

# Stereo channels with different temporal frequency tunings

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Received 11 March 2005; received in revised form 24 August 2006

## Abstract

To investigate the spatial and temporal frequency tunings for stereopsis, we measured the contrast sensitivity for depth discrimination with variable spatiotemporal frequencies and disparities using drifting sinusoidal gratings. The results showed that the contrast sensitivity changed with the stimulus disparity and the disparity tuning function varied with the spatial frequency. The disparity in the peak sensitivity decreased proportionally with the spatial frequency (size-disparity correlation). Although the temporal frequency exhibited a limited influence on the peak disparity, the temporal frequency tuning varied with the spatial frequency. The shape of the temporal frequency tuning function was lowpass for higher spatial frequencies, whereas it was bandpass for low spatial frequencies. These results suggest that more than one channel with different temporal as well as spatial frequency tunings contribute to stereopsis.

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**Keywords:** Stereopsis; Temporal frequency; Disparity tuning; Size-disparity correlation; Depth perception

## 1. Introduction

Stereopsis is the sense of depth derived from binocular disparities between the left and right retinal images. Similar to other visual functions, the sensitivity to stereopsis depends on the spatial and temporal frequencies of the retinal stimulation. To understand the spatiotemporal properties of the stereo mechanism, sensitivity measurements at various spatiotemporal conditions are necessary. There are two principal methods to investigate stereo sensitivity: contrast threshold and disparity threshold (stereoacuity or  $D_{\min}$ ) measurements. Several studies have determined contrast sensitivity as a function of spatial frequency for stereopsis by measuring the luminance contrast required for detecting depth (Frisby & Mayhew, 1978; Legge & Gu, 1989; Minematsu, Shioiri, & Yaguchi, 1996; Shioiri, Morinaga, & Yaguchi, 2002b; Smallman & MacLeod, 1994). As reported in these studies, the spatial frequency dependence of contrast sensitivity showed that the sensitiv-

ity peaks at a particular spatial frequency (bandpass frequency tuning). Although Frisby and Mayhew (1978) suggested that disparity does not influence spatial frequency tuning, subsequent studies demonstrated that the spatial frequency for peak sensitivity varied with the stimulus disparity (size-disparity correlation; Tyler, 1973, 1975) when eye movements were minimized during the measurements (Smallman & MacLeod, 1994). The decrease in the peak spatial frequency with an increase in disparity indicates that more than one channel with different tunings in both spatial-frequency and disparity contribute to stereopsis. This presumption is supported by masking studies that investigated the existence of spatial frequency channels for stereopsis (Prince, Eagle, & Rogers, 1998; Shioiri, Hatori, Yaguchi, & Kubo, 1994; Yang & Blake, 1991) as well as by other methods and reasoning (Julesz & Miller, 1975; Lehky & Sejnowski, 1990; Poggio, Gonzalez, & Krause, 1988; Richards, 1970, 1971).

Similar to contrast sensitivity, disparity thresholds depend on the stimulus spatial frequency (size-disparity correlation). Several studies showed a lower threshold with higher spatial frequencies, but only when the spatial

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frequency was lower than approximately 4 c/deg (Lee & Rogers, 1997; Schor & Wood, 1983; Schor, Wood, & Ogasawa, 1984; see also Tyler, 1973, 1975). Lee and Rogers showed that the disparity threshold decreased with the spatial frequency until approximately 4 c/deg and then it increased. The increase in the threshold at higher spatial frequencies is possibly because of a decrease in the effective contrast. When a fixed contrast is used, the change in the contrast sensitivity could influence the disparity threshold measurements. Although several studies used stimulus contrast equated among different conditions in terms of visibility (e.g., 30 times the threshold contrast), these results cannot be easily interpreted when the nonlinear relationship between the disparity threshold and contrast is considered (see below). To estimate spatiotemporal frequency tuning, we should take into account the dependence of the contrast threshold on disparity (Smallman & MacLeod, 1994) or the dependence of the disparity threshold on contrast (see Shioiri, Ito, Sakurai, & Yaguchi, 2002a for similar discussion on motion).

Experimental results in the literature show that the relationship between contrast and disparity cannot be easily summarized. First, several measurements of the disparity threshold with various contrasts revealed that the relationship was nonlinear (Legge & Gu, 1989; Cormack, Stevenson, & Schor, 1991). For example, Cormack et al. (1991) found that stereoacuity was proportional to the cube root of the contrast at just above threshold, while it became less dependent on contrast with an increase in contrast until it is approximately constant. Second, the relationship between the contrast and disparity threshold varied with the spatiotemporal frequency. In a previous study, we measured disparity threshold as a function of the spatial and temporal frequencies with various contrasts of the stimulus gratings (Lee, Shioiri, & Yaguchi, 2003a). When their data were plotted in order to show the dependence of disparity threshold on the stimulus contrast, the shape of the function varied according to the spatiotemporal conditions. For low spatial and high temporal frequencies, the threshold decreased as the contrast increased up to approximately 0.1; beyond this value, the threshold was approximately constant. For higher spatial frequencies, on the other hand, the threshold decreased with the contrast independent of the temporal frequency over almost the entire contrast range. It is evident that the disparity threshold with a fixed contrast with various spatiotemporal frequencies only yields a partial characteristic. Similarly, contrast sensitivity measurements with a fixed disparity also provide a partial understanding.

The abovementioned discussion indicates that it is necessary to measure contrast sensitivity as a function of disparity (or disparity threshold as a function of contrast) for each spatiotemporal frequency in order to investigate the spatiotemporal frequency characteristics of stereopsis. Although our previous study measured the disparity threshold with various contrasts for various combinations of spatial and temporal frequencies (Lee, Shioiri, & Yag-

uchi, 2003b), we found that such a measurement could not cover the sensitivities at large disparities. With a fixed contrast, depth is perceived within a range of disparities. To specify the range, the upper limit of disparity is required while only the lower limit is obtained by disparity threshold measurements. The measurements of disparity threshold access only the mechanism that is sensitive to small disparities available for each condition. In this view, the most important data are those obtained by Smallman and MacLeod (1994); they measured the contrast sensitivity with a number of combinations of spatial frequency and disparity. Their results revealed how the spatial frequency influences the contrast and disparity thresholds. However, they did not control the temporal property of the stimulus, except that they employed two display durations; this was insufficient for investigating the temporal frequency tuning of the underlying mechanisms. Temporal properties are important for stereopsis not only in their own right but also to consider the influence of the disparity information on the motion in depth (e.g., Regan, 1991; Shioiri, Saisho, & Yaguchi, 2000), relationship with the structure from motion (e.g., Uomori & Nishida, 1994) and other related perceptions. In this study, we conducted experiments in order to measure the contrast sensitivity as a function of the stimulus disparity for different combinations of spatial and temporal frequencies.

## 2. Experiment

### 2.1. Stimulus

The stimulus display comprised four squares arranged in a  $2 \times 2$  array with gaps of 0.3 deg (10 pixels) separating the squares (Fig. 1). The size of each square was  $4.3 \text{ deg} \times 4.3 \text{ deg}$  ( $128 \times 128$  pixels). Each square contained a drifting sinusoidal grating that moved along the same direction either leftward or rightward. The gratings in the upper right and lower left squares exhibited the same disparity; it was opposite to those in the other two squares (i.e., upper left and lower right were given a crossed disparity and the upper right and lower left were given an uncrossed disparity or vice versa). The observers responded which of the pairs appeared to be closer. The stimulus of a  $2 \times 2$  array was used for the following reasons. When one stimulus exists at the centre of the display, it tends to be perceived in front of the background even without a disparity difference from the background. When one pair of stimuli is arranged vertically, the upper

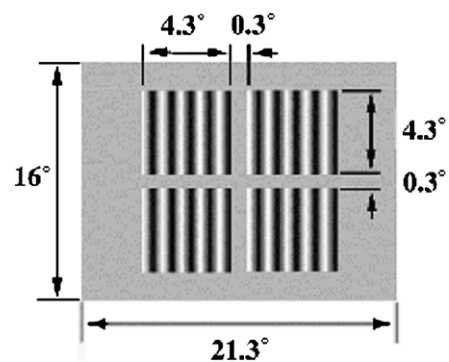


Fig. 1. Stimulus configuration. This is a fused view of the left and right eye images; these images differ only in the phase of the gratings.

stimulus tends to be perceived farther in depth than the lower one. The present task with a  $2 \times 2$  stimulus arrangement cancelled the influence of these undesired depth biases since the observer compared the depth between the upper left and lower right pair and the upper right and lower left pair. We did not employ a stimulus pair arranged horizontally because we assumed that the disparity change along the vertical axis might be more important. For example, Rogers and Graham, 1983 reported a vertical/horizontal anisotropy in which the sensitivity was greater for horizontally oriented corrugations than that for vertically oriented ones. This selection of the stimulus arrangement was rather arbitrary, and we found that the present results were not essentially different from those from previous experiments in different stimulus conditions (see Fig. 5).

## 2.2. Apparatus

The stimuli were generated on a colour monitor (Sony GDM-FW900) under the control of a graphic board (Cambridge Research, VSG 2/3). The frame rate of the display was 120 Hz, and the spatial resolution was  $640 \times 480$  pixels. Dichoptic separation was achieved by viewing the display through a pair of goggles (Crystal EYES3) that switched on and off alternately between the two eyes at a rate of 120 Hz in sync with the frame refresh of the display. In the system, the effective frame rate to each eye was 60 Hz. In general, this temporal resolution should be sufficient in order to investigate the visual system because the temporal resolution of the visual system is lower than 60 Hz even at high luminance stimulus conditions (Kelly, 1961). The average luminance of the display was  $6.3 \text{ cd/m}^2$  when viewed through the open shutter of the goggles. The luminance was  $0.5 \text{ cd/m}^2$  when viewed through the closed shutter. Although light through the closed shutter slightly changes the retinal disparity, the amounts of disparity change are predictable in our stimuli. Since the effect of cross talk is equivalent to adding another sinusoidal grating with a different phase and different contrast, the retinal image is also a sinusoidal grating with a phase and contrast that can be mathematically calculated (the maximum error was approximately 10%). The disparity values in the following sections indicated the values calibrated considering the cross talk. The viewing distance was 82 cm, where 1 pixel of the display corresponded to 2 arc min. A chin rest was used to stabilize the observer's head. The experiments were carried out in a dark room, where the observer waited for the experimenter to begin a session for around 1 min before each session.

## 2.3. Procedure

A two-alternative forced-choice response, indicating which of the two diagonal pairs of the patches appeared closer, was used. Threshold contrast for depth detection was measured by using a staircase procedure. A staircase procedure controlled the stimulus contrast by means of a 2-up-1-down staircase in which the contrast was assumed to converge at the value that gives 70.7% correct responses. One step of the contrast change was set as 1.12 dB. Fifteen reversals were measured in the staircase, and the average of the final five reversals was calculated as the threshold for that session. The motion direction was randomly chosen on each trial. Observers received no feedback concerning the validity of their response. A uniform grey field with an average luminance replaced the gratings between the trials. The shutters kept switching throughout a session to control the display in the same manner both during and between trials. The stimulus spatiotemporal frequency was a combination of one of the six temporal frequencies (0.15, 0.4, 1.5, 4, 10 and 20 Hz) and one of the four spatial frequencies (0.23, 0.94, 3.75 and 7.5 c/deg). The gratings drifted to control the temporal frequency. All the gratings moved in the same direction; however, the direction changed randomly from trial to trial. Phase disparities of  $0.36^\circ$ ,  $0.65^\circ$ ,  $1.3^\circ$ ,  $2.6^\circ$ ,  $5.2^\circ$ ,  $6.5^\circ$ ,  $13^\circ$ ,  $26^\circ$ ,  $40^\circ$ ,  $65^\circ$ ,  $104^\circ$  and  $130^\circ$  were used for each condition (disparity in absolute distance was a function of spatial frequency: disparity (deg in visual angle) =  $1/\text{frequency (c/deg)} \times \text{phase disparity (}^\circ)/360^\circ$ ). The data were not, however, obtained when the threshold was excessively high. An antialiasing technique was used to display phases with subpixel accuracy. Although only four pixels covered one cycle in the case of the grating with 7.5 c/deg,

our analysis regarding the effect of sampling rate confirmed that it would not cause problems in the measurements. By using a psychophysically obtained perceptual field profile (Rentschler & Fiorentini, 1974), we verified that the output of spatial filtering in the visual system does not change with a shift in the sampling points relative to the grating. That is, spatial filtering removes the high spatial frequency components in an image created as a result of screen sampling. This analysis is based on the data on foveal vision and the effect of sampling should be less in the peripheral stimuli used in our case. The stimulus presentation duration was fixed at 1 s. Before and after the stimulus presentation, the stimulus field became uniform grey with the same luminance as that of the average luminance of the gratings. The observer fixated on the centre of the screen, and the cross of the gaps between the grating squares acted as the fixation point. To verify the fixation with rapid stimulus movements, we measured the eye movements of one observer under the condition of 0.94 c/deg at 10 Hz (gratings moved 10.6 deg for a presentation duration of 1 s) for two trials (left and right motion). The largest deviations from the fixation point were 0.7 deg and 0.4 deg for the left and right trials. The average velocity was 5% (left) and 3% (right) of the stimulus velocity and velocity exceeded 50% of the stimulus velocity occasionally (2% (left) and 4% (right) of the stimulus presentation period) but never continued longer than 33 ms (the previous and next velocities in our 30 Hz sampling data were always less than 15% of the stimulus velocity). These results indicate that the eye movements in our conditions were within the range of fixational eye movements (Martinez-Conde, Macknik, & Hubel, 2004) and we assume that eye movements did not give any serious influence in our measurements.

For comparison, one observer participated in an experiment to measure the contrast threshold for stimulus detection with the same stimulus and equipment. The experiment used 1-up-1-down staircase for a yes/no (seen or unseen) decision.

## 2.4. Observers

The first author (SL) and a naive observer (JK) participated in the experiment. They had corrected-to-normal visual acuity, normal stereopsis and no history of any visual disorders. In each condition, SL ran three sessions and JK ran two sessions in each condition. JK ran also two sessions of each condition for determining the contrast threshold of stimulus detection.

## 3. Results

Figs. 2 and 3 show the contrast sensitivity as a function of disparity in all conditions. The results for different spatial and temporal frequencies are plotted in different panels in Figs. 2 and 3, respectively. Different symbols are used to indicate different temporal and spatial frequencies in Figs. 2 and 3. In these figures, the horizontal axis indicates the stimulus disparity from the fixation plane. The relative disparity between the two pairs of stimulus gratings should be doubled. The sensitivity peaked at a particular disparity in all the conditions. The shape of the disparity tuning function is similar across conditions, although the extent of tuning varied. Although the results of 20 Hz with 7.5 c/deg show only slight effect of disparity, similar feature can be seen around the peak. It should be noted that the sensitivity data close to 1 might have had influence of the physical limit of maximum contrast. In this plot, the tuning function tends to be wider at the intermediate spatial frequencies and narrower at high temporal frequencies; this is also the case when the data is plotted as a function of phase disparity (the shapes are the same in both the axes if they are

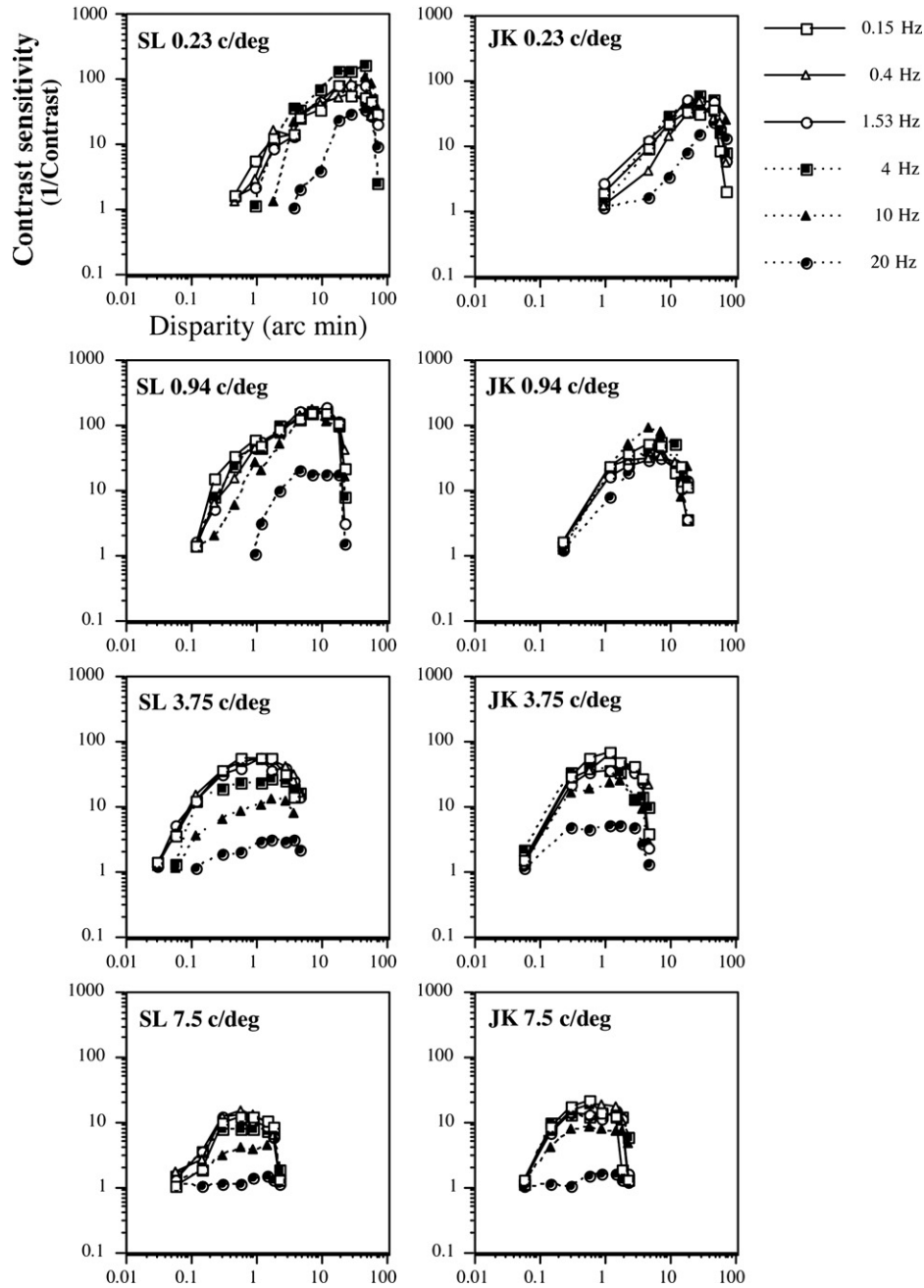


Fig. 2. Contrast sensitivity as functions of disparity. Results with different temporal frequencies for each spatial frequency are plotted in the same panel; the results for the SL and JK are shown separately.

in a logarithmic scale). The abrupt reduction in the sensitivity at large disparities is, at least partly, because of the stimulus used. Since we used periodic stimuli, the maximum disparity was limited by half the grating period, beyond which the disparity reversed and no correct response was expected. The disparity with the peak contrast sensitivity decreases proportionally with the spatial frequency; therefore, data from different spatial frequencies roughly coincide when the data are plotted against the phase disparity (not shown). The peak sensitivity occurs at approximately 50 deg in phase or 100 deg in relative phase in most of the conditions.

It can be seen in Fig. 3 that spatial frequency tuning changes with temporal frequency. For low temporal frequencies, the sensitivity is the highest at an intermediate spatial frequency. For high temporal frequencies, the sensitivity is the highest at the lowest spatial frequency. The change in the disparity tuning functions indicates that the temporal frequency in the stimulation influences the sensitivity to disparity in terms of both the contrast sensitivity and stereoacuity (or  $D_{min}$ ).

To compare the relative sensitivity among different temporal frequency conditions, we used the highest sensitivity among the different disparities in each temporal frequency

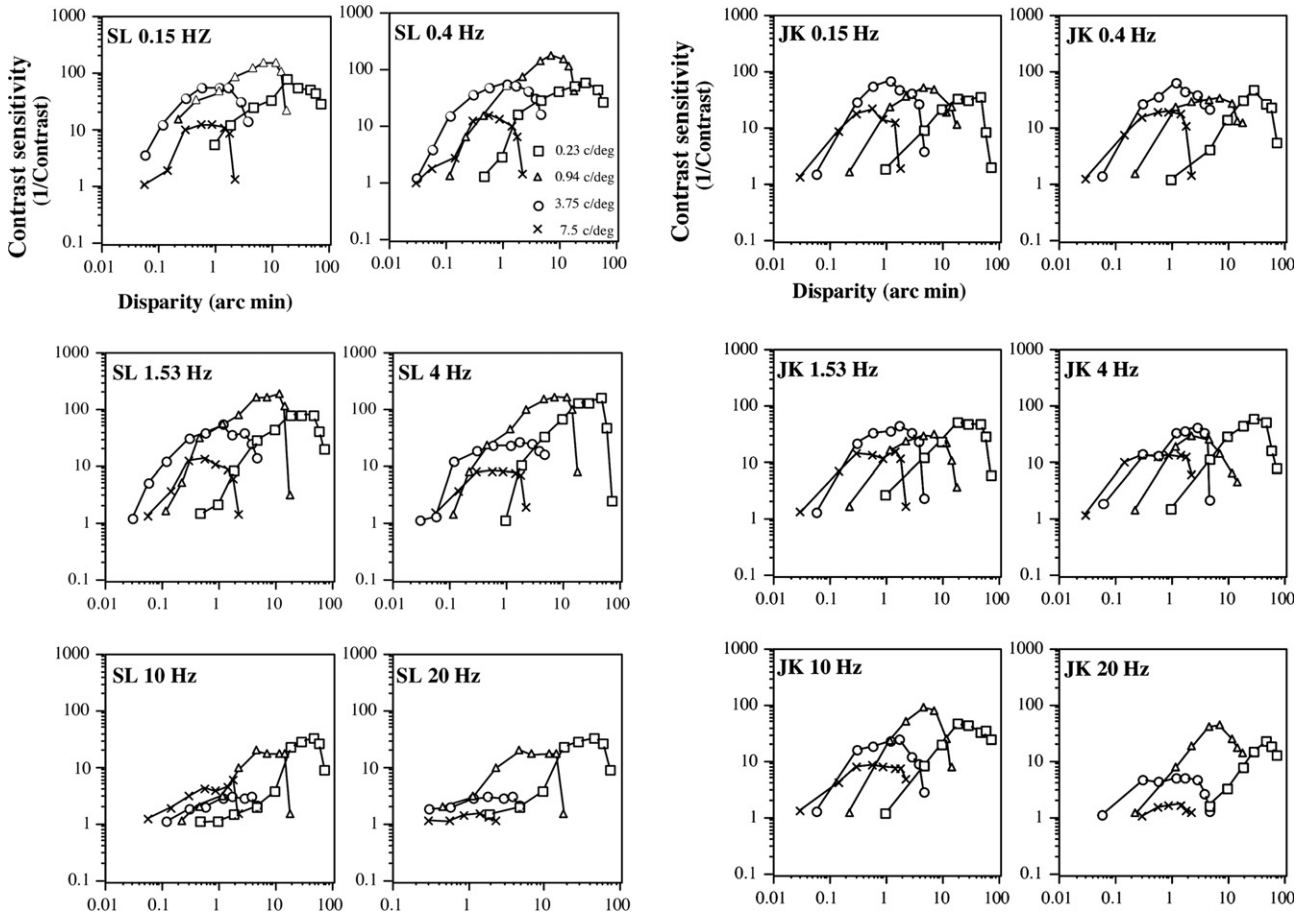


Fig. 3. Same data as that in Fig. 2; but, the results are plotted with different spatial frequencies for each temporal frequency in the same panel.

condition. The highest sensitivity is plotted as a function of temporal frequency in Fig. 4. Different symbols are used to represent different spatial frequencies. This figure shows that the temporal frequency tuning depends on the spatial frequency. For high spatial frequencies (3.75 and 7.5 c/deg), the shape of the temporal frequency tuning was low-

pass, whereas for low spatial frequencies (0.23 c/deg), it was bandpass with a peak between 5 and 10 Hz. For a spatial frequency of 0.94 c/deg, the shape of the tuning is low-pass for SL and bandpass for JK. It should be noted that these results are supported by the data for other disparity conditions shown in Fig. 2, although the temporal tuning

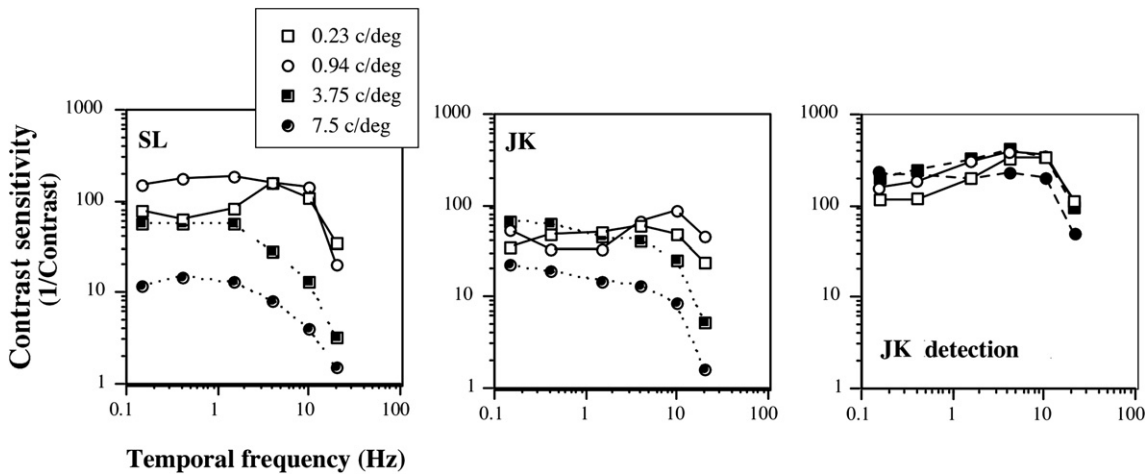


Fig. 4. Peak contrast sensitivity of each disparity tuning as a function of temporal frequency for SL and JK and contrast sensitivity for grating detection task for JK. Different symbols represent different spatial frequencies.

in Fig. 4 is based only on the peak disparity. The right most panel shows the contrast sensitivity required for grating detection. The temporal frequency tuning for each spatial frequency is similar to that for depth discrimination although variations in sensitivity among different spatial frequencies is much less than that for depth discrimination.

The difference in temporal frequency tuning at different spatial frequencies has important implications. This is an additional and important confirmation for the assumption that multiple channels contribute to stereopsis. Although the difference in spatial frequency tuning among different disparity conditions (i.e., size-disparity correlation) is consistent with the claim, it is not sufficient. A single channel can predict size-disparity correlation, as will be discussed using a model. However, the same analysis does not explain the difference in temporal frequency tunings at different spatial frequencies.

Each function in Fig. 3 contains information on  $D_{\min}$  (stereoacuity) and  $D_{\max}$  (the maximum disparity from which disparity can be discriminated).  $D_{\min}$  and  $D_{\max}$  can be obtained by drawing a horizontal line with a particular  $y$ -intercept and determining the intersections of the function with each line. The  $y$ -intercept of the line should correspond to the stimulus contrast. In other words, the results include information on the disparity thresholds with various contrasts. Although the  $D_{\min}$  and  $D_{\max}$  measurements might be constant with the spatial frequency in the high frequency region (e.g., above 2 c/deg, as suggested in Schor & Wood, 1983), our results indicate that such a characteristic could depend on the stimulus contrast.

With the contrast sensitivity required for detecting the gratings (Fig. 4 right most panel), our data can be compared with previous measurements on stereoacuity where the contrast was equated in terms of the threshold. For example, Patterson (1990) measured the disparity threshold for various spatiotemporal frequencies. His results showed that the disparity threshold increased with the temporal frequency for high spatial frequencies (a threshold of 8 c/deg for 20 Hz is 3.0 times that for 1 Hz), while they showed that the effect of the temporal frequency on the disparity threshold was minimal for intermediate and low spatial frequencies (a threshold of 1 c/deg for 20 Hz is 0.9 times that for 1 Hz). By using the disparity tuning functions in Fig. 3, we determined JK's stereo acuity for the stimulus with a 30 times threshold contrast. The obtained thresholds were similar to Patterson's data. A stereoacuity of 7.5 c/deg for 20 Hz is 3.3 times that for 1.53 Hz, and stereoacuity of 0.94 c/deg for 20 Hz is 0.8 times that for 1.53 Hz. This shows that our results include information on  $D_{\min}$ , which is comparable to  $D_{\min}$  measured in previous experiments (the same is expected with regard to  $D_{\max}$ ).

#### 4. Discussion

In this section, we discuss some technical issues related to our measurements; then, we discuss the physiological implications of the present results. First, the effect of the

number of cycles in the stimulus is considered. Sensitivities at 0.23 c/deg could have been underestimated because of the smaller number of cycles in the stimulus gratings. A decrease in the number of cycles is known to reduce the contrast sensitivity to grating detection, particularly when the number of cycles is less than eight (Robson & Graham, 1981). However, it is unlikely that this influenced our measurements of frequency tunings. The shape of the temporal frequency tuning for detecting gratings in our stimulus (Fig. 4, right) is similar to that of the temporal frequency tunings in the literature with greater number of cycles (i.e., temporally bandpass with low spatial frequency and temporally lowpass with high spatial frequency).

Second, the effects of the stimulus configuration and experimental setup are investigated. Our stimulus covered a relatively large retinal area and the observers' decision was probably based on the peripheral vision, which might have differed from the results from the fovea. Our grating stimuli may be different from the other types of stimuli such as random dot patterns. Our experimental setup used a multiplexing technique with a shutter goggle, which might yield different results as that from setups that use conventional stereoscopes. We compared our results with two previous experiments having smaller stimulus near the fovea with a conventional stereoscope using random dot patterns (Smallman & MacLeod, 1994; Kimura, Shioiri, Yaguchi, & Kubo, 1994; see Kimura et al.'s data in Shioiri et al., 2002b). The stimulus covered the central visual field within 5 deg in both the experiments, while the present experiment used much larger stimuli that covered a field exceeding 10 deg, where the centre of each grating square was approximately 3.5 deg away from the fovea.

To compare the results from previous studies and our study considering the effect of eccentricity, we used the cortical magnification factor for stereopsis estimated by Stevenson, Reed, and Yang (1999). They measured the size that yields an equivalent performance for disparity detection as a function of eccentricity (Fig. 9 in their study). Their results showed that the stimulus at the periphery of 3.5 deg (which corresponds to ours) required approximately 3 times the stimulus size in order to achieve the same performance at the fovea. That is, the stimulus at an eccentricity of 3.5 deg is equivalent to the stimulus with one-third its size at the fovea. Therefore, the horizontal axis of the present data was shifted towards the higher spatial frequency region by a factor of 3 in order to compare the central stimulus conditions. In Fig. 5, the data with similar disparity and temporal conditions are selected in order to compare the results from the three studies. Fig. 5 shows similar spatial frequency tunings even with differences in stimulus configurations and experimental setups. This suggests that our conclusions can be extended to the stereo mechanism in the central vision. Further, the differences in the stimulus configuration and experimental setup among the studies are not essential for the threshold measurements.

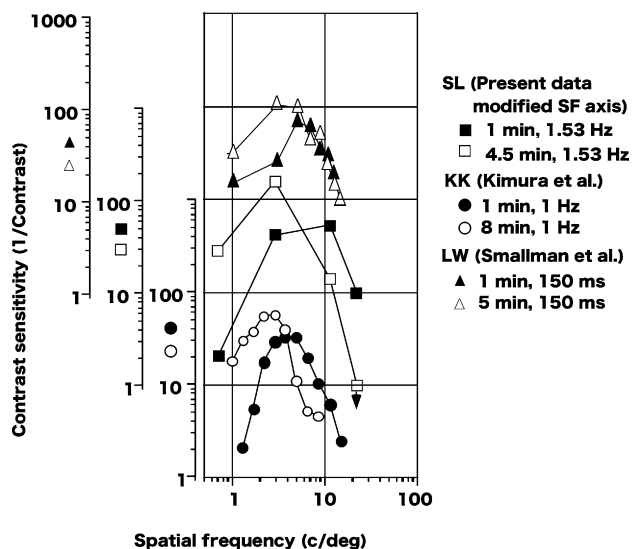


Fig. 5. Comparison of contrast sensitivity for disparity discrimination among three studies under similar temporal and disparity conditions (Smallman & MacLeod, 1994; Kimura et al., 1994). The present results were shifted by a factor of 3 along the spatial frequency axis according to the cortical magnification factor for disparity discrimination.

The present experiment revealed how spatial frequency, temporal frequency and disparity influence sensitivity of stereopsis. Contrast threshold measurements demonstrated that all the factors influenced the sensitivity. The effect of spatial frequency confirmed the size-disparity correlation for stereopsis (Smallman, 1995; Tyler, 1973). The peak of the disparity tuning depended on the spatial frequency of the stimulus. The effect of temporal frequency was different for different spatial frequencies. For high spatial frequency stimuli, the sensitivity to depth is the highest between 5 and 10 Hz (bandpass). For low spatial frequency stimuli, the sensitivity is the highest at temporal frequencies lower than 1 Hz (lowpass).

There are two important issues related to the effect of temporal frequencies on the sensitivity of disparity discrimination. First, this supports strongly that multiple channels contribute to the disparity detection. Although the change in the spatial frequency tuning with disparity (size-disparity correlation) is often considered as the evidence of multiple channels in stereopsis, this is not a sufficient condition because a single-channel model can predict size-disparity correlation as discussed below. From this point of view, temporal frequency characteristics is more important since the same model does not explain the differences in temporal tuning among conditions. To show that the size-disparity correlation does not necessarily indicate the existence of multiple channels, we calculated the responses of a disparity energy model. The disparity energy model is a model of a disparity-sensitive complex cell proposed by Ohzawa and his co-workers (Ohzawa, DeAngelis, & Freeman, 1990). Fig. 6 shows the simulation results of the spatial frequency tunings of a cell for several disparities and disparity tunings for several spatial frequencies (see Appendix A). This sim-

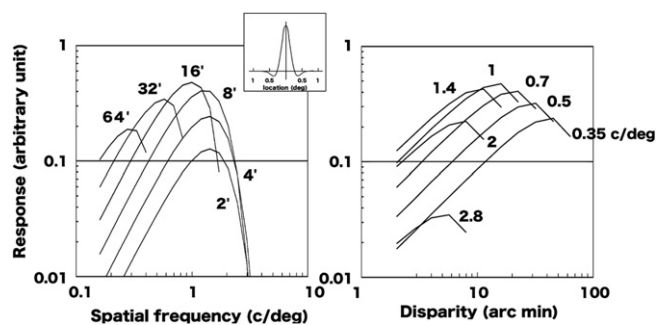


Fig. 6. Responses of a model complex cell sensitive to binocular disparity. Spatial frequency tunings for disparities of 2, 4, 8, 16, 32 and 64 arc min and disparity tunings for spatial frequencies of 0.35, 0.5, 0.7, 1, 1.4, 2 and 2.8 c/deg. The complex cell has simple cells as subunits and the profile of the left receptive field of one of the simple cells is shown in the inset.

ulation reveals that the spatial frequency peak changes with the stimulus disparity and the disparity peak changes with the stimulus spatial frequency; this results in the size-disparity correlation. The model predicts a size-disparity correlation even when a single channel is assumed.

Second, the effect of temporal frequency on disparity discrimination provides information of temporal characteristics of the visual pathways that convey disparity signals. Together with spatial frequency characteristics, we discuss whether both/either of the M and/or P pathways convey disparity signals. Although Hubel and Livingstone suggested that primate stereopsis are mediated only by the M pathway (Hubel & Livingstone, 1987; Livingstone & Hubel, 1987), subsequent studies reported the experimental results that disagree with this suggestion (Schiller, Logothetis, & Charles, 1990; Kontsevich & Tyler, 2000). For example, Schiller et al. showed that P-LGN lesions in monkeys disrupted the behavioural detection of cyclopean stereo targets with fine random dots, whereas M-LGN lesions had no effect on the performance of these targets. Kontsevich and Tyler showed psychophysically that the stereoscopic system is more sensitive to sustained stimuli than that to transient ones. Considering the spatial and temporal frequency tunings of the two pathways (Merigan & Maunsell, 1993), Kontsevich and Tyler concluded that their results imply that stereopsis is more strongly influenced by parvocellular inputs. Our results are consistent with those of Schiller et al. and Kontsevich and Tyler. To interpret our results, two mechanisms with different spatio-temporal frequency tunings are required. For high spatial frequency stimuli, the sensitivity to depth is the highest between 5 and 10 Hz (bandpass). For low spatial frequency stimuli, the sensitivity is the highest at a temporal frequency lower than 1 Hz (lowpass). These temporal frequency characteristics agree with those of the M and P pathways in monkeys that were obtained from a lesion study (Merigan & Maunsell, 1993). They also agree with the transient and sustained channels classified according to the temporal frequency tunings of human contrast sensitivity (van Nes, Koenderink, Nas, & Bouman, 1967); these channels are often related to the M and P pathways found in monkeys.

Therefore, our results support that both the M and P pathways convey disparity signals.

In conclusion, our analysis of contrast sensitivity measurements for depth discrimination suggests that there are at least two channels for stereoscopic depth perception with different spatiotemporal frequency tunings and different disparity tunings.

### Acknowledgments

This study was partially supported by MESSC (GASR-18330153) to SS and the Cooperative Research Project of RIEC at Tohoku University. The authors thank Koichi Yuge, Hideki Umamo and Taku Sato for their assistance in the experiment and the preparation of the manuscript. We also thank Philip Grove for his comments on an earlier version of the manuscript.

### Appendix A

We simulate the responses of a disparity-sensitive cell using a model termed as the disparity energy model, which was proposed by Ohzawa and his co-workers (Ohzawa et al., 1990). This model represents responses of a complex cell that has two simple cells as subunits. The receptive field profiles of the two simple cells are different in phase so that they can detect stimulus at different positions within the receptive field. The profiles may be expressed by sine Gabor and cosine Gabor functions. The simple cells have binocular receptive fields and the receptive field profiles are also different in phase between the left and right fields. Because of the binocular difference in phase, the cell is sensitive to binocular disparity. To simulate the responses of a disparity-sensitive cell to a set of stereo stimuli, we assumed that each receptive field profile of the simple cells is described as

$$G(x) = e^{-\frac{x^2}{2\sigma^2}} \cos(2\pi\omega x + \phi), \quad (\text{A1})$$

where  $G(x)$  represents the profile of a monocular receptive field;  $x$ , the spatial position;  $\sigma$ , the spatial spread of the function;  $\omega$ , the peak spatial frequency; and  $\phi$ , the phase shift. As an example, let us consider a complex cell that is sensitive to far disparity (far cell). The left and right receptive field profiles of a simple cell may be expressed by Gabor functions with  $\phi = 0$  and  $\phi = -\pi/2$  or  $\phi = \pi/2$  and  $\phi = 0$ . In the present simulation, we use only one combination of the phase properties ( $\phi = 0$  and  $\phi = -\pi/2$ ) as a representative. The response  $R$  of the cell to sinusoidal gratings can be described as follows:

$$R = \int G_{\text{left}}(x) \cdot I_{\text{left}}(x) dx + \int G_{\text{right}}(x) \cdot I_{\text{right}}(x) dx, \quad (\text{A2})$$

where  $I_{\text{left}}$  and  $I_{\text{right}}$  indicate the stimulus images on the left and right retinas. Suppose the stimulus is a pair of gratings that are described as follows:

$$\begin{aligned} I_{\text{left}} &= \cos(2\pi f) \\ I_{\text{right}} &= \cos(2\pi f - \theta) \end{aligned} \quad (\text{A3})$$

where  $f$  is the stimulus spatial frequency and  $\theta$  is the binocular phase disparity. The cell response  $R$  can be expressed as follows.

$$\begin{aligned} R &= \sin(-\theta) \int \exp(-x^2/2\sigma^2) \sin(2\pi\omega x) \cdot \sin(2\pi f x) dx \\ &\quad + \int \exp(-x^2/2\sigma^2) \cos(2\pi\omega x) \cdot \cos(2\pi f x) dx \\ &= \frac{1}{2} \sin(\theta) \int \exp(-x^2/2\sigma^2) (\cos(2\pi(\omega - f)x) \\ &\quad - \cos(2\pi(\omega + f)x)) dx \\ &\quad + \frac{1}{2} \int \exp(-x^2/2\sigma^2) \cos(2\pi(\omega + f)x) \\ &\quad + \cos(2\pi(\omega - f)x) dx \end{aligned} \quad (\text{A4})$$

Calculating the integral in this equation derives response  $R$  as follows.

$$\begin{aligned} R &= \frac{1}{2} \sin(\theta) (\exp(-2\pi^2(\omega - f)^2\sigma^2) - \exp(-2\pi^2(\omega + f)^2\sigma^2)) \\ &\quad + \frac{1}{2} (\exp(-2\pi^2(\omega + f)^2\sigma^2) + \exp(-2\pi^2(\omega - f)^2\sigma^2)). \end{aligned} \quad (\text{A5})$$

The second term of this equation is independent of  $\theta$ , the stimulus disparity; thus, its value is the same for near, far and zero disparity stimuli. Therefore, we use the value of the first term as the cell response. One method to explain the psychophysical results is to use the differences in the responses of near and far (or near/far and zero) sensitive cells. Such manipulation eliminates the second term of Eq. A5. In this simulation, however, we only use the first term as the response of the cell since this is essentially the same as the subtraction method. For the simulation, we adopt  $\omega = 1$  c/deg and  $\sigma = 0.2$  deg. These parameters are arbitrarily selected to have a typical receptive field profile in the simple cells. The left panel in Fig. 6 shows the response as a function of the spatial frequency with various disparities. The right panel shows the response as a function of disparity with various spatial frequencies. The receptive field profile of the hypothesized simple cell is shown in the inset of Fig. 6.

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