

PRECISE VELOCITY DISCRIMINATION DESPITE RANDOM VARIATIONS IN TEMPORAL FREQUENCY AND CONTRAST

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Abstract—Velocity discrimination is not affected by random changes in contrast or temporal frequency. Observers judged the relative velocity of a moving sinusoidal grating when target contrast was varied randomly from trial-to-trial over the range from 5 to 82%. The Weber fraction for the random mixture of interspersed contrast levels was about 0.06, comparable to velocity discrimination for targets presented at a fixed contrast. In a parallel experiment, the spatial frequency of the target was changed randomly from trial-to-trial, a procedure which produced concomitant random changes in the nominal temporal frequency. These variations had little effect on the velocity increment threshold; random changes in temporal frequency ranging from 2.25 to 8.25 Hz increased the Weber fraction from 0.05 to 0.07. Under identical experimental conditions, velocity discrimination was generally more precise than the discrimination of differences in temporal frequency, particularly when temporal frequency thresholds were measured with counterphase gratings. Our results indicate that velocity discrimination depends on velocity.

Velocity Motion Spatial frequency Temporal frequency

INTRODUCTION

Under most circumstances, a human observer can easily tell that a target moving at a velocity of 6 deg/sec is moving faster than a target moving 5 deg/sec. With practice, his judgments can be much more precise than that. The velocity Weber fraction hovers at 0.05 for velocities ranging from 3 to 70 deg/sec (McKee, 1981; McKee and Nakayama, 1984; Orban *et al.*, 1984). How does the observer know that one velocity is faster than another? What limits his performance?

Discrimination thresholds generally reflect the signal-to-noise characteristics of the underlying neural machinery. In the case of velocity discrimination, the observer must decide whether the signal produced by the motion of the target is generated by one velocity or by another very similar velocity; the "noisiness" of the two signals limits the precision of the judgment. Ideally, any stimulus perturbation which increases the "noise" of the velocity signals will degrade discrimination. One strategy for deciphering the neural velocity code is to introduce random fluctuations in stimulus dimensions other than velocity and observe the influence of these changes on the psychophysical thresholds. Random stimulus fluctuations can

increase the uncertainty of the observer about the exact characteristics of the relevant signal, resulting in some loss of precision. A more serious deficit will occur if random changes in other dimensions are confounded physiologically with genuine changes in the velocity dimension itself. In a sense, the most interesting stimulus variations are those that have *no* effect on velocity discrimination. Either the stimulus dimension is not a critical component of the velocity code, or its perturbing effects can be eliminated by neural operations within the velocity network.

To illustrate this strategy, consider a particularly simple model of velocity coding: velocity is signaled by neurons which vary their output as a monotonic function of the retinal velocity of stimulus. Although neurons which increase their output as a function of retinal velocity have been observed, the response of these units is affected by many other stimulus dimensions, including stimulus area, intensity and contrast (Grusser and Grusser-Cornehls, 1973). A model of velocity coding which is based on the output of such units has the weakness that changes in velocity can be easily mimicked by changes in stimulus contrast. Random changes in stimulus contrast would then be confounded with changes in velocity producing an increase

in velocity discrimination thresholds. To test whether velocity judgments are actually confounded by changes in contrast, we measured velocity discrimination for moving sinusoidal gratings, introducing random changes from trial-to-trial in the stimulus contrast over the range from 5 to 82% contrast. If our observers were unable to disentangle the velocity component from contrast-induced changes in the signal, random changes in contrast would degrade velocity discrimination.

An appealing alternative to a model based on a monotonic velocity sensor are models which assume that there are multiple mechanisms each tuned to different, but overlapping, velocity ranges (Thompson, 1984; Adelson and Bergen, 1985). In this type of model, contrast effects can be eliminated by an "opponent" stage which uses the ratio of the signals emerging from the separate tuned mechanisms to estimate velocity. But what establishes the differential tuning of the velocity mechanisms? If human motion detectors are correlators of the Reichardt (1961) variety, then velocity tuning depends jointly on the spacing (Δs) between the paired input receivers and the temporal characteristics (Δt) of the delaying network which joins the pair. In recent theoretical modifications of the Reichardt model, the spatial and temporal tuning depends on broad-band filters selectively responsive to a particular range of spatial and temporal frequencies (Van Santen and Sperling, 1985; Adelson and Bergen, 1985; Watson and Ahumada, 1985).

The velocity tuning of this type of mechanism is given by the ratio of the optimal temporal frequency to the optimal spatial frequency, but note that there are an infinite number of spatial and temporal frequency combinations which together specify the same velocity. Single neurons in monkey and cat striate cortex have a preferred spatial and temporal frequency, and thus a preferred velocity (Holub and Morton-Gibson, 1981; Movshon *et al.*, 1978), but, strictly speaking, these units are not "velocity mechanisms". They are only sensitive to a limited subset of the spatio-temporal frequencies which comprise a given velocity. This type of unit could only serve as the neural substrate for velocity if it is assumed that each velocity is coded by a narrow spatial frequency range. But perhaps this assumption about human velocity sensitivity is justified. Targets such as lines or dots which are broadly represented in the spatial frequency domain will easily stimulate the ap-

propriate velocity mechanism, providing an adequate representation of all visible velocities. Velocity discrimination would then reduce to the discrimination of temporal frequency.

It has been argued that motion-sensitive elements of the human visual system respond to temporal frequency, not velocity (Sekuler *et al.*, 1976). At first glance, it may seem that there is quite striking evidence for this assertion. The motion after-effect is direction specific, and the magnitude of this after-effect depends on the temporal frequency of the adapting sinusoidal grating, not the adapting velocity (Pantle, 1974). On the other hand, perceived shifts in apparent velocity depend on the velocity of the adapting stimulus, not its temporal frequency (Thompson, 1981). The results from the adaptation studies do not indicate decisively whether velocity is a primary dimension of sensory coding, or a derived dimension which depends chiefly on temporal frequency.

Do human observers actually respond to target velocity or only to target temporal frequency? To test this question psychophysically, we used sinusoidal gratings as our velocity stimuli, and randomly varied the target spatial frequency from trial-to-trial, asking our observers to ignore these variations and to judge target velocity alone. Random variations in spatial frequency necessarily introduce random variations in temporal frequency since temporal frequency is the product of velocity and spatial frequency. Randomizing temporal frequency would greatly increase the "noise" in a temporal frequency detector and should have disastrous effects on a discrimination based on temporal frequency alone. If our observers can make precise judgments of velocity in the face of such perturbations, then it is likely that the human visual system responds to velocity, not temporal frequency.

METHODS

Velocity discrimination was measured by the method of single stimuli. On each trial the observer was shown one of five velocities chosen from a narrow range and was forced to judge whether the single sample was faster or slower than the mean of the range. No specific standard was ever presented; instead the observer judged the velocity shown on each trial against an implicit mean established by the sequence of trials (McKee, 1981; McKee and Nakayama,

1984). For the studies in which target contrast or spatial frequency was randomly varied from trial to trial, this procedure had a special virtue. Because no standard was presented, the observer was forced to abstract the velocity standard, and his judgment was not influenced by the particular contrast or spatial frequency chosen for a standard stimulus. For the studies in which contrast or spatial frequency was a fixed parameter, feedback was provided if desired by the observer. In the studies in which contrast or spatial frequency was varied randomly from trial to trial, *no* feedback was given.

A psychometric function was generated by the percentage of trials on which the observer responded "faster" as a function of the five test velocities. Typically, the test velocities covered a range of $\pm 12\%$ of the mean, i.e. the stimulus step size was 6%. Probit analysis was used to fit a cumulative normal function to the data. The velocity threshold and standard error of the threshold were estimated from the fitted function. Threshold was defined as that incremental change in velocity which produced a change in the response level from 50% "faster" to 75% "faster", or specifically half the difference between the velocities corresponding to the 25% response level and the 75% response level respectively ($d' = 0.675$). The velocity corresponding to the Point of Subjective Equality (or more precisely, to the implicit standard used by the observer) was estimated from the fitted function as the stimulus value corresponding to the 50% response level. Each plotted threshold is based on at least 200 trials. For the studies employing random variations in contrast or spatial frequency, 600–1200 trials were used to estimate the combined threshold based on the summed data for all the intermixed contrast or spatial frequency levels.

The targets for all our experiments were vertical sinusoidal gratings which moved horizontally. The direction of motion was varied randomly from trial to trial. The sinusoidal pattern was generated by an Innesfree *Picasso* image generator and was displayed on a Hewlett-Packard 1332A CRT equipped with a P31 phosphor. Contrast and luminance were measured with a Pritchard photometer. The mean luminance was approximately 30 cd/m^2 for all experiments. Stimuli were viewed binocularly with natural pupils at a distance of either 57 or 74 cm, well within the accommodative range of the three authors who served as observers. The outer borders of the

grating measured $8 \times 10 \text{ cm}$. The subjects fixated the center of the screen.

If the moving targets had been presented for a fixed duration, observers could have judged the velocity by the distance traversed by the target on each trial. To minimize the use of distance and duration cues, duration was randomly varied by $\pm 20\%$ from trial to trial. Except where indicated, the mean duration was 450 msec. Variations in apparent contrast can also be used to judge velocity. Unless noted in the experimental description, on each trial, the contrast of the target was chosen randomly from one of four levels covering a narrow range. These random perturbations in contrast and duration make it likely that our thresholds represent a genuine response to target velocity, rather than a response based on other cues which ordinarily co-vary with changes in velocity.

RESULTS

Velocity discrimination with random variations in contrast

Our initial objective was to learn if random variations in contrast would degrade velocity discrimination. We began by establishing that each of the chosen suprathreshold contrasts was separately adequate to produce optimum discrimination. The curve drawn in Fig. 1 shows the Weber fraction as function of velocity for a

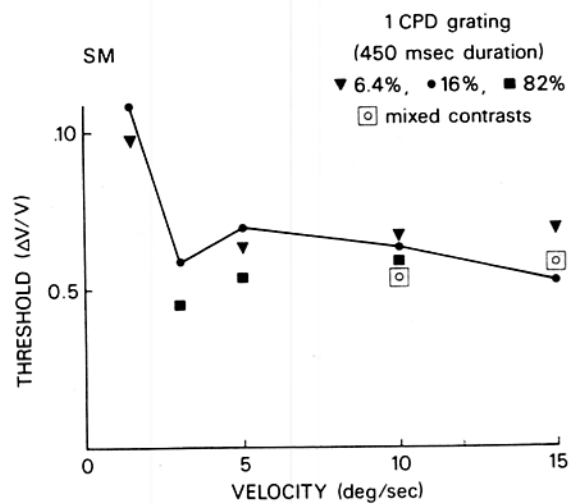


Fig. 1. Velocity discrimination thresholds as a function of stimulus velocity under a mixture of experimental conditions. Solid symbols represent discriminations obtained for gratings of fixed constant as marked. Boxed symbols represent the velocity discrimination thresholds for the condition where all three contrasts were randomly intermingled. Note that contrast or the random variation of contrast has essentially no effect on velocity discrimination thresholds.

	Separate Contrasts	Grouped Contrasts
<i>5 deg/sec</i>		
KN	.063	.066
GS	.053	.057
<i>10 deg/sec</i>		
KN	.063	.062
GS	.060	.059

Fig. 2. Discrimination of velocity for separately presented contrasts vs the same range of contrasts randomly intermingled for 5 and 10 deg/sec. Contrast values were 4.6, 10, 13.5, 27.6, 51.2, and 82%.

sinusoidal grating of 1 c/deg presented at a fixed contrast of 16%. The curve reaches its asymptotic value at a velocity of 3 deg/sec in agreement with earlier studies (McKee, 1981). The Weber fractions for two other fixed contrasts, 6.4 and 82%, cluster around this curve, showing no systematic effect of these contrast levels on velocity discrimination. We then randomly intermingled these same three contrast levels, and measured the Weber fraction for the mixture. The boxed points in Fig. 1 show that random variations in contrast had no effect on velocity discrimination.

Because the three contrast levels were so different in appearance, it seemed possible that the observer might somehow compensate for the random changes in contrast. To allay this worry, we repeated the experiment with six contrast levels: 4.6, 10, 13.5, 27.6, 51.2 and 82%. Figure 2 compares the average Weber fraction for the six contrast levels presented separately (Separate Contrasts) to the Weber fraction found when the contrast levels are randomly intermingled from trial to trial (Grouped Con-

trasts). Again the data show that velocity discrimination is insensitive to random variations in contrast. The changes in the visual signal produced by changes in suprathreshold contrast have no significant effect on the velocity thresholds, in agreement with earlier work by Pantle (1978).

Recent studies by Regan (personal communication) supply additional evidence that velocity discrimination is essentially independent of suprathreshold changes in contrast. The discrimination of orientation and of spatial frequency also show little dependence on contrast, provided that the stimulus is 2–3 times the absolute contrast threshold (Regan *et al.*, 1982; Regan and Beverley, 1985). The discrimination of direction, itself a motion threshold, shows a similar contrast independence at contrast values above 3% (Nakayama and Silverman, 1985).

Generally, energy models which determine the direction of motion by means of a type of Reichardt correlator are susceptible to variations in contrast (Watson and Ahumada, 1985). To remove the contrast dependence, a subsequent stage of processing is needed, one which takes the ratio of signals coming from two or more labeled neural groups. If velocity discrimination depends on the ratio of the signals in two groups of differentially-tuned neurons, velocity thresholds would be indifferent to contrast levels above some minimum value (Adelson and Bergen, 1985).

Velocity discrimination as a function of spatial frequency

We next measured the optimal spatial frequency range for velocity discrimination as a function of velocity. Pantle had measured the

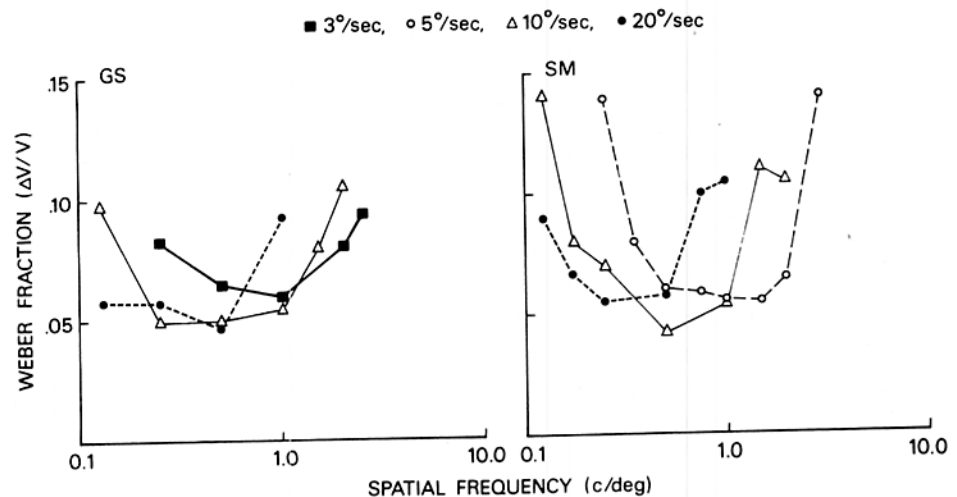


Fig. 3. Velocity discrimination thresholds as a function of spatial frequency for differing velocities.

Weber fraction for velocity using three spatial frequencies, 0.6, 4.8 and 10 c/deg (see also Thompson, 1983). There were indications in his data that velocity discrimination was much better at the lowest spatial frequency. We repeated the Pantle study with a more extensive set of spatial frequencies. To obscure velocity-induced changes in apparent contrast, we randomly varied contrast from trial-to-trial using four equally-spaced contrast levels which spanned the range from 40 to 60%.

The Weber fraction curves showed a shallow tuning for each of the tested velocities (see Fig. 3). The faster the velocity, the lower the optimal spatial frequency range. The thresholds for all the tested velocities were somewhat elevated at spatial frequencies greater than 2 c/deg, consistent with the expectation that motion-sensing elements of the human visual system are spatially coarse.

Following Pantle's lead, we have replotted the data from Fig. 3 as a function of temporal frequency (see Fig. 4). Except for the points for the velocity of 3 deg/sec, the data superimpose on a single function which reaches a shallow minimum at 5 Hz. The data for 3 deg/sec deserve some comment; they are not merely aberrant points associated with this observer. We have found this same type of shift to lower temporal frequencies in other observers at very slow velocities. It appears that slow velocities (<3 deg/sec) depend on a different temporal substrate than the faster velocities.

Note that temporal frequency "tuning" for velocity discrimination is quite broad. As Pantle (1978) demonstrated by measuring both contrast sensitivity and velocity discrimination as a

function of temporal frequency, the tuning associated with velocity discrimination is much broader than the flicker sensitivity curves. There is no *a priori* reason why a sensitivity function should predict discrimination thresholds. Wavelength discrimination, for example, shows no direct relation to the photopic sensitivity curve. Critical flicker fusion sets a limit on the velocity thresholds at the extremes. A sinusoidal grating of 5 c/deg moving at a velocity of 20 deg/sec has a temporal frequency of 100 Hz. Such a target would not even be visible, much less discriminable from other moving patterns. The minimum contrast required to detect flicker does not necessarily have much bearing on the discriminability of a temporal signal at suprathreshold contrast levels. Mandler (1984) has measured the Weber fraction for the discrimination of differences in temporal frequency as a function of temporal frequency. This function is quite different in shape from the contrast modulation function for temporal frequency.

Velocity discrimination with random variations in spatial frequency

We began this study by measuring the velocity increment threshold for a high contrast (82%) sinusoidal grating of 1 c/deg moving 5 deg/sec. The velocity Weber fraction for this stimulus was roughly 0.05. If the spatial frequency of the target is held constant, then changes in the velocity and temporal frequency are coupled. We then ran a number of sessions introducing different amounts of spatial frequency variation from trial to trial. By doing this, we were able to decouple the relationship between temporal frequency and velocity in a

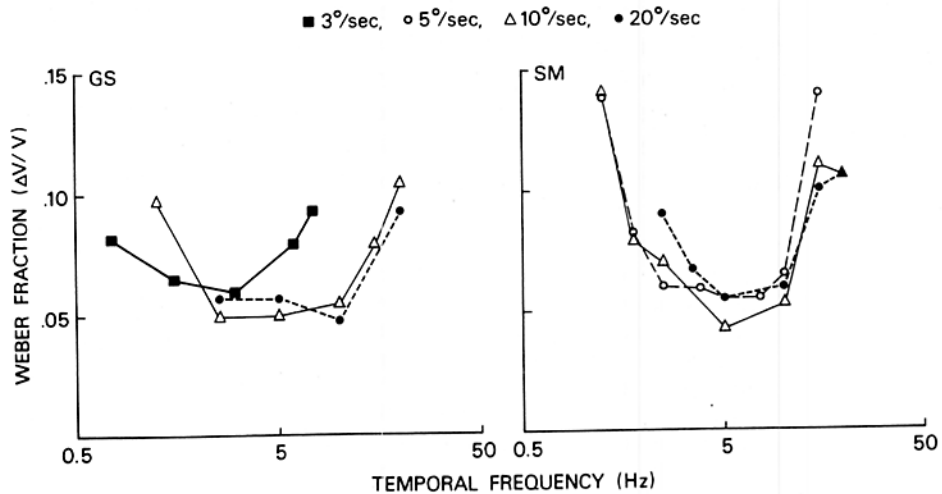


Fig. 4. Velocity discrimination thresholds as shown in Fig. 3, replotted as a function of temporal frequency.

Table 1. Random variations in spatial frequency (velocity range 4.5–5.5 deg/sec)

Spatial frequency range (c/deg)	Temporal frequency range (Hz)
1	4.5–5.5
0.94–1.06	4.2–5.8
0.88–1.13	4.0–6.2
0.75–1.25	3.4–6.9
0.5–1.5	2.25–8.25

Example of largest range:
 For velocity range 4.5–5.5 deg/sec
 0.5 c/deg varies from 2.25 to 2.75 Hz
 1.5 c/deg varies from 6.75 to 8.25 Hz

systematic manner. Recall that in this experiment our subjects were not shown a standard stimulus on each trial, and that they received no feedback about the accuracy of their judgments. Table 1 shows the five conditions employed in this experiment. For our largest range, we interspersed at random five spatial frequencies extending from 0.5 to 1.5 c/deg, e.g. 0.5, 0.75, 1.0, 1.25, and 1.5 c/deg—spatial frequencies which the previous experiment had shown to produce good velocity discrimination. Thus, for the velocity of 5 deg/sec, the nominal temporal frequency* could range from 2.25 to 8.25 Hz. Variations in temporal frequency covering almost two octaves only increased the velocity Weber fraction from 5 to 7%.

Consider the outcome of the experiment if the observer cannot respond to velocity, but bases his judgments on the temporal frequency alone. We will assume that the observer judges the target velocity as faster when the temporal frequency exceeds the mean temporal frequency (5 Hz) by a discriminable amount. As the spatial frequency range increases, velocity errors must increase dramatically. For example, all velocities from our test range would be judged as faster on the basis of temporal frequency when the spatial frequency of the target is 1.5 c/deg. The continuous curve in Fig. 5 shows the predicted Weber fractions given the assumption that the observer is responding only to temporal frequency and can detect a 5% incremental

*The durations used for all our stimuli are relatively brief, so it is incorrect to refer to "the" temporal frequency of the stimulus. The stimulus energy is actually distributed across a broad range of temporal frequencies peaking at the nominal temporal frequency of the stimulus. Nevertheless, changes in the nominal temporal frequency of the stimulus will produce marked shifts in the temporal frequency distribution. Discrimination by a broad-band temporal frequency detector should be affected adversely by these shifts even if the stimulus energy is itself distributed broadly.

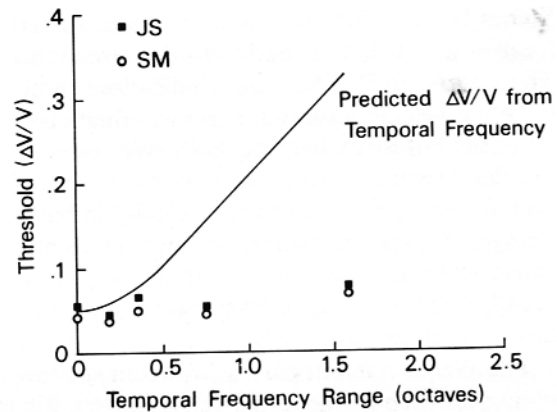


Fig. 5. Velocity discrimination thresholds in an experiment where temporal and spatial frequency were randomly varied from trial to trial. Velocity Weber fractions are plotted as a function of the range of temporal frequency variation. Solid line represents the results predicted if the observer was relying exclusively on temporal frequency to make the velocity discrimination. No feedback was given to the observers.

change in temporal frequency. The actual Weber fractions measured with an increasing spatial-temporal frequency range are also plotted in Fig. 5. The velocity Weber fractions are not dependent on temporal frequency.

It is possible that our observers were tracking the stimulus. Then the frame of the CRT and other objects in the room would have moved in the opposite direction at the appropriate velocity. In 500 msec, the pursuit velocity has reached a level of precision which is comparable to sensory velocity discrimination (Kowler and McKee, 1984). At shorter durations (<250 msec), pursuit is generally too imprecise to permit judgments of velocity amounting to 7%. As a control experiment for oculomotor pursuit, we repeated the experiment for the largest range of spatio-temporal frequencies at a duration of 230 msec. The velocity Weber fraction for the mixture of the five interspersed spatial frequencies presented at this shorter duration was 0.06. Therefore, the velocity judgments were probably based on our stimulus pattern, not the pursuit-induced motion of the surroundings.

There is another way to measure the influence of temporal frequency on velocity judgments. Although the spatial frequency of the stimulus changed randomly from trial to trial, the psychometric functions associated with each spatial frequency can be examined separately. If the spatial frequency, and thus the mean temporal frequency, of the stimulus was producing a systematic change in perceived mean velocity,

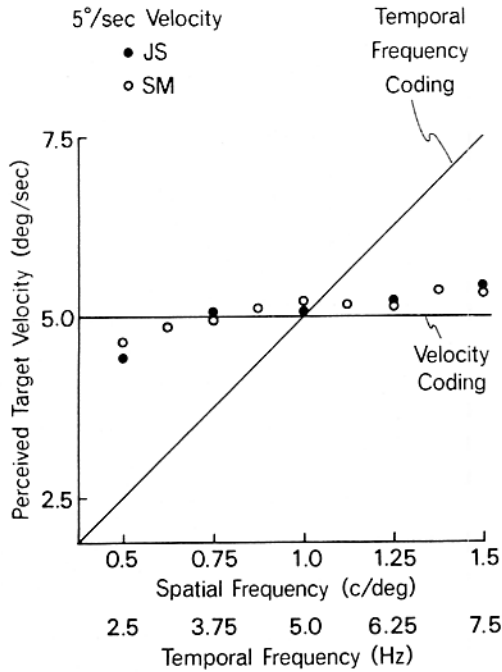


Fig. 6. Perceived target velocity as a function of the spatial and temporal frequency of the sinusoidal grating target. No feedback was given to the observers. If the observer were to rely on temporal frequency alone, results should conform to the 45 degree solid line.

then the mean of the psychometric function, commonly called the point of subjective equality (PSE), should have increased with increases in spatial frequency. In Fig. 6, we have plotted the PSE of the psychometric function for each spatial frequency. The shift with mean temporal frequency is discernible but falls far short of the shift which would have been predicted by a temporal frequency hypothesis (solid line in Fig. 6).

Perhaps our observers were performing some type of cognitive rescaling, adjusting their estimates of velocity to compensate for the target spatial frequency. When the target spatial frequency was high, the observer might have decided to judge the velocity as slower than what he actually perceived. One observer (J.S.) was shown only five spatial frequencies, and perhaps some re-scaling is likely for just five categories. The experiment was repeated with nine spatial frequencies with the second observer (S.M.) and her data are virtually identical to the results for the first subject (see Fig. 6).

Discrimination of temporal frequency with random variations in spatial frequency, velocity and contrast

While the agreement between the observers was excellent, these data did not rule out a

cognitive process in which the perceived velocity depended on the independent perception of spatial frequency and temporal frequency. There is one obvious way to address this question. If observers can make independent estimates of spatial and temporal frequency, then the Weber fraction for temporal frequency discrimination should be better or at least match the Weber fraction for velocity discrimination under identical experimental conditions.

In this study, we first measured velocity discrimination at 10 deg/sec for a random mixture of five spatial frequencies, summing the data from two separate sessions of 400 trials each. The spatial frequencies ranged from 0.5 to 1.5 c/deg, the mean duration was 230 msec ($\pm 20\%$), and the target contrast was randomized from trial to trial over the range from 14 to 24%. We then began training our observers with feedback to respond to variations in temporal frequency, given the same random trial-to-trial variations in spatial frequency, duration and contrast. On each trial the subject was shown one of five temporal frequencies chosen from a narrow range centered on 10 Hz and was required to judge whether the presented sample was higher or lower than the mean (10 Hz). When the temporal frequency threshold stabilized, we measured temporal frequency discrimination in two sessions of 400 trials each, pooling the data to obtain a grand estimate of the Webster fraction ($\Delta TF/TF$). The results of this confrontation between temporal frequency and velocity are shown in Fig. 7. After much practice, temporal frequency discrimination thresholds in drifting gratings can be as good as velocity thresholds (see results for K.N.) or significantly worse (see results for S.M.).

We were now faced with an experimental conundrum: did our observers judge velocity by making independent estimates of spatial and temporal frequency, or did they judge temporal frequency by making independent estimates of spatial frequency and velocity? Subjectively, the observers felt that they were responding to velocity and then inferentially judging temporal frequency by taking account of the spatial frequency. Because judgements of temporal frequency can be made with stationary targets, it was, of course, possible to measure temporal frequency thresholds in the absence of motion.

In order to match stimulus conditions as closely as possible, we measured temporal frequency discrimination for counterphase gratings, incorporating the random variations in

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WEBER FRACTIONS FOR A RANDOM MIXTURE OF FIVE SPATIAL FREQUENCIES

	$\Delta V/V$ V=10 deg/sec	$\Delta TF/TF$ Drifting TF=10 Hz	$\Delta TF/TF$ Counterphase TF=10 Hz
KN	.08 ± .005	.08 ± .005	.17 ± .01
SM	.07 ± .004	.11 ± .008	.14 ± .01

Fig. 7. Comparison of velocity discrimination thresholds and temporal frequency discrimination thresholds for drifting gratings and counterphase gratings.

duration, contrast, and spatial frequency used for the experiment with drifting gratings described above. Recall that counterphase gratings can be linearly decomposed into a rightward and leftward drifting grating of the same spatial and temporal frequency (Levinson and Sekuler, 1975). Human observers do not see simultaneous rightward and leftward motion in such gratings and this is best attributed to the opponent nature of motion sensing (Adelson and Bergen, 1985; Van Santen and Sperling, 1984). If the temporal frequency thresholds for drifting gratings are mediated by the velocity system, then the temporal frequency discrimination for counterphase gratings should be significantly worse.

The last column of Fig. 7 shows that temporal frequency discrimination was less precise for counterphase gratings. It is conceivable that, with greatly extended practice, the temporal frequency thresholds might reach the same values as the velocity thresholds, but we think this is unlikely. For one thing, our temporal frequency thresholds for counterphase gratings are in rough agreement with the thresholds for well-practiced observers judging temporal frequency changes in a uniform field flickering at 10 Hz (Mandler, 1984). Our results argue that, at this short duration, temporal frequency is only known indirectly through motion mechanisms whose fundamental dimension is velocity, not temporal frequency.

DISCUSSION

Velocity is a primary source of information about the visual environment. Image velocity can be used to encode depth, define object boundaries and contours, direct eye movements

*We want to thank Dr Jacob Nachmias for suggesting this experiment, and for his helpful commentary following the presentation of these results at the ARVO meeting in 1984.

and maintain posture (Rogers and Graham, 1979; Nakayama and Loomis, 1974; Rashbass, 1961; Lee and Aronson, 1974). For these purposes, velocity information should be relatively independent of the spatial or contrast characteristics of the stimulus, because there is seldom a meaningful correlation between the size, shape or contrast of an object and its velocity. It is thus not surprising that human velocity discrimination is unaffected by radical changes in contrast, spatial frequency and temporal frequency.

In the past, there have been a number of studies which have shown some dependence of perceived velocity on temporal frequency (Smith and Sherlock, 1957; Diener *et al.*, 1976). It must be stressed that our observers were performing a somewhat different task from these earlier studies. Our observers were asked to detect small changes in target velocity *per se*. In the other studies, the observers were asked to match the velocity to a standard, or to estimate the magnitude of a test velocity by reference to a standard. Unless extraordinary psychophysical procedures are used, changes in the velocity of a fixed contrast target are often accompanied by concurrent changes in apparent contrast, edge blur, distance traversed by the target, target duration, and—for repetitive targets—changes in local flicker (temporal frequency). When an observer is asked to relate the velocity of one target to another standard target which differs in all of these characteristics, he may try to minimize the differences on several dimensions. In the study by Diener *et al.* (1976), the standard for magnitude estimation was a square wave grating made of wide stripes (6 deg black stripes and 24 deg white stripes) moving 100 deg/sec. Test stimuli with narrower stripes were estimated to be moving faster than test stimuli with broader stripes. While their results can be interpreted as showing an imperfect dependence of perceived velocity on temporal frequency, the observers may have been using differences in apparent contrast in making their estimates of relative velocity. Recently Swift and Panish (1983) found little change in perceived velocity with changes in spatial frequency, in agreement with our results on discrimination.

The test targets used in some of these earlier studies were presented for a relatively long duration (many seconds). We have found that the small effect of temporal frequency on the velocity PSE's shown in Figure 6 can be exaggerated *slightly* at longer durations.* In fact, the Weber fraction for a random mixture of spatial

frequencies presented for 1 s is somewhat worse ($\Delta v/v \approx 0.1$) than the Weber fraction for a duration of 0.5 s. The increasing influence of temporal frequency on velocity discrimination thresholds for these long duration effects may be due to the effect of frequency on velocity would be back and practice. In a naïve observer, target frequency can affect *per se* target is shown long end cycles of a repetitive target location. Nevertheless, repetition rate at any one could have much to do with the discrimination. A target of 0.5 deg/sec moving at a velocity of 5 deg/sec moving at 230 msec, and excellent velocity discrimination.

Velocity discrimination is a result of temporal frequency. This result implies that temporal frequency is a basis of velocity coding. The dependence that motion (flicker) are processed by the visual system (cf. Hunzelman, 1983). The question is whether the visual system serves as the neural substrate for motion at some early stage. To imagine a visual motion without detecting velocity without detecting temporal frequency, one must concede that the visual circuitry responds to the stimulus, whether the stimulus is temporal frequency. That, for briefly-presented temporal signals, the visual machinery for velocity discrimination is different from the velocity system as the velocity system.

In Fig. 4, we show that the discrimination for fast velocity is centered on about 10 deg/sec. This finding is that the characteristics of all "fast" velocities are nearly identical. It would depend on the form of the underlying velocity system, this view would be "velocity metamorphosis".

*This term is borrowed from a well-known that indistinguishable dimensionality of

frequencies presented for 1350 msec is actually somewhat worse ($\Delta v/v \approx 0.09$) than the Weber fraction for a duration of 230 msec, reflecting the increasing influence of temporal frequency on velocity discrimination. We speculate that these long duration effects of temporal frequency on velocity would disappear with feedback and practice. In a naive observer, temporal frequency can affect *perceived* velocity if the target is shown long enough to permit many cycles of a repetitive target to pass a given location. Nevertheless, it is unlikely that the repetition rate at any one location (local flicker) could have much to do with velocity discrimination. A target of 0.5 c/deg moving at a velocity of 5 deg/sec moves through about 0.6 cycles in 230 msec, and such a target produces excellent velocity discrimination.

Velocity discrimination is superior to the discrimination of temporal frequency. Does this result imply that temporal frequency is *not* the basis of velocity coding? Certainly there is evidence that motion and temporal frequency (flicker) are processed by different visual mechanisms (cf. Hunzelmann and Spillmann, 1984). The question is whether temporal frequency serves as the neural substrate for velocity coding at some early stage. As it is almost impossible to imagine a visual mechanism that responds to velocity without detecting changes in time, we must concede that some level in the neural circuitry responds to the temporal aspect of the stimulus, whether the nomenclature is time or temporal frequency. *What our results do show is that, for briefly-presented targets, this temporal signal is so tightly embedded in the neural machinery for velocity that it cannot be extracted from the velocity signal with the same precision as the velocity signal itself.*

In Fig. 4, we show that velocity discrimination for fast velocities (≥ 5 deg/sec) depends on a common range of temporal frequencies centered on about 5 Hz. One interpretation of this finding is that the temporal filtering characteristics of all "fast" velocity mechanisms are nearly identical. If this were true, velocity tuning would depend chiefly on the spatial properties of the underlying mechanisms. In its simplest form, this view would argue for the existence of "velocity metamers"*—incremental changes in

*This term is borrowed from color vision where it is well-known that very different spectral distributions are indistinguishable, a consequence of the very limited dimensionality of the tri-chromatic system.

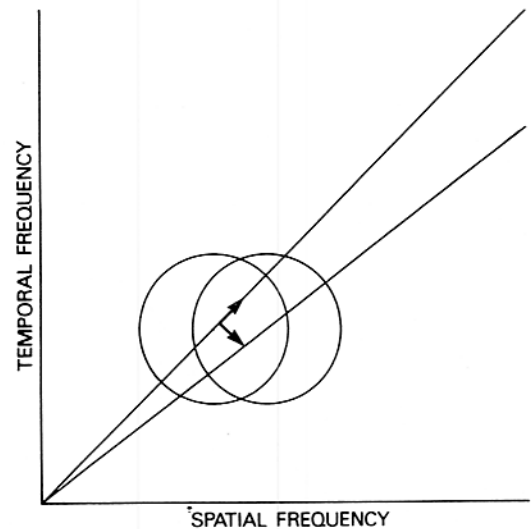


Fig. 8. Fourier representation of two spatio-temporal filters which would yield velocity "metamers". In this representation lines through the origin are the loci of constant velocity, the slope of this line being proportional to velocity. Two circles represent the isosensitivity profiles of the two spatio-temporal energy detectors. The two arrows represent changes in spatio-temporal energy, only one of which represents a change in velocity. Note, however, that either change will lead to identical ratios of signals for a pair of spatio-temporal energy detectors.

velocity which match incremental changes in spatial-temporal frequency without changing velocity. Figure 8 shows a spatio-temporal frequency representation of the velocity tuning for two hypothetical mechanisms which have the same temporal response; the diagonal lines indicate different velocities. If the perceived velocity depends on the ratio of the integrated stimulus energy detected by two or more overlapping mechanisms, then this ratio is unchanged whether the signal shifts downward to a different velocity (lower arrow) or outward along the same velocity line to a new combination of spatial and temporal frequencies. Our results show that human observers are never confused by these two events for short duration targets.

How does the human observer manage to discriminate between a shift in spatial-temporal frequency at the same velocity and a shift to a different velocity? One scenario invokes the existence of "stationary" spatial frequency detectors whose response declines monotonically with increasing temporal frequency (Adelson and Bergen, 1985; Thompson, 1984). While such mechanisms could easily remove the ambiguity diagrammed in Fig. 8, it is difficult to understand why these same detectors would not provide equally precise information about tem-

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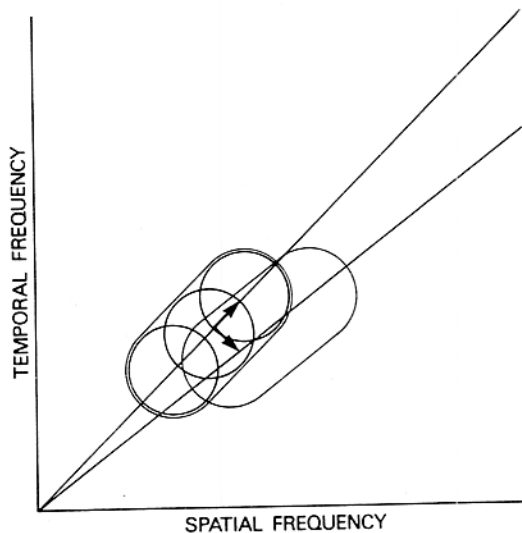


Fig. 9. Fourier representation of two hypothetical velocity detectors and their response to spatio-temporal energy changes. Velocity detectors (elliptical contours) are constructed from by summing spatio-temporal energy from subunits (circles) which share the same velocity. The spatio-temporal frequency sensitivity of such velocity detectors cannot be expressed as the product of spatial and temporal sensitivities. Note that the same change in spatio-temporal energy as shown in Fig. 8 (see arrows) will be discriminated by these hypothetical velocity detectors.

poral frequency; the thresholds for temporal frequency discrimination should match the velocity discrimination thresholds and they do not.

As an alternative, consider the arrangement drawn in Fig. 9: each velocity mechanism is served by multiple overlapping sub-units with different spatial and temporal frequency tuning but the same velocity tuning. All the signals from one velocity group are pooled and compared to the signals emerging from other adjacent velocity groups. Velocity discrimination would depend on the ratio of the pooled signals, an arrangement which would remove a significant dependence on suprathreshold contrast or spatial frequency. In contrast to the mechanisms proposed in Fig. 8, the changes depicted by the arrows would be easily distinguished. Newsome *et al.* reported the existence of units in MT which show exactly this type of behavior; the temporal frequency tuning of the response of these units depends on the spatial frequency of the target, consistent with a genuine response to velocity. One can speculate that the velocity units are actually built out of smaller sub-units optimally tuned to a particular spatial-temporal frequency combination. The broad tuning for spatial and temporal frequency noted in our results is consistent with this type of model. Moreover, if information

about temporal frequency is sensed indirectly via the underlying velocity mechanisms, then judging changes in temporal frequency would be more difficult than judging changes in velocity, which is exactly what we have demonstrated.

Our experiments are analogous to the crucial test for wavelength discrimination in the presence of fluctuations in luminance. If an observer can respond consistently to wavelength despite random variations in luminance, we conclude the observer has color vision. If an observer responds consistently to velocity despite random variations in temporal frequency, spatial frequency and contrast, we conclude he sees velocity.

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