A Joint Lateral Motion—Stereo Constraint

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Received: March 29, 2021 **Accepted:** November 17, 2021 **Published:** January 25, 2022

Citation: Chen Y, Yao Z, He Z, et al. A joint lateral motion—stereo constraint. *Invest Ophthalmol Vis Sci.* 2022;63(1):32. https://doi.org/10.1167/iovs.63.1.32 **P**URPOSE. We developed a stereo task that is based on a motion direction discrimination to examine the role that depth can play in disambiguating motion direction.

METHODS. In this study, we quantified normal adults' static and dynamic (i.e., laterally moving) stereoscopic performance using a psychophysical task, where we dichoptically presented randomly arranged, limited lifetime Gabor elements at two depth planes (one plane was at the fixation plane and the other at an uncrossed disparity relative to the fixation plane). Each plane contained half of the elements. For the dynamic condition, all elements were vertically oriented and moved to the left in one plane and to the right in another plane; for the static condition, the elements were horizontally oriented in one plane and vertically oriented in another plane.

RESULTS. For the range of motion speed that we measured (from $0.17^{\circ}/\text{s}$ to $5.33^{\circ}/\text{s}$), we observed clear speed tuning of the stereo sensitivity ($P = 3.0 \times 10^{-5}$). The shape of this tuning did not significantly change with different spatial frequencies. We also found a significant difference in stereo sensitivity between stereopsis with static and laterally moving stimuli (speed = $0.67^{\circ}/\text{s}$; P = 0.004). Such difference was not evident when we matched the task between the static and moving stimuli.

CONCLUSIONS. We report that lateral motion modulates human global depth perception. This motion/stereo constraint is related to motion velocity not stimulus temporal frequency. We speculate that the processing of motion-based stereopsis of the kind reported here occurs in dorsal extrastriate cortex.

Keywords: stereo vision, speed tuning function, lateral motion

There are several studies that demonstrate that our abil-L ity in detecting moving stereo target is different from that of static ones.¹⁻⁴ Stereopsis exhibits lowpass temporal properties⁵ in that the faster the disparity is modulated in time, generally the worse the stereo sensitivity (also see Hadani and Vardi⁶). The filtering properties of the underlying mechanisms are thought to be spatiotemporally separable and consistent with a spatiotemporal gradient limit.⁵ These results are pertinent to the early stages of cortical processing involving nondirectionally selective detectors.⁷ Separate from the temporal modulation of disparity is the dependence of stereopsis on lateral stimulus motion, a property that involves directionally selective detectors in early regions of the cortical pathway.⁸ In general, the faster the lateral motion, above about 2°/s, the worse the stereopsis.¹ For extended grating stimuli, Morgan and Castet⁹ argued for a fixed spatial phase limit for different spatial frequencies, consistent with a temporal frequency rather than velocity dependence. Hadani and Vardi⁶ found a very different dependence for a multielement stimulus where all the elements moved in a fixed direction across an abrupt disparity-defined trajectory. Stereopsis was impaired at low velocities $(1^{\circ}/s \text{ to } 3^{\circ}/s)$ and improved at higher velocities $(11^{\circ}/s)$ where it was equivalent to that for stationary elements. The findings of these two studies appear to be at odds but the stimuli and methods are so fundamentally different that it is likely they reflect very different neural limits.

Neither of these studies bear upon the question we address which involves the relationship between motion direction discrimination and stereopsis. Our task involved the disambiguation of motion direction based solely on stereopsis and neither of the previous studies have addressed this issue. This involves the conjoint processing of motion and stereopsis and is likely to reflect later parts of the cortical pathway, particularly the dorsal pathway.¹⁰⁻¹² We examined this issue using a limited lifetime, multielements display but with control over spatial frequency. The display consisted of two fields of spatial Gabors moving in opposite directions and distributed in one of two depth planes, one being the fixation plane that was arranged to not coincide with the screen plane. The subject was asked

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Investigative Ophthalmology & Visual Science

to identify the motion direction of the stimulus in depth (uncrossed disparity). We confined our task to one polarity of disparity to avoid any processing/sensitivity differences that might occur between uncrossed and crossed disparities.^{13–15} We wanted to know how disparity processing and lateral motion processing were related when both kinds of information were required to solve the task. Our intent was to use a task that would access processing at a higher stage in the pathway (i.e., extrastriate cortex) than involved in the simple depth detection of moving stimuli (i.e., striate cortex). Therefore an additional question, concerning the possible site of this stereo/motion interaction, was whether this was a velocity or temporal frequency dependence.

METHODS

Participants

Nine adults (average age = 24.78 ± 4.24 ; mean \pm standard deviation [SD]; three males) with normal or corrected-tonormal vision (20/20 or above) participated in this study. One subject was the first author. All other participants were naïve to the purpose of the study and provided informed written consent. Subjects were optimally refracted and optically corrected. The study was in line with the tenets of the Declaration of Helsinki and was approved by the Institutional Review Boards at Wenzhou Medical University.

Apparatus

We conducted experiments via in-house Matlab scripts using the PsychToolBox extension.¹⁶ All stimuli were presented on a gamma-corrected LG D2792PB 3D LED screen (LG Life Science, Seoul, Korea), which had a resolution of 1920 × 1080 pixels and a refresh rate of 60 Hz. We used Bits# Stimulus Processor (Cambridge Research Systems Ltd., Rochester, UK) to generate contrast resolution of 14-bit. Throughout the psychophysical experiments, we dichoptically displayed the stimuli using polarized glasses to the observers in a dark room at a viewing distance of 171 cm. The mean luminance through polarized glasses was 36.5 cd/m².

Design

In this study, we performed five experiments (Table). In Experiment 1, we measured the stereo-speed tuning curve at 3 cycles/degree (cyc/deg; local Gabor spatial frequency). In particular, we measured observers' stereoacuities using laterally moving Gabor arrays (the spatial frequency of each Gabor was 3 cyc/deg) at six different speeds: $0.17^{\circ}/s$, $0.33^{\circ}/s$, $0.67^{\circ}/s$, $1.33^{\circ}/s$, $2.67^{\circ}/s$, and $5.33^{\circ}/s$. Different speeds of

motion were measured in a randomized order. Then, eight of nine subjects completed Experiment 2-a control experiment to measure the stereo-speed tuning curves at three different local Gabor spatial frequencies-in which each Gabor had a spatial frequency of 0.75, 1.5 or 6 cyc/deg (see Fig. 1D) and moved at the same six speeds that we measured in Experiment 1 (0.17°/s, 0.33°/s, 0.67°/s, 1.33°/s, 2.67°/s, and 5.33°/s). As confirmed by fast Fourier transform applied to the whole three-dimensional (3D) spacetime image, when we changed the spatial frequency of Gabors, the global spatial frequency changed in an identical way, so too did the global temporal frequency. The same eight subjects who finished Experiment 2 also participated in another control experiment (Experiment 3), in which, we compared the difference of stereoacuity between laterally moving and static stimuli. For static, we measured the stereoacuity of the observers using static Gabor array at 0.75, 1.5, 3 and 6 cyc/deg (local Gabor spatial frequency), respectively.

It should be noted that in Experiment 3, we measured static stereoacuity using a different task to that used for dynamic stereoacuity. To rule out the effect of task difference on stereoacuity, we conducted an additional control test (Experiment 4), in which we measured observers' dynamic stereoacuities using stimuli of moving Gabor arrays with random directions around the clock (0°-360°) at a speed of 0.67°/s at four spatial frequencies of 0.75, 1.5, 3 and 6 cyc/deg (local Gabor spatial frequency; Experiment 4.1); the orientation of the Gabor arrays was matched with that of the static stereopsis measurement in Experiment 3. This allowed the measurement of stereoacuity using the same orientation discrimination task but with moving Gabor arrays. In Experiment 4.2, we measured the stereoacuity of the observers using randomly moving (random directions around the clock, 0°-360°) stimuli, whose spatial frequency was set at 3 cyc/deg, at another five speeds $(0.17^{\circ}/s, 0.33^{\circ}/s, 0.33^{\circ}/s)$ 1.33°/s, 2.67°/s, and 5.33°/s). Six of nine subjects completed this experiment.

In all the above-mentioned experiments, the stimuli presentation duration was set as 1000 ms. To rule out the potential effect of vergence eye movements on the stereo-speed tuning, we also measured the stereo-speed tuning curve at a local Gabor spatial frequency of 3 cyc/deg with a much shorter stimuli presentation duration—200 ms (Experiment 5). All setups in Experiment 5 were identical to Experiment 1, except the stimuli presentation duration was different. The same six subjects who completed Experiment 4 participated in this control test.

All but the visual task of Experiment 2, 3 and 4 at local Gabor spatial frequency of 0.75 cyc/deg had 50 Gabor elements (each had a size of one cycle), which were displayed to each eye at a randomized position

TABLE. A Summary of Experimental Designs

	Subjects Number	Spatial Frequency of Gabors (cyc/deg)	Speed (°/s)	Presentation Duration (ms)	Discrimination Task
Experiment 1	9	3	0.17~5.33	1000	Motion direction
Experiment 2	8	0.75, 1.5, 6	0.17~5.33	1000	Motion direction
Experiment 3	8	0.75, 1.5, 3, 6	0	1000	Orientation
Experiment 4.1	6	0.75, 1.5, 3, 6	0.67	1000	Orientation
Experiment 4.2	6	3	0.17~5.33 (except 0.67)	1000	Orientation
Experiment 5	6	3	0.17~5.33	200	Motion direction

Because Experiments 4.1, 4.2, and 5 were carried out later, some subjects were not able to participate in the experiments for personal reasons.



FIGURE 1. Stimuli and design. (A) The Alignment task. Observers were asked to align four dots so that the distance between the neighboring dots were equal. (**B&C**) There were two depth planes: one plane was at fixation plane and the other at an uncrossed disparity relative to the fixation plane. (**B**) Laterally moving stereoscopic visual stimuli which we used to assess human stereoscopic vision. Right panel, an illustration of the 3D stimuli in the dynamic stereoscopic measurement. The Gabor envelope and sinewave carrier moved together at the same speed. Observers were asked to answer which moving direction (either left or right, as indicated by the *red* or *blue arrows* separately) of Gabors was in the front fixation plane. Gabors in either orientations or moving directions were distributed equally in the circular display window. (**C**) Static (i.e., non-moving) or randomly moving stereoscopic measurement. Observers were asked to asswer which orientation (horizontal or vertical) of Gabors was in the front fixation plane. (**D**) Four different spatial frequencies of Gabor elements: 0.75, 1.5, 3, 6 cyc/deg. The size of each Gabor was maintained at one cycle. When the spatial frequency of each Gabor was set at 1.5, 3, 6 cyc/deg, 50 Gabor elements were displayed to each eye, and reduced to 24 elements for the local Gabor spatial frequency at 0.75 cyc/deg.

on the display (diameter = 6.15° in visual angle). There was an empty space (diameter = 1.11° in visual angle) around the center fixation point to facilitate fixation control. Limited to the size of display, the Gabor elements would be

reduced to 24 when spatial frequency of each Gabor was 0.75 cyc/deg. For all experiments with moving stimuli, the Gabor envelope and sinewave carrier moved together at the same speed. Each Gabor had a 5% probability of limited

lifetime in each presentation frame. Gabors that reached their lifetime were reborn at a random location of the display window. When a Gabor moved to the edge of the display window, it disappeared and immediately reappeared at the opposite edge. These were designed to minimize any tracking of individual Gabors.

In the experiment where we showed laterally moving stimuli, we included two depth planes (one plane was at fixation plane and the other at an uncrossed disparity relative to the fixation plane); one contained 25 (for local Gabor spatial frequency at 1.5, 3, 6 cyc/deg) or 12 (for local Gabor spatial frequency at 0.75 cyc/deg) vertical-oriented Gabor elements horizontally moving to the left and the other 25 or 12 vertical counterparts to the right (see Fig. 1B). Gabor elements assigned to the same depth plane always moved in the same direction. The subjects were asked to report whether the Gabor elements in the front fixation plane were moving in the left or right direction. In the measurement with static (Experiment 3) and randomly moving (Experiment 4) stimuli, we also included two depth planes; one contained 25 (for local Gabor spatial frequency at 1.5, 3, 6 cyc/deg) or 12 (for local Gabor spatial frequency at 0.75 cyc/deg) horizontal Gabor elements and the other 25 or 12 vertical counterparts (see Fig. 1C). The subjects were asked to report whether the Gabor elements in the front fixation plane were horizontal or vertical. Before the measurement, we provided practice trials for all subjects to familiarize them with the visual task.

Using the three-down/one-up staircase procedure, we measured the minimum uncrossed disparity that the observers needed to discriminate for the orientation or the movement direction (i.e., D_{min}) of the Gabor elements. We varied the disparity in each trial based on observer's performance with an initial relative step-size of 50% before the first reversal and 20% in all subsequent trials. We used subpixel interpolation for the stimuli by Gaussian windowing each Gabor element and recomputing the peak of the Gaussian function. At the sixth reversal point, the staircase was terminated. To more accurately measure the threshold for stereopsis, we repeated each staircase three times. We averaged the last five reversals of each repetition to compute the threshold and variance; there were 15 reversal points for each condition. Before completing each staircase, subjects performed the alignment task (see Fig. 1A) to ensure correct fusion between their two eyes. During the alignment task, subjects were asked to align four dots so that the distance between the neighboring dots was equal.

Procedure

For all the experiments where we displayed the static and moving stimuli, a dichoptic frame was shown before each trial throughout the visual task. We presented the dichoptic stimuli of the Gabor elements at two depth planes (one plane was at fixation plane and the other at an uncrossed disparity relative to the fixation plane) for 1000 ms (or 200 ms in Experiment 5). Subjects were asked to report whether the motion direction of the Gabor elements in the front fixation plane were to the right or left (experiment with the moving stimuli; see Fig. 1B), and whether the orientation of the Gabor elements in the front fixation plane were horizontal or vertical (experiment with the static or randomly moving stimuli; see Fig. 1C) under no time constraint. A fixation point in the center of the display was continually presented for the whole trial to ensure that moving stimuli were not tracked. Furthermore, the stimuli were composed

of limited lifetime Gabor elements so that the motion was carried by the Gabor population as a whole to ensure individual elements were not tracked. Finally, the fact that the motion directions were balanced (i.e., in opposite directions) was also a safe guard against tracking the stimuli. After the response, the next trial would begin 200 ms later. The initial disparity of the task was established at 40 pixels (i.e., equivalent to 1503 arc seconds). We provided auditory feedback to both correct and incorrect answers, and asked the subjects to remain fixated at the fixation point throughout the visual task.

Statistical Analysis

We recorded thresholds for stereopsis in pixel units throughout the measurement and converted them to stereo sensitivity (i.e., the reciprocal of thresholds for stereopsis = $1/D_{\mbox{\scriptsize min}})$ in arc seconds. Then, we analyzed the difference of stereo sensitivity across different speeds using a one-way repeated-measures analysis of variance (ANOVA) and that across different local Gabor spatial frequencies using a 2way repeated-measures ANOVA, with their effect size calculated as partial eta squared. We also performed post-hoc pairwise t-tests (with Bonferroni correction) for comparing the stereo sensitivity between each two local Gabor spatial frequencies. Linear mixed-effects models were applied to explore associations of local Gabor spatial frequency with the parameters of the speed tuning function. Furthermore, we compared the values of stereo sensitivity among the conditions shown with static and dynamic (i.e., laterally moving and randomly moving) stimuli at four different local Gabor spatial frequencies using a two-way repeatedmeasures ANOVA, and conducted a Pearson correlation test to find the relationship between them.

Curve Fits

The speed tuning function for the stereo sensitivities were fitted with a log Gaussian model, which has been used in a previous study to fit the speed tuning curves in cortical area Middle Temporal (MT) of macaque visual cortex^{17,18}:

$$\varphi = \varphi_0 + A \times exp\left[-\frac{1}{2 \times \sigma^2} \left(\log \frac{s}{s_p}\right)^2\right]$$
(1)

where φ is the stereo sensitivity and *s* corresponds to the stimulus speed in degrees per second. The function has four free parameters. φ_0 represents a general amplitude, *A* is the peak amplitude, σ determines the (logarithmic) tuning width, s_p represents the preferred speed.

An *F*-test for nested models was used to compare the preferred speed and tuning width among the speed tunings of 0.75, 1.5, 3, and 6 cyc/deg local Gabor spatial frequencies for each observer. In particular, we compare the full model where the speed tunings of four local Gabor spatial frequencies have different preferred speeds and tuning widths with the reduced model where the speed tunings of four local Gabor spatial frequencies have identical preferred speeds and tuning widths. For two nested models with k_{full} and $k_{reduced}$ parameters, the *F* statistic is defined as:

$$F(df_1, df_2) = \frac{\left(r_{full}^2 - r_{reduced}^2\right)/df_1}{\left(1 - r_{full}^2\right)/df_2}$$
(2)



FIGURE 2. The stereo sensitivity as a function of the motion speed at 3 cyc/deg local Gabor spatial frequency. Results of different observers are plotted in different panels. In each panel, individual's stereo sensitivity is plotted as a function of speed. *Error bars:* 95% confidence interval for individual's stereo sensitivity of each motion speed.

in which $df_1 = k_{full} - k_{reduced}$, and $df_2 = N - k_{full}$, for *N* data points. If these two models generate significantly different fits (i.e., P < 0.05), we choose the full model; otherwise, we take the prediction of the reduced model.

RESULTS

Experiment 1. The Effect of Motion Speed on Stereopsis for our Conjoint Motion/Stereo Task

To address whether speeds influence the stereo performance on our disparity increment task, we measured the stereo sensitivity of all subjects at six speeds at a local Gabor spatial frequency of 3 cyc/deg: $0.17^{\circ}/s$, $0.33^{\circ}/s$, $0.67^{\circ}/s$, $1.33^{\circ}/s$, $2.67^{\circ}/s$ and $5.33^{\circ}/s$. Figure 2 shows a plot of the stereo sensitivity of each subject as a function of the motion speed. We found that the stereo sensitivity is speed-tuned, as demonstrated by the bell-shape of the speed tuning curves, for which the peak occurs at around 0.33° /s to 1.33° /s. A one-way repeated-measures ANOVA showed that the stereo sensitivities of the observers were significantly different across different speeds: F(5, 40) = 7.901, $P = 3.0 \times 10^{-5}$, partial eta squared = 0.497. Note that this tuning for speed occurs at relatively slow speeds.

Because we found a bell-shape tuning for stereo sensitivity at different speeds, we performed a fit of the speed tuning function separately from all subjects' individual and averaged stereo sensitivities, using a log Gaussian model which has been used in a previous study to fit the speed tuning curves in cortical area MT of macaque visual cortex.^{17,18} We successfully fitted the individual data (the median R^2 value is 0.90) and the averaged data (see Fig. 3, $R^2 = 0.87$) using the model.



FIGURE 3. The average speed tuning function at 3 cyc/deg local Gabor spatial frequency. The average of stereo sensitivity is plotted as a function of speed. *Error bars*: standard errors across the nine subjects. The model that has been used in a previous study to fit the speed tuning curves in cortical area MT of macaque visual cortex¹⁸ fits our data well ($R^2 = 0.87$).

Experiment 2. The Effect of Stimulus Spatial Frequency on Speed Tuning for Stereopsis for our Conjoint Motion/Stereo Task

To address whether the speed tuning was dependent on the stimulus spatial frequency, we measured the stereo sensitivity at another three local Gabor spatial frequencies (0.75, 1.5, and 6 cyc/deg). We compared the speed tuning functions among four local Gabor spatial frequencies and found that they exhibited a similar bell-shape. We also successfully fitted the data measured at 0.75, 1.5, 3, and 6 cyc/deg of eight subjects using the log Gaussian model (see Fig. 4A, $R^2 = 0.86$, 0.91, 0.84, 0.87 separately). A twoway repeated-measure ANOVA revealed a significant difference in stereo sensitivity among different speeds (F(2.740, 19.181 = 15.459, $P = 3.3 \times 10^{-5}$, partial eta squared = 0.688) and different local Gabor spatial frequencies (F(3, 21) = 5.957, P = 0.004, partial eta squared = 0.460). No significant interaction was found between speed and local Gabor spatial frequency, F(6.258, 43.808) = 1.727, P =0.135, partial eta squared = 0.198. Post-hoc pairwise t-test (with Bonferroni correction) showed significant difference between 0.75 cyc/deg and 1.5 cyc/deg, 0.75 cyc/deg and 3 cyc/deg spatial frequencies of Gabors (P = 0.011, 0.001). The results suggested that spatial frequency of Gabors also could affect absolute stereoscopic performance.

We also conducted a two-way repeated-measure ANOVA on reaction time (see Fig. 4B). The results showed no difference in reaction time among different speeds (F(5, 35) = 2.134, P = 0.084, partial eta squared = 0.234), but a significant difference among different local Gabor spatial frequencies (F(3, 21) = 3.526, P = 0.033, partial eta squared = 0.335). No significant interaction was found between speed and local Gabor spatial frequency, F(15, 105) = 1.197, P = 0.286, partial eta squared = 0.146. The results indicated that such speed tuning function could not be accounted for by reaction times.

To assess whether stimulus spatial frequency influences the shape of the speed tuning function, we derived the positions of the peaks (i.e., preferred speeds) and bandwidths from each subject's tuning function for four different spatial frequencies (Fig. 5). A one-way repeated-measure ANOVA showed that there's no significant difference among four spatial frequencies for either preferred speed (F(1.279,



FIGURE 4. The effect of stimulus spatial frequency on stereoscopic performance with laterally moving stimuli. The stereo sensitivity (**A**) and reaction time (**B**) as a function of the motion speed at four different local Gabor spatial frequencies (6 cyc/deg in *green triangle* and *green solid line*, 3 cyc/deg in *red circle* and *red solid line*, 1.5 cyc/deg in *blue square* and *blue solid line*, 0.75 cyc/deg in *yellow rhombus* and *yellow solid line*). *Error bars*: standard errors across the eight subjects.



FIGURE 5. The preferred speed (**A**) and bandwidth (**B**) as a function of spatial frequency. Each color of dot represents results of one observer. *Rectangle* represents the average of stereo sensitivities at different spatial frequencies. *Error bars*: standard errors across the eight subjects.

8.956) = 1.696, *P* = 0.232, partial eta squared = 0.195) or bandwidth (F(3, 21) = 0.668, *P* = 0.581, partial eta squared = 0.087). Linear mixed-effects models also showed that the preferred speed and bandwidth were not significantly associated with spatial frequency (*P* = 0.091 for preferred speed; *P* = 0.283 for bandwidth).

We further conducted an F-test for nested models to statistically compare the difference in preferred speeds and tuning widths among the speed tunings of different local Gabor spatial frequencies. These fits are drawn in Figure 6. According to the F-test for nested models, the full model (with different preferred speeds and tuning widths among speed tunings of four local Gabor spatial frequencies) failed to generate better fits (all P > 0.05) than the reduced model (with the same preferred speeds and tuning widths among speed tunings of four local Gabor spatial frequencies), and the latter successfully accounted for 81.3% to 91.0% of the variance for all observers except S6, and the average observer. These results indicated that the preferred speeds and tuning widths among four speed tunings of different local Gabor spatial frequencies were not significantly different in these observers. For S6, the F-test for nested models showed that the full model generated better fitting (F =5.407, P = 0.016) than the reduced model and the former successfully accounted for 90.4% of the variance. Applying full model fitting for S6 generated the same conclusions with the present version. These results indicated that different spatial frequencies of Gabors did not make a significant change to the shape of the speed tuning function.

Experiments 3 & 4. Static versus Dynamic Stereopsis for our Conjoint Motion/Stereo Task

One interesting question was whether we have different stereoacuities between moving and static stereo stimuli. To

answer this, we compared the static stereo sensitivity with the dynamic stereo sensitivity measured at 0.67°/s. This is because the preferred speeds of individuals and the average results were at around 0.67°/s (Fig. 6, the average preferred speed of eight subjects and four local Gabor spatial frequencies was at $0.67^{\circ}/s \pm 0.31^{\circ}/s$; mean \pm SD). In Figure 7A, dynamic stereo sensitivities measured with laterally moving stimuli are plotted as a function of static stereo sensitivity at four different local Gabor spatial frequencies. It is obvious that most of the data points reside above the identity line, indicating that significant improvement of stereo sensitivity with laterally moving stimuli exist for all local Gabor spatial frequencies (two-way repeated measure ANOVA: Speed: F(1,7) = 16.980, P = 0.004, partial eta squared = 0.708; local Gabor spatial frequency: F(1.219, 8.532) =3.031, P = 0.114, partial eta squared = 0.302; Speed × Local Gabor spatial frequency: F(3,21) = 0.426, P =0.737, partial eta squared = 0.057). Moreover, a twotailed Pearson correlation test revealed a strong correlation between dynamic and static stereo sensitivities (r = 0.761, $P = 4.36 \times 10^{-7}$), suggesting that there might be partial common mechanism in stereopsis for static and dynamic stimuli.

It should be noted that the tasks that subjects were asked to do were different between dynamic and static conditions (e.g., moving direction discrimination vs. orientation discrimination). This would not affect our analysis of speedtuning curves as identical task was used in comparing stimuli of different speeds. However, this might affect our observation that there is a difference in stereopsis between moving and static stimuli. To address this, we conducted an additional test to measure stereoacuity using moving stimulus of random directions around the clock (0°–360°) having two different orientations (vertical and horizontal as Experiment 3) in the two planes. This would enable us to measure stereopsis for moving stimuli using the same orientation



FIGURE 6. The stereo sensitivity as a function of the motion speed at four local Gabor spatial frequencies. Results from eight subjects and their average are shown in different panels of the figure (6 cyc/deg in green triangle and green solid line, 3 cyc/deg in red circle and red solid line, 1.5 cyc/deg in blue square and blue solid line, 0.75 cyc/deg in yellow rhombus and yellow solid line). Error bars: for individual represent 95% confidence interval; error bars: for average represent standard errors across the eight subjects.

discrimination task as that previously used for the measure-

ment of stationary stimuli. Six subjects completed the experiment. In Figure 7B, the stereo sensitivity for the static Gabor elements is plotted against that for the randomly moving stimuli (speed = $0.67^{\circ}/s$). A two-tailed Pearson correlation test still revealed a strong correlation between dynamic and static stereo sensitivities (r = 0.733, $P = 4.70 \times 10^{-5}$). However, no significant difference was found between them for all local Gabor spatial frequencies (two-way repeated measure ANOVA: Speed: F(1,5) = 0.004, P = 0.955, partial eta squared = 0.001; local Gabor spatial frequency: F(3,15) = 9.033, P = 0.001, partial eta squared = 0.644; Speed \times Local Gabor spatial frequency: F(3,15) = 1.912, P = 0.171, partial eta squared = 0.277), which indicated that the difference of stereopsis we found in Experiment 3 was not evident when we matched the task between the static and moving stimuli.

When we used the orientation task, we didn't find any difference in stereo sensitivity between zero speed and a speed of 0.67°/s. Does this imply that there is no speed tuning of stereo judgements for the orientation task? To answer this, we measured stereoacuity using moving stimulus of random directions (0°-360°) at 3 cyc/deg at another five speeds. In Figure 8, we plotted the average stereo sensitivity measured with orientation task (orange filled circle) as a function of speed. We still found a clear speed tuning of stereo sensitivity for the orientation task (one-way repeated measure ANOVA: Speed: F(5, 25) = 3.579, P = 0.014, partial eta squared = 0.417).



FIGURE 7. Comparation between static and dynamic stereo sensitivities. Dynamic stereo sensitivity measured with laterally moving stimuli (**A**) and randomly moving stimuli (**B**) at $0.67^{\circ}/s$ as a function of static stereo sensitivity at four different local Gabor spatial frequencies. The *dash line* is the identity line. Each symbol represents results of one observer (6 cyc/deg in *green triangle*, 3 cyc/deg in *red circle*, 1.5 cyc/deg in *bule square*, 0.75 cyc/deg in *yellow rhombus*). The *gray* and *orange areas* indicate where observers having higher dynamic (speed = $0.67^{\circ}/s$) stereo sensitivity than static stereo sensitivity. *Crosshair* represents the average of stereo sensitivities; different colors correspond to different local Gabor spatial frequencies. *Error bars*: standard errors across the eight or six subjects. ** indicates P < 0.01 when comparing the static and dynamic stereo sensitivities.



FIGURE 8. The average speed tuning function for orientation task. The average of stereo sensitivity for orientation task (*orange line* and *filled circle*) is plotted as a function of speed. *Error bars*: standard errors across the six subjects.

Experiment 5. The Effect of Presentation Duration on Speed Tuning for Stereopsis for our Conjoint Motion/Stereo Task

As we mentioned in the design section, we measured all the above experiments at 1000 ms without eye tracking. Even though we provided a fixation point continually and instructed subjects to fix on it throughout the trial, only used Gabors with limited lifetime (each Gabor had a 5% probability of limited lifetime in each presentation frame), and set an empty space (diameter = 1.11° in visual angle) around the fixation point to facilitate good fixation, there could still be a concern that whether the speed tuning we found above was due to the potential effects of uncontrolled eye movements by the vergence or tracking movements. To address this, we measured the stereo sensitivity at a much shorter presentation duration of 200 ms in Experiment 5. If the uncontrolled eye movement is the exact cause of the speed tuning we observed, then at a presentation duration of 200 ms, the speed tuning would not exist.

In Figure 9, we plotted the average stereo sensitivity measured at 200 ms (black filled circle) and 1000 ms (red open circle) presentation duration separately as a function of speed. The data of 1000 ms presentation duration for six subjects are the same as Experiment 1. We found the stereo sensitivity is speed-tuned when presentation duration was 200 ms (two-way repeated measure ANOVA: Speed: F(5, 25) = 4.836, P = 0.003, partial eta squared = 0.492; Presentation duration: F(1, 5) = 9.042, P = 0.030, partial eta squared = 0.644; Speed × Presentation duration: F(5, 25) = 1.861, P = 0.137, partial eta squared = 0.271). An F-test for nested models revealed that the reduced model (assuming the tuning curves of 1000 ms and 200 ms presentation durations have same preferred speeds and tuning widths) could generate as good fit as the full model (assuming the tuning curves of 1000 ms and 200 ms presentation durations have different preferred speeds and tuning widths): F = 1.518, P =0.323. The reduced model successfully accounted for 92.2% for the average result (Fig. 9). These results indicated that the speed tuning function that we reported above could not be accounted for by the potential effects of eye movement.



FIGURE 9. The effect of presentation duration on stereoscopic performance with laterally moving stimuli. The average of stereo sensitivity measured at 200 ms (*black dashed line* and *filled circle*) and 1000 ms (*red line* and *open circle*) presentation duration are separately plotted as a function of speed. *Error bars*: standard errors across the six subjects.

DISCUSSION

Using a task that involved the discrimination of both motion and stereo involving two depth planes of randomly distributed, laterally moving, limited lifetime Gabors, we show that stereo sensitivity is tuned for stimulus movement, that this occurs at low speeds and that it involves velocity not temporal frequency. Furthermore, we show that although there was a difference in stereo sensitivity between laterally moving stimuli and static stimuli when measured in separate tasks (orientation vs. motion direction), this difference did not exist between static and moving stimuli that were measured using the same task.

Because our task, requiring as it did the joint discrimination of motion direction and depth and being global in nature, is very different from the tasks previously used to explore the dynamics of stereopsis, it is not surprising that our results are rather different from a number of earlier observations of stereo acuities for moving targets.^{1,4,9,19} Some previous studies^{1,19} have argued that stereo acuities for laterally moving line targets appeared no difference from the static stereopsis if the lateral motion is less than 2°/s motion speed, and increase monotonically at higher velocities. Others⁴ have argued that there is no difference between the static stereo acuity and stereo acuity at 2°/s motion speed, using random dot stimulus. Our results suggest that there is a bell-shaped dependence with a peak at around 0.67°/s (Fig. 6). Our stimuli (as well as our task) differed from those of previous studies in being locally spatial frequency narrowband and globally distributed in space.

In this study, we measured stereoacuity with laterally moving stimuli at six preset speeds (ranged from $0.17^{\circ}/s$ to $5.33^{\circ}/s$). This range was selected according to previous physiology and psychophysics studies. Physiology studies show that most MT neurons were tuned to slow speeds, in the range of 0°/s to 10°/s.^{17,20} Snowden and Kavanagh²¹

reported that the mean lower threshold of motion for the younger observers was $0.087^{\circ}/s$, which was much slower as the minimum speed we chose for our experiment. What's more, if our slowest stimulus was below the lower threshold of motion, the task (of recognizing which motion direction was in front and which behind) would be rendered impossible since motion would not be perceived. This verifies that the stimulus motion that we measured (from $0.17^{\circ}/s$ to $5.33^{\circ}/s$) was well above the lower threshold for motion for our subjects.

Another surprising finding compared with the purely temporal frequency dependence of local⁹ and global⁵ stereopsis reported in previous studies was the evidence for velocity tuning in the current study. It is likely that the use of random Gabor stimuli may necessitate a more global process that would occur at a later site in the pathway where the outputs of earlier spatiotemporally separable filter have been combined to extract motion velocity (e.g., Priebe, Lisberger and Movshon⁸). Consistent with this, the log Gaussian form of the tuning response we measure psychophysically is similar to that found for speed tuning dependence of MT neurons for random-dot stimuli,¹⁷ which in turn may suggest the involvement of area MT in process of stereopsis for spatially distributed stimuli of the sort used here. Studies for the speed tuning of macaque MT neurons also suggest that different units of MT neurons prefer different speeds, containing both slow and high speed within the range that we investigated.^{17,20} Because the tuning for speed we found occurs at relatively slow speeds with a preferred speed at around 0.67°/s, MT neurons tuned to very slow speeds may contribute to the stereo judgements in our study.

What's more, we found an improvement of stereo sensitivity with laterally moving stimuli, whereas such improvement doesn't exist when we matched the task between the static and moving stimuli. In the motion direction task, subjects were making motion direction judgements on the basis of depth not depth judgement for stimuli in motion. The orientation task involves discriminating orientation on the basis of depth; its temporal properties, although of interest, do not directly bear on the results for stimuli having opposite motion directions. Motion and orientation can be processed along different cortical streams.²²

Another concern is the effect of eye movement on the speed tuning of the stereo sensitivity. We didn't measure objects' eye tracking data during the experiments, which is a limitation of our study, but we think it's not likely to be a problem. The relevant eye movements here are vergence eye movements, and our control data for a short presentation duration show that these vergence movements are not an issue here. Tracking eye movements are not likely to be a problem for four reasons. First, the stimuli are global and composed of limited lifetime elements such that the motion is not carried by individual elements that can be tracked but across the population as a whole. Second, the motion is always directionally balanced, being in opposite directions, to provide limited stimulation for tracking in a particular direction. Third, the fact that we show bandpass tuning for velocity is also at odds with tracking, which would be expected to exhibit lowpass tuning. Last, using the orientation task with random directions of moving elements (i.e., Experiment 4.2), we still find evidence for speed tuning. Such a task involves depth, motion and orientation processes and might reflect different mechanisms from the motion-stereo constraint. Nevertheless, such results suggest that eye movements don't play an important part in our finding of stereo-speed tuning. In summary, our results suggest that for the motion/stereo task we used, involving spatially distributed, laterally moving micropatterns, stereo sensitivity is tuned for lateral motion velocity.

Acknowledgments

Supported by the National Natural Science Foundation of China Grant NSFC 31970975 the Natural Science Foundation for Distinguished Young Scholars of Zhejiang Province, China (LR22H120001), and the Project of State Key Laboratory of Ophthalmology, Optometry and Vision Science, Wenzhou Medical University (No. J02-20210203) to J.Z., The Zhejiang Medical Health Science and Technology Project 2020KY656 to Z.H., the NSERC grant 228103, and an ERA-NET Neuron grant JTC2015 to R.F.H.

Disclosure: Y. Chen, None; Z. Yao, None; Z. He, None; Z. Cheng, None; P.-C. Huang, None; S.H. Min, None; F. Lu, None; R.F. Hess, None; J. Zhou, None

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