

PERCEPTUAL INTEGRATION AND DIFFERENTIATION
OF DIRECTIONS IN MOVING PATTERNS

William P. Marshak

Captain, USAF

1981

Northwestern University

Doctor of Philosophy in Experimental Psychology

214 pages

ABSTRACT

Two or more directions of motion cannot be discriminated from one direction over separations of direction greater than 16 and less than 60 degrees at threshold contrast. The multiple directions produce a percept indistinguishable from a single direction. When the same stimuli are presented at six or more times threshold contrast, another kind of perception error occurs: the component directions are seen separately but their perceived directions repel one another.

In a series of experiments, contrast, directional content, pattern content and velocity determined the conditions under which directions of motion summate or repel one another. Stimulus changes increasing inhibition enhance repulsion; changes decreasing inhibition enhance summation.

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A three stage, vector model can explain these errors in directional perception. The first stage¹ of direction processing is excitation of directionally sensitive units. Such units may be portrayed in polar coordinates as vectors whose orientation is their optimal direction of sensitivity and whose length indicates the amount of activation. The second stage of motion perception is an inhibitory process limiting the distribution of excitation to units whose sensitivity is close to the direction of motion and suppressing activity in units sensitive to other directions. In the third stage, all remaining excitation is processed by a decision mechanism that determines the perceived direction of motion. Two decision processes, a peak detection and a vector summing process, are discussed.

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- Mather, G. and Moulden, B. A simultaneous shift in apparent direction: Further evidence for a "distribution-shift" model of direction coding, Quarterly Journal of Experimental Psychology, 1980, 32, 325-333.

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NORTHWESTERN UNIVERSITY

PERCEPTUAL INTEGRATION AND DIFFERENTIATION
OF DIRECTIONS IN MOVING PATTERNS

A DISSERTATION
SUBMITTED TO THE GRADUATE SCHOOL
IN PARTIAL FULFILLMENT OF THE REQUIREMENTS
for the degree

DOCTOR OF PHILOSOPHY
Field of Psychology

by

WILLIAM PAUL MARSHAK

Evanston, Illinois

June 1981

ABSTRACT

Two or more directions of motion cannot be discriminated from one direction over separations of direction greater than 16 and less than 60 degrees at threshold contrast. The multiple directions produce a percept indistinguishable from a single direction. When the same stimuli are presented at six or more times threshold contrast, another kind of perception error occurs: the component directions are seen separately but their perceived directions repel one another.

In a series of experiments, contrast, directional content, pattern content and velocity determined the conditions under which directions of motion summate or repel one another. Inhibition among motion sensitive units is the presumed underlying cause of these perceptual errors. Stimulus changes increasing inhibition enhance repulsion; changes decreasing inhibition enhance summation.

A three stage, vector model can explain these errors in directional perception. The first stage of direction processing is excitation of directionally sensitive units. Such units may be portrayed in polar coordinates as vectors whose orientation is their optimal direction of sensitivity and whose length indicates the amount of activation. The directional tuning of these units subserve motion detection

but contain too diffuse a distribution of excitation to determine direction alone. The second stage of motion perception is an inhibitory process limiting the distribution of excitation to units whose sensitivity is close to the direction of motion and suppressing activity in units sensitive to other directions. In the third stage, all remaining excitation is processed by a decision mechanism that determines the perceived direction of motion. Two decision processes, a peak detection and a vector summing process, are discussed.

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TABLE OF CONTENTS

Tables	vii
Figures	viii
Introduction	1
Models for the Perception of Motion and its Direction	2
Physiological Evidence Relevant to Perception of Direction	19
A Vector Model for the Perception of Motion and its Direction	21
The Experiments	38
Observers	38
Stimuli	38
Apparatus and Calibrations	39
Experimental Procedures	47
Part I: Contrast and the ability to see direction of motion	57
Experiment 1: Contrast threshold using random dot patterns	59
Experiment 2: Accuracy of perceived direction as a function of stimulus contrast	70
Part II: Summation of directions in moving stimuli	78
Experiment 3a: Contrast and motion conditions for the collapse of multiple directions in moving stimuli	88
Experiment 3b: Accuracy of perceived direction as a function of movement's duration ..	96
Experiment 4a: Summation of directions as a func- tion of number of dots in motion ...	105

Experiment 4b: Contrast threshold as a function of number of moving dots	107
Part III: Repulsions of directions in moving stimuli ...	118
Experiment 5: Repulsion as a function of bidirect- ional motion presentation	119
Experiment 6: Repulsion as a function of the number of dots in the influence pattern	128
Experiment 7: Velocity's effect on the repulsion phenomenon	133
Part IV: Summation of directions within motion after- effects	143
Experiment 8a: Isotropism of directionally sensitive mechanisms	151
Experiment 8b: Summation of directions in the after- effect of bidirectional motion	155
General Discussion	166
Summary of Results	166
Review of the Vector Model	170
Related Research	173
Future Applications of the Dissertation	179
Appendix 1: A Spatial and Temporal Description of Random Dot Stimuli	184
Footnotes	200
References	201
Vita	214

TABLES

<u>Table</u>	<u>Subject</u>	<u>Page</u>
Table A	Cumulative probability of $P(A)$ from a Monte Carlo simulation of the current experiments	52
Table B	Summary of Analysis of Variance for Experiment 1.	68
Table C	Summary of Analysis of Variance for Experiment 3a.	95
Table D	Size of absolute errors in perceived direction at threshold contrast in Experiment 1.	101
Table E	Summary of Analysis of Variance for Experiment 4a.	110
Table F	Summary of Analysis of Variance for Experiment 4b.	115
Table G	Summary of Analysis of Variance for Experiment 5.	125
Table H	Summary of Analysis of Variance for Experiment 7.	139
Table I	Temporal frequencies from onset and offset of stimuli.	198

FIGURES

<u>Figure</u>	<u>Subject</u>	<u>Page</u>
Figure 1	The ratio model for the perception of motion.	4
Figure 2	The vector model for the perception of motion.	28
Figure 3	A vector model interpretation for perceiving two directions of motion simultaneously.	32
Figure 4	The vector model interpretation for perception of two directions of motion without lateral inhibition's influence.	35
Figure 5	Dot contrast as a function of Z- voltage based on readings off the display face with the Spectra photometer.	41
Figure 6	A pattern of random dots moving along parallel paths at the same velocity at 45 degrees.	44
Figure 7	Comparative accuracy of the pointer orientation matching and verbal report for subjects indicating the direction of motion.	55
Figure 8	Contrast sensitivity of counterphase flickering gratings as a function of temporal frequency using spatial and temporal criteria (from Kulikowski and Tolhurst, 1973).	61
Figure 9	Contrast sensitivity ($1/\log$ contrast) for moving and stationary dots using spatial and temporal criterion.	66
Figure 10	Correlation of perceived and actual direction of motion as a function of dot pattern contrast.	73
Figure 11	Descriptions of dot motion in unidirectional, bidirectional, and polydirectional movement.	80

Figure 12	The possible positions with associated probability of a dot undergoing a random walk upward (90 degrees) and rightward (0 degrees) in a polydirectional stimulus over seven successive frames.	84
Figure 13	Discriminability of a unidirectional stimulus (90 degrees) from bidirectional and polydirectional stimuli as a function of angular differences in the multidirectional stimuli.	92
Figure 14	Accuracy of perceived direction as a function of the duration of the display.	98
Figure 15	Discrimination of unidirectional from bidirectional motion as a function of the total number of dots in the moving patterns.	108
Figure 16	Contrast sensitivity for a unidirectional moving dot pattern as a function of the number of dots in the pattern.	113
Figure 17	Perceptual error which results from the presence of a second direction of motion in the same visual space.	122
Figure 18	The repulsion reported within a bidirectional dot pattern whose target direction moved at 22 degrees and whose influence pattern moved at 0 degrees while containing varying numbers of dots.	130
Figure 19	Size of repulsion reported within a bidirectional dot pattern in which the velocity of motion in the influence direction varied.	136
Figure 20	A vector model representation of the effects of adapting motion on subsequent visual stimuli.	145
Figure 21	Duration of the secondary (long) component of motion aftereffect as a function of adapting direction.	153

Figure 22	Deviation of direction of motion aftereffect from the expected value of 180 degrees from adaptation direction as a function of adapting direction.	156
Figure 23	Deviation of direction of motion aftereffect from the expected vector sum of the individual component aftereffects with a bidirectional adapting stimulus containing different angular separations.	160
Figure 24	Diagram of the optical bench designed to measure the Fourier power spectrum of transparencies of the dot patterns.	185
Figure 25	The theoretic and measured relative amplitudes of a square wave grating up to the sixth harmonic frequency.	189
Figure 26	Photo of a 550 dot pattern whose arrangement is random except for the constraint that no two dots overlap.	191
Figure 27	Fourier power spectrum for a random dot pattern containing 550 and 200 dots.	193
Figure 28	Relative amplitude of energy as a function of spatial frequency of random dot patterns containing 550 and 200 dots.	195

INTRODUCTION

Our ability to recognize or identify the direction of motion in the fronto-parallel plane is usually quite good. For example, when observers judge the direction of a high contrast random dot pattern moving at 4 degrees per second, individual errors are less than 3-6 degrees and judgements average to within a degree of the actual direction (Marshak and Sekuler, 1979). But when two directions of motion are seen simultaneously in the same visual space, systematic errors in perceived direction as great as twenty degrees occur (Marshak and Sekuler, 1979; Mather and Moulden, 1980). This failure to perceive the direction of motion veridically provides clues to the nature of the responsible mechanism for perception of direction.

Perceptual errors and illusions have long played a role in theories of visual perception. The decomposition, transmission and synthesis of information by the eye and brain, perform introduce distortion into perception that are not normally noticed. Nevertheless, the same mechanism responsible for normal perception also produces misperceptions strong enough to be measured easily in the laboratory, if appropriate stimuli are used. Therefore, theories of visual perception must include explanations for these errors in perception.

Existing evidence and new evidence developed herein are inconsistent with contemporary models of motion perception. Existing models are particularly weak in explaining how direction of a moving stimulus is perceived. A review of these models will reveal their strengths and shortcomings. Next, the available evidence about how motion is perceived will be presented as a foundation for a new model of motion perception. This new model will distinguish between perception of direction and other aspects of motion, concerning itself primarily with direction. Then the model will be tested in a series of psychophysical experiments. Finally, the model's extension to cover other aspects of motion perception will be proposed.

Models for the Perception of Motion and its Direction

The earliest and most cited model of perception of motion is the ratio model. This model is inspired, in large part, by an attempt to explain the motion aftereffect (MAE). MAE is the illusory motion of stationary contours that occurs after prolonged viewing of similar moving contours. The direction of the illusory motion is 180 degrees from the adapting direction (Wohlgemuth, 1911). Both psychophysicists (Sutherland, 1961; Pantle and Sekuler, 1967; Moulden and Mather, 1978) and physiologists (Barlow and Levick, 1965;

Vautin and Berkley, 1977) have hypothesized that MAE is a consequence of adapting neural elements tuned to opposite directions. The outputs of directionally sensitive cells or mechanisms are compared to the outputs of those cells or mechanisms tuned to the opposite direction. A difference between these opponent mechanisms signals that motion is present (Figure 1). The comparison of oppositely tuned elements may involve a simple subtraction, or a ratio of the outputs. The latter is the source of the model's usual title, "the ratio model". The ratio model's comparison processes (subtraction or computing the ratio) will be treated as equivalent in this dissertation, and criticisms of the model will apply equally to either comparative process.

According to the ratio model, real motion is perceived when a moving stimulus activates a mechanism most sensitive to that direction of motion. This is compared to another mechanism sensitive to the opposite direction of motion, the opponent mechanism, whose response to the stimulus motion is less. The difference between the output of the mechanism sensitive to motion and the opponent mechanism signals the presence of motion. MAE is perceived because the prolonged motion has adapted one of the mechanisms, creating a difference in activity between it and its oppositely tuned mechan-

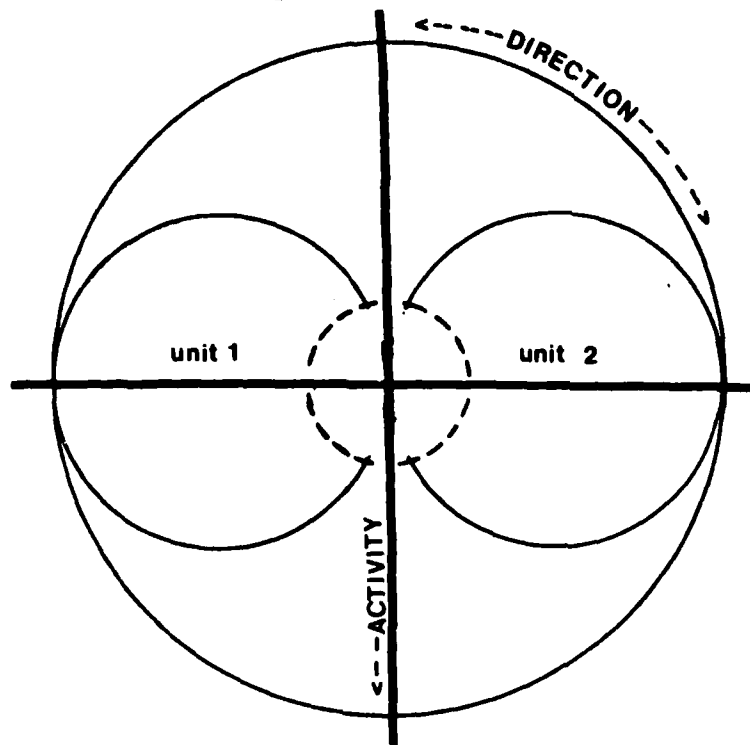
Figure 1: A schematic representation of the ratio model for the perception of motion.

- A. The sensitivity of two oppositely tuned, unidirectional motion sensitive units such as thought to underly the ratio model are shown in a polar coordinate system. The angle in this polar coordinate system corresponds to the direction of motion of a stimulus in a portion of the visual field to which both mechanisms are sensitive. The distance from the center represents the activity of the mechanism. The average unstimulated or base line activity level of all DS units is represented by the small dashed circle. When two dimensional motion is present in these unit's receptive field, their activity is specified by their tuning functions shown as solid circles. Motion of a high contrast moving stimulus along the orientation of any radius will result in activity proportional to the intersection of that radius with the tuning function. Less activation may result if the stimulus is of lesser contrast or of a velocity to which the unit is not optimumly

sensitive.

- B. The activity of the two mechanisms is now represented by bar graphs to simplify explanation of several states of the ratio model. When no motion is present, mechanism activity is the same as the resting or base line activity (dashed lines).
- C. When presented with prolonged stimulation in a single direction, the mechanism most sensitive to that direction increases its activation while the oppositely tuned unit remains at its normal base line activity level. The difference between the unit activity or their ratio differing from unity is interpreted as motion in the direction of stimulus motion. During this stimulation, the more active unit is becoming adapted.
- D. If a stationary stimulus follows the prolonged stimulation, the following situation occurs. The unit which had been active during the initial stimulation has entered a refractory period during which it cannot maintain base line activity. The unstimu-

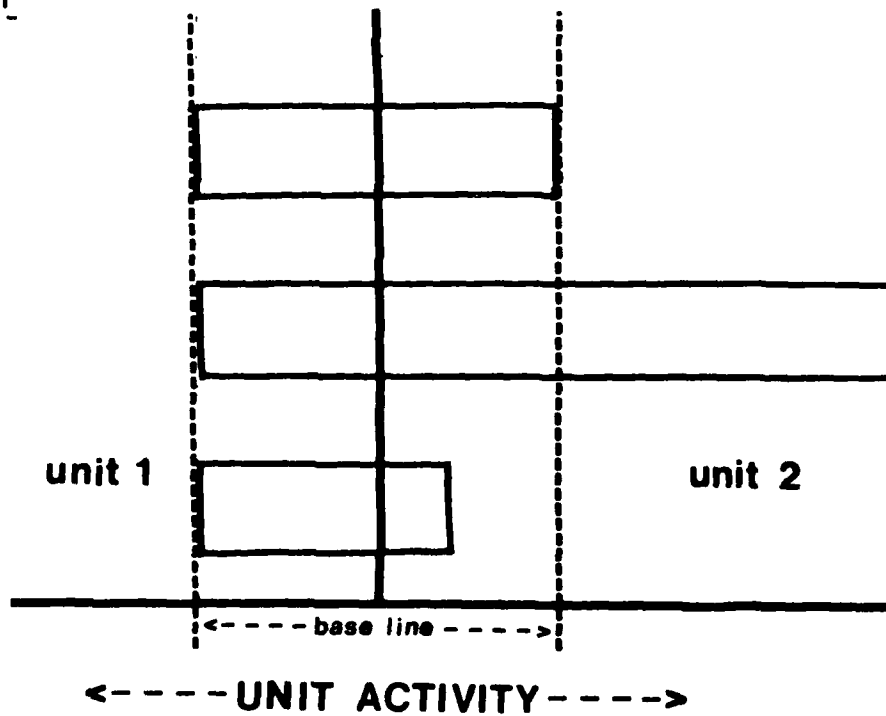
lated oppositely tuned unit maintains base line activity. What results is a difference between the unit outputs, or a ratio different from unity which the system interprets as motion in the direction opposite from the prolonged stimulation.



A

MOTION
STIMULUS PERCEPT

NONE	NONE
RIGHT	RIGHT
NONE	LEFT



B

C

D

ism. Adaptation with prolonged stimulation, key to the ratio explanation of MAE, has been observed in motion sensitive cells (Vautin and Berkley, 1977; Von der Heydt, Hanny and Adorjani, 1978). Although none of the ratio model's proposals have dealt explicitly with thresholds for detecting motion, many researchers (Pantle and Sekuler, 1967; Moulden and Mather, 1978) have postulated that the size of the ratio of the opponent mechanisms determines the threshold and that contrast helps determine outputs of the separate mechanisms.

The evidence concerning the ratio model for perception of direction is mixed. As mentioned before, physiologists (Vautin and Berkley, 1977; Von der Heydt, Hanny and Adorjani, 1978) have recorded from motion sensitive cells in cat and monkey and found that adaptation of motion sensitive cells occurs as a consequence of prolonged stimulation with moving contours. This reduced activation due to adaptation is consistent with, but not conclusive proof of the ratio explanation. However, psychophysical tests of the consequences of the ratio model have not been so favorable.

One ratio model prediction was tested by Sekuler, Lehr, Stone, and Wolf (1971). They argued that equal adaptation of both opponent mechanisms ought to result in no change in contrast threshold. This manipulation should result in the

simultaneous reduction in both the numerator and denominator of the ratio. Observers adapted to a square wave grating moving in alternating directions of motion, then were tested for threshold elevation in one test direction. The threshold elevation observed was not different from a control condition in which the opposite direction adaptation was replaced by a stationary grating. Contrast threshold for motion in one direction was independent of adaptation to motion in the opposite direction. This lack of interaction between opposite directions has been called the independence hypothesis.

The independence of opposite directions of motion at threshold contrasts was demonstrated in a different and ingenious way by Levinson and Sekuler (1973; 1975b). The thresholds of counterphase gratings (created by combining two sinusoid gratings of the same spatial frequency and contrast but moving in opposite directions) were compared to the thresholds of the individual grating components. Summation of the components in the counterphase results in twice the peak contrast of the single components. Their results indicated each of the components was independently detected at threshold. This independence of opposite thresholds suggests that the ratio model may not apply to detection of motion.

At higher contrasts, independence of oppositely tuned directionally sensitive mechanisms seems to be replaced by a form of reciprocal inhibition. Using combinations of contrast and velocity in counterphase gratings, Levinson and Sekuler (1975a) demonstrated that a oppositely moving grating reduced the ability of a grating to produce contrast threshold elevations. The opposite direction grating apparently inhibited the effects of adaptation.

The independence of opposite directions at threshold first observed by Sekuler et al. (1971) has recently been questioned by Moulden and Mather (1978). The latter authors sought to defend the ratio model by testing another of its predictions: adaptation of one direction ought to facilitate detection of motion in the opposite direction. In terms of the logic of the ratio model, this adaptation would be analogous to reducing the denominator of the ratio or creating a simple difference. Such a facilitation effect would contradict the independence of opposite directions found by Sekuler.

Moulden and Mather did not actually observe this facilitation in their raw data, but concluded that threshold elevation caused by the pattern of the stimulus obscured the expected direction-specific adaptation. To support their view, Moulden and Mather 'adjusted' their data by

subtracting the contrast threshold elevation observed in a control condition in which the subject adapted to a stationary grating. In the adjusted data, all observers exhibited a slight facilitation (.02 log units). No statistical tests for the significance of these differences were offered.

Several aspects of the Moulden and Mather experiment are questionable. Their statistical adjustment of the data assumes that motion and pattern specific adaptation sum linearly and without interaction. No proof of this assumption is offered in their paper. The size of the facilitation is quite small, contrary to the expectation from manipulating one part of a ratio or even by a subtractive process.

The ratio model has been the principle explanation for perception of motion for the twenty years since Sutherland's 1961 paper. Experimental tests of its predictions are not persuasively in the model's favor. Moreover, this model is incomplete in not incorporating a description of how other than opposite directions of motion interact. Strong interactions of motion in similar directions are reported for both simultaneous presentation (Marshak and Sekuler, 1979) and successive presentation (Levinson and Sekuler, 1980).

Theories of direction perception must be comprehensive enough to describe perception of directions in at least two-space and ultimately in three-space. Only relatively recently have researchers turned their attention to motion in depth (Beverly and Regan, 1973; Regan, Beverly and Cynader, 1979). This inability of the ratio model to explain directional interactions in other than opposite directions makes the model useless in dealing with the interaction of other than opposite directions. Even the most recent supporters of the ratio model, Moulden and Mather, have admitted the ratio model's shortcomings (Mather, 1980; Mather and Moulden, 1980) as we shall see a little later.

A second way of modeling the perception of motion and its direction is a mathematical analysis of the changing pattern of contrast. Several kinds of mathematical analysis have been forwarded. The mathematical operation of correlation has been proposed as a model of the perception of direction (Poggio and Reichardt, 1973; Sekuler, Pantle and Levinson, 1978). These models propose that motion sensitive neurons perform a cross- or auto-correlation on the contrast sweeping across the retina.

On a conceptual level, the correlation model is a formal mathematical embodiment of a shift-and-subtract model of

motion perception. The logic of such a model is that if you took two successive pictures of the same scene, converted one into a negative and summed the contrast at each point, the result would be zero where no change took place. If any change took place in the scene, as an object in motion, the result would be the image of the object. Mathematically, the operation correlates the corresponding points in successive frames to detect changes due to motion.

This correlation process is usually ascribed to individual neural units receiving temporally delayed inputs from other units separated by space and time. Motion perception in the fly has been described and physiologically tested with the correlation model (Reichardt and Poggio, 1976; Poggio and Reichardt, 1976). These correlational models concern themselves primarily with temporal changes of contrast on the retina. Lappin and Bell (1979) applied the correlation model to the ability of human observers to see movement in successive frames of dynamic random dot displays with some success. Gafni and Zeevi (1977; 1979) have expanded this kind of computational reasoning to other kinds of spatio-temporal information processing by the visual system.

Mathematical models of motion perception have two problems. First, very few tests of the perceptual consequences of these theories have been performed. Second, mathematical

models require the estimation of many free parameters. These parameters are fit to the data and do not correspond to any known physiological or psychophysical processes. For example, Lappin and Bell (1979) use a parameter phi to reflect the spatio-temporal separation of successive frames and a contribution to the total variance that is associated with the visual system's ability to detect matches in successive frames. Testing the descriptive powers of such a model is almost impossible because of the flexibility allowed by the free parameters.

There is little doubt that the future of modeling all neural processes must ultimately rest with mathematics. However, mathematical descriptions should conform to known physiology and the visual system's operating characteristics as determined by psychophysics.

The goal of this dissertation is the proposal of a new model of motion perception, one incorporating directional information processing into its basic structure. This model borrows from features of both ratio and mathematical models. Compared activity of motion sensitive units will play a central role, just as it does in the ratio model. Unlike the ratio model that compared only oppositely sensitive units, the new model will compare activity from mechanisms tuned to similar as well as mechanisms tuned to opposite directions.

Second, a mathematical description will be given of how information about a variety of directions is combined. Instead of difference, ratio or correlation, the proposed model uses vector algebra.

Before this new model can be derived, the physiology and psychophysical characteristics of direction sensitivity must be reviewed. The connection between physiology and the modeling process is held together by the fragile thread of linking hypotheses. Given the state of physiological research in the visual system, an abstract model of motion perception cannot be based entirely on that research. However, physiology provides useful clues in the derivation of an abstract mathematical model. Such a convergence of thinking should be mutually beneficial for future research in physiology and in psychophysics.

Physiological Foundations of Directional Sensitivity

Five main classes of motion sensitive neurons were identified by Grüsser and Grüsser-Cornehl (1973). One of these classes was described as follows:

Movement-detecting neurons for which neural activation depends on the direction of the moving stimulus (DS-neurons). The direction in which the stimulus has to be moved to elicit an optimal response is called the preferred direction; the direction in which no response or the weakest response occurs, the null direction. (pg. 342)

The subtleties of feature extraction, in this case motion and its direction, are beyond the scope of this discussion (Barlow, 1959). A unit or element of the visual system (which can be a cell, cell network or mechanism) will be said to be directionally sensitive (hereafter, DS) if its output could serve as a basis for the identification and/or discrimination of different directions of motion in visual space.

Physiologists have observed DS changes of firing rate in single cells of frog (Lettvin, Maturana, Pitts and McCulloch, 1961), rabbit (Hubel and Wiesel, 1968), and monkey (Hubel and Wiesel, 1968). There is psychophysical evidence for similar cells in man (Sekuler and Ganz, 1963). The description of a cell's directional sensitivity is usually in terms of its response sector (Grüsser and Grüsser-Cornehl, 1973) or tuning function. The cell's tuning function is its response, in impulses per second, for various directions of stimulus motion with contrast and velocity held constant. Tuning functions of DS cells come in two basic shapes: bidirectional and unidirectional. Bidirectional cells respond to motion in opposite directions but not to motion off this axis of sensitivity. Motion in either direction along or similar to this preferred axis increases the cell firing rate. Unidirectional cells have a

single preferred direction and are only sensitive to this single or adjacent directions.

Regardless whether this dichotomy is true, or that a continuum between the extremes exist, cells with bidirectional sensitivity are an unlikely candidate as a basis for directional perception. The independence of opposite directions of motion at threshold reported by Sekuler et al., (1971) is inconsistent with, but does not foreclose, a contribution to motion perception by these bidirectional cells. The independence hypothesis is more consistent with the notion that unidirectional cells underly motion perception. Consider now what is known about the unidirectional cells.

Physiological descriptions of unidirectional DS cells tuning functions are also reviewed by Grässer and Grässer-Cornehl (1973). Regardless of the species or level within the visual system, most tuning functions are broadly tuned, showing elevation in firing to directions as far as 45 degrees on either side the preferred direction. Cells in the peripheral retina have broader tuning functions than those in the central retina (Levick, Oyster and Takahashi, 1970).

Two hypotheses have been offered as to how cell receptive fields could be organized in a DS neuron. Hubel and

Wiesel (1959) thought asymmetrical interactions between excitatory and inhibitory areas of the receptive field caused direction specific response. Such asymmetrical interactions predict that DS should be non-uniform within different parts of the DS cell's receptive field. This prediction has been contradicted by studies in which DS was found to be relatively uniformly distributed (Barlow and Levick, 1965; Michael, 1968).

An alternative theory of DS was offered by Barlow and Levick (1965) and has been called the veto theory. This theory contains a network of temporally delayed inhibitory connections between DS cells. If motion is in the preferred direction, inhibition on a motion sensitive cell from neighboring neurons arrives too late to interfere with the rise of excitation. In the null direction of motion, lateral inhibition veto or nullifies the effects of excitation within the cell and activity is not increased over baseline, noise level. This explanation and the importance it attaches to lateral inhibition has been supported by single unit recordings and neurochemical studies. Both Benevento, Creutzfeldt and Kuhnt (1972) and Creutzfeldt, Kuhnt, and Benevento (1974) found evidence for inhibitory post-synaptic potentials when cells were stimulated with moving stimuli. DS behavior by a cell can be abolished by bicuculline, an

antagonist of the inhibitory neural transmitter GABA (Pettigrew and Daniels, 1974). This further indicates the importance of inhibitory processes in directional sensitivity.

Simulations of the DS cell's membrane further support the veto model. Torre and Poggio (1978) derived an equivalent electrical circuit for ion flow through the cell membrane; they claim close correspondence between their model and DS cell behavior. Houchin (1975) used a digital computer to show how spatial and temporal combinations of inhibitory and excitatory post synaptic potentials delivered to the cell membrane can mimic the recorded behavior of DS neurons. Both models result in DS mechanisms which are uniformly sensitive within the hypothetical cells receptive field, which is more consistent with the veto model than with the Hubel and Wiesel proposal.

Psychophysical Evidence Relevant to Perception of Direction

Psychophysical work on DS visual mechanisms in humans was begun by Sekuler and Ganz (1963). They reasoned that if DS cells existed, such units might be selectively adapted by prolonged stimulation in one direction. This DS adaptation should elevate threshold for motion in the adapting direction more than the threshold for motion in the opposite

direction. Since the grating's pattern information (spatial frequency and orientation) was identical for all conditions, the difference between conditions was attributed to the effect of adapting motion. This direction specific threshold elevation has been replicated psychophysically (Sekuler, Rubin and Cushman, 1968 ; Tolhurst, 1973) and with evoked potentials (Clarke, 1974).

Psychophysical estimates of the tuning function of the DS mechanism were made by Sekuler et al. (1968) and Levinson and Sekuler (1974). The former authors adapted one direction with moving square-wave gratings and then optically rotated their pattern, testing for threshold elevation at various directions. They found the directional differences of 45 degrees reduced the amount of direction specific threshold elevation by about one half. To prove that this difference was due to motion and not orientation differences between the adapt and test stimuli, they replicated the experiment adapting with stationary gratings. The angle at which the adaptation effect attenuated fifty percent was only 15-25 degrees in angular separation, substantially narrower than in the motion conditions. Thus, the tuning function for DS mechanisms in humans was shown to be much broader than the tuning function for orientation sensitivity.

Levinson and Sekuler (1980) replicated this experiment using a different stimulus, isotropic random dots. Such dot patterns have a broad spatial frequency spectrum, weighted toward the low frequencies, and equal energy in all orientations. These researchers took advantage of the fact that two distinct thresholds may exist for a moving target (Keesey, 1972; Tolhurst, 1973). Under certain conditions, the motion of a target can be seen before its pattern. When they measured threshold elevation using a "see motion" criterion, directionally sensitive mechanisms were found to be broadly tuned. However, a different result was obtained when a "see pattern" criterion was used. Levinson and Sekuler observed threshold elevations that were uniform in all directions, regardless of the adapting direction. Differential adaptation of motion and pattern sensitive mechanisms revealed those mechanisms can have different thresholds with dot patterns.

A Vector Model for the Perception of Motion and its Direction

Consider now a new model for the perception of motion and its direction. This new model draws two important concepts from the ratio model and the mathematical models. First, the activity of various motion sensitive units will play a central role, but in a way different from ratio

model. Second, mathematical notation will be used to describe the way in which the perceived direction of motion is determined from the interactions among the responses of different motion sensitive units.

The new model will be called the vector model, for reasons which will be apparent later. The vector model for motion perception consists of three stages of processing. These stages will be represented as operating in a serial fashion, but this is not a necessary feature of the model.

The model's first stage consists of a collection of directionally tuned, motion sensitive units. The response to motion of these units will be based on operating characteristics of visual neurons and the psychophysical evidence. Maximum activation of each unit is achieved by motion in the preferred direction; less activity results from motion in directions other than its preferred direction. The directional range of increased activity spans 45 degrees either side of the unit's preferred direction, gradually diminishing with increased deviation from that preferred direction. This assumption is based on the magnitude of threshold elevation observed in directions adjacent to adapting motion observed by Sekuler et al. (1968). A Gaussian distribution of amplitude will be assumed for simplicity sake. Two other assumptions are used: 1) all directionally sensitive units

have the same tuning functions and 2) preferred directions are equally distributed over the possible angles. None of these assumptions about symmetry, homogeneity, or density of units are necessary conditions for the vector model. In fact, some observations discussed later suggest some of these assumptions are false.

Each DS unit's output can be represented by a vector in a polar coordinate system; hence the model's name. The orientation of the unit's vector is the unit's preferred direction of motion; vector length indicates the activation of that unit. This simple conceptual representation can serve as a basis for the perception of direction, but also other dimensions of a moving target. Direction of motion is an important determinant of vector length and will be the principle source examined by the following research. However, it is easy to conceive of other contributors to the vector length.

Consider the available evidence on the directional tuning in the human visual system. The adaptation experiments of Sekuler et al. (1968) and Levinson and Sekuler (1980) both indicate that motion in any direction adapts units sensitive to a broad range of directions. But how can direction be judged precisely if the DS units are so broadly tuned? The vector model explains that accuracy by a second

stage of processing, inhibitory interactions among DS units. Inhibition's function would be analogous to its function in spatial vision in the visual system of the horseshoe crab, Limulus (Hartline and Ratliff, 1972). Unit activity along the spatial dimension is narrowed by inhibition in the Limulus visual system. The vector model proposes an analogous narrowing of activity along the directional dimension.

The vector model portrays the inhibitory stage of direction processing in the following fashion. Upon its stimulation, each DS unit exerts an inhibitory influence on units with similar preferred directions. The size of the inhibitory effect increases with directional differences from the unit's preferred direction up to a maximum, then diminish with greater directional separation. The adaptation studies cited earlier clearly demonstrated adaptation effects over broad ranges of angles. If adaptation occurred as a result of excitation, then units sensitive to similar directions would have their activity inhibited and the directional range of adaptation would be restricted. This strongly suggests that inhibition occurs at a stage subsequent to the initial adaptation.

This inhibition has several characteristics. First, the threshold for inhibition will be assumed to be higher than the threshold for excitation. One justification for this

assumption is that detection of motion is of too great a survival value to raise the detection threshold just to enhance accuracy of directional perception. Another justification is that an similar assumption is made for spatial inhibition in the Limulus eye. Second, the suppression of activity in similar directions would enhance motion detectability if a signal detection mechanism is responsible for threshold motion perception.

The existence of inhibition in direction perception leads to two unique predictions about the perception of direction. The accuracy of direction perception will be poor at detection threshold contrasts because inhibition will not be present. Also, above detection threshold the simultaneous presentation of two directions will alter the perceived direction of each component direction through the influence of each direction's inhibitory processes.

The final stage in direction perception is the decision stage which uses the net distribution of activation, the combination of excitation and inhibition, among the DS units to determine the perceived direction. There are two possibilities for the decision mechanism. The first is a mode or peak detector. This decision mechanism would seek the longest DS unit vector and take that unit's preferred direction as the perceived direction. This is a form of the "labeled

line" model used in vision and other domains (Lettvin et al., 1961). This peak detector is similar to the decision demon proposed by Selfridge (1959) in his Pandemonium model of vision. This decision mechanism is simple and is capable of accounting for at least part of the data to follow.

The second potential decision mechanism is modeled after the mathematical operation of vector summation. In this more complicated scheme, the DS unit vectors would be summed by vector algebra to determine the perceived direction of motion. The vector sum mechanism under most conditions makes the same predictions about perceived direction as the peak detector. The similar predictions of the two decision mechanisms makes choosing between them difficult, but experimental evidence will be presented later that will indicate a choice.

During the course of this dissertation's experiments and writing, a model similar to the vector model has been published. Mather (1980) has proposed what he calls a "distribution shift" model of direction perception. In his theory, Mather said there exists an array of motion sensitive element which served as the basis for perception of direction. Various illusions and distortions in direction perception are a result of changes in the distribution of activity within the array of motion sensitive elements. Mather

discusses the interaction of directions and the summation of motion aftereffects, two topics discussed in great detail later in this dissertation. Although the distribution shift and vector models have similar underlying logic, the vector model is much more explicit about the operation of its elements. The two models will be compared in more detail later. The fact that different theorists have arrived at similar ideas certainly indicates a convergence of thinking based on these new experiments.

We shall now consider how the vector model accounts for some existing data, and predicts the outcome of some experiments in this dissertation. Three examples of the model will be presented. The first example shows how an observer perceives the direction of a stimulus containing just a single direction of motion. Next, the perception of a complex moving stimulus containing two directions such as in the experiments of Part III and the prior work of Marshak and Sekuler (1979). Finally, the consequences of reducing inhibition among the DS units on the percept of two directions, a situation tested in Part II, are described.

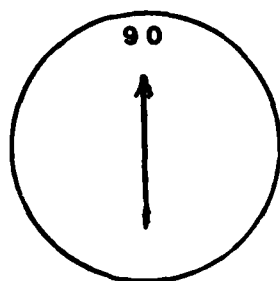
Figure 2A shows how the vector model interprets the effect of a single direction of motion. The first stage of directional information processing is an increase in unit vector length whose preferred direction lies along or in

Figure 2: A schematic representation of the vector model for the perception of motion.

- A. Motion is portrayed in a polar coordinate system. A stimulus moving through 90 degrees is presented to the model.
- B. The base line or unstimulated activity level of the DS units is represented by the dashed circle. Only representative vectors exceeding this activity level are represented. Each unit sensitive to 90 degree motion increases its activity in proportion to where that direction intersects the unit's tuning function (see Figure 1A). Unit activity is represented by a vector lying in the unit's preferred direction and whose length is proportionate to activation.
- C. At the same or subsequent level, active units exert inhibition on other units whose preferred direction is similar. This results in reduced activity in most units, but more pronounced in units whose direction is different from the direction of motion.

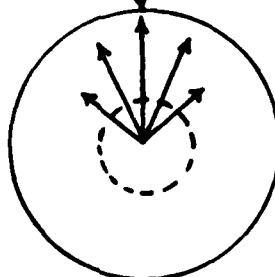
- D. The resulting distribution of activity is the basis for perceived direction. Two alternative decision mechanisms are proposed. Either the longest vector (peak) or average of the vectors (vector sum) determines perceived direction.

STIMULUS DIRECTION



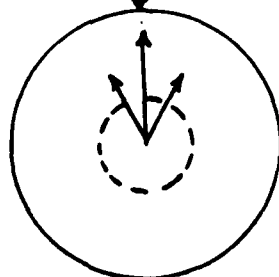
A

EXCITATION



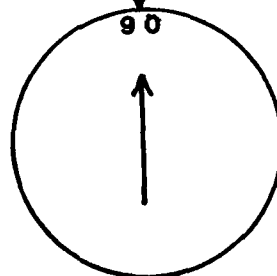
B

INHIBITION



C

DECISION



D

PERCEIVED DIRECTION

adjacent directions to that of stimulus motion. These vectors are shown in Figure 2B. The distribution of activation is over a range of angles of plus or minus 45 degrees. Units sensitive to other directions maintain their normal resting activity, represented by the dotted line. In the second stage of processing, the units exert inhibitory effects on other units with similar preferred directions. This restricts the activation to those units whose preferred direction is close to that of the direction of motion (Figure 2C). The final stage of processing is the decision mechanism which interprets the units' activity into perceived direction. Note that both the peak decision and vector sum decision mechanisms discussed before produce identical perceived directions, shown in Figure 2D.

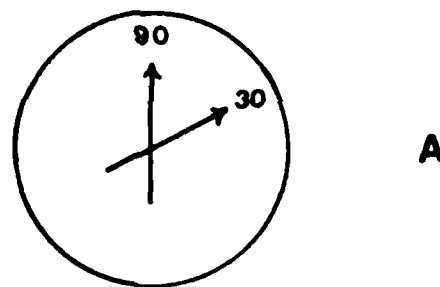
When two directions of motion are presented in the same visual space, the directions appear to repel one another (Marshak and Sekuler, 1979). The vector model would account for this repulsion in the following fashion. The stimulus in this example contains two directions of motion, at 30 and 90 degrees (Figure 3A). The excitatory processes produce a broad distribution of excitation amongst the DS units (Figure 3B). After inhibition modifies the distribution of activity in the DS units, the area of summed excitation is eliminated because of accumulated inhibition from both

Figure 3: A vector model interpretation for perceiving two directions of motion simultaneously.

- A. A stimulus containing two directions of motion, one at 30 and the other at 90 degrees, is presented to the model.
- b. Units sensitive to stimulus motion increase their activity, with summation in units sensitive to both directions.
- C. Inhibition modifies the pattern of excitation. This distorts the resulting distribution of activity in the population of DS units.
- D. A decision about perceived direction is made based on the modified distribution of activity. If peak detection is the basis for the decision, then the two peaks of activity have been shifted away from the true direction. If vector summing is the basis for the decision, two distinct distributions of activity exceed the base line, the vector sum of both is in error. Both processes predict the repulsion of directions.

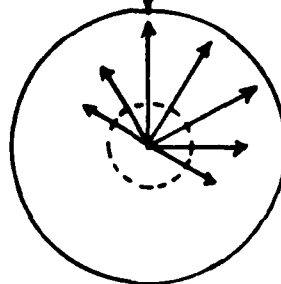
STIMULUS DIRECTION

33



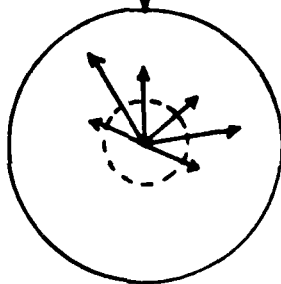
A

EXCITATION



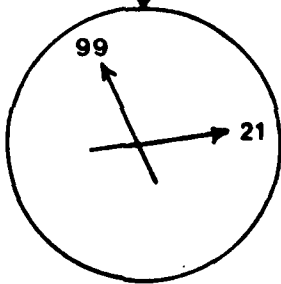
B

INHIBITION



C

DECISION



D

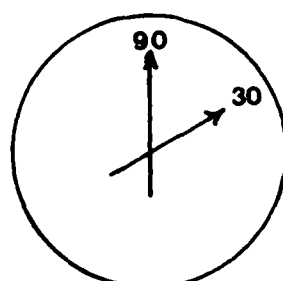
PERCEIVED DIRECTION

directions of motion (Figure 3C). In addition, the whole distribution of activity has been altered by the inhibition. Peak activity has been shifted from the real direction, away from the other direction and its inhibitory effects. The modal activity would determine perceived direction in a peak detecting decision model. The vector sum decision process accounts for the perception of two directions in a different fashion. s which exceed the resting activity level. Inhibition separates the vectors into two distinct distributions, interpreted as two distinct directions. A side effect of this differentiating process is that the vector sum no longer lies in the same direction as the original direction of motion. Thus, both the peak and vector sum decision mechanisms predict the perceived repulsion of two directions when simultaneously presented. Following this line of reasoning, the vector model predicts that the size of repulsion is dependent on the amount of inhibition generated by the stimulus.

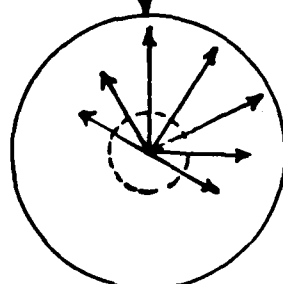
In the third example, the same two directional stimulus used above is now presented at a contrast just above the threshold for detection of motion (Figure 4). The model works as before (Figure 4A and 4B) with the following exception. Under the assumption that inhibition has a higher threshold than excitation, the inhibitory stage has been

Figure 4: The vector model representation of perception of two directions of motion in the absence of inhibition.

- A. Two directions of motion (30 and 90 degrees) are presented to the vector model.
- B. The excitatory process produces a range of activity in the DS unit population
- C. Now, the lateral inhibition which normally modifies the distribution of activation has been minimized or eliminated. Thus, the distribution of activation is submitted unmodified to the decision process.
- D. If activation is summed in units sensitive to the intermediate directions exceeds the activity of all other units, then the peak decision process predicts a single direction will be perceived. The vector sum decision process would determine a single perceived direction regardless of vector lengths because only one distribution of activity exists.

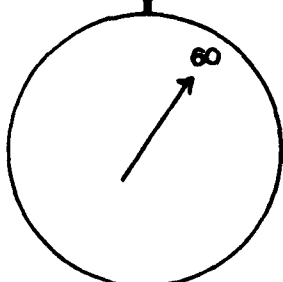
STIMULUS DIRECTION

↓
EXCITATION



↓
[INHIBITION]

↓
DECISION

**PERCEIVED DIRECTION**

attenuated or eliminated from the vector model (Figure 4c). Both the peak detector and the vector sum decision stages predict a single direction of motion will be perceived (Figure 4D).

The ability of the vector model to explain perceptual phenomenon will now be tested with a series of experiments. The separate stages of the model will be revealed by controlling the amount of lateral inhibition generated in the second stage of the vector model. The assumption that the threshold for excitation is lower than that for inhibition will be examined under conditions in which motion can be perceived and that inhibition is not likely to be operative. In other experiments, conditions conducive to inhibition will be created with the use of higher contrasts or the presence of a second direction of motion and its inhibitory influence on similar directions. Other experiments will try to isolate the source of inhibition and to determine which of the two alternative decision mechanisms is more plausible.

THE EXPERIMENTS

Observers

The author and five naive, paid volunteers served as subjects in the experiments. All the observers had experience as psychophysical observers and were free of known ocular pathology. Three observers were emmetropic while the other two were myopic. The myopic observers were corrected to 6/6 during all observations.

Stimuli

All stimuli used in these experiments were patterns of luminous dots on a dimmer background. Dot patterns have the ability to move in any direction without a change in their spatial characteristics. The spatial description of dots is mathematically complex, requiring a two dimensional luminous profile. These attributes are quite different from the other preferred stimulus in motion perception, the grating. Gratings are patterns whose luminance varies over only one dimension. The luminance profile of a grating is mathematically simple and its widespread use facilitates comparisons to other studies. However, gratings can only portray motion in the two directions orthogonal to the orientation of the luminance profile. Drastic changes in the spatial orientation characteristic of the grating are necessary to enable

the stimulus to show other directions of motion. The attribute of having constant spatial description regardless of direction gives dot patterns a distinct advantage over gratings for the studies in perceiving motion's direction.

Apparatus and Calibrations

The experiments were conducted using a Digital Equipment Corporation PDP-8/I computer to create stimuli, time events and record data. The stimuli were patterns of luminous dots whose spatial arrangement, motion and contrast were precisely controlled by the computer. This was accomplished using three computer-controlled, 12-bit digital to analog converters connected to the X, Y, and Z inputs of a Tektronix 604 monitor. The screen was 9.5 centimeters on each side and addressable as a matrix of 4096 by 4096 positions.

Each dot, approximately circular with a diameter of 39 microns, was made in the following fashion. First, position of the dot was determined by voltages applied to the X and Y inputs to the monitor. Next, a voltage was applied to the minus side of the differential amplifier (Z-) controlling screen luminance. The computer then triggered a signal generator to deliver a 200 microsecond pulse to the plus side of the differential amplifier (Z+) resulting in intensification of the dot. The sum of the fixed voltage from the

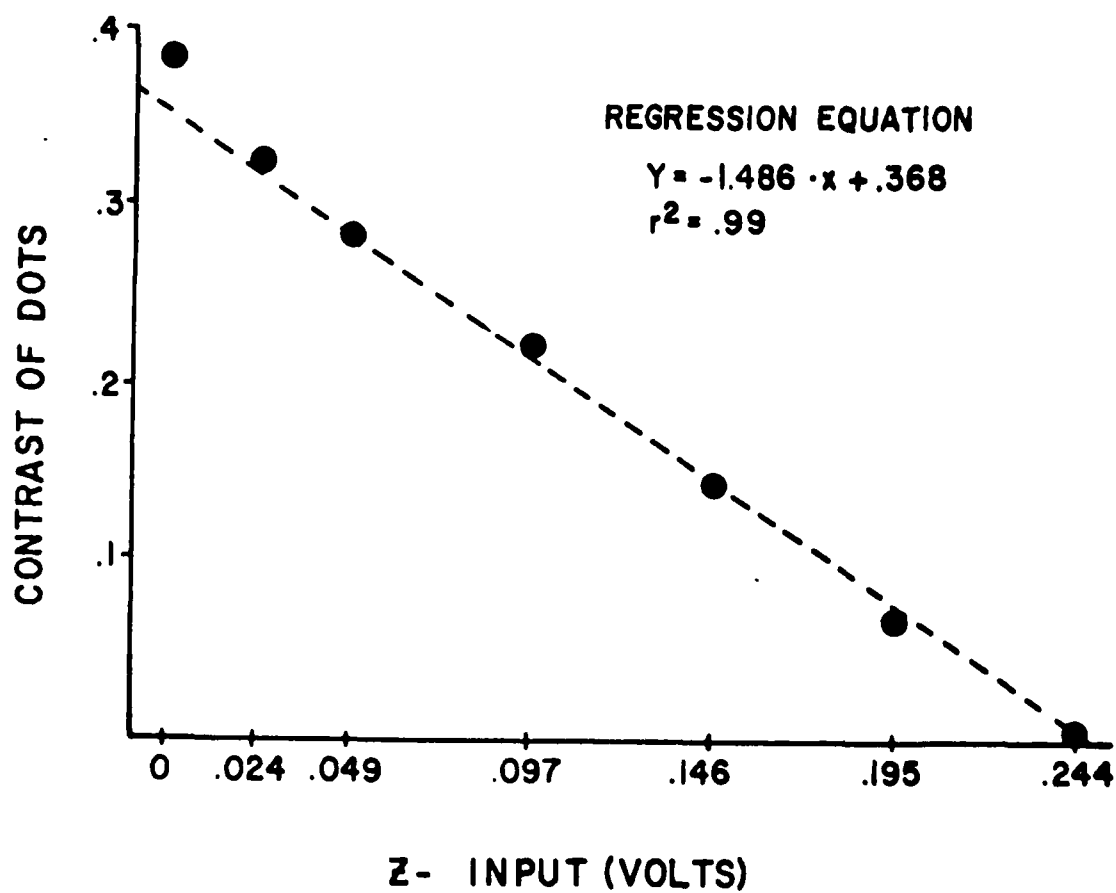
signal generator and the program controlled Z- voltage determined the brightness of the dot.

Calibration of dot luminance as a function of the programmable, Z- voltage was done as follows. A closely packed but non-overlapping dot pattern was measured using a Spectra Brightness Spot Meter Model 1815-SB. Luminance of the dots was an inverse linear function of the voltage applied by the computer to Z- input of the scope. Additional measurements of individual dots with a Gamma Model 2900 Auto Photometer verified that luminance of each dot was a linear function of voltage over the voltage range used in the experiments. A tungsten lamp raised the monitor face to a luminance of 1.9 candela/meter squared. The surround of the monitor was measured at 2.1 candela/meter squared. Since dots are aperiodic stimuli, the appropriate description of their contrast is the luminance increment of the dot pattern divided by the total background luminance (Boynton, 1966). Contrast calculated for the dot pattern as a function of Z- voltage is plotted in Figure 5. A regression equation was fit to these measurements

$$\text{Contrast} = -1.468 * \text{voltage} + .368$$

and that equation accounted for 99 percent of the variance.

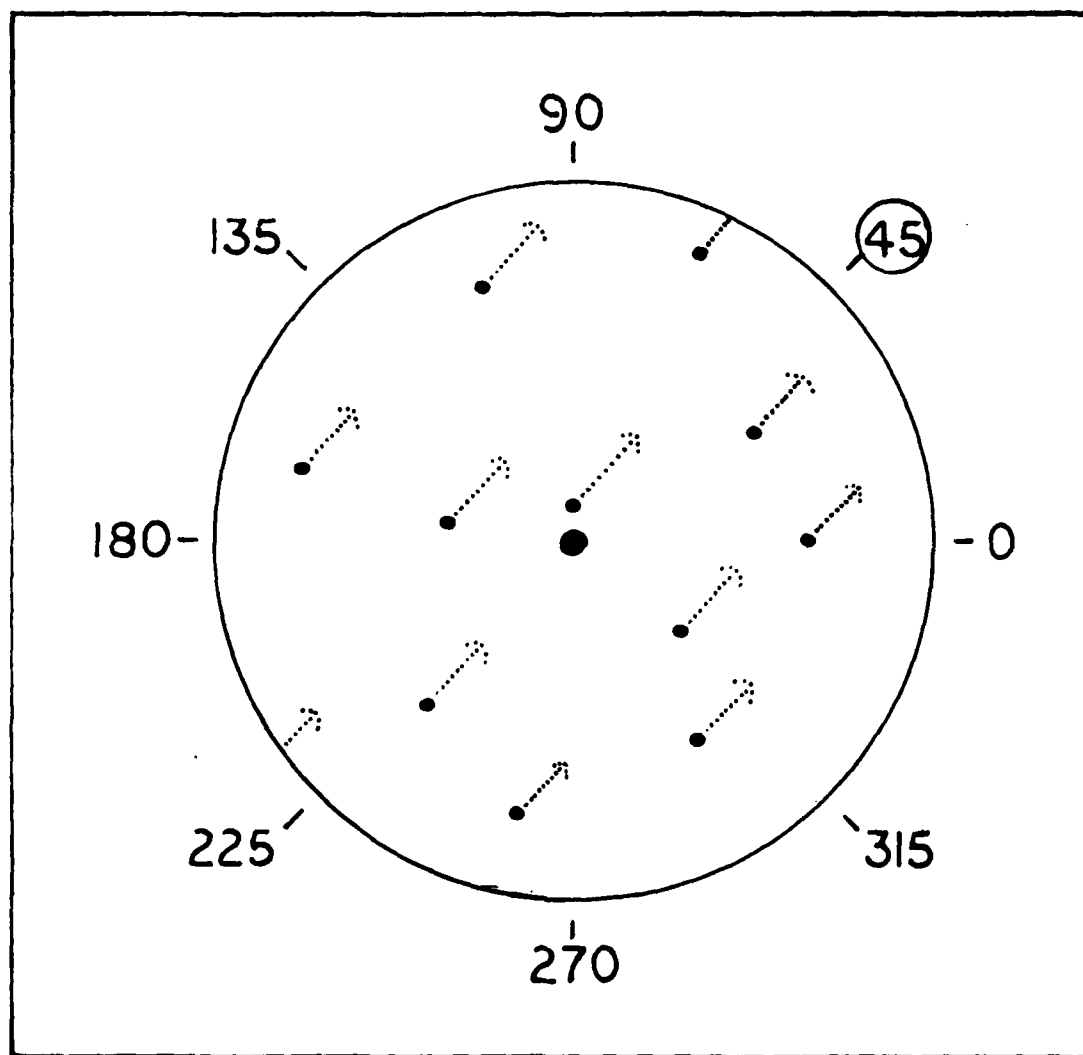
Figure 5: Dot contrast as a function of Z^- voltage based on the readings off the display face with the Spectra photometer. The dots were plotted in a square which filled the photometer's sensitive area. Distance from dot centers was .468 millimeters, to prevent dot overlap.



For a complete description, motion requires two parameters: direction and velocity. Direction in the dot displays will be characterized using imaginary radii of the circular aperture or mask through which the display was viewed. The radius whose path traced from the center of the mask points in the direction of motion will be used to identify that direction. Following the polar coordinate convention, zero indicates rightward motion. This directional nomenclature is represented with a pattern of dots moving through 45 degrees in Figure 6. Velocity of dots or dot patterns is measured by net displacement over unit time. A dot moving at 4 centimeters in one second has a velocity of 4 centimeters per second. A more appropriate metric of distance is how many degrees of visual angle does the distance represent. Since the display was viewed from 57 centimeters, each centimeter corresponds to one degree of visual angle. Thus, our example would have a velocity of 4 degrees per second.

The display was refreshed at a rate of 30.59 frames per second. This means 32.68 milliseconds elapsed between successive intensifications of the same dot. This refresh rate was sufficient to create smooth apparent motion. Smooth motion was perceived up to velocities of 32 degrees per second, the fastest velocity used in these experiments. The

Figure 6: A single pattern of random dots moving along parallel paths. The dots all moved at the same velocity and in the same direction relative to the center (in this example, 45 degrees). The larger central point is the stationary fixation point. No protractor marks or numbers were present on the circular mask when the pointer was used to indicate direction. A graduated mask (10 degree interval) was employed with the verbal procedure of reporting directions. The moving dots were brighter than their background, the opposite of what is pictured in the figure.



accuracy of directional control varied slightly as a function of velocity. This occurs because of the discrete voltages of the electronics used to define individual dot positions. Direction control was accurate to one degree at 4 degrees per second, the most commonly used speed in these experiments. On those occasions when lower velocities were used, motion was always along horizontal or vertical orientations. Directional accuracy was precise regardless of the velocity along the axis because dot motion required changes along only one dimension, which the electronics could precisely control.

A mask covered the perimeter of the display face, leaving exposed a circular display area with a diameter of 8 degrees of visual angle. To attenuate edge effects associated with display borders, the mask was kept at a luminance close to that of the display (Kelly, 1977). Luminance of the mask differed from that of the display face by less than 10 percent of the display's value. Kelly also pointed out that the rapid luminance transitions associated with stimulus onset and offset contribute temporal frequencies to the stimulus. A .28 second linear luminance ramp was used to fade in and fade out the presentation of stimuli. This means for a typical one second stimulus presentation, the maximum luminance was maintained for 0.54 seconds. This

mode of presentation was used with all stimuli which were presented at less than the maximum contrast. Stimulus onset and offset for experiments using full contrast used either ramped or abrupt step functions depending on the software used. Perception of low contrast stimuli may be enhanced by temporal frequencies produced by stimulus onset and offset. It is doubtful that the visibility of high contrast stimuli is changed. Each experiment will be identified as using either ramped or step stimulus presentation.

The display face contained a small dark fixation point of one millimeter diameter, assisting the observer to maintain fixation (see footnote 1). A chin rest and frame reduced observer fatigue and to insure that observers maintained proper viewing distance (57 centimeters). Observers viewed the display binocularly in all conditions.

Experimental Procedures

Three different kinds of methodology were employed in the following experiments. A variety of procedures were required because of the diverse phenomena being measured. These procedures include the method of adjustment, two category forced choice signal detection and direction matching.

The method of adjustment was used to determine contrast thresholds for random dot patterns. Presentation of the patterns was accomplished in the following way. Discrete stimulus presentations of one second duration with ramped onset and offset were used. A blank inter-stimulus interval separated the presentations to create a continuous cycle of stimulus, blank, stimulus, blank, etc.

Contrast adjustments made by the observers could be sampled by the computer during the interstimulus interval, allowing identical display control software to be used for threshold and other experiments. The observer adjusted the control by rotating a 10-turn precision potentiometer; this varied the voltage being applied to the computer's analog to digital converter. During each interstimulus interval, the computer compared the input voltage with the voltage obtained from the last sampling. The contrast of the next stimulus presentation was changed to match the direction and size of the voltage change. Contrast was initially set by the computer at a random value either well above or well below threshold. Probability of a high or low initial contrast was equal. In addition, the initial value of contrast had a random factor of between minus and plus 5 percent added to prevent initial potentiometer position from becoming a cue. Even at the most extreme initial contrasts, con-

trast was still substantially below or above the threshold. The continuous cycle of stimulus presentations continued until the observer was sure that stimulus contrast satisfied criterion specified by the instructions. At this point, the observer pressed a button to signal the computer to record the current contrast as a threshold setting and initiate the next measurement.

The second kind of experiment was a signal detection procedure employing a signal detection rating scale to measure performance. Observers were asked to rate their confidence as to whether a short stimulus presentation contained a stimulus designated as target or another stimulus designated as non-target. The frequency of each stimulus type was equal. This method was used to measure the observers ability to make the discrimination between the two different stimuli. Probability of target or non-target was equal in an order randomized by the computer. Observation intervals were signaled with a coextensive auditory tone. After each interval, observers reported their confidence about the interval's content using a six category rating scale shown below:

- 1) definitely target present
- 2) probably target present
- 3) possibly target present
- 4) possibly non-target present
- 5) probably non-target present
- 6) definitely non-target present

After each observation interval, the observer indicated his choice by pressing one of six buttons connected to the computer. This choice was recorded and feedback as to the correctness of the response was signaled by a series of short audible beeps. The 'correct' signal came if the observer responded target present when the target had been presented (presents 1-3) and when non-target response was chosen when the non-target was presented (responses 4-6). This feedback was designed to enhance observer performance.

Analysis of the confidence ratings was done using McNicol's (1972) method. A non-parametric signal detection statistic, $P(A)$ the area under the Receiver Operating Characteristic curve, measured discriminability of the stimuli. $P(A)$ is computed as:

$$P(A) = 1/2 [P_i(S|n) - P_{i-1}(S|N)] * [P_i(S|s) - P_{i-1}(S|s)]$$

where N = the number of rating scale categories, S = a yes response, s = a signal present, n = noise alone, i = the response category and $P(S|n)$ and $P(S|s)$ are the conditional probabilities of each rating scale category. The Z transform of $P(A)$ is linearly related to sensitivity (d'), so the transform was used for all data analysis.

When evaluating the results of signal detection experiments, it is important to know the $Z(P(A))$ which corresponds to chance performance. This chance level of performance was not available in the literature, so a Monte Carlo simulation of the signal detection experiments was run. The simulation used the same number of trials and equal probability of events as in the present experiments. A TRS-80 microcomputer with a proven pseudo-random number generator was employed to generate responses and calculate the $P(A)$ and $Z(P(A))$. The outcome of each of 505 simulated experiments was computed and used to develop cumulative probabilities for $P(A)$ with intervals .25 wide. Table A contains each $P(A)$ interval, its frequency of occurrence, the relative probability and cumulative probability. The probability of a $Z(P(A))$ greater than .34 (corresponding $P(A) > .633$) is less than five percent (one-tailed).

The third kind of experiment was a direction matching procedure. Observers reported the perceived direction of

Table A

Cumulative probability of $P(A)$ from a Monte Carlo simulation of some of the current experiments. (A total of 40 presentations of target and non-target stimuli were made with random assignment of one of six response categories.)

P(A) INTERVAL	FREQUENCY	PROBABILITY	CUM. PROBABILITY
0.000 - .2875	0	0.0000	0.0000
.2876 - .3125	4	.0079	.0079
.3126 - .3375	10	.0198	.0277
.3376 - .3625	9	.0178	.0455
.3626 - .3875	15	.0297	.0752
.3876 - .4125	24	.0475	.1228
.4126 - .4375	38	.0752	.1980
.4376 - .4625	45	.0891	.2871
.4626 - .4875	63	.1247	.4119
.4876 - .5125	65	.1287	.5406
.5126 - .5375	57	.1129	.6535
.5376 - .5625	50	.0990	.7524
.5626 - .5875	38	.0752	.8277
.5876 - .6125	40	.0792	.9069
.6126 - .6375	17	.0337	.9406
.6376 - .6625	15	.0297	.9703
.6626 - .6875	5	.0090	.9802
.6876 - .7125	7	.0139	.9941
.7126 - .7375	2	.0040	.9980
.7376 - .7625	1	.0020	1.0000
.7626 - 1.000	0	0.0000	1.0000
	505	1.0000	1.0000

all or some part pre-specified part of a moving dot stimulus. Estimates of stimulus direction were made in two ways. The principle method, using orientation matching, will be described now; a second procedure will be described later. On a typical trial, the observer views a moving dot pattern for one second. Immediately following the stimulus, a line segment subtending one half degree of visual angle appears on the outer edge of the display.

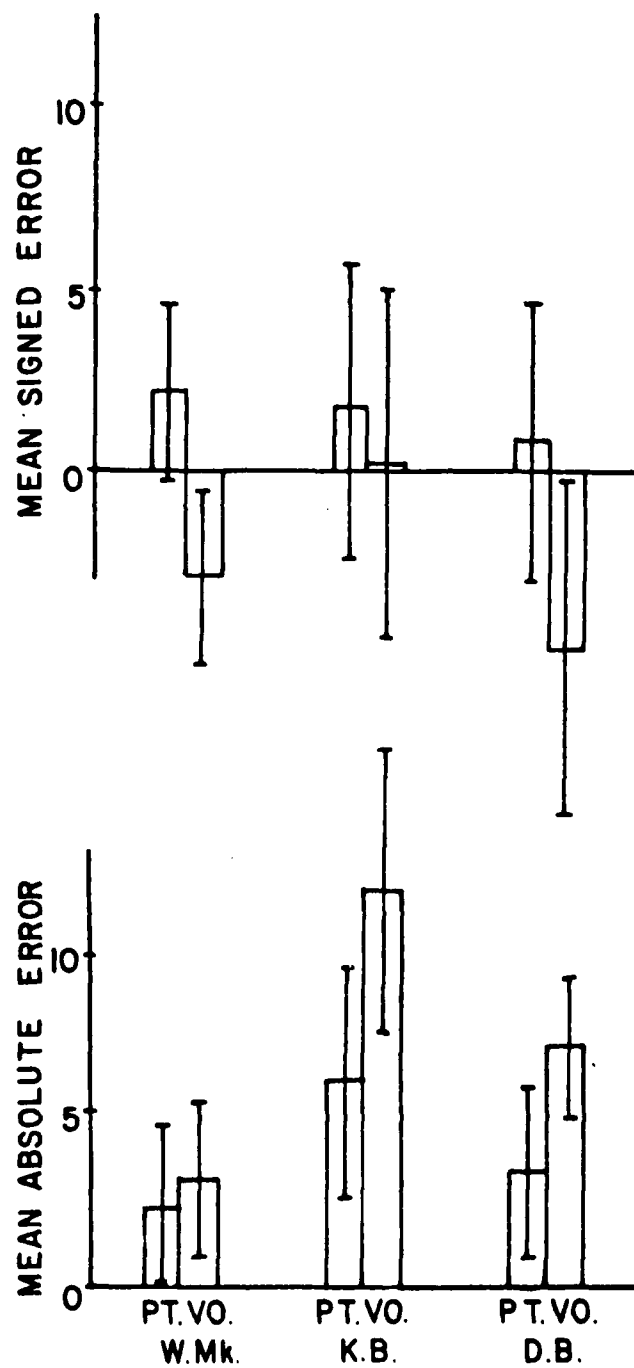
The observer reported the perceived direction of the stimulus by using the pointer's orientation to indicate the direction of motion to indicate which radius of the mask pointed in the stimulus direction. Rotation of a potentiometer by the observer caused the line segment 'pointer' to rotate around the display circumference with one degree resolution. Initial orientation of this pointer was randomized within a range plus or minus twenty degrees of the real direction of motion. This was sufficient to prevent initial position from serving as a significant directional cue. Once a satisfactory match was achieved, the observer notified the computer with a button press. The computer recorded the direction estimate and presented the next moving dot pattern. In some stimuli, more than one direction of motion is present in the display. When more than one direction was contained in a stimulus, the observer was

directed to report one particular component direction (such as motion not along the vertical orientation).

This orientation matching procedure of direction estimation is different from the verbal estimates observers made in my previous work (Marshak and Sekuler, 1979). In those earlier experiments and some of the current ones, a protractor scale surrounded the display mask and observers made a verbal report of the direction of the stimulus from the scale. The orientation matching procedure has two advantages. First, observers do not have to change fixation to read the protractor on each trial and second, data acquisition was automated, thus avoiding transcription of audio tapes.

Judgements of the direction in which dot patterns moved were made by three observers using both orientation matching and verbal reports. The results are shown in Figure 7. The accuracy of the perceived direction was measured by absolute and signed averaged error for the two methods of report. The standard deviations of the error measures were coextensive in all but one of the comparisons, indicating no difference in the methods of reporting perceived direction.

Figure 7: Comparative accuracy of the pointer orientation matching (PT.) and verbal report (VO.) of reporting perceived direction of motion. Mean signed error is the average accuracy of the perceived direction. Mean absolute error is the average magnitude of the individual errors. These were based on twenty estimates made by each observer with each method of report. Narrow lines represent the standard deviations of each observer.



Part I

Contrast and the ability to see direction of motion

Sensitivity to contrast has become a principal means of measuring the receptive field of individual visual neurons (Enroth-Cugell and Robson, 1966) and overall sensitivity to pattern of the visual system (Schade, 1965; Sekuler, 1974). Just as gradients of contrast determine the form of an object, temporal modulation of contrast can result in the perception of flicker or motion. The visual system extracts information about motion and its direction from these changing patterns of contrast on the retina.

The vector theory of motion perception described in the Introduction is based on the response of DS units whose output is (at least to some degree) also a function of stimulus contrast. Further, vector theory presupposes that two stages enter into the perception of direction: an excitatory stage and an inhibitory stage. The Limulus model (Hartline and Ratliff, 1972) of excitatory and inhibitory interaction in spatial vision usually attributes lower contrast thresholds to the excitatory process than the inhibition. This difference in threshold for the two processes may be a general characteristic worth exploring in the motion domain. The experiments of this section will first seek to determine

the contrast threshold for moving random dots, and address some relevant issues in measuring stimulus threshold. Once contrast threshold has been assessed, the accuracy of direction perception will be measured at various contrasts to see whether the presumed inhibitory sharpening process enhances accuracy at contrasts above threshold.

Several experiments have estimated the contrast sensitivity of motion sensitive elements of the human visual system (Pantle and Sekuler, 1969; Pantle, 1974; Keck, Palella and Pantle, 1976). All three experiments employed the motion aftereffect (MAE) to measure the contrast sensitivity of motion sensitive elements. Their collective results suggest a linear relationship between contrast and MAE up to a 5-6 times threshold, after which increasing contrast had no effect on aftereffect. The vector model intimately associates the activity of motion sensitive elements with the perception of motion's direction. Thus, the relationship between contrast and directional accuracy is of importance to the vector model.

At least two experiments are necessary to define the relationship between contrast threshold and perceived direction. First, the threshold of the stimulus, in this case isotropic random dots, must be measured. Second, the accuracy of direction perception must be measured as a function

of stimulus contrast. Then the contrast at which directional accuracy is best can then be compared with the stimulus threshold. The vector model would predict that more contrast is required to achieve accurate perception of direction than detection of motion because of the higher threshold of the inhibitory direction sharpening process.

Experiment 1: Contrast threshold using random dot patterns

Experiments that measure contrast threshold are complicated because the concept of threshold is so complex. Different methods of measurement can yield very different estimates of the threshold. There is an additional complication in measuring the contrast threshold for a stimulus in motion.

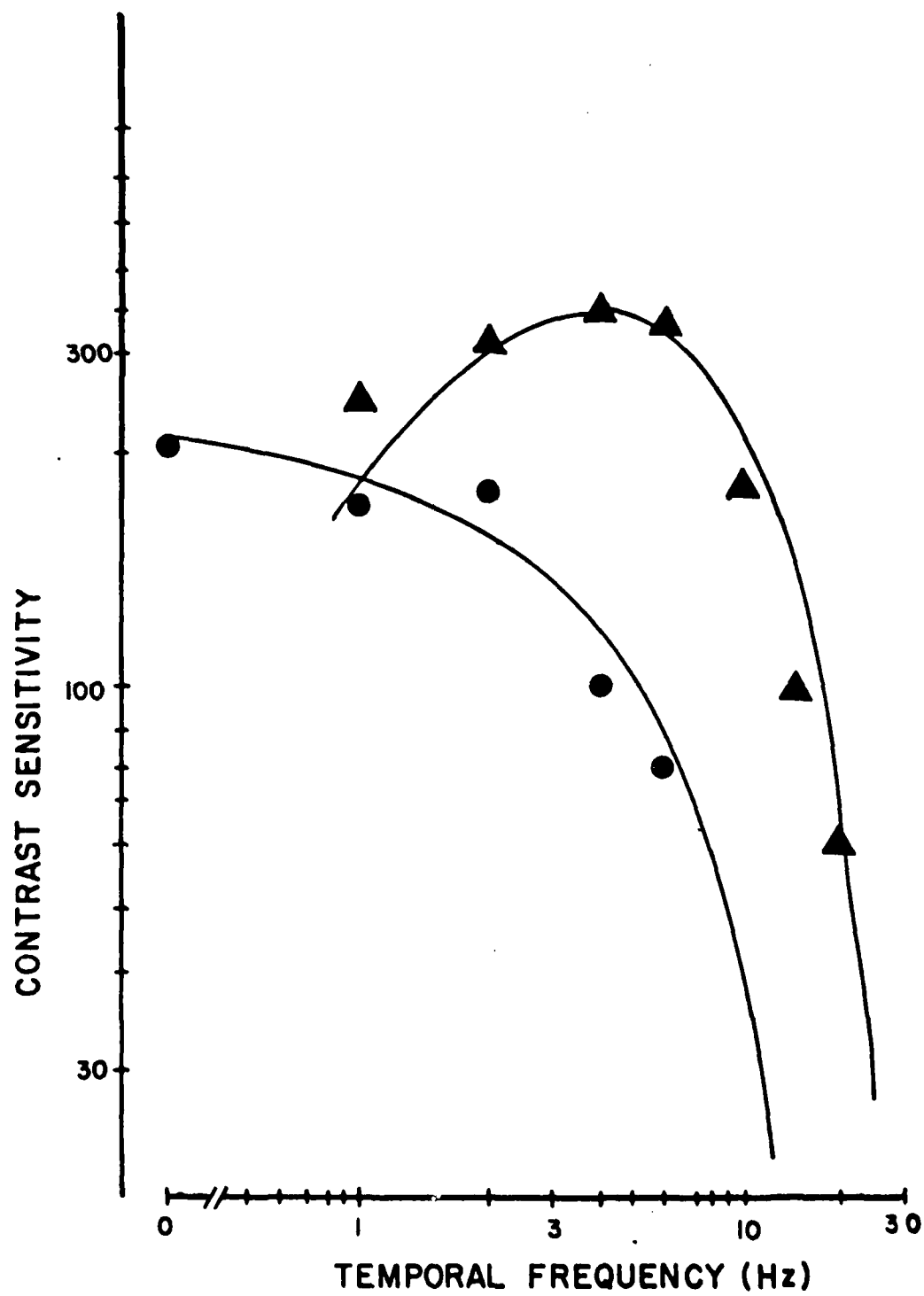
Two distinct contrast thresholds have been associated with a moving stimulus (Keeseey, 1972; Tolhurst, 1973; Kulikowski and Tolhurst, 1973). These experiments employed sinusoidal grating stimuli which were temporally modulated (changed over time) by moving or by flickering. If the grating contrast was increased from a value below contrast threshold, the observer first sees the flicker or motion without seeing the grating's bars. The pattern becomes visible only after a further increase in contrast. If the grating contrast is decreased from a initial value above

contrast threshold, the grating's pattern disappears at a higher contrast than the stimuli's flicker or motion.

Random dot patterns have significantly different spatial frequency content from grating patterns. Sinusoidal gratings have all their energy at a single spatial frequency and in a single orientation. Since the pattern can only show a displacement in the direction orthogonal to its orientation, only two opposite directions can be exhibited by gratings. Their motion results in a single temporal frequency, the product of their spatial frequency and velocity. Kulikowski and Tolhurst (1973) reported the contrast sensitivity function (the inverse of contrast thresholds) for flickering sinusoidal gratings as a function of temporal frequency of flicker. A figure from their paper has been reproduced in Figure 8. Each of the two curves reflects threshold for a particular criterion: either see flicker or see the grating's pattern. They observed differences based on observer criterion at intermediate temporal frequencies, but at the extremes the curves converged.

The random dot patterns used in these experiments have a spatial frequency spectrum concentrated in the lower frequencies (less than 1 cycle/degree). This energy is not all in one orientation as it is in gratings. Rather, it is uniformly spread in all orientations. A detailed description

Figure 8: Contrast sensitivity of counterphase flickering gratings as a function of temporal frequency using spatial (circles) and temporal (triangles) criteria (from Kulikowski and Tolhurst, 1973).



of the spatial frequency content of the dot patterns employed is contained in Appendix 1. When random dots move, they generate a range of temporal frequencies. The temporal frequencies resulting from spatial energy oriented orthogonal to the direction of motion are a simple product of spatial frequencies and velocity. Temporal changes in other directions are generated as well. The temporal frequency at other directions falls off as a cosine function of the difference between angle of motion's direction and angle of that other direction. Thus, the temporal frequencies generated by dot patterns tend to be very low, at a point on Kulikowski and Tolhurst's curve where the spatial and temporal thresholds converge. The prediction that the spatial and temporal thresholds are similar for dot stimuli will be tested in the process of establishing the contrast threshold for dot patterns.

The experiment was conducted in a booth protected from extraneous light other than the indirect lighting of the display face and the luminous dots themselves. At the display face luminance of 2.1 candela / meter squared, color perception was still possible. This indicated that the threshold measurements would be based on photopic sensitivity. The dark adaptation curve for photopic vision achieves maximum sensitivity after 5 to 7 minutes. Thus, at

least five minutes of dark adaptation and several more minutes of instructions preceded each session involving near threshold dot contrast.

Contrast threshold settings were made by three observers using the method of adjustment procedure. After the five minutes of dark adaptation, two experimental sessions were run in immediate succession. During the first session, observers set contrast so that "clear and distinct dots were just barely visible." These measurements are an estimate of the spatial threshold. The observers remained in the dark between sessions. The order of sessions was always spatial, then temporal so that any additional change in dark adaptation would favor finding a threshold difference. In each session an observer made 32 threshold settings.

The stimulus for these threshold settings was an isotropic random dot pattern composed of 650 dots. The pattern was so constrained so that no dot could overlay any other dot; this prevented points of higher than average contrast. Pattern onset and offset were phased over time as described earlier. On half the settings in both sessions, the dots moved rightward at 4 degrees per second. The other half of the settings were made with stationary dots. A temporal criterion was possible even with stationary dots because of the temporal changes caused by the discrete presentations

used in the method of adjustment.

The average threshold settings for moving and stationary dots using each criterion are presented in bar graph form in Figure 9. These data have been adjusted to account for the physical difference in luminance for moving and stationary dots observed in the display calibrations. The most striking feature of these results is the lack of differences among the four conditions. Experiments using gratings had found threshold differences as great as one log unit (Kulikowski and Tolhurst, 1973), yet the greatest differences in this experiment were no greater than .14 log units. An analysis of variance was performed on these data and the outcome presented in Table B. No statistically significant differences were observed between the various experimental conditions.

Differences based on observer criterion were in the expected direction (temporal sensitivity > spatial sensitivity) but were not statistically significant ($F=10.73$, $p < .10$) reflecting the small differences. For all practical purposes the thresholds using spatial and temporal criterion with these random dot patterns were equivalent.

Sensitivity for stationary dots was slightly greater than sensitivity for moving dots ($F=16.16$, $p < .10$). This

Figure 9: Contrast sensitivity ($1/\text{contrast}$) for moving and stationary dots using spatial and temporal criterion. Each category is the mean of 16 threshold settings by three observers. The standard error bars are also presented.

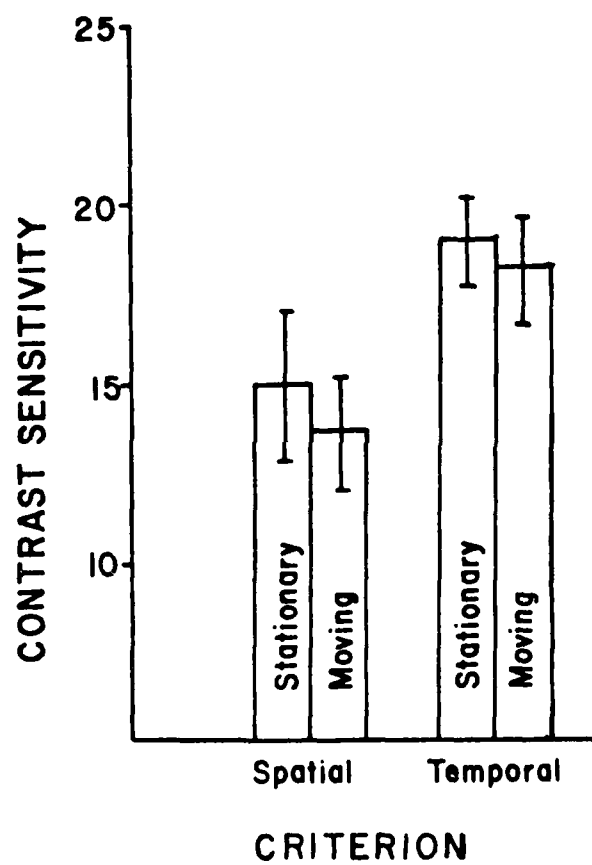


Table B

Analysis of Variance Summary Table for Experiment 1

SOURCE	DF	SS	MS	F	p
Subject	2	.53			
Motion	1	2.02	2.02	16.16	<.10
Subject x Motion	2	.25	.125		
Criterion	1	51.04	51.04	10.73	<.10
Subject x Criterion	2	9.51	4.76		
Criterion x Motion	1	.27	.27	.65	n.s.
Subject x Criterion x Motion	2	.38	.41		

difference was again not statistically significant and cannot be taken as meaningful. The criterion by motion interaction also failed to achieve significance as well ($F = .65$, n.s.). The comparison that parallels Keesey (1972) is that between the temporal versus spatial thresholds for the moving pattern. The sensitivity in these conditions were essentially the same.

Discussion:

The results of Experiment 1 failed to show significant differences in unadapted contrast threshold for spatial and temporal information using isotropic random dots as a stimulus. The lack of threshold differences are in line with our expectations based on the temporal frequencies generated by dot patterns and the findings of Kulikowski and Tolhurst (1973). The spatial and temporal thresholds coincide for random dot patterns. The only report of distinct spatial and temporal thresholds was made by Levinson and Sekuler (1980). They found that adaptation with moving random dots could elevate the temporal threshold while not effecting the spatial threshold. Perhaps the spatial and temporal thresholds which normally coincide for dot patterns can be differentially adapted to reveal their separate

existence.

The failure to measure two distinct thresholds for perception of moving stimuli permits me to average these data into a single approximate threshold, whose contrast is about .06. The scene is now set to see how the accuracy of perceived direction varies at contrasts around this estimate of contrast threshold. Description of directional accuracy as a function of stimulus contrast should reveal whether the Limulus model for excitatory-inhibitory interaction can be extended to human motion perception, whether a difference between threshold and accuracy asymptote exists as the vector model suggests and whether manipulating contrast can be used to control the amount of lateral inhibition operating in the observer's perception of motion's direction.

Experiment 2: Accuracy of perceived direction as a function of stimulus contrast

According to the vector model, the accuracy of perception of direction is based in part on an inhibitory process. Reasoning from other models of inhibition, it was presumed that the inhibitory mechanism would have a slightly higher threshold than the excitatory processes. These assumptions lead to the following prediction about the perceived direction of a moving stimulus: as contrast increases from below

threshold, the accuracy of perceived direction will increase up to some point above detection threshold where the inhibitory process is fully operational. Increasing contrast beyond that point will not improve accuracy of perceived direction.

Although the relation between contrast and direction has not been previously studied, the relationship between contrast and adaptation effects on motion sensitive mechanisms already has. Experiments using motion aftereffects produced with gratings (Pantle and Sekuler, 1969; Keck, Palella and Pantle, 1976) have estimated a point at which increased contrast of the adapting stimulus no longer affects the motion aftereffect. The present experiment will use a very different technique to estimate the contrast at which the directional perception mechanism reaches its maximum performance.

The stimulus consisted of the same pattern of random dots described in Experiment 1; all of the dots moved along parallel paths at a rate of 4 degrees per second. Each stimulus lasted one second, with ramped onset and offset of contrast. The direction of motion was randomized within a range of directions between 75 and 105 degrees. The restricted range of directions (plus or minus 15 degrees of vertical) were chosen to minimize elevation of threshold due

to uncertainty effects (Ball and Sekuler, 1981). Very little threshold elevation is expected within such a range of angles, so it is reasonable to assume thresholds are the same in both experiments.

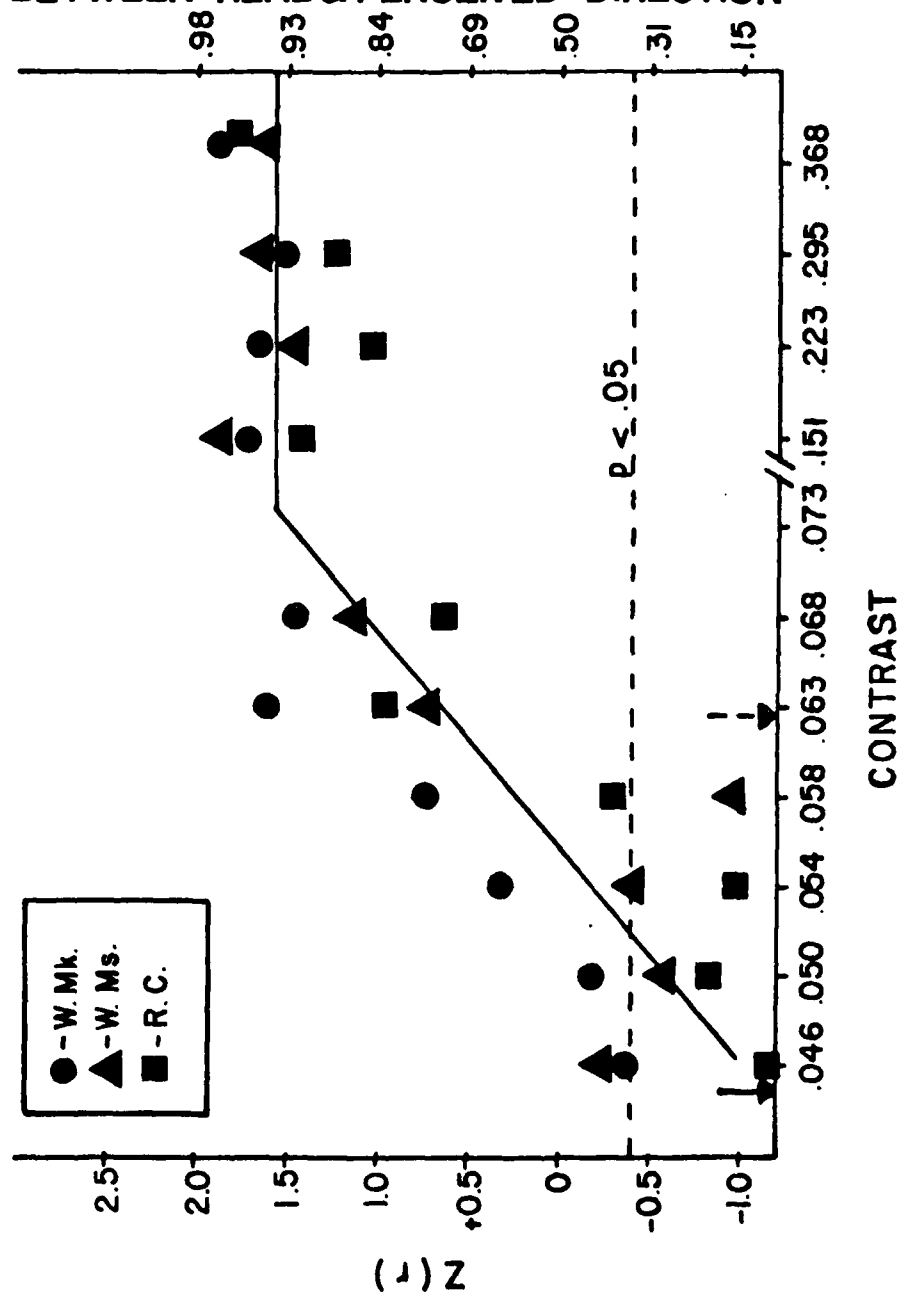
Directional estimates were made after each stimulus using the direction matching procedure with the potentiometer controlled pointer (described earlier). Three observers made a total of 20 directional estimates at each of 10 contrast levels. The sequence of contrasts started at maximum (.36) and changed in linear steps (.07) until the vicinity of threshold (.06) determined for the same observers in Experiment 1 was reached. Finer, log scaled steps were used (.004-.006) in the lower contrast range.

Directional accuracy was measured using the Pearson correlation between perceived and read direction of motion. Correlation was chosen as dependent measure because it concisely describes the relationship between percept and real stimulus and because it allowed a convenient test of when performance exceeded chance. The correlation coefficients for the three observers at the various contrasts are shown in Figure 10.

Various other kinds of information are also represented in Figure 10. Two estimates of threshold appear as arrows

Figure 10: Correlation of perceived and actual direction of motion as a function of dot pattern contrast. Dashed line is the correlation coefficient corresponding to chance performance. Dashed arrow is the method of adjustment threshold. Solid arrow is the averaged detection threshold for two of the observers (W.Mk.) and R.C.). The solid line is a least squares fit of the data for a two line segments constrained such that the right segment is horizontal (Bogartz, 1968).

r BETWEEN REAL & PERCEIVED DIRECTION



along the abscissa. One threshold is the contrast determined by all the method of adjustment observations from Experiment 1, a contrast of .06 .

The second threshold (the solid arrow along the abscissa) represents the contrast at which the moving dots are detected using a signal detection procedure. At each of the lower scale contrasts, two of the observers (W.Mk. and R.C.) observed 40 stimulus presentations, half of which contained moving dots (target) and half of which contained only veiling luminance (non-target). Observers reported their confidence that the interval contained the target or non-target on a bipolar rating scale in which a 1 was definitely target present and 6 was definitely non-target present. Their confidence rating scale judgements were converted into $Z(P(A))$ and the lowest contrast exceeding chance performance was determined. The chance level was determined with a Monte Carlo simulation of the experiment using random responses (for precise values see Table B). Both observers were able to detect moving dots at a contrast of .05.

Also shown in the figure is the best fitting pair of line segments determined by a method of least squares with the constraint that the right-hand segment have zero slope. The line segments were fit to the z transforms of the correlation coefficients (Bogartz, 1968).

Figure 10 shows several interesting things. First, the signal detection procedure produced lower estimates of contrast threshold than did method of adjustment. Second, at the signal detection threshold the observer had little or no idea of what direction the dots are going in. Performance in estimating the direction of motion was at chance levels at this contrast. Third, perception of direction exceeds chance performance at a contrast very near the signal detection threshold and well below the method of adjustment threshold. Fourth, the intersection of the least squares line segments occurred at a contrast of .07, only 1.6 times the signal detection threshold; at this contrast, accuracy of direction perception has asymptoted.

Discussion:

The difference between thresholds determined by signal detection and method of adjustment probably reflects a difference in criterion used by the observers. Typically, signal detection methods produce lower threshold estimates than adjustment procedures.

Poor perception of direction near the lower threshold estimate is consistent with the predictions of the vector model. At detection threshold, the observer has only the excitatory process to determine whether motion is present,

the inhibitory direction-sharpening process is absent. Directional accuracy continues to improve with higher contrast until the optimum levels of excitation and inhibition have been reached.

The contrast at which direction perception is asymptotic, estimated by the intersection of the lines, is .07. Unfortunately, this estimate falls into the transition between the small and large steps in contrast. Preliminary data estimated where the inflection point in the contrast sensitivity curve would occur and the small contrast steps chosen to cover this range. Unfortunately, performance of two of the subjects yielded data which moved the inflection point into that portion of the contrast continuum where the shift from smaller to larger contrast steps took place. Even with this handicap, the estimated point at which the direction sensitive mechanism reaches optimum performance is relatively low, only 1.07 times the method of adjustment threshold and only 1.6 times the threshold determined by signal detection. This minimum contrast at which direction perception effectively operates will be used in later experiments.

Part II

Summation of directions in moving stimuli

The vector model of motion perception proposes two processes, one excitatory and one inhibitory to underly the perception of direction. Most naturally occurring stimuli generate excitation and inhibition in such proportions to allow veridical perception of direction. The next two parts will explore ways in which these normal proportions may be imbalanced to create misperceptions. The vector model makes definite predictions about these misperceptions, providing evidence to support its explanation about how motion is perceived.

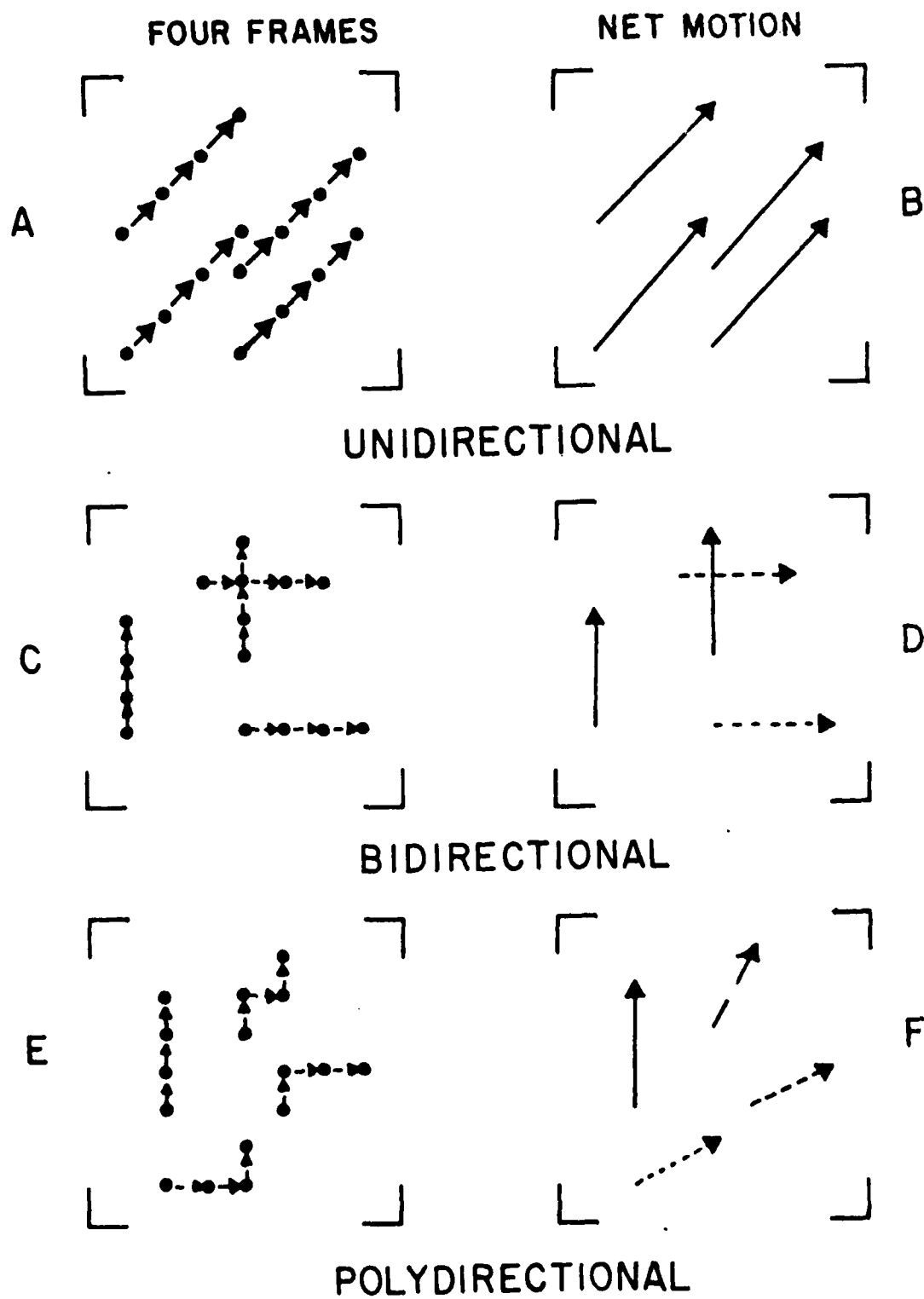
The experiments of Part II will deal with reducing the generation of inhibition. Recall that in the vector model, inhibition restricts excitation among the broadly tuned DS units to a narrow range of units tuned to the direction of stimulus motion and similar directions. When more than one direction is observed, inhibition helps to separate the resulting distribution of unit activity into two distinct parts. This allows two different directions to be perceived simultaneously. If a stimulus containing multiple directions were created in such a way as to reduce the inhibitory process, then the multiple directions will be perceived as

one direction. Since the nature of these stimuli is crucial to this reasoning, a complete description of these peculiar stimuli is necessary.

Consider first the stimuli used in Experiments 1 and 2. When random dots in the display all move in the same direction on parallel paths and at the same velocity, observers perceive a single texture or spatial pattern moving behind the display mask. The frame by frame motion of four dots from such a stimuli is presented in Figure 11A. Net displacement of dots over the same number of frames is represented in B of that same figure. The direction of net displacement corresponds to the direction in which the dot travels. I shall name stimuli for the number of directions of net displacement they contain. Hence the stimulus just described will be called a unidirectional stimulus.

But suppose a stimulus with a different kind of movement were created. In that stimulus, half of the dots within the display moved in one direction and the other half moved in another direction. Suppose further that each set moved in their direction at the same velocity along parallel paths. In such a display with sufficient angular separation between the directions, the observer might perceive two distinct dot patterns moving in two directions. Note however, that if the dots stopped moving, the observer could not tell which

Figure 11: Descriptions of dot motion in unidirectional, bidirectional and polydirectional movement. The display screen locations of four dots over four successive refreshes of the display for unidirectional (A), bidirectional (C) and polydirectional (E) motion are shown on the left. The corresponding net migration of each dot over the four frames are shown for each kind of motion in B, D, and F. See the text for further explanation.



dot belonged to which pattern. Stationarity destroys the percept of separate patterns. This percept of distinct pattern from motion characteristics of the stimulus has been labeled 'structure from motion' by Ullman (1979). The frame by frame motion of four dots in such a 2-direction, 2-pattern display is portrayed in Figure 11C. The net displacement of dots over the same duration is shown in D of the same figure. Again, the directions of displacement coincide with the frame by frame directions of the dots. This kind of stimulus will be called a bidirectional stimulus.

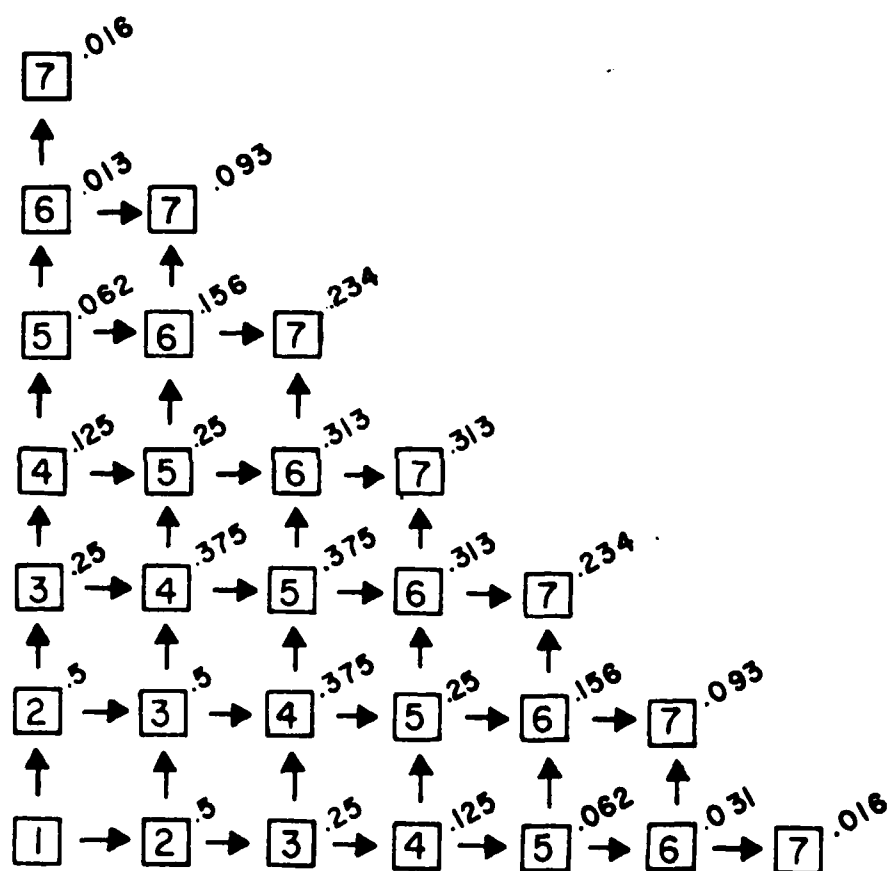
Now consider a stimulus in which dots move in two directions but in a different manner. The dots of the bidirectional stimulus move in either one of two directions only. Each dot travels in the same direction in each successive frame, associating each dot with one direction only. What if the constraint of associating each dot with only one direction were removed? What if, unlike the bidirectional stimulus (Figure 11C), any dot could move in either direction? No association between dot identity and dot direction would be possible. If the probability of each dot moving in one of two directions were 0.5 each dot would make a unbiased random walk. The frame by frame motion of four dots moving in this fashion is shown in Figure 11E. If you

examine the directions and number of dots moving in each successive frame, the motion represented in Figure 11C and Figure 11E are identical. Approximately the same number of dots (a result of the equal probability of the two directions) will move in each direction. If the directionally sensitive mechanisms in the visual system integrate only over two successive frames, bidirectional motion would be identical to this form of random walk.

But consider what happens over many successive frames; the net displacement of dots in random walk stimuli are different from those of the bidirectional stimulus. The displacement of four dots over four frames is presented in Figure 11F. A whole range of motion directions, not just two, is created by the net displacement of dots taking a random walk. This form of stimulus will be called a polydirectional stimulus. The directions of net displacement and their associated proportions of occurrence for seven frames of polydirectional stimulus are calculated in Figure 12. If the directionally sensitive visual mechanisms integrate over large numbers of successive frames, a Gaussian distribution of directions should be perceived.

Observers who viewed the polydirectional stimulus at full contrast describe the stimulus as individual dots making a wiggling traverse across the screen. No spatial

Figure 12: The possible successive screen locations of a single dot moving with polydirectional motion over seven screen refreshes. The squares represent the possible location after the appropriate number of refreshes. The decimal is the probability that the dot will finish in that location after those refreshes. The possible net migration direction of a dot in polydirectional motion is a binomial distribution of directions whose mean bisects the frame motion directions and whose range spans the frame motion directions.



structure is visible within the display; spatial relationships among the dots are changing constantly. Those same observers reported that only three distinct directions of motion are visible: the directions of the frame by frame motion and a third direction midway between them. Considering polydirectional motion contains only two directions of motion in a frame by frame sense and a Gaussian distribution of directions over which dots migrate, this percept of continuous motion in three directions is of great theoretic interest.

Consider the kind of integration the visual system must perform to see each kind of motion in the polydirectional display. Frame by frame motion requires integration across dots to be perceived as continuous. One could argue that confusion of dot identity could account for the continuity of motion. However, the central direction can only be perceived by integrating a single dot's motion over many, many frames. Maintenance of dot identity is important to this latter percept and as mentioned earlier, observers reported seeing the a wiggling traverse.

Frame by frame motion is identical to the stimuli used in the earlier experiments of Marshak and Sekuler (1979) in which significant amounts of inhibition were presumed to be generated. In the vector model, such directions are easily

differentiated because of the inhibition. The migratory motion over successive frames may not create the same degree of inhibition because of changing directions and the Gaussian distribution of directions. Without the inhibitory process, summation of directions of the intermediate directions may occur.

The vector model asserts that under some conditions multiple directions in a display will not be accurately perceived. If the conditions under which lateral inhibition operate are minimized or if the distribution of activity in the DS unit vectors is manipulated to create a single mode or vector sum, then multiple directions in a display will be mistaken for a single direction. Unfortunately, the alternative peak and vector sum decision processes make identical predictions about the summing of directions and will not be differentiated until later experiments.

The experiments of Part II will use these three types of stimuli (unidirectional, bidirectional and polydirectional) to create conditions under which multiple directions cannot be discriminated from a single direction. This failure in the ability to discriminate how many directions there are in a stimulus will be taken as evidence for the vector model of direction perception.

Experiment 3a: Contrast and motion conditions for the collapse of multiple directions in moving stimuli.

The component directions in bidirectional stimuli are easily distinguishable, although they may be inaccurately perceived. At high contrast, the two directions seem to repel one another (Marshak and Sekuler, 1979; Mather and Moulden, 1980). The peak and summing forms of the vector model both postulate that the distribution of activity in DS units will lead to the percept of a single direction. According to the model, the conditions which will create the collapse of multiple directions into a single one are conditions that minimize lateral inhibition among the directionally tuned units.

The source of the inhibition that is supposed to clearly delineate the directions contained in the multidirectional stimulus may be from motion and/or pattern of the stimulus. Reduction of the amount of lateral inhibition will be approached in two ways. One way to reduce inhibition's effects on motion perception is to use near threshold contrasts. The vector model assumes that inhibition requires more contrast to activate its influence than to generate excitation. A second way to minimize inhibition is to dis-

tribute its influence over a wide range of angles. This results in a reduction in excitation in all directions without creating selective reduction in similar directions as in the case of unidirectional motion. The polydirectional stimulus accomplishes this with its unique representation of multiple directions.

Observers performed a signal detection task. In one block of trials, they had to identify whether the stimulus interval contained unidirectional motion (Figure 11 A-B) or bidirectional motion (Figure 11 C-D). In the other block of trials, observers had to identify unidirectional motion from polydirectional motion (Figure 11 E-F). When a single direction was present, its direction was always upward (90 degrees). The stimuli containing multiple directions used frame to frame motion in the following directions with angular separations in parentheses: 84.5 and 95.5 (11), 82 and 98 (16), 77.5 and 102.5 (25), 71 and 109 (38), 60.5 and 119.5 (59), and 45 and 135 (90) degrees. The mean of these directional pairs are all 90 degrees.

The angles were symmetrical about 90 degrees so that if the two directions should perceptually sum, the resulting percept would be indistinguishable from the upward unidirectional motion. The number of dots moving in each direction was equal for bidirectional stimuli (325 dots) and

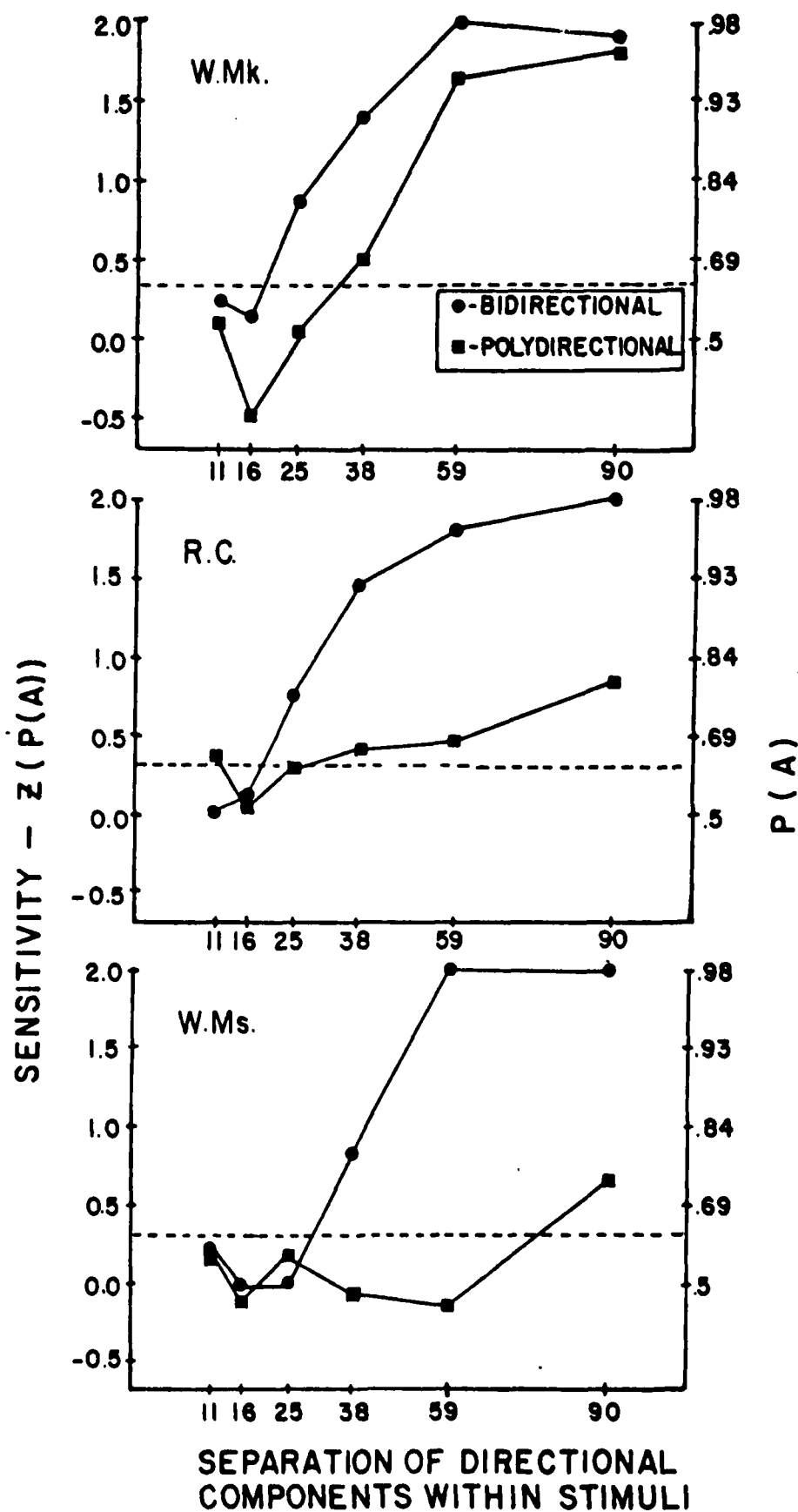
approximately equal for polydirectional stimuli (probability of motion in either direction was 0.5). The possibility existed that summed motion may appear slower than unidirectional motion, so velocity was varied to prevent this from being used as a cue. Velocity of the dots was randomized from trial to trial between 3.5 and 4.5 degrees per second. Contrast was set at .06, near the method of adjustment threshold for all three observers. Since the same observers had served in Experiment 2, I knew that their directional judgement performance was nearly asymptotic at this contrast.

The criterion for whether directional summation occurred was whether the observer could discriminate between the presence of one and more than one direction in a display using the signal detection procedure. On each trial, either one of the two types of motion was presented. The stimulus consisted of moving dots presented with ramped onset and offset of contrast over 1 second, with maximum contrast maintained for .54 seconds. The observer reported to the computer whether one or more than one direction was present. This initiated the next self paced trial after a short delay. Forty trials made up a block of trials. The order of presentation was randomized by the computer. In some blocks, the two types of motion were unidirectional and

bidirectional motion; in other blocks, the two types were unidirectional and polydirectional motion. Each block consisted of 20 presentations of one and 20 presentations of the other kind of motion. The multidirectional stimuli (poly or bidirectional) used six angular separations in their frame by frame motion. Observers were run on each block once. After each stimulus presentation, the observer used a six category rating scale judgement to indicate his confidence of whether one (target) or more directions (non-target) of motion were present. Performance was measured when the observer reported the percept and associated confidence in what he or she saw by pressing one of six buttons, which the computer recorded. The percept of a unidirectional stimulus was indicated with buttons 1-3, with a corresponding confidence of "definitely", "probably", or "possibly" present. If the observer perceived a multidirectional stimulus (bi- or polydirectional, as appropriate), buttons 4-6 were pressed to indicate confidence of "possibly", "probably" or "definitely" present.

The confidence ratings for the three subjects were converted into sensitivity scores $Z(P(A))$ at the six angular separations of bi- and polydirectional motion. These curves are presented in Figure 13 A-C. One curve represents the discriminability of uni- from bidirectional motion while the

Figure 13: Discriminability of a unidirectional stimulus (90 degrees) from bidirectional (circles) or polydirectional (squares) stimuli as a function of angular differences in the bi- and polydirectional stimuli. The dashed line represents chance levels of performance. The results are shown for observers W.Mk., R.C. and W.Ms..



second curve represents unidirectional from polydirectional motion. The Z-transform of each $P(A)$ was taken and the data subjected to analysis of variance. The summary of that analysis is presented in Table C.

Combination of multiple directions of motion separated by less than 30 degrees or so are indistinguishable from a unidirectional stimulus at this low contrast. Discrimination performance failed to exceed the chance level as determined by the Monte Carlo simulations at the narrow angular separations. Discrimination was generally poorer for the polydirectional form of multiple directions than for bidirectional motion ($F = 122.7$, $p < .001$).

Interesting individual differences can be seen in Figure 13. The experimenter (W.Mk.) was able to discriminate polydirectional motion from unidirectional motion at above chance level at larger angular separations than the other observers, although not as well as with bidirectional stimuli. The two less experienced observers never became really proficient at telling unidirectional from polydirectional motion. Since I had acquired considerable experience in creating the display, this may represent a practice effect.

Table C

Summary of Analysis of Variance for Experiment 3a

SOURCE	DF	SS	MS	F	p
Subject	2	.57	.28		
Motion	1	5.22	5.22	122.70	<.001
Subject x Motion	2	.09	.04		
Angle	5	16.47	3.29	20.56	<.01
Subject x Angle	10	1.60	.16		
Motion x Angle	5	3.76	.75	4.70	<.10
Subject x Motion x Angle	10	1.60	.16		

Experiment 3b: Accuracy of perceived direction as a function of movement's duration.

An issue raised in the description of the stimulus motion and in the outcome of the previous experiment is the temporal range over which motion sensitive elements of the human visual system integrate. The debilitating effect of the displacement directions of a polydirectional stimulus found in Experiment 3a indicates integration can occur over at least 3 stimulus frames (required to show the intermediate directions). What exactly is the lower limit of duration or displacement for the perception of direction? A better understanding of the duration/displacement required to perceive direction is necessary to understand how much of the information in the moving stimuli is available to the observer.

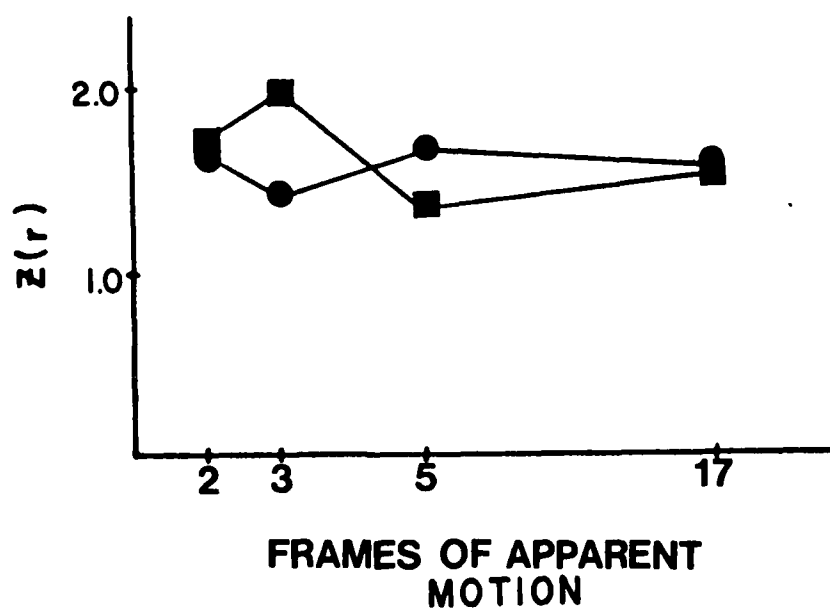
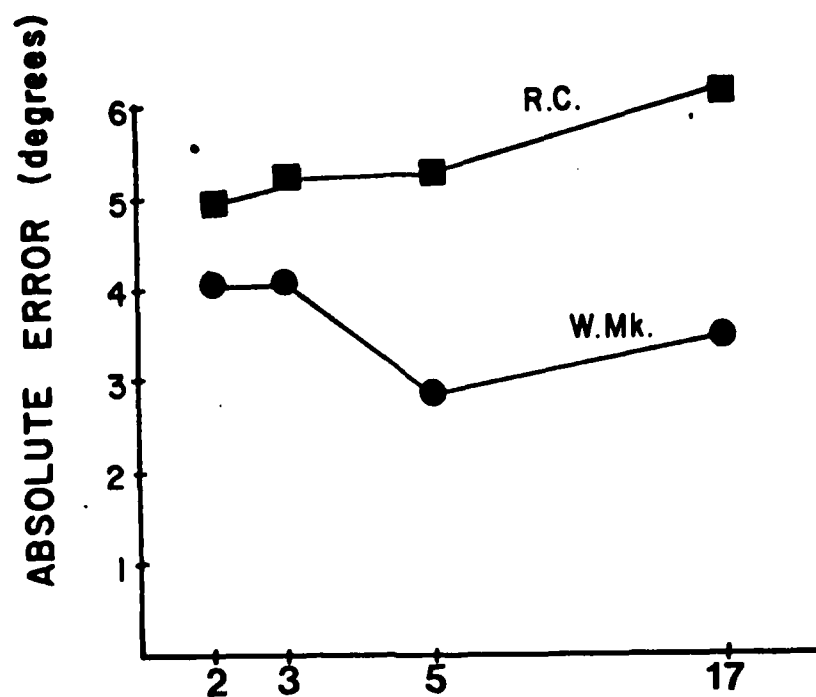
Since stimulus motion is in fact apparent motion, a result of successive 'still' frames, the duration variable is restricted to discrete numbers of frames in a display. Accuracy of perceived direction was measured in two observers by presenting a controlled number of frames of motion in an otherwise stationary dot display. The number of frames containing motion were 2, 3, 5 and 17. Only unidirectional motion was used, since it serves as a standard

against which the other kinds of motion are compared. All other details of the experiment were just as in Experiment 2. When the stimulus did move, its motion was in a direction within 15 degrees of upward (90 degrees) with uniform random placement within that range.

Since the concern in this experiment is with the interval over which motion is integrated, stimulus visibility is maximized. High contrast (.37) was employed using ramped onsets and offsets whose duration was .25 seconds or 6 successive frames. The motion always occurred during the maximum contrast. Directional judgements were made by the observer with the computer generated pointer as described in the directional matching procedure. A total of 20 directional estimates were made at each duration of motion.

The accuracy of directional judgements for each number of frames of motion is shown in Figure 14 expressed in two different metrics: Pearson correlation between perceived and actual direction and as mean absolute error size. Both measures clearly show that accuracy of perceived direction is as good as after two frames of motion as after 16 frames of motion. Accurate perception of direction does not require long durations/displacements to achieve maximum accuracy at high contrast. It could be this ability suffers at lower contrasts used in Experiment 3a. However, since

Figure 14: Accuracy of perceived direction as a function of duration of the display. The average absolute error and the z-transform of the correlation are plotted as a function of the number of frames of motion for two observers (W.Mk. and R.C.).



discrimination remained possible at the larger angular separations this is unlikely.

Discussion:

A single direction of motion was not distinguishable from multiple directions when 25-30 degrees differences in direction were present in the stimulus. Accuracy for single direction judgements of direction are presented in Table D to show the order of error made by the same three subjects with stimuli of the same contrast from Experiment 1. Discrimination of two directions from one occurred with angular differences four times the magnitude of directional errors at this contrast level.

The inability to discriminate one direction from two or more directions is incongruous with the earlier finding that directions repel one another. Marshak and Sekuler (1979) reported that perceived direction of one moving pattern is repulsed by the presence of a second pattern moving in a similar direction. It would seem that repulsion of directions between moving patterns would aid detecting the presence of more than one direction.

How can the same stimulus (bidirectional in that earlier paper) create two different perceptual errors based on a

Table D

Size of absolute errors committed at threshold contrast in Experiment 1.

OBSERVER	MEAN ABSOLUTE ERROR	STANDARD DEVIATION
W.Mk.	4.65	3.64
W.Ms.	4.95	4.68
R.C.	4.55	3.41

difference in the contrast level? The vector model can account for both kinds of errors based on the relative activity of the inhibitory process. At high contrast, inhibition is generated by each directional component and the distribution of excitation is altered by the presence of the other direction. When contrast is low, inhibition is attenuated and the broad excitation which characterizes the first stage of the vector model is allowed to pass unmodified to the decision stage. At the decision stage, the excitation either produces a peak of excitation between the component directions or the broad distribution is vector summed.

Brindley (1960) proposed that when physically different stimuli evoke indistinguishable neural responses, they cannot be discriminated. Creation of indiscriminable classes of stimuli was advocated by Ratliff and Sirovich (1979) as a means of identifying the important aspects of a stimulus. At low contrast, unidirectional and both kinds of multidirectional stimuli are stimuli in the sense of Ratliff and Sirovich, at least at acute angles. The vector model attributes their equivalence to the similarity of neural activity which the stimuli present to the decision stage. Indiscriminability does not require that neural activity be identical for stimuli to be members of an equivalent class;

only the crucial aspects of the neural activity must be identical.

Distribution of activity among the DS units is crucial to determining perceived direction so other factors affecting activation were carefully controlled. Bi- and polydirectional stimuli must create different temporal frequencies from unidirectional stimuli when moved. Activity differences based on temporal frequency were controlled to prevent them from becoming a cue. The velocity of the stimuli were varied in a random fashion to prevent vector length from serving as a cue in discriminating the stimuli.

The vector model can account for the poorer discrimination of a single direction from polydirectional than from bidirectional motion. The presence of stimulation in intermediate directions of motion in the polydirectional stimulus may contribute to a centrally located mode over larger angular separations, or facilitate the vector sum process by preventing reduced excitation from occurring between the component directions. Another possibility is that consistent motion may be more conducive to formation of inhibition than the wiggle of the polydirectional stimulus.

The polydirectional stimulus and its differentiation between directions of frame by frame motion and displacement

over frames raised the issue of which of those directions are available to the observer. The percept of three directions in polydirectional motion suggested both frame by frame and some aspect of displacement was being seen. Experiment 3b shows that frame by frame motion can be accurately perceived by the observer. In fact, the accuracy is as good with longer durations of motion and their associated longer displacements. The visibility of the intermediate direction with polydirectional motion indicates that stimulus displacement across frames also can lead to the percept of direction. However, not all the directions of displacement are perceived by the observer. Motion is only perceived in the most commonly traveled direction (see Figure 12), which happens to be the same direction as would result from peak or vector sum decision mechanisms.

One possible way to distinguish the two mechanisms would be to create a distribution of displacement directions for which most common direction and vector sum direction do not coincide. Unfortunately, the current computer and software available were not capable of creating this kind of stimulus arrangement.

Experiment 4a: Summation of directions as a function of number of dots in motion.

Summation of directional components has been reported by Levinson, Coyne and Gross (1980) using bidirectional motion. Experiments with discrimination and directional judgement show that two directions can sum and the perceived direction is half way between the component directions. A difference between their findings and my observations is that Levinson et al. report summation between directions separated by more than 30 degrees even when their moving dots are at supra-threshold contrast. Summation at contrasts above thresholds were never seen with my displays. A difference between Levinson's and my displays may explain this discrepancy. A total of 150 dots made up the two patterns in the experiments of Levinson et al. ; 650 dots was the normal number of dots in my experiments. The following experiments were performed to determine whether this stimulus parameter could account for the difference between my results and those of Levinson et al. and interpret the difference in terms of the vector model.

As in Experiment 3, observers judged whether one or two directions of motion were present in a one second ramped duration (.5 second maximum) stimulus presentation. Con-

trast was fixed at the averaged method of adjustment threshold (the contrast was similar for all three subjects) as determined for the same observers as in Experiment 2. On half the trials, only one direction of motion was present. Motion was unidirectional and upward (90 degrees). On the other half of the trials, the stimulus motion was bidirectional in movement; dot patterns were moving in directions 60.5 and 119.5 degrees, with an angular separation of 59 degrees centered on upward.

The basic difference between this experiment and Experiment 3a was the number of dots in the stimulus varied from 650 dots down to 210 dots in steps of 25 percent. Equal numbers of dots made up each pattern in the bidirectional stimulus. These changes in number of dots were made by elimination of the intensification pulse, and insertion of an appropriate number of null operations, for a specified number of dots. In this way, frame rate and dot luminance were unchanged from the other experiments. The number of dots in the unidirectional target stimulus was equal to the total dots moving in the bidirectional stimuli.

Discrimination performance at each number of dots was measured in blocks of forty observations. Stimuli containing uni- or bidirectional stimuli were presented twenty times each in an order randomized by the computer. The signal

detection procedure employing the rating scale response system was used. The $Z(P(A))$ observed at each number of dots was plotted in Figure 15 along with the .05 chance level of performance.

Discrimination of one direction from two becomes increasingly easier as the number of dots in motion increases. This was substantiated by an analysis of variance performed on the $Z(P(A))$ s and summarized in Table E. The change in performance due to the number of dots was statistically significant ($F = 5.12$, $p < .05$).

Experiment 4b: Contrast threshold as a function of the number of moving dots.

Subjective impressions were solicited from observers after each experiment. Those comments were particularly interesting for Experiment 4a. Observers reported the reason for poorer discrimination performance in Experiment 4a was that fewer dots seemed less visible. That is, the discrimination curves are a result of increasing failure to see the stimulus instead of a summation of their directions. This visibility explanation for the failure of discrimination seemed unlikely because at least one of the stimuli (unidirectional and 650 dots) was known to be at their

Figure 15: Discrimination of unidirectional from bidirectional motion as a function of the total number of dots in the moving patterns. Dashed line represents chance performance. Solid line is the average for all three observers.

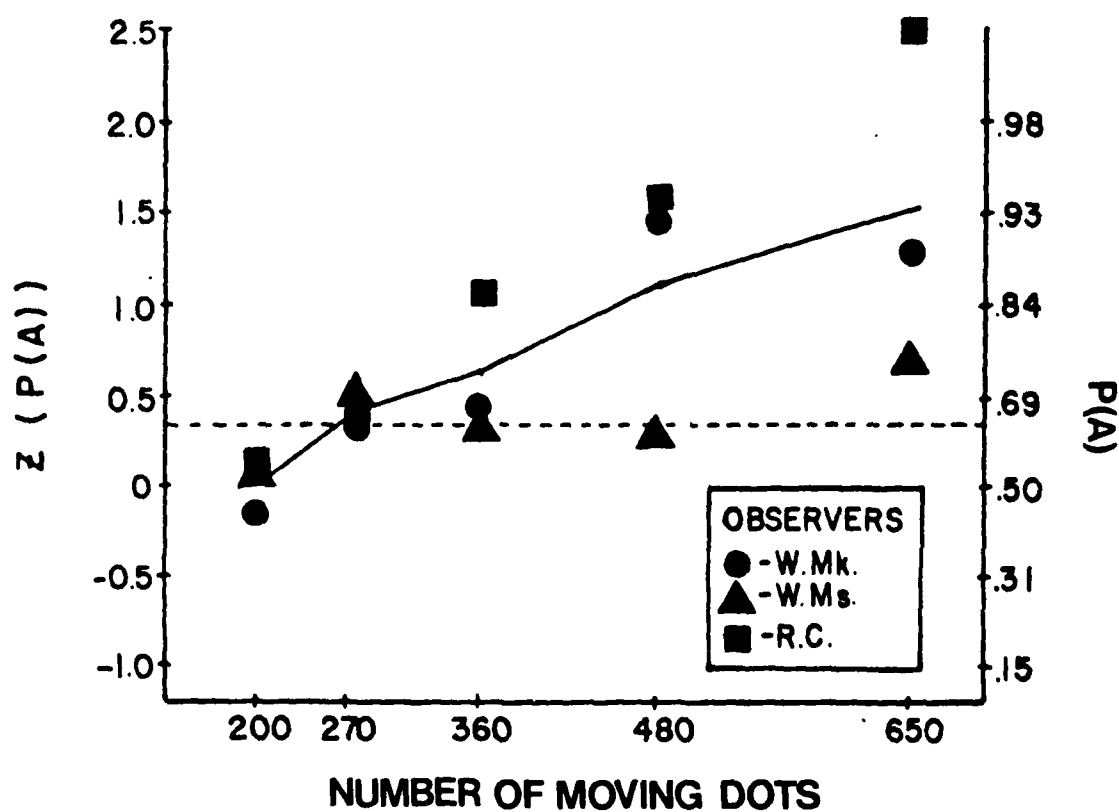


Table E

Summary of Analysis of Variance for Experiment 4a

SOURCE	DF	SS	MS	F	p
Subject	2	1.60	.80		
Number	4	4.10	1.02	5.12	<.05
Subject x Number	8	1.60	.20		

method of adjustment threshold (1.6 times detection threshold), as found in Experiment 1a. Besides, motion was always seen in the other experiments. The reduced numbers of dots used in Experiment 4a requires establishing the relationship between visibility and dot count to see if observer's reports about reduced visibility were true. The method of adjustment was used to determine contrast thresholds for unidirectional dot patterns moving upward (90 degrees) at 4 degrees per second. Two observers (R.C. was unavailable) set thresholds with displays containing of 50, 150, 250, 450, 650 dots. Ten threshold settings were made by each observer for each stimulus, starting with the high number of dots and going through successively lower numbers. This order was adopted to insure that dark adaptation would facilitate performance with fewer dots, to insure the effect was not confounded by adaptive state, even though sufficient adaptation time was allowed. This introduces the chance of a practice or criterion effect, but this was deemed less important than the potential impact of dark adaptation. Density was reduced without change in dot size or luminance (as described in the earlier experiment. All other details of the experiment were as in Experiment 1.

Contrast sensitivity was plotted as a function of the number of moving dots in Figure 16. Contrast sensitivity

falls off as the number of dots in the moving pattern is reduced. This substantiates the observer reports of their inability to see the sparser populated stimuli. The analysis of variance of these results is presented in Table F. Contrast sensitivity diminished significantly as number of dots was reduced ($F = 42.07$, $p < .01$). A 13 fold reduction in the number of dots reduced sensitivity by a factor of 2.4.

Discussion:

Levinson, Coyne and Gross observed summation of directions well above contrast threshold with dot displays containing only 150 dots. The function relating contrast sensitivity and dot count is a negatively accelerating curve. If Levinson et al. determined thresholds with a unidirectional stimulus at the full compliment (150 dots), the threshold for fewer dots moving in different directions is probably much elevated. Thus, summation would still be perceived at apparently supra-threshold contrasts.

The same reasoning can be applied to the results of Experiment 3a because of the reduced dot content of bidirectional and polydirectional stimuli. However, each experiment contained a unidirectional standard stimulus whose visibility (Experiment 1) and directional accuracy (Table D)

Figure 16: Contrast sensitivity for a unidirectional moving dot pattern as a function of the number of dots in the pattern for two observers (W.Mk. and J.M.).

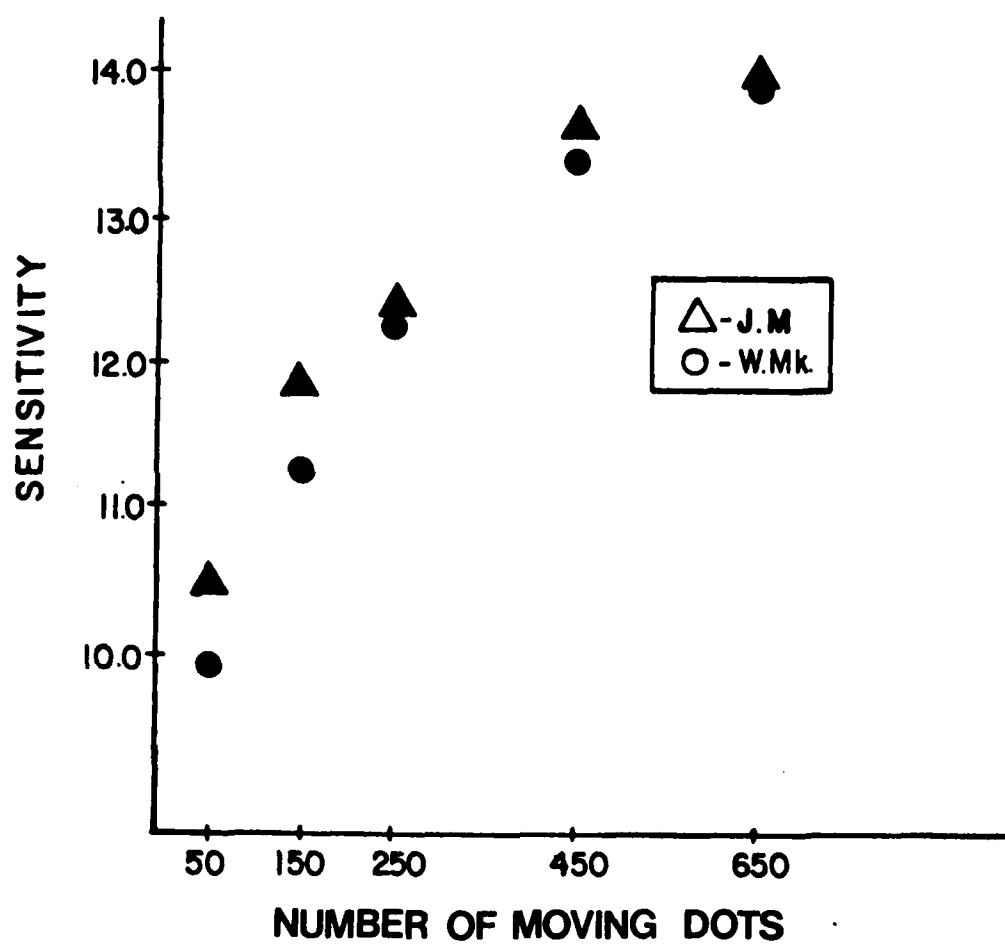


Table F

Summary of Analysis of Variance for Experiment 4b

SOURCE	DF	SS	MS	F	p
Subject	1	57.6	57.6		
Number	4	2700.06	675.01	42.07	<.01
Subject X Number	4	64.18	16.05		

is well documented. If stimuli in the interval containing two directions of motion were not visible, differential visibility of unidirectional and the other stimulus should have been sufficient for accurate discrimination. Other aspects of the outcome of Experiment 3a also discount the visibility interpretation. At large angles of directional separation, discrimination exceeds chance. Second, no visibility complaints were mentioned by the observers. Although some reduced visibility can be expected from the outcome of the results of Experiments 4a and 4b, the slope of the sensitivity curve is shallow with greater number of dots and little effect would be expected.

Two possible explanations can be offered for the decrease in contrast sensitivity with fewer moving dots. First, fewer moving dots may reduce the probability of perceiving the pattern. Thresholds for complex patterns are likely to depend in part on probability summation over space (Graham, 1977). Contrast threshold for one dot could be used to estimate the threshold for two or more dots based on the increased chance of seeing any one of the dots. This may contribute to the threshold elevation when fewer dots move, but an even more important variable is changing when the number of dots is varied. The spatio-temporal characteristics of the stimulus are dramatically changing.

The spectral consequences of changing numbers of dots are a more likely cause of the changes in threshold. The change in spatial frequency content and the corresponding effect on temporal frequency is described in Appendix 1. Fewer dots in the pattern increase the proportion of their energy at spatial frequencies below one cycle per degree. Since the spatio-temporal sensitivity surface is depressed at low spatial and temporal frequencies (Kelly, 1977), the elevation in threshold may result from lower temporal frequencies of the less dense, moving dot patterns.

Part III

Repulsion of directions in moving stimuli.

Bi- and polydirectional stimuli are indiscriminable from a single direction when presented at near threshold contrast and when their directional content ranges are restricted to acute angles. At contrast six times threshold, apparent repulsions between directions in bidirectional stimuli have been observed (Marshak and Sekuler, 1979). The same phenomenon was independently reported by Mather and Moulden (1980). Summation and repulsion of perceived directions are conflicting kinds of perceptual errors. The presence of opposite effects at different parts of the contrast continuum may indicate that two processes with opposite effects are present in the perceptual process.

Directional judgements of unidirectional stimuli were found to be generally accurate in Experiment 1. This accuracy may be achieved through the combination of two distinct processes; each process revealed at the particular contrast level. The contribution of two different mechanisms to the perceived direction is described in the vector model. Distribution of activity in the broadly tuned directional mechanism is modified by an inhibitory process. Activity is restricted to units whose optimal direction is close to the

direction of motion. Another purpose for inhibition is to prevent overlap of the distribution of activity resulting from two or more directions of motion. The final distribution of activity is the basis on which the peak or the alternative vector sum decision mechanism determines the perceived direction of motion.

The vector model predicts that manipulating the amount of inhibition will have profound affects on the perception of direction. In Part II, low contrast and lower numbers of dots were conducive to summation of directions. These same conditions conducive to the summation of directions at low contrast ought to produce reduced amounts of repulsion observed at high contrast. The experiments of Part III will closely examine the repulsion phenomenon to reveal the sources of the perceptual distortion and provide evidence about the reciprocal relationship between direction summation and inhibition.

Experiment 5: Repulsion as a function of bidirectional motion presentation.

When two directions of motion are seen on overlapping visual fields, mutual repulsion of the directions results (Marshak and Sekuler, 1979). According to the vector model,

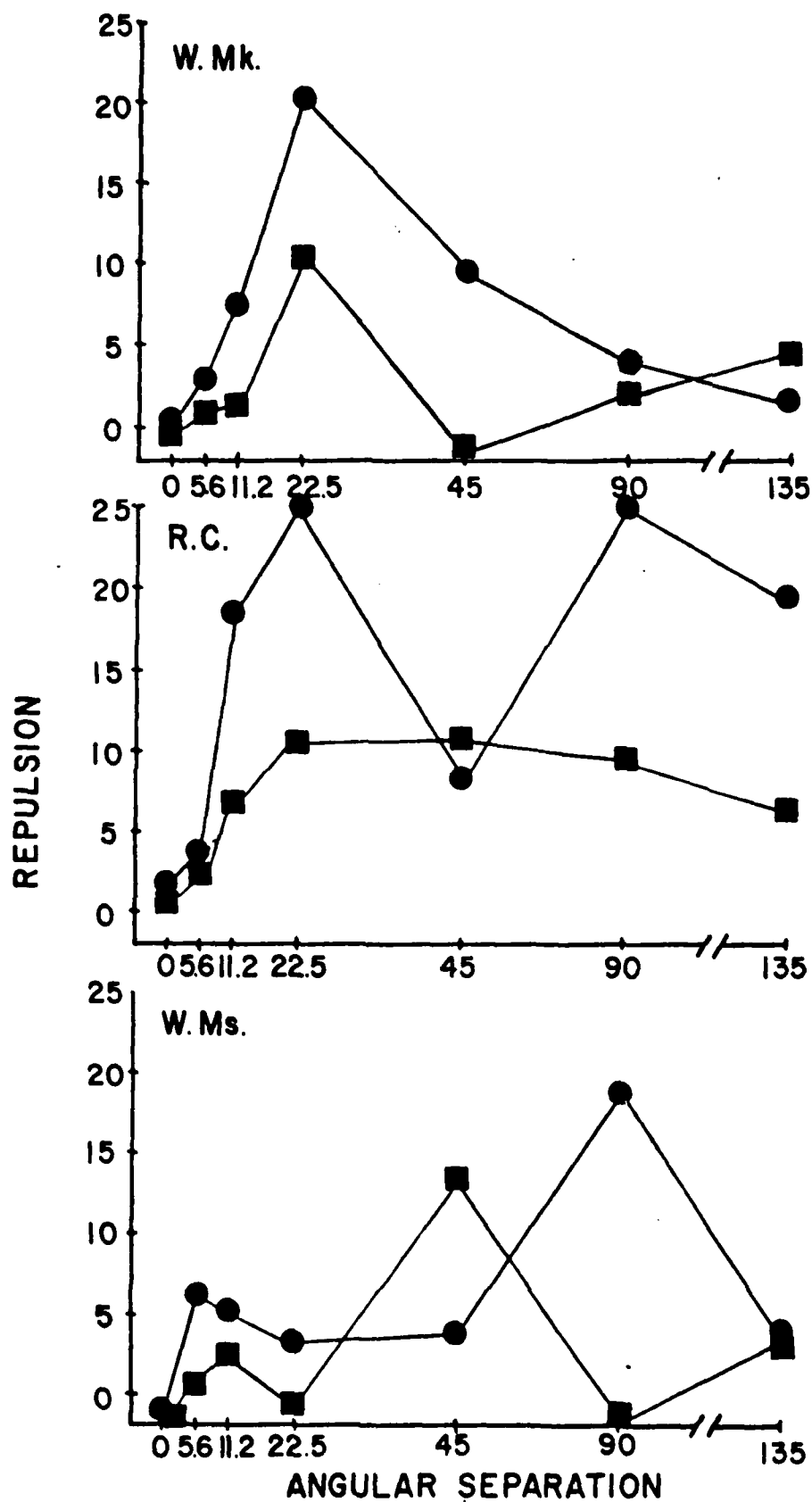
this repulsion is due to interaction of inhibitory effects generated by the other direction. Reduction of the inhibitory effects should result in more veridical percepts of the component directions in bi- and polydirectional stimuli. The current experiment seeks to demonstrate this by portraying two directions in such a way that is likely to minimize the amount of inhibition which is generated.

The size of repulsions between directional components of bidirectional stimuli like those employed in Experiment 3a was measured by having three observers estimate one of the two component directions. One component always moved upward (90 degrees) while the other component moved in a direction with some angular separation relative to the 90 degree component. Upward (90 degrees) motion was always present and observers were not asked to estimate this direction. Its purpose was to serve as a source of inhibition to influence the other simultaneously presented direction whose perceived direction was estimated by the observers. The directions were presented using 650 dots with bidirectional motion in one condition and with polydirectional motion in the other condition. Seven angular separations were employed: 0, 5, 11, 45, 90, and 135 degrees. All dots had a velocity of 4 degrees per second and a contrast of .37, which is six to eight times the detection threshold.

The stimuli were presented for a duration of one second with ramped onset and offset, after which a pointer appeared indicating a direction within plus or minus 40 degrees from the target's true direction. The restricted range was chosen to reduce the amount of adjustment the observer had to make. Orientation of the pointer was random with uniform distribution over that range to minimize any inadvertent cues. Observers adjusted the computer-interfaced potentiometer to move the pointer around the circumference of the display until its orientation matched the perceived direction of the target. The order of presentation for the angular separations was random; each observer made ten settings for each combination of directions. Trials were blocked by kind of motion, but each block contained all the directional combinations. The perceived direction of the target directional component is converted into a measure of repulsion by computing the mean signed difference between perceived direction and real direction. A plus sign indicates the direction was judged to be deflected away from the influence component; a minus sign shows deflection toward the influence component.

The size of repulsion is plotted as a function of angle between target and influence directions for each subject in Figure 17 A-C. Separate curves represent directional esti-

Figure 17: Perceptual error which results from the presence of a second direction of motion in the same visual space. In one set of data (circles), the motion was bidirectional with each of three observers estimating the direction of one directional component. In the other data set (squares), motion was polydirectional with the observers estimating one directional component. The measure of error, repulsion, is the signed difference between perceived direction and actual direction.



mates made with bidirectional and polydirectional stimuli. The most experienced observer (W.Mk.) exhibited the inverted-U relationship between angular separation and repulsion reported in earlier work (Marshak and Sekuler, 1979). The other two observers reported irregular repulsion curves. The repulsion measurements were analyzed and the summary for that analysis of variance is shown in Table G. Polydirectional presentation of directional components resulted in significantly less repulsion than did presentation of bidirectional stimuli ($F = 66.99$). Trend analysis was performed on the size of repulsion over the angles separating influence and target directions. The linear ($F=3.25$) and quadratic ($F=4.18$) components failed to attain significance.

Discussion:

Two of the observers (R.C. and W.Ms.) exhibited repulsion curves unlike those reported in Marshak and Sekuler (1979). The original observations used a series of angular separations all within the same quadrant to make a series of acute angles. The measurements in Experiment 5 were made with the target angle alternating on both sides of vertical. It may be more confusing for observers to make judgements whose directions were divided between several quadrants, as

Table G

Summary for Analysis of Variance for Experiment 5

SOURCE	DF	SS	MS	F	p
Subject	2	888.52			
Motion	1	167.40	167.40	66.98	<.025
Subject x Motion	2	4.99	2.49		
Angle	6				
Linear	1	536.93	563.93	3.25	n.s.
Quadratic	1	165.03	165.03	4.18	n.s.
Residual	4	100.99	25.50	.41	n.s.
Subject x Angle	6				
Subject x Linear	2	346.56	173.28		
Subject x Quadratic	2	78.97	39.48		
Subject x Residual	8	490.63	61.33		
Motion x Angle	6	164.93	27.49	1.10	n.s.
Subject x Motion x Angle	12	299.02	24.92		

in the present experiment. Two of the observers (W.Mk. and R.C.) made directional estimates using bidirectional stimuli and the angular relationships similar to that of Marshak and Sekuler (1979). These observations replicated the earlier findings. Similar results with a slightly different stimulus were observed by Mather and Moulden (1980). They moved stimuli in two directions using dynamically changing dots which persisted only a few display frames and found repulsions in perceived directions similar to Marshak and Sekuler.

There are two possible reasons why these results differ from the earlier findings. First, the standard error of the judgements were twice those observed in the earlier repulsion experiments. Perhaps observers could not make as consistent directional estimates of stimuli occurring in two quadrants as easily as when they occurred in one. Another factor may be differences in the distribution of inhibition in different directions. Marshak and Sekuler (1979) reported that repulsion between directions is reciprocal, but it is not symmetrical. The size of repulsion effects based on direction of target and influence directions of motion requires further examination.

Despite the variability in the data, clearly more repulsion occurred with bidirectional motion than with

polydirectional motion. The direction of components in the polydirectional motion were more veridically seen than in bidirectional motion. Considering the complexity of motion in the polydirectional stimuli, it is remarkable that this kind of stimulus should result in less error.

Marshak and Sekuler attributed repulsion to the influence of lateral inhibition between directions in bidirectional stimuli. The present results are consistent with the idea that more inhibition is generated with bidirectional than with polydirectional presentation of motion. This in turn is consistent with the vector model's proposal that inhibition isolates different directions, preventing summation.

If inhibition is proportional to activity of the DS units, then stimuli preferred by those units will generate more inhibition. Directional changes made by the individual dots cannot be as potent in stimulating the DS unit as a dot which maintains a single direction of motion through the unit's receptive field. Subjective reports about polydirectional motion indicate that the directions are not as distinct as in uni- or bidirectional motion.

The last experiment replicated the repulsion effect and showed how the alternative portrayal of two directions,

polydirectional motion, could reduce the size of repulsion. Other changes in the stimulus can be made that enhance generation of inhibition and increase the amount of repulsion. One of these possible changes will be tested in the next experiment.

Experiment 6: Repulsion as a function of number of dots in the influence pattern.

Experiment 4b showed that number of dots can influence the visibility of a moving dot pattern; more dots make near threshold contrast patterns more visible. Greater dot densities in moving random dot patterns put more energy in spatial and temporal frequencies to which the visual system has greater sensitivity (Appendix 1). This boost in energy should enhance both excitation and inhibition created within the vector model. The present experiment will use changes in number of dots in the influence part of a bidirectional stimulus to modify its inhibitory influence.

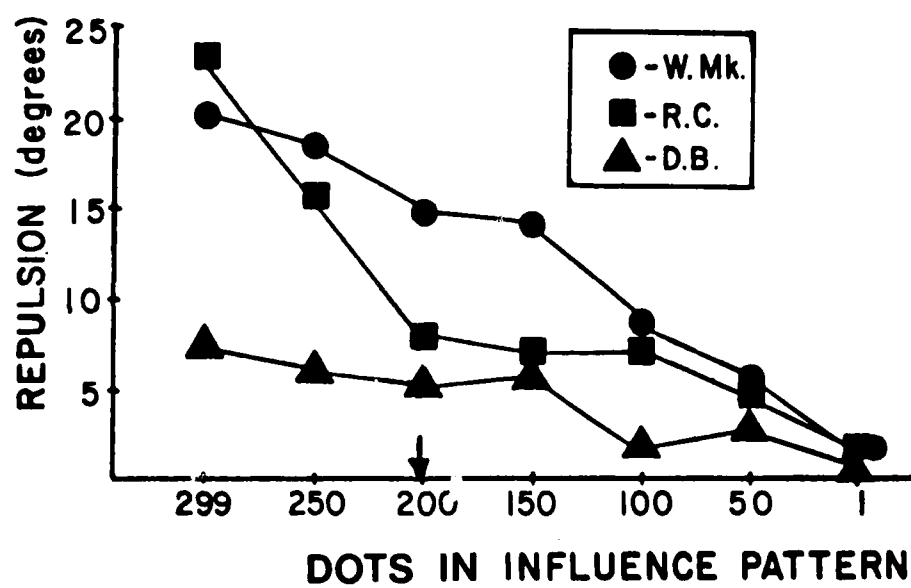
Stimuli in this experiment were bidirectional random dots as described earlier (Figure 11 C-D). Dots moving in the direction designated as target always numbered 200 and moved in the direction of 22 degrees. Dots moving in the other direction traveled rightward (0.0 degrees) and acted

as the source of influencing inhibition on the target direction. The number of dots moving in the influence direction varied between 1 and 300 dots. All dots moved for 1 second per presentation with a contrast of .37 and a velocity of 4 degrees per second in their respective directions. Onset and offset of the stimuli were abrupt, so maximum contrast was present for the whole 1 second interval.

Three observers (W.Mk., D.B. and R.C.) made 20 directional estimates at each density of the influence pattern using the verbal report form of the directional estimate procedure. Recall that in this procedure, the observer watched each stimulus presentation and then indicated direction by matching his percept to a protractor scale surrounding the display circumference. The report was recorded on tape and analyzed later. Order of the dot content in the influence direction was randomized by the computer. The stimuli were presented at 6 second intervals to allow time for the verbal report.

The size of repulsion is measured again by the signed error in directional judgement (perceived direction minus actual direction) and is shown for each observer at each influence density in Figure 18. Repulsion was a linear function of number of dots in the influence pattern for all subjects, although differences in slope for individual

Figure 18: The repulsion reported by three observers within a bidirectional dot pattern whose target direction moved at 22 degrees and whose influence pattern moved a 0 degrees and contained varying numbers of dots.



subjects can be seen. In addition, linear regression was performed on these data for each observer:

$$\text{W.Mk.} \quad y = .068 x + -.215 \quad \{r = .84\}$$

$$\text{R.C.} \quad y = .070 x + 2.465 \quad \{r = .94\}$$

$$\text{D.B.} \quad y = .022 x + 2.536 \quad \{r = .85\}$$

where y is the angle of repulsion in the percept of target direction and x is the number of dots in the influence direction. The amount of variance accounted for by the regression equations for all three observers exceeded the level of statistical significance ($p < .001$).

Discussion:

The target direction in this experiment never changed. The author (W.Mk.) was aware of this fact, but the other two observers were not so informed. Neither naive observer noticed the lack of variation in the target direction and both were surprised when informed of the fact. This is a tribute to the dependence of the target pattern's perceived direction on the influence pattern's dot content.

Varying the number of dots affects the visibility of the pattern (Experiment 4b) and the percept of similar directions. Low numbers of dots increase the energy in the low

spatial frequencies of the dot patterns which lowers the temporal frequencies generated when they move. The visual system is less sensitive to low spatio-temporal frequencies (Kelly, 1977). This accounts for the elevation of contrast threshold in Experiment 4b. If sparse dot patterns are less effective than denser ones in stimulating the visual system at low contrast, they may be less effective at the higher contrasts of Experiment 6 (5-8 times threshold) as well. This reduced effectiveness takes the form of an inability to generate as much inhibition and less manifest repulsion in that experiment.

Since the sensitivity to motion is dependent on the temporal properties of the stimulus (Pantle, 1974; Movshon, 1980), it follows that the other determinant of temporal frequency, velocity, may also affect the generation of inhibition. The next experiment will explore this possibility.

Experiment 7: Velocity's effect on the repulsion phenomenon.

This experiment is designed to reveal how stimulus temporal frequency, manipulated by changing velocity, affects the generation of inhibition which is thought to underly the repulsion effect. A stationary dot pattern should have no effect on a second moving dot pattern's perceived direction.

Increasing the influencing dot patterns velocity in a bidirectional stimulus should stimulate the DS units and create inhibition. Inhibition will be maximal when the temporal frequencies are optimal to stimulate the DS units. After the optimal velocity is exceeded, the DS units will reduce their output and inhibition will fall off. Thus, an inverted U-shaped function between velocity of the influence pattern and magnitude of repulsion is predicted by the vector model. Recall that dot patterns have a spatial spectra which extends over a wide range of spatial frequencies but weighted in the low frequencies (Appendix 1). This suggests that repulsion will persist at even high velocities of the influence pattern, since moderate temporal frequencies will persist.

The stimuli were bidirectional random dots as described before. Two directions were present: an influence direction, containing 200 dots moving at 0.0 degrees, and a target direction, containing an equal number of dots moving at 22.5 degrees. Contrast was .37 for all presentations and the duration was one second, with abrupt onset and offset of contrast. The velocity in the target direction was held constant at 4 degrees per second while the velocity in the influence direction varied between 0.0 and 32.0 degrees per second. The order of velocities in the influence direction

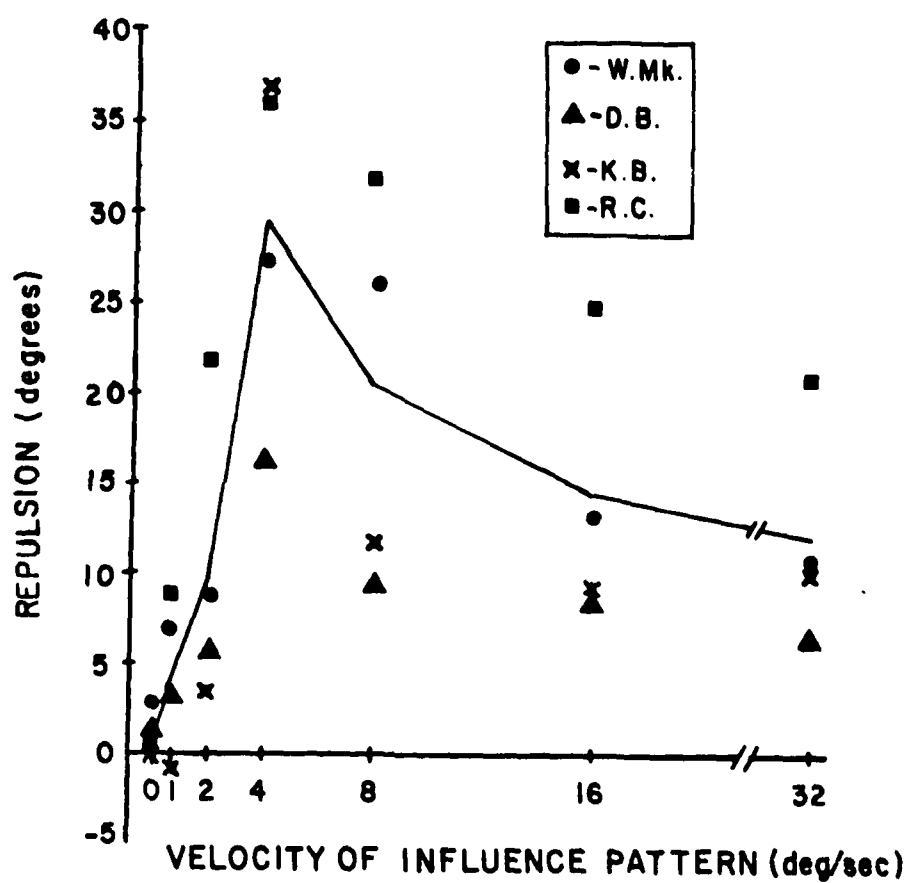
was randomized by the computer.

Four observers (W.Mk., R.C., D.B. and K.B.) made twenty directional estimates at each velocity using the verbal report version of the direction matching procedure. A condition with velocity of zero served as a control condition to see if observers had constant error. Only one observer, K.B. exhibited constant error (12 degrees) and her data were adjusted by subtracting out the average constant error in the zero direction condition. This was the only observer to exhibit any constant error. It could be that in observing some non-vertical movement in all conditions, the observer shifted her reference of vertical. This was the only experiment this observer was used in.

The repulsion of the target direction away from the influencing direction as a function of influencing stimulus velocity is plotted for the four observers in Figure 19. Repulsion was maximum when target and influence direction moved at the same velocity. Slowing the influence pattern reduced the error in judgement until at stationarity, the error disappears. Increasing influence pattern velocity also reduces the size of error, but at 32 degrees per second a sizable amount of repulsion remains in the data.

An analysis of variance with trend components supported

Figure 19: Size of repulsion reported by 4 observers within a bidirectional dot pattern in which the velocity of motion in the influence direction was manipulated. The target pattern moved at 22 degrees and the influence pattern moved at 0 degrees at the various velocities.



this interpretation and is presented in Table H. Apparent direction of the target pattern is repulsed away from the influence pattern (linear trend component $F = 18.08$, $p < .025$). The amount of repulsion is maximal when target and influence patterns move at the same velocity and fall off with velocity differential (quadratic trend component $F = 30.04$, $p < .025$). The second inflection in the curve results in a significant cubic trend ($F = 15.83$, $p < .025$). After falling off from 4 degrees per second velocity, repulsion levels off at the higher velocities. The residual variance of the trend analysis was also significant, but I have no explanation to account for the effect.

The reduction of repulsion at the higher velocities has a simple explanation. At 32 degrees per second, the dot pattern is almost a blur. The temporal frequencies generated by this velocity of the random dots are very high (.25 cycles per degree spatial frequency or above yields 8 hertz or more temporal frequency). Motion sensitive elements should be less than optimally stimulated.

Discussion:

Both psychophysical (Pantle, 1974) and physiological (Movshon, 1980) research indicates the crucial characteristic of a moving stimulus is the temporal frequencies it

Table H

Summary of Analysis of Variance for Experiment 7

SOURCE	DF	SS	MS	F	P
Subject	3	654.59	218.20		
Velocity	7				
Linear	1	576.26	576.26	18.08	<.025
Quadratic	1	933.33	933.33	30.04	<.025
Cubic	1	54.6	154.60	15.83	<.025
Residual	4	600.61	150.15	5.93	<.05
Subject x Velocity					
Subject x Linear	3	95.61	31.87		
Subject x Quadratic	3	93.22	31.07		
Subject x Cubic	3	10.37	3.45		
Subject x Residual	9	227.22	25.21		

generates. The vector model attributes repulsion between similar directions of motion to an inhibitory process. Apparently, the generation of inhibition is also dependent on the temporal properties of the stimulus. The expected inverted U-shaped velocity function was observed. Repulsion did not occur when the influence pattern was stationary and fell off at high velocities. Maximum repulsion occurred when the target and influence patterns moved at the same velocities. It is not certain whether repulsion is velocity tuned (similar velocity moving patterns repulse one another maximumly) or whether four degrees per second is just an optimal temporal frequency. Further work is required to separate these possibilities.

The persistence of repulsion at very high velocities (32 degrees per second) has two possible causes. First, the low spatial frequencies in the dot patterns spatial spectrum may be sufficiently low to generate temporal frequencies to which the visual units are still sensitive (recall $\text{temporal frequency} = \text{spatial frequency} \times \text{velocity}$). Thus, inhibition continues to be generated amongst the DS units as proposed by the vector model. An alternative explanation can be offered based on the appearance of such high velocity dots. The dots appear nearly as streaks, tracing lines across the screen. It might be that the dots are no longer

stimulating motion sensitive elements, but now stimulate pattern sensitive elements. Georgeson (personal communication) observed a repulsion effect with moving dot patterns. Instead of using another moving pattern to influence the target pattern's direction, Georgeson used a superimposed grating pattern. Repulsion of the perceived direction of motion away from the orientation of the grating was observed. This suggests that pattern sensitive units may influence motion's direction, just as the influence pattern motion has in these experiments.

The experiments of Part III show a reciprocal relationship between the ability of a stimulus to encourage summation (Experiment 3a) and repulsion (Experiment 5) of perceived directions. The same inverse relationship between the perceptual errors can be seen in the effects of increased dot pattern density with reduced visibility and summation of directions and enhanced repulsion (Experiments 4a, 4b and Experiment 6). Just such a reciprocal relationship between the conditions conducive to summation and repulsion is suggested by the vector model. Thus, the outcome of these experiments are consistent with the proposed model. The evidence indicates that the repulsion effect may have at least two sources. The velocity effect reported in Experiment 7 is indicative of inhibitory interactions

between directional sensitive elements. Yet the residual effect at high velocities of influence directions, suggests that spatial factors may play a role in perception of direction.

Since two directions cannot be presented without the development of some inhibition, it is difficult to demonstrate how the final stage of the vector model operates alone. Elimination of inhibitory influences, shown to be so powerful in Part III, may yet be demonstrated. The experiments of the last part will deal with one way inhibitory effects may be eliminated, and the consequences examined, through use of aftereffects.

Part IV

Summation of perceived direction within motion aftereffects

The experiments of Part II demonstrated that summation of directions requires reduced dot density, low contrast, or polydirectional motion. The vector model attributes the success of these stimulus manipulations in encouraging summation of directions to the reduction of inhibition amongst the DS units. If this were true, the stimulus most conducive to directional summation should generate little or no lateral inhibition. The before mentioned conditions approach this requirement, but at considerable cost to the excitatory process as well. No moving stimulus can provide this ideal situation of excitation without inhibition. However, it may be possible to create a situation similar to this with a motion aftereffect (MAE).

When a pattern moves in one direction for some length of time and then stops, illusory motion in the opposite direction follows (Wohlgemuth, 1911). Motion aftereffect presents a unique problem for the vector model. How are the consequences of adapting motion interpreted by the decision process as motion? It turns out that explaining MAE can provide evidence about the plausibility of the two alternative decision processes.

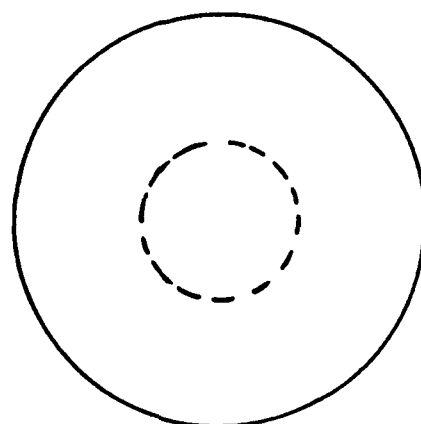
The peak decision process has difficulty explaining MAE because there is no 'peak' in unit activity following adapting motion. Levinson and Sekuler (1975a) did suggest inhibition of the opposite direction occurred during adaptation, providing a subsequent facilitation in the opposite direction after adaptation. This has not been physiologically observed nor has any psychophysical evidence been reported to support their notion. The peak decision process has no basis on which to report the direction of motion aftereffect.

The vector sum decision process can explain both motion aftereffect and other consequences of adapting motion like the directional distortions reported by Levinson and Sekuler (1976). The distributions of unit vectors for two sequences of visual stimulation are presented in Figure 20. When no motion is present (Figure 20A), all the vectors exhibit their base line or normal resting activity level (dotted line). This base line represents the average activity of all the unit vectors. When prolonged adapting motion is experienced (Figure 20B), those units sensitive to that direction of motion become more active. The base line level of activity is increased because the overall average activity level has increased.

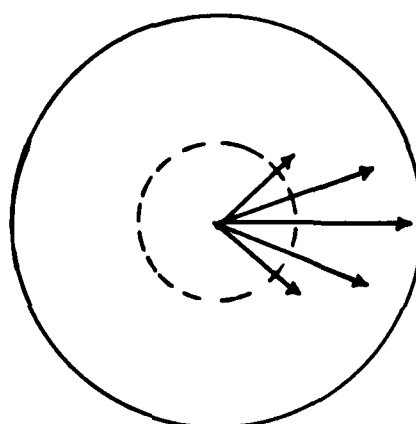
Figure 20: A vector model interpretation of the effects of adapting motion on subsequently stimuli.

- A. Resting- The vector model's polar coordinate system is shown. Each direction sensitive unit exhibits a resting or base line activity level when not stimulated by motion (dotted circle).
- B. Adaptation- Prolonged stimulation of units sensitive to the direction of motion results in increased activity of those units and a subsequent refractory period when their ability to respond is reduced.
- C. Post Adaptation- A stationary pattern subsequent to the moving one results in normal baseline activity in unadapted cells and reduced activity from those cells which had been adapted. No unit will be "most active", leaving a peak decision mechanism without a basis for perceiving direction. The vector sum of activity predicts motion in the opposite direction.
- D. Post Adaptation- A stimulus is subsequently moved in a direction similar to the one used

during adaptation, then the distribution of vectors will be distorted. Some units will be less active because of the adaptation and both the peak and vector sum of the resulting vectors will be displaced away from the direction of prior adaptation and the real direction of motion.

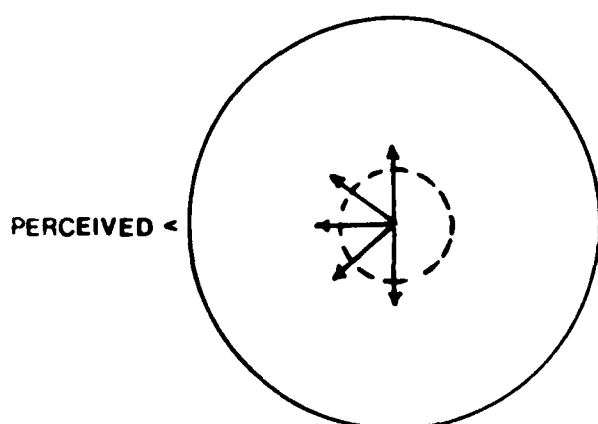


NO MOTION



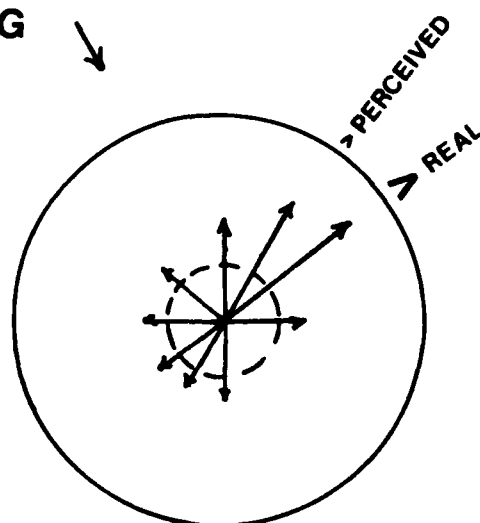
> REAL + PERCEIVED

ADAPTING
MOTION



PERCEIVED <

MOTION AFTEREFFECT



> PERCEIVED
> REAL

SUBSEQUENT MOTION

The left side branch of Figure 20 (C) shows the consequence of the adapting motion on a subsequent stationary stimulus. The base line activity level is depressed because the units affected by adaptation are in a refractory period of less activity. Vector summing of all these units, or just units which exceed the now depressed average activity level will result in the perception of motion in the direction opposite of adaptation.

The depressed activity of adapted units can also affect the perception of subsequent motion (Figure 20D). Following adapting motion, a second stimulus moving in a similar direction has a distorted distribution of activity among the unit vectors. The reduced capacity of adapted units to respond shifts the vector sum of activity away from the direction of adapting motion. This will only affect directions similar to the adapting direction, exactly the finding of Levinson and Sekuler (1976).

The consequence of adapting motion is a distribution of excitation without any of the inhibition which accompanies the perception of real motion. The vector sum of this distribution is in the direction opposite to adaptation. There is evidence to support this explanation. The standard errors for determining direction of MAE are higher than for real motion as we will see in the next experiment. This

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suggests the inhibitory sharpening process present in real motion, according to the vector model, is not present in motion aftereffect. Thus, we have a stimulus that creates a distribution of excitation similar to real motion without the usually accompany inhibitory influences.

Consider the adaptive consequences of multidirectional stimuli, which contain more than one direction. A somewhat similar stimulus has been created by Riggs and Day (1980). They created two color contingent motion aftereffects by alternately adapting with gratings or dots of two different colors moving in two different directions separated by 90 degrees. When dots of each color were showed following adaptation, an appropriate aftereffect was observed. However, if the observer was shown an achromatic dot pattern, a vector sum of the aftereffects resulted. Riggs and Day demonstrated that two adapting motions produced two aftereffects, and if the color differences were eliminated, those aftereffects would sum. The authors conclude that this summation was a product of "a synthesis of unperceived components" (pg. 418). Each component direction creates its own aftereffect which, without some source of identification, undergoes a summation process over wide ranges of angles.

An assumption can simplify and allow simple predictions to be made based on the vector model. The assumption is that at least the excitatory processes of the DS units are all equally sensitive to motion. If those units were not equally sensitive, the decision process would have to compensate for the variation in unit output. This is possible, but predicting the results of the decision process would be significantly more complicated than if they were equally sensitive. A preliminary experiment would determine if the DS units exhibit the characteristic of equal sensitivity or isotropism to see if simple predictions about summation are possible.

Adaptation with bidirectional motion adapts DS units sensitive to two different directions of motion simultaneously, instead of the alternating adaptation of Riggs and Day. When the dots of the bidirectional stimulus cease to move, the percept of two distinct adapting dot patterns disappears because the basis of their identity, pattern from motion (Ullman, 1979) has been eliminated. In their place, there is a single dot pattern double the original component pattern's density. This leaves the visual system with one pattern with which to represent two directions of MAE. Based on the findings of Riggs and Day, one can expect that the motion aftereffects will vector sum. This experiment

will be performed and its consequences related to the vector model will be discussed in the rest of this part.

Experiment 8a: Isotropism of directionally sensitive mechanisms.

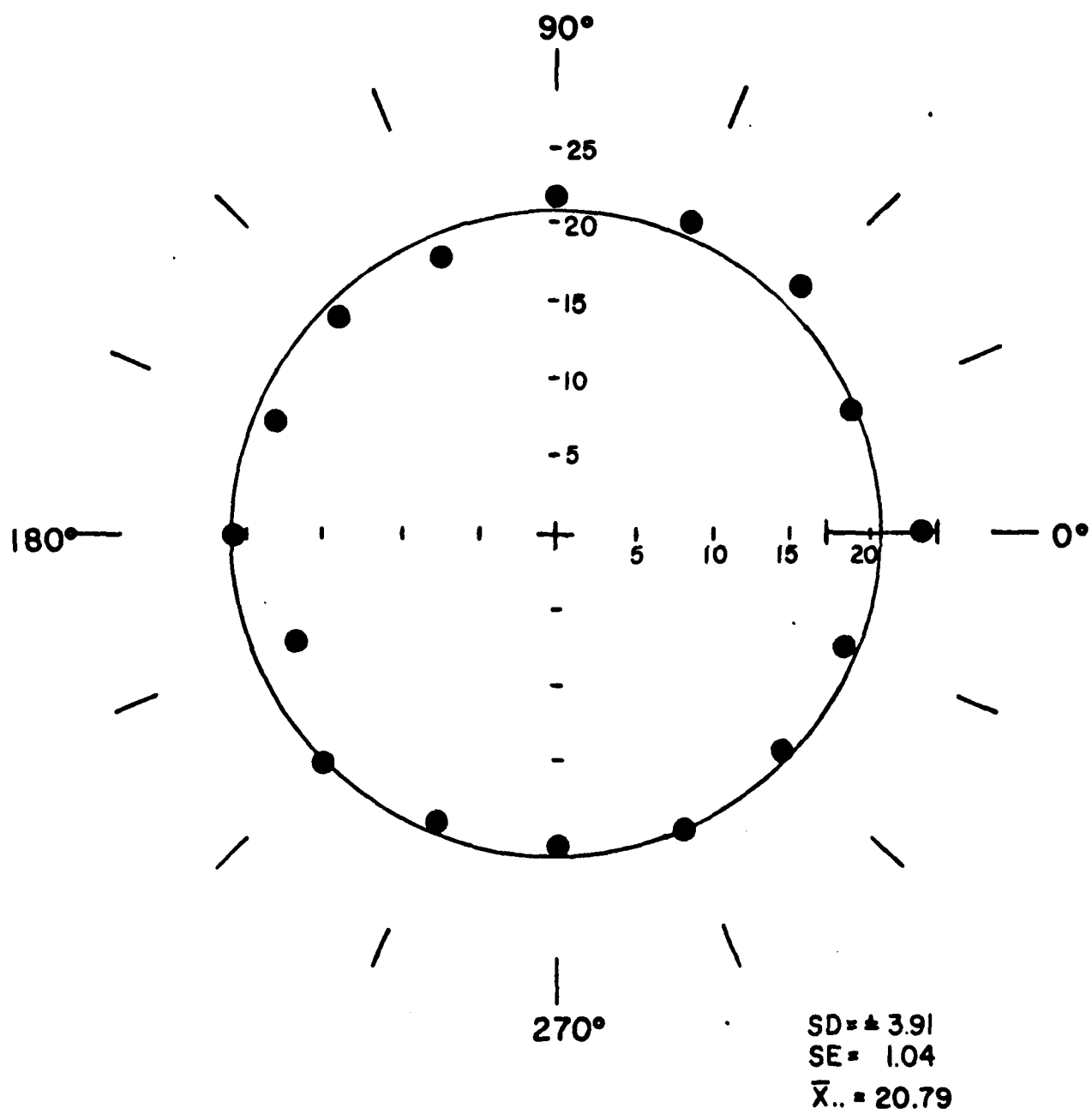
The design and interpretation of an experiment that will study summation of directions would be easier if the motion sensitive mechanisms were isotropic, equally sensitive in all directions. Gross differences in sensitivity based on directional differences would make interpretation of the resulting summed directions very difficult. Such isotropism cannot be assumed in the visual system because exceptions in the visual domain and certain motion aftereffects are already known to exist (Scott, Lavender, McWhirt and Powell, 1966). It is important to establish the equal sensitivity of the motion sensitive elements to facilitate interpretation of directional summation experiments in the terms of the vector model. Unequal sensitivity would prevent making of definitive predictions about the outcomes of those experiments.

There are two prior demonstrations of isotropism in the perception of motion. Levinson and Sekuler (1980) showed that the motion and pattern thresholds for moving dots were the same in all directions. Ball and Sekuler (1981) showed

that the reaction time to onset of motion was the same regardless of direction. The present experiment will extend these observations of isotropism in motion perception to aftereffect of single directions of motion.

Two different measurements of isotropism in MAE were made: its duration and its direction. Isotropism of MAE duration was measured in a single observer (W.Mk.) who adapted to a unidirectional stimulus composed of 400 random dots at a contrast of .37 (six times threshold). During adaptation the dots moved at 4 degrees per second for 60 seconds. Immediately after adaptation, the dots stopped and their contrast was reduced in half. This combination of high adapting contrast and low test contrast was found to produce the largest possible aftereffects (Keck, Palella and Pantle, 1976). The computer timed the interval between cessation of motion and when the observer pressed a button signifying cessation of MAE. The criterion for cessation was the end of MAE's secondary or slow component (Masland, 1969). In Figure 21, MAE duration is plotted in polar coordinates as a function of adapting direction. Duration of MAE is uniform across the 16 directions of motion measured. The circle in Figure 21 has as its radius the mean MAE duration, 20.79 seconds. Variability of points about this mean circle accounted for 79 percent of the total variance of the

Figure 21: Duration of the secondary (long) component of motion aftereffect as a function of adapting direction for one observer (W.Mk.). Each point represents twenty observations.

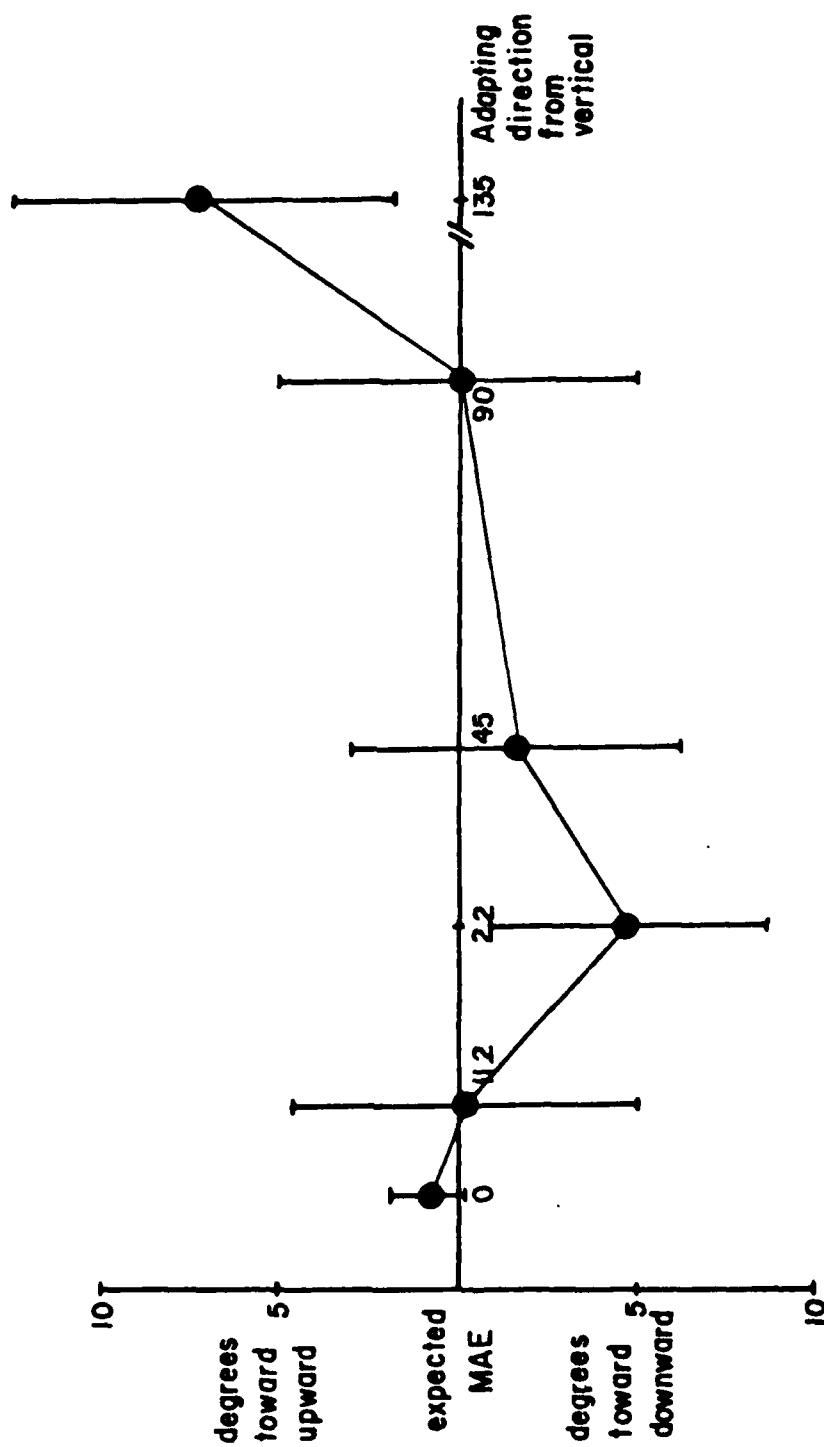


points.

Isotropism of MAE direction was tested with the same observer (W.Mk.). Adapting stimulus were created with a different software arrangement using 650 random dots which moved in unidirectional motion for 40 seconds at a contrast of .37 in directions of 0, 11, 22, 45, 90 and 135 degrees. Immediately following adaptation, the contrast was reduced in half and stationary dots remained visible for 5 seconds. Then the dots were replaced by the pointer which the observer adjusted to indicate direction. Five directional estimates were made at each direction of motion with directions coming in random order.

The direction of MAE as a deviation toward or away from downward from the 180 degree expected value is presented in Figure 22. Perceived direction of MAE conformed closely to the 180 degree prediction. The variance accounted for by a line based on the 180 degree prediction accounted for 88 percent of the total variance in the directional judgements. Thus, both duration and directional measures indicate that MAE is isotropic, comparable in all directions.

Figure 22: Deviation of direction of motion aftereffect from the expected value of 180 degrees from adaptation direction as a function of the direction of the adapting motion. Each point represents 10 observations with one observer (W.Mk.).



DEVIATION OF MAE FROM VECTOR PREDICTION

Experiment 8b: Summation of directions in the aftereffect of bidirectional motion.

The purpose of this experiment is to see if MAE components summate as predicted by the vector model and as suggested in the Riggs and Day (1980) findings. Summation of directions in motion aftereffects have also been reported by Mather and Moulden (1980) which reflect on the present experiment. Discussion of this latter study will be reserved till later, since certain differences in outcome occurred.

The experiment was conducted in the following fashion. On each trial, the observer maintained fixation while viewing a bidirectional stimulus for 40 seconds. This adapting stimulus consisted of a total of 650 dots equally divided into two patterns, each moving in its own direction at 4 degrees per second. Contrast of the adapting patterns was .37. Immediately after the adapting interval, the dot patterns ceased moving and the contrast dropped to .15 or approximately half.

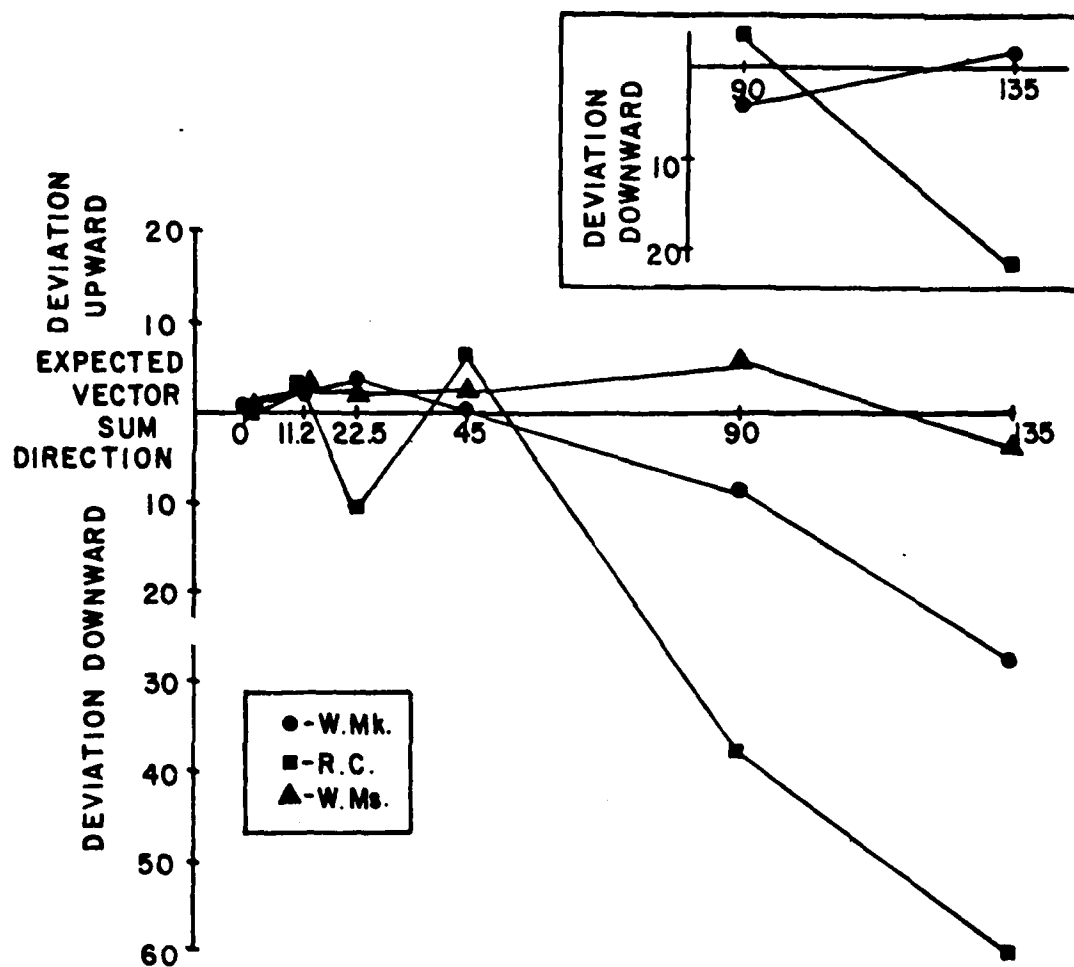
One component of the bidirectional adapting stimulus always moved at 90 degrees (upward motion); the second component moved at various directions greater or less than 90 degrees. The differences between the directions were either

0, 11, 22, 45, 90 or 135 degrees. Directions were randomly placed either side of upward and their order of presentation was also determined by chance. Adaptation was followed by a test stimulus, also of 650 dots that remained visible for five seconds. After this, the dot pattern disappeared and a pointer appeared on the screen, randomly oriented with uniform distribution over the range of 180 to 360 degrees. The observer used a potentiometer to rotate the pointer until it matched the direction of the perceived MAE. He then pressed a button to notify the computer of a satisfactory match between orientation and MAE direction.

All three observers, and several others who had seen the display, reported that a single direction of aftereffect results as a consequence of adapting with two directions of motion. It is as though the visual system resolves the dilemma of seeing a single test pattern move in two directions of aftereffect by summing the component directions.

The perceived direction of the motion aftereffect is shown as the deviation from that expected by a vector sum prediction for three observers in Figure 23. The conformity to prediction is quite good up to 45 degrees, where at the two wider angular separations two observers show a significant departure of perceived direction toward downward.

Figure 23: Deviations of direction of motion aftereffect from the expected vector sum of the individual component aftereffects of a bidirectional adapting stimuli with different angular separations. Insert is a rerun of the points for W.Mk and R.C. to counterbalance possible carryover effects.



All three observers noted that the speed and duration of the aftereffect at the larger angular separations to be less than at smaller separations. This observation, coupled with the fact that each stimulus contained upward motion, strongly suggested that adaptation from the vertical component of prior trials may be affecting directional summation of the weaker MAE that result from wide angular separations. Since each trial contained an upward moving motion component, the resulting adaptation could have accumulated resulting in a more powerful MAE in this direction. This would result in a deflection downward of the summed after-effects. The two wider adaptation angles of separation were run again with the two observers who experienced the apparent carry over effect adapting angles of 45 and 135 degrees for a 90 degree separation and 202 and 337 degrees for a 135 degree separation. This arrangement of adapting angles eliminated carry over effects by balancing them against one another. The direction of MAE was found to conform to the vector sum of the components under these conditions (insert, Figure 23). It is interesting to note that only two of the three subjects experienced this carry over effect. I cannot provide an explanation for this interesting individual difference.

Discussion:

Isotropism of direction perception, equal sensitivity to all directions of motion, is a prerequisite for the accurate summation of directions. The outcome of Experiment 8a is consistent with the isotropism of direction perception. Contradictory findings are reported by Mather (1980). Mather also tested isotropism using an adapting stimulus of random dots in which dots moved smoothly for 288 milliseconds, then disappeared to reappear in a random location and move again. This was done to prevent "permanent landmarks" (pattern) and prevent afterimages. Various directions were sequentially adapted and tested as in Experiment 8a and isotropism was not observed. Rather, greater aftereffects were observed for motion along the vertical orientation than for horizontal or oblique motion. Mather concludes that direction perception contains an anisotropy caused by reduced sensitivity of horizontal motion detectors, probably caused by the predominance of horizontal motion in the visual environment. These differences are difficult to reconcile, with only the differences in the nature of the display as a possible cause.

In that same paper, Mather reports observing the effects of the anisotropy in motion aftereffects after adapting with his form of bidirectional motion. Those deviations from the expected vector sum seem similar to the outcome of Experi-

ment 8b before the carry over effects were controlled. Mather used a vertical component in each adapting stimulus with only one minute between successive trials. When determining direction of aftereffect, he had observers watch until the aftereffect was no longer observed. This probably was not sufficient to prevent carry over between trials, since motion aftereffect is known to persist for long periods of time and to spontaneously recover (Masland, 1969). Thus, Mather's report of anisotropy in the summation of motion aftereffects was probably due to accumulation of effect from the repeated vertical motion component.

The observation that motion aftereffects sum, extends Wohlgenuth's (1911) observation that alternating, opposite directions of adapting motion create aftereffects that cancel. In my case, directional summation results from non-opposite adapting directions. The reduction of MAE with increasing angular separation which was noticed by the observers indicated some sort of cancellation occurs. Vector summation is the directional consequence of the combination of two non-opposite directions.

An attempt was made to isolate and perceive the component directions in the aftereffect as Riggs and Day (1980) were able to do with color contingency. Since color was not a controllable display parameter, distinctive spatial

arrangements of the dots were tried. In this attempt, dots moving in one direction were arranged in vertical oriented dot pairs or dipoles while dots moving in the second direction were members of a horizontally oriented dipoles. The test pattern contained only one kind of dipole. Summation of the aftereffects still occurred. Only small differences in the Fourier analysis of random dots and random dot dipoles could be discerned. Too few dipole pairs could be plotted to create a meaningful difference in the stimulus spectra. Apparently the spatial arrangement manipulation was not as effective in isolating component directions as the manipulation of color. An alternative explanation is that simultaneous adaptation of directions is not equivalent to sequential adaptation, and that component directions have no have a separate existence.

GENERAL DISCUSSION

Summary of Results

The contrast thresholds for moving and stationary dot patterns were measured by method of adjustment and signal detection theory using spatial and temporal criterion. Spatial and temporal thresholds were approximately the same, a result attributed to the low temporal frequencies of random dot patterns (Experiment 1). This common threshold was used as a reference for the contrast at which the accuracy of directionally sensitive mechanisms reach asymptotic performance. Increasing contrast beyond 1.7 times threshold failed to improve the accuracy of perceived direction of motion (Experiment 2). Accurate perception of direction is achieved at contrasts very close to the method of adjustment threshold.

At contrasts near threshold, two or more directions of motion could not be discriminated from one direction. Discrimination was impossible even when the direction differed by far greater than expected from the error data for perception of a single direction (Experiment 3a). This failure in discrimination reflects perceptual summation of the stimuli's component directions. According to the vector model, this summation is a consequence of attenuating the effects of lateral inhibition. A polydirectional stimulus

produces summation with even larger differences among the component directions. Such a stimulus contains a range of directions of net displacement. Bidirectional stimuli, which contain only two directions of net displacement, produce summation over a narrower range of differences between the component directions.

The accurate perception of motion requires only that two display frames be presented, the minimum needed to even produce apparent motion (Experiment 3b). This observation is important in several respects. First, the neural sharpening process postulated by the vector model must be very fast. Second, the perception of polydirectional motion involves integration of motion information over a wide range of temporal intervals. This explains why the observer of a polydirectional stimulus can perceive the two directions in which a dot may travel across two successive frames.

Discrimination of unidirectional from bidirectional stimuli becomes increasingly more difficult as fewer dots are in motion (Experiment 4a). Observers reported they could not discriminate one from multiple directions of motion because of reduced visibility of the dots. When the number of moving dots is reduced by a factor of 13, contrast threshold for the pattern increased by a factor of 2.4 (Experiment 4b). This elevation in threshold explains why

Levinson et al. (1980) observed directional summation at higher physical contrasts than I did.

There exists a reciprocal relationship between the occurrence of summation and repulsion in the various kinds of multidirectional stimuli. Polydirectional stimuli that enhance summation at low contrast, attenuate repulsion at high contrast. Conversely, bidirectional stimuli that show summation over narrower angular differences at low contrast enhance repulsion at high contrast (Experiments 3a and 5). The explanation for this reciprocity between summation and repulsion lies in the amount of inhibition postulated by the vector model. Large amounts of inhibition reduces summation and encourage repulsion. High contrast and bidirectional motion encourage inhibition. Low contrast and motion distributed over many directions reduce inhibition.

Other factors may also affect the formation of inhibition. Increasing the number of dots in the pattern results in more lateral inhibition and larger repulsion effects (Experiment 6). The finding that apparent repulsion of directions varies with velocity indicates that inhibition is dependent on the temporal frequency of the stimulus. Persistence of repulsion at high temporal frequencies suggests either that the low frequency components of these fast moving dots can still produce the inhibition responsible for

repulsion, or other aspects of the stimulus such as orientation of the near streak motion can also create inhibition.

The mechanisms responsible for motion aftereffect (MAE) were shown to be isotropic for duration and directional accuracy (Experiment 8a). This conflicts with findings of Mather and Moulden (1980). This discrepancy may be attributable to persistence of the aftereffect over successive trials and stimulus differences. Isotropy allows simple predictions to be made about the summation of aftereffects. The summation of two directions in aftereffect was shown to conform closely to predictions based on the vector sum of directions expected from separate component aftereffects (Experiment 8b).

Finally, there is a striking similarity between the summation of directions with apparent motion in Experiment 3a and with MAE in Experiment 8b. This does not prove that the same mechanisms underlie both phenomena. Weisstein (1969) has criticized the use of aftereffects as a vehicle for studying visual mechanisms because they allow numerous alternative explanations. However, the vector model provides a single structure to explain the perception of real and illusory motion. By assuming the same mechanism is responsible for both percepts, my model is further specified. The overall reasoning of the vector model will be

re-evaluated in the next section.

Review of the Vector Model

The vector model was proposed to explain the perception of directional information. The model consists of three distinct stages of processing (Figure 2). First, broadly tuned directionally sensitive units are stimulated by the moving target. Second, the spread of excitation is restricted by lateral inhibition, principally arising from motion sensitive units, which sharpens the neural response to motion. Additionally, this inhibition creates distinct zones of activity within the population of DS units limiting integration of directions so that distinct directions can be seen in bi- or polydirectional stimuli (see Figure 3). Third, the resulting distributions of excitation is processed by a decision mechanism that determines the direction of perceived motion.

A number of experiments were offered that presumably control the amount of inhibition generated by visual stimuli. Inhibition is reduced in the experiments of Part II and IV and summation of directions (demonstrated by the failure to discriminate two or more directions from one or summation of MAE) is observed. Inhibition was enhanced in Part III which resulted in a repulsion of perceived

directions. These findings are consistent with the vector model.

Two candidates for the decision process were proposed in the introduction of the vector model. One process was a identification of peaks of activation among the DS units; the other was a more elaborate, vector summation process. Both peak detection and vector summation can account for the results of the apparent motion experiments reported in Parts II and III. If the model is also applied to the motion aftereffect experiments, then a choice of decision mechanism can be made. A peak detecting process cannot account for aftereffects, because adaptation by a moving stimulus does not create a unique peak in the subsequent activity of DS units. Even if the arguments of Levinson and Sekuler (1975b) are accepted, and a rebound occurred in units sensitive to the opposite direction, the peaks in activity do not correspond to the direction of the single aftereffect resulting from bidirectional adapting motion!

The MAE experiments indicate a more involved process for deciding perceived direction: a process that integrates the activity of several directionally sensitive units. If vector summation is the decision process, the vector model can account for a wider variety of visual phenomenon.

Finally, a very similar theory to the vector model has recently been published by Mather and Moulden (Mather and Moulden, 1980; Mather, 1980). Until very recently (Moulden and Mather, 1979), these researchers had tried to uphold the ratio model of motion perception. Apparently based experiments similar to those I have performed, they have altered their stance. Moulden and Mather used a random dot stimulus that consisted of correlated successive frames, not the smooth motion reported in these experiments. With this stimulus, they observed the repulsion effect reported earlier by Marshak and Sekuler (1979) and the summation of motion aftereffects reported by Riggs and Day (1980) and also reported here.

These findings led Mather and Moulden to propose that motion perception resulted from an array of motion sensitive elements. Perceptual errors and motion aftereffects result from shifts in the distribution of activity within the array. This is basically the same as the vector model presented here. The difference between Mather and Moulden's model and mine is that I am much more explicit about how the modification of activity in the DS unit population takes place. The vector model describes in detail the interplay of excitation and inhibition which produces the final percept. Mather (1980) is vague about how this takes place.

That paper includes a vector diagram showing how directions of motion aftereffect combine, but offers no clue about the mechanism responsible for the combination. Neither does Mather consider the consequences of such a mechanism for the perception of real motion, other than to mention other papers which report distortions in direction perception. Although similar in basic logic, the vector model offers a more comprehensive treatment of how direction is perceived.

Related Research

Two recent reports relate to the present findings. Lennie (1980) has questioned whether distinct spatial and temporal thresholds exist. Recall in Part I that criterion differences in determining the threshold for moving dots was not large. Lennie has taken issue with other researchers (Rowe and Stone, 1977; Georgeson, 1976) that the X/Y distinction among retinal ganglion cells indicates distinctive processing of pattern and motion. Physiologically, the conduction velocities of the two classes of neurons were shown not to be different as it is often been supposed, eliminating the any difference for processing the two kinds of visual information.

Psychophysical experiments with humans, also presented by Lennie, show that spatial and temporal thresholds

converge when 1) sufficiently high temporal frequencies are used and 2) when a stringent criterion for determining spatial criterion (discrimination between gratings of different spatial frequency) are used. The findings in Experiment 1 add to this list that threshold differences may not be as great with random dot patterns as they are with gratings. This may be attributed to the distribution of energy within the spatial frequency spectrum of the dot patterns.

The observed characteristics of motion sensitive visual neurons are consistent with the hypothetical units that are the basis for the vector model. Movshon (1980) has recorded the directional tuning function of complex cells in cat visual cortex. When stimulated with unidirectional moving random dot patterns, such cells responded to a broader range of directions than with gratings as the stimulus. Movshon attributed this broadened tuning function to the spatio-temporal characteristics of the random dot patterns (for review see Appendix 1). Pantle (1974) had already shown that temporal frequencies of visual stimuli were the crucial stimulus characteristic for stimulating motion sensitive mechanism. Since dot patterns have power in all orientations, Movshon argued that a range of temporal frequencies are generated at varying angular differences from the direction of motion. Moving dot patterns generate temporal fre-

quencies to which cells are sensitive in directions other than their direction of motion. When dots were moved at velocities higher than the cells optimum velocity, a strange bi-lobed tuning function was observed. This was again attributed to the distribution of temporal frequencies over directions observed with moving dots. At such high velocities, complex cells are most sensitive to temporal frequencies generated in other than the direction of motion. Since those optimum temporal frequencies can be found either side the direction of motion, a bi-lobed tuning function resulted.

Movshon also recorded the response of complex cells to bidirectional moving dot patterns. One pattern of dots was moved in the cell's optimum direction while another pattern was moved in similar directions. A powerful inhibition on the cell's normal response to the optimum stimulus was observed. The directionally tuning of this inhibition was similar to the excitatory tuning function, suggesting these were due to the same directionally tuned mechanism. This inhibition is strikingly similar to the inhibition postulated to be operating in the vector model's second stage.

While the polydirectional display was in development, I was not sure whether motion would be perceived under such dynamic conditions. The reason for this doubt was that such

motion superficially resembled dynamic visual noise and that the crossing of paths during each dots random walk would create confusion. Morgan and Ward (1980) measured the spatial and temporal boundaries for the perception of unidirectional motion in dynamic visual noise. They described spatial and temporal boundaries within which motion was perceived. The polydirectional motion employed in these experiments contained temporal separations of 32 milliseconds (the frame rate) and spatial separations of 5.86 minutes of arc (displacement associated with a velocity of 4 degrees per second) between successive plots of each dot. These values were well within the boundary conditions Morgan and Ward described for the perception of motion.

The spatial form or pattern of a moving stimulus may affect the preception of stimulus direction. The two dimensional Fourier spectrum of the stimulus determines, along with velocity, the temporal frequencies which are generated on the retina. The persistence of repulsion at high temporal frequencies has an alternative explanation that involves possible pattern influences on motion perception. Consider now several other reports of pattern effect on motion perception in the literature.

An unpublished study by Georgeson (personal communication) suggests a spatial influence on motion. The perceived

direction of a moving random dot pattern (unidirectional motion) was estimated when a square wave grating pattern was superimposed. At narrow angles between grating orientation and dot pattern direction, observers reported an attraction between the grating and motion's direction. At wider angular differences, the dots were repulsed away from the orientation of the grating. The attraction of the dots to the grating's orientation is similar to the summation of directions reported in Parts II and IV. The repulsion of the dots from the grating's orientation is much like the repulsions observed at high contrast in bidirectional dot motion in Part III. This indicates that spatial influences can intrude into the domain of motion perception.

In a second study, Georgeson (1976) reported a different kind of interaction between motion and pattern perception. He adapted observers to moving dot patterns and collected reports of pattern aftereffects. This result was attributed to inhibition between motion and pattern sensitive mechanisms. This observation suggests that pattern affects the perception of direction. But, Georgeson's interpretation has been criticized by MacKay and MacKay (1976) who provided an alternative explanation based on orientation sensitive mechanisms.

Two studies by Kulikowski (Kulikowski and MacCana, 1980; Kulikowski and Vidyasager, 1979) also demonstrate interactions between motion and pattern sensitive visual mechanisms. The first paper reports that perceived velocity is modified by adaptation to stationary gratings. Another finding was that adaptation to stationary gratings can reduce the threshold for perceiving motion. The latter report shows that contrast reversal changes the apparent spatial frequency of flickering gratings. A disinhibition of motion mechanism again reported by adapting the stationary patterns. These results generally support the idea of motion-pattern interactions.

The vector summation decision mechanism of the vector model would predict that if the range over which summation were not restricted, opposite directions of motion would cancel and a stationary stimulus would be perceived. This unique percept has actually been reported by Clarke (1977). Random dot patterns moving in opposite directions were shown in alternation to observers. At alternation rates of less than 12 hertz, observers reported seeing a single dot pattern moving first one direction and then reversing to go in the opposite direction. Above 40 hertz, two dot patterns were perceived to be moving in opposite directions. This is analogous to the percept of a bidirectional stimulus with

directions 180 degrees apart. At intermediate alternation rates (12 - 40 hertz) the stimulus appeared as dynamic visual noise; no single direction was seen. This breakdown in perception of motion was taken by Clarke as the result of a balance between oppositely tuned direction sensitive mechanisms and supportive of the ratio model. In the case of opposite directions, the vector and ratio model have similar predictions.

However, the vector model predicts a non-moving stimulus with other than opposite directions! Consider alternation of three dot patterns whose directions are separated by 120 degrees. A ratio model would predict 3 perceived directions, but a vector model would predict stationarity. It is unclear precisely how Clarke's displays circumvented the inhibitory separation of directions. However the observation of stationarity is certainly consistent with the vector model's predictions.

Future Applications and Extensions of the Dissertation

This dissertation has introduced a simple member of a large class of new visual stimuli allowing the directional content to be controlled and disassociated from pattern aspects of the moving stimulus. The polydirectional stimuli used in these experiments used a Gaussian distribution of

directions because of equal probability of the component directions. Other distributions of directions could be used to test the summation process further. I suggested earlier that a distribution of directions containing a notch could be used to distinguish between the peak and vector sum decision processes in the vector model. The dynamic dot motion used by Moulden and Mather (1980) has some advantages over the polydirectional motion because directions of frame by frame motion can be used without any net migration which is characteristic of polydirectional motion. Also, balance of directions in polydirectional stimuli could also be used to explore the phenomenon of stopping motion with moving dot patterns (Clarke, 1977). The potential usefulness of the varieties of multi-directional stimuli to study direction perception may be analogous to what the grating has been to the study of spatial vision.

Next, the vector model can be extended to stimulus dimensions other than direction in 2-space. The model could easily be extended to include motion in 3-space by postulating the existence of visual units sensitive to motion in depth. Evidence supporting the existence of units sensitive to depth has been reported psychophysically (Beverly and Regan, 1973) and physiologically (Regan, Beverly and Cynader, 1979). It would be interesting to see if the

phenomena of direction summation and repulsion were present in three dimensional motion.

Another dimension the vector model could potentially encompass is stimulus velocity. Vector length may be a convenient way to express velocity of real motion as well as the velocity and duration of MAE. Testable predictions about velocity or MAE duration can be derived from the density and direction of adapting stimulus motion. Observers reported in Experiment 8b that MAE from adapting stimuli whose directions were widely separated were weaker than MAEs produced by the combination of two similar directions. This is consistent with a vector length explanation of MAE velocity and duration.

Mather (1980) as conducted such motion aftereffect experiments, looking at aftereffect duration as a function of the angular separation of the adapting component directions. He found that duration fell off as a function of increasing angular separation. The relationship between directional separation of adapting motion and directional separation was not linear. Mather was able to explain this by assuming summation between the broadly tuned DS units, especially at small directional separations.

Finally, the vector model proposed in this dissertation

resembles several other theories of motion perception. For example, Johansson (1975) has theorized that motion perception is a vector analysis of directions which is based on projective geometry. The vector analysis portion of his theory utilizes summation and differentiation of angles based on the spatial interpretation of their motion. The implication that spatial characteristics of the stimulus may affect perception of motion (Experiment 7 and other studies) link Johansson's theory and the vector model. Inhibition would be the means of interaction between the two domains.

Johansson provides several demonstrations in which the direction of motion of several dots is interpreted as though they were points on a solid object. The percept seems influenced by the apparent spatial structure of the moving dots. If pattern can influence direction, as Georgeson (unpublished) has demonstrated, then spatial aspects of the stimulus (real or apparent) may act as sources of inhibition in the vector model to modify the perceived direction of the dot's motion. The common characteristics of Johansson's analysis of motion perception and the vector model demand further attention.

Another, more formal theory of direction perception that is related to the vector model, is Ullman's (1979) computational model for motion perception. Extending Marr's (1976)

computational descriptions of stationary patterns to the perception of patterns in motion, Ullman proposes that two fundamental interpretive processes operate in the spatio-temporal description of moving stimuli. The first process is the perception of spatial structure from motion information. An example of this is the percept of two distinct dot patterns in bidirectional moving stimuli. The identification of any dot with one pattern is because of its common motion characteristics. When motion stops, identity is lost. Ullman is less explicit about the second process, motion derived from structure. The various influences of pattern on motion may be what Ullman is referring to.

In conclusion, the vector model offers a flexible alternative explanation of the perception of motion than other current theories. The application of the vector model here has been confined to perception of direction in two dimensional motion. The model may be readily extended to three dimensional motion and to other motion parameters such as velocity. For these reasons, I believe the vector model will provide a useful impetus for further research in motion perception.

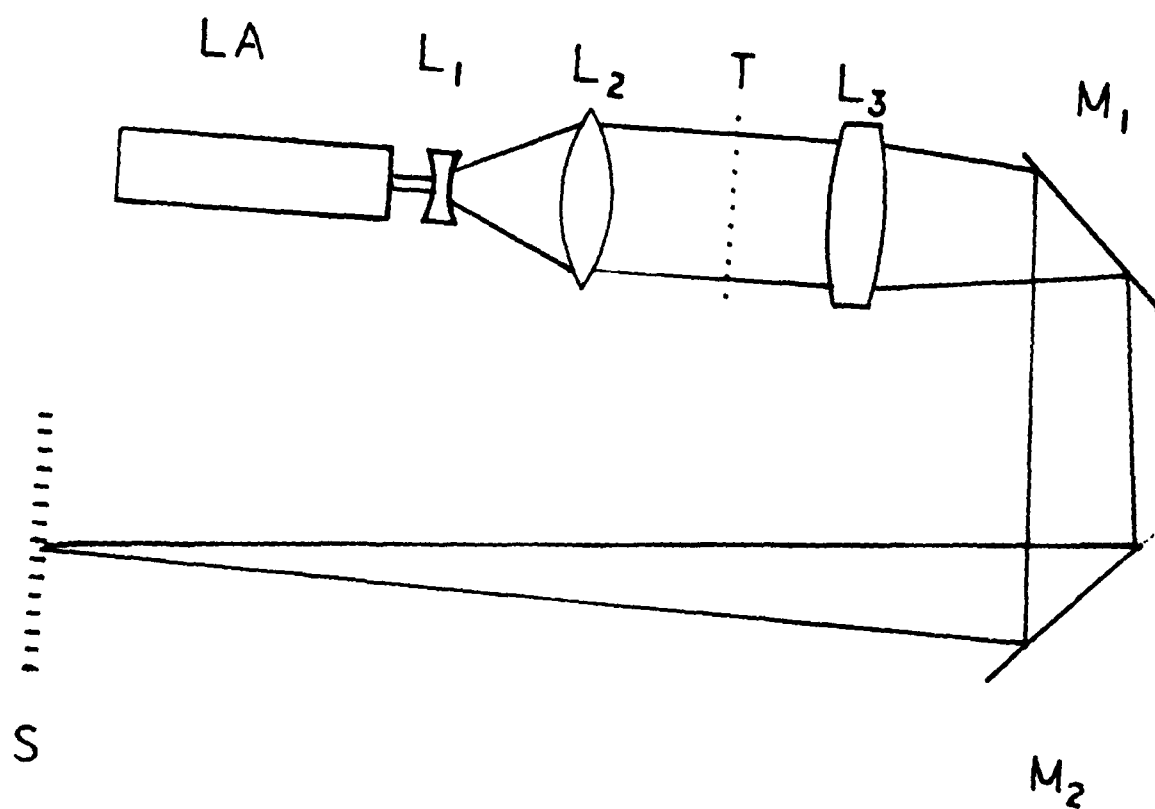
Appendix I

A Spatial and Temporal Description of Random Dot Stimuli

The spatial frequency content of random dot stimuli used in this dissertation was measured using an optical Fourier spatial frequency analyzer which was described in Lipson (1972). The general configuration of the analyzer is pictured in Figure 24. The beam of the 1/4 milliwatt laser LA was diverged by lens L1, and then collimated by lens L2 to increase the beam size. This enlarged beam was passed through a small positive transparency. The beam was brought back to convergence after reflection on mirrors M1 and M2 onto a semitransparent screen S.

This process projects on the screen the Fourier power spectrum of the stimulus. Small variations in contrast, focus and negative density modified the absolute energy which reached the screen. Because of this variation, all measurements were normalized for each target. Energy measurements were made from the rear from screen with the Gamma photometer. This instrument was not sensitive enough to measure small amounts of energy at high frequencies because of the low power of the laser. This limited normalization of energy to within the sensitive range of that instrument.

Figure 24: Diagram of the optical bench designed to measure the Fourier power spectrum of transparencies of the dot patterns. LA is a laser, L1 is a diverging lens; L2 is a collimating lens; T is the transparency whose spectrum is being measured; L3 is a converging lens; M1 and M2 are front surface mirrors; and S is a semitransparent screen.



Measurements were calibrated for spatial frequency using a high quality square wave grating. The frequency of the grating was obtained relative to the dot patterns by using an eye loupe to count the number of cycles of the grating occurred within the diameter of the screen image. This was 11 cycles per screen diameter. Since the mask was 8 degrees of visual angle in diameter, the grating was 1.38 cycles per degree. When the square wave was inserted at T in the optical bench, its power spectrum was projected on the screen. The Fourier spectrum of a square wave is the infinite series

$$F = f + (1/3 * 3f) + (1/5 * 5f) + (1/7 * 7f) + \dots$$

which in the power spectrum is represented as a series of blips of energy at the odd harmonics of F. Since the fundamental frequency of the grating was estimated to be 1.38 cycles per degree, the blips served as landmarks identifying frequencies of 1.38, 4.14, 6.90 ... cycles per degree.

The accuracy of the photometer measurements were calibrated by measuring the energy in the square wave grating. Square roots of the photometer readings were taken to convert them from power to amplitude measurements. These amplitude measurements were summed over the sensitive range of the photometer and the percent of the total amplitude was computed, a kind of relative amplitude. The theoretic rela-

tive amplitude up to 20 cycles per degree was computed for the square wave spectrum and is plotted with the observed relative amplitudes in Figure 25. Agreement was generally good.

Using the screen positions for the square wave components as spatial references, a random dot target of 550 dots (Figure 26) was placed in the optical bench and its Fourier spectrum was recorded photographically (Figure 27a). In order to see the effects of density on the power spectrum, another random dot pattern with approximately half the number of dots (200) was also analyzed (Figure 27b). Energy of both patterns was concentrated in the low spatial frequencies (center) with spattering of energy at higher frequencies (not shown in the photo). Energy is approximately uniform in all orientations, and the range of the central energy is approximately the same. However, the lower density pattern seems to have a larger proportion of energy in the very low frequencies (in the center).

This observation is substantiated by the relative amplitudes of frequency components presented in Figure 28. Measurements were made by scanning a horizontal slice starting at center (D.C.) and moving outward at intervals of .23 cycles per degree. The 550 dot pattern has about 40 percent of its amplitude below 1 cycle per degree, but the 200 dot

Figure 25: The theoretic and measured relative amplitude of a square wave grating up to the sixth harmonic frequency.

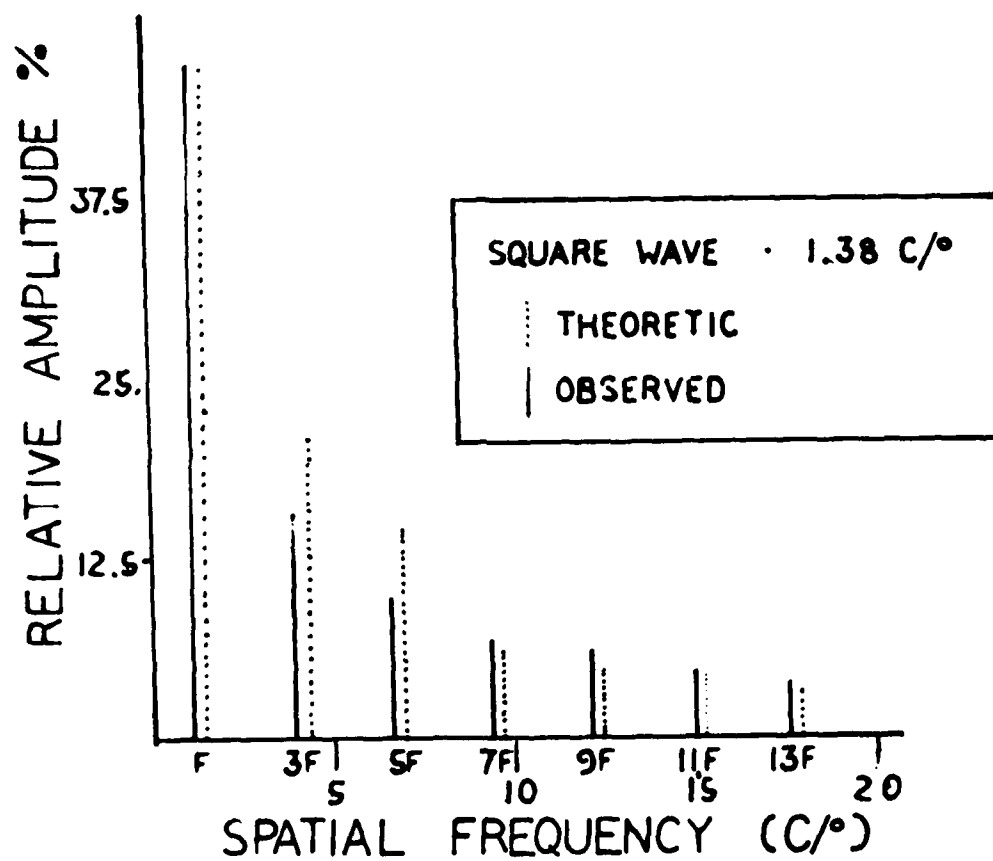


Figure 26: Photo of a 550 dot pattern whose arrangement is random except for the constraint that no two dots overlap.



Figure 27: Fourier power spectrum for a random dot pattern containing 550 dots (A) and 200 dots (B).

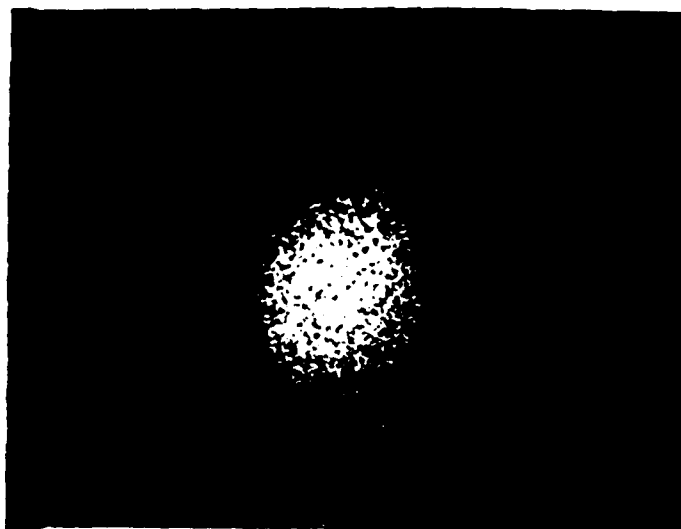
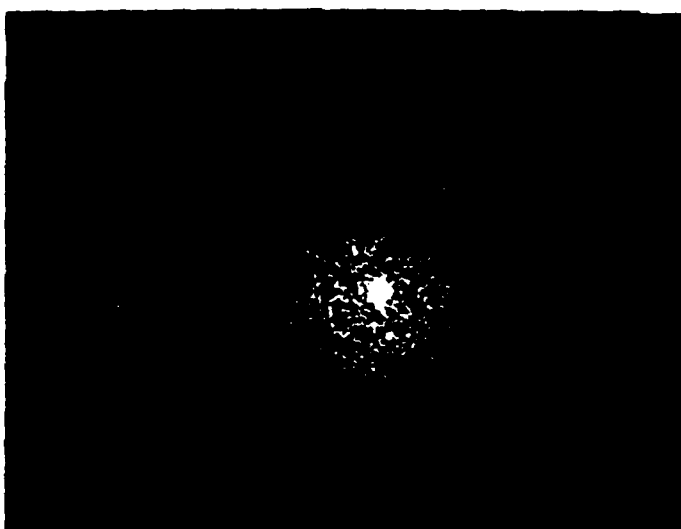
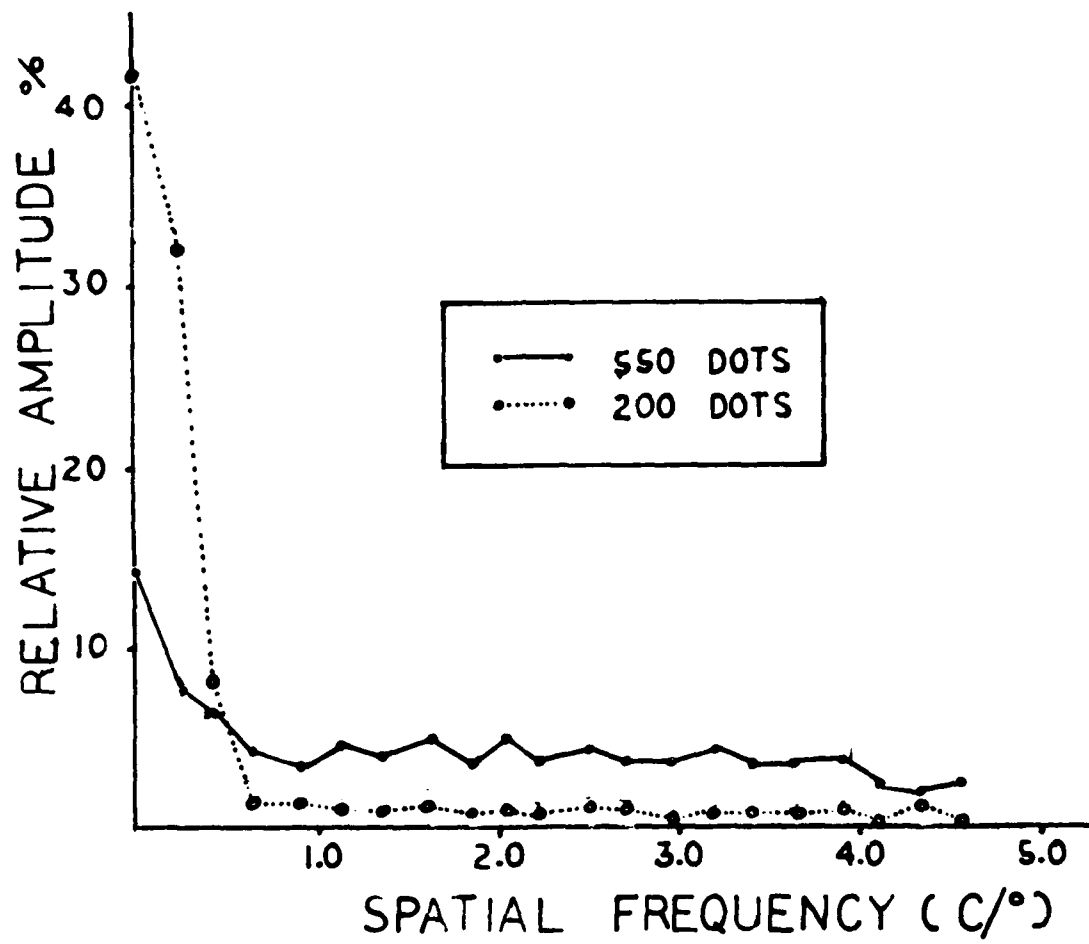
**A****B**

Figure 28: Relative amplitude of energy as a function of spatial frequency for random dot patterns containing 550 and 200 dots.



pattern has 86 percent of its energy below 1 cycle per degree.

Motion of these low frequency stimuli will result in very low temporal frequencies. At a velocity of 4 degrees per second, one used in many experiments of this dissertation, the temporal frequencies will be primarily below 4 hertz. Some caution is necessary in evaluating the effectiveness of these temporal frequencies compared to say, gratings. Only a small portion of the random dot pattern's total energy lies along the axis of motion, unlike the grating which contains all its energy along the axis of motion. The remaining energy is in all other orientations and although they do contribute to the temporal frequencies, the frequency is reduced by a cosine function with their orientation's angular difference from the direction of motion (Movshon, 1980).

The temporal frequency contribution of stimulus onset and offset was analyzed for both the ramped and edge onset of contrast in Table I. The contrast profile as a function of time was analyzed by a program written by Sekuler (personal communication) and adapted by me to run on a TRS-80 microcomputer. The program describes the frequency content as a Fourier series. Ramped onset and offset eliminates significant temporal components above 2 hertz, while edge

Table I

Temporal Frequencies from Onset and Offset
of Stimuli

- Freq (Hz)	RAMPED ON/OFFSET		EDGE ON/OFFSET	
	Sine	Cosine	Sine	Cosine
1	0	-6.3	0	-10.21
2	0	-2.81	0	0
3	0	-.40	0	3.46
4	0	0	0	0
5	0	-.35	0	-2.15
6	0	-.29	0	0
7	0	0	0	1.62
8	0	0	0	0
9	0	-.14	0	-1.35
10	0	-.08	0	0
11	0	.05	0	1.21
12	0	0	0	0
13	0	-.08	0	-1.15
14	0	0	0	0

onset has larger components at much higher temporal frequencies.

FOOTNOTES

1. In their paper, Marshak and Sekuler (1979) discounted the possible explanation that their results were due to eye movements because of a control procedure. Small afterimages were produced on the retina with a electronic flash to make an observer aware of the fixation point. Experience enabled the observer to resist the tendency to follow the dots and to hold a fixation point for one second presentation of stimuli such as the ones used in this dissertation.

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