Detection of relative and uniform motion

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We measured the lowest velocity (velocity threshold) for discriminating motion direction in relative and uniform motion stimuli, varying the contrast and the spatial frequency of the stimulus gratings. The results showed significant differences in the effects of contrast and spatial frequency on the threshold, as well as on the absolute threshold level between the two motion conditions, except when the contrast was 1% or lower. Little effect of spatial frequency was found for uniform motion, whereas a bandpass property with a peak at approximately 5 cycles per degree was found for relative motion. It was also found that contrast had little effect on uniform motion, whereas the threshold decreased with increases in contrast up to 85% for relative motion. These differences cannot be attributed to possible differences in eye movements between the relative and the uniform motion conditions, because the spatial-frequency characteristics differed in the two conditions even when the presentation duration was short enough to prevent eye movements. The differences also cannot be attributed to detecting positional changes, because the velocity threshold was not determined by the total distance of the stimulus movements. These results suggest that there are two different motion pathways: one that specializes in relative motion and one that specializes in uniform or global motion. A simulation showed that the difference in the response functions of the two possible pathways accounts for the differences in the spatial-frequency and contrast dependency of the velocity threshold. © 2002 Optical Society of America

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1. INTRODUCTION

The perception of motion depends not only on the velocity of an image in a given retinal area but also on the velocity of the surrounding images. Two types of interaction between signals from adjacent areas are possible. First, presenting either a stationary or a moving stimulus in the opposite direction in the surrounding area strengthens the motion impression of a moving target[1–8] as well as the motion aftereffect.[9–21] To accommodate this fact, a relative motion detector is often modeled as being a motion-sensitive unit with a center-surround antagonistic receptive field.[4,7,22,23] A typical model of a relative motion detector has a preferred direction at the center of the receptive field with both/either inhibitory signals from the direction and/or excitatory signals in the opposite direction in the surrounding area, i.e., a center-surround antagonistic receptive field.[22,23] Second, coherent motion signals in a large field produce the perception of global motion. It is widely accepted that the visual system has a motion detector that specializes in global motion.[24–27] Morrone *et al.*, for example, have reported a spatial integration effect of global motion signals within a large field (10-deg diameter).[25] The signal-to-noise sensitivity for discriminating the direction of radial, circular, and translational motion increases with the total area of the stimulus field. This suggests that the visual system has global motion detectors to integrate motion signals with gradual velocity changes across a large visual field. Image motion is perhaps detected locally, giving rise to a large array of motion vectors at different image locations. Then these local motion signals are integrated across space into regions that share a common velocity, giving a percept of global coherent motion.[26] Such a global motion process can be parallel to the relative motion detector.

The presumption of separate pathways for relative and uniform motion signals is supported by psychophysical and physiological studies.[28–31] Shioiri *et al*. have reported a selective desensitization effect for relative and uniform motion stimuli.[28] The results show that the threshold for discriminating the direction of relative motion is higher after exposure to relative motion than after exposure to uniform motion, whereas little difference is found in the threshold for discriminating the direction of uniform motion. Born and Tootell have suggested the existence of two different pathways in the visual system that specialize in processing different types of motion stimulation based on the results of single-cell recordings.[29] Their results show that some monkey MT cells are sensitive to relative motion (antagonistic receptive field surround) while other cells are sensitive to global motion (receptive field surround that reinforces the center).

The purpose of the present study is to investigate possible differences between the sensitivities to relative and uniform motion, which possibly reflect the differences between the relative and global motion mechanisms. We compare the spatial-frequency and luminance contrast dependency of the sensitivity to relative and uniform motion signals in experiment 1, because several studies have suggested that these features might be related to the differences between the analyses of relative and uniform motion signals. Although spatial-frequency tuning for motion perception shows low-pass characteristics,[32] bandpass spatial-frequency tunings have also been reported in several experiments.[33–41] For example, induced motion, which is perceived motion in the stationary field induced by motion in the surrounding area, has a bandpass spatial-frequency tuning.[39] The well-known contrast saturation for motion perception[42–44] is not seen for motion induction either.[40] Since motion induction can be regarded as a motion enhancement in the direction opposite to the surrounding motion, we might expect differences in the spatial-frequency and contrast characteristics between relative and uniform motion signals.

Experiment 2 investigates the effects of eye movements, positional cues, and the border between stimulus and background. These factors might alter the performance of the analyses of relative and uniform motion even when there is no difference in the underlying mechanisms between the two types of motion analyses. The effects of stimulus presentation duration and stimulus size are investigated for this purpose. The details are described in Section 3.

2. EXPERIMENT 1

A. Method

1. Apparatus

The apparatus was a Macintosh IIcx with a black-and-white 21-in. graphic display (Nanao Flexscan 6500) with a 640 × 480-pixel resolution (67-Hz noninterlace). The distance between the observer and the display was 200 cm (1 arc min/pixel). Luminance levels of approximately 12 bits were achieved by using the technique developed by Pelli and Zhang.[45] This higher luminance resolution allowed us to use velocities that are slower than the limitation of the pixel resolution by means of a subpixel motion technique. The subpixel motion technique makes the assumption that the visual system blurs the individual pixels sufficiently and that displacements smaller than the pixel size may be represented by adjusting the luminance values appropriately. When the system sets the stimulus at a very slow speed, only a small number of pixels will change the luminance. At least 30% of the pixels in the stimulus field changed the luminance at each refresh of the video frame (1/67 s), even in the worst case in our experiment.

2. Stimulus

The stimulus in the relative and uniform motion conditions was the same vertical stacks of two horizontal bands filled with vertical sinusoidal gratings that moved either rightward or leftward. The size of each band was either 5.3 deg wide × 1.0 deg high with a 0.3-deg gap between them or 5.3 deg wide × 0.06 deg high with a 0.03-deg gap. In the relative motion condition, two gratings moved in opposite directions [Fig. 1(a)]. In the uniform motion condition, the two gratings moved in the same direction, so that there was no relative motion component between them [Fig. 1(b)]. The spatial frequency of the gratings varied between 0.75 and 12 cycles per degree (c/deg). The mean luminance of the grating was 50.0 cd/m^2, and the contrast varied between 0.5% and 85%. Data were not measurable in some conditions with lower contrasts because the threshold was too high. The area outside the gratings was always dark (<0.5 cd/m^2), and the display frame was barely visible in a dark room. The stimulus field was uniform gray (50.0 cd/m^2) before and after the presentation of the drifting gratings. It should be noted that the stimulus in the uniform condition contained relative motion cues, which were the stationary borders between the moving gratings and the dark background. We chose this stimulus because our intent was to compare the mechanism that is sensitive to relative motion in adjacent areas and the mechanism that is sensitive to motion in a large field, which is not necessarily sensitive to the full field motion. Usually, a large sensitivity reduction is found in a uniform motion field of several degrees.[1,6,7,28] The effect of the border was investigated in experiment 2.

3. Procedure

The velocity of the stimulus was varied from trial to trial to obtain a threshold velocity by the method of constant stimuli. The spatial frequency and the contrast were fixed in each session. The gratings moved with a constant velocity throughout the 960 ms of presentation. The observer reported the direction of the grating movement with the two-alternative forced-choice method (the direction of the upper band was reported in the relative motion condition). Two observers who had corrected-to-normal vision participated.

B. Results: 1-deg Band

We defined the threshold as the velocity that gave 75% correct responses after a cumulative normal distribution function was fitted to the data points. We used Probit analysis for the fitting, scaling the output of the fitting function to vary between 50% and 100%. The number of trials to determine each threshold value was 375 (15 velocities × 25 trials). Figure 2 compares the velocity thresholds in the relative and uniform motion condi-

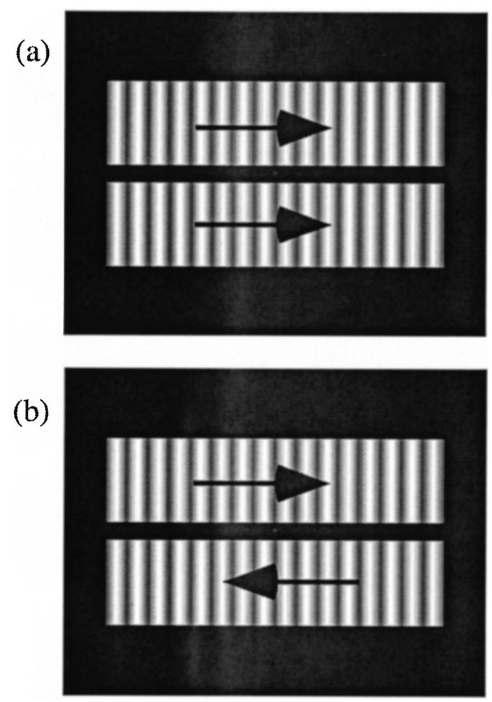

Fig. 1. Schematic diagram of the stimuli. The gratings of the two bands moved (a) in the same direction in the uniform motion condition and (b) in opposite directions in the relative motion condition. Arrows indicate the motion direction of the gratings. The actual direction varied from trial to trial.

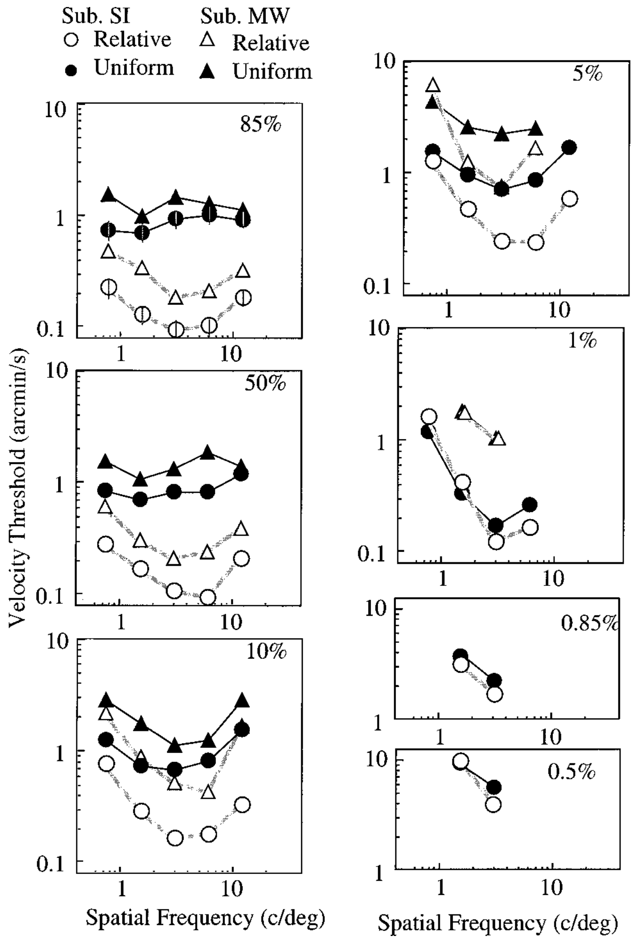

Fig. 2. Velocity thresholds as a function of spatial frequency with the 1-deg-band stimulus. Each plot shows the result for each contrast of the stimulus grating. The open symbols represent threshold data in the relative motion condition, and the filled symbols represent those in the uniform motion condition. Error bars, attached to data in some condition as examples, indicate the 95% confidence interval obtained from the variance estimated by Probit analysis for the reciprocal value of the slope of the cumulated normal distribution function fitted to the data.

tions as a function of spatial frequency. The different plots show the results with different contrasts.

It is evident that the velocity threshold differed between the two motion conditions in two aspects, except when the stimulus contrast was 1% or lower. First, the threshold was always lower in the relative motion condition. Second, the shape of the velocity threshold function was different in the two conditions. In the relative motion condition, the velocity threshold was lowest at approximately 5 c/deg with a gradual increase on both sides. In the uniform motion condition, the velocity threshold was approximately constant with a value of roughly 1 arc min/s when the contrast was high (50% and 85%). When the contrast was lower than 1%, the spatial-frequency characteristics resemble those in the relative motion condition.

The effect of contrast on velocity threshold was also very different between the two motion conditions. Figure 3 shows velocity threshold as a function of stimulus contrast for each spatial frequency. In the relative motion condition, the threshold decreased monotonically with the increase in contrast over the range used. In the uniform motion condition, the threshold also decreased, but only up to 5%, beyond which it was approximately constant. Despite these significant differences at higher contrasts, the threshold was almost identical in the two conditions when the contrast was 1% or lower.

C. Results: 0.06-deg Band

Figures 4 and 5 compare the velocity threshold functions against spatial-frequency and contrast in the two motion conditions, respectively. The different plots show the results for the different contrasts in Fig. 4 or the different spatial frequencies in Fig. 5. The results for the 0.06-deg band are similar to those for the 1-deg band (Figs. 2 and 3) in terms of the differences between the two motion conditions. When the contrast was high (85%), the threshold decreased with spatial frequencies within the spatial-frequency range in the relative motion condition, whereas the threshold was approximately constant across the spatial frequencies in the uniform motion condition. When the contrast was low (10% and 5%), the spatial-frequency characteristics resemble each other in the two conditions. The threshold decreased monotonically with contrast in the relative motion condition, whereas it was approximately constant for contrasts higher than roughly 10% in the uniform motion condition.

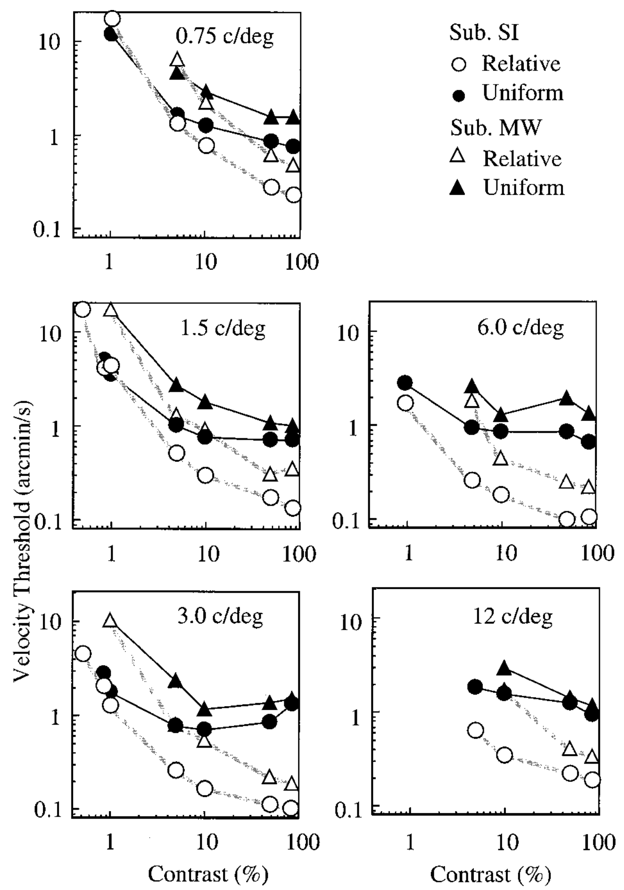

Fig. 3. Velocity thresholds as a function of contrast with the 1-deg-band stimulus. Each plot shows the result for each spatial frequency of the stimulus grating. The open symbols represent threshold data in the relative motion condition, and the filled symbols represent those in the uniform motion condition.

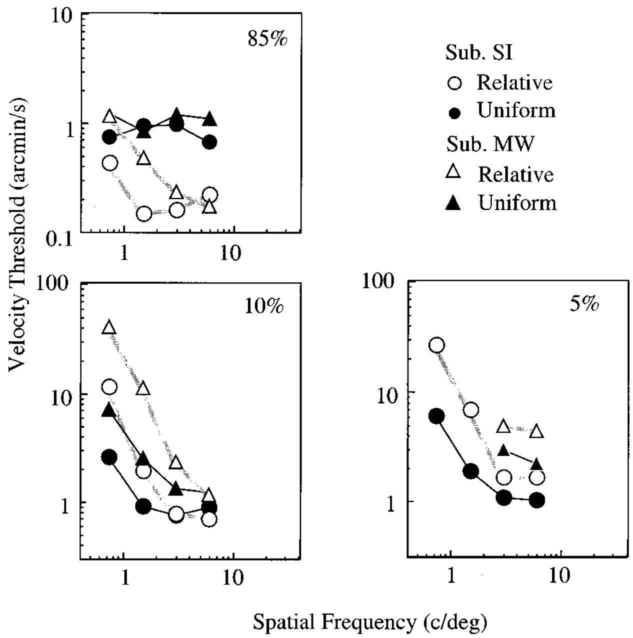

Fig. 4. Velocity thresholds as a function of spatial frequency with the 0.06-deg-band stimulus. Each plot shows the result for each contrast of the stimulus grating. The open symbols represent thresholds in the relative motion condition, and the filled symbols represent those in the uniform motion condition.

An important difference from the 1-deg-band condition was that the threshold for the relative motion was higher than that for the uniform motion in the low-contrast conditions. In the 1-deg-band condition, the threshold for the relative motion was never higher than that for the uniform motion throughout the contrast range used. A comparison of the data between the two band sizes shows that narrowing the bands elevated the threshold largely in the relative motion condition and only slightly in the uniform motion condition. This suggests that the mechanism that is responsible for relative motion is much more sensitive to band size than that which is responsible for uniform motion.

D. Discussion

The differences in spatial-frequency and contrast characteristics between the motion conditions suggest that different motion detectors determine the velocity threshold for relative and uniform motion. Assuming two different mechanisms or pathways for relative and uniform motion is the simplest interpretation for the large differences in the two motion conditions. The strongest support for this interpretation comes from the change in relative sensitivity between the motion conditions with contrast for the 0.06-deg band. The threshold in the relative motion condition was lower at higher contrasts but higher at lower contrasts than that in the uniform motion condition. It is difficult to explain the reversal of the relative sensitivity between the motion conditions dependent only on the stimulus contrast without assuming separate mechanisms. An increase in the stimulus contrast should affect the threshold similarly in the two conditions if an identical motion detector determines threshold in the relative and uniform motion conditions. The threshold may become the same at high contrasts in the two conditions because of the response saturation, but it should not reverse.

Three factors should be considered before attributing the differences in the velocity threshold between the two motion conditions to differences in the underlying mechanisms. The first is the effect of eye movements. Tracking eye movements reduces the retinal velocity of the uniform motion, whereas there is no reduction in the retinal relative velocity. When the eye tracks a moving stimulus, it might cause differences in the thresholds between the two conditions. The second is the effect of positional changes. The relative phase between the top and bottom gratings varies with time in the relative motion condition, and the change from the beginning to the end of the stimulus presentation should provide a cue for the direction of stimulus motion. Thresholds in the relative motion condition can be determined by this cue if the sensitivity to the change is higher than the sensitivity to velocity. Since the spatial-frequency and contrast characteristics differ between the detection of patterns and motions, the results of experiment 1 may simply indicate another aspect of the differences between the pattern and motion mechanisms. The third is the effect of the border between the gratings and the background. Although our uniform motion stimulus does not have relative motion between the grating bands, the gratings move relative to the stationary borders. If the relative velocity to the border influences the threshold measurements, the results for the uniform motion may be attributed to a motion detector that is sensitive to relative motion against the sta-

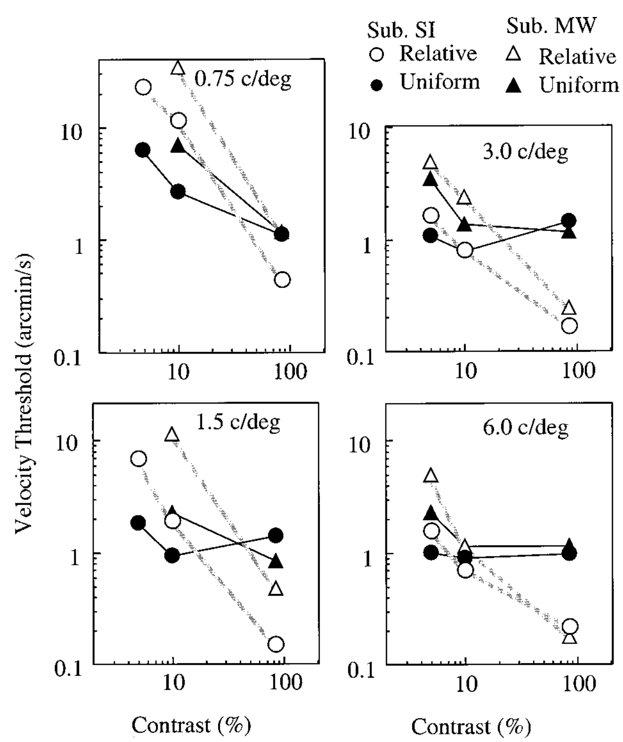

Fig. 5. Velocity thresholds as a function of contrast with the 0.06-deg-band stimulus. Each plot shows the result for each spatial frequency of the stimulus grating. The open symbols represent the thresholds in the relative motion condition, and the filled symbols represent those in the uniform motion condition.

tionary border. We conducted experiment 2 to examine the effects of these factors on our threshold measurements.

3. EXPERIMENT 2

In experiment 2, we investigated the effects of the stimulus duration and size on the threshold measurements. The first purpose of the experiment was to examine whether tracking eye movements were the primary cause of the threshold differences between the two motion conditions. Although the velocities of interest were at the threshold level in our measurements, the eyes may still have tracked the moving gratings.[46] We measured the spatial-frequency characteristics with short presentations (133 ms), as well as with long presentations (1067 ms), to investigate the effect of eye movements. The duration of 133 ms was short enough to prevent tracking eye movements.[47] If eye movements were the cause of the different results in the relative and uniform motion conditions, the differences obtained in the long-presentation condition should have disappeared in the short-presentation condition.

The second purpose of the experiment was to examine whether the different results between the two motion conditions could be attributed to the effect of sensing positional changes or the change in the relative phase of the gratings in the relative motion condition. Since the amount of positional change is expressed by the total distance of the stimulus motion, the effect can be investigated by varying the presentation duration. The velocity threshold should decrease with an increase in the duration if the observer responds to the direction of motion based on the total distance of the stimulus motion. This is because the speed should be slower for a longer duration in order to maintain a constant total distance. If, on the other hand, the motion signal determines the threshold, the velocity threshold should be constant. Note that we must consider the results at durations longer than the temporal summation limit, to examine whether velocity or displacement determines the threshold. The temporal summation limit is the time within which the mechanism that is responsible for the threshold in focus integrates the corresponding signals.[48] For a typical threshold measurement, the threshold achieves a constant level at a certain time of presentation duration, although the time may not always be obtained clearly.

The third purpose of the experiment was to examine the effect of the border between the gratings and the background. We varied the stimulus width to examine whether the visibility of the border, which decreased with eccentricity, was significant for the measurements. As an additional condition, the height of the stimulus was varied as a control. This was done to investigate the effect of the stimulus area without changing the visibility of the border. How the area influences our measurements is important, since the width change confounds the changes in the area and the visibility of the border. The stimulus area increases with the increase in the stimulus width, which may decrease the threshold, while the visibility of the border decreases with the increase in the stimulus width, which may increase the threshold.

A. Method

1. *Apparatus*

The apparatus was a 17-in. graphic display (Sony CPD-17GS) controlled by a video board (Cambridge Research Systems VSG2/3) viewed from a distance of 181 cm. The resolution of the monitor was 640×480 pixels, and the frame rate was 120 Hz. Each phosphor was driven by a 12-bit digital-to-analog converter, and the same subpixel motion technique was used to achieve slow speeds as that in experiment 1.

2. *Stimulus*

The stimuli were the same as those in experiment 1 with some exceptions. The mean luminance of the grating was 27.5 cd/m^2, and the contrast was either 10% or 85%. The spatial frequency of the gratings was varied in the first condition with a constant duration of 133 or 1067 ms. The stimulus presentation duration was varied in the second condition with a constant spatial frequency of 3 c/deg. The width or the height of the stimulus bands was varied with a fixed gap size of 0.3 deg in the third condition. The spatial frequency and the contrast were also fixed at 3 c/deg and 85%, respectively. The gratings moved with a constant velocity throughout the presentation. A temporal Gaussian envelope with a standard deviation of one quarter of the total duration was used to remove abrupt contrast changes.

3. *Procedure*

The task was to discriminate motion direction as in experiment 1, and the direction of the stimulus motion was varied from trial to trial. A conventional staircase technique (two up, one down) controlled the stimulus velocity. The threshold was defined as the velocity that gave 75% correct responses through Probit analysis applied to the data pooled over a total of 400 trials or more. Two new observers who had corrected-to-normal vision participated in all conditions.

B. Results and Discussion: Spatial-Frequency Characteristics

Figure 6 compares the spatial-frequency characteristics of the velocity threshold for short and long presentations. The characteristics of the long presentation were similar to those shown in experiment 1. The threshold was lowest at a middle spatial frequency in the relative motion condition. The dependency on spatial frequency was much smaller in the uniform motion condition, showing the largest difference at a middle spatial frequency. The differences in the spatial-frequency characteristics remained for the short presentation. For a clearer comparison, the threshold ratio between the relative and uniform motion conditions is plotted as a function of spatial frequency in Fig. 7. The gray curves indicate the average ratio over the four data points (two contrasts for the two observers). The average ratio shows the largest advantage in the relative motion condition at spatial frequencies of approximately 5 c/deg for both long and short presentations. Since eye movements should have little or no influence on the measurements in the short-presentation

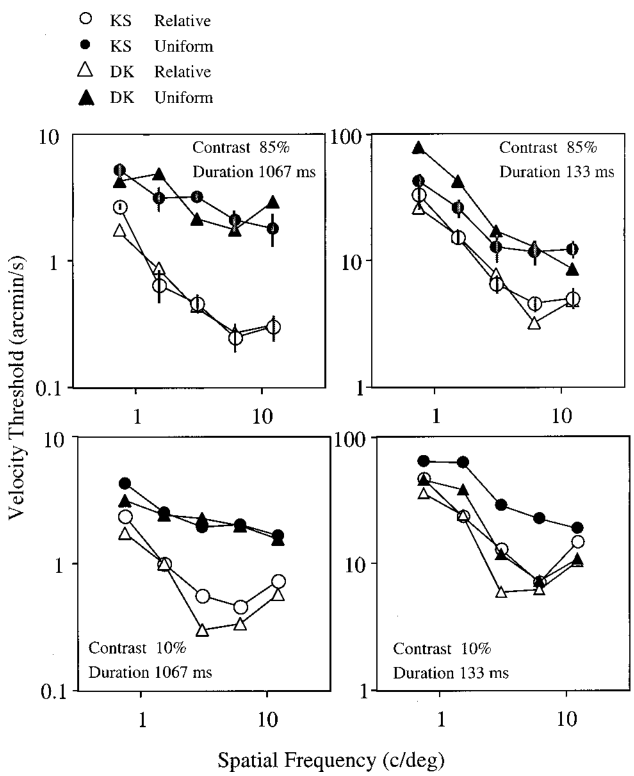

Fig. 6. Velocity thresholds as a function of spatial frequency for long (left) and short (right) presentations. The top plots show the results for observer KS, and the bottom plots do so for observer DK. The open symbols represent thresholds in the relative motion condition, and the filled symbols represent those in the uniform motion condition. Error bars, attached to data in some conditions as examples, indicate the 95% confidence interval obtained from the variance estimated by Probit analysis for the point of 75% correction.

conditions, the difference between the two motion conditions cannot be attributed to the different effects of eye movements.

A question that remained is the effect of eye movement in the long-presentation conditions. The results of the short exposure showed smaller differences in the two conditions than those of the long exposure. This may indicate that eye movements elevate the threshold velocity in the uniform motion condition by reducing the retinal velocity when the presentation duration is long. To explain the threshold difference of approximately 5 c/deg between the two motion conditions by the different influences of eye movements (Fig. 7), the gain of the tracking eye movement induced by moving stimuli should be largest at approximately 5 c/deg, producing the largest loss of retinal velocity in the uniform motion condition at the spatial frequency. However, the effect of spatial frequency on tracking eye movements in the literature is inconsistent with this notion. Hughes *et al.* showed that the gain of pursuit eye movements for moving gratings was larger for a 0.5-c/deg stimulus than for a 5-c/deg stimulus.[49] It is unlikely that eye movements cause differences between relative and uniform motion conditions. The reduction of the sensitivity difference between the two motion conditions in the short-presentation condition may be attributed to the decrease of the effective contrast by shortening the exposure duration. This presumption is supported by the fact that the effect of shortening of stimulus exposure is similar to that of the decrease of stimulus contrast.

C. Results and Discussion: Effect of Duration

Figure 8(a) shows velocity threshold as a function of stimulus duration in each motion condition. In the relative motion condition, the velocity threshold decreases up to approximately 1 s, beyond which it is roughly constant. The decrease in the threshold with presentation duration is typical in visual psychophysics and can be explained by the temporal summation of the motion signals. When the threshold is expressed in terms of the total distance of the stimulus movement, i.e., displacement threshold, the threshold increases at durations longer than 1 s [Fig. 8(b)]. If a positional cue were the determining factor, the threshold expressed in distance should be constant for the durations, under the assumption that the cue is based on the difference between the positional information at the beginning and the end of the presentation. These results clearly indicate that the observer's performance is based on velocity, not position, in our measurements.

Threshold for uniform motion decreases within the duration used, while the slope of the function becomes shallower for longer durations. When the threshold is expressed by total distance [Fig. 8(b)], the value increases with duration at 1 s or longer, consistent with previous studies.[50–53] The present results, together with others, suggest that velocity is the determining factor of the threshold.

D. Results and Discussion: Stimulus Size

Figure 9(a) shows velocity thresholds as a function of stimulus width. In the uniform motion condition, the threshold increases slightly with an increase in stimulus width up to approximately 3 deg. However, stimulus width has little influence on threshold when it is 3 deg or larger, up to 10 deg. This suggests that the location of the border between the gratings and the background does not play an important role in our measurements with 5.3

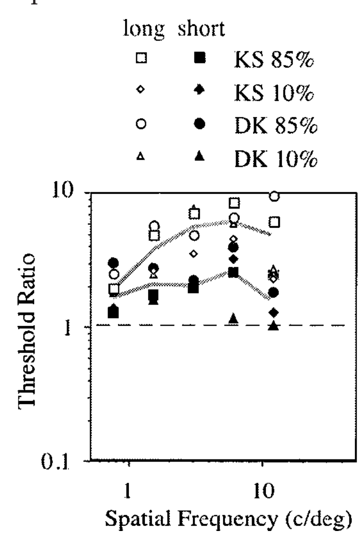

Fig. 7. Ratio of velocity threshold in the uniform motion condition to that in the relative motion condition as a function of spatial frequency. The open symbols represent the results for the long presentation, and the filled symbols represent those in the short presentation.

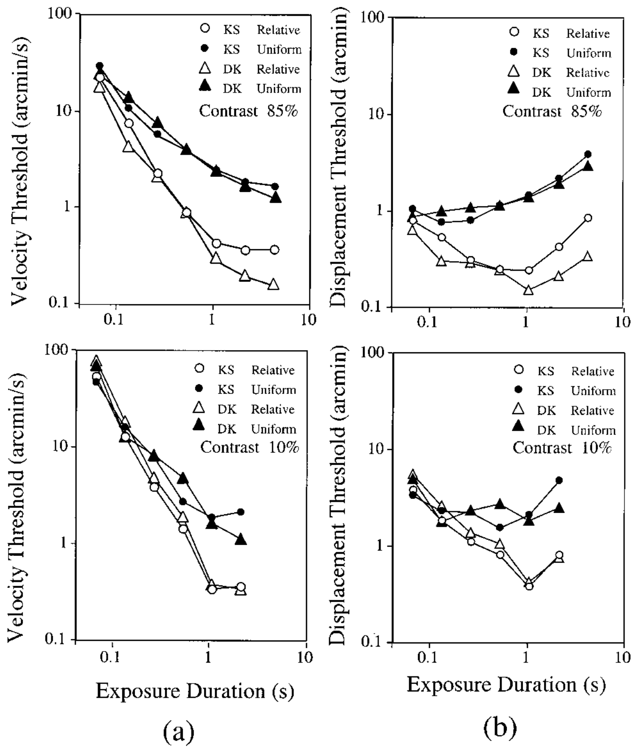

Fig. 8. (a) Velocity thresholds as a function of presentation duration. The top plot shows the results with 85% contrast stimulus, and the bottom plot shows those with 10% contrast stimulus. The open symbols represent the thresholds in the relative motion condition, and the filled symbols represent those in the uniform motion condition. The circles represent the results of KS, and the triangles represent those of DK. (b) Displacement thresholds as a function of presentation duration. The threshold in (a) is replotted as the total distance of movement during the presentation. Symbols are the same as those in (a).

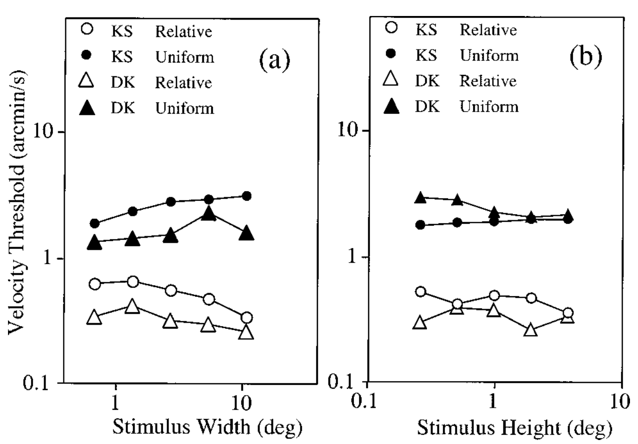

Fig. 9. Velocity thresholds as a function of (a) bandwidth and (b) band height for two observers. The open symbols represent the results for relative motion, and the filled symbols for uniform motion. The circles represent the results of KS, and the triangles represent the results of DK.

deg of width, although it may cause some influence on the threshold when the stimulus width becomes smaller than 3 deg. Figure 9(b) shows velocity threshold as a function of stimulus height. In the uniform motion condition, threshold is approximately constant as a function of stimulus height. This indicates that the change in the stimulus area did not influence the threshold measurements.

In the relative motion condition, threshold decreases slightly with width and height. This is consistent with the effect of band size obtained in Experiment 1. Reduction of band height from 1 to 0.06 deg elevated the threshold drastically (but note that the gap size also varied). The assumption that the summation area for relative motion is larger than that for uniform motion explains the different effects of stimulus size in the two conditions, although it is not clear what information this provides about the underlying mechanisms.

4. GENERAL DISCUSSION

The present experiments showed three major differences in the velocity threshold between relative and uniform motion conditions. First, the threshold velocity for relative motion was lower than that for uniform motion. The difference was more than a factor of 10 in some conditions. Second, the sensitivity to the relative motion had a peak at approximately 5 c/deg, whereas the sensitivity to uniform motion varied little with spatial frequency when the stimulus contrast was high. Third, the threshold decreased with an increase in contrast up to the highest contrast (85%) in the relative motion condition, whereas it decreased with an increase in contrast up to approximately 5% in the uniform motion condition. These differences suggest that the visual system has separate underlying mechanisms: one for relative motion and one for uniform motion.

A. Spatiotemporal-Frequency Characteristics

Figure 10(a) expresses velocity thresholds in a spatiotemporal-frequency diagram to summarize the results in the two motion conditions. The plot shows the velocity threshold in terms of temporal frequency as a function of spatial frequency in each contrast condition for the 1-deg band of observer SI. This plot is equivalent to a contour plot of the contrast sensitivity function in the spatiotemporal-frequency diagram. The differences between the two motion conditions can be viewed as the differences in the spatiotemporal-frequency characteristics of the underlying mechanisms.

The most significant difference is in the lower temporal-frequency limit. In the uniform motion condition, the contours are close to the gray line of 1 arc min/s when the contrast is high. Neither stimulus contrast nor spatial frequency influenced the lowest velocity at which an observer identifies motion direction, as has been shown in previous measurements.[44,54] The result is very different for the relative motion condition. No simple relationship can be seen between spatial frequency and temporal frequency or velocity. These differences in spatiotemporal-frequency characteristics perhaps reflect the difference in the underlying mechanisms.

B. Response Function of the Underlying Mechanisms

To attribute the differences in spatiotemporal-frequency characteristics to differences in the underlying mechanisms, we estimated the response functions of the mecha-

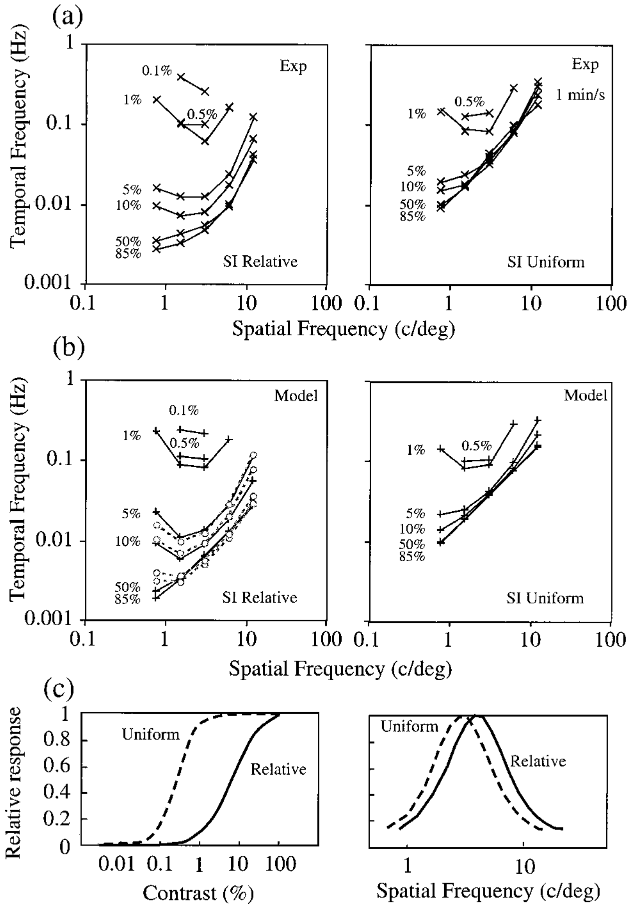

Fig. 10. (a) Velocity threshold of the 1-deg band for SI expressed by temporal frequency as a function of spatial frequency for each contrast. The left plot shows the data in the relative motion condition, and the right plot shows the data in the uniform motion condition. This corresponds to the contrast sensitivity function in the spatiotemporal-frequency domain. (b) Model prediction of the velocity thresholds in (a). The open circles connected by dashed lines are from fitting without data at contrasts of 1% or lower. (c) Contrast response functions and spatial-frequency tuning functions estimated from the model in each condition.

nisms responsible for threshold measurements in the two conditions. We assumed a nonlinear response function before the analysis of the quasi-linear motion detector.[55–57] The response of a motion detector may be expressed by the following equation:

$$R = Sf(cg(f_x))h(v),$$

where R represents the response of the motion detector, c stimulus contrast, f_x spatial frequency, v stimulus velocity, and S sensitivity. In this model, the input to the detector from the previous stage is characterized by the response function f and the spatial-frequency tuning function g. The input is multiplied by the velocity dependency of the response h. We do not consider spatial-frequency tunings of the motion detectors because the tuning in the model is too narrow to explain the spatial-frequency dependency found in our experiments. In other words, we assume that different detectors with different spatial-frequency tunings work for different spatial-frequency stimuli. We also do not consider the response nonlinearity of the motion detector. Since our threshold measurements indicate the velocity with which response reaches a certain threshold, our data do not have any information on the response changes of the detector with contrast but do have information on the relative effects between the stimulus contrast and velocity on the detector. This implies that the effect of contrast on the velocity threshold is determined by the contrast response function before the first-stage motion detector (the local motion detector) and the velocity tuning of the motion detector. This contrasts with the study of Edwards *et al.*,[43] who addressed the effect of the response function of the local motion detector, measuring the signal-to-noise ratio for perceiving coherent motion.

A Naka–Rushton-type equation is used to model the contrast response saturation function:

$$f(c) = R_{\max}c^n/(c^n + c_{50}^n),$$

where $R_{\max}$ represents the maximum obtainable response, n the exponent governing the steepness of the contrast dependency, and c_{50} the half-saturation contrast yielding a response of $R_{\max}/2$. Spatial-frequency tuning functions are modeled by Gaussian functions in logarithmic scale:

$$g(f_x) = \exp\{-[\log(f_x) - \log(f_{x0})]^2/\sigma^2/2\},$$

where f_{x0} indicates the peak spatial frequency and σ the spatial constant or bandwidth. We assume that the motion detector's response is proportional with stimulus velocity $[h(v) = kv]$, following Burr and Corsale, who use instantaneous local variation in luminance by the first derivative of the luminance distribution with respect to time. A simple simulation using a motion energy model[55] reveals that this approximation is precise enough for the slow velocities as velocity thresholds in the present experiments.

Fitting the model functions to data for all spatial-frequency and contrast stimuli with the 1-deg band in experiment 1 by a least-squares procedure, we estimate n, c_{50}, f_{x0}, and σ with the response values multiplied by the coefficient of the velocity function kS, to achieve $R = 1$ (Table 1). The model prediction in the spatiotemporal-frequency domain is shown in Figs. 10(b) and 10(c) for ob-

Table 1. Model Parameters for the Least-Squares Fitting[a]

	Relative		Uniform	
	SI	MW	SI	MW
c_{50}	0.051 (0.15)	0.112 (0.17)	0.014	0.036
n	1.48 (0.69)	1.46 (1.11)	1.52	1.57
f_{x0}	3.92 (3.67)	3.29 (3.36)	3.00	2.98
σ	0.39 (0.29)	0.37 (0.33)	0.35	0.41
kS	7.62 (13.08)	4.35 (5.50)	1.28	0.80

[a] Values in parentheses indicate the results obtained without data at contrasts of 1% or lower.

server SI with the contrast response and spatial-frequency functions. Comparing Figs. 10(a) and 10(b) reveals that the basic characteristics are predicted well by the model. That is, the threshold is constant for different spatial frequencies (straight line with a slope of 45 deg in the spatiotemporal-frequency domain) and different contrasts (considerable overlap of the contours for contrasts higher than or equal to 5%) in the uniform motion condition, while it shows the minimum at a middle spatial frequency (curved downward in the spatiotemporal-frequency domain) and dependency on contrast (little overlap of the contours) in the relative motion condition. One exception is that the prediction with high contrast closely follows a straight line in the relative motion condition, which is different from experimental data. Better predictions for relative motion are possible if fittings are made without data at contrasts of 1% or lower. The fittings are shown by dashed curves in Fig. 10(b), and the fitting parameters are shown in parentheses in Table 1. The effect of spatial frequency in the fittings is closer to experimental results than that in the original fittings. Since the thresholds are similar in the two motion conditions at low contrast, they were likely to be determined by the same mechanism. Thresholds at low contrast in the relative condition, therefore, may not reflect the characteristics of the underlying mechanism for relative motion. The fittings without data at low contrast perhaps provide a better estimation of the characteristics of the underlying mechanism.

The estimated response saturation functions differ between relative and uniform motion conditions, as expected from the threshold results. The half-saturation contrast for relative motion is approximately three times that for uniform motion for both observers. The estimated half-saturation contrast may be compared with the physiological results of parvocellular and magnocellular LGN cells. For both relative and uniform motion, it is smaller than approximately 0.1 (or 0.15 when data at low contrasts are removed from analysis in the relative motion condition), which is much smaller than the half-saturation contrast of parvocellular LGN cells (approximately 0.5). It is rather closer to the value for magnocellular LGN cells (approximately 0.1).[58] Differences in the contrast characteristics in the velocity threshold are not likely to be related to the dichotomy of the parvocellular and magnocellular pathways.[59,60]

Interestingly, the estimated spatial-frequency tuning functions from the model fitting are similar in the two conditions, although the peak spatial frequency is slightly higher for relative motion. The model reveals that different response functions result in a difference in the spatial-frequency characteristics in the velocity threshold. The spatial-frequency characteristics obtained from the simulation are similar to those for detecting static stimulus gratings, peaking at approximately 5 c/deg with a broad spatial-frequency tuning. To confirm the results, we repeated the fittings with independent values of kS for different spatial frequencies and found essentially the same results. The spatial-frequency tuning with a peak at approximately 5 c/deg is consistent with that of the parvocellular pathway. Here, too, the differences in the spatial-frequency characteristics in velocity threshold are not likely to be related to the dichotomy of the parvocellular and magnocellular pathways. The response functions are similar to those of the magnocellular cells, whereas the spatial-frequency tunings are similar to those of the parvocellular pathway for both relative and uniform motion stimuli.

These results are consistent with the claim that both the magnocellular and parvocellular pathways contribute to motion analysis.[38] Although motion is usually conceived as characterizing the magnocellular pathway, the contribution of the parvocellular pathway to motion perception is still possible.[38,61–64] De Valois *et al.*[38] suggest that directional V1 cells have inputs from magnocellular and parvocellular pathways, pointing out the importance of combining signals from cells with slow responses with those with fast responses to construct direction selectivity in a cell. For our measurements, it is possible that the cells with the lowest temporal-frequency tunings contribute to the analysis of both relative and uniform motion because we measured the lowest velocity to identify motion directions.

The above discussions indicate that the differences in the relative and uniform motion conditions in the present experiments can be attributed to the difference in the response saturation of the underlying mechanisms, both of which may have contributions from both the magnocellular and parvocellular pathways. It should be noted, however, that our analysis is based on many assumptions, and further investigation is necessary to assess the validity of the analysis.

C. Functional Difference between Relative Motion and Uniform Motion Detectors

Here we discuss possible functional differences between two types of motion detectors, which we call relative and uniform motion detectors. The discussion is based on the assumption that the motion detectors that are responsible in our measurements in the relative and uniform motion conditions are also responsible for processing relative and uniform or global motion signals in general.

The threshold in the uniform motion condition showed little dependency on either spatial frequency or contrast. This suggests that the motion detector that is responsible for detecting uniform motion is sensitive to speed independent of the stimulus conditions. Our model suggests that this can be achieved by a strong response saturation of the underlying mechanisms. This is an important feature related to two aspects of motion analysis. First, setting a criterion for the minimum speed to see uniform motion should minimize the erroneous motion perception derived by the signals from the retinal motion caused by involuntary eye movement.[65,66] This should help to extract signals of object motion from retinal motion signals. Although the speed limit of approximately 1 arc min/s found in the present experiment may be too slow to remove all retinal motion due to fixational eye movements,[67,68] much can still be removed from motion analysis. Second, the signal that codes speed is useful for evaluating the stimulus speed independently for shape, size, surface texture, and other object features, for example to detect expansion/contraction, rotation, and translation. Such global motions should be detected in the spatial distribution of velocity with a variety of stimulus features in a large field.

One may think that speed perception independent of stimulus conditions contradicts the reports of the dependency of perceived speed on contrast and spatial frequency. However, such dependency of perceived speed on stimulus conditions is not conclusive. It has been suggested that experimental conditions alter the dependency of perceived speed on stimulus conditions. A large effect of contrast on perceived speed has been shown between stimuli presented simultaneously, whereas there is little effect between stimuli presented sequentially.[69,70] It may be the case that a speed comparison between stimuli presented sequentially is based on the signal of the uniform motion pathway whereas a speed comparison between stimuli presented simultaneously is not, and it may be based on the signal of the relative motion pathway.

The results in the relative motion condition were different. The threshold varied across conditions. The motion detector that is responsible in a condition may be designed to detect velocity differences at adjacent areas as sensitively as possible within physiological restrictions. Our model shows that a weaker response saturation results in a dependency of the velocity threshold on spatial frequency and contrast. Such a motion detector is perhaps important to detecting motion borders. To distinguish objects from backgrounds by using motion cues, a higher sensitivity is useful while no speed estimation is required.

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