induce a cyclopean illusion of drifting motion (Shadlen & Carney, 1986). Here, we use an inversed version of the previous method by which a perception of a counter-phased grating is achieved by dichoptic presentation of sine-wave gratings drifting in opposite directions to left and right eyes. In the situation depicted in Figure 2A, the left eye views a vertically oriented sine-wave grating drifting rightward. An identical grating is presented to the right eye and is drifted in the opposite, i.e. leftward direction. Attainment of a fused binocular percept is assisted by observation of the green circle and red cross presented to the left and right eyes, respectively, such that fusion produces a percept of the cross within the circle as illustrated in the figure. Binocular fusion of the two opposite drifting sine-wave images is expected via wave theory to produce a counter-phase grating (oscillating and constant in position) whose amplitude is twice that of the individual monocular sine-wave gratings.

The testing procedure is illustrated in Figure 2B. A subject is positioned in the chin rest and is assisted with the adjustments as described above. Each trial begins with a view of a frame containing a dichoptic cross to assist binocular fusion (Ding & Levi, 2011). The subject is instructed to maintain perception of the red cross within the green circle to help retention of optimal binocular fusion during testing. When the subject is ready to begin, he or she presses the space bar on the key pad to initiate a trial. To provide a transition prior to the test run, two vertical gratings (identical except for contrast which is fixed at 48% for one eye and varies from 3% to 48% for the other eye) move in the same direction (left or right). Presentations are varied randomly so that either eye can receive the high contrast grating. H and L represents high and low contrasts, respectively, and a bold letter (**H** or **L**) designates direction change (see below). Following a short delay after the presentation begins (2 to 3 seconds), a reversal of direction of one of the two gratings occurs to induce perception of a counter-phased grating. Subjects indicate that they detect the counter-phase condition by pressing the space bar and the reaction time is recorded. As depicted in Figure 2B, direction changes result in four possible combinations of high and low contrast (**H**–L, H–**L**, **H–L**, and H–L). A bold H or L indicates that a direction change occurred for a high or low contrast grating, respectively. For half the trials, direction change occurs for both high and low contrast gratings or there is no direction alteration. For these control trials (**H–L** and H–L), subjects are instructed to not press the space bar. We tested four different spatial frequencies (0.25, 0.5, 1, and 2 cycles/deg.) at each of five octave separated contrast levels (3, 6, 12, 24, and 48%). The number of complete conditions for the experimental runs is 80 (four spatial frequencies times five contrast levels times four possible combinations of direction change).

It is important to note that we made a considerable effort to insure that subjects were very clear about the visual conditions presented and that they understood that it was critical for them to pay close attention to each response. To assist in this effort, we demonstrated each visual condition so that they understood the difference between drifting, and counter-phasing grating stimuli. Obviously, for the specific purpose of the study, the perception of stationary counter-phased gratings was critical. For all three subjects, we were confident they understood and did their best to provide accurate responses. Furthermore, our analysis demonstrates that the subjects actually perceived counter-phase gratings and did not simply respond to a change in motion direction (see more details in Discussion).

Results

Data for three subjects and their mean composite values are shown in density plots in Figure 3A, C, E, G. Values for the variable contrast grating, from 3% to 48% in octave steps, are plotted on the abscissa. Spatial frequency is plotted on the ordinate from 0.25 to 2 cycles per degree, also in octave steps. Correct answers, in percent, for each stimulus condition are coded in density plots to the right of each graph from 50 to 100% with dark to light signifying lower to higher percentage correct values, respectively. Data for all three subjects are quite similar. They show high levels of correct identification of counter-phase grating perception that occur even for substantial differences in contrast between the two eyes with nearly perfect responses for combinations of 24%/48% or 48%/48%. Even for a combination of 12% and 48%, counter-phase grating detection is substantial especially at a spatial frequency of 0.5 cycles per degree. Perception of fusion in the form of counter-phase detection falls off markedly when contrast differences are at the highest levels, i.e., 3% or 6% contrast for one eye combined with 48% for the other. The other clear finding exhibited by these data is that perceptual combination of the two opposite drifting gratings into a single counter-phase perception is best for two of the three subjects at 0.5 cycles per degree. The performance level of the third subject, BH, is comparable at 0.5 and 1 cycles per degree. This result indicates that there is not a simple inverse relationship between spatial frequency and detectability of a counter-phase grating. This finding is more explicitly illustrated below in Figure 4.

In Figure 3B, D, F, and H, each row of the density matrix in **A, C, E** and **G** is re-plotted to show with psychometric style curves the effects of unequal monocular contrast values on detectability of counter- phase gratings. Contrast in octave steps is again represented on the abscissa and percent correct identification of counter-phase gratings is plotted on the ordinate. There are four sets of data points for each subject but for visual clarity, only two sets are shown in the figure. Each set of data points represents a specific spatial frequency condition. Black and gray symbols represent 0.5 and 2 cycles per degree, respectively. Mean values for each subject and for all subjects together (composite) are represented by red data points and curves. The psychometric curves are fitted with a Weibull function as follows:

$$P_{\text{correct}} = 1 - 0.5\ \exp\left[-(x/\alpha)^{\beta}\right]$$

where $P_{correct}$ is the percentage of correct response, x is the varied-eye contrast, α and β are free parameters which determine threshold and slope of the function, respectively.

Note that for all three subjects, response curves, which have sigmoid shapes, generally show higher percentages of correct counter-phase grating perception for lower spatial frequency conditions. However, for the limited number of spatial frequencies tested (four), there is not a completely linear relationship between counter-phase grating detectability and spatial frequency. Additional details of the relationship are given below.

We next reverse the variables of contrast and spatial frequency in order to see in more detail how the perception of counter-phase gratings varies with spatial frequency. In Figure 4, spatial frequency is on the abscissa and contrast is plotted on the ordinate. The density plots for individual subjects (**A, C**, and **E**) and summarized by mean composite values in **G**, show a clear progression of counter-phase detectability as the difference in contrast between the two combined gratings is reduced. Detectability is markedly affected when the contrast of one of the grating pairs is 3 or 6%. Counter-phase is most frequently observed at a spatial frequency of 0.5 cycles per degree. As in Figure 3, the density matrix on the left has been transformed on the right (**B, D, F, & H**) such that each row is re-plotted to show effects of spatial frequency on detectability of counter-phase gratings. Data points from light gray to black represent contrast differences between the two gratings of small (light gray) to large (black). Data points in red represent mean values for each subject and for the mean composite for all three subjects. The clear result here, as expected, is that counter-phase detection increases progressively as contrast differences between the two component gratings is reduced (from black to light gray data points). In addition, for two of the three subjects, correct counter- phase detection is best for a spatial frequency of 0.5 cycles per degree. This tendency is also observed for the combined composite data (**H**), and it is statistically significant (one-sided bootstrap test, 0.25 vs. 0.5: $p<10^{-4}$, 0.5 vs. 1: $p<10^{-2}$, 0.5 vs. 2: $p<10^{-4}$). Effects of spatial frequency on counter-phase grating detectability are more apparent in the mid-level contrast range (i.e., 6, 12, or 24%) compared with the lowest or highest contrast. Although these data are suggestive, additional spatial frequencies should be tested to establish a clear relationship.

Finally, our protocol includes data on reaction times of subject responses. In Figure 5A, C, E, and G, contrast of one of the two component gratings is given on the abscissa with reaction time on the ordinate. The data are presented in box- plots. Each box contains a thick horizontal line which represents the median [50th percentile] level for that variable. For example, subject TK exhibits a reaction time of just under 1 second when contrast is reduced in one of the grating pairs to 3%. The top and bottom edges of each box represent 25th and 75th percentiles of the data set, respectively. Vertical lines above and below the middle of each box indicate 99% of the data distribution range. Gray crosses outside each range represent outliers. As the data show, there is a small but consistent reduction in reaction times as contrast differences between the two component gratings are reduced, i.e., as one of the two gratings increases in contrast from 3% to 48%. Similar box plots are shown in the right column (Figure 5B, D, F and H). In this case, spatial frequency is plotted on the abscissa and reaction time on the ordinate. Boxes and symbols are the same as for the left column. These data also show a small consistent effect in which reaction times tend to increase as spatial frequency rises. Considered together, the data of Figure 5 indicate that the more difficult the task of detecting counter-phase in the combined two gratings, the greater the reaction time. This is expected when the contrast differences between the two gratings are high as shown in the left column. It is interesting to note that when spatial frequency is the variable, as in the right column of Figure 5, reaction times are least for the lowest spatial frequencies (0.25 and 0.5 cycles per degree). These values are below the peak of a standard spatial frequency sensitivity curve in human subjects, i.e., 2–3 cycles/degree. The shortest reaction times for the lowest spatial frequencies may be due to the relatively fast speed of motion during that condition. Since temporal frequency is fixed at 2Hz, the lowest spatial frequency occurs with the fastest moving speed.

Discussion

We have addressed an apparent discrepancy between neurophysiological and psychophysical data concerning binocular integration in the visual system. Previous single neuron studies in the visual cortex have demonstrated an apparent specific gain mechanism by which differences in contrast of monocular stimuli do not substantially affect the resulting binocular interaction profiles for phase-varying grating stimuli (Freeman & Ohzawa, 1990; Ohzawa & Freeman, 1994; Truchard *et al.*, 2000). On the other hand, behavioral studies have shown that fine binocular function, such as stereoscopic depth discrimination, is clearly impaired if there is a relatively small difference in quality of left and right eye images (Legge & Gu, 1989; Schor & Heckmann, 1989; Cormack *et al.*, 1997; Stevenson & Cormack, 2000).

In addition to the behavioral study on stereopsis mentioned in the Introduction (Legge & Gu, 1989), other similar investigations have been conducted. In one, use of a low spatial frequency grating (0.8 cycles per degree), with contrasts of 25% and 50% for left and right eyes, respectively, caused a large increase in stereo threshold (Schor & Heckmann, 1989). Similar findings were reported in a subsequent study which the authors refer to as a stereo contrast paradox (Cormack *et al.*, 1997). In a later paper, the same group extended the findings to include motion detection and vernier acuity and the result is again referred to as a contrast paradox (Stevenson & Cormack, 2000). Note that for any intraocular contrast difference between the two eyes, a reduction in stereo sensitivity is predicted based on requirements for effective binocular processing.

In the current study, when left and right eye images have unequal contrast values but the contrast differences are not large, subjects reported that they could differentiate whether the two images were moving in the same or in opposite directions. This is relevant to whether our subjects actually perceived counter-phase gratings. Their perception for these conditions may not be the same as that for an intact counter-phase grating. There is a possibility that subjects simply responded when they detected a change in motion direction regardless of binocular integration. However, this seems very unlikely for the following reasons. In our experimental design, the detection of motion direction change must rely on the high rather than the low contrast stimulus. Therefore, if subjects responded when they detected a change in motion direction, two undesired effects on behavioral performance would result: 1) the percentage of correct responses (hit vs. miss) in the H–**L** condition would be significantly lower than that for the **H**–L condition. 2) the false alarm rate for the **H–L** condition would be much higher than that for the H–L condition. Our results show clearly that neither of these undesired effects occurred. When the varied eye contrast changes from 3 to 48% in octave steps, two observations are relevant. 1) The percentage of correct responses are similarly increased in the H–**L** condition (11%– 33% – 73% – 92% – 96%) and the **H**–L condition (13% – 34% – 72% – 94% – 98%). 2) The false alarm rates are very low for both **H–L** (4% – 4% – 2% – 1% – 3%) and H–L (2% –2% – 2% – %3 – 1%) conditions.

When different images are shown to left and right eyes, a default outcome may be binocular rivalry, which can occur when binocular correspondence cannot be established (Blake, 1989). This possibility is relevant in the case of interocular contrast differences. We were careful to facilitate binocular fusion and minimize rivalry with our training procedure which was specifically focused on emphasizing to subjects the need to maintain perception of the fixation cross contained within the green circle (Figure 2). Our subjects reacted to the specific perception of a counter phased flickering grating. Even if they perceived occasional motion in depth, that could have resulted only via the binocular system during fusion of left and right eye stimuli. If opposite drifting gratings are viewed monocularly, subjects may determine whether movement is in the same or in opposite directions even when contrast differences between gratings are quite large. This will be clear since monocular combination provides a constant level of contrast in the same direction of movement but in the opposite direction case, modulated grating perception applies. In the binocular viewing condition used in the current study, each monocular grating contrast is constant independent of direction of movement. Perception of counter phase during binocular viewing relies on completely different visual cues compared to the monocular case. Counter phase perception relies only on binocular combination.

There have been many theoretical treatments of binocular vision including gain control assessments that we have previously published in neurophysiological work (Ohzawa *et al.*, 1985; Sclar *et al.*, 1985; Truchard *et al.*, 2000). One proposal regarding signal strength differences between the two eyes is that the contribution of low contrast stimuli to binocular integration is smaller than that predicted by linear summation (Ding & Sperling, 2006). Our current results show that detection of counter phase is not difficult with a contrast ratio of 0.5, i.e., a combination of 24% and 48% contrast in monocular images. It is not clear if the current results are relevant to the findings of the Ding and Sperling, since their experimental conditions were completely different than ours.

Two previous investigations related to our current study but with different goals (Georgeson & Scott-Samuel, 1999; Rainville *et al.*, 2005) concern tests of predictions of the energy model which has had widespread attention in various vision studies (e.g., Adelson & Bergen, 1985; Watson & Ahumada, 1985; Ohzawa *et al.*, 1990). In the first study, differences of energy are measured by use of gratings with different contrasts moving in opposite directions. The main finding was that opponent energy was not a good predictor of direction discrimination. Instead, directional motion energies were used to derive motion contrast which yielded good predictions of direction discrimination over a range of different contrasts. These results were used to modify an opponent energy model to make it relevant to cortical neurophysiology. The follow-up study compared two masking procedures to differentially activate local and remote processes. Results were consistent with activity of local motion detectors with spatial properties derived from motion detectors. In both studies, tests were conducted under normal viewing conditions in which binocular fusion was not required.

Our current results are significant because they show that there is a range of dissimilarity between left and right eye image quality within which, some binocular function is retained. Binocular integration of visual information is first achieved in the primary visual cortex. Many neurons in this area and subsequent cortical stages show binocular disparity tuning (Poggio *et al.*, 1988; Gonzalez & Perez, 1998; Cumming & DeAngelis, 2001; Read, 2005). And there is increasing evidence that disparity processing in extra-striate areas is responsible for encoding of more complicated and perceptually relevant stimulus properties compared to that in the primary visual cortex. For example, binocular neurons in the macaque primary visual cortex are selective for absolute but not relative disparity (Cumming & Parker, 1999). On the other hand, those in V4 or inferior temporal cortex (IT) show relative disparity tuning and their neural activity is well correlated with perceptual choice in fine depth discrimination tasks (Uka *et al.*, 2005; Shiozaki *et al.*, 2012). The results we report here demonstrate that a form of binocular integration, although relatively crude, is possible with extended stimuli even when relatively large differences in image quality exist between the two eyes. We speculate that this process may be accomplished by neurons in primary visual cortex.

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References

Adelson EH, Bergen JR. Spatiotemporal energy models for the perception of motion. J. Opt. Soc. Am. A. 1985; 2:284–299. [PubMed: 3973762]

Anderson P, Movshon J. Binocular combination of contrast signals. Vision Res. 1989; 29:1115–1132. [PubMed: 2617860]

Blake R. A neural theory of binocular rivalry. Psychol. Rev. 1989; 96:145–167. [PubMed: 2648445]

Blake R, Fox R. The psychophysical inquiry into binocular summation. Percept. Psychophys. 1973; 14:161–185.

Cormack LK, Stevenson SB, Landers DD. Interactions of spatial frequency and unequal monocular contrasts in stereopsis. Perception. 1997; 26:1121–1136. [PubMed: 9509147]

Cumming BG, DeAngelis GC. The physiology of stereopsis. Annu. Rev. Neurosci. 2001; 24:203–238. [PubMed: 11283310]

Cumming BG, Parker AJ. Binocular neurons in V1 of awake monkeys are selective for absolute, not relative, disparity. J. Neurosci. 1999; 19:5602–5618. [PubMed: 10377367]

Ding J, Levi DM. Recovery of stereopsis through perceptual learning in human adults with abnormal binocular vision. Proc. Natl. Acad. Sci. U. S. A. 2011; 108:E733–E741. [PubMed: 21896742]

Ding J, Sperling G. A gain-control theory of binocular combination. Proc. Natl. Acad. Sci. 2006; 103:1141–1146. [PubMed: 16410354]

Freeman RD, Ohzawa I. On the neurophysiological organization of binocular vision. Vision Res. 1990; 30:1661–1676. [PubMed: 2288082]

Georgeson MA, Scott-Samuel NE. Motion contrast: a new metric for direction discrimination. Vision Res. 1999; 39:4393–4402. [PubMed: 10789432]

Gonzalez F, Perez R. Neural mechanisms underlying stereoscopic vision. Prog. Neurobiol. 1998; 55:191–224. [PubMed: 9643554]

Legge GE, Gu YC. Stereopsis and contrast. Vision Res. 1989; 29:989–1004. [PubMed: 2629214]

Ohzawa I, DeAngelis G, Freeman R. Stereoscopic depth discrimination in the visual cortex: neurons ideally suited as disparity detectors. Science. 1990; 249:1037–1041. [PubMed: 2396096]

Ohzawa I, Freeman RD. The binocular organization of simple cells in the cat's visual cortex. J. Neurophysiol. 1986a; 56:221–242. [PubMed: 3746398]

Ohzawa I, Freeman RD. The binocular organization of complex cells in the cat's visual cortex. J. Neurophysiol. 1986b; 56:243–259. [PubMed: 3746399]

Ohzawa, I., Freeman, RD. Monocular and binocular mechanisms of contrast gain control. In: Lawton, TB., editor. Computational Vision Based on Neurobiology. International Society for Optics and Photonics; 1994. p. 43-51.

Ohzawa I, Sclar G, Freeman R. Contrast gain control in the cat's visual system. J Neurophysiol. 1985; 54:651–667. [PubMed: 4045542]

Poggio GF, Gonzalez F, Krause F. Stereoscopic mechanisms in monkey visual cortex: binocular correlation and disparity selectivity. J. Neurosci. 1988; 8:4531–4550. [PubMed: 3199191]

Rainville SJM, Makous WL, Scott-Samuel NE. Opponent-motion mechanisms are self-normalizing. Vision Res. 2005; 45:1115–1127. [PubMed: 15707920]

Read J. Early computational processing in binocular vision and depth perception. Prog. Biophys. Mol. Biol. 2005; 87:77–108. [PubMed: 15471592]

Schor C, Heckmann T. Interocular differences in contrast and spatial frequency: Effects on stereopsis and fusion. Vision Res. 1989; 29:837–847. [PubMed: 2623826]

Sclar G, Ohzawa I, Freeman RD. Contrast gain control in the kitten's visual system. J. Neurophysiol. 1985; 54:668–675. [PubMed: 4045543]

Shadlen M, Carney T. Mechanisms of human motion perception revealed by a new cyclopean illusion. Science. 1986; 232:95–97. [PubMed: 3952502]

Shiozaki HM, Tanabe S, Doi T, Fujita I. Neural Activity in Cortical Area V4 Underlies Fine Disparity Discrimination. J. Neurosci. 2012; 32:3830–3841. [PubMed: 22423103]

Smith EL, Chino YM, Ni J, Ridder WH, Crawford ML. Binocular spatial phase tuning characteristics of neurons in the macaque striate cortex. J. Neurophysiol. 1997; 78:351–365. [PubMed: 9242285]

Stevenson SB, Cormack LK. A contrast paradox in stereopsis, motion detection, and vernier acuity. Vision Res. 2000; 40:2881–2884. [PubMed: 11000389]

Truchard AM, Ohzawa I, Freeman RD. Contrast gain control in the visual cortex: monocular versus binocular mechanisms. J. Neurosci. 2000; 20:3017–3032. [PubMed: 10751454]

Uka T, Tanabe S, Watanabe M, Fujita I. Neural correlates of fine depth discrimination in monkey inferior temporal cortex. J. Neurosci. 2005; 25:10796–10802. [PubMed: 16291953]

Watson AB, Ahumada AJ. Model of human visual-motion sensing. J. Opt. Soc. Am. A Opt. image Sci. 1985; 2:322–341.

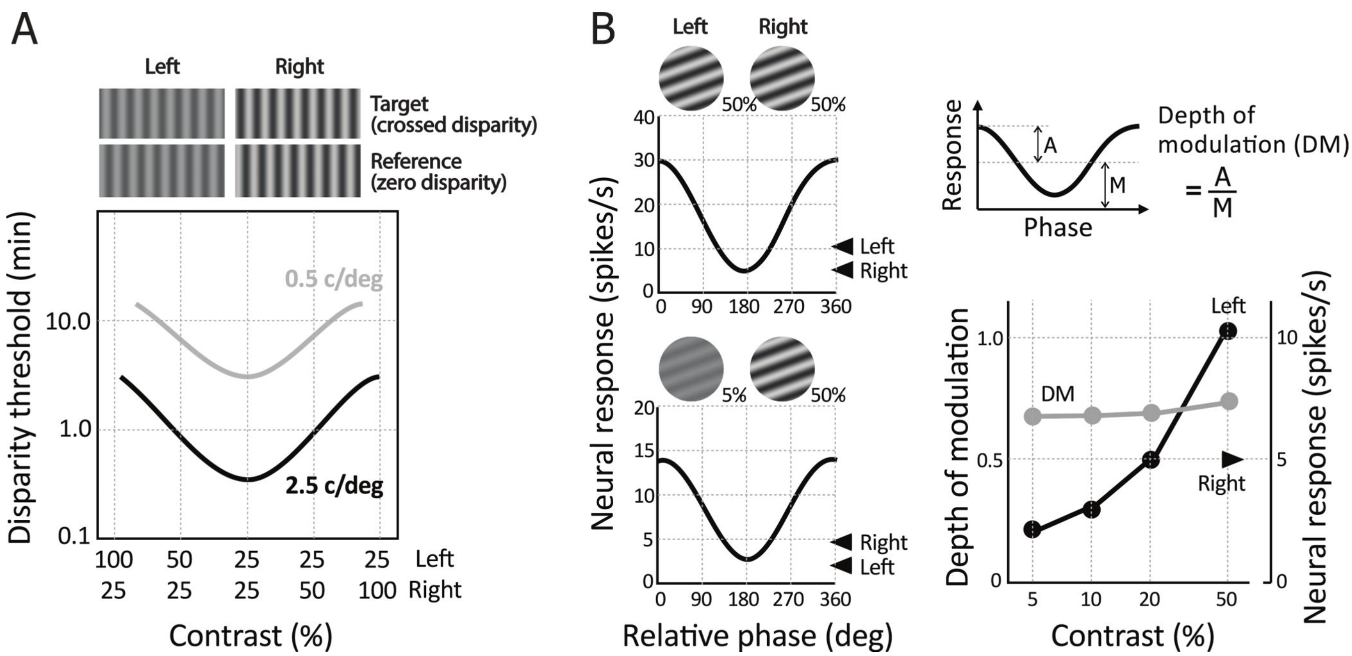

Figure 1. Previous studies: effects of unequal monocular contrast on disparity sensitivity (psychophysics) and binocular phase tuning (neurophysiology)

A. Replotted from Legge & Gu (1989). Disparity threshold was measured as a function of spatial frequency and unequal monocular contrast. Human subjects were provided with four panels of vertical sign-wave gratings. Left and right eyes could see only the left and right columns of the panels, respectively. The bottom pair of grating panels formed a reference stereo image (zero disparity). The top pair of grating panels, which are identical to the reference except for spatial phase, formed a near (crossed disparity, phase-shifted inward as shown at the top of A) or far (uncrossed disparity) target stereo image. When an equal stimulus contrast (25%) was used for left and right eye stimulation, subjects could easily detect a target image with a small disparity. However, as stimulus contrast for one eye became higher (i.e., unequal monocular contrast), the disparity detectability of a target was gradually impaired. Similar effects were found for two spatial frequencies as shown. **B**. Neurophysiological data from single cells in visual cortex. Gratings at optimal orientation and spatial frequency are presented at 50% contrast to left and right eyes as relative intraocular phase is varied. (**B** top). A similar test is shown (**B** bottom) for the same cell in which contrast of the grating for one eye is reduced by a log unit to 5%. Although overall response is reduced, relative phase tuning is closely similar to that for equal left and right eye contrast stimulation. Depth of modulation (DM), computed as illustrated in the upper right, is plotted against varied- eye contrast (lower right). As shown, DM is nearly flat across a range of contrast differences between left and right eyes. For comparison, a contrast response function is shown for the left eye alone.

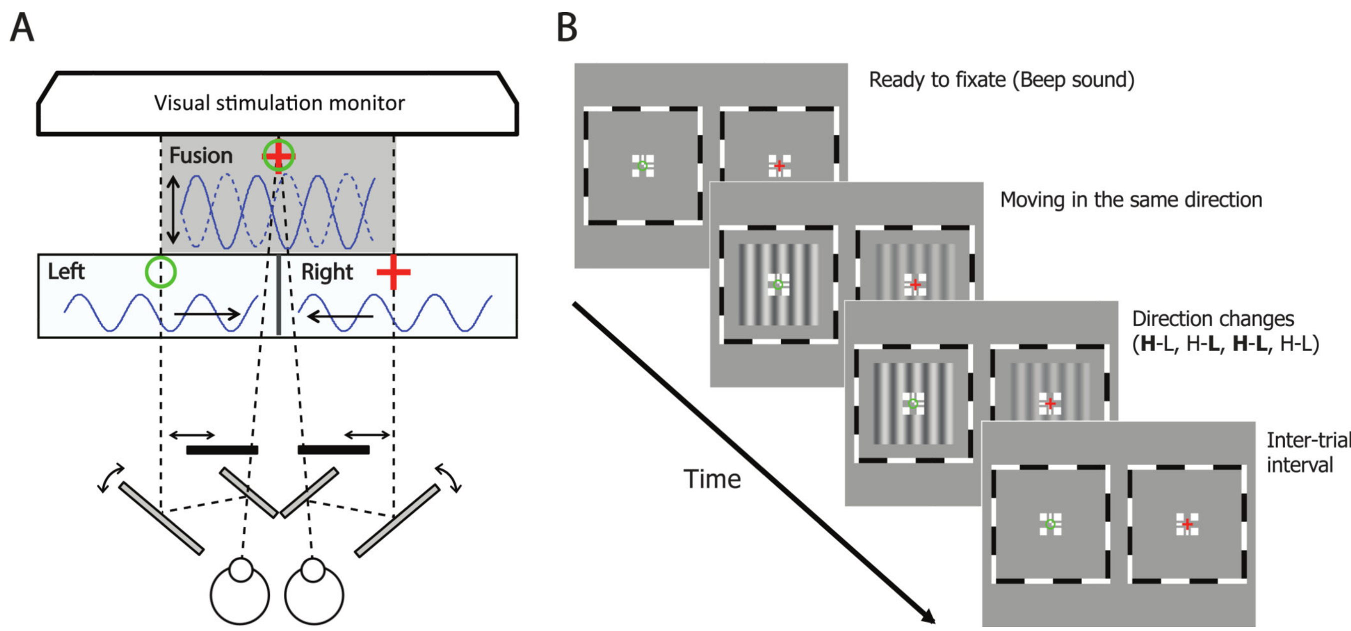

Figure 2. Apparatus and stimuli

A. A mirror haploscope is used to present two separate views to each eye. It consists of two pairs of vertically mounted mirrors (gray rectangles) and a pair of screens (black rectangles) in front of them toward the visual stimulation monitor. The angles of the two large mirrors and horizontal positions of the two screens are adjusted by individual subjects to achieve optimal fusion of left and right eye images. In the depicted situation, the left eye is stimulated with a vertical sign-wave grating drifting rightward. The grating stimulus in the right visual field is the same as that for the left, but it moves in the opposite (leftward) direction. Binocular fusion of these two stimuli is expected to result in the perception of a counter-phase flickering grating. **B**. Each trial begins with a view of binocular-fusion-assisting frames and a dichoptic cross (Ding & Levi, 2011). Left and right frames contain opposite halves of the cross, which are combined during optimal fusion. Subjects are instructed to try to maintain perception of a red cross within a green circle just before activating the space bar to report detection of the counter-phase grating. A beep signals presentation of two vertical sign-wave gratings, which are identical except for contrast. (One is fixed at 48%, and the other has the same or a lower contrast. The eye presented with a higher contrast is varied). At first, the gratings move in the same direction at 0.5 cycles/sec. Position of the higher contrast grating and direction of motion (left or right) are randomly chosen in each trial. After a delay of 2 to 3 seconds, also randomly chosen, a direction change occurs for one of the two grating stimuli. For each trial, **H**–L, H–**L**, or H & L indicate higher or lower contrast stimuli, respectively. The bold character means that a direction change occurs for that stimulus so as to form a counter-phase grating. If the subject detects this change, they report it and abort the trial by pressing the space bar and the reaction time is recorded. On half of the total trials, direction change occurs for both (**H–L**) and (H–L) conditions of grating stimuli. For these conditions, subjects are instructed to wait until the trial ends (5 seconds after stimulus onset) without depressing the space bar. Inter-trial interval is 5 seconds. The number of total stimulus conditions is 80 (4×5×4): Spatial

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frequencies (0.25, 0.5, 1, 2 cycles/deg), contrasts (3, 6, 12, 24, 48%), direction changes (**H**–L, H–**L**, **H–L**, H–L).

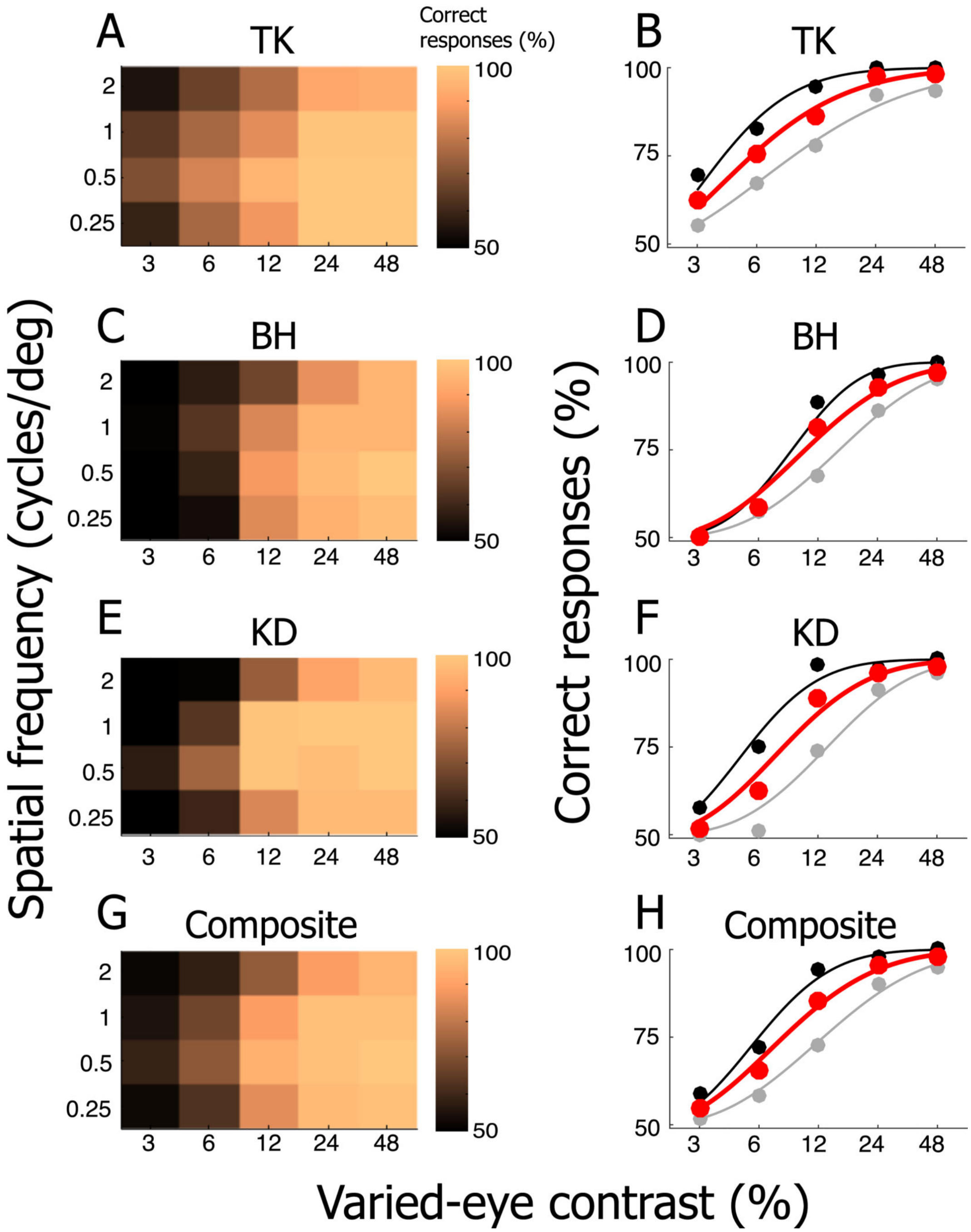

Figure 3. Effects of unequal monocular contrast on detection of counter-phase gratings

A, C, E, G. Color matrices in left column show performance levels of three individual subjects and their average or composite values for the counter-phase grating detection task as a function of stimulus contrast (x-axis) and spatial frequency (y-axis). The brighter the color, the higher the percentage of correct answers. **B, D, F, H**. Each row of color matrix data in the left column is replotted to show effects of unequal monocular contrast on detectability of counter-phase gratings. Only two out of four sets of data are shown here for visual clarity (Black: 0.5 cycles/deg; Gray: 2 cycles/deg). Red points represent mean values for all spatial frequency conditions. Psychometric curves are fitted with Weibull functions, $P_{\text{correct}} = 1 - 0.5\ \exp\left[-(x/\alpha)^{\beta}\right]$. For all subjects, percentages of correct answers are lowest for highest spatial frequency condition. However, the relationship between detectability of counter-phase gratings and spatial frequency is non-linear (see more detail in Figure 4).

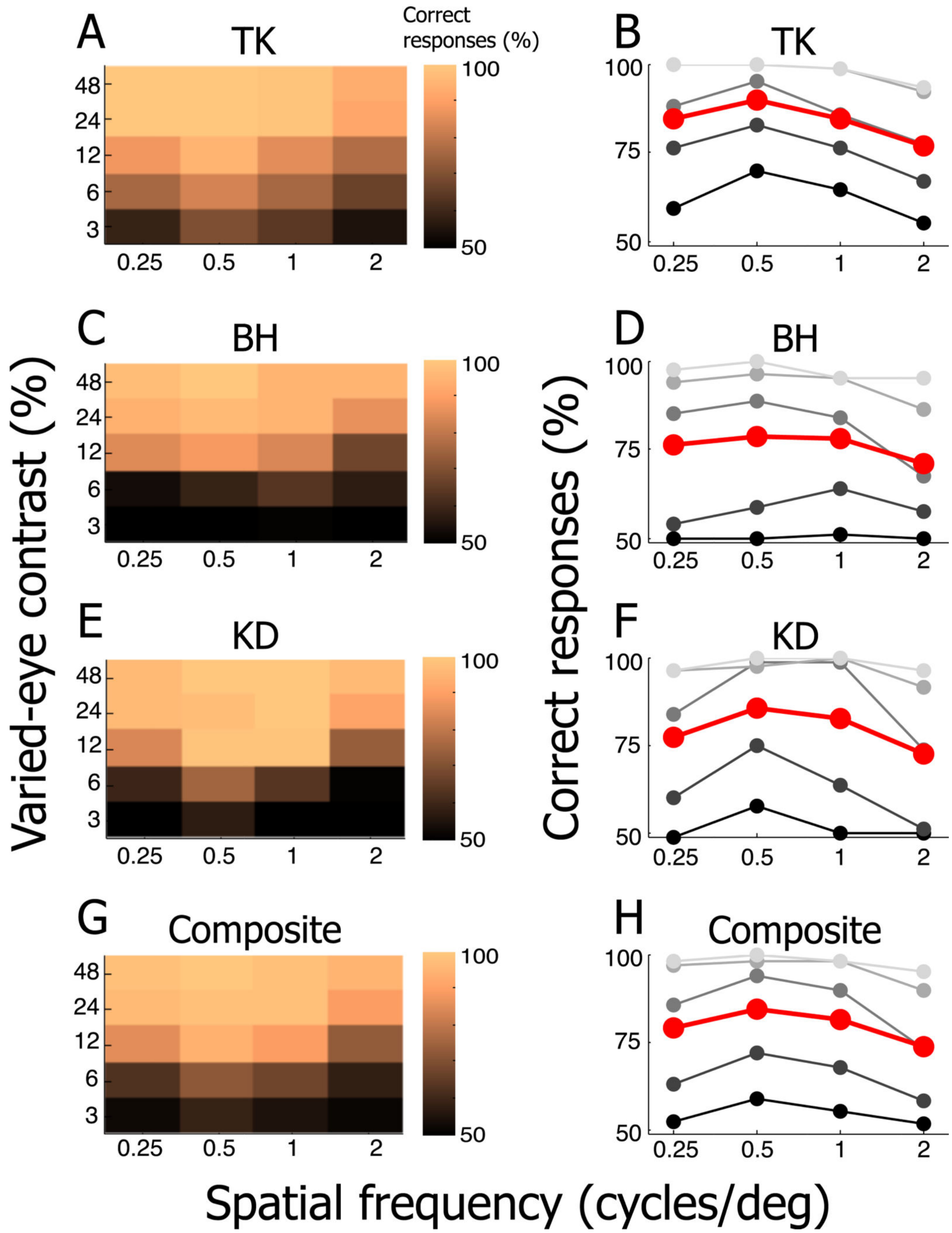

Figure 4. Effects of spatial frequency on detection of counter-phase gratings

A, C, E, G. Color matrices in left column contain the same information as that in Figure 3. But they are transformed to show stimulus contrast on the y-axis and spatial frequency on the x-axis. The brighter the color, the higher the percentage of correct answers. **B, D, F, H**. Each row of the color matrix in the left column is replotted to show effects of spatial frequency on detectability of counter-phase gratings. The brighter the data point, the higher the contrast condition. Red points represent mean values for all contrast conditions. Note that the best performance is observed at 0.5 cycles/deg., which is intermediate in the spatial frequency range we used.

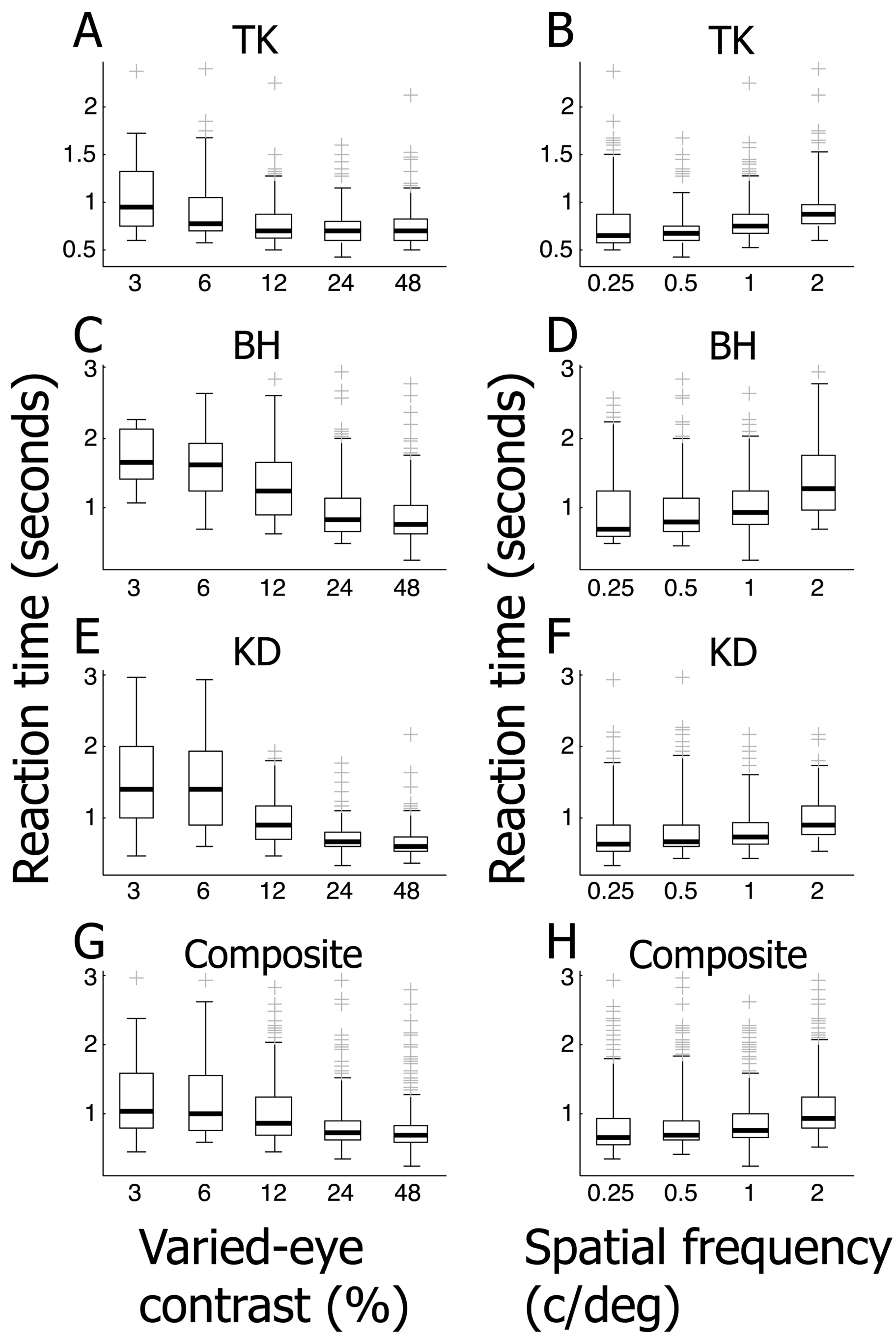

Figure 5. Reaction times for detection of counter-phase gratings

A, C, E, G. Reaction time distributions for the counter-phase grating detection task, are plotted against grating stimulus contrast. For each boxplot, the thick horizontal line within the box is the median (50th percentile), and the top and bottom edges of the box specify the 25th and 75th percentiles of the data set, respectively. The sum of the vertical lines above and below the boxes covers 99% of the entire data distribution. The gray cross marks outside this range indicate outliers. Reaction times are gradually reduced as stimulus contrast of the varied-eye increases. **B, D, F, H**. Reaction time distributions for the counter-phase grating detection task are plotted against spatial frequency. The same conventions are used as in the left column. Reaction times tend to increase with higher spatial frequency values.