



## Coherence of early motion signals

Joseph S. Lappin<sup>a,\*</sup>, Michael P. Donnelly<sup>a</sup>, Haruyuki Kojima<sup>b</sup>

<sup>a</sup> *Vanderbilt Vision Research Center, 301 Wilson Hall, Vanderbilt University, 111 21st Ave. South, Nashville, TN 37240-0009, USA*

<sup>b</sup> *Kanazawa University, Japan*

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### Abstract

Oscillation thresholds were evaluated for detecting motion and discriminating relative motion. Three horizontally aligned Gaussian blobs oscillated horizontally, with the center in-phase or out-of-phase with the two flankers. Motion thresholds were well below those for static bisection, and involved small contrast changes ( $< 0.25\%$ ). Remarkably, acuity was better for discriminating phase relations than for detecting rigid motion, averaging 8.7 and 11.0 arcsec, respectively, for 100 arcmin between blobs. Phase discrimination acuities were robust over separations of 20–320 arcmin and temporal frequencies of 1.5–6 Hz. Motion phase relations must be coherent among spatially separate retinal signals, carrying information about intrinsic image structure. © 2001 Elsevier Science Ltd. All rights reserved.

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Relative motion is an important form of visual information. Differential motions of some features relative to others provide visible information for segregating objects, discriminating depths, perceiving 3D spatial structure of connected objects and scenes, and guiding locomotion. The extensive experimental and theoretical literature on these topics precludes review here, but several reviews and collections of papers are available (Epstein & Rogers, 1995; Jansson et al., 1994; Lappin & van de Grind, 2000; Nakayama, 1985; Papathomas et al., 1995; Watanabe, 1998). This literature demonstrates that vision is highly sensitive to relative motion as a form of spatial information.

The present study investigated minimum oscillation amplitudes for discriminating phase differences between multiple features. The aim was to test ideas about early visual encoding of spatial positions and motions.

One conception of the mechanisms underlying motion perception involves what may be called ‘local energy’ models. Such models characterize the receptive fields of individual mechanisms and quantify their input–output sensitivities to spatiotemporal contrast en-

ergy (Adelson & Bergen, 1985; Anderson & Burr, 1991; Morgan & Chubb, 1999; Lu & Sperling, 1995; Reichardt, 1961; van Santen & Sperling, 1985; Watson & Ahumada, 1985; Watson, Barlow, & Robson, 1983; Watson & Turano, 1995). Similar versions of such models provide quantitative accounts of sensitivities to spatial texture, contrast, and motion.

How might such mechanisms represent relative positions and motions of multiple features? One possibility is that spatially separate mechanisms provide independent information about spatial position and motion.<sup>1</sup> If local mechanisms are linearly independent, then the perception of global patterns can be induced from the psychophysical sensitivities of the local mechanisms. This theoretical strategy is implicit in much of the psychophysical literature on the mechanisms of early vision. In research on acuity, for example, the spatial positions of image features often are thought to be encoded by the visual mechanisms they stimulate; and

<sup>1</sup> We define independence psychophysically: Spatial signals are said to be locally independent if thresholds for discriminating differential motions in separate locations are predictable as differences between independent random variables whose magnitudes are given by the thresholds for detecting the individual local motions. Questions about independence or correlation of physiological signals are addressed in Section 5.

\* Corresponding author. Tel.: +1-615-3222398; fax: +1-615-3438449.

E-mail address: joe.lappin@vanderbilt.edu (J.S. Lappin).

the retinal positions of these mechanisms usually are conceived as anatomically defined by local signs (Levi, 1997; McKee, Welch, Taylor, & Bowne, 1990; Rose, 1999). If separate mechanisms are locally independent, then sensitivity necessarily will be less for relative motions of multiple features than for motions of individual features — because the variance of a difference between two independent variables equals the sum of the two variances. The present experiments test this prediction.

Despite the theoretical appeal of locally independent mechanisms, a substantial amount of both psychophysical (Kim & Wilson, 1997; Smeets & Brenner, 1994; Takeuchi & De Valois, 2000) and physiological (Albrecht & Geisler, 1991; Bonds, 1989; De Valois & Tootell, 1983; Heeger, 1993; Tolhurst & Dean, 1991) evidence shows that sensitivity to motion at one location may be influenced by motion in neighboring locations. How such interactive effects might be involved in acuities for relative motions is not yet known.

A different theoretical approach involves what may be called ‘image structure’ models.<sup>2</sup> This approach is rooted historically in Gestalt ideas about the perceptual organization of stimulus fields. Much of the research on perceiving structure from motion has stemmed from Gestalt research on ‘phi motion’ and ‘common fate’. Descendants of this approach include Gibson’s (1979) description of the optic array, Johansson’s research on perceptual vector analysis (see Jansson et al., 1994), Koenderink and van Doorn’s (1976, 1992b) analyses of optic flow, and Warren’s (1995) research on visually guided locomotion. The principal idea is that positions and motions are visually represented relative to the surrounding image structure, independent of retinal position per se. The mechanisms underlying this representation have been unclear, however.

Fig. 1 offers schematic illustrations of these two different conceptions of mechanisms for representing spatial positions and motions. In local energy models, information about relative motion derives from differences between local motion signals. In image structure models, relative motion is defined by changes in retinal image structure. The principal difference is whether relative motion is specified after or before motion signals for individual features. Thus, an empirical test compares sensitivity to relative motion with sensitivity to the common motion of multiple features. Motion energy models predict that the threshold for relative motion, based on signal  $m(p) - m(q)$  in Fig. 1(A), is

substantially larger than that for common motion, based on signal  $m(p)$  or  $m(q)$  or both. Image structure models, however, predict that the threshold for relative motion, based on signal  $F$  in Fig. 1(B), may be similar or lower than that for common motion, based on signal  $E$ .

Human vision exhibits ‘hyperacuity’ for image motion — with thresholds well below the eye’s point spread function and the optical diffraction limit (e.g. Biederman-Thorson et al., 1971). Westheimer (1978) found that thresholds for discriminating the displacement direction of sine-wave gratings (50% contrast) were constant at  $\sim 10$  arcsec, independent of spatial frequency.

Such hyperacuities, however, seem to involve neighboring image structure as a reference frame. Legge and Campbell (1981) measured displacement thresholds for a small target within a surrounding annulus. With no annulus, the threshold was  $\sim 1.5$  arcmin; but with an annular surround, the threshold dropped as low as 18 arcsec, with little effect of the radial distance between target and annulus. McKee et al. (1990) also have documented the importance of reference features for achieving good motion acuity.

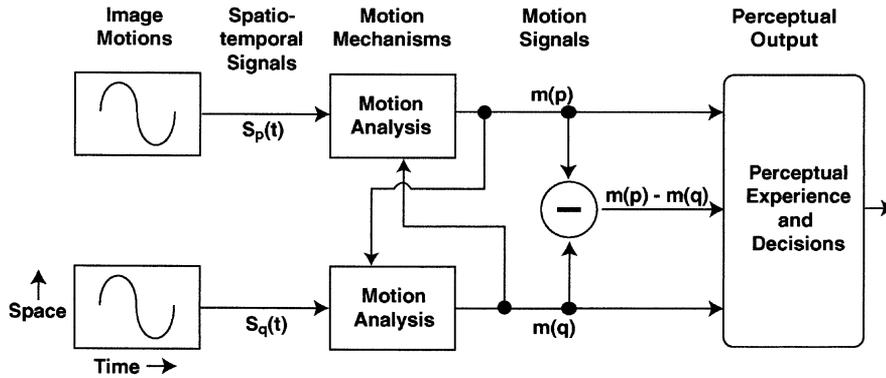
Indeed, many experiments have found hyperacuity for relative motion. Nakayama and Tyler (1981) and Nakayama (1981) used dense random-dot patterns undergoing differential shearing motions, and found displacement thresholds of only  $\sim 5$  arcsec! Comparable estimates were reported by Norman and Lappin (1992) and Lappin (1994) for detecting 3D structure in moving random-dot patterns simulating smoothly curved surfaces. Hyperacuities also have been found for even sparse patterns of widely separated features (Mowafy et al., 1990; Lappin & Ahlström, 1996; Lappin & Craft, 2000; Silverstein & Klein, 1994; Silverstein, 1999). Displacement thresholds were found in several studies to be approximately proportional to the spatial distance between adjacent features, with Weber fractions of  $\sim 0.1$ – $0.3\%$  (e.g. Lappin & Craft, 2000).

The present study differed from these previous experiments in two ways: First, this study more directly compared acuities for discriminating relative motion and detecting common motion. This comparison offers evidence about the optical stimuli for visual motion signals and about the elementary mechanisms for detecting these stimuli.

Second, the present experiments evaluated acuities for blurred features without sharp contrast edges. Many previous experiments on motion acuity have used high-contrast dots with sharp edges and well-defined spatial positions. Motions of features with steep contrast gradients produce large changes in local contrast. The present features, however, had gradual contrast gradients, and small motions produced small changes in local contrast. The diameter of the present features was

<sup>2</sup> The label ‘image structure models’ has been used by Geisler, Thornton, Gallogly, and Perry (2000) to refer to models for the perceptual organization of textured images — based on similarities and proximities of texture elements. Geisler et al. (2000) contrast the image structure models with ‘channel energy models’. Essentially the same theoretical comparison is intended by present use of the terms ‘image structure’ and ‘local energy’ models for motion perception.

### A. Local Energy Models



### B. Image Structure Models

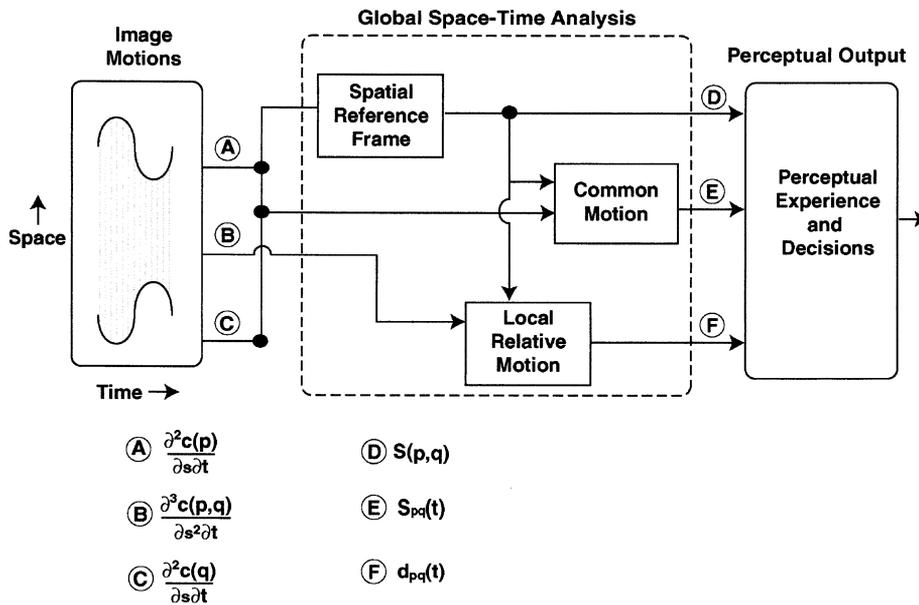


Fig. 1. Schematic illustrations of two conceptions of visual information about spatial positions and motions, with differing assumptions about the signals for local and relative motion. Neither illustration is intended as a well-defined quantitative model. (A) In local energy models, independent motion signals arise from two separate retinal locations. Interactions among local signals occur after initial analyses of spatial position and motion, and information about relative motion is derived from differences between the local signals. The symbol  $s_p(t)$  is a time-varying signal of spatial position at location  $p$ , and  $m(p)$  is the motion signal at that position. (B) In image structure models, temporal signals from separate retinal locations are coherent over space, carrying information about intrinsic structure of the image field. Visual information about relative motion is derived directly from the changing image structure, independent of the perceived common motion. The symbol  $c(p)$  is the contrast distribution at location  $p$ ; and the second-order derivative of this quantity represents image motion of this feature. The third-order derivative  $\partial^3 c(p,q)/\partial s^2 \partial t$  represents the changing spatial relationship between the two features. The three output signals at D–F, represent, respectively, a stable spatial reference frame for the two-feature pattern, common motion of the two-feature pattern, and differential motion.

more than two orders of magnitude larger than the hyperacuity threshold for motion detection. The retinal images of these features spread over thousands of neighboring photoreceptors and receptive fields. Thus, motion acuities in the present study required information about smaller contrast changes over larger spatial areas involving larger numbers of receptors and neurons.

Contemporary models of visual motion mechanisms often describe the optical input in terms of contrast

change rather than spatial displacements as such. Nakayama and Silverman (1985) tested this hypothesis by measuring contrast sensitivity thresholds for detecting and discriminating displacements of sine-wave gratings. For 2 cyc/deg gratings, thresholds were proportional to the contrast change between the initial and shifted gratings, with thresholds of  $\sim 0.2\%$  for detection and  $0.3\%$  for discriminating direction. Higher frequencies yielded higher thresholds. Phase shift and

grating contrast traded with one another to yield the threshold contrast change.<sup>3</sup> Displacement thresholds asymptoted at contrasts of  $\sim 2\%$ , however, yielding minimum phase shifts of  $\sim 10^\circ$  for 2 cyc/deg gratings, equal to (only) a 50 arcsec spatial displacement. Westheimer (1978) obtained significantly lower displacement thresholds than Nakayama and Silverman, probably because Westheimer used higher contrasts. In any case, more evidence is needed about the roles of contrast and contrast changes in spatial acuity.

## 1. General method

The stimulus patterns were three horizontally aligned Gaussian luminance blobs. The motions were small-amplitude sinusoidal horizontal oscillations. In Motion Detection tasks, observers discriminated between moving and stationary patterns.<sup>4</sup> In Phase Discrimination tasks, observers discriminated whether the central blob oscillated In-Phase or Anti-Phase relative to the two flanking blobs. This motion Phase Discrimination task was an oscillating version of a static Bisection Acuity task, which we also tested.<sup>5</sup>

<sup>3</sup> The difference,  $D$ , between two sine-wave gratings that have the same frequency and amplitude and differ only in phase is also a sine wave of the same frequency with an amplitude determined by the phase difference,  $D = 2A \sin(\phi/2)$ , where  $A$  is the amplitude of the two sine waves and  $\phi$  is the phase difference between the two. The amplitude of this difference is greatest, of course, when the phase shift is  $180^\circ$ . For discriminating between two directions of phase shift,  $\phi$  versus  $-\phi$ , the difference between the two differential patterns varies as  $A \sin(\phi)$ , with a maximum for phase shifts of  $\phi = 90^\circ$ .

<sup>4</sup> The motions of individual features in these experiments should not be regarded as 'absolute' or retinally defined: (1) The images in these experiments were not retinally stabilized; and eye movements were neither experimentally controlled nor measured. (2) Observers were consciously aware of moving their eyes on some trials. (3) The stimulus displays were viewed in low photopic illumination in which the edges of the video monitor and other stable spatial features of the room were easily visible. The rationale for this experimental arrangement is as follows: First, if acuities for relative motion were derived from differences in local retinal motions of individual features, and if local motion information were reduced by eye movements, then acuities for relative and individual motions alike would be hindered by such eye movements. Second, the visibility of other potential reference features might improve the acuity for an individual feature, but would not improve acuity for relative motions of multiple features. Thus, the present experimental arrangement is conservative, minimizing rather than enhancing the potential differences in visibility of relative as compared to common motions.

<sup>5</sup> In pilot experiments we also investigated acuities for relative motion in a Vernier arrangement of three vertically aligned blobs that oscillated horizontally. Thresholds for discriminating In-Phase and Anti-Phase oscillations were very similar to those obtained with the present horizontal bisection arrangement. We chose the horizontal bisection arrangement for the main experiments because static Vernier acuity thresholds were low, and for some observers only slightly higher than those for motion phase discrimination. Acuity thresholds for static bisection, however, were much higher than those for the motion phase discriminations, insuring that the latter involved perception of motion rather than static spatial acuity.

Relative motion amplitude depended on both the phase difference and the common motion amplitude. The phase difference was  $180^\circ$  in Exps. 1 and 3, producing relative motions with twice the amplitude of the common motion. Difficulty of the motion detection and phase discrimination tasks was controlled in Exps. 1 and 3 by the oscillation amplitude. In Exp. 2, smaller phase differences and larger oscillations controlled the relative motion amplitude.

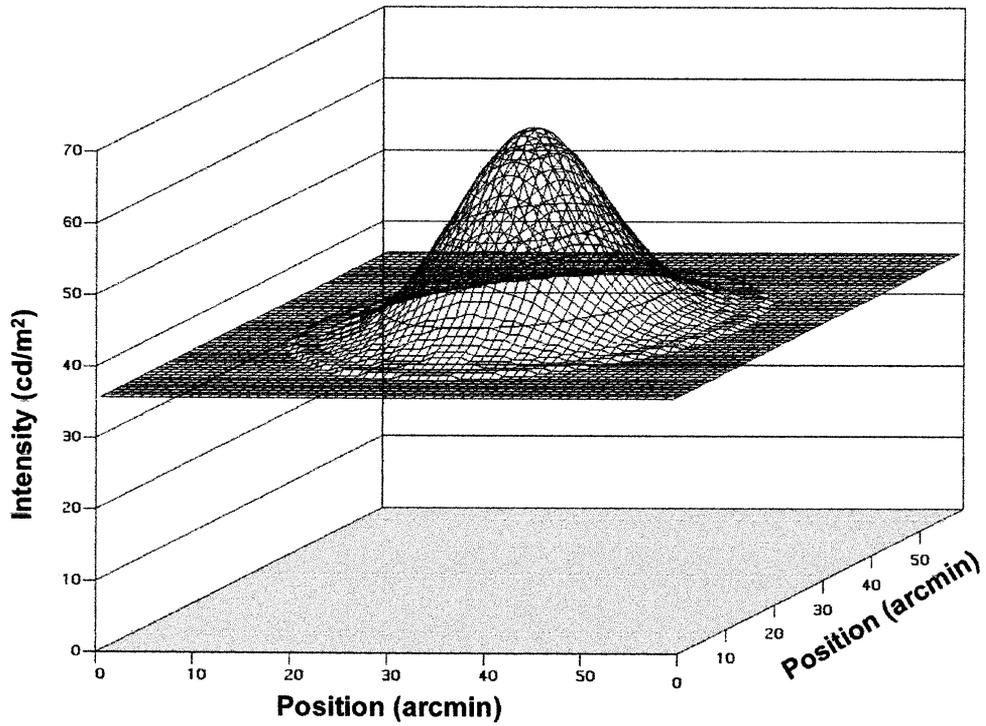
The full diameter of the 2D Gaussian blobs was 40 arcmin, with  $\sigma = 7.07$  arcmin = 7.07 pixels. The background luminance was  $35.4 \text{ cd/m}^2$ , and the maximum luminance at the center of the blob was  $63 \text{ cd/m}^2$ . Oscillations usually were less than a single pixel, so sub-pixel motions were approximated by small changes in gray-levels of multiple pixels. The display was first linearized by measuring the luminance value for each of the 256 gray-scale outputs using a Minolta Luminance Meter (model LS 110), and then fitting a gamma-correction function; and the values were then remeasured and readjusted as necessary. Stimulus patterns were created in MATLAB using the Psychophysics Toolbox (Brainard, 1997) and VideoToolbox (Pelli, 1997), then displayed on a Sony Multiscan 15sx monitor with  $1024 \times 768$  spatial resolution, 72 Hz. Viewing distance was 90 cm, yielding  $1 \times 1$  arcmin visual angle for each pixel. The display was viewed with normal room illumination, with  $4.8 \text{ cd/m}^2$  ambient illumination at the nominal zero gray-level. The borders of the display screen as well as other objects in the room were fully visible. Fig. 2 illustrates the profile of a single Gaussian blob — in Fig. 2(A) as a surface and in 2(B) at a cross-section through the center. The relative luminance changes produced by a displacement of the blob to the left by 0.14 pixels is shown at the bottom of Fig. 2(B).

One of two equally likely stimulus patterns, e.g. a stationary pattern versus one in which the three blobs oscillated rigidly, was displayed for 2 s on each trial, and the observer identified which of the two was presented. Trials were in blocks of 40, with 20 trials for each of the two stimuli. All other stimulus parameters were constant within each block. The observers were always previously practiced and familiar with the two stimulus alternatives. Linear psychometric functions —  $d'$  versus motion amplitude — were estimated from the obtained performance at 3–6 values of oscillation amplitude. Thresholds were estimated as the oscillation amplitude at which  $d' = 1.0$ , corresponding to one standard deviation of positional uncertainty.

## 2. Experiment 1: Acuities for common and relative motions

The purpose was to evaluate acuity for relative motion as compared with that for common motion. These

**A.**



**B.**

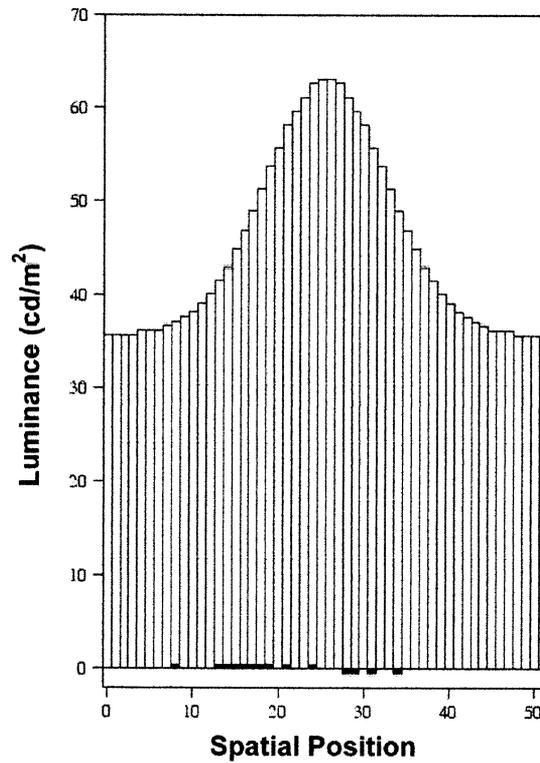


Fig. 2. Luminance profile of the Gaussian blobs used in the present experiments. (A) is a smoothed surface plot of the relative luminances. (B) shows a more detailed histogram of the luminance values in each 1 arcmin<sup>2</sup> pixel at a cross-section through the center of the blob. The bottom of the histogram in part B shows the luminance changes at that cross-section produced by a displacement of 0.14 pixel, shown as darker bars. The amplitude of these luminance changes was 1 gray-scale unit ( $\sim 0.5$  cd/m<sup>2</sup>), with increments shown as positive values and decrements shown as negative values. With this displacement, 20% of the 1272 pixels changed by this amount.

motion acuities were also compared with the bisection acuity for static patterns.

Four conditions included: (a) In-Phase Motion Detection (discriminating in-phase motions from stationary patterns); (b) Anti-Phase Motion Detection (discriminating anti-phase motions from stationary patterns); (c) Phase Discrimination (in-phase versus anti-phase); and (d) Bisection Acuity (static patterns with the central blob either left or right of center).

According to local energy models, acuities should be equal for the In-Phase and Anti-Phase Detections, and thresholds for Phase Discrimination should be roughly twice those for In-Phase Detection.<sup>6</sup> Motion acuities should be lower than acuities for static bisection, though the expected magnitude of this difference is not clear a priori.

### 2.1. Stimulus patterns

The center-to-center separation between adjacent blobs was 100 arcmin (100 pixels), 14 times the spatial scale parameter,  $\sigma = 7.1$ , of the Gaussian blobs. The oscillation frequency was 1.5 Hz.

### 2.2. Procedures

Acuities for each of these four detection and discrimination conditions were estimated by the discrimination accuracy's for five different amplitudes chosen by pilot work for each observer and condition. The oscillation amplitudes ranged from 0.3 to 0.1 arcmin in steps of 0.05 arcmin. In the Static Bisection task, the amplitudes ranged from 1.2 to 0.4 arcmin (in steps of 0.2 arcmin) for observers MD and HK and from 1.4 to 0.6 arcmin for JL.

Each condition was tested in a separate session ( $\sim 30$  min), in which the five amplitudes were presented in descending order. The four discrimination conditions were presented in random orders in successive sets of four sessions, and the entire set of experimental conditions was repeated four times for each observer.

<sup>6</sup> If motions of the central and both flanking blobs were equally detectable and independent, and if detectability,  $d'$ , was proportional to the amplitude of the motion, then the threshold (at the amplitude for which  $d' = 1.0$ ) for detecting motion of either the center or flanking blobs or both would be equal to  $1/\sqrt{2}$  times the threshold for either component alone. Similarly, the acuity threshold for the difference between the two visually independent motions would be  $\sqrt{2}$  times greater than that for either of the components alone — since the standard deviation of a difference between two identically distributed independent variables equals  $\sqrt{2}$  times the standard deviations of the two component variables. Accordingly, the Motion Detection and Phase Discrimination acuity thresholds would differ by a factor of  $\sim 2.0$ .

produced 160 trials for each observer at each displacement amplitude for each of the four conditions. The observers were the three authors.

### 2.3. Results and discussion

Results are summarized in Fig. 3, which shows acuity thresholds for each observer in each condition. More numerical details are given in Table 1, which reports both the acuity thresholds and inverse slopes (arcmin/ $d'$ ) of the psychometric functions for each observer and condition. The inverse slopes offer a second estimate of the standard deviation of spatial resolution. Psychometric functions —  $d'$  versus amplitude — generally were well fit by straight lines intersecting the horizontal axis between the origin and 0.1 arcmin, though the functions were less consistent in the Static Bisection task.

Three results are noteworthy: First, the motion acuity thresholds were small. The average threshold was 0.14 arcmin (8.1 arcsec) for Anti-Phase Detection, 0.18 arcmin (11.0 arcsec) for In-Phase Detection, and 0.14 arcmin (8.7 arcsec) for Phase Discrimination. Not surprisingly, thresholds for Static Bisection were noticeably larger — 0.79 arcmin (47.1 arcsec) — though this too represents good acuity for relative position,  $< 1\%$  of the distance between features. Motion acuity thresholds were even lower when estimated by the inverse slopes of the psychometric functions. Motion thresholds were also  $< 1\%$  of the diameter (40 arcmin) of these blobs, producing only small changes in contrast over the 1272 arcmin<sup>2</sup> area of the blob, with no change in positions of either the maximum luminance or the outside edges. Thus, the positions of these features were accurately specified by relations among distributed neural signals.

Second, and more important, observers had hyperacuity for motion phase relations among separate fea-

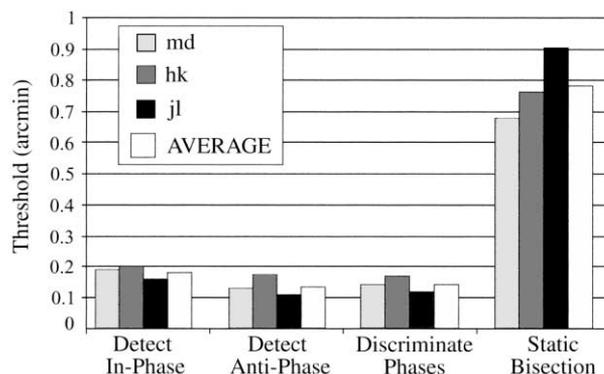


Fig. 3. Acuity thresholds (at  $d' = 1.0$ ) for each observer in each discrimination condition of Exp. 1.

Table 1  
Acuity thresholds ( $S$ , in arcmin, at  $d' = 1.0$ ) and inverse psychometric slopes (arcmin/ $d'$ , in parentheses) for each observer in each of the four main conditions of Exp. 1.

Observers	Discrimination conditions and performance measures							
	In-Phase Detection		Anti-Phase Detection		Phase Discrimination		Static Bisection	
	$S$	Slope <sup>-1</sup>	$S$	Slope <sup>-1</sup>	$S$	Slope <sup>-1</sup>	$S$	Slope <sup>-1</sup>
MD	0.191	(0.149)	0.127	(0.120)	0.146	(0.081)	0.687	(1.11)
HK	0.200	(0.111)	0.174	(0.061)	0.168	(0.064)	0.764	(0.588)
JL	0.157	(0.078)	0.104	(0.068)	0.119	(0.064)	0.906	(0.909)
Average	0.183	(0.113)	0.135	(0.083)	0.145	(0.070)	0.786	(0.869)

tures. Indeed, acuities were reliably better for both Phase Discrimination and Anti-Phase Detection than for In-Phase Detection of rigid common motion. Accuracy's were higher for Phase Discrimination than for In-Phase Detection in 14 of 15 cases (five amplitudes and three observers), and were higher for Anti-Phase than In-Phase Detection in 14 of 15 cases. Phase Discrimination and Anti-Phase Detection were not reliably different. Clearly, the relative motions produced by phase differences were highly visible.

The superior acuity for relative motion did not derive from locally independent motion signals for individual features. To show this, we estimated correlations between motion signals associated with the two components — center and flankers — pertinent to these tasks. Phase Discrimination required information about a motion difference between the center and flankers, and In-Phase Detection tested redundant information about a sum of motion signals from either center or flankers or both. The Appendix shows how thresholds for these two tasks estimate the visual correlation between center and flankers. This analysis assumes nothing about the relative sensitivity to one or two flankers or about the presence or absence of probability summation among the two flankers.

For a phase difference of 180°, the amplitude of relative motion was twice the oscillation amplitude of the individual features, so the relative motion thresholds were taken as twice the values for Phase Discrimination given in Table 1. (Exp. 2 supports this measure of relative motion, corresponding to what the Appendix calls a 'coherent phase model'.) Correlations estimated for MD, HK, and JL, respectively, were  $r = 0.645$ ,  $0.543$ , and  $0.652$ . Using the inverse slopes (arcmin/ $d'$ ) the estimated correlation was  $r = 0.762$  for the average observer. (By a 'total energy model', using the Phase Discrimination thresholds in Table 1, the correlation for the average observer was  $r = 0.918$ .) These correlations are similar to that found in a recent experiment in which detection thresholds were estimated separately for the center alone and for flankers alone, and the relative motion acuity was estimated by

the same phase discrimination task (Lappin and Whittier, submitted).

A third interesting result is that these motion sensitivities were also impressive when measured by their associated contrast changes. At the Phase Discrimination threshold of 0.14 arcmin, gray-scale values changed by just one unit ( $0.5 \text{ cd/m}^2$ ) — roughly 1% of the initial value — in just 20% of the 1272 pixels of the blob. Relative to the total blob luminance, this contrast change was just 0.24%. This sensitivity is especially impressive because it involved a relationship between contrast changes at separate locations.

### 3. Experiment 2: Effects of spatial separation on motion phase discrimination

Acuity for relative motion reflects visual organization. It may also provide evidence about the mechanisms that underly this organization. If perceived relative motion involves stimulation of a common receptive field by motion signals from separate features, then phase discriminations should decline as the separation between features increases.

#### 3.1. Methods

The methods were similar to those in the previous experiment, but with the following changes. First, the center-to-center separation between blobs was either 20, 40, 80, 160, or 320 arcmin, in separate blocks of trials. Second, only the Phase Discrimination task was used.

Third, discrimination difficulty was controlled by the phase lag between the center and flanking blobs, instead of by the oscillation amplitude as in Exp. 1. The purposes of this method were to demonstrate the visibility of smaller phase differences and to generalize the form of relative motion. The amplitude of differential motion,  $D$ , the phase difference,  $\phi$ , and the amplitude of common motion,  $A$ , are related by the formula:  $D = 2 A \sin(\phi/2)$ . The common motion amplitude was 0.4 arcmin for the three smallest blob separations (20,

Table 2  
Acuity thresholds ( $S_D$ , in arcmin, at  $d' = 1.0$ ) and inverse psychometric slopes (arcmin/ $d'$ , in parentheses) for Phase Discriminations by each observer at each of five blob separations in Exp. 2<sup>a</sup>

Observers	Spatial separations									
	20 arcmin		40 arcmin		80 arcmin		160 arcmin		320 arcmin	
	$S_D$	Slope <sup>-1</sup>	$S_D$	Slope <sup>-1</sup>	$S_D$	Slope <sup>-1</sup>	$S_D$	Slope <sup>-1</sup>	$S_D$	Slope <sup>-1</sup>
MD	0.197	(0.132)	0.265	(0.117)	0.262	(0.172)	0.385	(0.227)	0.580	(0.283)
HK	0.231	(0.127)	0.268	(0.142)	0.265	(0.148)	0.362	(0.252)	0.498	(0.262)
JL	0.198	(0.123)	0.240	(0.115)	0.204	(0.129)	0.325	(0.153)	0.406	(0.227)
Average	0.209	(0.127)	0.258	(0.125)	0.243	(0.150)	0.357	(0.211)	0.494	(0.257)

<sup>a</sup> Note that the present thresholds are defined in terms of the relative motions of the center and flanks, whereas in Exp. 1 they were defined relative to display coordinates. Phase Discrimination thresholds in Exp. 1 should be multiplied by 2 to obtain the present relative motions thresholds.

40, and 80 arcmin), and was 0.8, and 1.6 arcmin, respectively, for separations of 160 and 320 arcmin. The acuity threshold at each spatial separation was estimated from three values of phase lag. For the three smallest blob separations (20, 40, and 80 arcmin), the phase lags were 47, 35, and 23°, producing relative motions of 0.32, 0.24, and 0.16 arcmin, respectively. The same phase differences for 160 arcmin separation produced 0.64, 0.48, and 0.32 arcmin relative motion. For 320 arcmin separation, phase lags of 35, 23, and 11°, produced 0.96, 0.64, and 0.32 arcmin relative motion, respectively.

Each experimental session was devoted to a different spatial separation. The sequence of the five separations was randomized for each observer and each successive set of five sessions. In each session, the three phase differences were presented in descending order in three blocks of 40 trials. Each observer completed three blocks of trials for each separation and phase difference, totalling 120 trials at each point. The observers were the same as in Exp. 1.

### 3.2. Results and discussion

The results are shown in Table 2 and Fig. 4, which give the thresholds for relative motion at each spatial separation. Spatial separations between 20 and 80 arcmin had little effect on acuity for relative motion. Acuity thresholds increased for separations between 80 and 320 arcmin, though this four-fold increase in separation increased the acuity thresholds by a factor of only ~2. The effect of separation was less when acuity is measured by the inverse slope, approximately doubling as a result of the 16-fold increase in separation from 20 to 320 arcmin. Thus, relative to the separation between features, Weber fractions for relative motion improved with spatial separation. For 20 arcmin separation, the Weber fraction was ~1% (0.64% by the inverse slope); but for 320 arcmin separation, the Weber fraction was ~0.15% (0.08% by the inverse slope).

With separations of 20 and 40 arcmin, the blobs overlap and many receptive fields are jointly stimulated by two moving blobs; but with separations of 160 and 320 arcmin, different blobs stimulate far fewer of the same receptive fields. Evidently, the visual system is very efficient in maintaining information about spatiotemporal relations over spatially distributed regions.

These results also demonstrate the visibility of small motion phase differences. The acuity threshold at 320 arcmin separation corresponds to a phase difference less than 18°. The primary limitation, however, seems to involve the amplitude of relative motion rather than either the phase difference or retinal motion. Acuity thresholds for 80 arcmin separation in Exp. 2 were similar to those in Exp. 1 with 180° phase difference.

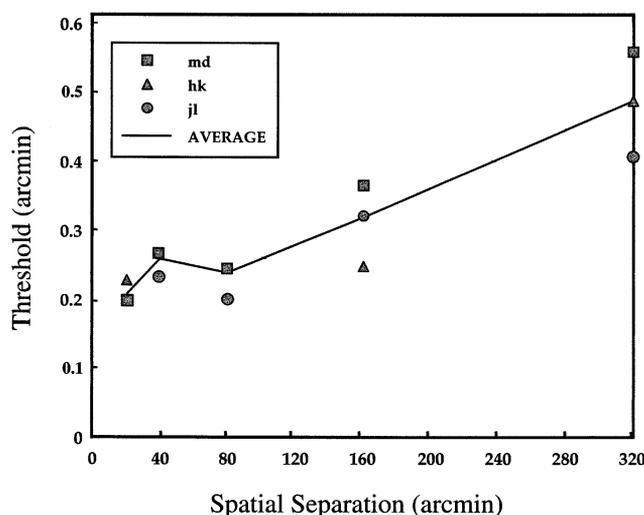


Fig. 4. Acuity thresholds for each observer at each spatial separation in Exp. 2. Unlike the data Exps. 1 and 3, the threshold values in this figure are defined by the amplitude of the differential motion of the center blob relative to the two flanking blobs, whereas in Exps. 1 and 3 they are defined by the motion amplitude of an individual blob relative to coordinates of the display screen. For comparison, the thresholds in Exps. 1 (Fig. 2) and 3 (Fig. 5) may be multiplied by 2.

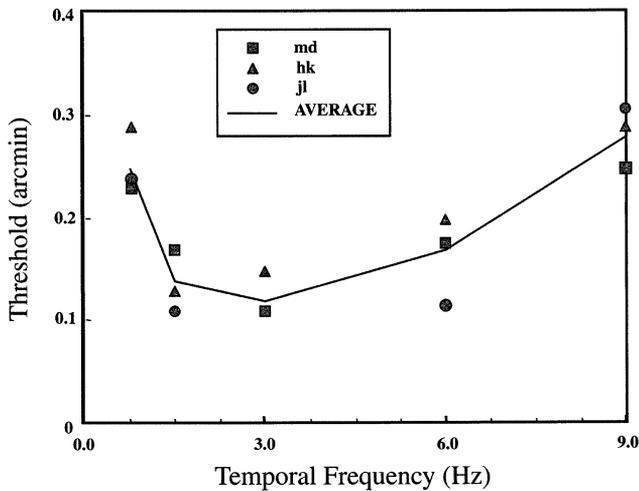


Fig. 5. Acuity thresholds for each observer at each temporal frequency in Exp. 3.

#### 4. Experiment 3: Effects of temporal frequency on motion phase discrimination

Next, we investigated the effects of temporal frequency on visual sensitivity to relative motion.

##### 4.1. Methods

The stimulus displays and procedures were similar to those for Phase Discriminations in Exp. 1. The phase difference was either 0 or 180°. Five temporal frequencies were tested — 0.75, 1.5, 3.0, 6.0, and 9.0 Hz.<sup>7</sup> The blobs were separated by 100 arcmin, as in Exp. 1.

The same three observers each participated in 15 sessions. Each session was devoted to a single temporal frequency and there were three sessions for each temporal frequency. The five temporal frequencies were tested in a randomly permuted order within each successive set of five sessions for each observer. Each session consisted of three or four successive blocks of 40 trials, with successively smaller values of oscillation amplitude. For temporal frequencies of 1.5, 3.0, and 6.0 Hz, the oscillation amplitudes were 0.3, 0.2, and 0.1 arcmin; and for 0.75 and 9.0 Hz, there was a fourth amplitude of 0.4 arcmin.

##### 4.2. Results and discussion

The results are shown in Fig. 5. As may be seen, phase discriminations were relatively constant for fre-

quencies of 1.5–6.0 Hz. This four-fold range of oscillation rates produced very visible changes in motion speed but little change in detectability of relative motion.

Oscillations of 0.75 Hz were too slow to yield visually clear motions, tending toward static bisection patterns. At 9.0 Hz, temporal summation made the small local contrast changes less visible. Similar results have been found by Silverstein and Klein (1994) and Silverstein (1999). In earlier studies with discrete displacements of high-contrast points, we routinely used rates of 10 or 20 frames per sec and found that acuities for relative motions were maintained at these and higher temporal rates (Lappin et al., 1991; Lappin & Craft, 1997, 2000). Vision seems to be sensitive to the high-frequency spatial and temporal components of such patterns. The limitations in perceiving rigidly moving spatial structure probably arise from temporal summation rather than either local or relative velocity per se.

#### 5. General discussion

The principal finding was that vision is very sensitive to relative motion. Indeed, the acuity was better for discriminating relative motion than for detecting common motion. From the perspective of traditional ideas about local motion-sensitive mechanisms, this is a puzzling result. What are the visual mechanisms for detecting relationships among spatially separate motions? The present results indicate that motion phase relations among barely detectable oscillations must be coherent (synchronous, correlated) over spatially separate image regions.

##### 5.1. Coherence of early motion signals

If acuities for relative motion involve correlations among spatially separate signals, then these correlations must exist in the retina: Precise spatiotemporal relations could not be reconstructed in the cortex if the stimulus information were lost by the retinal signals. As Brindley (1970) pointed out, behavioral discrimination implies a difference in retinal signals. That is, physiological entropy cannot decrease and acuity cannot increase over successive neural stages (Lappin & Craft, 2000). Acuity thresholds estimate upper bounds on the spatial uncertainty of retinal signals.

Perceptual sensitivity to spatial relations among separate moving features also has been found in experiments on the perceptual grouping of moving features (Alais, Blake, & Lee, 1998a; Alais, van der Smagt, van den Berg, & van de Grind, 1998b; Lappin, Norman, Loken, & Fukuda, 1990; Lorenceau & Shiffrar, 1992; Mingolla, Todd, & Norman, 1992). These perceptual grouping phenomena resemble the present results, and

<sup>7</sup> The video monitor's frame rate of 72 Hz rendered investigation of higher temporal frequencies impractical. Informal observations with 18 Hz demonstrated that these were much less visible than any of the slower oscillations, so we limited study to the fastest practical oscillation frequency of 9.0 Hz, as the decline in performance with higher frequencies was obvious.

they might involve similar mechanisms. Temporal synchrony of cortical processes (Singer, 1990; Singer & Gray, 1995) has been considered as a basis for perceptual binding, but temporal synchrony also arises from image motions. Additional information about the image structure cannot originate in the cortex.

Physiological evidence of the coherence of retinal signals was obtained recently by Bart Borghuis, Martin Lankheet, Wim van de Grind, and the first author (JSL) at Universiteit Utrecht. Spike trains in cat retinal ganglion cells were recorded in response to near-threshold oscillations of a vertical bar. The spike trains were reliably modulated by the oscillating bar, with high correlations between spike trains produced by the same stimulus on different trials. Lower contrasts produced fewer spikes, but the oscillating bar positions were specified independently of contrast by the synchronized temporal organization of the spike trains. In some conditions two additional flanking bars oscillated outside the cell's receptive field, either in-phase or anti-phase with the central bar. Spike trains stimulated by the central bar were unaffected by the flanking bars. Thus, information about the spatiotemporal stimulation was carried by the temporal structure of the retinal spike trains, with no detectable retinal interactions between the separate local signals. The present psychophysical results probably derive from similar retinal signals.

The hypothesis that vision is sensitive to small time differences in separate retinal signals is supported by additional psychophysical evidence. Benham's top produces perceived hue changes from stimulus time differences < 1 ms (Both & von Campenhausen, 1978). Binocular temporal disparities of 0.2 ms yield discriminable depth differences (Burr & Ross, 1979).

### 5.2. Image structure as an intrinsic visual reference frame

Measures of spatial position and motion require a reference frame. The reference frame for vision has been assumed to be the anatomy of the retina (Rose, 1999), though this belief does not derive from empirical evidence. The finding of superior acuity for relative motion points to an alternative hypothesis — that the reference frame for vision is the neighboring image structure.

Gestalt psychologists proposed that perceived spatial relations and motions arise from sensory fields analogous to electromagnetic, fluid, or gravitational fields in physics (Köhler, 1930, 1940; Lappin & van de Grind, 2000; Wertheimer, 1912; Westheimer, 1999). Köhler (1940) argued that both retinal stimulation and neural responses are properly characterized by their spatial and temporal order, not by the stimulus intensities or neural responses at local points.

Fields may be characterized by their differential structures, involving partial derivatives over space and time. These differential structures are invariant with respect to position in an extrinsic reference frame. Retinal images may be described by differentials of the form  $\partial i/\partial r$ ,  $\partial^2 i/\partial r^2$ ,  $\partial^2 i/\partial r \partial t$ , etc. where  $i$ ,  $r$ , and  $t$  designate values of intensity, retinal position, and time, respectively. ( $\partial i/\partial r$  represents a spatial contrast gradient, and  $\partial^2 i/\partial r \partial t$  represents motion.) These expressions depend on differentials of the retinal coordinates but not on the coordinate positions as such. Invariance of differential image structure under translations and rotations requires only that the retinal coordinates are homogeneous over the regions of these transformations. Scaling of the retinal coordinates is not directly relevant. Field structure is associated with second-order differentials and the topology of critical points (extrema, inflections, and singularities).

How can visual mechanisms be more sensitive to differences in position than to the local component positions? Doesn't discrimination of a difference require perception of the component values? Certainly not. Visual sensitivity to contrast rather than to individual intensity values or retinal positions is a familiar example. More generally, higher-order derivatives may be computed directly, without first computing lower-order properties (Koenderink, 1990; Koenderink & van Doorn, 1992a). Lappin and Craft (2000) report additional evidence that early spatial signals are based on image structure rather than retinal coordinates. Indeed, the intrinsic image structure constitutes information about the 3D structure of environmental objects (Koenderink & van Doorn, 1992b; Lappin & Craft, 2000; Perotti et al., 1998).

### 5.3. Motion and multi-local contrast changes

Image motions entail changes in local contrast. The present results demonstrate hyperacuity for relationships among small contrast changes in separate locations.

When the present acuity for relative motion ( $\sim 0.14$  arcmin) is expressed in terms of contrast, dividing the absolute values of local luminance changes by the total luminance of the blob, then the resulting ratio, 0.24%, describes good contrast sensitivity ( $1/0.0024 = 416$ ). This is similar to Nakayama and Silverman's (1985) results for detecting displacements of 2 cd sine-wave gratings (higher frequencies yielded higher thresholds), and it is better than the thresholds reported by Kelly (1985) for moving gratings. The present contrast sensitivity for relative motion is all the more impressive because it involved comparisons of contrast changes at separate locations.

Do the present hyperacuities for relative motion require perceived motion? Perhaps vision is comparably

sensitive to changing contrast without motion. Lappin and Whittier (submitted) investigated this question using blobs with bilaterally symmetric contrast oscillations, increasing and decreasing equally on both sides of the blob so that its centroid did not move. Detectability of these non-moving contrast oscillations was equivalent to that for moving blobs, but phase discrimination was much worse for non-moving than for moving patterns. Moreover, increases in spatial separation and temporal frequency both produced large decrements in phase discrimination. Thus, unlike moving patterns, the non-moving contrast oscillations were visually incoherent, without discriminable phase relations. Evidently, motion is critical for visual organization.

## 6. Conclusion

This study found that vision may be more sensitive to relative motion and relative contrast change than to local motion and local contrast change. Mechanisms that encode such relationships are not understood in detail, but they must involve coherent retinal signals that preserve the spatiotemporal image structure. Current ideas about local mechanisms for signaling spatial position, motion, and contrast warrant re-examination. Further research is needed to understand how early visual signals accurately specify global image structure.

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## Appendix A. Estimating the visual correlation between motion components

We wish to estimate the correlation between visual motion signals produced by the center and flanking components of the patterns in these experiments. We first develop the rationale and equations for a ‘total energy’ model, and then we consider a modified version called the ‘coherent phase’ model that takes account of the spatiotemporal phase relations between the components. These two models involve different assumptions about the stimulus information for visual motion sig-

nals and different rationale for estimating the correlation between these signals.

The total energy model assumes that the thresholds for detecting motion are based on the temporally integrated motion energy relative to the retina. That is, motion detection is assumed to reflect changes in position without necessary information about its direction or phase.

The coherent phase model, on the other hand, assumes that retinal motion signals carry information about the phase or direction of motion. If this spatiotemporal phase information is coherent across spatially separate retinal positions, then these phase relations may be signalled more precisely than the retinally defined positions from which they originated. The differential motion,  $D$ , of two neighboring features oscillating with the same temporal frequency and amplitude depends jointly on both the amplitude and phase difference of their oscillations, with  $D = 2 A \sin(\phi/2)$ , where  $A$  is the oscillation amplitude and  $\phi$  is the phase difference.

To summarize, the total energy model assumes that acuity for detecting relative motion depends on the overall oscillation amplitude, and the coherent phase model assumes that the relative motion acuity depends on the differential amplitude. Equations for the coherent phase model involve simple modifications of those for the total energy model, so we first develop the equations for the total energy model.

### A.1. Total energy model

Consider the three-blob motion patterns as composed of two parts — center and flanks. Suppose that the visibilities of these two signals are represented by vectors — say  $\mathbf{C}$  and  $\mathbf{F}$ . The correlation coefficient is equivalent to the cosine of the angle between these two vectors. We show here how this angular cosine, or correlation coefficient, may be estimated by the relative lengths of these vectors and that of a third vector representing either the difference,  $\mathbf{D}$ , or the sum,  $\mathbf{B}$ , of the two components  $\mathbf{C}$  and  $\mathbf{F}$ . We show here how the correlation between the  $\mathbf{C}$  and  $\mathbf{F}$  motion signals may be computed from the relative lengths of the difference vector,  $\mathbf{D}$ , as estimated by the Phase Discriminations, and their sum,  $\mathbf{B}$ , as estimated by the In-Phase Detections. Now the lengths of these visibility vectors may be associated with either the displacement threshold,  $S$ , or the detectability measure,  $d'$ , and we will need both of these measures, which are approximately reciprocals of one another.

Using the law of cosines, the lengths of the  $\mathbf{C}$ ,  $\mathbf{F}$ , and  $\mathbf{D}$  vectors are related by the following equation:

$$S_D^2 = S_C^2 + S_F^2 - 2S_C S_F \cos \delta, \quad (\text{A1})$$

where  $\delta$  is the angle between **C** and **F**, and the standard deviations  $S_C$ ,  $S_F$ , and  $S_D$  (the estimated acuity thresholds) are the three vector lengths. This equation is the same as the familiar statistical equation for the variance of a difference between two variables with the correlation coefficient  $r$  in place of the parameter  $\cos \delta$ . In this trigonometric representation the two vectors **C** and **F** are joined at their base, and the difference vector **D** joins the two ends, opposite the angle  $\delta$ . As the correlation between **C** and **F** varies between 0.0 and 1.0, the angle  $\delta$  varies correspondingly from 90 to 0°, and the squared length of **D**,  $S_D^2$ , varies from  $S_C^2 + S_F^2$  to 0.0.

A similar equation describes the relation between **C**, **F**, and **B**. Now we use the vector length to represent detectability as measured by  $d'$  for some given amplitude of motion. The vector **B** represents the detection of either or both of the two components, corresponding to the addition of **C** or **F**, depicted by joining the base of one to the end of the other, and the resultant vector **B** is the long diagonal of the parallelogram formed by **C** and **F**. The relative vector lengths are given by:

$$d_B^2 = d_C^2 + d_F^2 - 2d_C d_F \cos \beta, \quad (\text{A2})$$

where  $\beta$  is the (obtuse) angle opposite **B** formed by joining the base of **F** to the end of **C**. If  $\delta$  represents the other angle in this parallelogram, between **C** and **F** joined at their bases, then  $\beta + \delta = 180^\circ$ , and  $\cos \beta = -\cos \delta$ . Thus, Eqn. A2 can be expressed in terms of  $\cos \delta$ :

$$d_B^2 = d_C^2 + d_F^2 + 2d_C d_F \cos \delta. \quad (\text{A3})$$

To solve for the correlation,  $\cos \delta$ , we use two simplifying assumptions. First, assume that the motion detection thresholds of the two components are equal:  $S_C = S_F$ , and  $d'_C = d'_F$ . This is a dubious assumption, but it is conservative in the sense that its violation would only increase the estimated correlation. Second, assume that  $d'$  is proportional to the amplitude of oscillation. Although plausible, this assumption is not actually valid; the psychometric functions for these tasks were shifted slightly to the right of the origin,  $\sim d' = m(A - k)$ , where  $A$  is the oscillation amplitude,  $m$  is the slope, and  $k$  is the horizontal intercept, with an average value of  $\sim 0.07$  arcmin. Assuming that the intercept,  $k$ , is zero simplifies the equations relating the observable measures  $S$  and  $d'$ . This too is a conservative assumption that reduces (slightly) the estimated correlation. Thus, using the first assumption, equations A1 and A3 may be simplified to

$$S_D^2 = 2S_C^2 (1 - \cos \delta),$$

$$1 - \cos \delta = S_D^2 / (2S_C^2); \quad (\text{A4})$$

$$d_B^2 = 2d_C^2 (1 + \cos \delta),$$

$$1 + \cos \delta = d_B^2 / (2d_C^2) \quad (\text{A5})$$

Assuming that  $d' = m A$ , and given that  $S$  is defined as the value of  $A$  at the point on the psychometric function where  $d' = 1$ , then  $1 = m S$ ,  $m = 1/S$ , and  $d' = (1/S) A$ . Substituting this expression into equation (A5), we have

$$1 + \cos \delta = (A/S_D)^2 / (2 (A/S_C)^2)$$

$$= S_C^2 / (2S_D^2). \quad (\text{A6})$$

Multiplying equations A4 and A6 then yields an estimate of the angle  $\delta$  based on the relative values of the thresholds for the Phase Discrimination and In-Phase Detection tasks:

$$(1 - \cos \delta) (1 + \cos \delta) = (S_D^2 S_C^2) / (4 S_C^2 S_B^2)$$

$$1 - \cos^2 \delta = \sin^2 \delta = S_D^2 / (2 S_B^2)^2$$

$$\sin \delta = S_D / (2S_B) \quad (\text{A7})$$

$$r = \cos [\arcsin (S_D / (2S_B))] \quad (\text{A8})$$

### A.2. Coherent phase model

The total energy model assumes that the threshold for detecting relative motion,  $S_D$ , is defined by the oscillation amplitudes, regardless of the phase difference between the center and flankers. The oscillating spatial separation between the center and flankers depends on the phase difference between the two oscillations. As noted previously, the temporal frequency of the oscillating spatial separation is the same as that of the components, with amplitude  $D = 2 A \sin (\phi/2)$ . If  $\phi = 180^\circ$ , then  $D/A = 2$ , and the differential amplitude is twice that of the individual component features. In the total energy model, the threshold amplitude of the difference vector **D** was defined by the common oscillation amplitude of the individual components, but in the coherent phase model, the threshold,  $S_D$ , should be defined by a value of  $D = 2 A \sin (\phi/2)$ . The validity of this definition is supported by the results of Exp. 2. For a phase difference of  $\phi = 180^\circ$ ,  $D = 2 A$ . Accordingly, the threshold is larger and the correlation is smaller than computed by the total energy model.

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