



Temporal phase discrimination depends critically on separation

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Received 20 August 2001; received in revised form 28 January 2002

Abstract

Temporal phase discrimination was measured as a function of spatial separation of the stimulus components. In contrast to many previous studies, phase discrimination thresholds were measured directly, rather than inferred from the ability to discriminate synchronous from antiphase stimuli, or from segregation or shape tasks. For abutting bars, relative phase thresholds were closely proportional to temporal frequency. The proportionality corresponded to a threshold temporal offset of 2.5–9.5 ms, across subjects. Introduction of a small gap (0.125° or greater) led to a dramatic (3- to 7-fold) increase in thresholds for temporal phase discrimination, and thresholds were no longer proportional to temporal frequency. Insertion of a third bar filling the gap resulted in a recovery of the low thresholds, provided that its modulation was consistent with apparent motion across the three bars. Below 8 Hz, phase discrimination thresholds across three bars were equivalent to thresholds for two abutting bars. Above 8 Hz, phase discrimination thresholds for the three bar combination were lower than thresholds for two adjacent bars, implying that phase information was integrated across all three bars.

Phase discrimination thresholds do not appear to reflect the properties of a single mechanism. Especially at high temporal frequencies, low thresholds for phase discrimination are closely tied to the presence of apparent motion. Temporal phase discrimination is markedly impaired by a small separation of stimulus components. Moreover, the inability to detect phase differences across gaps corresponds to the loss of phase-dependence of vernier acuity thresholds across gaps.

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1. Introduction

Vernier acuity and the formation of illusory contours are two manifestations of the processing of local features by early vision. Vernier acuity thresholds for abutting stimuli of like polarity are several times lower than thresholds for stimuli of opposite polarity (Levi & Westheimer, 1987; Mather & Morgan, 1986; O'Shea & Mitchell, 1990). This strong polarity dependence falls off markedly when stimuli are separated by a gap (Levi, Jiang, & Klein, 1990; O'Shea & Mitchell, 1990; Waugh & Levi, 1993). An analogous observation holds for sinusoidally luminance-modulated vernier targets: there is a strong dependence of displacement thresholds on temporal phase when stimuli are abutting (Victor & Conte, 1999), but nearly no dependence with separations as small as 8 min (Victor & Conte, 2000a).

Illusory contour formation, on the other hand, is relatively independent of the luminance phase of the

inducers. Small polarity-dependent changes in the strength of illusory contours have been observed for a variety of static stimuli, using both subjective measures of illusory contour strength (He & Ooi, 1998), and objective but indirect measures (Spehar, 2000; Victor and Conte, 2000a). However, in contrast to vernier acuity, there is virtually no effect of relative temporal phase of dynamic inducers on illusory contour strength (Fahle & Koch, 1995; Victor & Conte, 2000a).

These observations are consistent with the notion that there are two regimes underlying the processing of the stimulus components (see further discussion in Victor and Conte (1999)). In the local regime, performance is governed by individual receptive fields or spatial filters (Klein & Levi, 1985; Wilson, 1986), and is thus sensitive to stimulus polarity (as well as contrast, orientation, and spatial frequency). In the long-range regime, the position of activated local filters is encoded (Burbeck, 1987; Kooi, De Valois, & Switkes, 1991; Levi & Waugh, 1996; Morgan, Ward, & Hole, 1990). Performance is limited by the positional uncertainty of this encoding process, and is thus insensitive to the details of the stimulus parameters. While this view was originally proposed to

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account for vernier performance, it would appear to apply equally well to other aspects of integration of stimulus components across space, including illusory contour formation and linking (Field, Hayes, & Hess, 1993; Kovacs & Julesz, 1993).

Thus, the interactions of temporal phase and position seen in vernier and illusory contour paradigms may reflect a more general aspect of the difference between local and longer-range processing. In particular, we hypothesize that the loss of sensitivity to temporal phase with increasing distance between stimulus components, independent of whether the stimulus components are used to make a spatial judgment, suffices to account for the lack of a temporal phase effect on illusory contour strength. However, there is a problem with this view. When *static* inducers have opposite polarity, the strength of the illusory contour is weakened (He & Ooi, 1998; Spehar, 2000; Victor & Conte, 2000a). Some previous studies of the frequency dependence of phase discrimination suggest that phase thresholds increase as temporal frequency decreases from 4 Hz towards DC (Forte, Hogben, & Ross, 1999). Others were performed with non-sinusoidal stimuli (Fahle, 1993; Kandil & Fahle, 2001; Leonards, Singer, & Fahle, 1996), so that the frequency dependence was unclear. Moreover, these studies used a grouping (Fahle, 1993; Kandil & Fahle, 2001) or segregation (Forte et al., 1999; Leonards et al., 1996) task as a surrogate for phase discrimination. If indeed phase discrimination worsens as temporal frequency decreases, it would be difficult to account both for the fact that illusory contour strength is independent of relative phase for *flickering* stimuli, but does depend on relative polarity of the inducers for *static* stimuli. Rather, one would have to postulate that illusory contour formation has a fundamentally different dependence on the temporal aspects of the stimulus than does vernier acuity.

Our experiments measure temporal phase discrimination thresholds directly for a simple stimulus configuration and sinusoidal contrast modulation. In contrast to previous studies described above, we find that phase discrimination thresholds improve monotonically with decreasing frequency. In common with a previous study (Forte et al., 1999) that examined the interaction of component separation, we also find a profound increase in threshold when components are separated. This dependence is sufficiently strong to account for the disparate dependence of vernier acuity and illusory contour formation on temporal phase, without invoking differential use of temporal information by vernier alignment and illusory contour formation.

The studies mentioned above (Fahle, 1993; Forte et al., 1999; Kandil & Fahle, 2001; Leonards et al., 1996), as well as others (Farid & Adelson, 2001; Lee & Blake, 1999a,b), have emphasized how temporal phase can influence segregation and grouping. Here we demonstrate

the converse: that temporal phase discrimination depends markedly on spatial context. By adding stimulus components that are neutral as far as providing phase information, but which either facilitate or inhibit the percept of apparent motion, temporal phase thresholds can be made to vary dramatically. This suggests a close relationship between mechanisms of temporal phase discrimination and apparent motion.

2. Methods

2.1. Subjects

Studies were conducted in nine normal subjects (three male, six female), ages 21–46. Subject MC participated in both experiments; the remaining subjects were naïve to the purpose of the experiments but underwent substantial practice, as described below. All subjects were practiced psychophysical observers and had visual acuities (corrected if necessary) of 20/20 or better.

2.2. Display

Visual stimuli were produced on a Sony Multiscan 17seII monitor, with signals driven by a PC-controlled Cambridge Research VSG2/3 graphics processor programmed in Delphi II. The resulting 768×1024 pixel display had a mean luminance of 81 cd/m^2 , a refresh rate of 100 Hz and subtended $11^\circ \times 15^\circ$ (approximately 1 min/pixel) at the viewing distance of 114 cm. The intensity vs. voltage behavior of the monitor was linearized by photometry and lookup table adjustments provided by VSG software.

2.3. Visual stimuli

The basic visual stimulus consisted of two aligned horizontal bars ($0.125^\circ \times 1.0^\circ$, maximal contrast $c = 0.8$) presented centrally (Fig. 1A). The edges of the bars were blurred by a Gaussian along the vertical axis, to match precisely the stimuli used in previous vernier experiments (Victor & Conte, 1999, 2000b). Bars were sinusoidally flickered at the same frequency f (2, 4, 8, 12, or 16 Hz). The temporal phases of the two bars differed by an amount $\Delta\phi$, with the leading phase randomly assigned to either the left or the right bar. Stimuli were presented for a time $T = 1 \text{ s}$, windowed by a cosine bell. From trial to trial, the starting phases of the bars were randomized so that initial phase of either bar was not available as a cue to phase difference. Thus, for a trial characterized by temporal frequency f and relative phase $\Delta\phi$, the temporal signal that modulated the contrast of the two bars was:

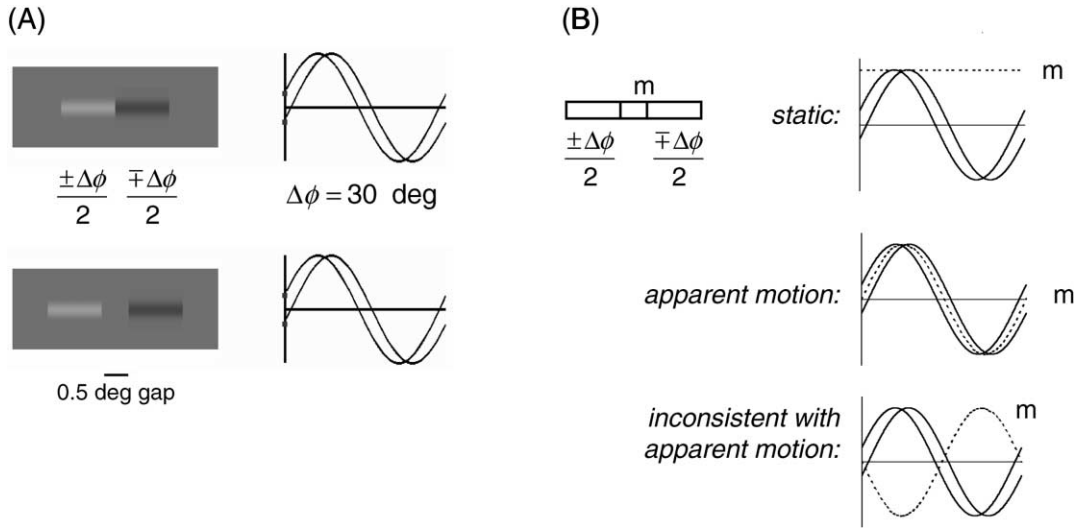


Fig. 1. (A) A diagram of the two-bar stimuli. Left: grayscale image of the center panel of the display during a frame in which the bars have opposite luminance polarity. Right: time course of contrast modulation for the two bars, for a phase difference $\Delta\phi = 30^\circ$. (B) A diagram of the three-bar stimuli. Left: diagram showing the spatial configuration. Right: time course of contrast modulation for the three varieties of three-bar stimuli.

$$c_{\text{left}}(t) = c \frac{1 - \cos(2\pi t/T)}{2} \cos \left[2\pi \left(ft + \frac{\phi_{\text{init}}}{360} + s \frac{\Delta\phi}{180} \right) \right]$$

and

$$c_{\text{right}}(t) = c \frac{1 - \cos(2\pi t/T)}{2} \cos \left[2\pi \left(ft + \frac{\phi_{\text{init}}}{360} - s \frac{\Delta\phi}{180} \right) \right],$$

where phases are expressed in degrees, and the initial mean phase ϕ_{init} is chosen randomly around the unit circle, and s is randomly assigned to +1 or -1.

In some experiments, a third bar was placed in a gap between the left and right bars in one of three modes. The length of the third bar was equal to the size of the gap (see Fig. 1B). In the “static” variation, its contrast was determined by the cosine bell temporal window alone:

$$c_{\text{middle:unmod}}(t) = c \frac{1 - \cos(2\pi t/T)}{2}.$$

In the “apparent motion” variation, it was modulated at the frequency f , and the phase was halfway between that of the left and right bars:

$$c_{\text{middle:AM}}(t) = c \frac{1 - \cos(2\pi t/T)}{2} \cos \left[2\pi \left(ft + \frac{\phi_{\text{init}}}{360} \right) \right].$$

In the “inconsistent with apparent motion” variation, the modulation signal was in antiphase to the apparent motion variation.

For production of these stimuli, the contrast values $c_{\text{left}}(t)$, $c_{\text{right}}(t)$, and $c_{\text{middle}}(t)$ were recomputed for each value of $\Delta\phi$ and ϕ_{init} , rather than simply shift a standard profile. This enabled accurate rendering of phase shifts that corresponded to far less than the 10 ms interframe interval of the display.

2.4. Psychophysical procedures

Subjects were asked to judge which of the two bars led the other in temporal phase. Thresholds (71% correct) were determined by a 2-AFC staircase procedure, without feedback, but only after substantial practice and stabilization of performance. Practice was initially with feedback and longer presentation times (2–4 s). Most subjects noted an apparent motion cue, and that at high temporal frequencies (12 and 16 Hz), the interface between the two bars appeared to pulsate or bleed from one bar to the other. Subjects who did not notice these cues spontaneously were acquainted with them early in the practice sessions. Over the 3–4 h of practice required for performance stabilization, presentation times were gradually reduced to 1 s and feedback was eliminated. Brief “refresher” practice trials were given at the beginning of each session of data collection. Once performance had stabilized during training, feedback was eliminated during data collection to reduce the likelihood that learning would take place (Herzog & Fahle, 1997).

Since relative phase is a cyclic quantity, there are potential difficulties in using a staircase method to measure thresholds (Mechler & Victor, 2000). Random responses would eventually lead to reversals of the staircase parameter, and the phase discrimination threshold might appear to be finite. To guard against this, we aborted a staircase if the staircase parameter approached 180° . Moreover, we only accepted a completed staircase as defining a valid threshold if the fraction of correct answers in the staircase was not statistically different from 71% correct (by a chi-squared test).

Relative phase discriminations are expected to be difficult not only near $\Delta\phi = 0$ but also near $\Delta\phi = 180$. Based on this as well as on the analogy with apparent motion (e.g., Nakayama & Silverman, 1985) one would expect that relative phase discrimination would be easiest in the quadrature condition, namely $\Delta\phi = 90^\circ$. Because of this consideration, the psychophysical staircase began with a relative phase parameter of $\Delta\phi = 30^\circ$. In the first two staircase reversals, relative phase changed by an octave; in the subsequent reversals, relative phase changed by one-third of an octave. For each completed staircase that satisfied the above criteria of fraction correct and non-divergence, a threshold was determined by the geometric mean of the final eight reversals. This procedure provided a margin of safety in case one of the initial responses was spuriously incorrect, and avoided excessively long staircases for conditions in which the threshold was substantially below 30° .

For each condition, 24 staircases (conditions with no gap) or 12 staircases (conditions with gaps) were run in block-randomized order balanced across subjects. For some conditions, typically those with high temporal frequencies, few if any of the staircases met the above criteria for validity. In these cases, we considered the threshold to be greater than 90° , the largest value that could be reliably measured. (Note that occasionally staircases would converge to thresholds of greater than 90° . If these staircases met the above validity conditions of fraction correct and non-divergence, then the threshold derived from the average of the final eight reversals was accepted.) If at least 2/3 of the staircases met the validity criteria, an overall threshold was determined from the geometric mean of the thresholds across the valid staircases. Confidence limits on these threshold measures were determined by *t*-tests applied to the logarithm of the thresholds estimated from each staircase.

3. Results

3.1. Experiment I: interaction of gap and temporal frequency

Fig. 2 shows the dependence of relative phase threshold on gap size at 4 Hz, for four of the five subjects who participated in this experiment. With no gap between the bars, phase thresholds ranged from approximately 4° to 15° , corresponding to a temporal shift of 3–10 ms. Phase discrimination thresholds increased as a gap between the bars was introduced. In all subjects, most of this elevation occurred with the smallest gap tested, 0.125° . Error bars are smallest for the no-gap condition because these measurements were derived from twice as many staircases as the other conditions. Thresholds became more variable once they exceed approximately 30° . This reflects the instabilities of the

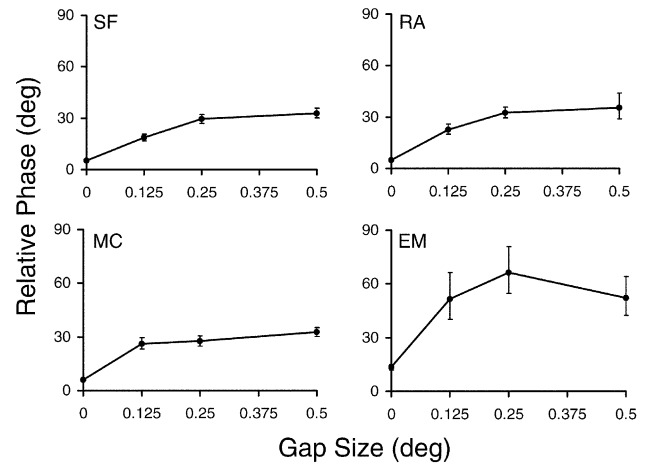


Fig. 2. Temporal phase discrimination thresholds for bars modulated sinusoidally at 4 Hz, as a function of gap size. Error bars represent $\pm 95\%$ confidence limits (two-tailed *t*-test) based on repeated staircases (24 for gap = 0, 12 for gaps > 0).

staircase procedure as described in Section 2. Comparable behavior of thresholds was seen at 2 and 8 Hz, with threshold elevations associated with a gap of 0.125° ranging from 3- to 7-fold and 5- to 10-fold for a gap of 0.5° .

Fig. 3 examines the same dataset as a function of temporal frequency, for the two extremes of gap size examined. With no gap, the dependence of phase threshold on temporal frequency was well approximated by a straight line with a *y*-intercept near zero, i.e., a proportionality. A proportionality of phase threshold and temporal frequency (i.e., a straight line with a *y*-

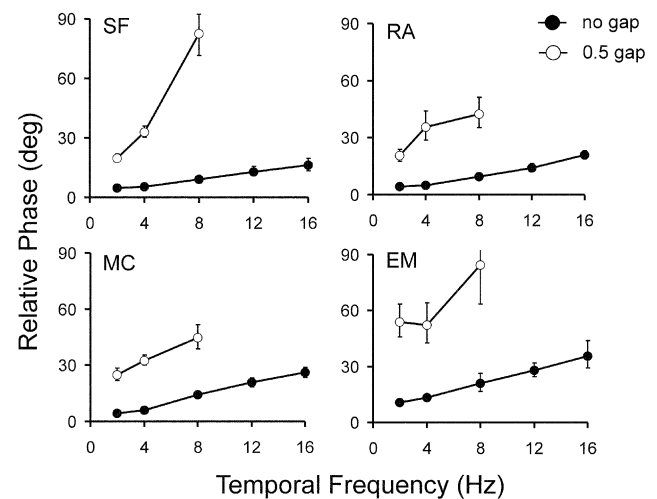


Fig. 3. Temporal phase discrimination thresholds for abutting bars (filled symbols) and bars separated by a gap of 0.5° (open symbols), as a function of temporal frequency. Missing data points represent conditions in which staircases diverged, indicating thresholds of greater than 90° , as detailed in Section 2. Error bars as in Fig. 2.

intercept of 0) is the expected behavior for phase discrimination if it were limited by a critical timing difference. With the introduction of a gap, phase thresholds became unmeasurable (i.e., greater than 90°) at 12 and 16 Hz. Even though there were only three temporal frequencies for which phase thresholds were measurable (2, 4, and 8 Hz), inspection of the 0.5° gap data (Fig. 3) suggests that the dependence of phase threshold on temporal frequency was no longer well described by a proportionality, at least for subjects MC, EM, and RA.

This difference between thresholds without a gap (near proportionality) and thresholds with a gap (not well described by proportionality) is confirmed by a regression analysis, summarized in Table 1. Phase threshold $\Delta\phi_{\text{threshold}}$ was regressed against temporal frequency f , $\Delta\phi_{\text{threshold}} = mf + b$, for each of the 15 datasets (five subjects, three gap sizes). For the no-gap data (Fig. 3, filled symbols), the estimated y -intercepts varied from 0.6° to 7.1°, and only two were significantly different from 0 (subjects EM and SF). For the 0.5° gap data (Fig. 3, open symbols), the estimated y -intercepts ranged from -5.6° (subject SF) to 41.0° (subject EM), and four of the five were significantly greater than 0 (all but subject SF). For 10 of the 15 gap conditions, the y -intercept was significantly larger than for the corresponding no-gap condition in the same subject, and it was never significantly lower. Across subjects, average y -intercepts were 2.3° (no gap), 16.3° (gap of 0.125°), 18.9° (gap of 0.25°), and 19.3° (gap of 0.5). There is an abrupt rise in the y -intercept between the no-gap condition and the 0.125° gap condition, but little further rise beyond that. This suggests a qualitative difference between performance without a gap and performance with a gap, regardless of gap size.

To the extent that the thresholds are well fit by a proportionality, the regression slope m can be converted into a timing difference (in ms) by $T_{\text{crit}} = (m/360) \times 1000$. Values of T_{crit} estimated in this fashion ranged from 2.5 ms (subject SF) to 9.5 ms (subject AC), with a mean of 5.0 ms across subjects. Subject AC also had the most variable thresholds.

3.2. Experiment II: dependence on what fills the gap

Since phase discrimination threshold was elevated dramatically by a small gap, we next examined thresholds in related stimuli. A third bar was inserted that matched the two end bars in contrast, dynamics, or both. In the static variation, the third bar was held at the peak contrast of the modulated bars. In the apparent motion variation, the third bar was modulated at the same temporal frequency, and at a phase halfway between that of the two end bars. In both cases, when the end bars were at their peak contrast, all components of the stimuli matched in contrast. At these instances, they could be perceived as a single object. However, the bar itself provided no cue as to the correct response. There was no relative phase information at the interface between an end bar and the central bar in the static variation. The relative phase shift at this interface in the apparent motion variation was $\pm\Delta\phi/2$, half of the overall phase shift between the left and right bars. A third variation, “inconsistent with apparent motion”, was similar to the apparent motion variation, but with an inverted polarity of the middle bar. In this stimulus, the phase shift at the interface between the end bars and the central bar was $\pm(\Delta\phi/2) + 180$. These three variations are diagrammed in Fig. 1B.

In Fig. 4, the upper panels show that when the phase of the third bar is consistent with apparent motion across the three bars, phase discrimination thresholds approximate the low thresholds seen for two bar stimuli. However, a static bar results in very little improvement over the thresholds measured in the presence of a gap, as seen in the lower panels. Only the two subjects whose data are shown had measurable thresholds over the entire frequency range for these conditions. For the “inconsistent with apparent motion” condition, all subjects were unable to perform the task at better than chance levels despite extensive practice.

As shown in Fig. 5, the slight difference between the apparent motion condition and the no-gap condition was consistent across subjects, and had systematic

Table 1
Regression analysis for thresholds as a function of temporal frequency in the absence of a gap, and with the three gap sizes

	No gap		Gap size					
			0.125°		0.25°		0.5°	
	y -int	T_{crit}	y -int	T_{crit}	y -int	T_{crit}	y -int	T_{crit}
MC	0.9 (0.5)	4.6 (0.2)	10.6 (2.1)	10.5 (1.1)	14.9 (3.7)	10.4 (2.0)	18.8 (2.8)	9.5 (1.5)
EM	7.1 (1.3)	5.3 (0.4)	38.3 (6.9)	11.3 (3.7)	62.3 (9.3)	7.5 (5.0)	41.0 (8.1)	14.5 (4.5)
RA	0.7 (0.4)	3.3 (0.1)	4.8 (3.4)	14.8 (1.8)	0.1 (4.5)	23.5 (2.4)	17.5 (4.4)	10.1 (2.3)
AC	0.6 (2.5)	9.5 (0.8)	20.3 (6.2)	20.9 (3.3)	16.7 (7.1)	27.0 (3.8)	25.1 (8.3)	22.9 (4.3)
SF	2.4 (0.5)	2.5 (0.2)	7.5 (1.9)	8.0 (1.0)	0.8 (3.6)	21.8 (1.9)	-5.6 (4.2)	30.6 (2.2)

Regressions are based on the thresholds from each staircase, i.e., multiple measures at each temporal frequency. Regression slopes m and their standard errors are quoted in terms of an equivalent timing difference in milliseconds, namely, $T_{\text{crit}} = (m/360) \times 1000$. Standard errors for each value are shown in parentheses.

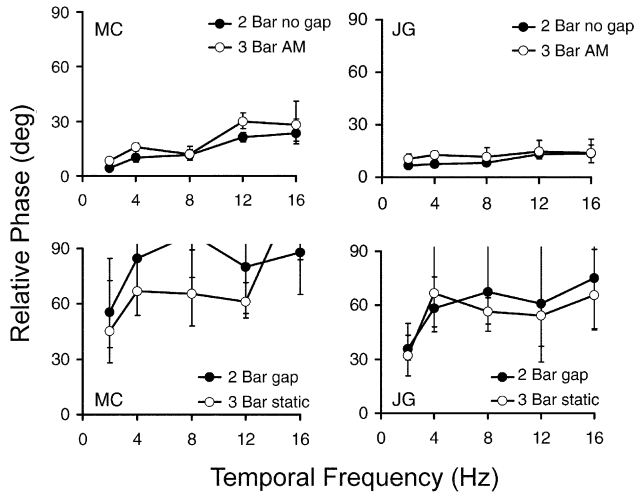


Fig. 4. Comparison of phase discrimination thresholds for abutting bars (two bar no gap) and three variations of stimuli in which the bars are separated by a gap (three bar AM, two bar gap, three bar static). For the three-bar “inconsistent with apparent motion” condition, no subjects were able to complete any valid staircases, indicating thresholds of $>90^\circ$. These data are not plotted. Gap size: 0.5° . Error bars as in Fig. 2.

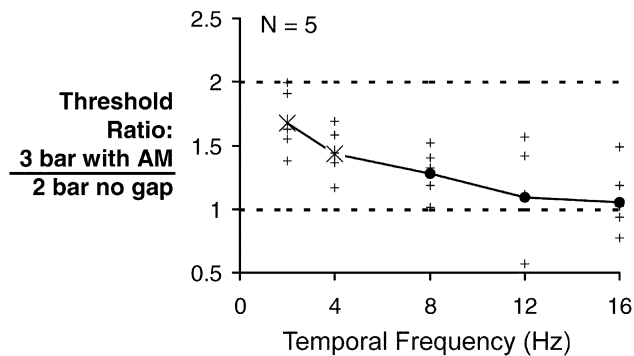


Fig. 5. Geometric mean (large symbols) across subjects and individual subject values (+) of threshold ratios for phase discrimination for three bars in the apparent motion condition and the no-gap condition. Data points marked by asterisks are significantly different from 1 via a paired *t*-test (one-tailed, applied to the logs of the thresholds).

temporal frequency dependence. The threshold ratios declined monotonically with increasing temporal frequency, approaching 2 at low temporal frequencies and 1 at high temporal frequencies. A threshold ratio of 2 would indicate that at threshold, the phase difference between adjacent bars (end and middle) of the three bar configuration matched the phase difference between the two bars in the no-gap condition. However, at high temporal frequencies, phase thresholds for the two stimuli were nearly identical, indicating that the phase difference between the end bars corresponded to the threshold phase in the two bar condition. This suggests that at high frequencies, phase information in the three-bar stimulus was integrated across both interfaces, because the phase discrimination at each interface alone

was half of threshold. Nevertheless, the middle bar was demonstrably used, since in its absence, thresholds were substantially higher, as shown in the lower half of Fig. 4. This shift from a local strategy to a global strategy was also consistent with the subjects’ reports that they used a particular strategy—looking at an edge—at low temporal frequencies.

4. Discussion

4.1. A temporal mechanism?

Phase thresholds for abutting stimulus components are small and proportional to temporal frequency, and thus well described by a temporal limit (Fig. 3). Introduction of a small gap between the stimulus components leads to thresholds that are several times greater (Fig. 2) and no longer approximately proportional to temporal frequency (*y*-intercept data of Table 1). Moreover, the low thresholds seen for abutting stimulus components can be recovered by adding a stimulus component that is formally uninformative, but promotes the percept of apparent motion (Fig. 4). Thus, thresholds for temporal phase discrimination cannot be considered as the consequences of a purely temporal mechanism.

For drifting vernier targets, it has been previously shown that there is a wide range of conditions for which spatial displacement thresholds correspond to a fixed temporal offset (Carney, Silverstein, & Klein, 1995). However, one cannot infer that a purely temporal mechanism is responsible for these thresholds. In a previous study, we compared displacement thresholds for drifting vernier stimuli based on gratings with relative phase thresholds of stationary sinusoidal reversing gratings. Both of these thresholds can be converted into temporal equivalents. Although the stimuli were matched for temporal cues, the equivalent temporal threshold in the relative phase task was severalfold higher than for the vernier task (Mechler & Victor, 2000). Here we show that several manipulations of the stimulus that leave the temporal cues unchanged have a dramatic effect on phase discrimination thresholds. The conditions in which thresholds are lowest are the conditions that facilitate the perception of apparent motion. Thus, both phase discrimination and drifting vernier tasks, which might appear to be governed by temporal limits of vision, more likely reflect the operation of spatiotemporal mechanisms, especially those related to short-range motion (Braddick, 1974).

Westheimer and McKee (1977) studied thresholds for temporal order discrimination for transiently presented adjacent lines. They found similar thresholds of 3 ms under optimal conditions, a comparable elevation of threshold for very modest separations (above 6 min), and also noted that thresholds were increased by dich-

optic presentation. This study identified a stimulus configuration in which perception of apparent motion was not necessary for low thresholds. The stimulus components were presented as the horizontal and vertical arms of a cross, and were spatially overlapping but temporally asynchronous. It is likely, however, that local motion detectors lying between the arms of the cross nevertheless provide unambiguous signals as to temporal order, even though the spatial integration of these local signals do not lead to global apparent motion percepts (Curran & Braddick, 2000; Qian, Andersen, & Adelson, 1994) since they are locally balanced. That is, failure to perceive apparent motion likely reflects cancellation of nearby opposing local motion signals at a later stage of processing (Braddick, 1997), but local motion signals may still be available for extraction of temporal information.

The relationship between temporal phase discrimination and apparent motion is further strengthened by the results illustrated in Fig. 5. In the high-frequency regime, the threshold for discrimination of relative phase of two bars separated by a third modulated bar is identical to the threshold when the two bars are abutting. This performance cannot be accounted for by a comparison of the end bars alone, since performance at this phase difference was at chance when these bars are separated by a gap. It also cannot be accounted for by probability summation of signals originating from the subthreshold phase signals between either of the two end bars and the middle bar. Rather, it requires synergistic processing of signals across the entire stimulus, much as local motion signals are processed synergistically along a motion trajectory (Verghese, Watamaniuk, McKee, & Grzywacz, 1999; Watamaniuk, McKee, & Grzywacz, 1995). This synergy is specific to the temporal phase judgment, and was not observed for a vernier offset judgment in a comparable spatial configuration (Victor & Conte, 1999).

We can rule out explanations based on probability summation in two ways. First, using Quick’s approach (Quick, 1974) with the customary probability summation exponent β of 4, we would anticipate in the three bar configuration that probability summation of signals at the two interfaces would result in an observed threshold that was lower by a factor of $2^{1/4}$ from the 2-fold increase that one would expect from fully independent processing. (The independent processing expectation reflects the fact that the phase difference between the end bars, the quantity plotted along the abscissa in Fig. 5, is twice the phase difference at each interface.) The probability summation prediction, approximately a 20% reduction, likely accounts for the low-frequency behavior in Fig. 5. However, reduction by a factor of two would be required to account for the high-frequency findings, since at threshold for the three bar configuration, the phase difference at each interface is approxi-

mately half of the phase threshold for two abutting bars in isolation. The transition between the independent processing regime at low frequencies and the synergistic processing regime at high frequencies is gradual, but is complete by 12 Hz. This is consistent with the 100 ms integration time estimate obtained by Watamaniuk et al. (Fig. 9 of Watamaniuk et al. (1995)).

An information-theoretic analysis leads to the same conclusion that combination of subthreshold signals alone cannot account for the high-frequency behavior. Assuming that the psychometric function is approximately linear between a phase difference of 0 (50% correct) and the measured threshold (70.7% correct), we can estimate that at half the measured threshold, performance would be approximately 60% correct. In a 2-AFC task in which the subject makes optimal use of the information available, the information H required to achieve a fraction correct f is the transmitted information in the 2×2 table

$$\begin{bmatrix} \frac{f}{2} & \frac{1-f}{2} \\ \frac{1-f}{2} & \frac{f}{2} \end{bmatrix}.$$

The transmitted information in this table is given by (Cover & Thomas, 1991)

$$H(f) = 1 + f \log_2 f + (1 - f) \log_2 (1 - f).$$

Thus, $f = 60\%$ correct performance estimated at half-criterion corresponds to $H = 0.0311$ bits of information from the border between the central bar and each end bar. Accordingly, $2 \times 0.0311 = 0.0622$ bits of information would be available in the three bar configuration from the two interfaces combined (assuming complete independence). $H = 0.0622$ bits, translated back to performance in a 2-AFC task by the above relation, corresponds to $f = 65\%$ correct performance. This substantially underestimates measured performance, which is at the defined threshold level of $f = 70.7\%$ correct. (The information equivalent of this level of performance requires $H = 0.1274$ bits of information.)

4.2. Implications for dynamics in vernier acuity and illusory contour formation

Vernier acuity and illusory contour formation are two processes in early vision in which the perceptual relationship between tokens depends critically on their spatial alignment. For dynamic stimuli, vernier acuity thresholds are highly dependent on the relative phase of the stimulus components (Victor & Conte, 1999), while illusory contour formation is insensitive to stimulus phase (Victor & Conte, 2000a). The striking dependence of temporal phase sensitivity on the gap accounts for this difference.

For a vernier task with abutting contours, the peak sensitivity to relative phase is at approximately 4 Hz, and elevations of vernier thresholds begin at a phase offset of approximately 45° (Figs. 8 and 9 of Victor and Conte (1999)). As seen in Fig. 3 (filled symbols), this is approximately 6–10 times the phase discrimination threshold. Illusory contour stimuli, by their nature, require a gap between the stimulus components. In the presence of a gap, the phase discrimination threshold is elevated to more than 30° (open symbols in Fig. 3). That is, in the presence of a gap, phase offsets of 6–10 times the threshold, greater than 180°, simply cannot be achieved. In other words, one need not postulate that vernier and illusory contour formation have fundamentally different dynamics, but merely that phase information is only retained over very short distances. This is consistent with our findings (Victor & Conte, 2000a) that the temporal phase dependence of vernier thresholds is also eliminated by small gaps.

4.3. Comparison with studies of temporal phase and spatial grouping

In addition to the above study of Westheimer and McKee (1977), other workers have measured temporal phase thresholds for perceptual tasks (Fahle, 1993; Forte et al., 1999; Kandil & Fahle, 2001; Leonards et al., 1996). The primary goal of those studies was to examine the role of temporal factors in grouping (Fahle, 1993; Kandil & Fahle, 2001) or segregation (Farid & Adelson, 2001; Forte et al., 1999; Lee & Blake, 1999a,b; Leonards et al., 1996), rather than determination of the limits of phase discrimination. Consequently, those studies do not determine phase discrimination thresholds per se, nor how these thresholds depend on temporal frequency and spatial separation—the limits that our study was designed to measure.

In some of these studies, phase differences of modulated stimuli were parametrically varied (Kandil & Fahle, 2001; Leonards et al., 1996 #4). The equivalent temporal thresholds were approximately 10 ms in the best subjects, somewhat higher than our results (5 ms average across subjects). This may reflect the fact that phase discrimination was not directly measured, but rather, a surrogate task of grouping or segregation was used. The surrogate task may have placed additional “upstream” limits on performance. Fahle (1993) using a figure-ground segregation task, found a lower threshold of 5 ms across a wide frequency range (1.3–30 Hz), but stimuli were presented with abrupt onset and offset. Thus, it is unclear whether thresholds were governed by phase discrimination at the fundamental frequency of the stimulus, or rather, its higher harmonics.

In the only study in which the influence of spatial separation was explicitly examined (Forte et al., 1999), stimulus components were kept in counterphase, while

another stimulus parameter, such as contrast or temporal frequency, was varied. Our results of a dramatic effect of spatial separation agree with that Forte et al., but in other respects, our results differ. In particular, we find that phase sensitivity increases as temporal frequency decreases towards DC (as would be expected for an equivalent temporal threshold), while Forte et al. (1999) find that phase discrimination threshold increases below 4 Hz.

We suspect that this low-frequency difference stems from the fact that we measured phase discrimination directly (by reducing phase differences to the limits of detectability), while Forte et al. (1999) extrapolated phase thresholds from performance under counterphase conditions. There are two concerns with the latter approach. First, inferring thresholds for high-contrast stimuli presented with small phase differences from responses to low-contrast stimuli presented with large phase differences requires an assumption of linearity. Second, it is likely that magnocellular neurons play a role in transmitting high-precision temporal information (Schiller, Logothetis, & Charles, 1990), and a major subclass of these neurons may be useless for discrimination under counterphase circumstances, because of frequency-doubling (Kaplan & Shapley, 1982, 1986). Thus, under counterphase conditions, collections of tokens can be segregated even though their phases cannot be discriminated (Ramachandran & Rogers-Ramachandran, 1991; Rogers-Ramachandran & Ramachandran, 1998).

This low-frequency behavior has an important functional consequence related to understanding the dynamics of illusory contour formation. Only because phase sensitivity increases as temporal frequency decreases towards DC can we account for the fact that polarity affects illusory contour strength for static stimuli (see above), but phase difference does not affect illusory contour strength for flickering stimuli.

Acknowledgements

This work was presented in part at the 2000 meeting of the Association for Research in Vision and Ophthalmology, Ft. Lauderdale, FL, and was supported by NIH NEI EY7977. We thank Jeremy Perlman for programming assistance and Tal Levin for her assistance with data collection and analysis.

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