Pattern perception at high velocities

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Background: When objects are stationary, human pattern vision is exquisitely acute. A number of studies show, however, that Vernier acuity for lines is greatly impaired when the target velocity exceeds about 5 deg $\sec^{-1}$. The degradation of line Vernier acuity under image motion appears to be a consequence of a shift in the spatial scale of analysis to low spatial frequencies. If correct, this implies that Vernier acuity may not be subject to a strict velocity limit, and that with appropriate low spatial frequency stimuli, Vernier acuity might be preserved at high velocities. To test this notion, we measured Vernier acuity and contrast discrimination using low spatial frequency periodic gratings drifting over a wide range of velocities.

Results: Vernier acuity and contrast discrimination for low spatial frequency periodic gratings are both possible at velocities as high as 1000 deg $\sec^{-1}$. When both are specified in the same units (as Weber fractions), Vernier acuities are closely predicted by the observers' contrast discrimination thresholds. Our results suggest that Vernier acuity is subject to a spatiotemporal limit, rather than to a strict velocity limit. At temporal frequencies less than about 10 Hertz, Vernier acuity is independent of velocity, but is strongly dependent on stimulus contrast. At high temporal frequencies Vernier acuity is markedly degraded, and shows little dependence on contrast.

Conclusions: Two mechanisms, which may have their neuronal counterparts early in the visual pathway, appear to limit the perception of moving targets at low and high temporal frequencies. Taken together with other recent work the present results suggest that the process of spatio-temporal interpolation in pattern analysis can operate at very high velocities.

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Background

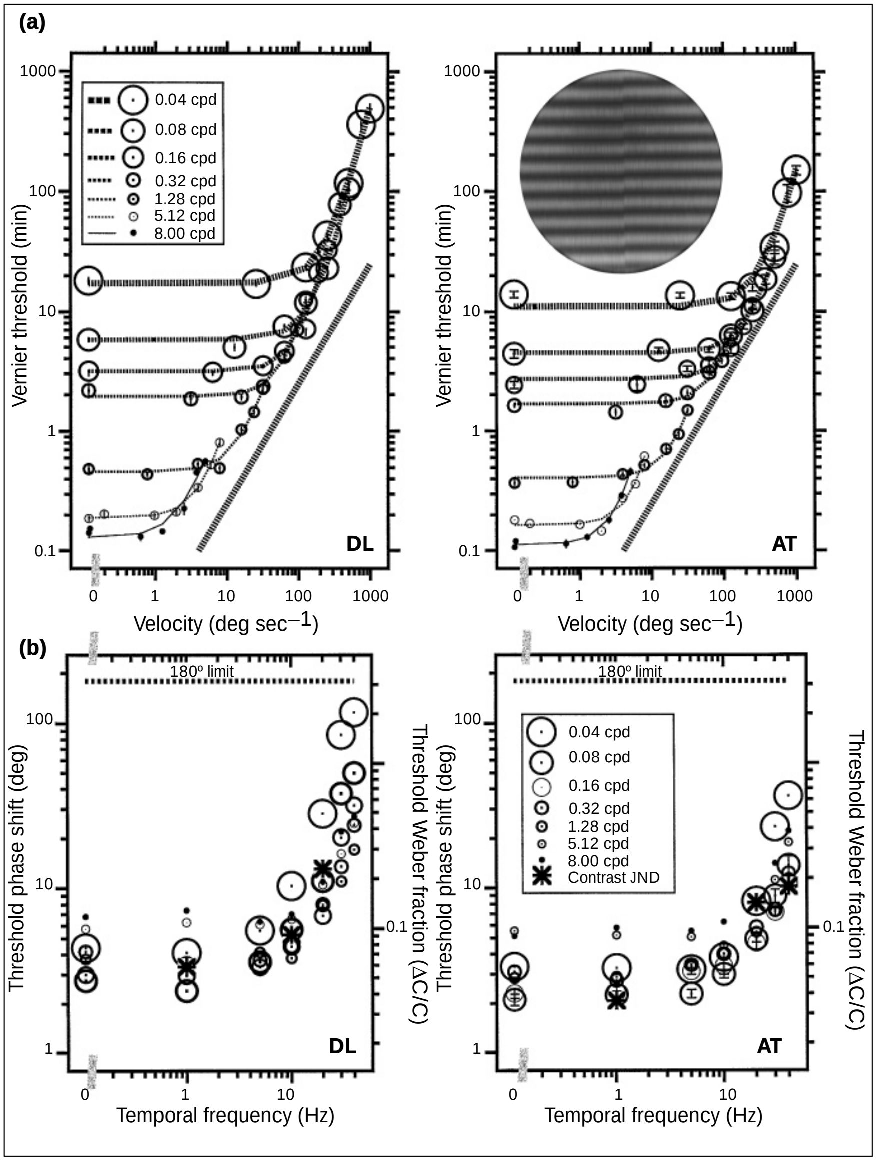
When objects are stationary, human pattern vision is exquisitely acute. For example, we are capable of discriminating a Vernier offset much smaller than the size of a foveal photoreceptor [1]; however, Vernier acuity for lines is degraded when the target velocity exceeds about 5 deg $\sec^{-1}$ [2–4]. Recent work suggests that the degradation of line Vernier acuity under image motion is a consequence of a shift in the spatial scale of analysis to low spatial frequencies [4]. If correct, this implies that Vernier acuity may not be subject to a strict velocity limit and, with appropriate low spatial frequency (large) stimuli, that Vernier acuity might be preserved at high velocities. In line with this notion, recent experiments suggest that the limitation on moving-line Vernier acuity might be a spatiotemporal one [4–6], as it is for stereoacuity [6], rather than a strict velocity limit. To test this idea, Vernier acuity was measured over a wide range of velocities using sinusoidal gratings (inset in Fig. 1a). By varying the spatial frequency (SF) of the grating — the number of cycles per degree (cpd) of visual angle — target velocity (V in deg $\sec^{-1}$) and temporal frequency (TF in Hertz) could be manipulated independently [6,7]. Temporal frequency is the rate of flicker of a fluorescent lamp, for example. Applied to a moving target, it is the rate of flicker at a photocell as the pattern moves over it. Velocity, in degrees per second, is the number of times per second that an object whirled on a bit of string would go round the head. For sinusoidal gratings, $V = TF/SF$.

Here, I report that Vernier acuity is not subject to a strict velocity limit. Vernier and contrast discrimination, like contrast sensitivity [7] and stereopsis [6], are feasible with low spatial frequency gratings at velocities as high as 1000 deg $\sec^{-1}$. At low temporal frequencies, Vernier acuity is strongly dependent on stimulus contrast; at high temporal frequencies, Vernier thresholds show much weaker dependence on contrast. Different mechanisms, which may have their neuronal counterparts early in the visual pathway, appear to limit the perception of moving targets at low and high temporal frequencies.

Results

Two highly experienced observers, AT and DL, were shown sinusoidal gratings. The gratings were displaced vertically (randomly up or down), and the task was to judge whether the right grating was higher or lower than the left one, and to rate the magnitude of the offset. For contrast

Figure 1



(a) Vernier threshold (min arc) as a function of velocity. The inset illustrates the stimuli (horizontal, sinusoidal gratings with a Vernier offset between the left and right gratings). Michelson contrast was 85 %. The oblique line indicates a temporal delay between the right and left gratings (spatial offset divided by velocity) of 0.67 msec. This limit [5,6] is consistent with the 10 Hz corner frequency (below). **(b)** The data are replotted with the left ordinate specified as a phase shift, and the abscissa as the temporal frequency. The horizontal dotted line represents the 180 phase shift limit for Vernier acuity. The right ordinate shows Vernier thresholds specified as a Weber fraction (ΔC/C; see Materials and methods), and the asterisks show contrast discrimination thresholds specified in the same way (ΔC/C) where C, the pedestal contrast, was 60 %.

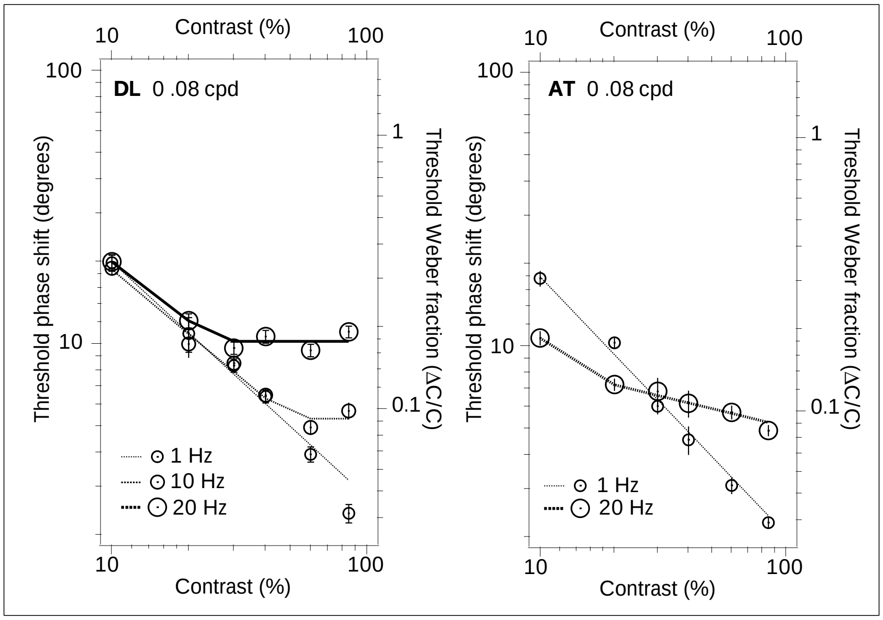
discrimination thresholds, the gratings were aligned and the observer judged whether the contrast of the right grating was higher or lower than that of the left grating.

Vernier thresholds were strongly dependent on stimulus spatial frequency (Fig. 1a). For each spatial frequency, thresholds were fairly constant over a range of velocities, and then increased in rough proportion to the target velocity. Above the ‘corner velocity’, Vernier thresholds were independent of spatial frequency. The corner velocity increased as spatial frequency decreased, consistent with a temporal limit rather than a strict velocity limit. The oblique line in Figure 1a indicates that there was a limiting temporal delay of 0.67 milliseconds between the right and left gratings — the threshold spatial offset divided by velocity. This temporal delay limit [5,6] may simply reflect the temporal tuning of cortical neurons with a corner frequency of approximately 10–20 Hertz (see below).

When the results were replotted as a function of temporal frequency, the strong influence of temporal frequency could be seen (Fig. 1b; the left ordinate is specified as the threshold spatial phase shift). For temporal frequencies below about 10 Hertz, the threshold phase shift was, on average, about 3 degrees, similar to thresholds reported for static sinewave Vernier [8], and to the best thresholds for stereopsis [6]. At higher temporal frequencies, the threshold phase shift increased sharply. Note that, even at the lowest spatial frequency (0.04 cpd) and highest temporal frequency (40 Hertz), corresponding to 1000 deg sec^{-1},

Figure 2

Threshold phase shift *versus* grating contrast (left ordinate) for a 0.08 cpd grating drifting at 1, 10 or 20 Hz (12.5, 125 or 250 deg sec^{-1}). The right-hand ordinate shows the Vernier thresholds specified as a contrast Weber fraction (ΔC/C) [8,9].



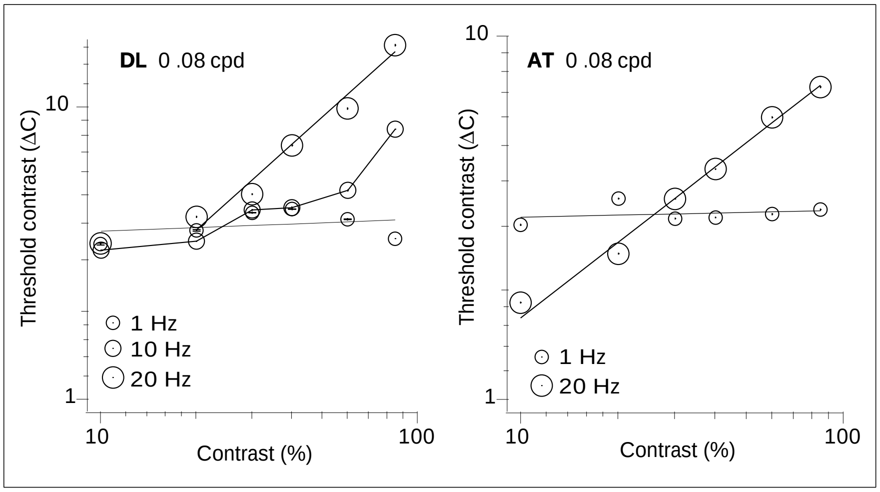
Vernier acuity was below the theoretical limit of a 180 degree phase shift (dotted line in Fig. 1b).

The asterisks in Figure 1b show that contrast discrimination thresholds (expressed as a Weber fraction — ΔC/C; right ordinate) followed a similar function of temporal frequency, and that when Vernier thresholds were expressed in the same units (ΔC/C; see Materials and methods), they were closely similar (see also [8,9]). This result is consistent with computational models of Vernier acuity based on the assumption that Vernier acuity is limited by the observers' ability to discriminate local contrast differences [8–12]. There is a strong effect of temporal frequency on both Vernier and contrast discrimination at high contrast levels; however, even at high temporal frequencies (corresponding to velocities approaching 1000 deg sec^{-1}) contrast Weber fractions were well below the theoretical limit (ΔC/C = 1).

In Vernier acuity, as in life, contrast is critical [8,9,12,13]. Strong contrast dependence occurred at low temporal frequencies, resulting in low Vernier thresholds, but broke down at high temporal frequencies, where Vernier thresholds asymptote as contrast was increased (Fig. 2). The differential effect of contrast at low and high temporal

Figure 3

Vernier thresholds of Figure 2 are replotted with the ordinate specified as a contrast increment threshold (ΔC) rather than as Weber fraction (as in Fig. 2).



frequencies is quite striking: at low temporal frequencies the effect of contrast is strong; at high temporal frequencies it is weaker.

Discussion

The present results suggest two separate limitations on pattern vision: at low temporal frequencies, Vernier acuity is a constant small phase shift, and is strongly dependent on contrast. A phase shift of approximately 3 degrees could be detected by orientation-tuned cortical mechanisms, and corresponds to a constant orientation cue (approximately 1 degree) if the length of the mechanism scales with spatial frequency. Orientation-tuned cortical neurons respond to Vernier offsets [14], and at least some individual cortical neurons are sensitive to orientation changes on the order of 1 degree [15]. At temporal frequencies above about 10 Hertz, Vernier acuity degrades sharply, and shows little dependence on contrast. The different contrast dependence at low and high temporal frequencies is qualitatively consistent with recent data on contrast discrimination for flickering stimuli [16], for contrast discrimination at very low spatial frequencies (D.M.L., unpublished observations), and for speed perception [17].

The data presented here are at least partially consistent with the known properties of neurons in the retina and lateral geniculate nucleus which provide inputs to the cortex. The strong dependence of Vernier (expressed as $\Delta C/C$) on contrast at low temporal frequencies indicates that the local contrast cue (ΔC) is nearly independent of contrast (Fig. 3), consistent with the linear behaviour of low gain neurons in the parvocellular (P) pathway. The weak dependence of Vernier (expressed as $\Delta C/C$) on contrast at high temporal frequencies indicates that the local contrast cue (ΔC) is strongly dependent on contrast (Fig. 3), consistent with the high gain, saturating, magnocellular (M) pathway in the primate visual system [18–20]. M neurons are more sensitive than P neurons to stimuli which are high in temporal frequency [21], and low in spatial frequency, and lesions in the M pathway abolish perception of rapidly flickering stimuli [22], with little effect on static targets. These two pathways produce distinctive neural increment contrast functions [16], which are similar to those obtained here. Indeed, a recent physiological study of macaque retinal ganglion cells shows that M-cells show only a small (saturating) effect of the contrast of a Vernier target, whereas P-cells show a strong effect [23], similar to the effects seen in Figure 2. At high temporal frequencies, the present results seem consistent with the properties of the M pathway. Without additional knowledge of the effects of pooling and noise, it is less clear whether the strong contrast dependence of Vernier at low temporal frequencies is mediated by P-cells. Taken together with other recent work [6,7] the present results suggest that pattern analysis can operate at very high velocities and may involve the large spatio-temporal receptive fields which have been described psychophysically [24].

Materials and methods

Stimuli were generated by a Neuroscientific Venus, and displayed on a Tektronix 608 monitor with a mean luminance of 100 cd m^{-2}, and a frame-rate of 278 Hz. Spatial frequencies of 0.64 cpd and below, were viewed monocularly from 14 cm (with appropriate lenses). At this distance the circular field had a diameter of 37 degrees. Higher spatial frequencies were viewed at proportionally larger distances. Gratings were moved at the desired rate by displacing them vertically (randomly up or down). To preclude tracking, stimulus duration was 150 msec. The observers' task was to judge whether the right grating was higher or lower than the left one, and to rate the magnitude of the offset [8]. Thresholds were estimated using signal-detection methodology [8], and represent the offset required for 84 % correct performance. Thresholds are the weighted mean of at least four runs (125 trials per run).

To specify Vernier acuity as a contrast Weber fraction, the local contrast increment was calculated. The contrast increment produced by the introduction of a Vernier offset

$$\begin{aligned} &= (C\cos(2\pi fx + \phi) - C\cos(2\pi fx - \phi))/2 \\ &= \Delta C \sin(2\pi fx) \qquad (1) \end{aligned}$$

where ΔC is given by:

$$\Delta C = C\sin(\phi) \qquad (2)$$

where C is the pedestal contrast, x is the position in degrees, f is the spatial frequency in cpd and the phase shift, ϕ, can be expressed in terms of the threshold displacement, d (degrees) by:

$$\phi = 2\pi fd \qquad (3)$$

Contrast discrimination thresholds (asterisks in Fig. 1b) were measured under identical conditions, except that the observers' task was to judge whether the right-hand grating (pedestal plus test) had lower or higher contrast than the left-hand grating (pedestal alone). For contrast discrimination tasks, the test grating was similar to equation (2), except that it was in phase with the pedestal instead of being 90 degrees out of phase:

$$= \Delta C \cos 2\pi fx \qquad (4)$$

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