

Dichoptic Activation of the Early Motion System

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The short range or early motion system has long been considered incapable of binocular integration. We have developed dichoptic motion stimuli which are based upon the decomposition of traveling sinewave gratings into the sum of two standing waves in spatial and temporal quadrature. The monocular views of such displays appear as counterphase flicker but when presented dichoptically the perception is of movement in a unique direction. Two lines of evidence are presented for the binocularity of early motion mechanisms in human vision. First, adaptation to dichoptic motion sinewave gratings is found to result in a motion aftereffect. Second, random texture motion displays based on the quadrature decomposition are found to support dichoptic perception of motion direction, but not figure/ground. Unlike random dot kinematograms, these displays do not necessitate alternating the direction of motion during dichoptic presentation. This encumbrance, and the reliance on figure/ground discrimination, may have been responsible for prior failure to achieve dichoptic motion perception with short range stimuli.

Motion perception Dichoptic Short range Motion aftereffect Early motion system Binocular vision
Cyclopean

INTRODUCTION

Exner (1875) demonstrated that discrete stimulus presentations can elicit the perception of motion at intervals too short for temporal order judgments, thereby concluding that motion perception is a primary sensation, not simply inferred from an object's change in position over time (see Boring, 1942). The powerful sense of motion elicited with discretely presented stimuli suggests that a common mechanism is involved in the perception of real and apparent motion (Gregory, 1966; Clatworthy & Frisby, 1973; Frisby, 1972; Gibson, 1950; Green, 1983; Green & von Grunau, 1983). Support for this position includes demonstrations of subthreshold summation (Barbur, 1981) and cross adaptation effects for real and apparent motion (Anstis, Giaschi & Cogan, 1985). Evidence for a common physiological substrate is derived from recordings of direction selective neurons which are activated by both types of motion (Barlow & Levick, 1965; Emerson & Gerstein, 1977; Mikami, Newsome & Wurtz, 1986). On the other hand, phenomenological differences between real and apparent motion, have led others to conclude that they are processed by different mechanisms (Kolers, 1972; Kaufman, Cyulnick, Kaplowitz, Melnick & Stof, 1971). One approach to resolving these issues emphasizes a two

process model of apparent motion perception (Anstis, 1978, 1980; Braddick, 1980; Nakayama, 1985).

In a series of classic papers, Oliver Braddick proposed that the analysis of apparent motion is subserved by at least two systems, a short range and a long range system (Braddick, 1973, 1974). He noted that when form cues are eliminated, as in random dot kinematograms, the perception of motion is more labile. If an object is defined by the abrupt displacement of a region of random dots within a larger field of random dots, the range of spatial (and temporal) displacements that maintain object identity is limited. This finding suggests a motion system which does not require form information, a system which may be conceptualized as extracting motion cues, *per se*, without prior knowledge of what is moving. This short range motion system was originally characterized by those parameters which delimit the perception of motion in random dot displays, relegating other types of motion perception to the long range system. The short range system or early motion system presumably reflects the operation of direction selective neurons which are responsive to real motion. Experiments utilizing an entirely different type of stimulus, the Ternus display (Ternus, 1938), also support a dual process model of apparent motion (Pantle & Picciano, 1976; Petersik, 1989; Petersik & Pantle, 1979).

The standard distinctions between the short and long range systems listed in Table 1 are derived from similar tables presented by Marr (1982), Anstis (1980), Braddick and Adlard (1978), Braddick (1980) and Petersik (1989). Advances in our understanding of motion processing

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TABLE 1. The processing of motion information is often characterized as occurring in two distinct systems, an early or short range system and an interpretive or long range system

Early motion system (low level, short range)	Interpretive motion system (high level, long range)
Spatial shift 15 min arc or less	Displacement of several degrees
Interstimulus interval < 100 msec	ISI > 300 msec
Bright ISI disrupts motion perception	Light or dark ISI acceptable
Monocular system	Can be stimulated dichoptically
Does not respect color information	Utilizes luminance and color
Adapts neural motion detectors to give motion aftereffect	Little or no motion aftereffect
Supports reverse ϕ	
Motion perception between frames precedes edge extraction	Edge extraction precedes motion perception

have forced revision of several of these distinctions between short and long range systems (Cavanagh & Mather, 1990). For example, the 15 min spatial limit, D_{\max} , is now known to depend on element size or spatial frequency content. The original finding reflected the use of small stimulus targets rather than a fundamental limit of the visual system. Similarly, we argue that the characterization of the short range, motion system as monocular reflects inappropriate stimulus conditions rather than a fundamental limitation of the early motion system. We approach this issue by first establishing the presence of a motion aftereffect after adaptation to a display that requires binocular integration to achieve the perception of motion. Next a new random dot "short-range" stimulus is introduced which is shown to adhere to many of the same phenomenological distinctions described by Braddick, with a key exception, it gives rise to a *cyclopean* perception of motion. In light of these findings we conclude that the short range, or early, motion system is capable of integrating information binocularly.

CYCLOPEAN MOTION AFTEREFFECT

After viewing unidirectional motion, stationary patterns appear to move in the opposite direction. This phenomenon, described by Adams (1834) after viewing a waterfall, has come to be known as the motion aftereffect (MAE). The MAE is thought to reflect a change in the responsiveness of direction selective neurons after adaptation to unidirectional motion (Sekuler & Ganz, 1963; Barlow & Hill, 1963, Vautin & Berkley, 1977; Sekuler & Pantle, 1967, 1974; Peterson, Baker & Allman, 1985). It is easily attained upon adaptation to various types of patterns such as sinewave gratings and random dot motion displays (Smith & Hammond, 1985; Smith, Musselwhite & Hammond, 1984; Turano & Pantle, 1985). Even patterns in apparent motion can produce a MAE so long as the spatial displacement from frame to frame is small (Banks & Kane, 1972). However, as spatial displacement is increased, the short range

system is bypassed and the MAE becomes vanishingly small.

The MAE has been shown to transfer interocularly (Smith & Hammond, 1985; Wade, 1976; Mitchell, Reardon & Muir, 1975; Ware & Mitchell, 1974; Price & Keck, 1982). After adapting to motion viewed monocularly, an aftereffect can be observed using the other eye. Interocular transfer of aftereffects is thought to be mediated by binocular cortical neurons (Coltheart, 1973; Anstis & Duncan, 1983). In primates and cats direction sensitivity is first expressed in the visual cortex where neurons characteristically receive input from both eyes (Hubel & Wiesel, 1962, 1968; Schiller, Finlay & Volman, 1976). Indeed adaptation to drifting bars, gratings or random dot patterns results in cortical cell response properties which are felt to underly the MAE (Vautin & Berkley, 1977; Hammond, Mouat & Smith, 1985, 1986). Based on these neurophysiological observations, one might expect the short range motion system to be identified with binocular visual processing. Yet attempts to elicit dichoptic short range motion perception in humans have been unsuccessful (Braddick, 1974; Green & Blake, 1981; Pantle & Picciano, 1976), suggesting the system is unable to integrate information from the two retinal images.

Perhaps these results reflect inappropriate stimulus conditions rather than a fundamental limitation of the early motion system. A class of dichoptic visual displays has been described which produce a strong perception of motion only when left and right eye patterns are integrated binocularly (Shadlen & Carney, 1985). These stimuli are unique in that binocular integration yields a purely unidirectional motion cue. As a first step in demonstrating the binocular nature of the early motion system, we have evaluated the presence of a MAE after adaptation to such a dichoptic motion display.

Methods

Subjects. Two of the participants were the authors and two were naive observers with little practice in dichoptic tasks. The observers were either emmetropic or had their refractive error corrected.

Apparatus. The stimuli were presented dichoptically on two Tektronix 602 display oscilloscopes, using a one-dimensional pattern generator driven by an IBM-PC computer. The oscilloscopes were placed on either side of the observer at a distance of 114 cm such that the circular aperture covering each display subtended 4 deg. To align the displays dichoptically, corner cubes were positioned in front of each eye of the observer. To prevent eye movements and thereby enhance the generation of a direction selective aftereffect, fixation spots were affixed to each display (Carney, 1982).

The adaptation and test stimuli were *horizontally* oriented sinewave gratings viewed dichoptically. Three adaptation stimuli were used: (1) blank screen at mean luminance (11 ft-L); (2) sinewave gratings drifting upward in real (rigid) motion; (3) counterphase modulated sinewave gratings before the left and right eyes in

spatio-temporal quadrature, where the left and right eye patterns are displaced by one-quarter of a spatial period and one-quarter of a temporal period. The intensity profiles of the gratings in quadrature may be represented as a product of spatial and temporal sinusoidal modulations,

$$L_{\text{left}}(y,t) = L_{\text{mean}}[1 + m \cos(fy)\cos(\omega t)], \quad (1)$$

and

$$L_{\text{right}}(y,t) = L_{\text{mean}}[1 + m \sin(fy)\sin(\omega t)], \quad (2)$$

where f represents spatial frequency (rad/deg visual angle), ω represents temporal frequency (rad/sec), L_{mean} is mean luminance, and m is the depth of modulation. The quarter cycle differences in space and time are reflected by substitution of sin for cos in equation (2). The sum of left and right intensity profiles is a drifting grating:

$$L_{\text{left}}(y,t) + L_{\text{right}}(y,t) = L_{\text{mean}}[2 + m \cos(fx - \omega t)]. \quad (3)$$

The binocular integration of motion information achieved in this way is unrelated to the stereoscopic perception of depth since in the case of horizontal gratings the spatial phase shift introduces no horizontal disparity information. The resulting motion perception is *cyclopean* in the sense that it requires integration of left and right eye inputs. It should not be confused with the motion of features in random dot stereograms, defined by horizontal disparity (Julesz, 1971; Patterson, Ricker, McGary & Rose, 1992) and hence depth. We use the adjective cyclopean when referring to properties of the visual perception which are only emergent from the fused binocular image. The term, dichoptic, is used generally to refer to the viewing conditions in which different stimuli are presented to either eye.

We used 1 c/deg gratings, modulated at a temporal rate of 3 Hz ($\omega/f = 3$ deg/sec). The contrast of the adaptation gratings were 5.0 and 2.5% for the dichoptic (quadrature) and real (rigid) motion conditions, respectively. In both cases the algebraic sum of left and right eye waveforms would possess contrast of 5%.

Procedure. Observers viewed the adaptation pattern for 5 min. During this period the position (i.e. absolute spatial phase) of gratings with respect to the fixation points was altered randomly every 10 sec. The interocular phase relationship (i.e. vertical disparity) was not affected. This manipulation served to shift the position of peaks and nodes in the counterphase gratings to different retinal locations. It served no purpose during adaptation to rigid motion but was performed to make the protocols as similar as possible.

The strength of the MAE was measured by nulling the MAE with a moving 1 c/deg test grating (5% contrast). The test gratings were presented binocularly in random order covering seven stimulus speeds and spanning both directions of motion. Both eyes viewed the identical test grating. The subject's task was to indicate the perceived direction, up or down, by pressing the appropriate button. A trial consisted of 4 sec of additional adaptation followed by a 500 msec delay blank screen and

finally the test grating, presented for 500 msec. After the test period the adaptation pattern was presented again. The cycle was reinitialized by the observer's response.

Sixty responses per stimulus speed were collected in three, 140 trial, sessions. The results were subjected to probit analysis (Finney, 1971) and an estimate of the nulling velocity was obtained. The velocity required to null the MAE served to estimate the latter's strength. We compared adaptation to dichoptic motion with adaptation to rigid motion and with the no adaptation control condition.

Results

The ability of four observers to identify the direction of slowly moving horizontal gratings before and after adaptation to downward rigid and dichoptic motion was examined. Data are presented in Fig. 1. The percentage of trials in which a test grating was reported as moving upward is plotted as a function of test grating velocity. The solid curves are maximum likelihood fits to a cumulative normal distribution [probit analysis (Finney, 1971)]. Three curves are shown for each observer, reflecting performance after adaptation to rigid motion, dichoptic motion, and in the unadapted state.

In the unadapted state, performance was predictable from the test grating velocity. The fraction of trials identified as upward increased with speed of upward motion and decreased with speed of downward motion. Stationary test patterns were about equally likely to be reported upward as downward. Of course, in the unadapted state, a stationary pattern appears to be stationary.

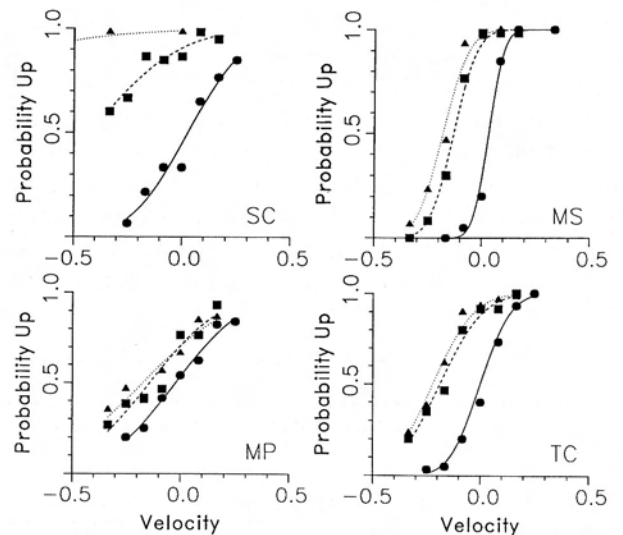


FIGURE 1. Measurement of MAEs in four subjects after adaptation to a blank screen (circles), drifting grating viewed binocularly (triangles), or dichoptic motion stimulus (squares). The percentage of trials in which motion of the test stimulus was judged as upward is plotted against test stimulus velocity (positive velocity upward; negative velocity downward). After adaptation to a blank luminance field, the percentage of upward responses increased with upward test stimulus velocity. After adaptation to both types of downward moving displays, stationary test gratings appeared to move upward. The likelihood of an upward judgment increased at all test velocities, as reflected by the shift of psychometric function to the left.

Adaptation to rigid and dichoptic downward motion produced a compelling MAE. Qualitatively, this was described as the appearance of upward motion in stationary test patterns. The MAE is reflected quantitatively by the left shift of the psychometric functions in Fig. 1. Larger downward velocities were necessary to support a perception of downward after adaptation to downward rigid and dichoptic motion. All subjects exhibited marked left shifts in their psychometric functions after adaptation to rigid and dichoptic motion. Extremely large MAEs were reported by observer SC, as reflected by the exaggerated leftward shift of her functions. Additional trials were provided for this subject over a broader range of velocities to establish the magnitude of shift in her psychometric function.

The velocity at which upward and downward judgments are equally likely (probability up = 0.5) is the nulling velocity of the MAE and serves to estimate its magnitude. It is the speed of the test grating that is exactly offset by the MAE to yield no net movement perception. Nulling velocities for four observers are summarized in Table 2. In the unadapted state, nulling velocities were approximately zero for all observers, and psychometric functions (Fig. 1) are symmetric about the point, velocity = 0.0, percent up = 50. However, after adaptation to downward motion, the test grating perceived as stationary was actually moving downward. Nulling velocities were approx. 0.20 deg/sec after adaptation to rigid motion and 0.15 deg/sec after adaptation to the dichoptic motion display (excluding SC's values).

Subjectively, the MAE obtained dichoptically was less powerful than that obtained with rigid motion. This trend is reflected in Fig. 1 and Table 2, achieving statistical significance for two observers (MS and SC). One possible explanation is that the motion signal in the dichoptic stimulus was attenuated because of fixation error. Any vertical interocular variation in fixation would introduce stimulus energy in the opposite direction of motion. If the error were to approach 7–15 min arc the perceived direction of the adaptation stimulus would actually reverse. Horizontally oriented patterns were employed to minimize this source of instability since vertical eye alignment errors have a smaller range

and drift more slowly (Leigh & Zee, 1991). Any eye alignment errors during adaptation would be expected to attenuate the aftereffect.

Alternatively the difference between rigid and dichoptic adapting conditions may reflect monocular contributions to the MAE. During adaptation to dichoptic motion, each eye views a counterphase grating which may be decomposed as the sum of an upward plus a downward moving grating. Ideally, within binocular mechanisms there is superposition of the downward components and cancellation of the upward components. Near threshold, this idealized summation appears to hold (Arditi, Anderson & Movshon, 1981; Watson, Thompson, Murphy & Nachmias, 1980; Shadlen & Carney, 1986). Monocular motion detectors cannot summate the two patterns, so conflicting directions of motion are represented in the population of monocular motion detectors and they cannot contribute to the MAE. Assuming detection of counterphase gratings is mediated independently by upward and downward mechanisms (Levinson & Sekuler, 1975; Watson *et al.*, 1980), there is a 3–6 dB range of contrasts above detection thresholds for dichoptic motion in which monocular contributions to perception should be minimal. Indeed, in our experience low contrast dichoptic motion gratings look the same as rigid grating motion. Unfortunately, at such low contrasts the strength of MAEs are only 50–75% of maximum (Pantle *et al.*, 1978). At 5% contrast (5–10 times threshold) monocular mechanisms contribute to perception and to the MAE. During adaptation to dichoptic motion these mechanisms are stimulated by flicker but they cannot contribute to the MAE. During adaptation to rigid motion, monocular mechanisms are exposed to lower effective contrast than binocular mechanisms, but the direction of motion is consistent. Thus both monocular and binocular mechanisms may contribute to the MAE. The small differences observed in three of four subjects raises the possibility that the monocular contribution is small and that the site of the MAE is predominantly in binocular mechanisms capable of integrating input from one or both eyes.

Discussion

The MAE has been proposed as a distinguishing characteristic of the early motion system (Anstis, 1980) and a signature of low level motion detectors (Pantle, 1974). However, Braddick (1974) refrained from linking the MAE with the short range system for two reasons, (i) the demonstration of a MAE after adaptation to apparent motion with 4 deg spatial displacements, and (ii) the observation that a MAE could be elicited with a dichoptic display sharing many properties with the one employed here (Anstis & Moulden, 1970).

The first objection must be withdrawn in light of subsequent recognition that D_{\max} is not a fixed 15 min arc, but increases with decreasing stimulus spatial frequency (Bischof & Di Lollo, 1990; Chang & Julesz, 1983a; Cleary & Braddick, 1990a, b). Indeed, to obtain a MAE with 1 deg displacements, Anstis and Moulden

TABLE 2. Magnitude of the MAE expressed as a nulling velocity for four observers

Observer	Velocity appearing stationary (deg/sec)		
	No adaptation	Adaptation to real motion	Adaptation to dichoptic motion
TC	0.00 ± 0.001	0.22 ± 0.04	0.19 ± 0.035
SC	0.03 ± 0.03	1.54 ± 0.17	0.42 (0.32–0.65)
MP	0.02 ± 0.02	0.17 ± 0.07	0.14 ± 0.05
MS	–0.03 ± 0.02	0.18 ± 0.02	0.13 ± 0.02

Values reflect the velocity of a test grating which is equally likely to be seen as upward or downward after adaptation to downward motion. Velocity is in deg/sec; positive values denote direction of test grating motion opposite to the aftereffect, or the same as the adapting motion. Error terms represent 95% confidence intervals from maximum likelihood probit analysis; they are approximately symmetric except where indicated.

found it necessary to place a ground glass in front of their display, thereby attenuating all but the low spatial frequency components. Using more conventional methods, Banks and Kane (1972) found MAEs with displacements not exceeding 12.5 min arc. It may be surmised that whenever a large displacement gives rise to a MAE, there is a motion cue present which would activate low level detectors (Pantle, 1974). With few exceptions, stimuli designed to selectively activate long range processes do not produce MAEs.

The second objection is more axiomatic: the MAE cannot be a signature of short range processes precisely because it can be elicited dichoptically. The position is based entirely on the premise that short range motion perception cannot be elicited dichoptically. Therefore, the critical question is whether dichoptic motion perception is possible in a short range display like Braddick's. If so, then there would be no grounds for excluding the MAE as a signature of short range (or early or low level) processes. Then the existence of a dichoptic MAE may be regarded as evidence for binocular short range motion processes.

We have reported cyclopean motion perception in one dimensional noise patterns (Shadlen & Carney, 1985) based on a generalization of the quadrature relationships in equations (1) and (2). In the next section the same quadrature spatiotemporal relationship is extended to develop a random texture motion stimulus comparable to Braddick's random dot kinematogram.

A NEW SHORT RANGE MOTION DISPLAY

The short range motion system was characterized as monocular because random dot kinematograms were not found to support dichoptic perception of motion in a manner requiring binocular integration (Braddick, 1974). In Braddick's display a set of random dots was flashed before the left and right eyes in alternation. The monocular patterns were uncorrelated except for a central rectangle within which dots were displaced by a fixed distance in the two views. Observers were required to report the orientation of the central rectangle: either vertical or horizontal. Observers found this task extremely difficult compared to the case in which alternate frames were viewed by the same eye. In this section we describe a new random texture stimulus which resembles Braddick's random dot kinematograms. However, when viewed dichoptically this stimulus supports a cyclopean perception of motion. In the following sections we set out to develop the display, establish it as a "short range" stimulus (see Expts 2.1 and 2.2) and then examine its ability to support dichoptic motion perception (see Expts 2.3 and 2.4).

Quadrature motion display

Our random texture motion displays are based on a generalization of the quadrature relationship exploited in Expt 1. It is convenient to consider each column of

pixels as a one-dimensional pattern composed of many spatial frequencies of random spatial phase (1D noise). When multiplied by a cosinusoidal temporal function the intensity of pixels in the column may be represented by:

$$L_{\text{left}}(y,t) = L_{\text{mean}} \left[1 + \frac{2}{N} \sum_{i=1}^{N/2} m_i \cos(f_i y - \phi_i) \cos(\omega t) \right], \quad (4)$$

where f_i , m_i and ϕ_i represent spatial frequency, depth of modulation and phase of the i th frequency component for $i = 1$ to $N/2$ cycles per vertical column subtense. The phase, ϕ_i , is a uniformly distributed random value between 0 and 2π . N is the number of pixels in the column and ω is temporal frequency. The noise is generated so that m_i is a constant which scales the intensity range of the display. Thus, the spectrum is that of an idealized white noise signal.

A two-dimensional random texture is created from a collection of independent 1D noise patterns, each 1 pixel wide in the horizontal dimension of the display. Intensity along this dimension is random and uncorrelated, resulting in the static intensity profile of a two-dimensional random texture [Fig. 2(A)]. Temporal modulation by cosine introduces contrast reversal, and the pattern appears as a flickering random texture. Like its counterphase grating components, it does not possess unambiguous motion information. To achieve this a second texture is required.

The pattern on the right side of Fig. 2(A) is made by shifting each frequency component of a column of pixels on the left by 90 deg phase so that corresponding columns of pixels are in spatial quadrature. This pattern is temporally modulated as well, but the counterphase cycle also differs by 90 deg phase. The quarter cycle difference in space and time between corresponding columns in Fig. 2(A) is reflected by the substitution of sine for cosine in equation (4) (i.e. Hilbert transform)

$$L_{\text{right}}(y,t) = L_{\text{mean}} \left[1 + \frac{2}{N} \sum_{i=1}^{N/2} m_i \sin(f_i y - \phi_i) \sin(\omega t) \right]. \quad (5)$$

The sum of corresponding left and right columns is a superposition of traveling waves of common temporal frequency and direction

$$L_{\text{left}}(y,t) + L_{\text{right}}(y,t) = L_{\text{mean}} \left[2 + \frac{2}{N} \sum_{i=1}^{N/2} m_i \cos(f_i y - \phi_i - \omega t) \right]. \quad (6)$$

Therefore, each column, and hence the entire pattern, turns into its negative image every half temporal period and is restored to its original image at the completion of one temporal period.

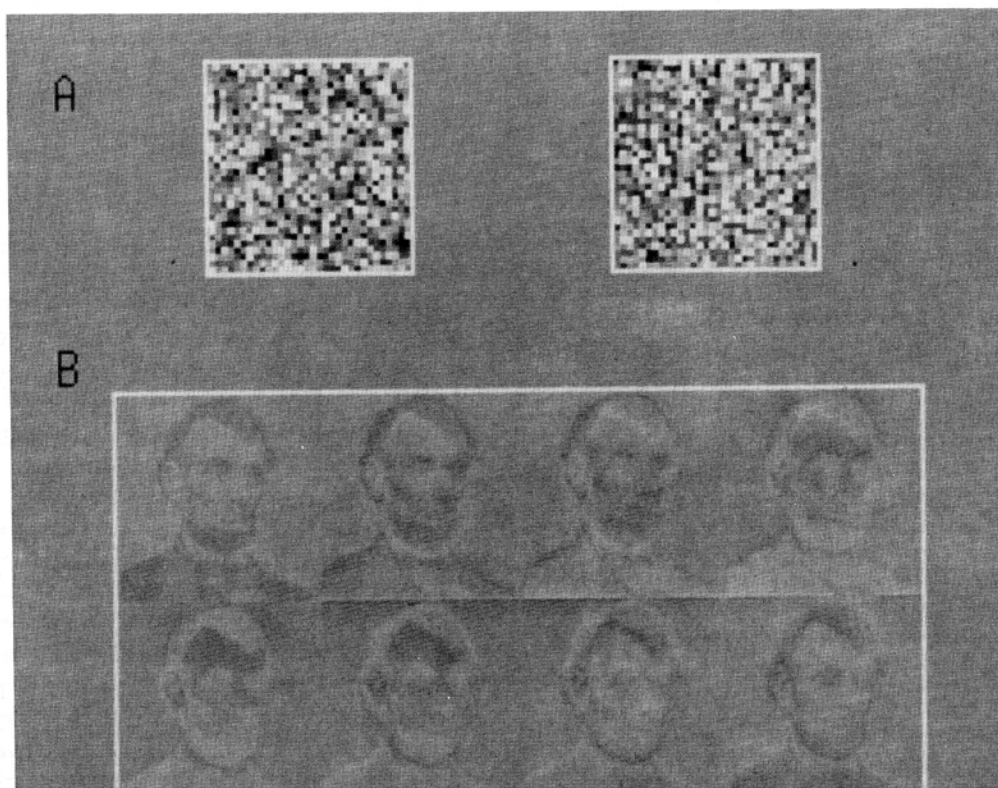


FIGURE 2. (A) Two-dimensional noise textures in spatial quadrature. Each column of pixels in the left texture is composed of a collection of sinusoids of random phase. Corresponding columns in the right pattern contain the same sinusoidal components shifted by 90 deg of phase. The dichoptic motion display is constructed by temporally modulating the contrast of left and right patterns by sine and cosine, respectively. Their sum or superposition contains only upward (or downward) motion energy (see text). (B) Film loop example of a motion energy display in which the distortions above are applied to a well known portrait. The frames are derived from a 64×64 pixel digitized portrait of Abraham Lincoln. Each frame is formed from the weighted sum of this portrait and its column by column Hilbert transform. The original and quadrature images appear in the first and third frames of the sequence (counting left to right). Weighting functions are cosine and sine, respectively, and each frame of the film loop represents a step of one-eighth temporal cycle. Notice that pairs of frames separated by half the film loop (e.g. 1 and 5) are positive and negative. When viewed as a film loop the sequence gives rise to a continuous perception of upward movement.

In summary, the dichoptic two-dimensional random texture display is created from a collection of independent one-dimensional noise columns, each one pixel wide, and their Hilbert transforms. The sum of corresponding columns of pixels in the two images is the sum of two counterphased waveforms in quadrature. Neither component alone, left or right eye column, would lead to motion perception, whereas the sum has motion in only one direction, up or down. Notice that either monocular pattern can be presented for an arbitrary duration without introducing a direction cue. This is not possible with most standard rigid motion displays in which alternate frames are presented to either eye, since successive frames of either monocular view contain motion cues.

In the experiments below, stimulus motion direction is always vertical; however motion in any direction can be produced by a simple generalization of the procedure described above. Note that the column Hilbert transform (substituting sine for cosine in the Fourier series) is equivalent to convolution with a hyperbolic filter, $1/\pi y$ (Bracewell, 1978). In our patterns this is approximately equivalent to two-dimensional convolution with a filter specified by a hyperbola along each column and a delta function (or very narrow pulse) in x ,

the row. Motion in other directions may be achieved by rotating the filter in the xy plane (Shadlen, Carney & Switkes, 1987).

The sum of a pair of patterns in spatial quadrature with temporal modulations in quadrature contains motion in only one direction (see Appendix 2). An intuitive sense for the motion sequence may be gained by studying Fig. 2(B). The sequence is created from a digitized portrait of Abraham Lincoln, shown in the upper left frame. After column by column Hilbert transform of this frame we obtain the quadrature portrait, frame 3 of the first row [Fig. 2(B)]. The remaining frames are generated by adding the original Lincoln and its quadrature image, weighted by cosine and sine functions of time (i.e. rank in the sequence), respectively. Thus each frame represents a 45 deg phase shift of all spatial frequency components composing each column of pixels. When these eight frames are shown as a film loop, Abraham Lincoln appears to move continuously upward, although he remains centered in each frame. Notice that halfway through the film loop Lincoln has metamorphosed into his negative. In this way, the motion illusion resembles the reversed phi phenomenon described by Anstis and Rogers (1975, 1986; Anstis, 1970). Notice, however, that identifiable features of

Lincoln are never actually displaced.* We will employ the term quadrature motion to distinguish this type of noncoherent motion display from those which incorporate rigid displacement of texture elements.

The random textures employed experimentally undergo similar transformations. To construct figure/ground or structure from motion tasks similar to those employed by Braddick, the motion direction of a rectangular region of the display was set opposite to that of the surrounding area. This was achieved by introducing a 180 deg phase shift in one spatial pattern or one temporal modulation over the area of interest.

Having achieved the development of a random texture display which is amenable to decomposition into left and right components of a dichoptic motion display, we now turn to the experimental results. The first two experiments establish the monocular quadrature random texture motion display as a short range stimulus. To do this we have followed Braddick's methods fairly closely, including his reliance on reaction times as a measure of perceptual difficulty. We then examine the capacity for dichoptic motion perception in our display. Finally a transient display is introduced which permits brief pulses of directionally unambiguous motion to be presented in dichoptic and nondichoptic displays.

General methods

Stimuli. Stimuli were viewed through natural pupils at a distance of 114 cm where they subtended 4 deg of visual angle. Random textures were constructed on a 64×64 pixel array with 8-bit gray scale resolution using a Number Nine Computer Co. graphics board. Pixel size was 3.75 min arc. Sixty-four such images could be stored on the graphics board and presented in any arbitrary order on the display monitor to create a prolonged motion sequence. Such patterns were used to generate two types of motion: rigid motion in which the pattern undergoes constant spatial shifts from frame to frame, and quadrature motion in which each spatial frequency component undergoes a constant spatial phase shift from frame to frame thereby continually deforming the image as described above. The direction of stimulus motion was always either up or down.

TABLE 3. Summary of conditions comprising Expt 2

Experiment	Display		Viewing	
	Rigid	Quadrature	Dichoptic	Nondichoptic
2.1	Δy , Velocity	Δ phase, TF		+
2.2	ISI	ISI		+
2.3	Velocity	TF	+	
2.4		Duration	+	+

The main parameter manipulations are shown for rigid and quadrature motion displays where ISI, TF, ΔY and Δ phase are interstimulus interval, temporal frequency, rigid vertical displacement and vertical phase shift, respectively. The viewing condition, dichoptic or nondichoptic, for the various display parameters is indicated by the presence of the + symbol.

Procedures. The capacity to discriminate direction of motion was assessed using the method of constant stimuli in a single-interval, two-choice task. Two types of discriminations were performed: the direction of stimulus movement (entire image motion: up or down) and the orientation of a central rectangle defined by its direction of motion opposite to that of the surround. In both tasks the direction of motion was randomized on each trial; in the figure/ground task the orientation of the central rectangle was also randomized. The image field was a 4 deg square and the central rectangle subtended 1×2 deg. In addition to percent correct, Braddick (1974) measured reaction time to assess the effect of motion display parameters on short range perception. Therefore, we have incorporated this measurement in Expts 2.1 and 2.2 which are designed to establish our textures as short range stimuli.

Analogous manipulations of spatial and temporal display parameters (e.g. displacement and phase shift) were applied to rigid and quadrature motion stimuli in separate runs. These manipulations will be described fully in the corresponding sections. For convenience, a summary of the main parameters and viewing conditions are listed in Table 3. Our main goal was to assess dichoptic motion perception in the quadrature random texture. As a preliminary step two experiments were conducted using customary binocular viewing (both eyes viewed the same stimulus). We will refer to this viewing condition as *nondichoptic*.

Experiment 2.1. Spatial and phase displacement limits

Much emphasis has been placed upon the magnitude of spatial displacement capable of providing an early motion cue (Bischof & Groner, 1985; Lappin & Bell, 1976). Braddick (1974) showed that the maximum displacement (D_{\max}) capable of eliciting motion perception in random dot displays is approx. 15 min arc irrespective of pixel size. Later studies demonstrated D_{\max} increases with field size and retinal location (Nakayama & Silverman, 1984; Baker & Braddick, 1982a, b, 1985a; Chang & Julesz, 1983b; Petersik, Pufahl & Kransoff, 1983). Moreover, it has been shown that D_{\max} depends on stimulus coarseness or spatial frequency content (Chang & Julesz, 1983a; Baker, Baydala & Zeitouni, 1989; Bischof & Di Lollo, 1990; Cleary & Braddick, 1990a, b; Morgan, 1992). Coarser textures may undergo

*The distortion introduced by the quadrature filtering poses serious problems for any feature detection scheme. Perhaps a most relevant example is the model proposed by Morrone and Burr (1988) which uses a quadrature decomposition very similar to that which is embodied in our stimuli. This model would identify independent sets of features in quadrature images (e.g. frames 1 and 3 of [Fig. 2(b)] which are explicitly excluded from providing any basis of correspondence. Indeed any model of feature detection which requires registration of primitives across multiple bandpass filtered representations (e.g. Marr & Hildreth, 1980) will fail to track features since the quadrature distortion destroys this alignment. Of course, primitives (e.g. zerocrossings) extracted from *within* appropriately filtered representations must undergo displacement in a consistent direction, and early motion detectors [e.g. energy mechanisms like Adelson and Bergen (1985)] could be described as "tracking" such primitives (Morgan, 1992). However, this description must be distinguished from the feature tracking associated with long range motion perception.

larger stimulus jumps, yet give rise to a motion perception. Thus the expected value for D_{\max} depends on the stimulus and testing conditions. Nevertheless, Braddick's observation remains valid; there is a displacement limit beyond which motion perception is not obtained in random textures, implying that the perception of motion in such patterns must be mediated by mechanisms which are incapable of processing large displacements. In this and the following section, our goal is to establish our random textures as short range stimuli by repeating Braddick's experiments with rigid motion. At the same time, we shall develop analogous spatio-temporal manipulations of the quadrature random texture motion display which will ultimately be utilized to test dichoptic motion perception.

2.1. Method. Random textures were presented in rigid translation with frame to frame spatial shifts ranging from 3.75 to 60.0 min arc. The effect of displacement magnitude was assessed in two ways. One set of measurements was made by presenting the static frames of the motion sequence for a fixed 80 msec duration (dwell time). Hence the effective speed varied with shift size from 0.8 to 12.5 deg/sec (variable speed, constant dwell condition). Alternatively, the dwell time was varied with displacement to yield a constant speed of 3.13 deg/sec (constant speed, variable dwell condition). Changes in spatial displacement may then be conceptualized as changes in the sampling rate of a rigid motion display possessing a unique velocity (see Appendix 1).

Analogous displacements were applied to the quadrature motion displays by varying the magnitude of the phase shifts in the apparent motion sequence. Recall that the columns of the texture are described by the superposition of traveling waves sharing a common temporal frequency. The phase jumps are naturally bounded by 180 deg since any larger displacement is equivalent to its difference from 180 deg in the opposite direction. We therefore examined performance for phase shifts from 22.5 to 157.5 deg. As for rigid motion this was accomplished in two ways, using a constant frame duration of 80 msec, the temporal frequency varied as a function of phase shift from 0.78 to 5.47 Hz (variable TF, constant dwell). Alternatively, frame duration was covaried with the phase shift to maintain a constant temporal frequency of 3.1 Hz (constant TF, variable dwell).

The combination of the stimulus conditions, figure/ground or direction discrimination, quadrature or rigid motion, and constant or variable dwell, comprise eight experiments. For each experiment the various stimulus levels were presented 40 times each, in random order. The direction of field motion (up/down) or figure orientation (horizontal/vertical) was randomized from trial to trial.

2.1. Results. Reaction times for the segregation of figure from ground as well as the perception of direction are plotted in Fig. 3(A,B) as a function of spatial displacement in the rigid translation display. The results in Fig. 3(A) were obtained under the variable speed (constant dwell) condition while those in Fig. 3(B) were obtained under the constant speed (variable dwell)

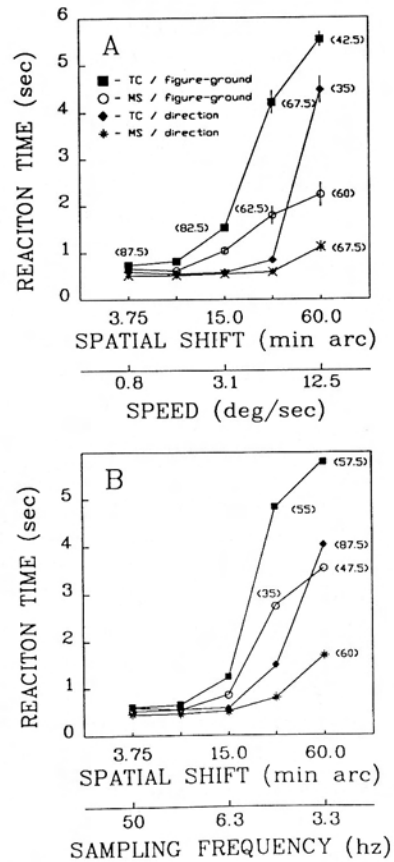


FIGURE 3. Spatial displacement limits for direction discrimination and figure/ground segregation tasks in random texture kinematograms for observers MS and TC. Reaction time is plotted as a function of stimulus displacement. Error bars indicate one SE and are shown only when larger than the symbols. Performance exceeded 90% correct except where indicated. (A) Constant dwell, variable speed condition. Velocity covaried with displacement. (B) Variable dwell, constant speed condition. Sampling frequency covaried with displacement at a fixed speed of 3.13 deg/sec. For both conditions, performance deteriorated when spatial displacement exceeded 15 min.

condition. To identify performance deterioration, the percentage of correct responses is indicated in the figure when performance dropped below 90% correct. These measures of performance reveal deterioration with displacements of 30 min arc. With the exception of TC's performance under the constant speed condition [Fig. 3(B) diamond symbols], direction discrimination was indistinguishable from chance for displacements exceeding 30 min arc. Performance on the figure/ground task deteriorated to chance with displacements of 30 min arc ($P < 0.01$). Comparable values were obtained under the constant speed and constant dwell conditions.

We have plotted the reaction times as a function of displacement because this was the strategy employed by Braddick (1974) in his seminal investigation. The metric seems to reflect some change in the difficulty of the task which is not necessarily sufficient to reduce the percentage of correct responses. Recall that the point of this preparatory experiment was to establish that the textures we utilized would necessitate activation of the short range system according to Braddick's scheme. The comparison between Fig. 3 and to Braddick's original data (1974, Fig. 2) is reasonable. Our estimates of D_{\max} are

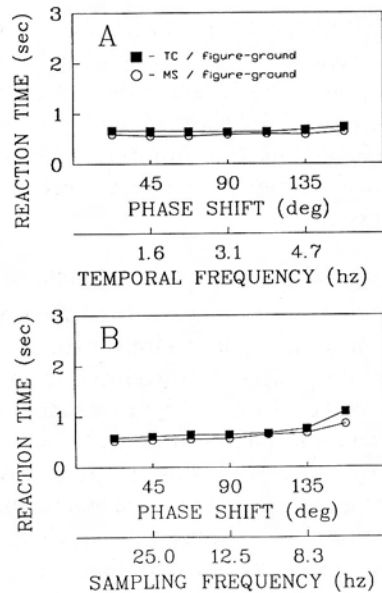


FIGURE 4. Spatial phase displacement limits for the figure/ground segregation task employing quadrature motion kinematograms. Percent correct was $>90\%$ for all conditions. (A) Constant dwell, variable temporal frequency condition. Sampling frequency was constant, so temporal frequency increased with spatial phase shift. (B) Variable dwell, constant temporal frequency condition. Temporal frequency of the sinusoidal components was fixed so sampling frequency varied inversely with spatial phase shift.

slightly larger, possibly because of differences in gray scale of the patterns. Braddick used black-white random pixel patterns (two gray levels) which result in more power at all spatial frequencies relative to a gray scale display with the same intensity limits and pixel size. The resulting high contrast high spatial frequency components in black-white displays should decrease estimates of D_{\max} relative to the gray level display (see Appendix 1). Minor differences aside we may conclude, like Braddick, that mechanisms responsible for perception of motion in these textures fail when spatial displacement exceeds some short range.

In the quadrature motion display all spatial frequency components undergo synchronous phase shift, so the analogy to apparent motion is realized by introducing discrete phase shifts. The effect of phase displacement magnitude on performance in the figure/ground task is shown in Fig. 4. In Fig. 4(A) the dwell duration was adjusted to yield a constant temporal frequency of 3.1 Hz.

Performance on the figure/ground task was virtually flawless ($>90\%$ correct) at all spatial phase displacements, although the quality of the perception was diminished at 157.5 deg as reflected in the lengthened reaction times. The results were virtually identical for both constant and variable temporal frequency conditions. Results on the direction discrimination task are not shown. Both observers exhibited flawless performance at all phase shifts. Of course performance must deteriorate to chance as the phase shift approaches 180 deg, but we

did not explore this range of displacements systematically.

The results obtained with rigid displacement demonstrate that motion perception in our random textures must be governed by a short range process. Since the same random textures are utilized in the quadrature display, it follows that the perception of motion in these displays must also be governed by a short range process. Yet the perception appears to be more robust to manipulations analogous to increasing displacement. In both types of displays the introduction of discrete jumps (in space or phase) is equivalent to sampling a continuous movement in time. Thus the failure of motion discrimination at large displacements must be attributed to visual information introduced by undersampling which would activate opposing motion mechanisms (Carney, 1983; Watson, 1990). For the quadrature display this sampling energy is weaker than the intended motion signal at all spatial frequencies, for phase shifts up to 180 deg (see Appendix 1).

Experiment 2.2. Interstimulus interval limitations

Braddick (1974) suggested that the early motion system operates over only a short range of time as well as distance. If successive frames of a rigid random dot motion display are separated by an interstimulus interval (ISI) exceeding approx. 100 msec, motion perception is degraded (Braddick, 1974; Baker & Braddick, 1985b). The effect is particularly dramatic if a bright field is introduced during the ISI. In this section we examine the effect of manipulating the ISI on the perception of motion in rigidly moving textures identical to those employed in the quadrature display, and apply the same manipulations to our quadrature display in order to further establish our random texture motion display as a "short range" stimulus.

2.2. Method. For rigid translation, static two-dimensional noise patterns were presented for 80 msec followed by a variable length ISI,* ranging from 20 to 160 msec. During the ISI the screen was either a bright (twice mean luminance) or dark homogeneous field. Following the ISI, the texture appeared displaced up or down by 1 pixel (3.75 min arc) as viewed through a static window. As before, the figure/ground stimulus was defined by the relative motion of a rectangular area relative to its surround. The effective speed of the pattern covaried with ISI from 14.4 to 37.5 min/sec.

The analogous ISI experiment was performed using quadrature random texture motion displays. Static patterns were presented for 80 msec and shifted a constant phase after a variable ISI. In this case temporal frequency covaries with ISI from 1.04 to 2.5 Hz. For both types of experiments, viewing was nondichoptic.

2.2. Results. Results are shown in Fig. 5. Reaction times are plotted as a function of ISI for figure/ground and direction discrimination tasks employing rigid translation and quadrature motion displays. For dark ISIs, performance on both tasks was virtually flawless. However, when a bright ISI was employed, performance deteriorated for 160 msec ISIs.

*Interstimulus interval refers to the period between the static images of the apparent motion sequence, not the period between trials.

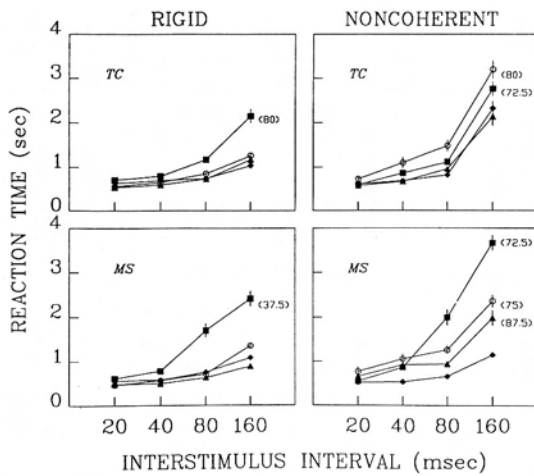


FIGURE 5. Interstimulus temporal interval limits for both rigid and quadrature motion random texture kinematograms. Reaction time and performance are plotted as in Fig. 3. Figure/ground task with bright ISI (solid squares); direction task with bright ISI (open circles); figure/ground task with dark ISI (solid diamonds); direction task with dark ISI (solid triangles).

Again, the reaction times provide a clearer picture of the perceptual quality as a function of ISI for both tasks. For all conditions, reaction time was found to increase as a function of ISI. This was most apparent between 80 and 160 msec. The pattern of results was strikingly similar for both rigid and quadrature motion as well as for direction and figure/ground tasks. On all corresponding tasks a bright ISI resulted in longer reaction times. These results are in agreement with those obtained by Braddick (1974), although in his most comparable condition (2.7 min arc pixel size, one pixel displacement, 75 msec dwell time) the deterioration in reaction time occurred at shorter ISIs. Again, this discrepancy may be due to the higher contrasts in binary intensity patterns or differences in adaptation state. For our purposes we are only trying to show that these stimuli do not support motion perception with large displacements and ISI, and therefore necessitate processing by a motion system which is only capable of operating over a restricted spatial and temporal range. The present findings serve to demonstrate that the random textures employed in our display activate "short range" motion processes, in accordance with Braddick's formulation. The finding of D_{max} suggests that the visual system is incapable of identifying distinct features in the pattern and tracking them over arbitrary distances. Successful motion extraction must therefore be due to some mechanism which is incapable of attentional tracking of texture features.

Regardless of the ultimate fate of "short range" as a concept, and regardless of its physiological identity, the processes responsible for motion perception in random dot patterns must also be activated to achieve motion perception in our textures. When these mechanisms fail, motion perception fails. Therefore, when motion perception is observed with the same textures set in quadrature motion, we may conclude that it is the "short range" or early motion system which is mediating such perception. All this may seem superfluous to many readers, since the use of random textures is often viewed as sufficient

grounds to implicate short range processes. Yet, the short range system has been characterized as monocular precisely because of the failure to demonstrate dichoptic motion perception with "short range" stimuli. As we are about to challenge this, it is important to document that the stimuli we employ do indeed necessitate "short range" processes.

Experiment 2.3. Dichoptic rigid and quadrature motion

We are now ready to ask whether dichoptic motion perception can occur with random texture stimuli. The quadrature motion displays introduced in the preceding sections are derived from a pair of random textures in column by column quadrature which are temporally modulated by sine and cosine, respectively. Pixel columns from either component image may be described as a superposition of standing waves, while the sum of corresponding pixel columns in the two images is a superposition of traveling waves. The latter is perceived as moving through a process mediated by short range mechanisms. The dichoptic display is constructed identically, except that rather than adding the two patterns on the display, they are presented dichoptically to either eye. Now the visual system must perform the addition. The monocular images are flickering and cannot contribute to the perception of direction, no matter how long they are viewed.

2.3. Methods. Stimuli were 128×128 or 64×64 pixel random texture noise patterns possessing the column by column quadrature relationship described above. Temporal frequencies were presented ranging from 0.2 to 11.3 Hz. Patterns were viewed dichoptically by free fusion. For direction discrimination experiments there is no comparison study employing rigidly moving textures. This is because the successive frames of a rigidly moving image contain monocular motion cues and cannot be readily used to test dichoptic perception of movement direction.

In addition, dichoptic figure/ground discrimination was tested using rigid translation and quadrature displays. As in Expts 2.1 and 2.2, the orientation of a central rectangle was identified and reaction time recorded. Figure and ground were distinguished by their opposing direction of motion. For the rigid translation display the direction of motion was reversed throughout the display on every other frame. Therefore, monocular patterns were flashing stationary images. For the quadrature case, the directions of figure and surround were chosen randomly for each trial but then maintained for the duration of the trial. Monocular patterns were counterphase modulated textures.

2.3. Results. Results on the dichoptic direction discrimination task are shown in Fig. 6. As in the preceding sections, reaction time is plotted against stimulus temporal frequency and performance below 90% is indicated. Performance was generally flawless for observer MS at all temporal frequencies and for observer TC for frequencies > 1 Hz. The reaction times obtained on this dichoptic motion task are comparable to those seen in preceding sections employing monocular displays. This

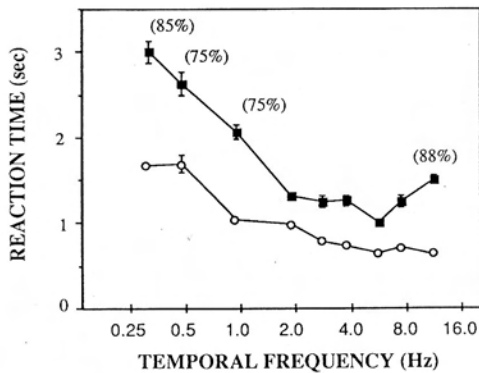


FIGURE 6. Direction discrimination using random texture kinematograms presented dichoptically in spatio-temporal quadrature. Reaction time is plotted against temporal frequency. Percent correct exceeds 90% except where indicated. Both subjects readily perceived dichoptic motion perception, demonstrating that the early motion system is capable of binocular integration. Solid symbols, subject TC; open symbols, subject MS.

result demonstrates that dichoptic motion perception is not precluded by the use of random texture stimuli, and that the early motion system is capable of binocular integration.

Since collecting this data we have gained considerable experience testing naive observers. Almost all observers with normal binocular vision achieve cyclopean perception of direction. However, it is commonly observed that the quality is much worse than that obtained monocularly and that this difference is more remarkable for random textures than the analogous comparison between dichoptic motion of sine-wave gratings and their rigid translation. This is not unexpected since any horizontal vergence errors must disrupt the correspondence between pixel columns and hence degrade motion perception with two-dimensional but not one-dimensional patterns. Similarly, small errors in vertical eye alignment result in degradation of the quadrature relationship at higher spatial frequencies. We know from our work with sinewave gratings that dichoptic motion perception deteriorates between 4 and 8 c/deg (Shadlen & Carney, 1985). The random textures employed in the present experiments were composed of sinusoidal frequencies from 0.25 to 8 c/deg.

These observations may be relevant to the results obtained on the figure/ground task. Like Braddick (1974) we found figure/ground segregation in dichoptic rigid motion displays to be difficult to impossible. Observer TC performed at chance for all stimulus conditions while MS was capable of weak motion perception only at the lower stimulus velocities (data not shown). Dichoptic figure/ground segregation using the quadrature motion displays was also disappointing (Fig. 7). The data appear to reflect a weak capacity for figure/ground segregation under a restricted set of temporal frequencies for TC and the entire temporal frequency range tested for MS; but we believe this is misleading. Neither observer actually perceived figure/ground segregation. The direction of motion was apparent throughout different regions of the pattern, and on that basis the orientation of the rectangular region with opposing motion

could be deduced. The striking contours which emerge at the boundaries of figure and surround in the nondichoptic version of the display were conspicuously absent.

In summary, these results reveal a capacity for dichoptic motion perception in random texture displays. In addition, they permit us to reconcile previous failures to demonstrate dichoptic motion perception with rigid type displays. The quadrature display permits us to test the discrimination of one direction of motion without introducing frequent reversals. With rigid motion displays, monocular cues are customarily eliminated by reversing the direction of motion after every other frame. Thus in prior studies a task more difficult than direction discrimination was employed, namely, segregation of a figure moving back and forth from its dynamic surround. Our results suggest two possible explanations for failure on this task: (i) the absence of consistent direction, and (ii) the possibility that figure/ground segregation may fail in spite of successful binocular integration of motion cues.

In the next and final experiment we will examine the effect of stimulus duration on dichoptic motion perception. We will take up the discrepancy between motion detection and figure/ground segregation in the discussion.

Experiment 2.4. A transient early motion display

We have demonstrated cyclopean perception of motion using random textures which appear to activate the short range system. To do this we have exploited a quadrature relationship between spatiotemporal luminance modulations which serves to decompose a traveling wave into two standing waves. Either component may be viewed for any duration without introducing a direction cue. In rigid motion displays, direction must be reversed every other frame in order to preclude monocular direction cues. Thus one possible explanation for the success of our display is that a consistent direction cue can be introduced for a substantial length of time.

There are two factors to be distinguished: the consistency of direction and the duration of presentation. Several studies have demonstrated facilitation effects for multiframe motion sequences (McKee & Welch, 1985;

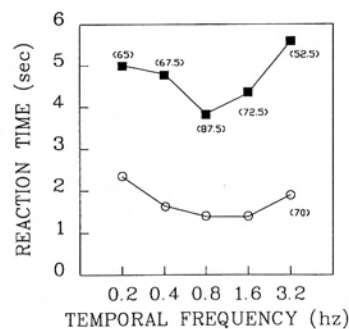


FIGURE 7. Figure/ground segregation of random texture kinematograms presented dichoptically in spatio-temporal quadrature. Reaction time and performance are shown as in preceding figures. Although the task was performed successfully under certain conditions, neither subject experienced compelling figure/ground perception, but based judgments on local (cyclopean) motion direction cues.

Solid symbols, subject TC; open symbols, subject MS.

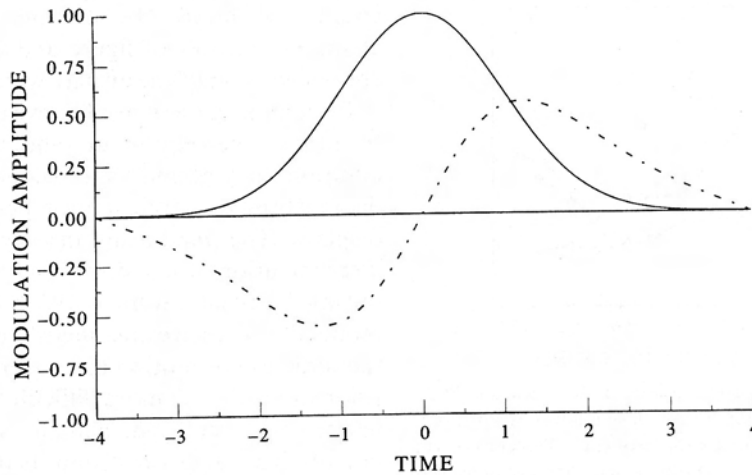


FIGURE 8. Temporal modulation functions employed in the transient "moving snapshot" stimulus. A Gaussian function (solid line) and its Hilbert transform (dashed line) are delayed by four standard deviations with respect to $t = 0$. Abscissa is in units of standard deviation [τ in equation (A2.3)].

Nakayama & Silverman, 1984; Ramachandran & Anstis, 1983; Georgeson & Shackleton, 1989). In this section we examine the effect of stimulus duration on dichoptic motion perception in random texture displays. To do this we have developed a transient version of the quadrature motion display which preserves its unidirectional character.

To control stimulus duration, it is customary to present a stimulus in a temporal window with Gaussian or half cosine contour. This type of modulation introduces motion energy in opposing directions (like counterphase). We wish to preserve the unidirectional character of our display so that the integrated motion signal contains motion energy in only one direction. Therefore we have incorporated the temporal window into the stimulus by replacing cosine and sine temporal modulations with a delayed Gaussian time function and its Hilbert transform, as illustrated in Fig. 8. Simply put, one pattern is pulsed on and off while the other is pulsed on, contrast reversed, and pulsed off. Again, neither pattern contains a direction cue, but the sum contains only one direction. As shown in Appendix 2, the sum

contains unidirectional motion energy distributed across a broad range of spatial and temporal frequencies. The briefer the pulse, the broader the range of temporal frequencies. We shall refer to these displays as *moving snapshots* since they appear as a brief pulse of unidirectional motion energy.

2.4. Methods. As in the previous sections, two types of discriminations were tested: direction and figure/ground. Direction of motion was up or down and the central rectangle was vertical or horizontal. The quadrature spatiotemporal components were either superimposed on a single screen (nondichoptic) or presented dichoptically to either eye. Eight stimulus durations were employed, from 20 msec to 2.5 sec. These values correspond to the width at half height of the even symmetric Gaussian pulse or 2.36τ (see Appendix 2). Both duration and direction were randomly interleaved for 40 trials per condition. Performance on dichoptic, nondichoptic, direction, and figure/ground tasks was tested in separate sessions. Reaction time was not measured.

2.4. Results. Performance on the nondichoptic figure/ground segregation task and the dichoptic direction discrimination task is shown in Fig. 9. Percent correct is plotted for each stimulus duration. When both components of the quadrature display were superimposed (nondichoptic condition), the task was performed effortlessly. Direction discrimination was perfect (data not shown) and figure/ground segregation was compelling at all but the shortest duration, where limitations in the display apparatus may be contributory. When the two components of the transient display were presented dichoptically, direction discrimination was still possible. As shown in Fig. 9, successful integration of motion cues was observed over a broad range of stimulus durations, with peak performance at 80–320 msec. These presentations are perceptually brief; yet they support dichoptic motion perception in random texture displays. On the other hand, figure/ground segregation was impossible. In spite of successful integration of dichoptic motion cues, the orientation of a central rectangle could not be discerned.

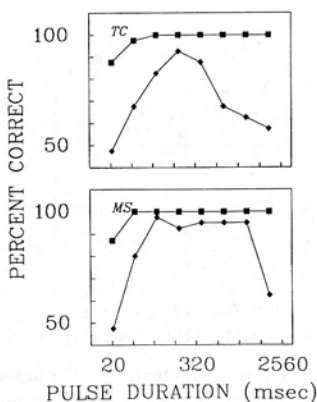


FIGURE 9. Motion perception of moving snapshot displays. Percent correct for nondichoptic figure/ground segregation (solid squares) and dichoptic direction discrimination (solid diamonds) tasks. Stimulus duration is defined as width of the temporal Gaussian at half height [2.35τ in equation (A2.3)].

These results suggest that the duration of presentation is not crucial for dichoptic motion perception. Therefore, the failure of dichoptic perception in random dot kinematograms is unlikely to be attributed to brief presentation. Rather, it would appear to be due to the presence of conflicting motion cues, introduced by alternating direction every two frames, and/or to the reliance on figure/ground segregation as an indicator of motion perception. Our observations reveal that figure/ground segregation may be poor or absent in spite of successful motion perception.

DISCUSSION

We have presented evidence supporting the binocular nature of the early motion system, and in the process have introduced a new class of stimuli which might be called "motion energy displays". The principal finding is the existence of a strong MAE upon adaptation to a stimulus whose motion cues are obtained only through binocular integration. Thus one site of adaptation is after the integration of monocular channels. The finding compliments prior demonstrations of interocular transfer of the MAE after monocular adaptation (Mitchell *et al.*, 1975; Price & Keck, 1982; Swift & Smith, 1985; Wade, 1976; Ware & Mitchell, 1974). To the extent that the MAE may be considered a signature of the early motion system, our results indicate that the latter is capable of binocular integration.

Is the MAE a signature of the early motion system? In all likelihood, the neural mechanisms responsible for the earliest extraction of motion information are the very ones that adapt to give rise to the MAE. Direction selectivity in primates and cats is first expressed in central visual pathways by neurons which characteristically receive binocular input (Hubel & Wiesel, 1962; Schiller *et al.*, 1976; Hammond & Pomfrett, 1989; Maunsell & Van Essen, 1983). Moreover, these neurons have been shown to exhibit adaptation effects consistent with a MAE (Barlow & Hill, 1963; Vautin & Berkley, 1977; Hammond *et al.*, 1985, 1986; Marlin, Hasan & Cynader, 1988; Peterson *et al.*, 1985). Presumably, these are the same mechanisms that fail to signal a consistent motion direction for textures undergoing apparent motion with displacements exceeding an appropriately scaled D_{max} (Mikami *et al.*, 1986). In displays containing both short- and long-range motion cues in competition, the MAE is always predicted by the "short range" component (Mather, Cavanagh & Anstis, 1985). Therefore, if a long-range based MAE exists, at best it is weak and easily masked by a short-range MAE.

Several investigators have described aftereffects of long-range or second order motion perception (von Grunau, 1986; Mather, 1991; Petersik, Shepard & Malsch, 1984), but a critical examination raises questions about the identity of these effects with conventional MAEs. For example, adaptation to a high spatial frequency filtered patch undergoing relatively large displacements (e.g. >180 deg phase with respect to dominant spatial frequency components) does not give

rise to a conventional MAE, but biases the perceived direction of a counterphase test grating (von Grunau, 1986). This bias should not be equated with the perception of a static grating as moving or a drifting grating as static (nulled motion). Similarly, the second order or three-dimensional MAE reported by Petersik *et al.* (1984) is also based on a bias in the perceived direction of an ambiguous dynamic test stimulus. In addition, the lengthy duration of this "MAE", followed by an apparent positive aftereffect distinguishes it from conventional MAEs. Mather (1991) reported a brief MAE using a novel stimulus designed to provide opposing motion signals to local detectors in spite of overall motion in a consistent direction. He randomly exchanged the polarity of elements between light and dark as they were sequentially spatially displaced. Hence the display was composed of standard apparent motion plus an opposing reversed phi. Adaptation gave rise to a weak aftereffect which Mather attributed to second order processes. An alternative interpretation is that the reversed phi signal is not of sufficient magnitude to cancel the apparent motion signal and therefore only weakens its aftereffect.

Measuring the MAE can be challenging and possibly misleading. Because the adaptation period is informative to even naive observers, the direction of motion of a stationary or ambiguous test target may be reported as opposite to the adapting stimulus even when no phenomenal illusion of motion is present. The commonest metric, MAE duration, is surely subject to bias, and since it is usually analyzed on a scale beginning with zero seconds, it virtually presupposes the existence of the MAE. Our methods do not assume the presence of a MAE and do not assess for bias in interpretation. We randomly interleaved test stimuli with various speeds of motion in the direction of the expected MAE, in the opposite direction, and with zero velocity. Although the adaptation period was still informative to the observer, it would have been difficult to generate psychometric functions of perceived direction as a function of target velocity based on this expectation.

We are left with the dogmatic position that the MAE cannot be a signature of the early motion system because the early motion system is monocular whereas the MAE transfers interocularly and can be elicited dichoptically. The argument rests entirely upon the previous inability to achieve dichoptic motion perception with short range displays; but this must be abandoned in light of our second result.

We have introduced a random texture motion display that supports dichoptic motion perception. We demonstrated that these random textures obey the phenomenology of a short range motion stimulus when undergoing rigid displacements. Yet when put in quadrature motion they may be used to support dichoptic motion perception. Quadrature motion is simply a superposition of traveling waves: drifting gratings of various spatial frequencies and random phase. Except for the transient display used in Expt 2.4, there is only one temporal frequency for all sinusoidal

components. Thus the display cycles in time without any net displacement. This is not obvious perceptually because the illusion of continuous texture motion is not contradicted by the lack of displacement of familiar features. It is apparent in the sequence depicted in Fig. 2(b), where illusory motion is sensed strongly in spite of Lincoln's persistence in one location.

Our dichoptic display exploits the trigonometric expression of a traveling wave as the sum of two standing waves in quadrature. Binocular motion mechanisms which are sensitive to upward motion are expected to sense the upward components of the monocular standing waves (Levinson & Sekuler, 1975), while mechanisms sensitive to downward motion sense the downward components. In one direction the components are superimposed while in the other direction they cancel. Ideally, the superposition and cancellation reflects linear summation of monocular signals which are themselves linearly related to luminance modulation. Ohzawa, DeAngelis and Freeman (1990) and Ohzawa and Freeman (1986a, b) have shown that binocular receptive field properties of simple and complex cells in cat striate cortex arise from the linear summation of such signals. This appears to be true for direction selective and nonselective cells (Ohzawa, personal communication). Linear binocular summation has also been observed psychophysically in contrast detection tasks over the spatial and temporal frequency range supporting cyclopean motion perception (Arditi *et al.*, 1981; Shadlen & Carney, 1986). This summation may be restricted to direction selective mechanisms since oppositely moving gratings do not add (Arditi *et al.*, 1981). Thus there is no cyclopean perception of counterphase, but rather rivalry.

On the other hand, it has been suggested that the capacity to detect dichoptic motion in grating stimuli may be based on tracking the changing location of features in the monocular patterns, rendering binocular integration unnecessary (Georgeson & Shackleton, 1989, 1992). This reservation is weakened in light of the capacity to detect motion dichoptically in random textures. Not only are features camouflaged, but they undergo distortion without any net displacement (see also Carney & Shadlen, 1992).

How can we account for the discrepancy between our results and the longstanding failure to achieve dichoptic motion perception in random dot displays? There are several contributing factors which ensue from the decomposition of a rigidly moving image into two components for dichoptic presentation. The sequence of rigid displacements which constitutes a random dot kinematogram can be divided into even and odd numbered frames, but each set contains a motion signal. One cannot present alternate frames to either eye without introducing monocular direction cues. The accepted solution has been to reverse the direction of motion after every two frames (Braddick, 1974) or to employ stimulus durations of only two frames (Green & Blake, 1981). Thus each eye sees a stationary pattern and all motion perception must arise as a consequence of binocular

integration. However, the binocular signal is the sum of two sampled stationary images. It does not contain an unambiguous motion signal and would not be expected to activate motion mechanisms selective for any one direction.

Georgeson and Shackleton (1989) adopted a creative solution to avoid reversing directions. They presented alternating frames of a one-dimensional random element display to either eye, but employed spatial displacements large enough to minimize monocular contributions to motion perception. They observed binocular motion detection which could not be accounted for by monocular performance or their combination through probability summation. Nevertheless, performance was poor, owing in part to the use of large spatial displacements.

Our quadrature motion display avoids these problems. Displacement magnitude may be chosen to be optimal at all spatial scales simultaneously because it is realized by a phase shift. Monocular signals are ambiguous while binocular signals convey only one direction of motion. Thus unidirectional motion can be presented dichoptically for any duration without introducing monocular cues. Yet, the capacity to discriminate direction in dichoptic moving snapshot displays (Expt 2.4) suggests that it is not the duration of the motion signal that is critical, but rather its consistent direction.

Finally, the use of figure/ground discrimination to test the capacity for dichoptic motion perception may have been problematic. In the past this strategy was necessary since a direction discrimination task was precluded by the reversals introduced every other frame. It could hardly have been anticipated that figure/ground segregation may fail in spite of successful dichoptic motion perception. Yet this has been our experience. Distinctions between figure/ground segregation and direction discrimination in random dot motion displays have been noted previously. Anstis (1989) reported marked differences between figure/ground segregation in central and peripheral vision that cannot be explained on the basis of motion detection mechanisms. Using random dot kinematograms, Chang and Julesz (1983b) found that D_{\max} for direction discrimination is almost double that for pattern detection. They suggest that these tasks may involve two different levels of short range processes. Thus, detection of local direction signals is necessary but not sufficient to segregate figure from surround in random dot (texture) kinematograms.

What property of the dichoptic motion display prevents figure/ground segregation? One possibility is that fine spatial detail is excluded from the cyclopean perception. Small vergence errors would be expected to produce interocular phase discrepancies from the intended quadrature relationship, leading to ambiguous or even incorrect motion signals at higher spatial frequencies. If figure/ground segregation requires consistent boundary information across spatial scales, then the inconsistent direction information at high spatial frequencies could prevent segregation.

An alternative explanation is that left and right eye images are sufficiently different in appearance to result in

binocular rivalry, which in turn disrupts figure/ground segregation. It has been shown that binocular integration of visual information can be achieved during binocular rivalry (Blake, Westendorf & Overton, 1980; Lehmkuhle & Fox, 1975). This is certainly true for dichoptic motion perception. When a pair of sinusoidal gratings in spatiotemporal quadrature are constructed from different colored lights, they support dichoptic motion perception in spite of the presence of binocular rivalry (Carney, Shadlen & Switkes, 1987). This phenomenon is felt to reflect the underlying parallel organization of pathways devoted to the analysis of motion and color. Perhaps the same is true of motion and form. Our quadrature texture displays are generated by a process that distorts one eye's image with respect to the other. It is not unreasonable to suspect that these images may be rivalrous. It is worth noting that a dichoptic motion sequence made from the portrait of Abraham Lincoln [counterphasing in temporal quadrature frames 1 and 5 of Fig. 2(b)] evokes a strong perception of motion; yet Lincoln is not recognizable. Therefore we speculate that rivalry might interfere with the successful integration of motion cues for figure/ground or form perception. An intriguing possibility is that form perception depends critically upon signals in monocular mechanisms (Livingstone & Hubel, 1988).

Whatever the explanation, we must accept that the use of figure/ground segregation to assess dichoptic integration of motion cues can lead to false conclusions. Thus far we have attributed prior failure of dichoptic motion perception to methodological constraints posed by the use of random dot kinematograms. In addition to escaping these pitfalls, our quadrature motion stimulus may facilitate dichoptic motion perception because it reflects the organization of neuronal receptive fields underlying direction selectivity. The idea that such receptive fields are constructed from spatial weighting functions in quadrature (e.g. so-called bar and edge detectors) has received theoretical (Adelson & Bergen, 1985; van Santen & Sperling, 1985, 1984; Watson & Ahumada, 1985) and experimental support (Reid, Soodak & Shapley, 1987). Such receptive field subunits are probably identified with striate simple cells which are for the most part binocular (Hubel & Wiesel, 1962; Schiller *et al.*, 1976) and have been shown to combine left and right eye stimulation linearly (Ohzawa & Freeman, 1986b). Thus the quadrature decomposition of motion energy stimuli may be ideally suited to activate direction selective mechanisms dichoptically.

Characterization of the early motion system as binocular is consistent with the most conservative notions regarding its physiological identity. For without fingering a particular cortical area, it is known that sensitivity to direction is achieved at or beyond the convergence of monocular vision pathways. Thus we may revise the distinctions between psychophysical processes devoted to motion perception in terms which may be physiologically relevant and which are not confined to the operating constraints of a particular display (e.g. D_{max}). It would appear that the short range or early motion

system might be characterized by (i) its sensitivity to motion energy, thus embracing local spatial and temporal constraints and (ii) binocularity, in the either eye or both sense.

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APPENDIX 1

Effect of temporal sampling on rigid and quadrature motion

An apparent motion sequence is constructed from a series of static frames obtained by temporally sampling a continuous motion. Therefore the perception of apparent motion is predicted by the visibility of an idealized continuous motion combined with the products of sampling. This approach and its associated formalisms have been examined by Fahle and Poggio (1981), Carney (1983), Burr *et al.* (1986) and Watson, Ahumada and Farrell (1983). These authors have emphasized the utility of frequency domain description of apparent motion displays. Here, we shall apply these results to compare rigid and quadrature motion sequences. Since movement occurs along only one direction, it will simplify matters to consider only one spatial dimension. As in the derivation of the quadrature display, we shall consider a column of pixels as a one-dimensional idealized white noise waveform.

For one-dimensional random noise, we may regard the spatial Fourier transform as flat, on average. When set in rigid motion, the space-time Fourier transform (STFT) is oriented such that it is nonzero only at spatial-temporal frequency combinations lying on a line through the origin [Fig. A1 (A)]. This support is the projection of the STFT on the spatial-temporal frequency plane. It is symmetric about the (0,0) point and its slope reflects velocity. Notice that values in quadrants 1 and 3 correspond to motion in one direction, while values in the other pair of quadrants would correspond to the opposing motion. Thus, regardless of the exact mechanism, a direction sensor must behave as a filter with passband over kitty-corner quadrants, as depicted by the shaded and open ellipses in Fig. A1.

The quadrature motion displays employed in Expts 2.1–2.3 possess only one temporal frequency. All spatial frequency components cycle through phase in synchrony. Ideally, its STFT is nonzero at a unique temporal frequency, so its support is flat and symmetric about 0,0 [Fig. A1 (B)].

Temporal sampling has the effect of introducing copies of the original STFT along the temporal frequency axis at intervals of the sampling frequency. These supports are shown in Fig. A1 (C, D) This

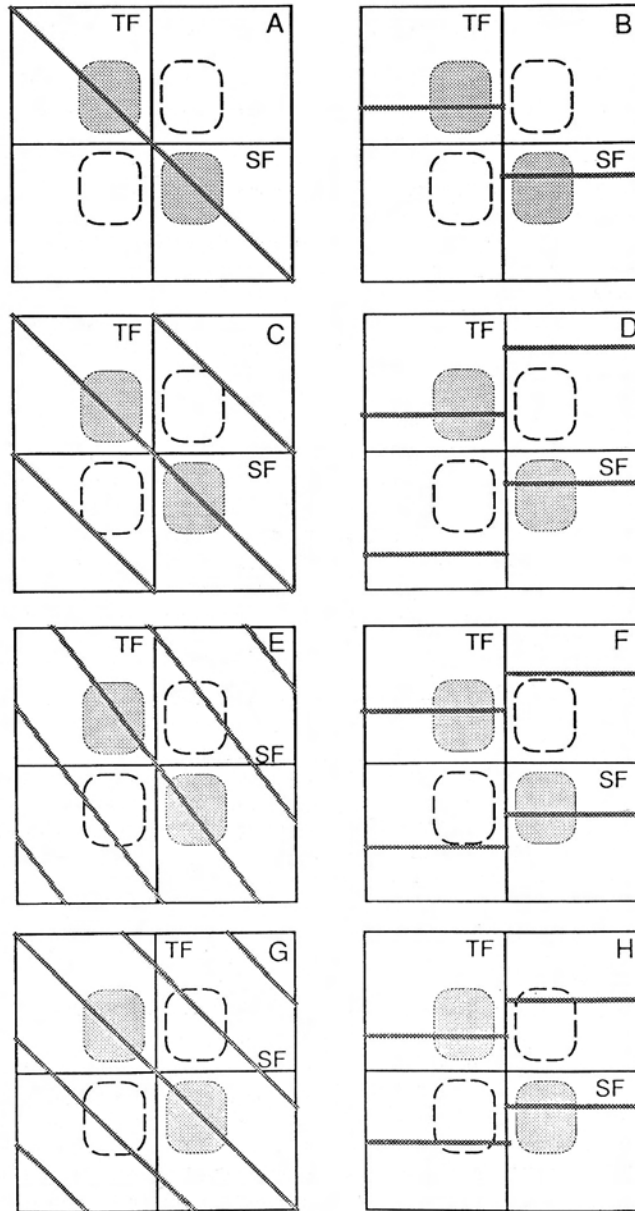


FIGURE A1. Effect of sampling on rigid (left column) and quadrature (right column) motion displays. Plots are projections of the display space-time Fourier transform upon the spatial temporal frequency plane. The lines or supports reflect the location of non-zero values of amplitude. Axes labeled SF and TF refer to stimulus spatial and temporal frequency, respectively. The enclosing box represents the limits of visual sensitivity. Shaded regions represent the passband of putative direction sensors which are sensitive to the intended direction of the display. Corresponding open regions would represent similar mechanisms sensitive to the opposite direction of motion. Analogous rigid and quadrature display transforms are shown side by side. The lower two rows (E-H) depict conditions in which the rigid motion display fails to result in short range motion perception while quadrature motion is still perceived. (A) Ideally sampled rigid motion. (B) Ideally sampled quadrature motion. (C) Apparent motion with adequate temporal sampling. Sampling artefact is visible, but directional information is preserved. (D) Apparent quadrature motion with the same sampling as in (C). (E) Displacement magnitude and speed are increased by 50% with sampling rate the same as in (C). The increase in speed is reflected by the change slope of the supports. Portions of the aliased supports lie within the passband of opposing motion sensors, often at lower values of temporal frequency and hence possess greater amplitude. (F) Phase displacement and temporal frequency are increased by 50% with sampling rate unchanged from (C) and (D). Some aliased support enters the passband of the opposing sensor, but always at a higher TF and is therefore more attenuated. (G) Displacement magnitude is increased by 50% with compensatory reduction in sampling frequency to maintain speed as in (A) and (C). Aliased support enters the passband of opposing motion sensors, in some places at lower values of TF, hence greater amplitude. (H) Phase displacement is increased by 50% with compensatory reduction in sampling frequency to maintain TF as in (B) and (D). Although aliased supports fall within the passband of opposing sensors, they occupy higher TFs and are therefore attenuated relative to the intended direction of motion.

would accurately depict a stroboscopically sampled display, but apparent motion sequences are constructed by sampling and then holding the current spatial configuration until the next sample. This is equivalent to convolving the stroboscopically sampled display with a temporal pulse as long as the holding period (dwell). In turn, this

attenuates the STFT along the temporal frequency axis by a sinc function [$\text{sinc } w = \sin(\pi T\omega)/\pi\omega$, where T is the dwell duration and ω is temporal frequency]. That is, the further a value is from $TF = 0$, the lower its amplitude (approximately). The attenuation is steeper with longer dwell times.

In Expt 2.1, rigid displacement was varied in two ways. Either the dwell was maintained constant so that velocity covaries with displacement, or it was lengthened to maintain a constant velocity. In the constant dwell condition, the angle of the support increases away from the spatial frequency axis, but its copies remain interspaced by the same amount on the TF axis since the sampling rate is unchanged [Fig. A1 (E)]. In the variable dwell (constant speed) case, the supports maintain their orientation but are spaced closer to one another on the TF axis [Fig. A1 (G)]. In addition, the attenuation as a function of TF is more rapid since the dwell time is extended. Notice that either of these manipulations inevitably introduce non-zero values into the pair of quadrants which contain the representation of the opposite direction of motion. It is reasonable to presume that the deterioration in motion perception is accounted for by the increasing visibility of this aliased representation. Exactly how much energy leads to degradation is a matter to be settled experimentally. Assumptions about the nature of motion detecting mechanisms, and particularly the shapes of their transfer functions, become important. For present purposes, it is sufficient to appreciate that as displacement size is increased, the values introduced in the wrong quadrants are aliased to lower TFs than in the original support and are therefore less attenuated. Thus Fig. A1 (E, G) could represent failure of the early motion system (i.e. displacement $> D_{\max}$).

The analogous manipulations to the quadrature display [Fig. A1 (F, H)] result in either increasing the TF or decreasing the sampling rate. Here too, the aliased supports enter the quadrants for the opposite direction of motion [Fig. A1 (F, H)]. Yet, since they are flat, they do not attain values of TF lower than those in the original support until the sampling frequency is less than twice the intended TF. This would occur only with phase displacements > 180 deg which are better described by the equivalent phase displacement in the opposite direction. Thus for any phase displacement < 180 deg, aliased motion energy is more attenuated than the original support. We offer this as an explanation for the robust perception of quadrature motion with respect to sampling frequency.

APPENDIX 2

Derivation of the transient motion energy display

Consider the two dimensional texture $f(x,y)$ as a collection of independent one dimensional columns, $f(y)$. A second texture $f'(x,y)$ is constructed so as to be in column by column quadrature with the first pattern. We can ignore the x dimension and represent each column by a spatial waveform and its hilbert transform. For random textures, $f(x)$ is a white noise sample, and

$$f'(x) = f(x) * \pm \frac{1}{\pi x} = \pm \frac{1}{\pi} \int_{-\infty}^{\infty} \frac{f(\sigma)}{x - \sigma} d\sigma, \quad (\text{A2.1})$$

where the asterisk denotes convolution, and the sign determines whether the quadrature waveform will lead or lag the original by 90 deg phase. This determines the direction of motion, ultimately. The column pairs are temporally modulated by a pair of time functions which are also in quadrature, and the two pairs of space-time separable functions are added to generate a motion energy stimulus:

$$\phi(y,t) = g(t)f(x) + g'(t)f'(x). \quad (\text{A2.2})$$

The temporal modulation functions used in this study were either cosine and sine or, for the transient display (Expt 2.4), a delayed Gaussian and its hilbert transform. Notice that $g(t)$ and $g'(t)$ must be chosen so as not to violate causality; they must be zero for $t < 0$. Theoretically, this cannot be achieved for functions with low pass fourier transforms (e.g. Gaussians) because the odd symmetric component decays hyperbolically. Practically, however, a sufficient delay may be chosen which leaves negligible values at $t < 0$. Therefore

$$g(t) = \exp\left(-\frac{(t - k\tau)^2}{\tau^2}\right) k > 3. \quad (\text{A2.3})$$

As shown in Fig. 7, a delay of three to four standard deviations is sufficient.

It is convenient to consider the Fourier transform of f , which may be represented by

$$\phi(\omega, \lambda) = G(\omega)F(\lambda) + G'(\omega)F'(\lambda) \quad (\text{A2.4})$$

where $F(\lambda)$ is the spectrum of white noise and $G(\omega)$ is a lowpass Gaussian function whose width is the reciprocal of the time constant in $g(t)$. In the frequency domain, the hilbert transform is performed by complex multiplication with $\pm i$, for positive and negative frequencies, respectively. Therefore

$$\phi(\omega, \lambda) = G(\omega)F(\lambda) - \text{sgn}(\omega)\text{sgn}(\lambda)G(\omega)F(\lambda) \quad (\text{A2.5})$$

$$= G(\omega)F(\lambda) \left. \begin{array}{l} \omega \text{ and } \lambda \text{ opposite sign} \\ 0 \end{array} \right\} \omega \text{ and } \lambda \text{ same sign.} \quad (\text{A2.6})$$

The Fourier transform is nonzero over kitty-corner quadrants of the spatiotemporal frequency plane. This region contains all possible downward moving sinusoids while the opposite quadrant pair contains all possible upward moving sinusoids. Thus, the display contains only unidirectional motion energy (Watson & Ahumada, 1983, 1985; Adelson & Bergen, 1985). A sign reversal in f, f', g , or g' will select the alternate quadrant pair; hence the opposite direction of motion.