Opponent Processes in Human Motion Perception: Shear and Compression Sensitivity, Induced Motion and Motion Capture.

A Thesis submitted for the degree of
Doctor of Philosophy

by

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Abstract

Sensitivity to differential motion components, shearing and compressive (opposed) motion, was examined. The hypothesis that the visual system contains local mechanisms specifically sensitive to these types of motion was tested. Stimuli consisted of two moving sinusoidal gratings. Sensitivity to shear and compression was compared with sensitivity for linear motion. Lower thresholds of motion and contrast sensitivities were obtained. Subjects were more sensitive to opposed than to non-opposed motion for a range of grating orientations and different grating spatial frequencies. However sensitivity for opposed motion decreased in the presence of a second added linear motion. The hypothesis of local shear and compression mechanisms was rejected in favour of antagonistic (opponent) interactions between local motion mechanisms.

Motion capture was examined. Stimuli were made up of a circular test grating surrounded by another grating. Subjects were required to judge the direction of motion of the test grating. Experiments examined the effects on motion capture of: centre grating size; orientation of surround; relative contrast of centre and surround; plaids in the surround. Conditions favouring motion capture were: with the smallest centre grating; with surround and centre orientations within thirty degrees; with surround had higher contrast than the centre; and only when a plaid surround contained a component of similar orientation as the centre. For conditions of motion capture relative to those of no-capture, increased velocity thresholds for judging the centre direction were found. This was associated with a shift in the bias point between opposed directions with no change in overall sensitivity to motion.

It is suggested that a cooperative network of local motion mechanisms featuring centre-surround opponency can account for all the results of this study.

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Chapter 1

1.1 General

The study has two parts. The first part was particularly concerned with the analysis of retinal flow fields by the visual system. The nature of the retinal flow field depends upon the optic flow field. The optic flow field is the changing pattern of light intensities, in different visual directions, about any observation point in space, as an observer or objects in the environment move. The Optic Flow Field is sampled by both eyes, giving rise to changing patterns of retinal stimulation. The retinal flow field is the changing pattern of light on the retina (Gibson 1950). The retinal flow field contains much information which is useful to the observer in trying to understand the structure of his environment and his position in it (Gibson 1950). For example, from an analysis of the information contained in the retinal flow field the observer is able to specify distances to objects, three dimensional shapes of stationary objects, the time to contacting an object, his direction of self motion and the structure and motion of a moving object. It is however not known how the visual system analyses retinal flows. It has been shown that when a retinal flow field is considered as a vector field, such that every point in the instantaneous retinal image is specified by a direction and a speed, (Longuet-Higgins and Prandzy 1980, Koenderink and Van-Doorn 1975, Koenderink, 1985) a global retinal flow field can be analysed (using vector calculus) into a set of independent local motion components vectors (differential motion vectors), namely a translation, an expansion/contraction (divergence), a rigid rotation (curl) and a deformation (shear and compression; see figure 1). Further, that once the components of retinal flow have been analysed, useful aspects of the flow can be computed e.g. the separation of self motion from motion of objects in the environment (Longuet-Higgins and Prandzy 1980). In the light of this work it has been hypothesised by some authors (Regan 1986, Koenderink 1985) that one way in which the visual system may obtain information from retinal flows is by analyzing them into their differential flow field components. That is the visual system analyses the retinal flow field by carrying out a process approximating a vector analysis of the flow field, obtaining local estimates of the various first order differential components of the flow. According to Regan (1986) this may be done via visual mechanisms specifically sensitive to the components of retinal flows. The experiments of part one were concerned with testing this hypothesis for the two components of deformation, shear and compression. From these experiments the aim was to produce a model of how shear and compressive motions are processed by the visual system.

The question as to how the observer analyses retinal flow fields is interesting when one considers the input to the visual system. The observer is frequently confronted with a changing pattern of light from which he or she requires to make

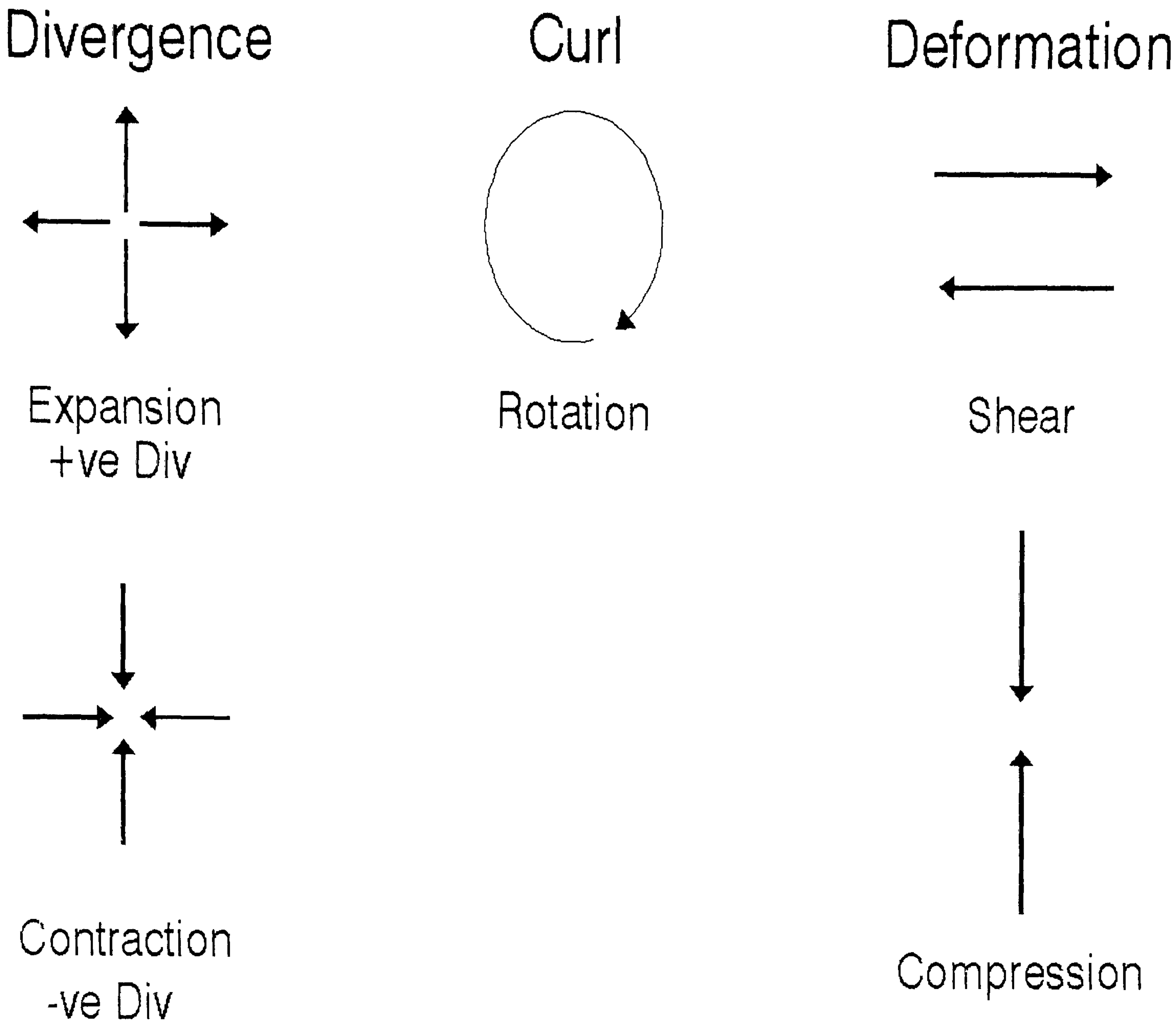


Figure 1: Differential motion components of optic flow fields.

judgements. Relative motion between objects in the environment is a common natural motion type occurring for example when an object moves relative to a stationary background, and shear and compression are both forms of relative motion. An understanding of how the visual system processes this type of motion would therefore be very useful in trying to understand how humans as observers perceive their environment.

The second part of the study was concerned with an examination of illusory motion, specifically motion capture (eg Mackay, 1961; Chang and Julesz, 1984; Ramachandran and Cavanagh, 1987) and induced motion (eg Porterfield, 1759; Dunker, 1938; Wade and Swanston, 1987). The aim of these experiments was to examine the stimulus conditions which favoured motion capture and those that favour induced motion. It was a further aim to test current models of motion capture and induced motion and to produce a model of these phenomena.

Motion capture and induced motion represent conditions where the perceived direction of motion of a stimulus is affected by motion in other parts of the visual field. Under certain conditions a moving stimulus in one part of the visual field may appear to move in the same direction as a moving stimulus in surrounding parts of the visual field when physically the motion is in the opposite direction to the surrounding motion (motion capture). Under other conditions the motion in one part of the visual field may appear to move in the opposite direction to surrounding motion when physically that motion is in the same direction as the surrounding motion (induced motion). The experience of motion capture and induced motion suggests that different motion signals in different parts of the visual field can interact with each other to alter the nature of the resultant motion percept (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993). As motion capture and induced motion give rise to very different perceptual effects, studying the conditions favouring these effects allows an assessment to be made of the ways in which these motion signals interact with each other across space and the conditions that favour particular types of interaction.

Opposed motion displays (motion in opposite directions in different parts of the visual field) were used in both parts of this study, hence the results from the two sets of experiments were directly comparable. It was of interest to see if there was any consistency between models generated to explain both induced motion/motion capture and shear/compression sensitivity.

1.2 Motion Sensitive Mechanisms

Throughout this study mention was made of local motion sensitive mechanisms. It is important at this stage to describe what is meant by this.

It should be noted that as far as this study is concerned the precise nature of the local motion mechanisms is unimportant. This is because in this study interest is focused on processes that occur after local motion signals have been detected. No argument will therefore be made in favour of any of the various local motion detection algorithms that have been proposed (eg Adelson and Bergen, 1985; Van Santen and Sperling, 1985; Watson and Ahumada, 1985). It is assumed that the visual system has the ability to detect local motion signals by what ever means.

The model of Adelson and Bergen (1985) will be described as an example of this general class of model. This is because this model is consistent with the known physiology of the visual system (eg. Adelson and Bergen, 1985; Snowden et al, 1991; Emerson et al, 1992) and with psychophysical results (eg. Snowden, 1989). Adelson and Bergen (1985) argue that moving stimuli may be represented as occupying a three dimensional space. This three dimensional space consists of two spatial dimensions, x and y and a third temporal dimension, t. Consider figure 2. Figure 2a shows a vertical bar moving towards the right. The three dimensional spatio-temporal representation of this motion (x-y-t space) is shown in figure 2b. Note how the bar slopes in the x-t plane. In figure 2c only the x-t dimensions are plotted. This is because there is no change in the y dimension i.e. the bar only has a horizontal motion (to the right) component and no vertical (y) component. In the x-t plot the moving bar is seen as a sloping strip. The direction of the slope of the strip represents the direction of motion of the bar and the magnitude of the slope represents the velocity of the bar i.e. velocity can be considered to be the gradient of the slope (distance travelled in the x dimension divided by the time taken to travel the distance). Figure 2d shows the x-t plot for the bar moving to the left. Note how the slope direction is negative compared to that of the rightward moving strip (figure 2c). Thus it is argued that motion can be considered to be analogous to an orientation in x-t (or x-y-t) space i.e. as a spatiotemporal orientation. Given that motion may be represented in this way, Adelson and Bergen (1985) argue that the problem of detecting motion is then how to detect spatiotemporal orientation. These authors state that this problem can be solved by the existence of cells which feature receptive field organisations that are oriented in both space and time. Thus such a cell (referred to as a spatiotemporal filter), dependent upon its spatiotemporal orientation, would have a preference for a particular direction of stimulus motion (this is shown in figure

Figure 2a: x-y plot of a moving bar

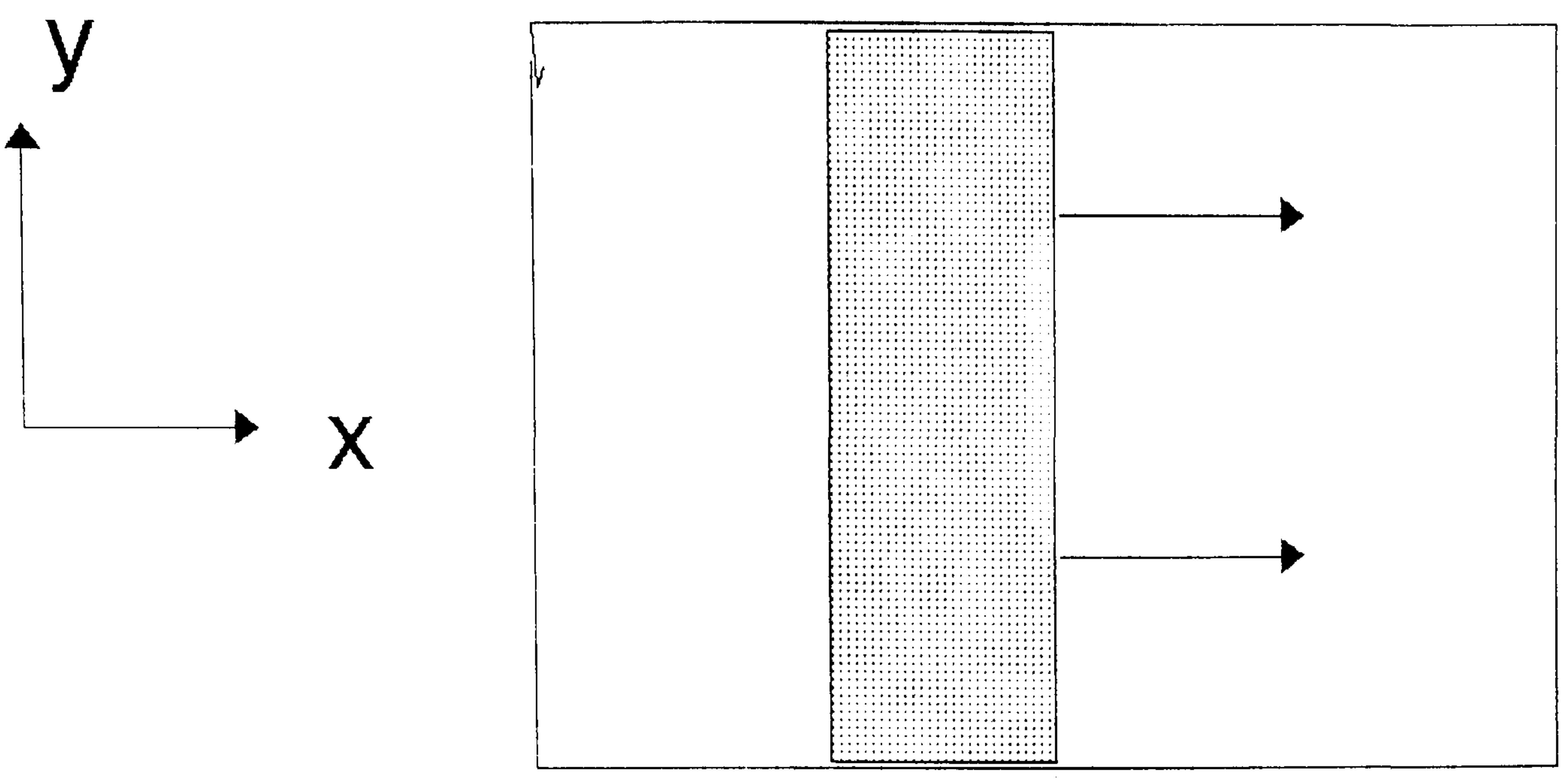


Figure 2b: x-y-t plot of a moving bar

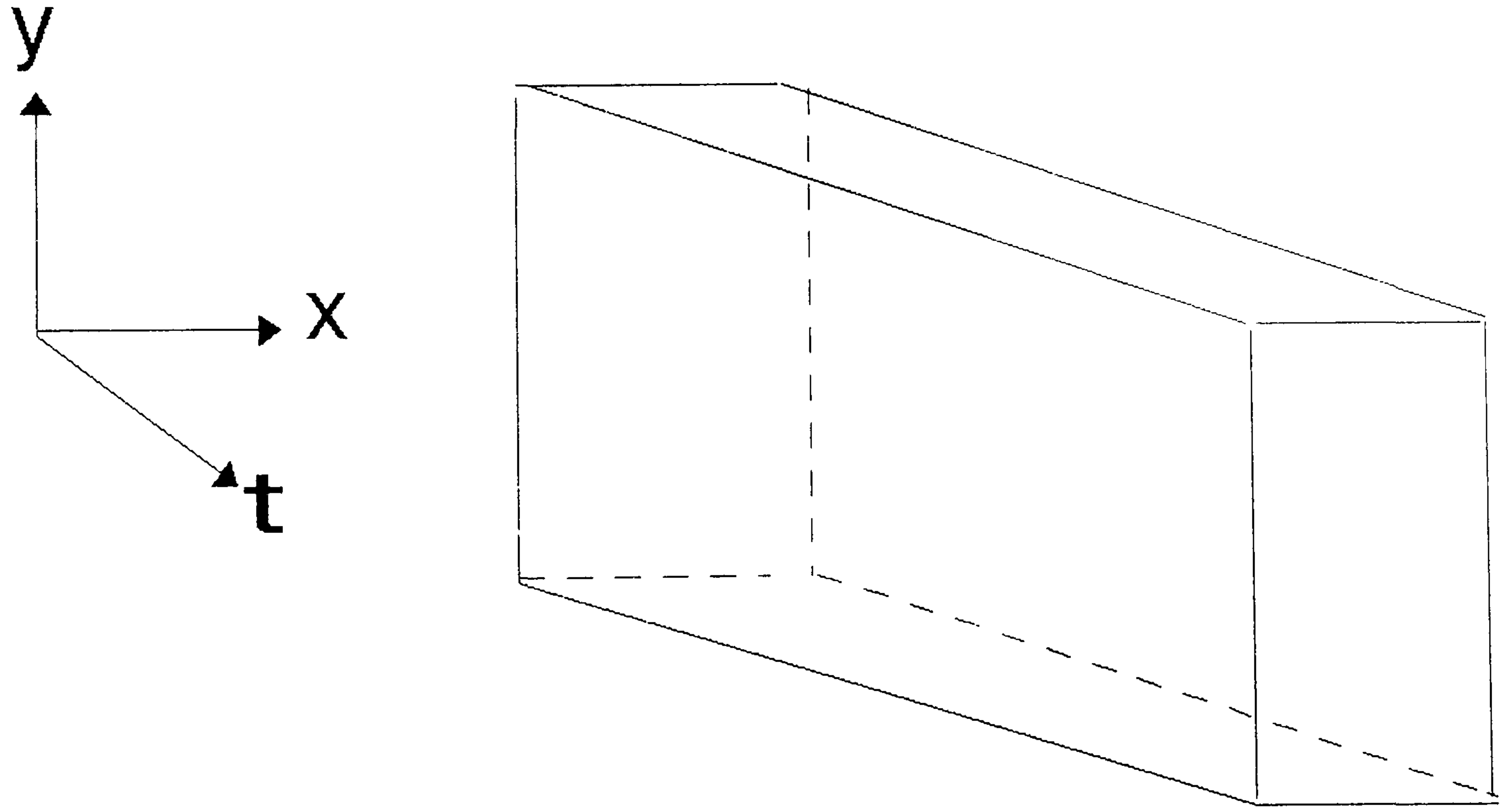


Figure 2c: x-t plot of rightward motion

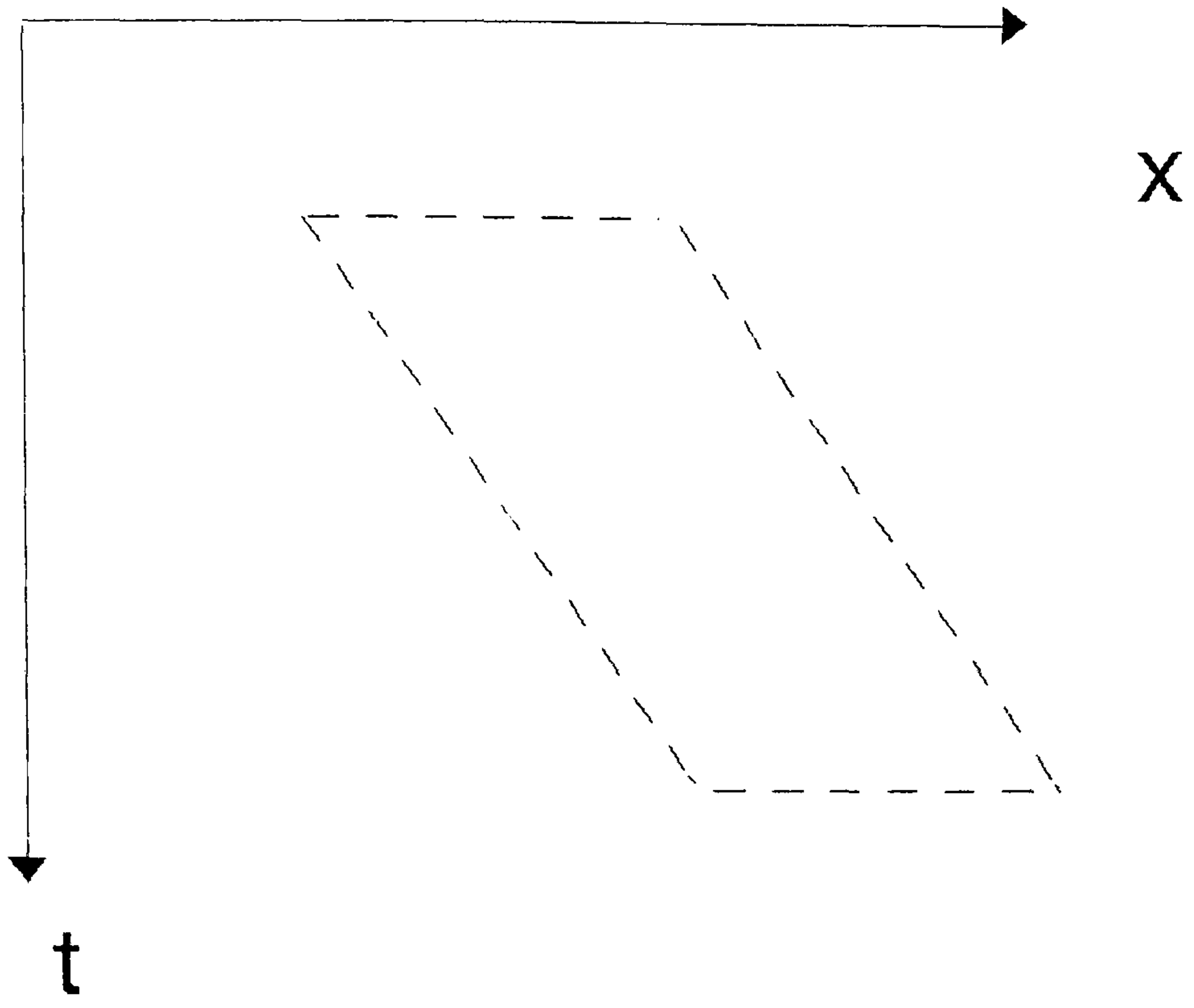


Figure 2d: x-t plot of leftward motion

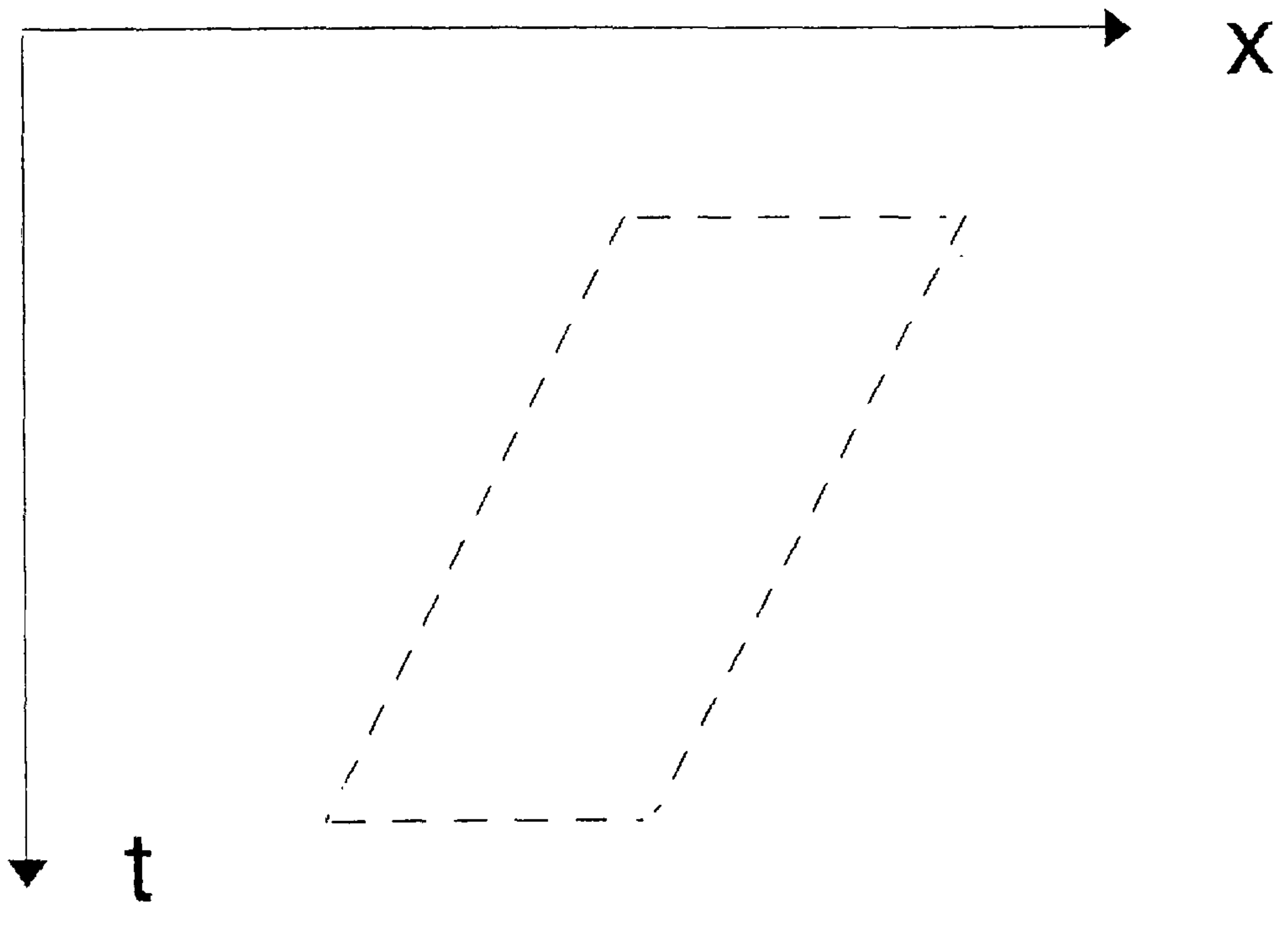
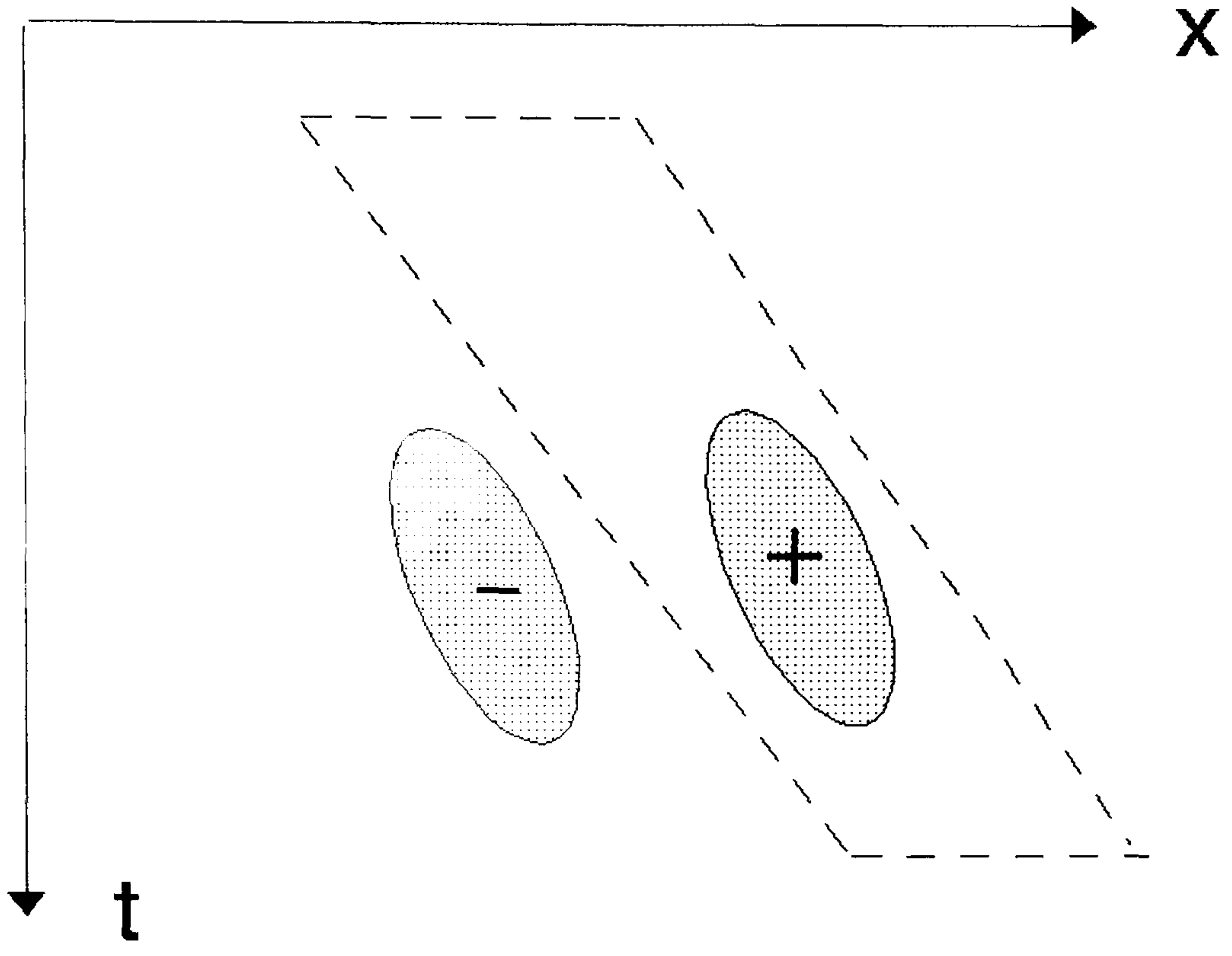
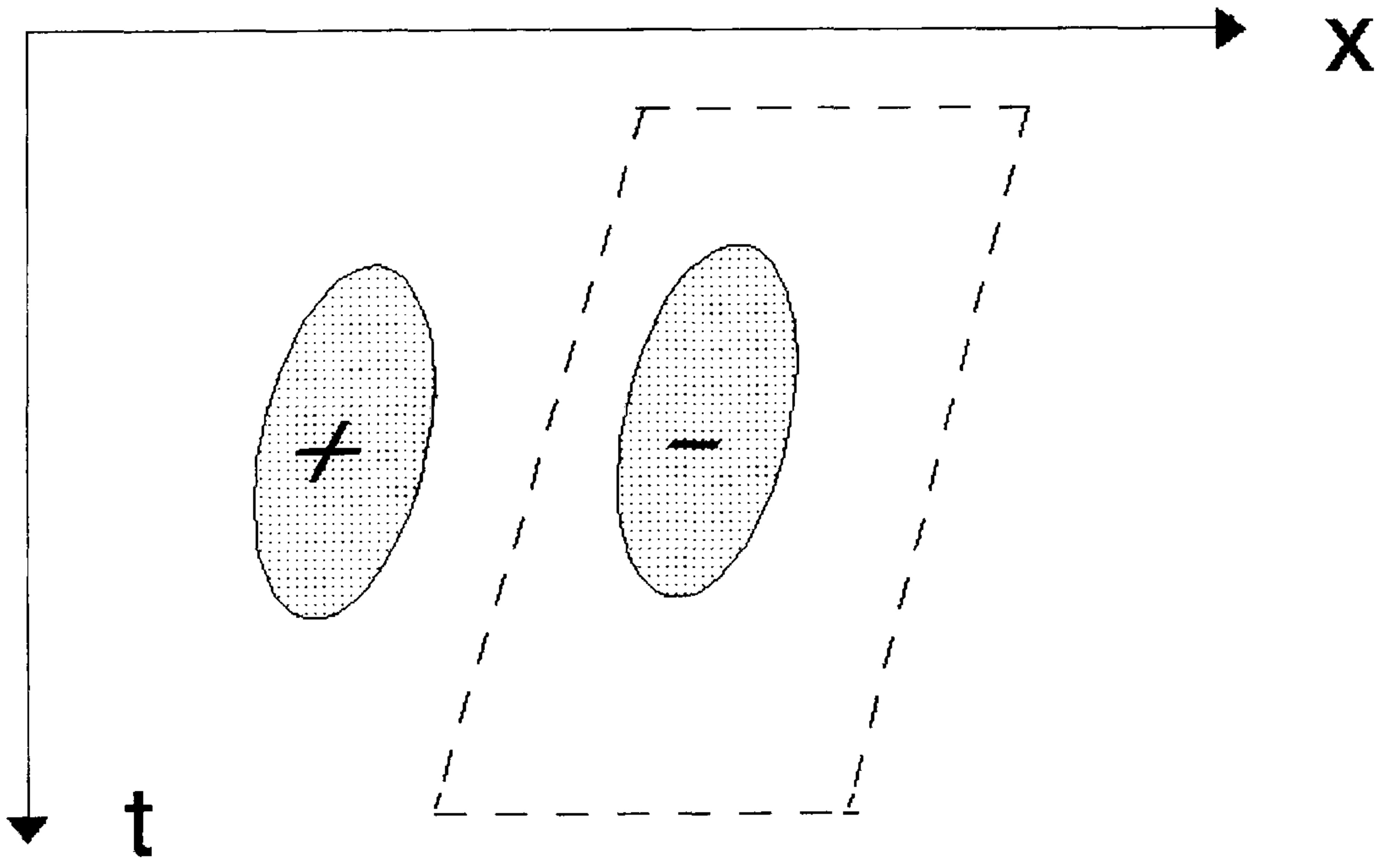


Figure 2e:

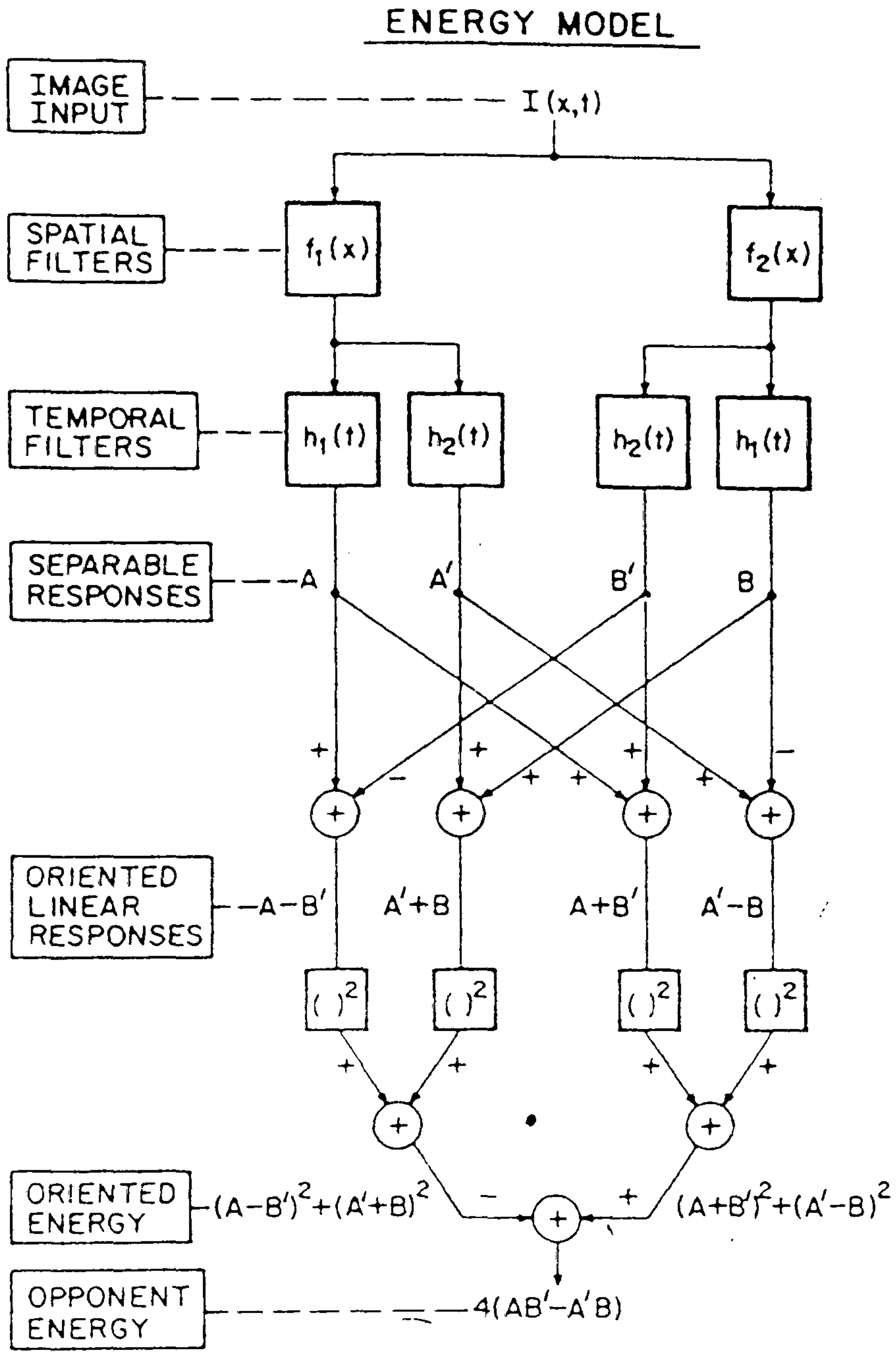


Right Sensitive Mechanism



Left Sensitive Mechanism

Figure 2f:Motion Energy Model (Adelson and Bergen, 1985)



2e). The first cell in figure 2e has a receptive field that is oriented so that motion to the right will excite the cell while leftward movement will inhibit it (excitatory, +, regions will be stimulated by movement to the right, while inhibitory,-, regions will be stimulated by leftward movement). The second cell of figure 2e is oriented so that motion to the left will maximally excite it. Adelson and Bergen propose that pairs of these spatiotemporal filters are connected, each sensitive to the same direction of motion but with sensitivities 90 degrees out of phase. Such arrangements are called energy detectors in the model. The outputs of these pairs of filters are then squared and summed, the results of which are then subjected to a compressive non-linearity. Leftward and rightward energy detectors are combined to produce opponent energy signals. The opponent energy is signed in response to the direction of motion of the stimulus, with opposite sign to opposite directions of local motion. The model can be seen formally represented in figure 2f. The spatial and temporal filters constitute the spatiotemporal filter part of the model. Pairs of spatiotemporal filters are connected and give rise to the 'oriented linear responses'. The oriented linear responses are then subject to squaring and summing to produce oriented spatiotemporal energy signals. The spatiotemporal energy signals are then combined to produce opponent energy signals. It may be noted that this model features opponency. It is important at this stage to distinguish the type of opponency described within this model and the type of opponency described later in this study. Within the model of Adelson and Bergen (1985) opponency refers to opponent processes between local sub-units which respond to motion in the same retinal location. In contrast, opponency as described in this study refers to opponency between motion sensitive mechanism across space i.e. between mechanisms responding to motion in different retinal locations. This distinction has recently been made by Raymond (1993).

Thus this model gives rise to a motion response that is localized in space, time and spatial frequency. The output of this model therefore gives information about the direction of motion within a given spatial frequency band at a given instant of time.

Part 1

Human Sensitivity to Shearing and Compressional Motion

Chapter 2

2.1 General Introduction to Part 1

The experiments of part one were concerned with how the visual system processes retinal flow components, particularly shear and compression. The aim was to test the hypothesis (Regan, 1986) that there does exist specific sensitivities in the visual system to shear and compression components of retinal flow fields. Previous research concerning sensitivity to shear and compression has been contradictory as to whether the visual system contains shear and compression specific mechanisms (see section 2.3). In attempt to resolve the disagreement between these previous studies and to introduce a new paradigm into the study of shear and compression sensitivity, the current set of experiments were carried out.

Some psychophysical evidence has been found to support the notion that the visual system is able to analyse a retinal flow field into it's components. Warren and Hannon (1990) examined the effect of pursuit eye movements upon the determination of heading. They noted that translation of an observer through a static environment generates an optic flow field in which the focus of outflow specifies the direction of motion. However on the retina, this flow pattern (retinal flow) contains not only translational changes due to the motion of the observer in the direction he is heading, but also rotational changes due to pursuit eye movements. Clearly in order to compute the direction of heading the visual system needs to separate the translational information from the rotational information. They found that in a structured three dimensional environment the visual system is able to decompose the retinal flow field into the two sets of components on the basis of flow field information alone. This was done without reference to multiple fixations or oculomotor information. This result indicates that an analysis of retinal flow based upon the detection of local retinal flow field components was carried out in order to compute the direction of self motion.

Given that the visual system is capable of analyzing retinal flows into their constituent components as Warren and Hannon (1990) indicate, it is interesting to ask how the visual system carries out this analysis. Regan (1986) has proposed that retinal flow fields may be analysed by mechanisms selectively responsive to the local components of retinal flow. Regan thus proposes that the visual system contains mechanisms (detectors) sensitive to local deformation, rotation, expansion/contraction and translation. Some psychophysical evidence has been reported for the existence of such mechanisms. For example evidence has been obtained for mechanisms selective for looming (Regan and Beverley, 1978; Freeman and Harris, 1992) and rotation (Regan and Beverley, 1984; Freeman and Harris, 1992). However the evidence for the existence of mechanisms selective for shearing and compressional motion is somewhat inconclusive, for example

Richards and Lieberman (1982) and Regan (1986) report data that is consistent with the presence of shear and compression specific mechanisms, while Van Doorn and Koenderink (1983); Nakayama (1981); and Braddick and Holliday (1991) report data inconsistent with the existence of such mechanisms.

Consider two objects moving side by side but at different velocities, this is a shearing motion and the resultant retinal flow field will contain a sizable shearing component. Similarly, consider motion parallax effects. Such effects will be observed when an observer is moving relative to a stationary background. An example of this is when an observer looks out of the window of a moving train. In this case foreground objects appear to move in an opposite direction to background objects relative to the fixation point. Thus under these circumstances the retinal flow field will contain a sizable shearing motion component due to the differences in velocity between the moving object and its background. Clearly a sensitivity to shearing motion would greatly help in analyzing the retinal flow field produced by such motions. For example in the case of motion parallax, the detection of shearing motion could serve as a powerful clue to the effect that what was being observed was a motion relative to a stationary background.

A similar logic applies as regards examining sensitivity to compressive motions. As deformation is made up both of a shearing and compressive component sensitivity to compression is vital for the observer to correctly perceive the magnitude of deformation present in a retinal flow field.

2.2 What characterises Shearing and Compressive Motion ?

Shearing motion can be defined as follows (see figure 3a,3b and 3c). A pure

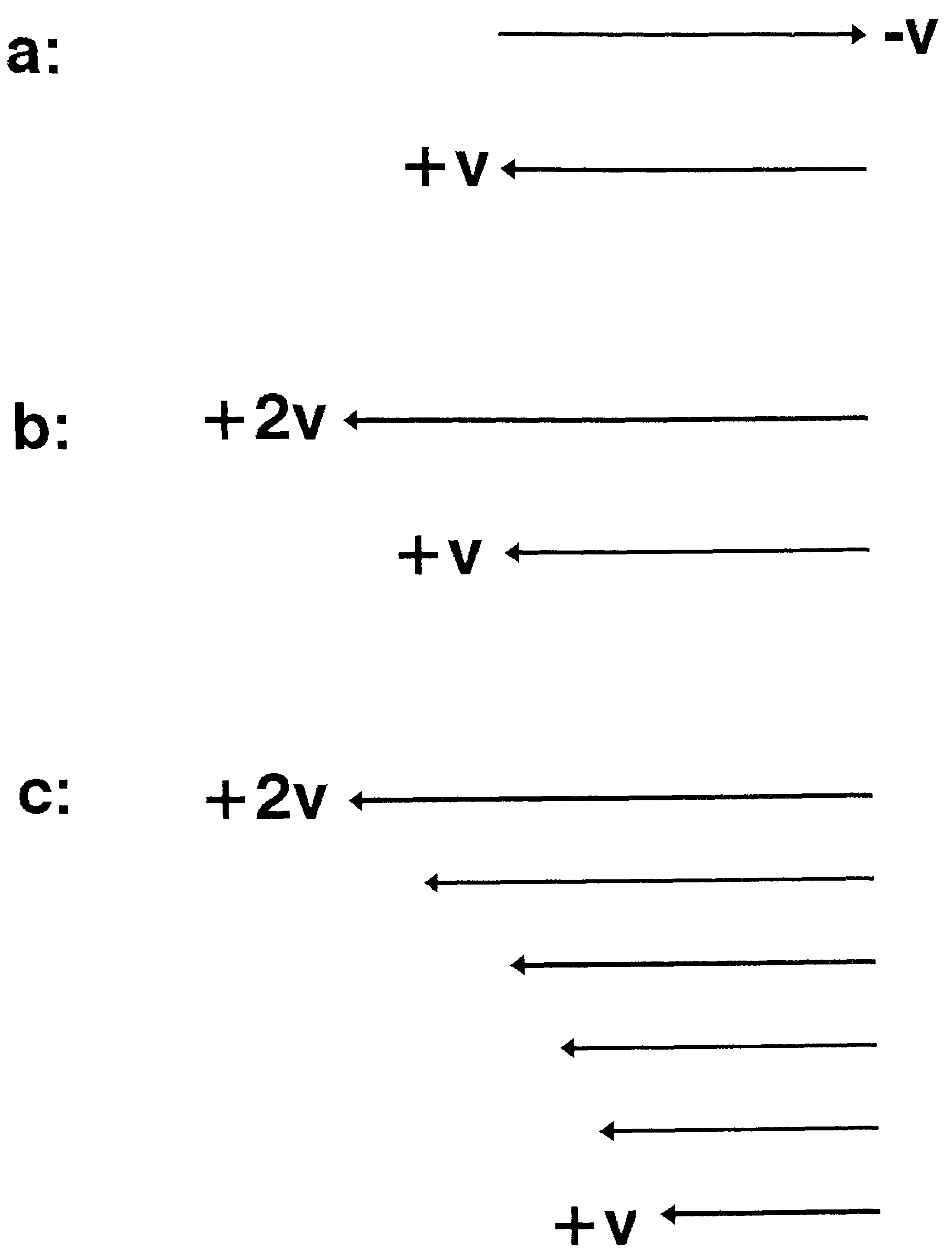


Figure 3: Three types of shearing motion. a) difference in direction of motion; b) difference in speed of motion; c) graded velocity.

shearing motion consists of a discontinuity in the retinal flow field such that the velocity varies perpendicularly to the direction of motion or equivalently velocity varies in a direction parallel to the boundary between two points. This can take the form of differences in direction of motion between two spatially separated locations (eg two oppositely moving gratings each moving with equal speed, one spatially above the other), in speed (eg two gratings one moving faster than the other in the same direction) or in some combination of the two. It is important to note that as well as conditions where only two different motion signals exist across space (as described above), shear is the dominant motion type in velocities that are graded across space. In such circumstances, local velocity varies continuously across space, essentially there are several different velocities within a region of space. Concerning this study, the existence of this type of motion was noted. However it was not considered in these experiments. Instead shearing displays were generated with only two different velocities. Such displays were used as this is similar to the retinal flow conditions that exist when an object, is observed to move with constant velocity, against a static background, by a static observer. The definition of shear used conforms to that of Regan (1986).

A compression (see figure 4a and 4b) is defined as a discontinuity in the retinal flow field such that the velocity across the field varies in a direction perpendicular to the boundary between two points in the field. This can take the form of differences in the direction of motion between two spatially separated points in the field, such that the motion directions are opposite to each other and moving towards each other (the type of compression used here). Similarly the speed of motion could vary across the flow field such that motion is in the same

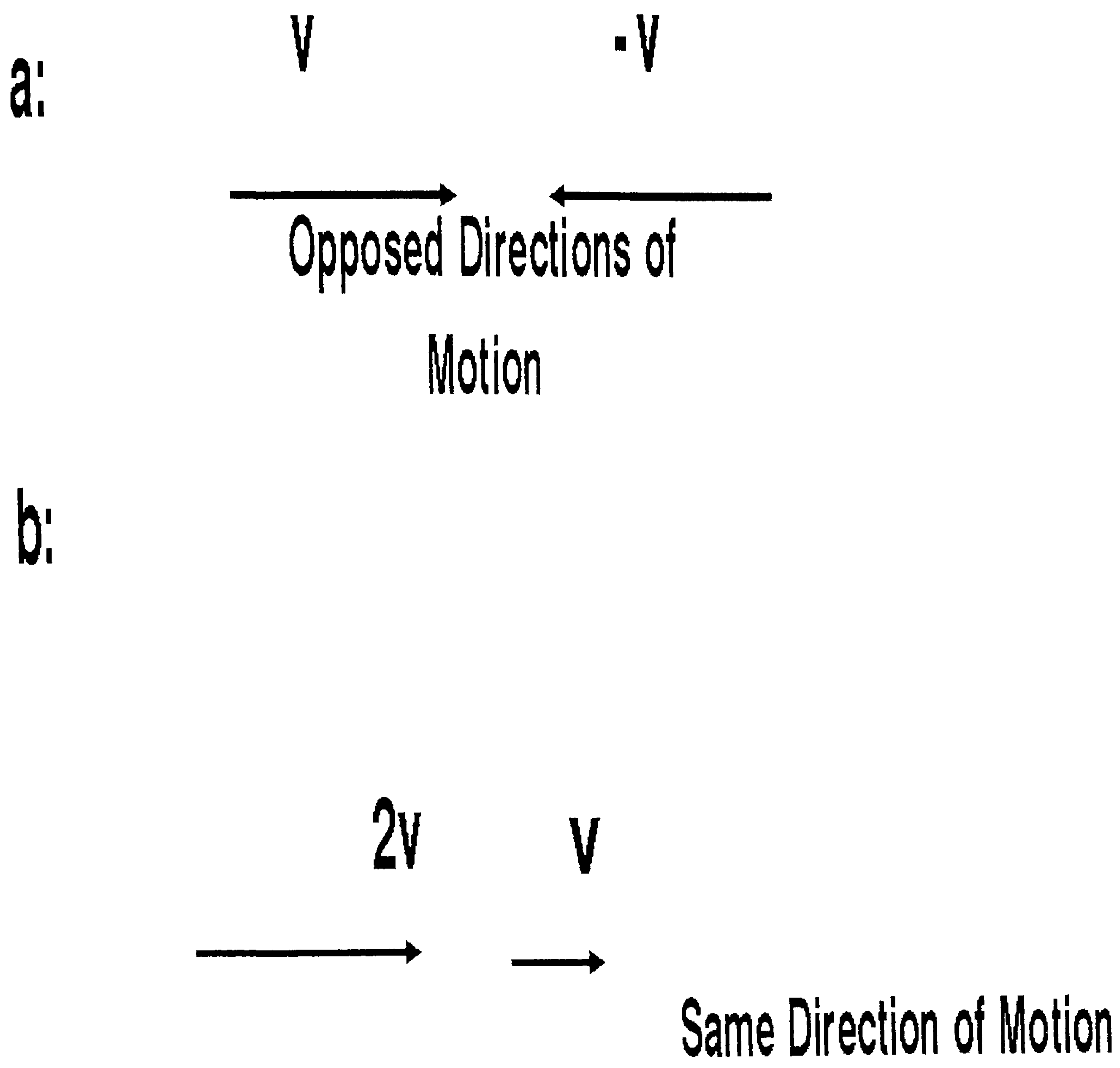


Figure 4: Two Types of Compression

direction across the field, but in one part of the field the speed of motion is faster than in an other part. In conditions where the directions of motion are opposite to and moving away from each other, there exists an expansion (a negative compression) in the flow field.

2.3 Previous Research on Shear and Compression Sensitivity

Most of the previous work on shearing and compression motion sensitivity has been concerned only with the respective detection thresholds for shearing and compressional motions; it has not compared responses to shearing or compressional motion with other types of image motion; and it has mostly used random dot stimuli as opposed to gratings. Much of this previous work, is also contradictory as to the existence of shear and compression specific mechanisms. Some results indicate differences in the way shear is processed compared with compression, while other studies indicate no difference in the sensitivities to shear and compression.

Richards and Lieberman (1982) presented random dot patterns to their subjects, which defined either a shearing boundary or an compressional boundary. They found that when the displays were presented to the parafovea of subjects, approximately 20% of their subjects could not locate the boundary in the shearing display type, but all subjects could locate the boundary in the compressional type display. This they took to indicate that there exist separate mechanisms processing shear and compressional motion. Regan (1986) measured detection threshold elevation for boundaries defined by shear and compression in a cross adaptation experiment. He found that the threshold elevation for detecting one boundary type (eg. shear) after adapting to the same boundary type was greater than the threshold elevation for adapting to the other boundary type (eg compression), however the threshold elevations were small in all conditions (approximately 44% post adaptation change). This Regan took to indicate that compression and shear boundaries are detected differently and is also consistent with what would be expected if the visual system contained mechanisms specifically sensitive to shear and compression.

In contrast to the above two studies the following studies produced little evidence for shear and/or compression specific mechanisms. Regan (1986) reported data from an experiment examining shearing detection thresholds using random dots. It was found that sensitivity to shear and compressional motion was equivalent with respect to velocity detection thresholds for all stimulus widths (widths of bars of moving random dots defining the motion types) and display presentation times. This result indicated that there is no difference in the way in which shear and compression are processed, and argues against specific shear sensitivities.

Van Doorn and Koenderink (1983) measured the sensitivity of observers to discontinuities in the motion of a field of random dots. The field of dots was split in half, different dot velocities were assigned to each half field. In their first experiment the dots in both fields moved in the same direction but with different speeds, the boundary between the two half fields was set to be either at right angles to (compression) or parallel to (shear) the difference in speed. There was no difference between the detection threshold results for both conditions, indicating that the orientation of the border between the two half fields was immaterial to the detection of the motion discontinuity. Thus there was no difference in the way in which the shear and compression boundaries were detected. This result is contrary to the result that would be expected for shear and compression sensitive mechanisms having different sensitivities. In their second experiment the dots moved with equal speed but in different directions. The stimuli were arranged so that the boarder between the two half fields lay along the bisectrix or perpendicular to the bisectrix of the two velocity directions. When the velocity difference lay along the bisectrix two possible conditions were used, convergence (the two velocities moving towards each other) and divergence (the two velocities moving away from each other). It was again found that the orientation of the border between the two half fields was of minor importance in determining the detection threshold of the velocity discontinuities (ie the shapes of the psychometric functions for all three conditions were equivalent). Instead they found that it was the direction difference between the moving patterns which determined the detection thresholds. (Interestingly when a shear type motion was presented it had the lowest detection threshold of all, the threshold being lower than that for pure divergence and pure convergence. This indicates that shear was processed differently to convergence and divergence and is therefore consistent with the sort of results that would be expected of a shear sensitive mechanism, although it does not give unequivocal support to the notion of shear detectors). Van Doorn and Koenderink suggested that from their results there was no evidence for velocity transient mechanisms (mechanisms sensitive to the components of retinal flow e.g. shear or compression).

Nakayama (1981) examined detection thresholds for horizontal shearing motion in the presence of common image motion. He found that the detection thresholds increased with the addition of common image motion such that common motion directions closest to the horizontal caused the greatest increase in detection threshold. This study argued against specific shear sensitive mechanisms. This is because one of the purposes of flow field component detectors is to separate different types of motion in the retinal flow field (in this case the added translational motion and the shearing motion). If there exist detectors for the particular retinal flow components, then it would be expected that the detection thresholds for shear would be invariant with added common motion, as in order for the detectors to adequately separate two different types of image motion the (shear) detectors should signal the presence of e.g. shear (which was still present in the display), irrespective of the added common motion. In this experiment this did not occur.

Braddick and Holliday (1991) carried out a study in which they examined the ability of subjects to detect the presence of deformation (shear and compression) within a moving display. Following from the work of Treisman (1988) it was predicted that if deformation specific mechanisms exist the time taken to detect a target which differed in sign of deformation from other elements in the display would be independent of the number of other elements in the display. This was predicted because the existence of such deformation specific mechanisms would give rise to a retinotropic feature map of the magnitude of deformation at any point in the display. A feature map of this sort could then be examined by a processes acting in parallel across the visual field which would mean that any target differing in magnitude or sign of deformation would appear to pop out of the display. In this experiment displays were set up which consisted of 3, 5 or 9 rectangular elements. The centre of each rectangle remained stationary. The aspect ration of each rectangle was varied going from a long horizontal rectangle through a square to a tall thin vertical rectangle. The target rectangle went through this sequence in the opposite direction to the other rectangles in the display, thus the target was a deformation of opposite sign to that of the other rectangles. In some trials the target was present and in others it was absent. The task of the subject was to report as quickly as possible if the display contained the target rectangle (one key press) or if the display did not contain the target (another key press). It was found that the time taken to detect the presence of the target was dependent upon the number of other elements in the display, increasing as the number of other elements increased. This was in contrast to the findings for a single line element undergoing the opposite direction of motion to the other line elements where the time to report the presence of the target was independent of the number of other elements. These results were therefore inconsistent with the notion of deformation specific detectors.

2.4 Introduction to the Methodology

Watson and Robson (1981) were interested in how an observer is able to distinguish one stimulus from another and proposed that this could be done by labelled detectors. When a labelled detector responds the observer is immediately able to distinguish the particular detectors response from that of any other. Labelled detectors signal not only the presence of a particular stimulus type but also what that stimulus is. This leads to the idea that if detectors for a particular stimulus type are labelled detectors then the observer should be able to discriminate two stimuli from each other at the same point/threshold at which he detected the presence of the stimuli. This idea of labelled detectors is particularly applicable to the study of specific sensitivities to retinal flow components. For example if there existed detectors specifically sensitive to shearing or compressional motions then one would expect that once a stimulus is detected the observer would be able to identify it as being a shear or compression, and would also be able to discriminate that stimulus from other type of motion.

In experiments 1 and 2 detection and discrimination contrast thresholds were obtained for shearing (experiments 1a and 2a) and compressive (experiments 1b and 2b) motions. In both experiments 1 and 2 the discrimination task involved discriminating the shear or compression from linear motion. In experiment 3 to 7 discrimination thresholds for shear and linear motions (experiments 3a,4a,5a,6a and 7a) and compression and linear (experiments 3b,4b,5b,6b and 7b) were examined for suprathreshold stimuli.

In each of the experiments sensitivity to shearing or compressive motion was compared to that for linear motion using sinusoidal grating displays. This enabled the comparison of shear or compression sensitivity with that for another type of motion rather than just comparing shear and compressional motion sensitivities as has been done in most previous experiments. Also this methodology introduced the use of sinusoidal gratings into tests of shearing and compression sensitivity.

Chapter 3: Do shear and compression mechanisms exist in the visual system ?

In this chapter three experiments will be reported which were concerned with testing for the existence of mechanisms with specific sensitivities to shearing and compressive motion in the human visual system.

3.1 Introduction

Experiments 1a and 1b: Contrast Sensitivity for Shear and Compression

Experiment 1a examined contrast detection and discrimination thresholds for shearing and linear type motion, while experiment 1b examined these thresholds for compression and linear motion, over a range of grating velocities. Following from Watson and Robson (1981) (see above) if there exists a specific sensitivity to shearing motion (shear detectors) or compressive motion (compression detectors) one would expect that the detection and discrimination thresholds would be equal in for the shear stimuli (experiment 1a) and the compression stimuli (experiment 1b). If no such equalities were found then evidence against the existence of specific mechanisms would have been obtained.

Experiment 2a and 2b: The effect of Added Common Image Motion upon Sensitivity to Shear and Compression

Experiment 2a examined contrast detection and discrimination thresholds for shearing and linear type motions and experiment 2b examined these thresholds for compression and linear motion in the presence of added common image motion of various velocities. If there exists a specific sensitivity to shearing and compressive motion then it would be expected that the detection and discrimination thresholds for shear and compression would be equal for all added common image motion velocities and these thresholds would be invariant with added common image motion i.e. thresholds should be unaffected by added common motion. If on the other hand the thresholds are increased (Nakayama 1981), then evidence against specific shearing or compressive mechanisms would be obtained.

Experiment 3a and 3b: Shear and Compression Sensitivity at Suprathreshold Contrasts

Experiment 3a examined velocity discrimination thresholds for shearing and linear type motion, and experiment 3b examined velocity discrimination thresholds for compression and linear motion, at suprathreshold contrasts over a range of grating spatial frequencies. Discriminations were made between moving stimuli and stationary stimuli, as well as between moving stimuli (experiment 3a: shear or linear/ experiment 3b: compression or linear).

If there exists specific sensitivity to shearing or compressive motion then it would be expected that the thresholds for discriminating a moving stimulus (shear or compression) from linear or a stationary stimulus stationary should be equal. This due to the fact that with such a specific sensitivity to shear or compression, as soon as a stimuli is perceived as moving then the stimulus type would be known.

3.2 Methods: Experiments 1 to 3

Apparatus

Patterns were generated for all three experiments by an Innisfree Picasso under microcomputer control, from a CED 1708 interface. They were displayed on a Tektronix 608 monitor with a P31 phosphor. Each frame in the display could be specified independently. The frame rate was 202 Hz. Responses were obtained using a two button response key.

Experimental Displays

The basic display for all 3 experiments consisted of 2 vertical sine wave gratings displayed on the viewing screen. For all experiments the gratings filled the screen from left to right, each grating covered an equal area of the screen. The display subtended a visual angle of 1.9 deg at the viewing distance of 300 cms that was kept constant for all experiments. The drift rate of each grating was used to define the velocities of the gratings for all three experiments (in experiment 3 it was the dependent variable), this was controlled via phase control giving 7 bit resolution of spatial phase per frame.

The starting phase of each grating was randomised from trial to trial to prevent the use of vernier cues in detecting and discriminating the gratings. In each of the moving displays used, the velocity of each grating was equal. Differences existed between the shear and compressive displays. These will be detailed below.

Displays for Experiments 1a, 2a and 3a

In the case of experiments concerned with shear sensitivity (experiments 1a, 2a and 3a) the two gratings were displayed one vertically above the other separated from each other by a vertical distance of 0.8 cm. The on-screen distance was used so as to eliminate any effects of vernier cues. Vernier acuity is known to diminish over distance (Westheimer and Mckee, 1975). Had the gratings been generated so that they were in contact with each other it may have been possible to use vernier cues to identify the presence of an offset in the relative positions of the two gratings far more readily than with a gap between the two gratings.

Shear displays consisted of the two gratings moving with equal velocities but in opposite directions, linear displays consisted of the gratings moving in the same direction with equal velocities (see figure 5).

The directions of motion of the gratings were varied from trial to trial such that for shear one grating could move left or right in each trial (the other grating moving in the corresponding direction to preserve the shear) and likewise for the linear motion the gratings could move both left or right randomly from trial to trial.

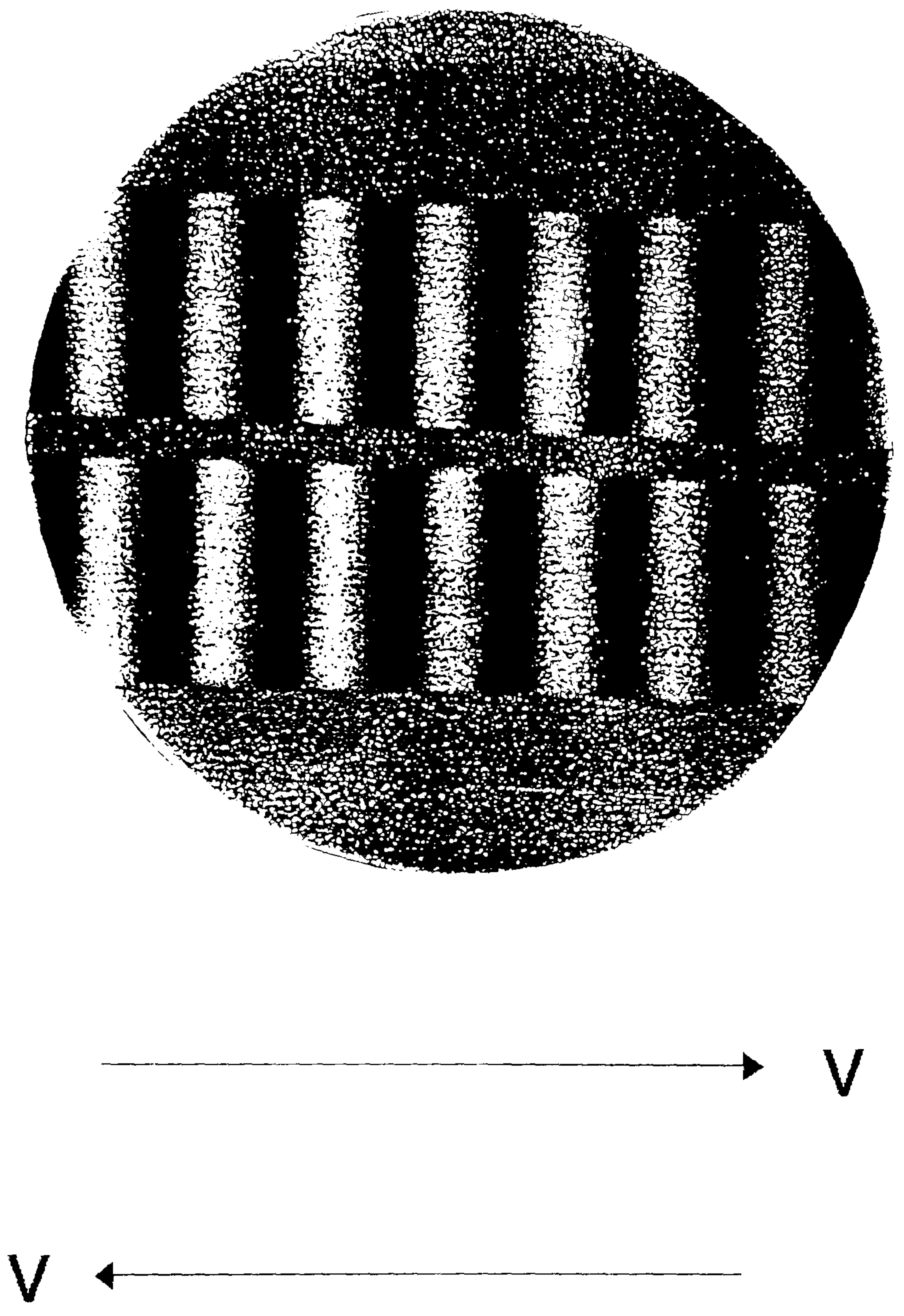


Figure 5:Basic Shear Display

Displays for Experiments 1b, 2b and 3b

In the case of the experiments concerned with compression sensitivity (experiments 1b, 2b and 3b) the two gratings were displayed next to each other, one to the left and one to the right of the display and were separated by an horizontal distance of 0.8 cm (see figure 6). The windows were displayed so that the actual area of the screen covered by the display was equal to that for the shearing displays of experiments 1a, 2a and 3a. In experiments 1b, 2b and 3b four types of display were defined. Compressive, expanding and linear moving displays and a stationary display. The Compressive display consisted of two gratings moving in opposite directions of motion, towards each other. The expanding display consisted of the two gratings moving in opposite directions away from each other. The linear motion displays consisted of the two gratings moving in the same direction (the direction of motion of each of the gratings defining linear motion was randomised from trial to trial) and stationary displays were made of two gratings with zero velocity. Although in these experiments we were interested in the responses to compressive motion an expanding stimulus (see figure 7) was used as a control stimulus type. The reason for this is that if displays were used that were either linear or compressive, then the identification of the type of motion could be done on the basis of the direction of one of the components. For example if presented with a linear motion moving then the motion is in the same direction in both display gratings. For the compression the motion in one of the gratings is the same as that in the linear display but opposite the linear direction in the other grating. The directions of motion of the linear display can be leftward or rightward in both gratings. However for the

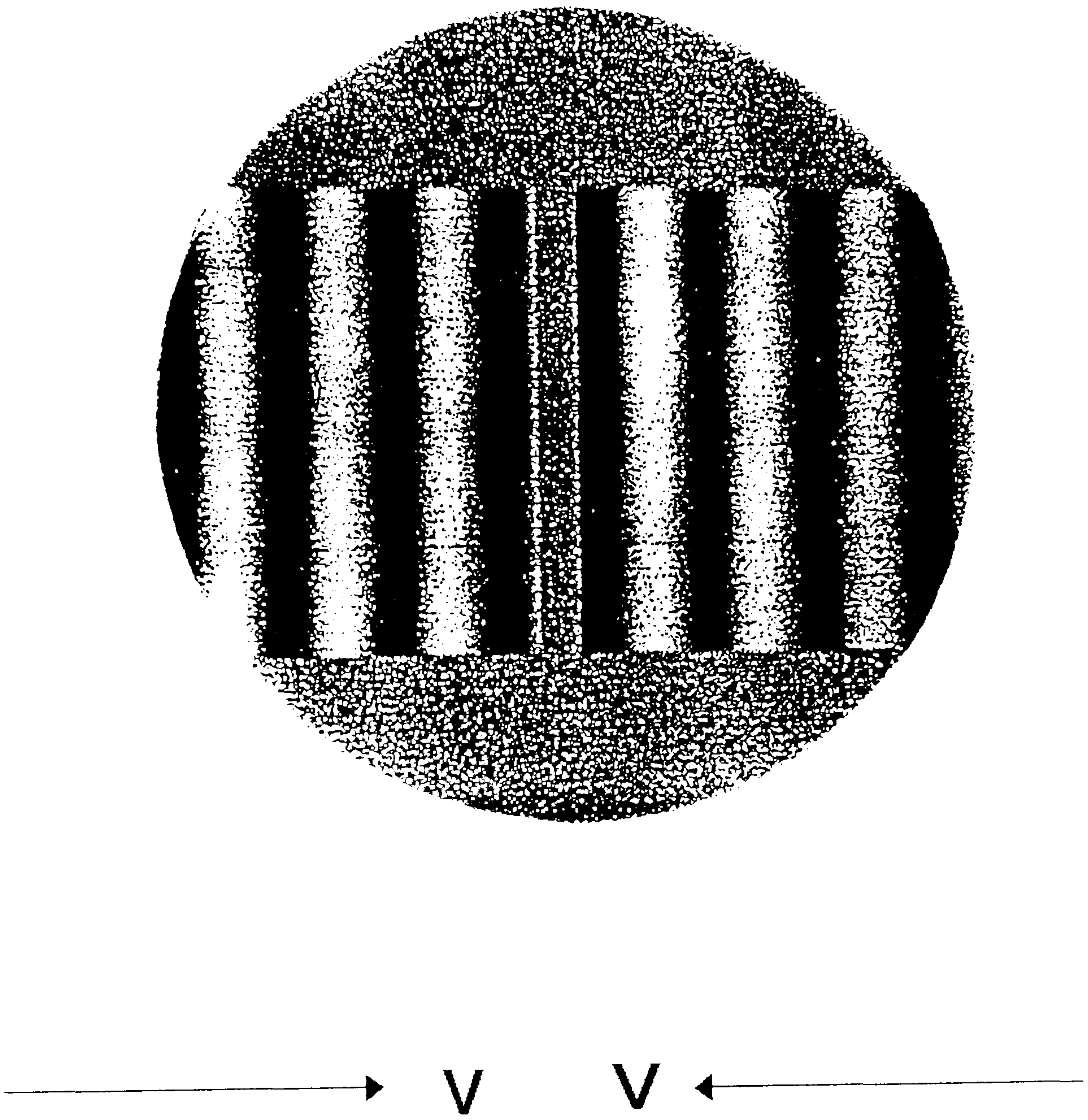


Figure 6: Basic Compression Display

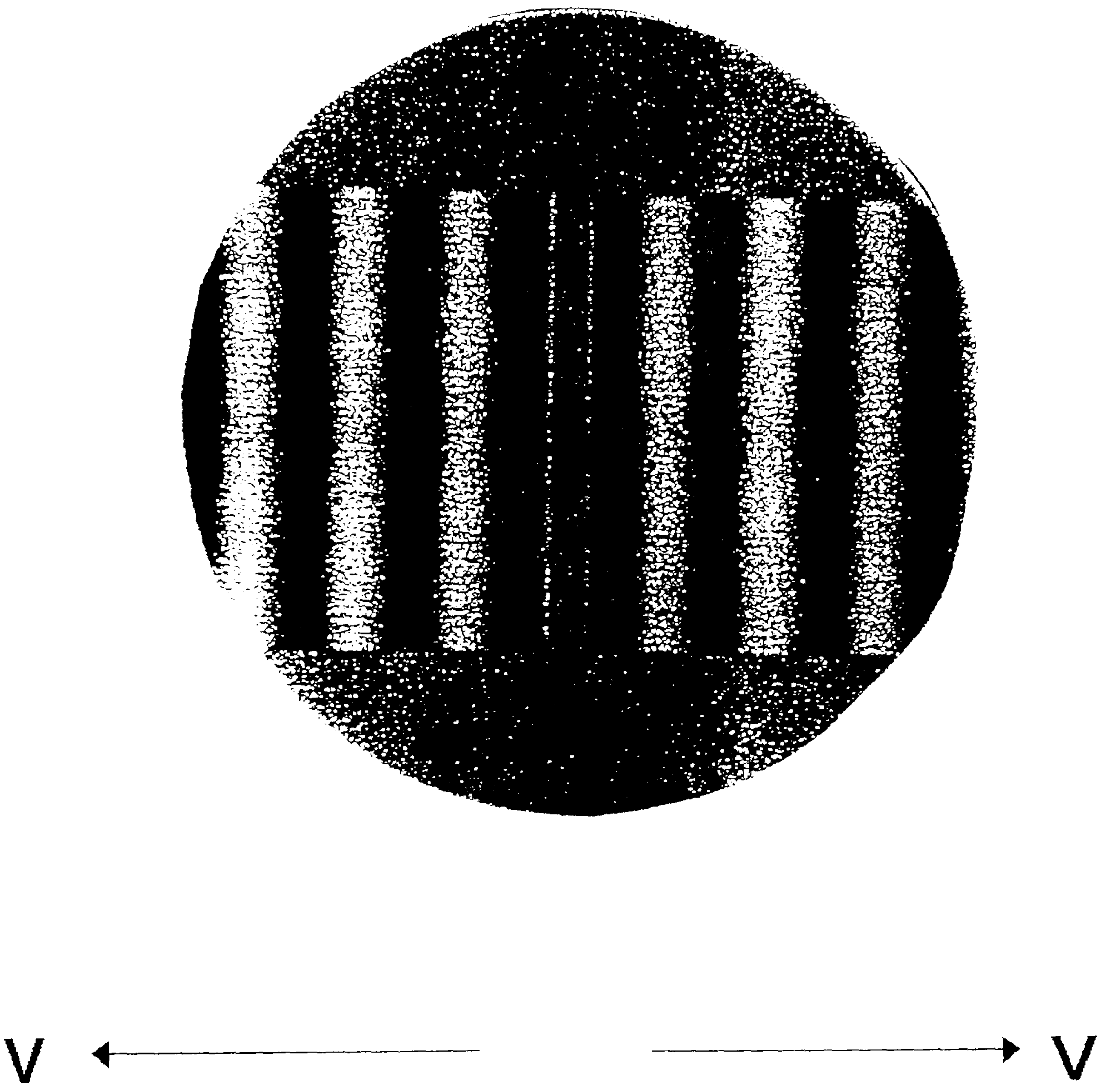


Figure 7: Basic Expansion Display

compressive display, in order to maintain the presence of compression, the direction of motion must be to the right in the left hand grating and to the left in the right hand grating. If these directions were to be reversed then the display would become an expansion. Thus if the a rightward direction of motion was found for the righthand grating of the display, the observer could in principle know that the type of motion present was not compression but linear as the compressive stimulus will by definition, never feature a rightward motion of the right grating. The same logic applies for the left grating direction of motion i.e. compression never has a leftward direction of motion for the left grating while linear motion does.

The introduction of the expanding motion type means that in order to identify the motion type, then the observer has to examine both directions of motion. As we were only interested in the responses to linear and compressive motion, no data was recorded for the expanding motion. The gratings making up the expanding display were given the same speed as the current grating speed for the detection of compression.

General Procedure: Experiments 1 to 3

For all experiments a two alternative forced choice procedure was used. Each experimental run was separated into a series of trials.

On any given trial the type of stimuli to be presented was selected randomly. The stimuli could be presented in one of two time intervals, the interval into which it was placed was decided randomly. Each time interval was of 100 msec duration and each interval was separated by an interval of 100 msec. This time interval was used so as to eliminate any possible effects of pursuit eye movements, which have a latency of approximately 200 - 250 msecs (Alpern, 1989), longer than the display duration. An experimental run was initiated in all experiments by the observer depressing one of the response keys. For each experiment the thresholds (contrast for experiments 1a/1b and 2a/2b, velocity experiment 3a/3b) were calculated using a staircase procedure set to track the 75% correct point. For all experiments the display screen was viewed binocularly from a distance of 300 cm. All these experiments were carried out under photopic conditions with a mean background luminance of 5cd/square metre.[1]

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[1] **Procedural Note for Experiments 1b, 2b and 3b**
As described in the display section these experiments contained an expanding motion as a control stimulus. No data was obtained for this type of motion. When presented with the experimental display responses to the expansion were obtained, so as not to interrupt the flow of the experiment. The observer was required to indicate the interval in which the motion occurred with his first response, his second response was to identify the motion type. If the subject thought that the motion type was expansion, his second key response would be to press the third key on the response box. Pressing the third key initiated a new trial. No data was obtained for the expansion stimulus. It was noted that while data was obtained for both types of shear (top moving left/ bottom right and vice versa) and why should data not have been obtained for expansion as well as compression? One of the reasons for this is that the phenomenal appearance of the two types of shear stimulus is constant i.e. a shear in both situations. However it is argued that this does not apply to compression and expansion, indeed the naive observer, VJH, reported that the phenomenal relationship between expansion and compression did not appear equivalent to the relationship between the two types of shear. In addition to this as each experimental run was up to 20 minutes in duration (which the observers reported as being just comfortable), it was felt that the addition of data collection for expansion would have further increased the time for each run, possibly introducing fatigue effects into the experiment. Technically the use of the expanding control stimulus makes the design a 3AFC experiment, however in the procedure the design is referred to as 2AFC as no data was collected for the expansion stimulus.

Procedure Experiment 1a

In this experiment there was no stationary stimulus used. The moving stimulus was randomly shear or linear motion and could occur in either interval 1 or 2 which was chosen randomly. Each interval was indicated by an audible tone that lasted for the duration of the time interval. The interval in which no stimulus occurred was characterised by a blank screen of mean screen luminance. On being presented with the stimulus the subjects task was to make two successive key presses. The first key press was to indicate the interval in which he thought the stimulus had occurred (detection), key 1 for first interval, key 2 for the second. The second response was to indicate the type of stimulus observed (discrimination), key 1 for linear motion, key 2 for shearing motion. The second key press ended the trial and initiated a new one.

Four separate staircases were used in determining the four thresholds of this experiment. A correct response gave rise to a decrease in the contrast of the stimulus on the next presentation of that stimulus, an incorrect response resulted in an increase in the contrast of that stimulus.

Six velocities of image motion were used in this experiment, 0.06, 0.1, 0.5, 1.0, 1.5 and 3.0 degrees per second. The experiment was repeated for each of the velocities listed. The reported thresholds are for at least 3 separate runs at each velocity.

Procedure Experiment 1b

This experiment used an identical procedure to that of experiment 1a except that compression replaced shearing motion and an expansion motion was introduced as a control.

Procedure Experiment 2a

The protocol of this experiment was exactly the same as that for experiment 1. The main differences were that this experiment utilised eight staircases as opposed to four as in experiment 2.

In this experiment the contrast thresholds for detection and discrimination of shearing and linear motion were assessed for a variety of added common motions of the stimuli. A standard stimulus was defined. This featured the two gratings making up each display moving at 1.0 deg/sec. To this standard display, depending on the experimental condition, was added a common image velocity (see figure 8a). The added velocities were 0.0, 0.5, 1.0, 1.5, 2.0 and 2.5 deg/sec. The added velocity was always from right to left across the display screen, (from the point of view of the observer).

An experimental run in this experiment was identical to that for experiment 2. Within a given run, a common velocity was added to the stimuli (linear and shear) for each stimulus presentation. Experimental runs were completed for each of the possible added common velocities. The reported thresholds for this experiment are the results of at least three experimental runs at each added velocity.

Detection and discrimination results for four types of stimuli are reported i.e. Linear A, Linear B, Shear C and Shear D stimuli. This was due to the fact that there exists two types of linear and two types of shearing motion in this experiment (ie a leftward moving linear, a rightward moving linear, a shear with

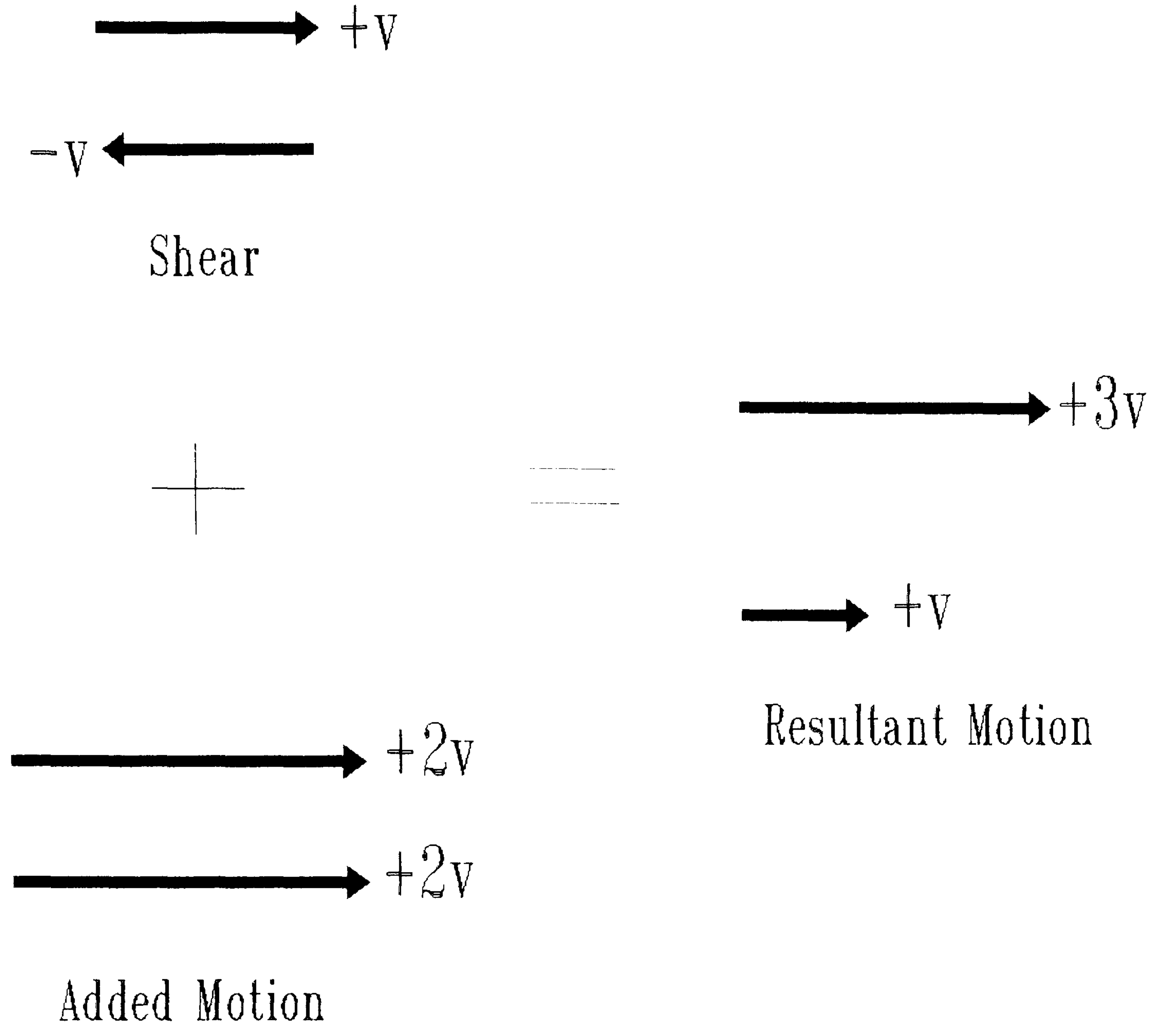


Figure 8a: Effect of adding a rightward motion to a shear

the upper grating moving to the left and lower grating moving to the right and a shear with the upper grating moving right and the lower to the left) which are affected differently by the added common motion. In the previous two experiments, as we were only interested in responses to the motion type and the two types of linear (and the two types of shear) did not differ from each other the thresholds were determine by averaging the responses to the two types of linear and two types of shear. In this experiment due to the addition of common image motion, the two types of each motion did differ from each other, e.g. the leftward linear motion when leftward common image motion was added became a leftward motion with greater leftward velocity (linear A stimulus); the rightward linear with added leftward velocity moved with reduced velocity to the right, ultimately moving to the left (linear B stimulus); the first type of shear (upper grating moving left) had an increased upper grating velocity left and a reduced lower rightward grating velocity (shear C stimulus); the effects of the added common motion on the second type of shear was exactly opposite to those of the first (shear D stimulus). Given this we could not be sure that the results for each different type of stimulus motion would be equivalent and so the thresholds had to be recorded separately. This explains the use of the eight staircases, one for detection and discrimination of each of the four stimuli. The use of the eight staircases gives rise to very complex graphical representations of the results. For this reason the results for all eight staircases were not presented in the graphs. Rather only the results that show the main effects found by these experiments were presented. This is represented by plots for linear stimulus A and shear stimulus C and linear stimulus A and compression stimulus C. The ANOVA tests the

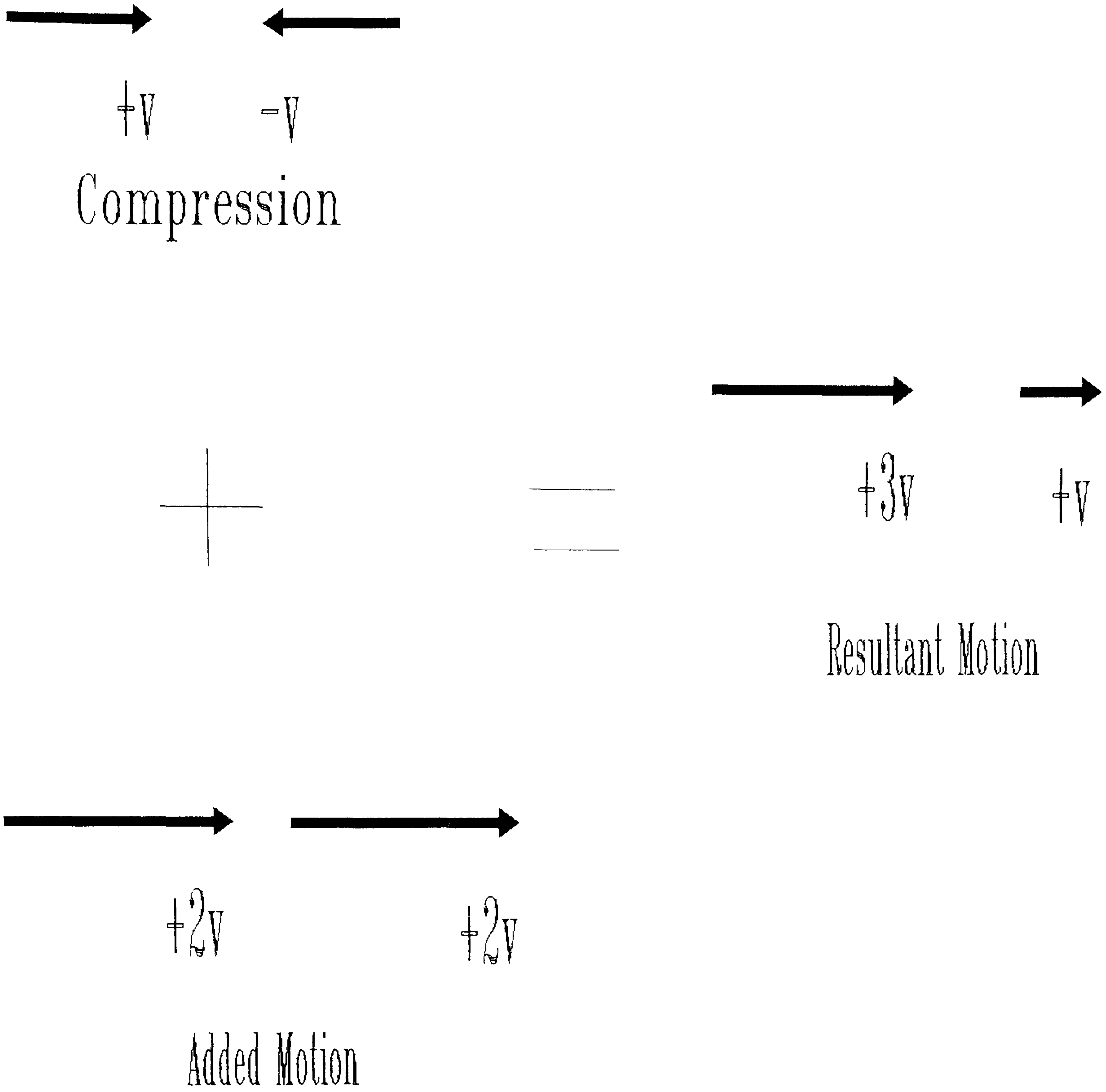


Figure 8b: Effect of adding a rightward motion to a compression

effects of the eight different types of stimuli.

Procedure Experiment 2b

This experiment utilised an identical procedure and data are reported in a similar way to those of experiment 2a, except that compression was substituted for shearing motion and an expansion motion was introduced as a control (see figure 8b).

Procedure Experiment 3a

On any given trial the observer was presented with two types of grating pattern, one moving and the other stationary. The moving pattern could be either the linear or shear type motion. The moving and stationary patterns were randomly placed into one or other of the display time intervals. All gratings in this experiment were displayed at 50% contrast. The speeds of the two gratings were equal and in opposite directions.

The task of the subject after presentation of the stimuli was to make two successive key responses. The first was to signal in which of the two intervals he thought the moving stimuli had occurred, pressing response key 1 indicated the first interval, response key 2 the second interval. Thus the first response was to discriminate the moving (linear or shear) display from the stationary display. The second key press was to indicate which type of moving stimuli was seen, key 1 if he had seen linear motion, key 2 if he had seen shearing motion. Thus the second response was to discriminate the two types of moving stimulus (linear or shear). On making the second response the trial was ended and a new trial was initiated.

Four separate staircases were used in this experiment to control the speed of motion of the moving gratings. Each of the staircases was related to one of the perceptual judgements (discriminations) of the experiment. There were four types of trial in these experiments each corresponding to one of the perceptual judgements. In the first type of trial the observer's task was to discriminate linear motion from stationary motion by stating in which interval the moving stimulus occurred (the first key press response controlled the staircase). The second type of trial was where linear motion was physically present and the observer's task was to discriminate linear from shear motion by identifying the type of motion present (the second key press response controlled the staircase). The third type of trial was where shear motion was present and the observer's task was to discriminate shear motion from the stationary stimulus by responding in which time interval the moving stimulus occurred (the first key press response controlled the staircase). The fourth type of trial was where shear motion was present and the observer's task was to discriminate shear from linear motion by identifying the motion type (the second key press response controlled the staircase). Thus on any given trial only one of the key presses actually had an effect on a staircase and this depended upon the type of trial. A correct response resulted in a decrease in the velocity the next time the particular stimulus type was presented, an incorrect response resulted in an increase in the stimulus velocity. The type of trial was randomly selected from trial to trial. When a staircase had reached threshold and if any of the other staircases had yet to reach threshold, it was still possible for a trial to be of the type controlled by the staircase. In these circumstances the speed given to the gratings in the display was the threshold speed identified by that staircase, but no data was collected for the responses to the stimuli. In practice it was found that the four staircases reached threshold in a similar number of trials, usually within 3-5 trials of each other. It was never the case that one staircase reached threshold much faster than the other three and only a maximum of 1-2 trials were required with a completed staircase at threshold.

Five grating spatial frequencies were used in this experiment, 1.1, 2.2, 4.4, 8.8, 17.6 cycles/degree. This experiment was repeated for each of these spatial frequencies. The reported thresholds (results) are for at least 3 separate runs for each spatial frequency. The thresholds are in terms of the lower threshold of motion (velocity, deg/sec) for each display and task type.

Procedure Experiment 3b

This experiment used the same procedure as experiment 3a, except that compressive motion replaced shearing motion and an expansion motion was introduced as a control.

Subjects

The subjects for experiments 1 to 3 were the author KAR and VJH. KAR was aged 25, has normal vision and is an experienced psychophysical observer. VJH was aged 24, has normal vision and was naive to the aims of the experiment.

3.3 Results

Results Experiment 1a

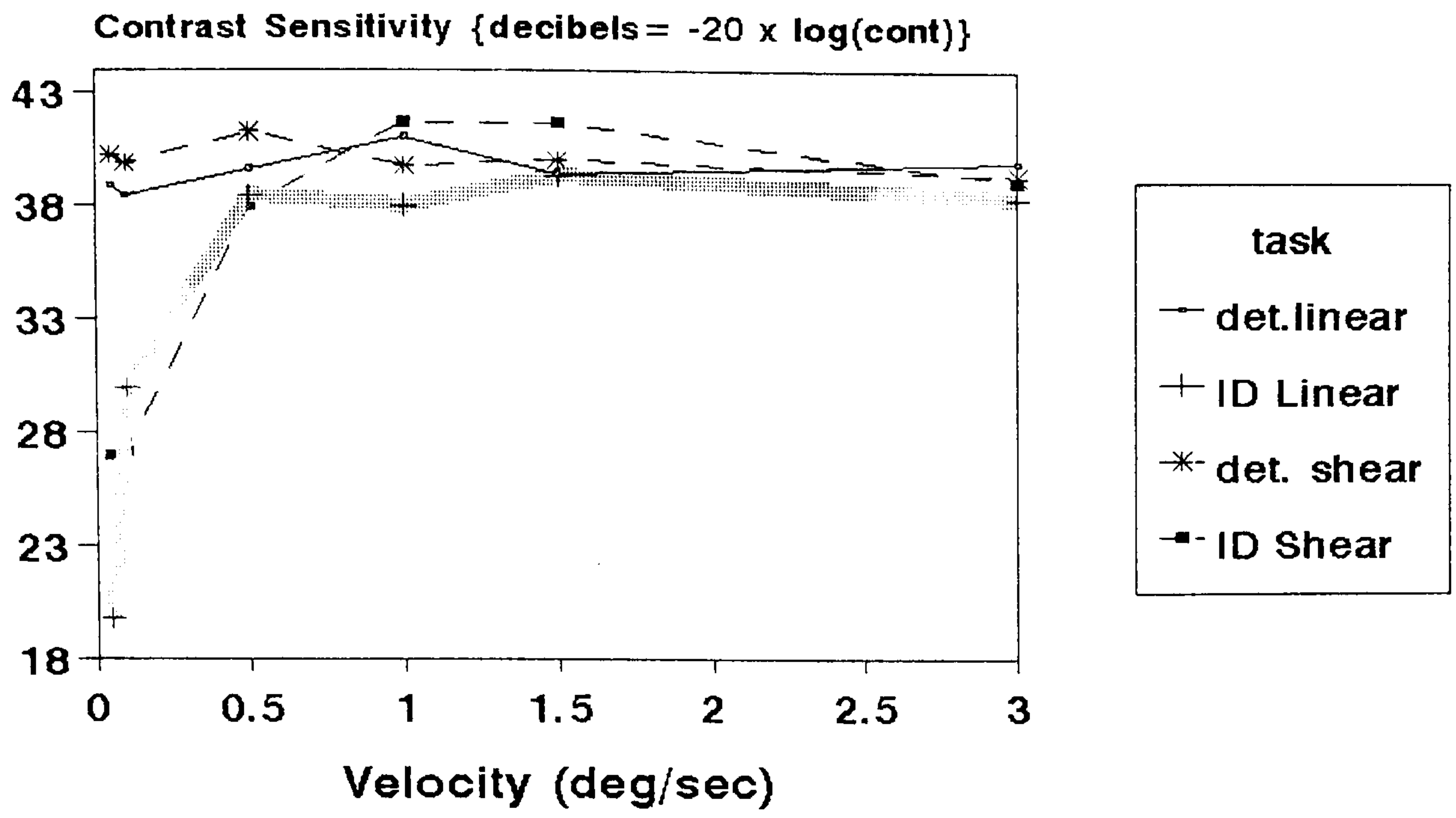
(See figure 9a) It can be seen from an examination of the results that for all image velocities the contrast sensitivities for detection for both types of motion were invariant over the range of velocities used. The detection contrast sensitivities over the range of velocities used were equivalent for both types of motion.

The discrimination contrast sensitivities for both types of motion were equivalent to the respective detection contrast sensitivities for velocities of 0.5 deg/sec and greater. Also for velocities in this range the discrimination contrast sensitivities for both types of motion were equal to each to each other and were also invariant with velocity.

For velocities between 0.06 deg/sec and 0.5 deg/sec the discrimination contrast sensitivities were reduced for both types of motion, velocity of 0.06 deg/sec for linear motion. At 0.06 deg/sec the shear discrimination contrast sensitivity was superior to that of the linear motion.

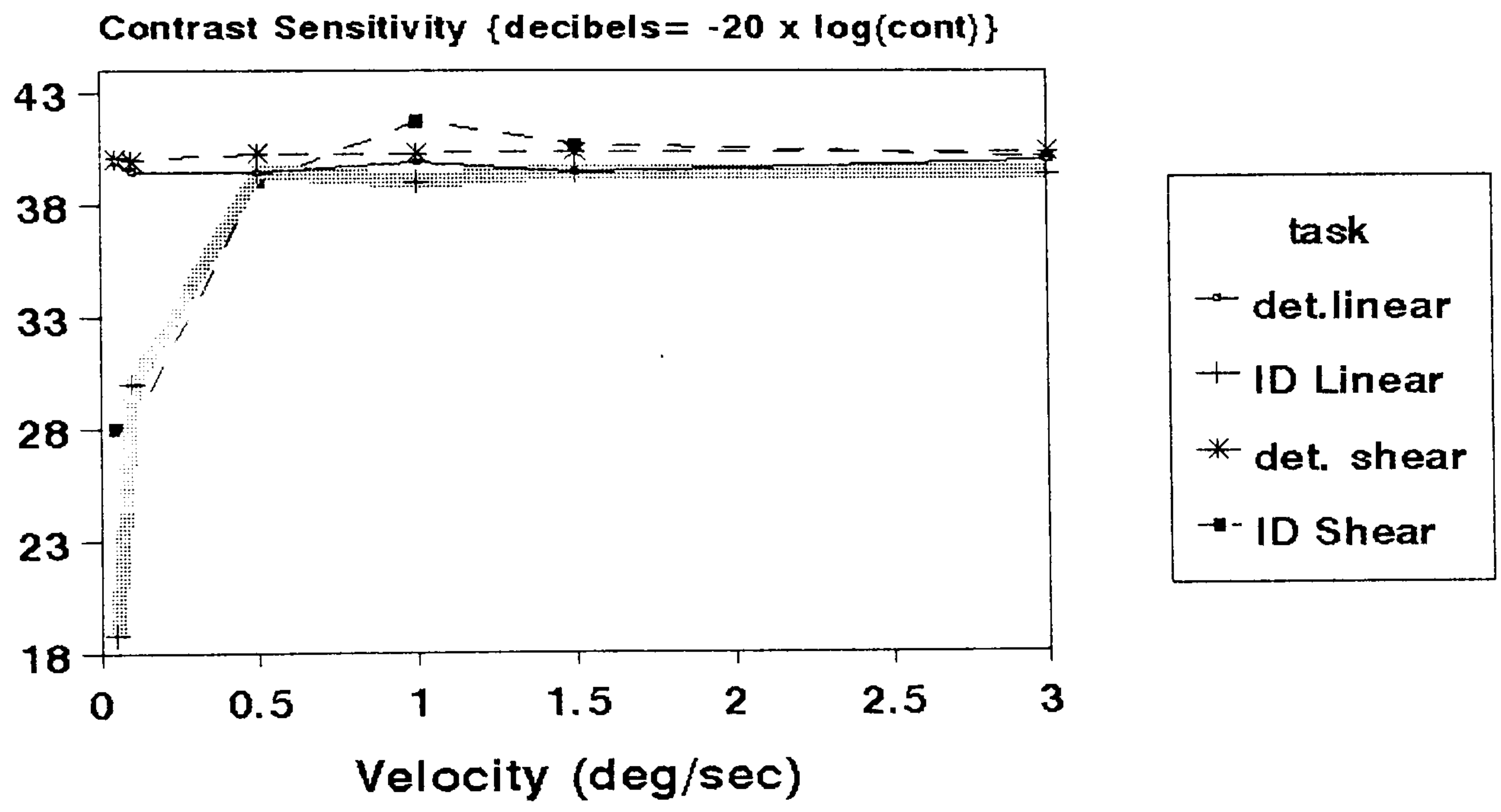
The equivalence of the contrast sensitivities for detection and discrimination for both types of motion for velocities of 0.5 deg/sec and over is consistent with what would be expected of mechanisms sensitive selectively to shear and linear motions. At the lowest velocities the non-equivalence of the detection and discrimination contrast sensitivities for shear and for linear motions is contrary to the expectations of a system featuring specific sensitivities to shear and linear motions.

Subject: KAR



(SF = 4.4 c/deg)

Subject: VJH



(SF = 4.4 c/deg)

Figure 9a: Contrast sensitivity for the detection and identification of shear. Experiment 1a

Results Experiment 1b

(See fig 9b) The results of this experiment are very similar to those of experiment 1a.

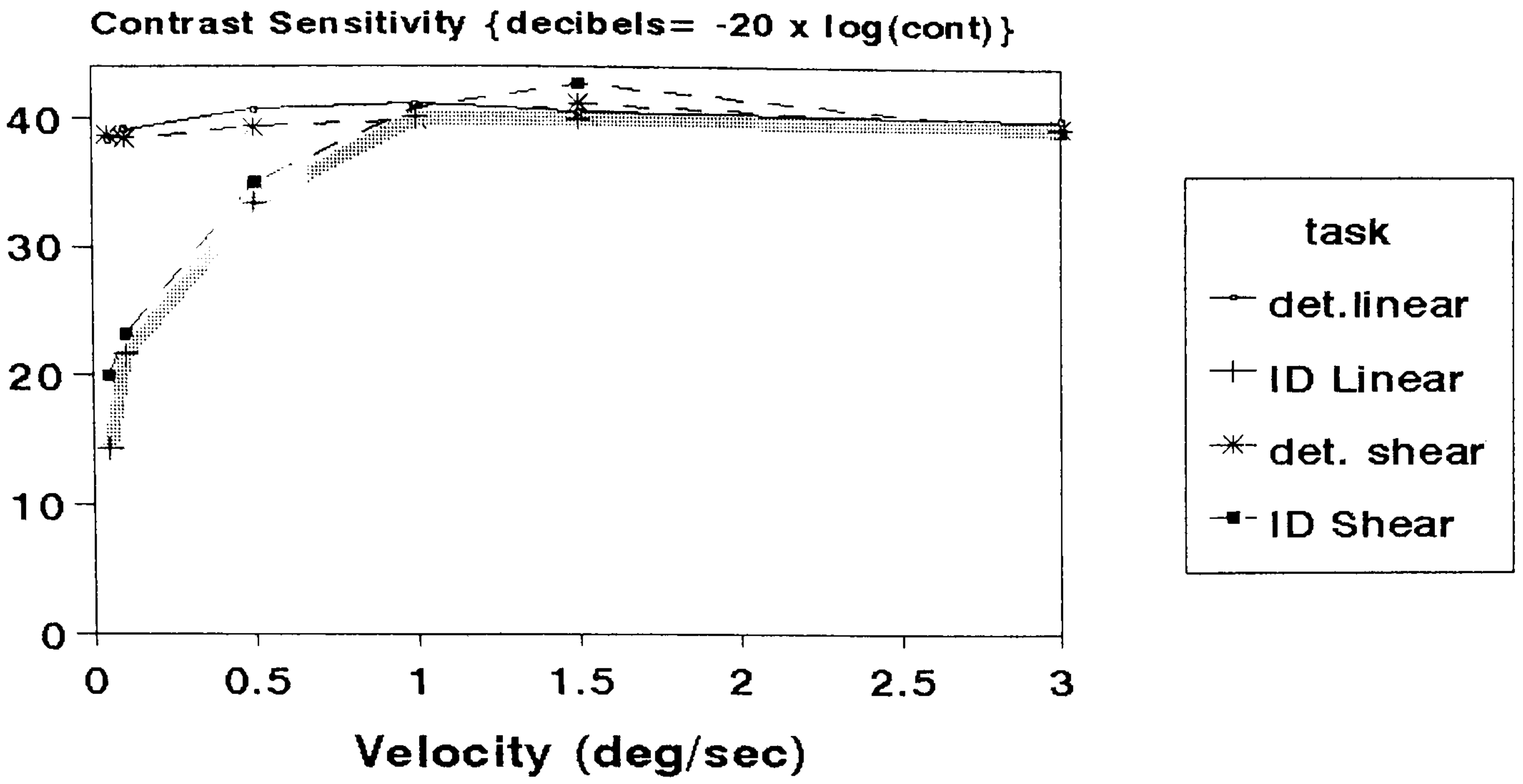
Again for all image velocities the contrast sensitivities for detection for both types of motion were invariant over the range of velocities used. The detection contrast sensitivities over the range of velocities used were also equivalent for both types of motion.

The equivalence of the contrast sensitivities for detection and discrimination for both types of motion for velocities of 0.5 deg/sec and over is consistent with what would be expected of mechanisms sensitive selectively to compressive and linear motions. At the lowest velocities the non-equivalence of the detection and discrimination contrast sensitivities for shear and for linear motions is contrary to the expectations of a system featuring specific sensitivities to compressive and linear motions.

Results Experiment 2a

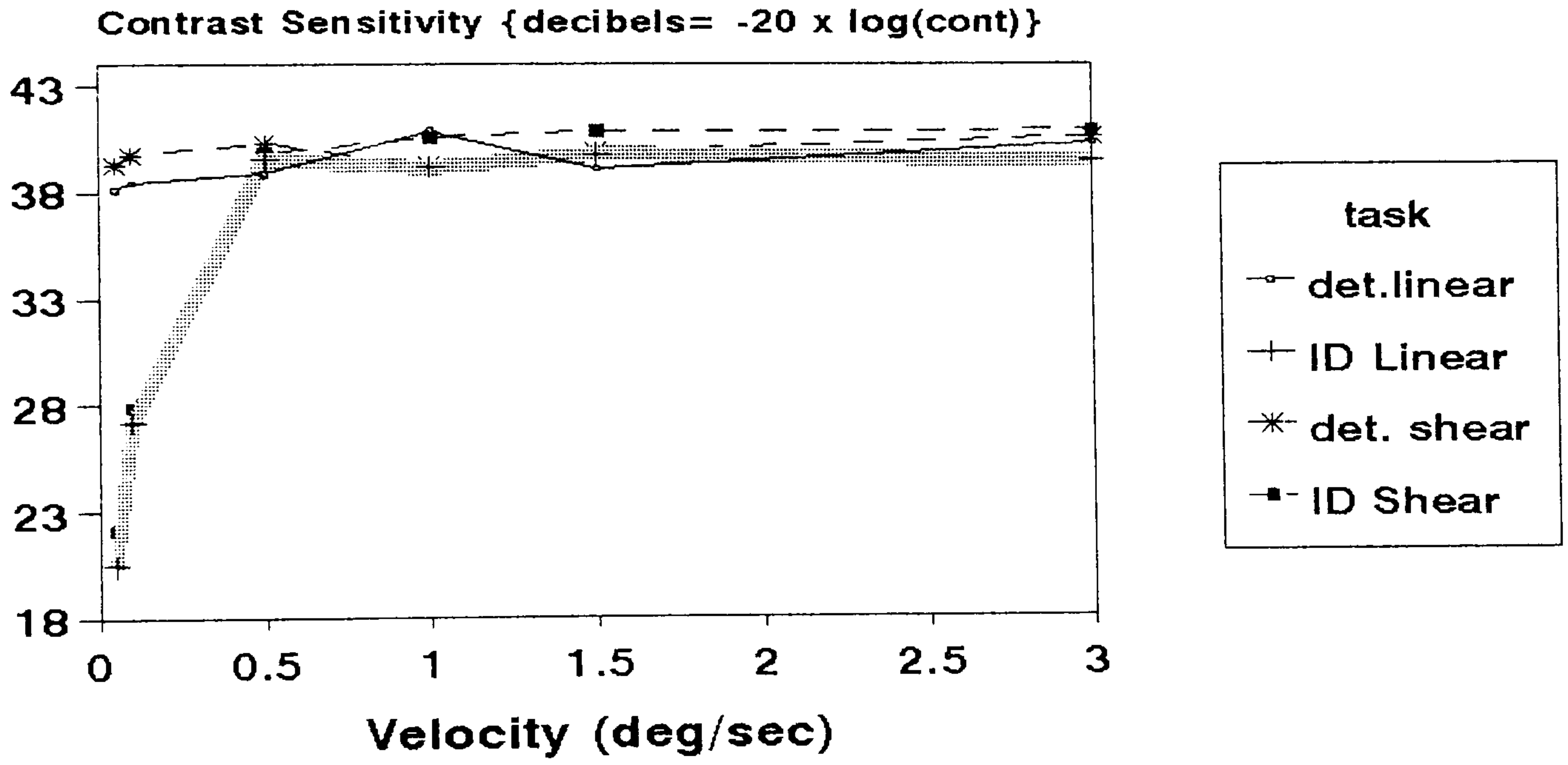
(See fig 10a, 10b, 10c and 10d) It can be seen from an examination of the results that the contrast sensitivities for the discrimination of the shear and linear motion reduce with added common motion. This can be seen especially clearly by examining the linear trend of the data (see figs 10b and 10d). The detection thresholds for both types of motion were more stable with added common velocity than the discrimination thresholds for both types of motion. However all, except linear motion B exhibit a small downwards trend with added common velocity, this trend is less than that for the discrimination sensitivities.

Subject: KAR



(SF = 4.4 c/deg)

Subject: VJH



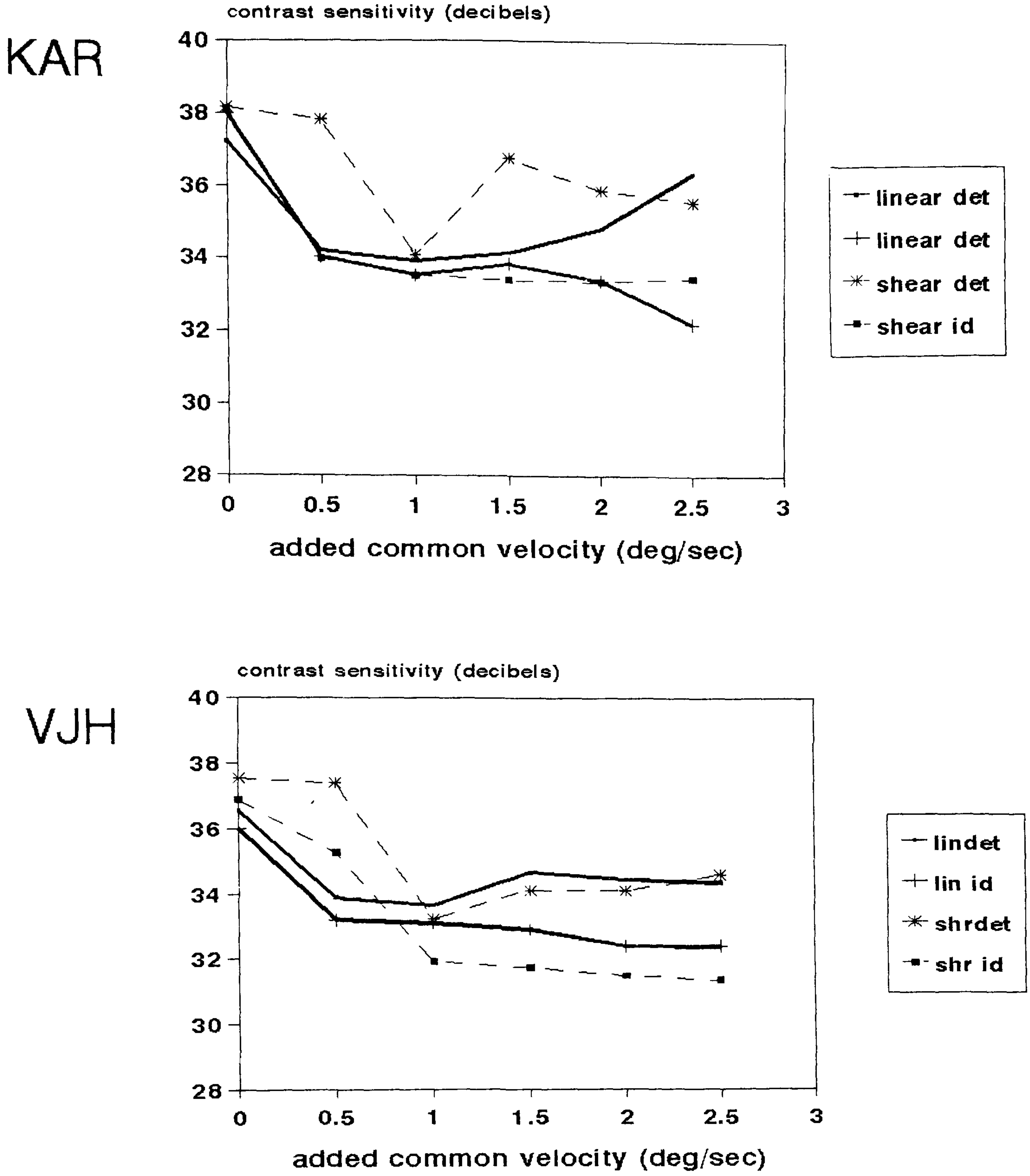
(SF = 4.4 c/deg)

Figure 9b: Contrast sensitivity for the detection and identification of compression. Experiment 1b.

Analysis of variance revealed that there was no significant effect of stimulus type (linear or shear) on the results ($F=1.499;DF=3;p>0.05$), and that there was a significant interaction between task type (detection or discrimination) and added common velocity in determining these results ($F=3.444;DF=5;p<0.01$). All other interactions were insignificant. Analysis of variance also revealed significant effects of added common velocity ($F=22.560;DF=5;P<0.01$) and task type ($F=79.143;DF=1;p<0.01$). This pattern of results suggests that the type of stimulus is unimportant in determining the detection and discrimination sensitivities, and suggests that what is important is the added common velocity and the task type.

It therefore appears that for a given added velocity and a given task there is no significant difference in the sensitivity to shear or linear motion of the visual system, both in terms of detection sensitivity and discrimination sensitivity. The detection and discrimination sensitivities for all added common velocities were not equal as would be expected of labelled detectors. These results are inconsistent with the hypothesis of labelled shear specific detectors in the visual system due to the reduction in discrimination sensitivity with greater added common velocity and the inequality of the detection and discrimination sensitivities for the shear type motion. The lack of significant effects of the stimulus type suggests that shear and linear motions are processed in a similar way possibly by the same underlying system of detectors.

The values of the contrast sensitivity for detection and discrimination for all stimulus types at zero added common velocity were lower than those in experiment 1a (1.0 deg/sec). Because there was eight separate staircases



Subject: VJH (sf= 4 c/deg)

Figure 10a: Experiment 2a Shear Plus Common Motion. Contrast Sensitivity

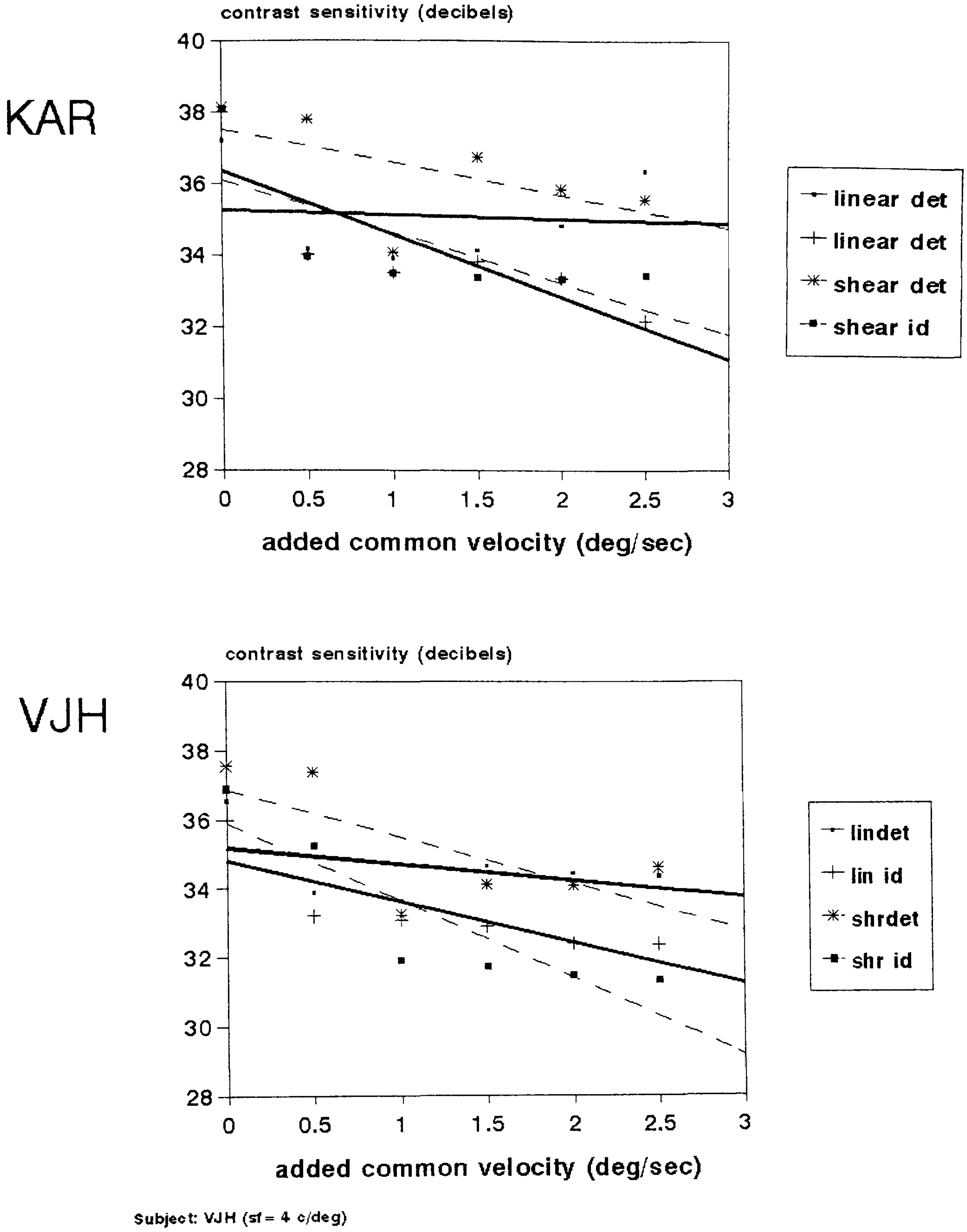


Figure 10b: Experiment 2a (Linear Trends)

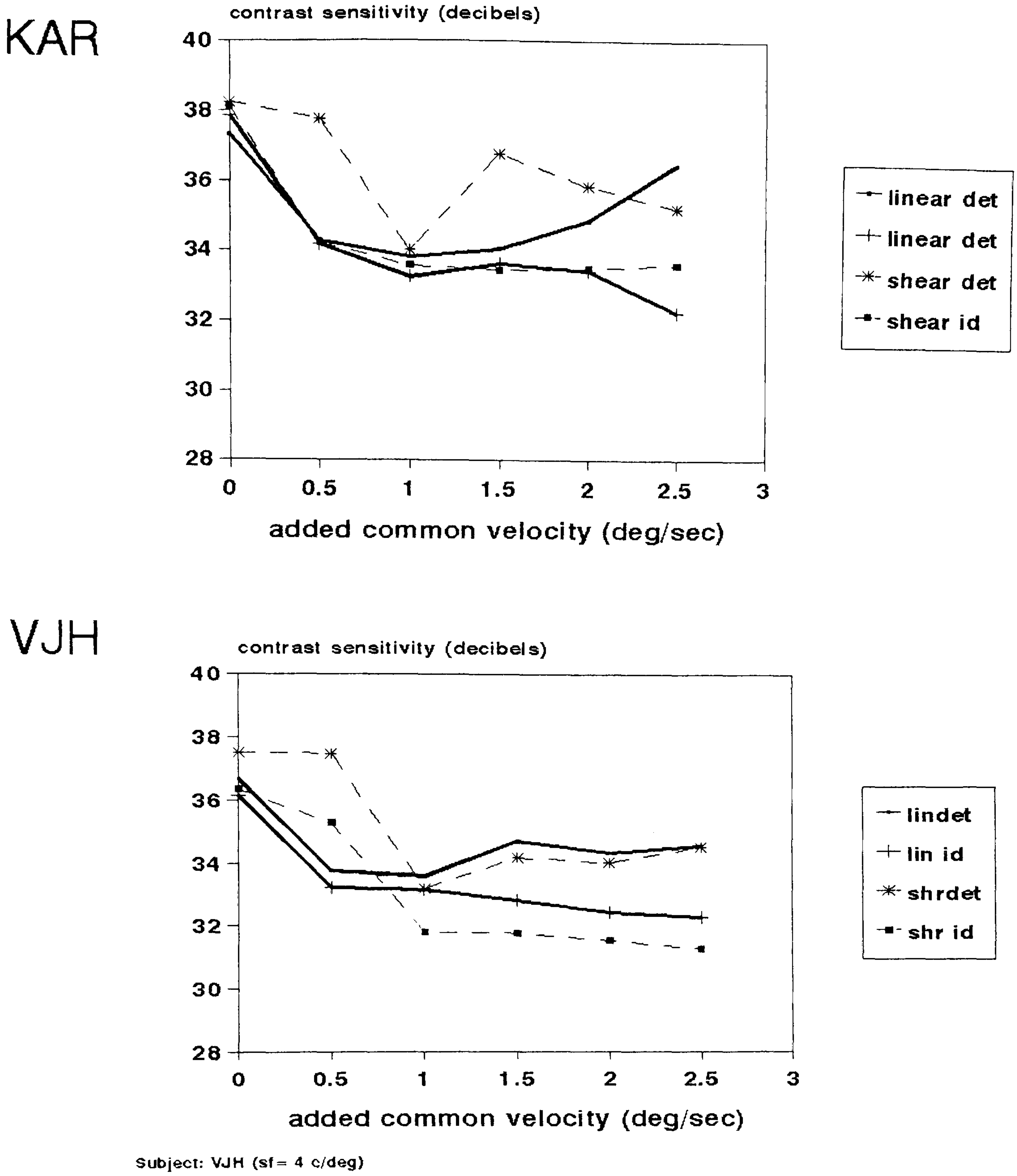
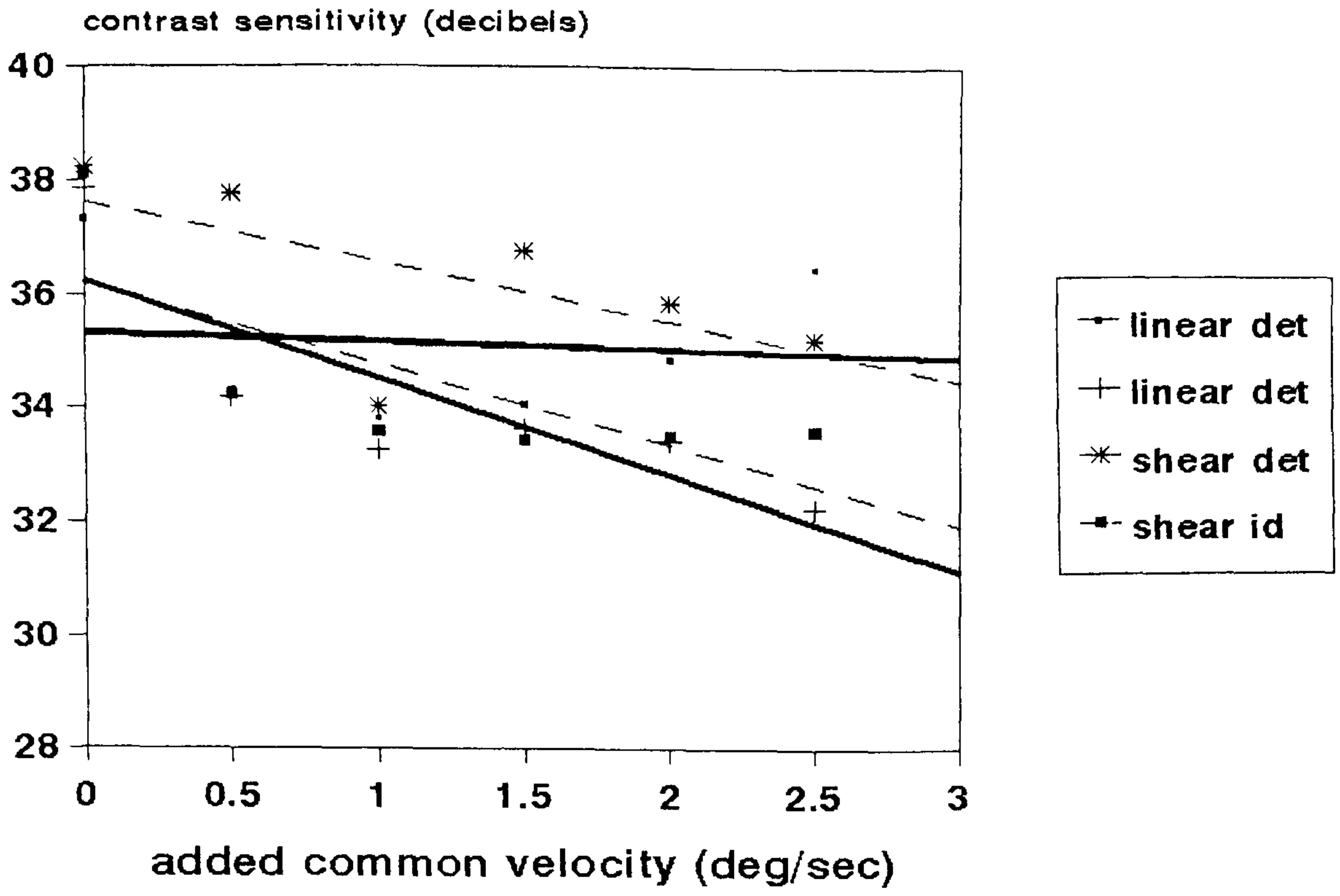
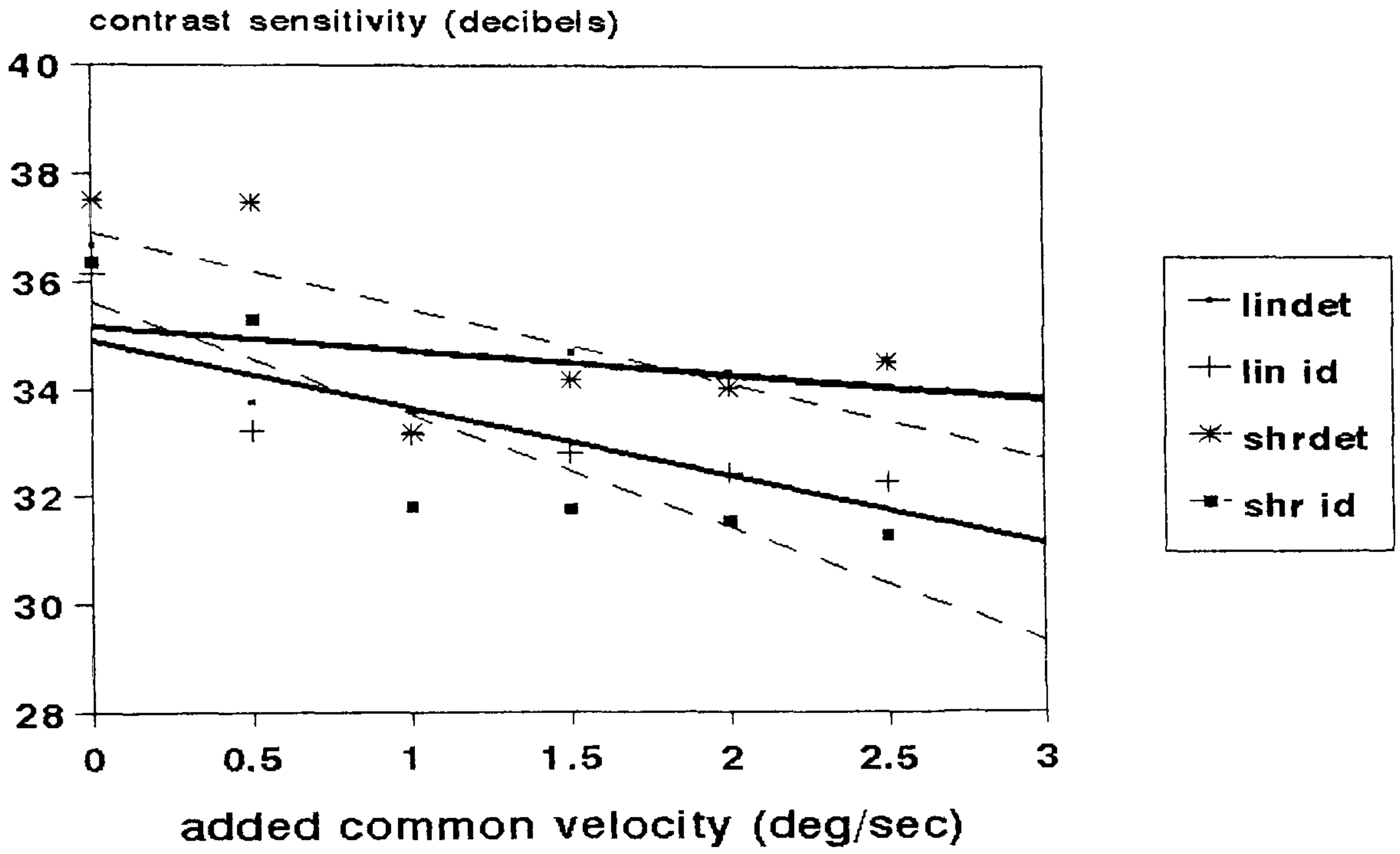


Figure 10c: Experiment 2a
Shear Plus Common Motion.
(Second set of staircases,
see text for explanation)

KAR



VJH



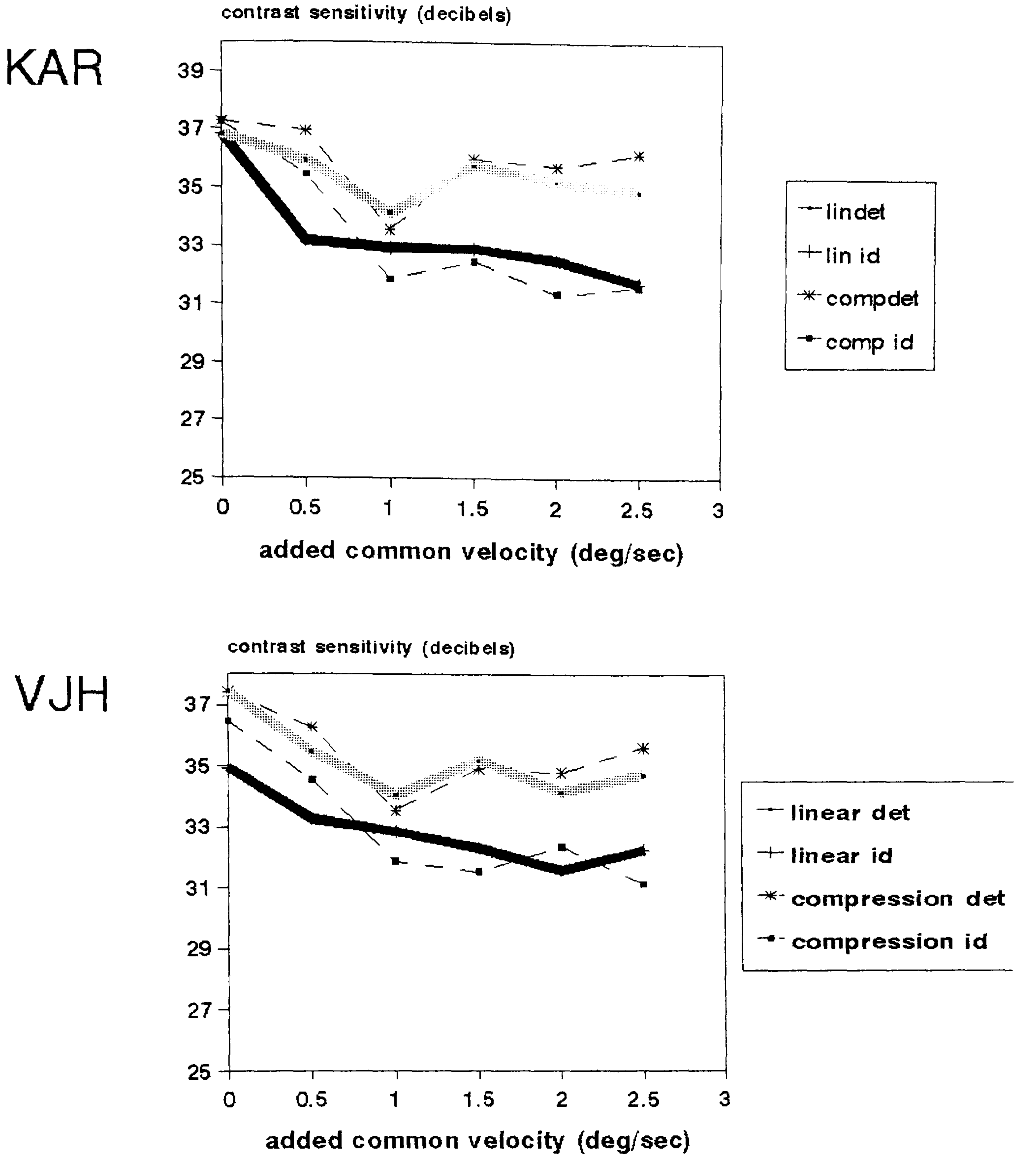
Subject: VJH (sf= 4 c/deg)

Figure 10d: Experiment 2a Shear Plus Common Motion. Linear trends. (Second set of staircases, see text for explanation) controlling the experiment it is possible that with such a long experiment (each run was on average 35 mins long) fatigue effects could play a part in determining the threshold, with a resultant decrease in sensitivity especially towards the end of each experimental run.

Results Experiment 2b

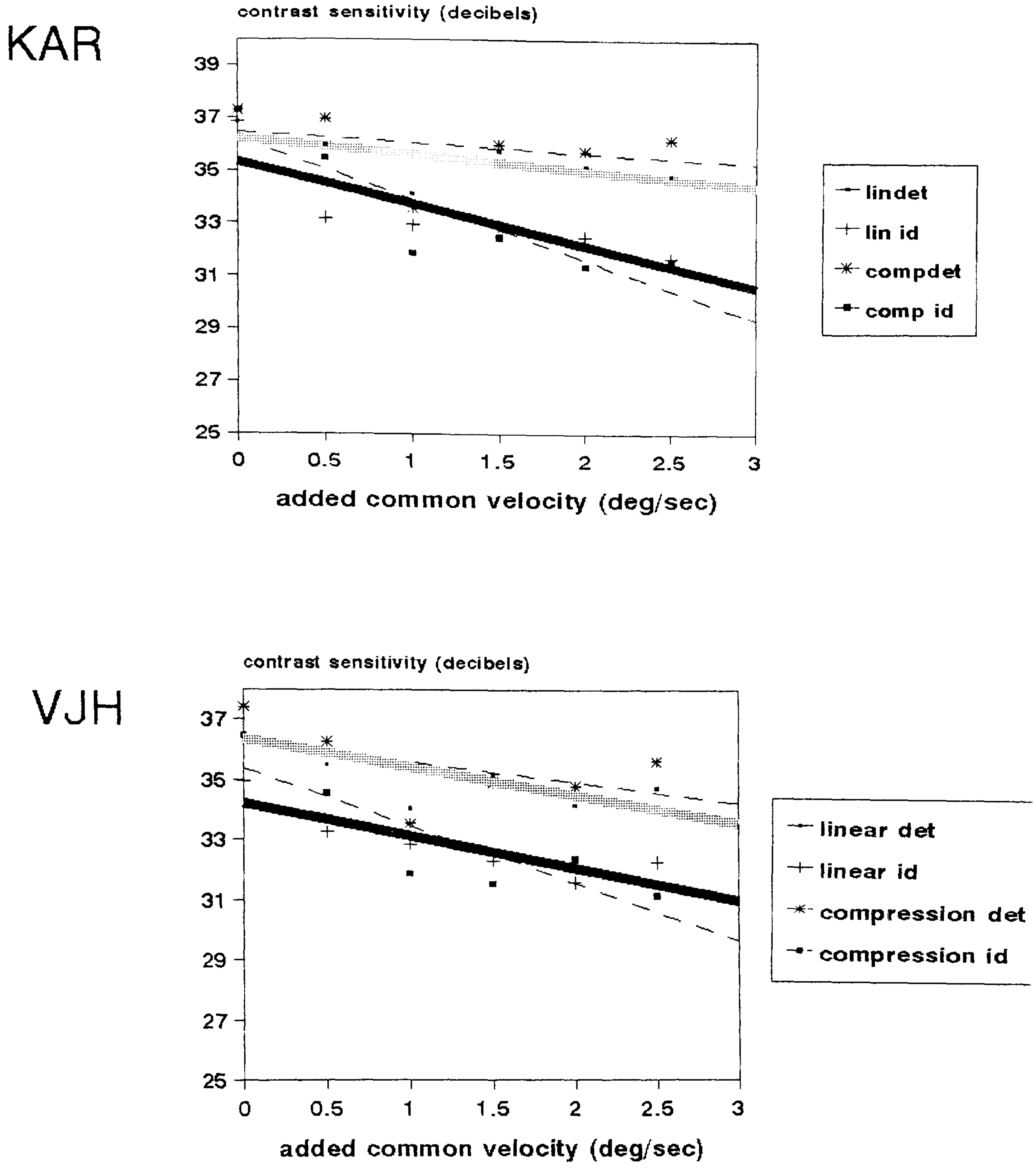
The results of this experiment are similar to those of experiment 2a (See fig 11a, 11b, 11c and 11d). It can be seen from an examination of the results that the contrast sensitivities for the discrimination of the compressive and linear motion reduce with added common motion. This can be seen especially clearly by examining the linear trend of the data (see figs 11b and 11d). The detection thresholds for both types of motion were more stable with added common velocity than the discrimination thresholds. All except linear motion B exhibit a small downwards trend with added common velocity, this trend is less than that for the discrimination sensitivities.

Analysis of variance revealed that there was no significant effect of stimulus type (linear or compression) on the results ($F=1.499; DF=3; p>0.05$), and that there was a significant interaction between task type (detection or discrimination) and added common velocity in determining these results ($F=3.444; DF=5; p<0.01$). All other interactions were insignificant. Analysis of variance also revealed significant effects of added common velocity ($F=22.560; DF=5; P<0.01$) and task type ($F=79.143; DF=1; p<0.01$). As with experiment 2a this pattern of results suggests that the type of stimulus is unimportant in determining the detection and discrimination sensitivities, and



Subject: VJH (sf= 4 c/deg)

Figure 11a: Compression with Common Motion (Contrast Sensitivity). Detection and identification of stimuli. Experiment 2b



Subject: VJH (sf = 4 c/deg)

Figure 11b: Compression plus Common Motion Linear Trend

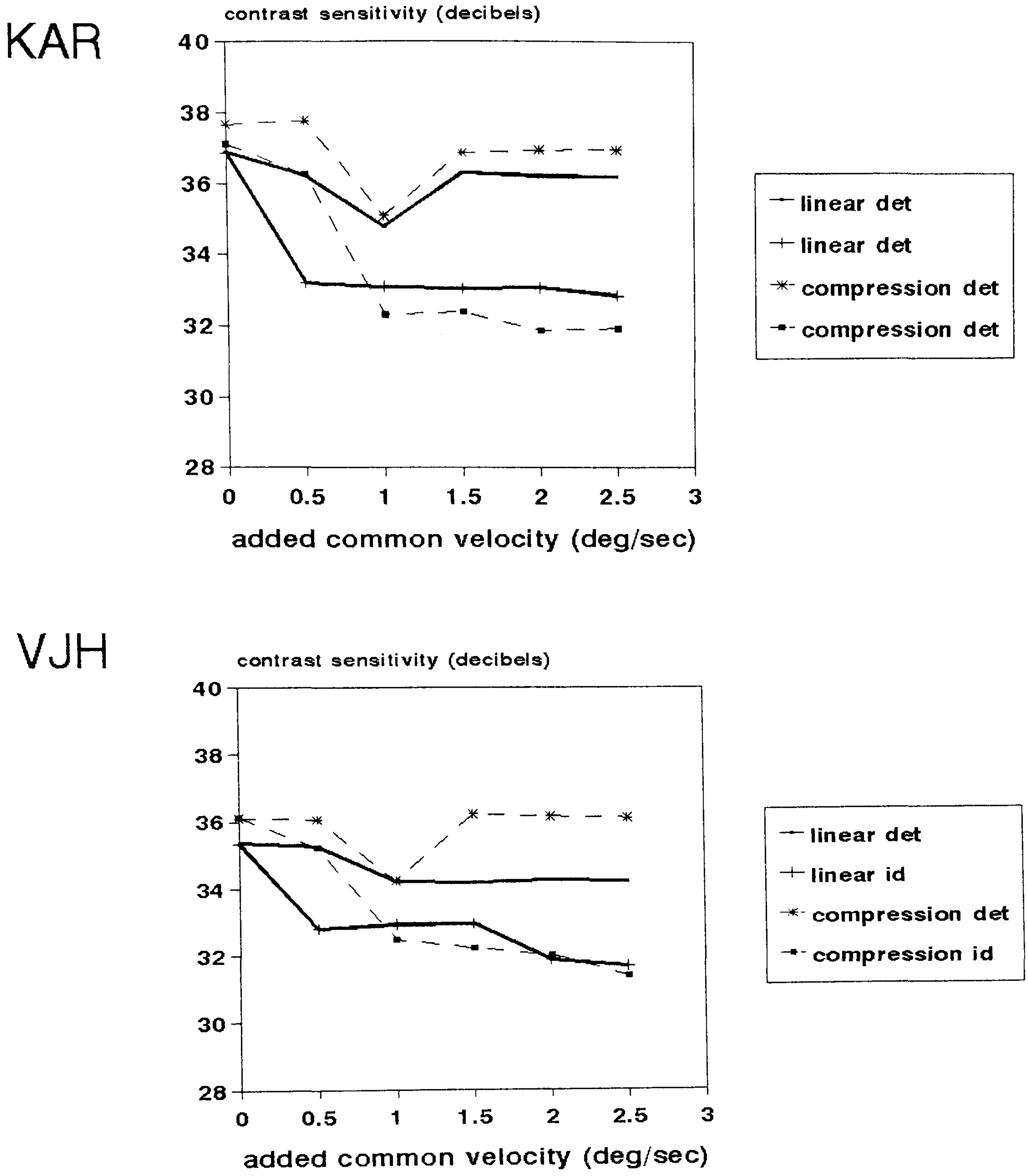


Figure 11c: Experiment 2b Compression Plus Common Motion. (Second set of staircases, see text for explanation)

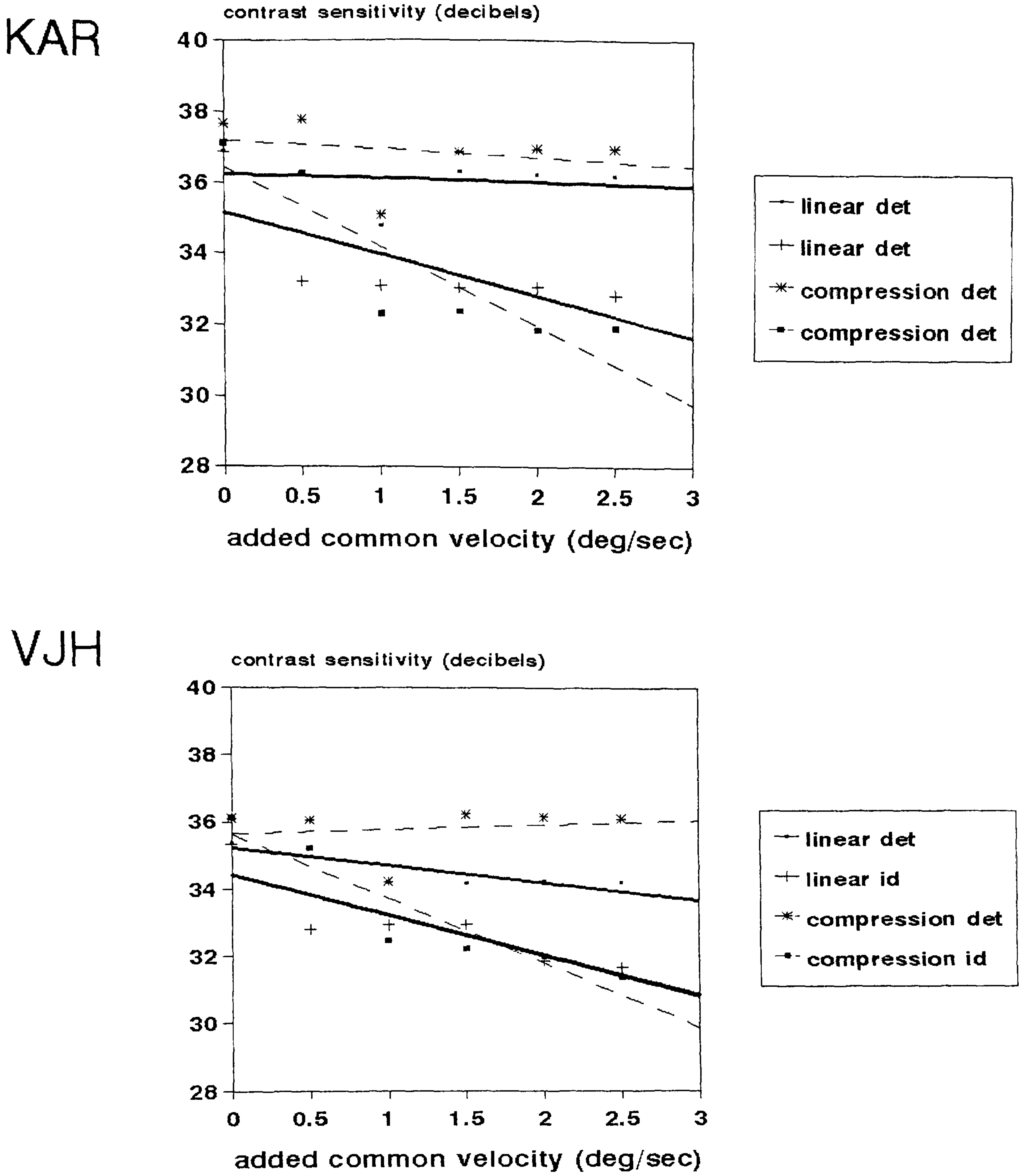


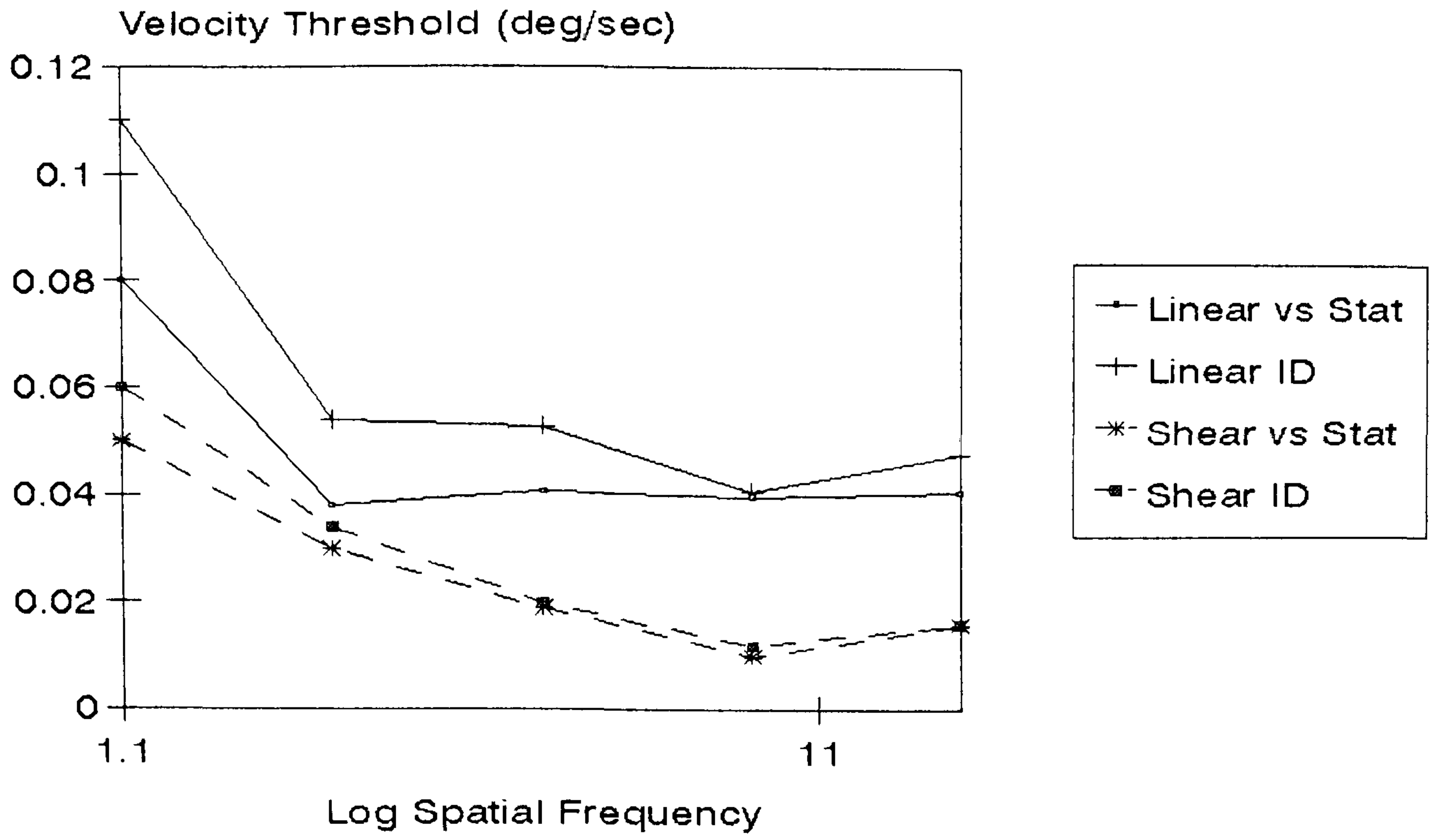
Figure 11d: Experiment 2b
Compressionr Plus Common Motion.
Linear trends.
(Second set of staircases,
see text for explanation)

suggests that what is important is the added common velocity and the task type. Thus it appears that for a given added velocity and a given task there is no significant difference in the sensitivity of the visual system to compression or linear motion, both in terms of detection sensitivity and discrimination sensitivity. The detection and discrimination sensitivities for all added common velocities were not equal as would be expected of labelled detectors. These results are inconsistent with the hypothesis of labelled compression-specific detectors. The lack of significant effects of the stimulus type suggests that compression and linear motions are processed in a similar way possibly by the same underlying system of detectors.

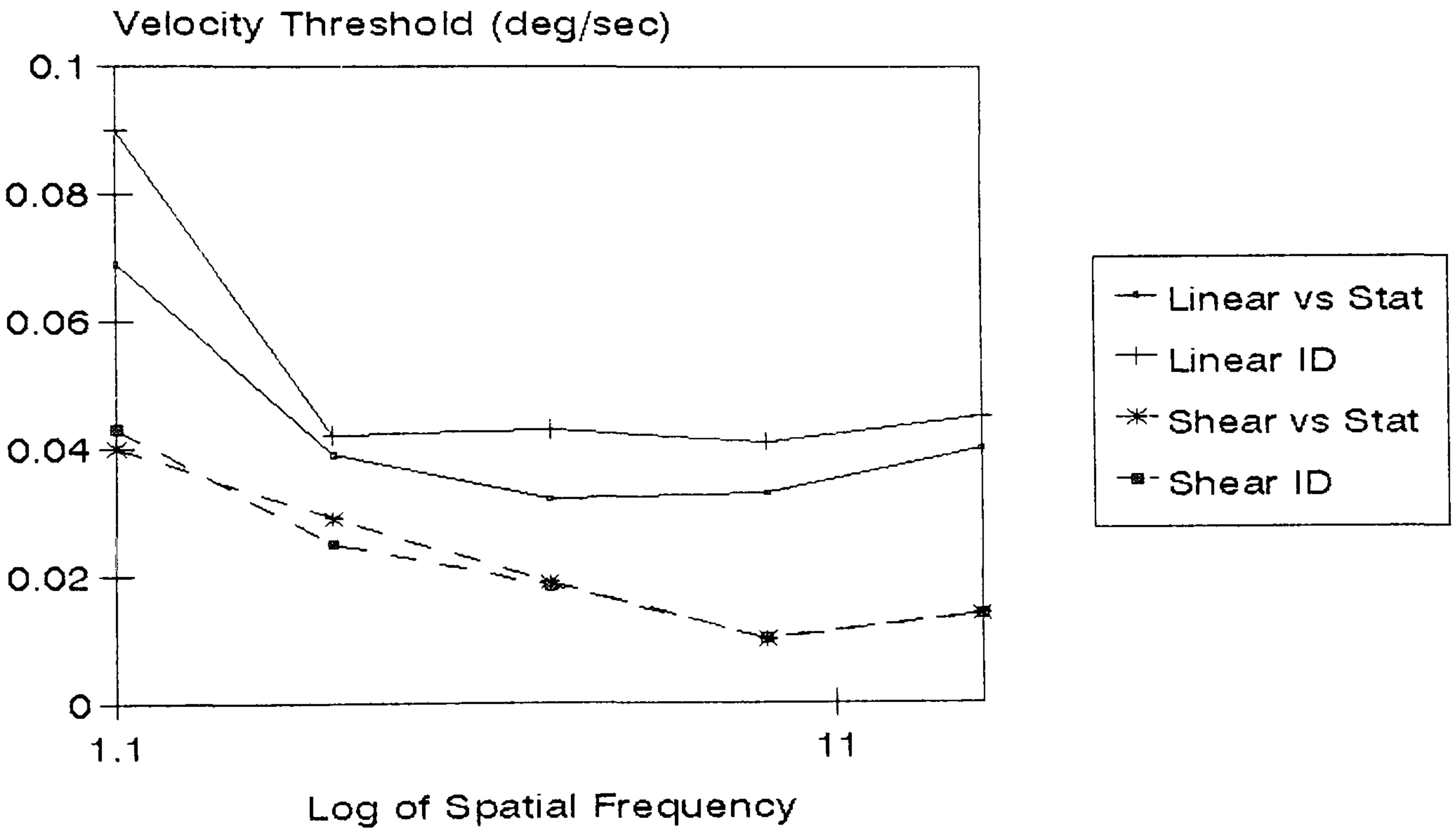
The values of the contrast sensitivity for detection and discrimination for all stimulus types at zero added common velocity were lower than those in experiment 1b (1.0 deg/sec). It is likely that as there were eight separate staircases controlling the experiment with such a long experiment (each run was on average 19 mins long) fatigue effects could play a part in determining the threshold, with a resultant decrease in sensitivity and thus increase in contrast threshold especially towards the end of each experimental run.

Results Experiment 3a

(see fig 12a) It can be seen from an examination of the results that the subject appeared to have a greater sensitivity to shearing motion than to linear motion, (the lower discrimination thresholds when shear was the stimulus than when linear was the stimulus) this was a statistically significant finding i.e. for the interaction between spatial frequency and stimulus type ($F=2.625; df=4; p<0.05$).



KAR



VJH

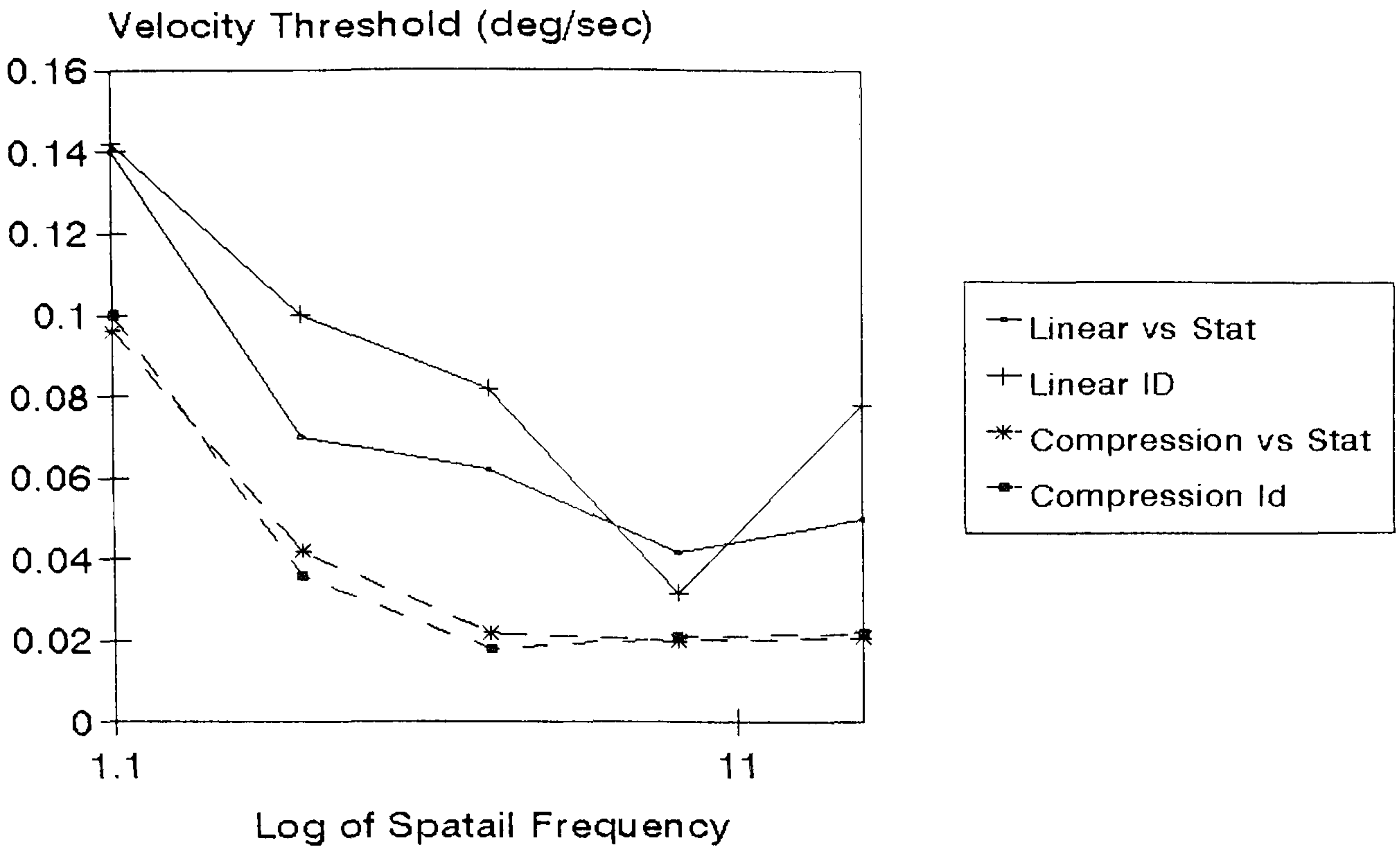
Figure 12a: Lower thresholds of motion for shear. Experiment 3a.

For spatial frequencies in excess of 4.4 cycles per degree, the velocity thresholds were invariant with spatial frequency for both linear and shear motions. Sensitivity to both types of motion was reduced with the lowest spatial frequencies used, however even at the lowest spatial frequencies the superiority in the sensitivity to shear over linear motion was preserved. For both shear and linear motions the threshold for discriminating moving (shear or linear) from non-moving stimuli and for discriminating shear and linear from each other, were equivalent, the thresholds being statistically insignificantly different i.e. the insignificant interaction between discrimination type and stimulus type ($F=3.254; df=1; p>0.05$).

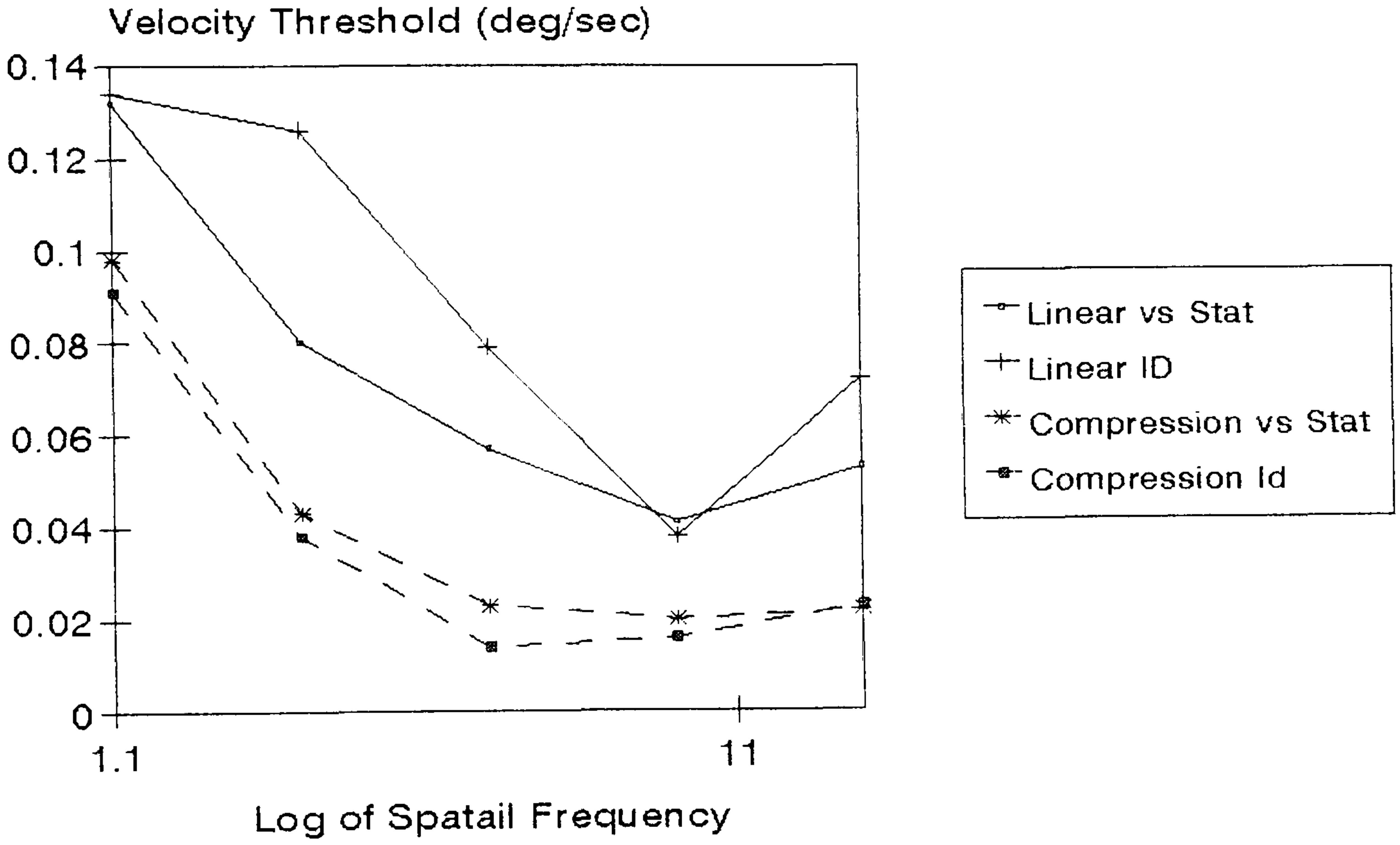
The equivalence of the discrimination thresholds for shearing motion is consistent with the results that would be expected from shear sensitive mechanisms, and gives us evidence for specific sensitivity to shearing motion in the visual system. The difference in the thresholds for shear and linear motion is consistent with the idea that the two types of motion are processed differently and is also therefore consistent with the expectations of a system featuring shear sensitivity. It should be noted, however that these results indicate that if there exists shear sensitive mechanisms then at low spatial frequencies these mechanisms have reduced shear sensitivity.

Results Experiment 3b

The results of this experiment can be seen with reference to figure 12b. These results are generally similar to those of experiment 1a. It can be seen from an examination of the results that the subject appeared to have a greater sensitivity



KAR



VJH

Figure 12b:Lower thresholds of motion for compression. Experiment 3b.

to compressive motion than to linear motion. This was a statistically significant finding i.e. the observed significant interaction between spatial frequency and stimulus type ($F=4.533; df=4; p<0.001$) and the significant effect of the stimulus type ($F=201.705; df=1; p<0.001$).

As in experiment 3a, the velocity thresholds were invariant with spatial frequency beyond a spatial frequency of 4.4 cycles per degree for both linear and shear. Sensitivity to both types of motion was reduced at the lowest spatial frequencies used.

There was no effect of the task type ($F=1.856; df=1; p>0.05$) indicating due to the significance of the stimulus type (see above) and the spatial frequency ($F=121.214; df=4; p<0.00$) that the pattern of results was probably due to the type of stimulus and the spatial frequency (as found for experiment 3a).

There was a significant interaction between the stimulus type and the task type ($F=5.069; df=1; p<0.05$). This probably reflects the significant effect of the stimulus type rather than any effect of the task.

It is worth noting that data was obtained in a supplementary informal experiment to see if carrying out the experiment with one grating vertically above the other (as for the shear stimulus display) effected the results. It was found that similar results were obtained to those reported above and so it appears that the use of the compressive gratings 'side by side' display as used in experiment 3b has no effect upon the pattern of results.

3.4 Discussion

Discussion: Experiments 1a and 1b

Taking the findings of experiments 1a and 1b together, it appears that the visual system is equally sensitive to the presence of linear, compressive or shearing motion (the equivalence of the detection thresholds). At low velocities (less than 0.5 deg/sec) the visual system is unable at the point of detection to identify (and therefore discriminate) the type of motion. When, at the higher velocities (0.5 - 3.0 deg/sec) this becomes possible shear and linear motion and compression and linear motion are discriminated at the same threshold.

It was hypothesised that if there exist detectors specifically sensitive to shearing or compressive motion then the detection and discrimination thresholds would be equal. This is only the case for the higher velocities used. This means that in order to explain these results in terms of local labelled detectors for compression and shear then one must also postulate local labelled linear detectors (a sensible proposition given that translational - linear type - motions are one of the four local components of retinal flow see introduction). If such detectors exist they are only labelled detectors for their preferred type of motion at higher velocities, at low velocities these hypothesised detectors are unable to signal the type of motion at the point of detection.

Thus, to summarise experiment 1, if there exist local labelled shear or compression sensitive mechanisms then they are accompanied by local linear sensitive mechanisms. At detection threshold (low contrasts) these mechanisms are only labelled (for motion type) at the higher velocities used. At low velocities these mechanisms are only capable of signalling the presence or absence of motion.

There is however no obvious reason why specific local detectors should not be labelled at low velocities, because a good proportion of the motion that an observer sees is in the low velocity range used here. If the visual system is to make use of local detectors, one would expect that they would be able to signal shear, compression or linear motion over all velocities and at the point of detection. If this were not so, little processing economy would be achieved, some other mechanism would need to be used to detect these types of motion at lower velocities.

It is possible to offer another explanation not requiring the existence of local detectors. It is suggested that the detection of the motion types is subserved by local directionally selective mechanisms. These mechanisms could be of the type proposed Adelson and Bergen (1985). Such mechanisms operate upon the retinal image in parallel signalling local leftward or rightward motion and are selective for that particular direction of motion. Thus in this experiment the shearing and compressive stimuli presents the visual system with two oppositely moving gratings. It is suggested that the visual system does not analyse these motions as local shear or compression but analyses the pattern into its local motion directions i.e. as rightward and leftward motion in different parts of the visual field. Similarly with the linear motion the visual system obtains local motion signals which indicate e.g. rightward motion, in all parts of the visual field. The information from the local analysis of image movement direction is then fed to a higher level in the visual system, where a particular type of motion e.g. shear or linear, is identified. One way in which this could be done is by global mechanisms sensitive to the type of image motion that summate (integrate) the local directional information provided by the local motion directional detectors. As shear and compression differ in the direction of the opposed motion relative to the motion boundary, in order to unambiguously identify the motion type these higher order processes would have to have inputs which specified the orientation of the motion boundary. This model explains the fact that the two types of motion (compression and linear or shear and linear) have equivalent detection sensitivities for all velocities tested. As local motion direction detectors with opposite directional preferences are equally sensitive to image motion in their preferred directions (Ball and Sekuler,1980), they will signal the direction of local motion for all parts of the visual field at the same contrast for leftward and rightward motion. As these detectors respond only at a local level they have no sensitivity to the different types of motion present and so signal either leftward or rightward local motion irrespective of whether linear or shear motions give rise to their responses. Hence the local motion detectors will signal the presence of motion at the same contrast for both types of motion used in this experiment, giving rise to equal detection sensitivities. Also explained is the equivalence of the discrimination and detection sensitivities for the higher velocities. If discrimination is mediated by the ability to detect the directions of motion of the gratings, then when these have been analysed the visual system would know what type of motion is present, merely from the number of motion directions present in the image. As the leftward and rightward sensitive local motion detectors have equal sensitivity, local left and right motions are detected at the same contrast. Only two detector responses are required (one from each half of the visual field corresponding to each of the two moving gratings) to signal the type of motion i.e. left and right motion parallel to the motion boundary signals shear motion, left and right motion perpendicular to the motion boundary signals compressive motion, left and left signals linear motion. As the local motion detectors operate in parallel, as soon as at least two detectors respond from different halves of the visual field, (which will occur at the same threshold contrast), then the type of motion is known. Thus the motion type can be discriminated from other motions at the threshold of detection.

A problem exists as to how to explain the results for the low velocities used. The present model can not explain why discrimination is not equal to detection at these velocities. The model needs to be modified to account for these results.

Thompson (1984) carried out a similar experiment to those reported here. He examined detection and discrimination sensitivities for gratings moving in opposite directions while varying spatial and temporal frequency of the gratings used. He found that for the lowest temporal frequencies and the highest spatial frequencies used the ability to correctly discriminate oppositely moving gratings was impaired, while for other combinations of temporal and spatial frequency discrimination was indicative of labelled (directional) channels in the visual system. He suggested that one possible interpretation of these findings was that at detection threshold low temporal frequency channels have a directional preference (preferred direction of motion) but they also respond to some extent to slow movements in the opposite direction. He proposed that if this limit to the sensitivity in the null (non-preferred) direction were to be some constant velocity, then in spatial frequency terms the overlap in sensitivity of oppositely tuned slow channels would be small at low spatial frequencies and high at high spatial frequencies. The channels would remain directionally selective labelled channels, but at high spatial frequencies, slow moving stimuli would be detected by either of two different channels labelled for opposite directions of motion. Thus the actual direction of the stimulus motion would not be discernable to the visual system. This idea may be applied to the present results for the low velocities used. Thompson proposed that the velocity limit of the sensitivity to opposite direction could be 0.3 deg/sec. An examination of the results of the present experiments reveals that two of the low velocities used in this experiment are below this limit. It is at these velocities where the discrimination of the stimuli is not equal to the detection sensitivity. I have proposed that it is directional sensitive mechanisms that underlie the results of this experiment.

Clearly if Thompson's hypothesis is correct, and at detection threshold and at low velocities the visual system can not be sure in which direction the stimuli move, then more information is required by the visual system to disambiguate the responses of the directional mechanisms. This is evidenced by the reduced discrimination sensitivities at low velocities. Detection thresholds remain constant at the low velocities used as the directionally selective mechanisms, although having some sensitivity to opposite directions of motion, signal the presence of a moving stimuli merely by a response irrespective of the direction that is signalled.

Another possible explanation of the observed reduction in the discrimination sensitivities at low velocities is the hypothesised existence of two separate systems to process static and moving stimuli (eg Ikeda and Wright, 1972; Tolhurst, 1973;

Watson and Ahmuda, 1985). These two systems are thought to be distinct in their spatio-temporal sensitivities. The motion system is most responsive to rapidly moving patterns (low spatial frequency and high temporal frequency) while the static system is most responsive to slowly moving or stationary patterns (high spatial and low temporal frequencies). The motion system is thought to be directionally selective and responsible for assigning directional information to image components, while the static system is not. Evidence to support such a conclusion is the finding that direction is judged correctly at threshold contrasts only at velocities of image motion above 1 deg/sec (Watson et al 1980, Thompson 1984) and the fact that the summation of contrasts is directionally selective only above 1 deg/sec (Watson et al 1980). An examination of the results of this experiment show that for velocities below 1 deg/sec discrimination performance is reduced. As these velocities are in the range of the static system then the discrimination process will be impaired at detection threshold contrasts for these lower velocities. This is because the static system does not provide any directional information about the display, and so it will be correspondingly harder to identify the type of motion present. The equivalence of detection sensitivities for the linear and opposed (shear or compression) types of motion for all velocities used in these experiments, could be explained within this scheme if the sensitivities of the two systems (static and motion) were equivalent for the detection of the presence of a stimuli irrespective of the stimulus velocity.

Discussion Experiments 2a and 2b

Taking the results of experiments 2a and 2b together, the observed decrease in the discrimination sensitivities of the stimuli with greater added common velocity, indicates that as greater velocity is added the stimuli become more difficult to discriminate. This is consistent with the findings of Nakayama (1981) and argues against the presence of local shear or compression detectors (at threshold contrasts).

The results indicate that the discrimination of shearing and compressive motion breaks down in the presence of added translational motion. It appears that the visual system is unable to analyse shearing or compressive motion from a translating retinal flow field at threshold contrast. The non-equivalence of the detection and discrimination sensitivities for all added common image velocities indicates that detection is not mediated by local shear or compression (or linear) sensitive labelled detectors.

It is possible to explain these results by suggesting that detection of the motion is mediated by directionally selective motion detectors as discussed in experiment one. When presented with the displays of these experiments the local motion detectors would signal the presence and direction of local motion irrespective of the amount of added common motion or of the stimulus type. Such a suggestion could explain the lack of a significant effect of the stimulus type upon the results of both experiments, such that if detection is mediated by local directionally selective mechanisms then it would not be expected that the type of stimulus would affect the processing and hence the detection and discrimination sensitivities. This is because (as in experiment one), local directional mechanisms only give out information about local directions of motion, and at a local level (within the range of response of these local detectors) there is nothing in the shear, compression or linear displays to indicate what type of motion is present. The problem for the visual system arises when it attempts to discriminate the type of motion present. As more common motion is added to a shear or compression the motion is still a shear or compression but its components are now both moving in the same directions. The signals from the local directional detectors will indicate that for both linear and shear motion (experiment 1a) or linear and compressive motion (experiment 1b) the local direction of motion is in the same direction e.g. to the left or to the right. In the case of shear or compression one of the gratings is moving faster than the other, (indeed the difference between the two grating speeds is constant for all added common image velocities), however the visual system is unable at detection to discriminate the types of motion present as the local directionally selective mechanisms are themselves unable to signal stimulus velocity (Borst and Egelhaaf, 1989).

It therefore appears that the system responsible for the identification (and hence discrimination) of the type of motion does not respond to the difference in image velocity, (otherwise the discrimination would be unaffected by added common velocity and would, as at zero added common velocity, be equal to the detection threshold for this velocity (1.1 deg/sec)). It seems that the system responsible for the discrimination is most responsive to the local directions of image motion. This may be explained if one refers to the discussion for experiment 1. Here it was proposed that either global mechanisms sensitive to shear and compression or cognitive inferential mechanisms could be responsible for the discrimination. These mechanisms it was hypothesised responded to the directions of local motion signalled by the local directional mechanisms. Thus such higher level mechanisms when faced with increasing added common motion at detection threshold, have increasing difficulty in discriminating the type of motion as their responses are dependent upon the sensitivity of local motion detectors to the local directions of motion in the display. A shear or compressive motion, (in directional terms), becomes more like a linear motion with greater added common velocity, i.e. consists of two gratings moving in the same direction. Clearly local direction signals alone give ambiguous information as to the type of motion present. Hence more information is required by the higher level global or cognitive mechanisms in order to discriminate the true type of motion present. This is exhibited in the form of increased contrast for discrimination and hence reduced discrimination sensitivities.

It is worth noting what would be expected if there existed local shear and compression sensitive mechanisms. As the added common velocity was increased the sensitivity would remain invariant. This is because in order to be useful in analyzing retinal flows, such mechanisms should be able to signal their preferred motion type, as the discontinuity between the two halves of the retinal flow field is preserved regardless of the amount of common image motion.

Discussion Experiments 3a and 3b

If there exist shear specific mechanisms in the visual system then one would expect that the discrimination thresholds in each experiment would be equal. This has been found by this experiment.

The gratings presented in this experiment were suprathreshold and were clearly visible to the observer. Thus the observer has no difficulty in detecting the gratings. The problem for the visual system is at what velocity can it just detect that the gratings have moved and thus discriminate the type of movement. Given that the gratings are clearly visible, then it is possible that the mechanisms used to discriminate the different types of motion are in fact cognitive inferential mechanisms that respond to local directional motion signals. The local directional signals could be produced by local directionally selective mechanisms as described above. Two opposite directions of motion signalled from different parts of the visual field corresponding to the positions of the two gratings would be interpreted as being a shearing or compression motion, two same direction signals would be interpreted as being a linear motion, no directional signal would be interpreted as a stationary pattern.

The problem with such an explanation is that there is no obvious reason why shearing and compressive motion should have superior discrimination thresholds to linear motion. Inferences as to the type of motion are only constrained by the ability to detect the local direction of motion, and as such it would be expected that the discrimination thresholds for all three types of motion should be equal.

It could be that these results indicate the presence of mechanisms that respond not specifically to compression, shear or linear motions but a wide range of motion types. It could be that these mechanisms due to their receptive field organisation, give rise to a stronger response to shearing and compressive motions than to linear motion. In order for a mechanism to have such a response it would be required to respond more strongly to two opposed directions of motion which were separated in space than to two similar directions of motion. This hypothetical mechanism would also have to integrate directional signals from more than one location in order to be able to signal the type of motion present (for example shear and compression feature two opposite motion directions at different locations in the retinal flow field).

One possible mechanism is one that responds to the signalled directions of motion from many local directionally selective mechanisms and has a receptive field that covers at least as wide an area as the size of the display in these experiments (ie 1.9 deg of visual angle). It would feature centre surround organisation such that the centre responds selectively to one direction of motion and the surround responds to the opposite direction of motion. The mechanism would respond most strongly when motion in one direction was signalled by the local directional mechanisms for retinal locations in the centre of the mechanisms receptive field and a motion in the opposite direction was signalled for retinal locations in the mechanisms surround.

An example of a mechanisms that could operate in this way is one in which its receptive field centre received excitatory inputs from local directional units having the same preferred direction of motion and its surround would be defined by excitatory inputs from units having the opposite preferred direction of motion. It is likely that the centre of the receptive field would be inhibited by directions of motion opposite to its preferred direction of motion and this would also be the case for the surround e.g. Stromeyer et al (1984) (see figure 13a). This could thus be described as a centre-surround opponent motion mechanisms.

Such mechanisms as this have been proposed previously e.g. Nakayama and

Figure 13a: Centre-surround opponent mechanism as proposed by Murakami and Shimojo (1991,1992,1993)

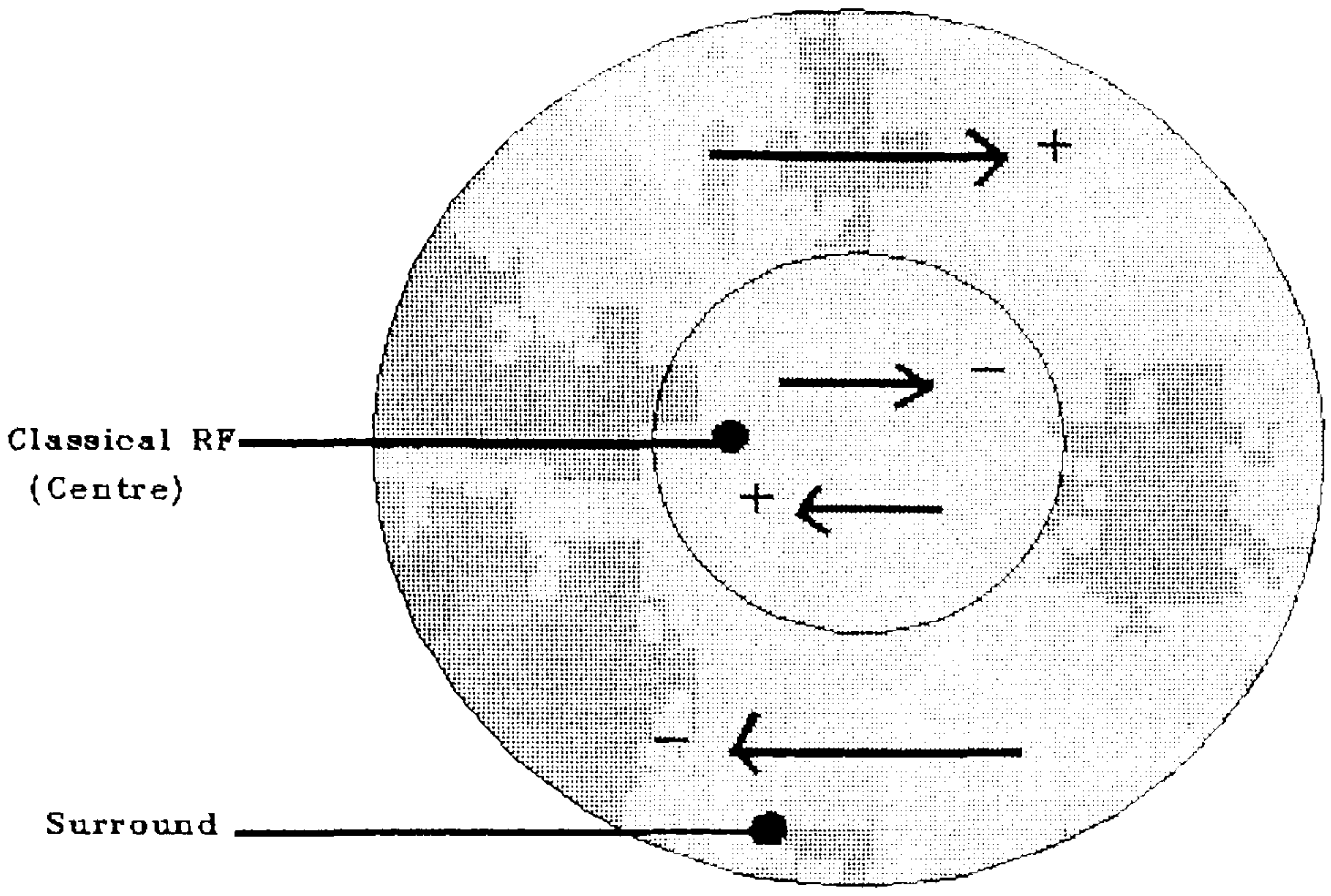
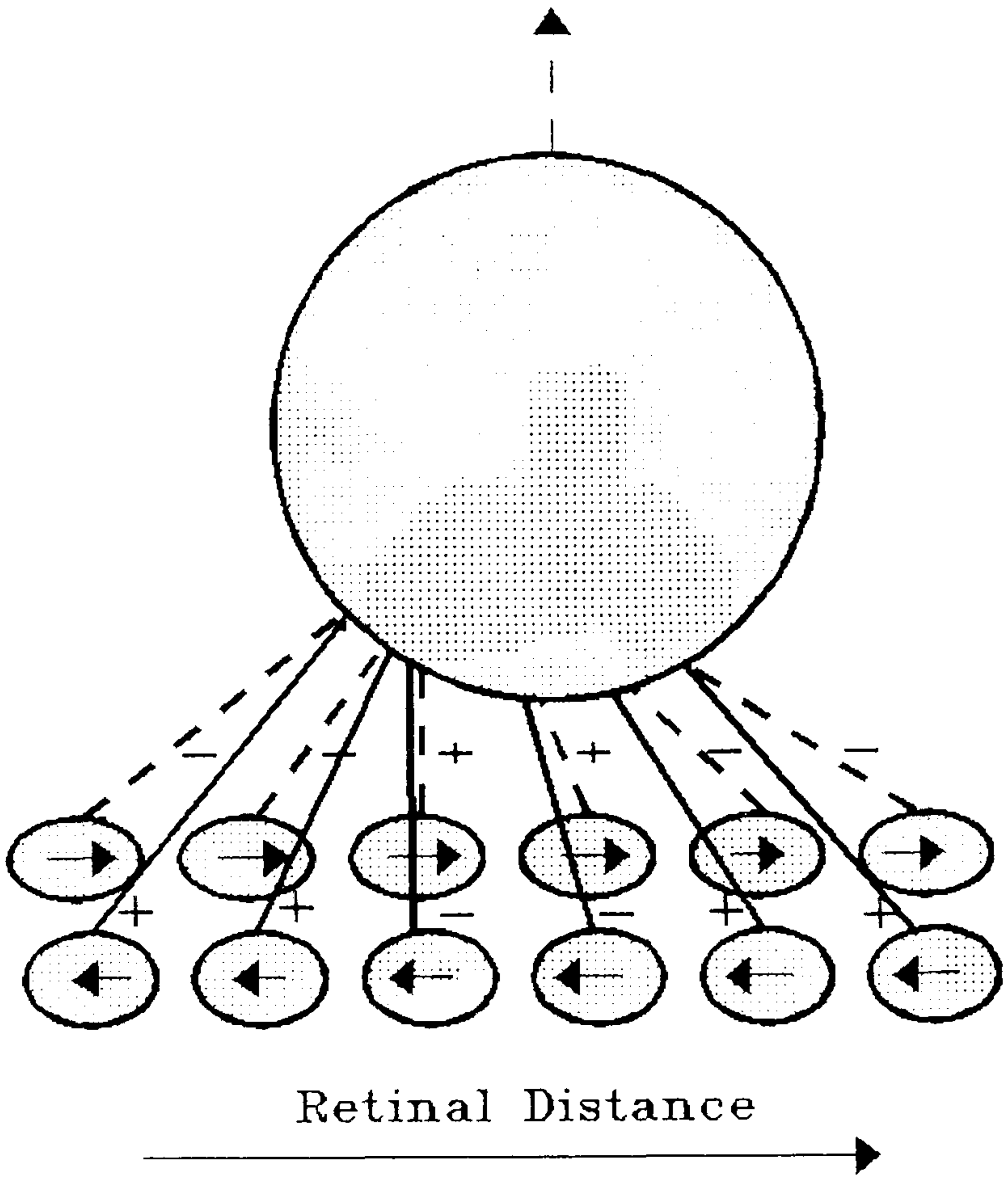


Figure 13b: Local motion detectors feeding into higher level opponent motion mechanism. Note how opposed local motion at the same retinal location inhibits the mechanism, while it is excited by opposed motion from different retinal locations.



Tyler (1981), and Nakayama and Loomis (1974) to explain the detection of shear in optic flows and to explain motion hyperacuity. Murakami and Shimojo (1991,1992,1993) have proposed a similar mechanisms to account for motion capture and induced motion. The model of Murakami and Shimojo (1991,1992,1993) requires that there be a stream of processing starting with an array of local directional units of the type described by Adelson and Bergen (1985) feeding into an array of higher level centre surround opponent mechanisms. Such an arrangement is described in figure (13b). It may be seen how within this scheme greater response to shearing and compressive motion would be expected due to the presence of two opposite directions of motion in the visual field, while reduced responses to linear motion would occur due to the presence of the same directions of motion in all parts of the visual field, leading to greater inhibition of the mechanism. The geometry of the centre surround mechanism is not described by the model for example Murakami and Shimojo (1993) state that they do not assume circular symmetry of the centre-surround mechanism.

Another possibility is to propose that these results are not due to the activity of a centre-surround opponent motion mechanisms per se, but are due to co-operative and competitive interactions between local directionally selective mechanisms. Within this scheme, the interactions between local directionally selective motion mechanisms are excitatory over a short spatial range and inhibitory over a longer spatial range (Nawrot and Sekuler, 1990). Unlike the previously described mechanism, the signals generated by local motion mechanisms are not fed into a higher level centre-surround unit. Within a local patch of the visual field mechanisms with similar directional preferences interact

Figure 14a: Line Element Model of Nawrot and Sekuler (1990. Note how opposed motion signals from the same retinal location inhibit each other while from different locations they facilitate each other.

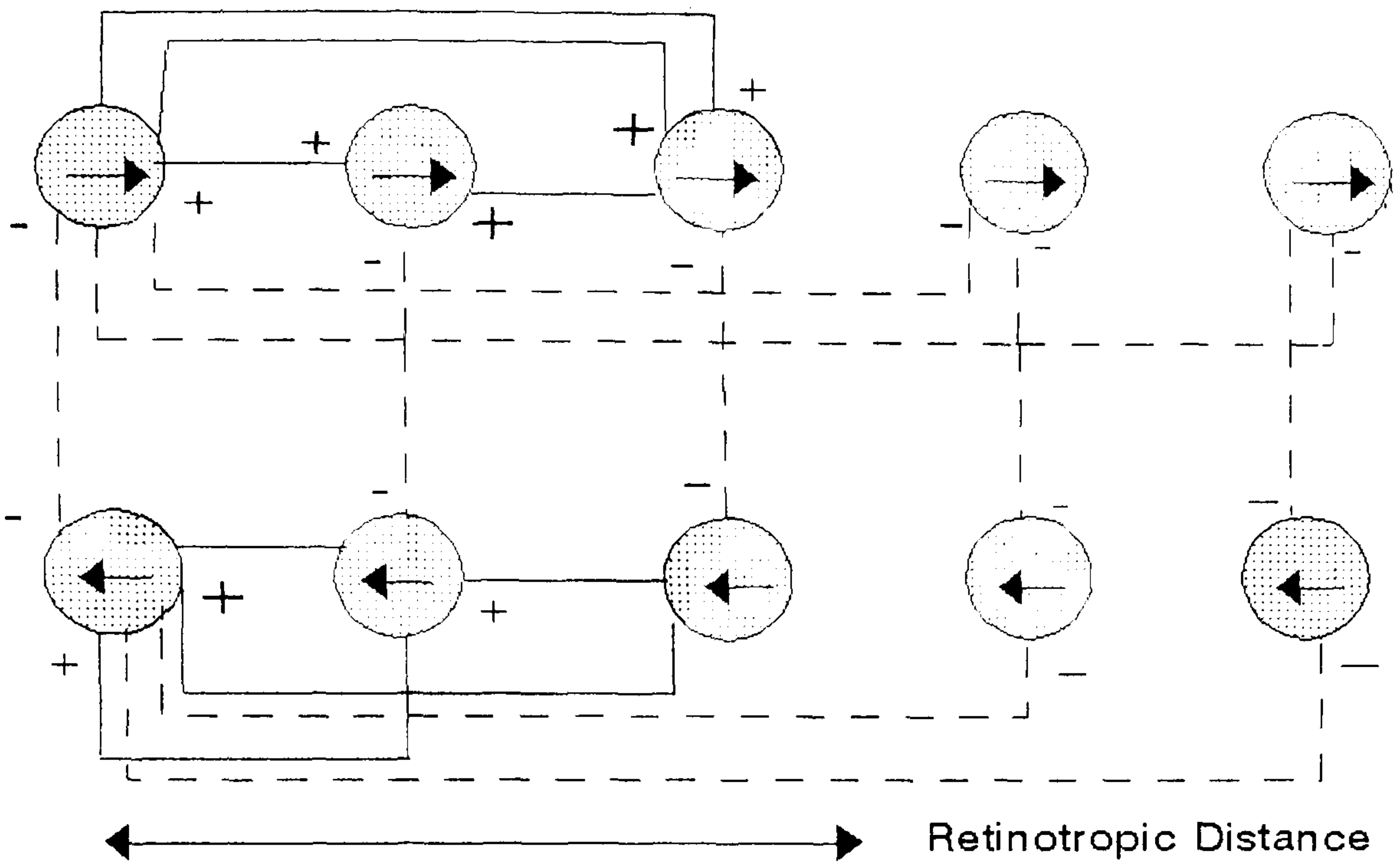
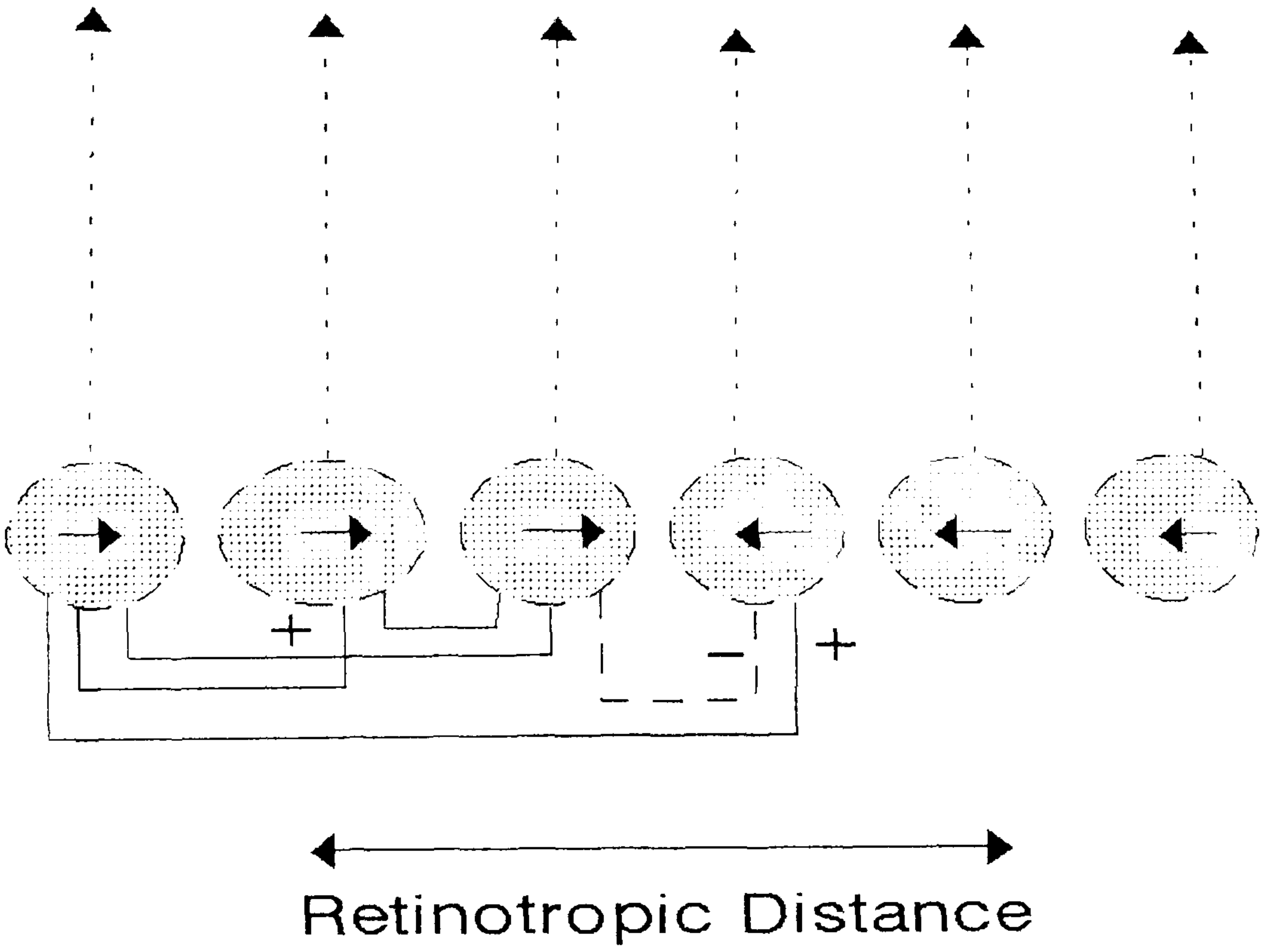


Figure 14b: Line Element Model Showing How Outputs From Each Directional Unit Are Passed on to Higher Level Processes



with each other in an excitatory way, while mechanisms of opposed directional sensitivity interact in an inhibitory way (see figure 14a). Over a larger spatial range mechanisms with opposite directional preference excite one another while mechanisms with the same directional preference inhibit one another. Opposed motion types such as shear or compression thus give rise to lower motion thresholds than are produced by linear motion. This model's structure can be seen by reference to figure 14b. This type of mechanisms has been proposed by Nawrot and Sekuler (1990) in their model of motion capture and induced motion.

It is important to note that these mechanisms are not a shear or compression mechanism per se, rather they are opponent motion mechanism responding most strongly to any type of opposed motion signal.

Some neurophysiological evidence for such mechanisms, with large receptive fields (2 deg at the fovea) has been found in the pigeon e.g. Frost and Nakayama (1983). Allman et al (1985) have also found evidence for directionally opponent interactions within MT cells of the owl monkey i.e. an MT directionally selective cell was maximally stimulated when its preferred direction was presented to the centre of the cells receptive field (the cells classical receptive field) and its non-preferred direction of motion was presented to a region surrounding the classical receptive field and Born and Tootell (1992,1993) have obtained similar results in macaque area MT. The current data does not, however allow any conclusions to be drawn as to which of these two explanations of the lower thresholds for opposed motion should be favoured.

Snowden (1993) obtained similar results to this study. In an experiment using random dot stimuli, he found that the movement thresholds for shearing patterns were less than those for simple (linear) motion. His data revealed that shear thresholds were approximately one half those for linear motion.

Our results at low spatial frequencies imply that the visual system is more sensitive to high spatial frequency patterns moving at slow velocities than to low spatial frequencies moving at slow velocity. This result for suprathreshold contrasts fits in with work on the contrast sensitivity to moving patterns (Robson, 1966; Koenderink and van-Doorn, 1979; Kelley, 1977) which has shown that the low spatial frequency motion sensors of the visual system respond to higher velocities than do the high spatial frequency motion sensors (assuming that one may extrapolate these threshold findings to suprathreshold stimuli).

Thus to summarise experiment 3; the results of this experiment may be explained either by postulating the existence of local shear, compression and linear specific mechanisms, with the shear and linear mechanisms being more sensitive to image motion than the linear mechanisms. This suggestion seems unlikely however on account of the results obtained in experiment 2, where shear and compression sensitivity was observed to be influenced by the presence of common image motion (see discussion of experiment 2 and general discussion). Alternatively there exists some form of opponency in the visual system such that greater responses are generated to opposed motion (shear and compression) then to linear motion. This opponency may take the form of a higher level mechanisms with centre surround receptive field organisation that receive inputs from local directionally selective mechanisms or may be the result of interactions between lower level motion sensitive mechanisms.

The motion opponency explanation is the preferred option, in that it is consistent with the known neurophysiology and also because such an explanation is sensible in terms of processing economy i.e. there is no requirement for several different motion mechanisms each sensitive to a single different motion type.

As this experiment was performed at high suprathreshold contrasts then it is the case that these conclusions are only applicable at contrasts above detection threshold.

3.4 General Discussion (experiments 1, 2 and 3)

The results of these experiments indicate that there is a difference in the way in which shear and compression is processed at low contrasts (detection threshold) and high contrasts (suprathreshold contrasts). At detection threshold it appears that processing of shear and compression is not done by local mechanisms with specific sensitivities to these differential invariants. In addition to this the lack of difference between the detection thresholds for linear and shearing and for linear and compressive motions (experiments 1a and 1b) indicates that the same underlying mechanism mediates their detection. It was proposed that this mechanism is associated with local directionally selective units which analyse the retinal flow pattern into local direction of motion estimates. The response of just one of these units signals the presence of a moving stimulus irrespective of the stimulus type (detection).

At low velocities it was proposed that detection is mediated by non-directional mechanisms. It was argued that identification (and discrimination) at detection threshold for higher velocities, is based upon higher level (than the local directional mechanisms) global mechanisms, which receive inputs from the local directional mechanisms. At low velocities of image motion these high level mechanisms fail in their attempt to identify the type of motion at detection threshold due to detection being carried out by directionally non-selective mechanisms. At detection threshold contrasts, the dependence upon local estimates of direction information in the processing of shear and compression is a finding consistent with the work of Werkhoven and Koenderink (1991) on rotary motion, they proposed that '..the estimation of rotary motion is mediated by local estimations of linear velocity'. Also Kappers et al (1993) found that the detection of divergence was critically dependent upon the translational motion component rather than detection of the divergence per se. This work as well as our current findings are consistent with the suggestion of Van de Grind that 'local information on optic flow fields is obtained by combining bilocal detectors into flow instance detectors; there appears to be no detectors of pure local differential components like divergence, rotation or shear' (van de Grind, 1993).

For higher contrasts it was proposed that there is some form of spatial opponency between locally signalled directions of motion. This gives rise to greater responses to shearing and compressive (opposed) motion than to linear motion. This opponency could be realised by either a specific neural unit with centre surround spatial organisation or by opponent interactions between local directionally sensitive motion mechanisms.

The task now is to propose a scheme into which the findings for the different contrast levels fit. It seems that for the idea of opponency to be viable, this opponency must only occur when the contrast is above a certain level. If this were not so then the results for the detection threshold experiments would indicate a greater sensitivity for shear and compression than for linear motion.

The idea that opponency may occur only at suprathreshold contrasts is consistent with the findings of Stromeyer et al (1984). They found that at detection threshold contrasts two directions of motion were detected by unidirectional mechanisms. For suprathreshold contrast displays they found evidence for mechanisms which were highly sensitive to the difference between the two directions of motion. (It is worth noting also that Stromeyer et al's finding that at threshold contrasts the two directions of motion were detected independently is consistent with the ideas expressed here about the way in which detection is carried out, see discussion of experiment 1).

Why is it the case that opponency occurs only at suprathreshold contrasts ? In order for the effects of opponency to be observed two spatially opposed directions of motion need to be signalled by the local motion mechanisms. If one considers a population of detector mechanisms such as directionally selective units. In terms of contrast the probability of any such mechanism firing in response to its favoured stimulus characteristic, increases with increasing contrast[2]. Hence at low, detection threshold contrasts the probability of any given directional mechanism responding is lower than at higher contrast. The effect of this would be that at low contrasts it is less likely that two motion mechanisms sensitive to opposite directions of motion, will respond than it is at higher suprathreshold contrasts. Clearly this would mean that opponency effects would be less likely at

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[2] As regards motion mechanisms it has generally been found that the lower threshold of motion for discriminating the direction of motion of a grating decreases as contrast increases for contrasts up to 5% (eg Johnston and Wright, 1985). Thus the ability to discriminate the direction of motion of a grating improves up to contrast levels of 5%.

detection threshold contrasts than at suprathreshold contrasts.

The above suggestion is consistent with the work of Stromeyer et al (1984). They suggested that opponency effects would only be observed after some contrast threshold was reached. It should be noted that there is a distinction between the type of opponency described by Stromeyer et al (1984), and that referred to in these experiments. Stromeyer et al refer to opponency between motion mechanisms which respond to motion in the same retinal location i.e. spatially localised opponency. By contrast opponency in these experiments refers to opponency between motion mechanisms which respond to motion in different retinal locations i.e. spatial opponency. This distinction has been made also by Raymond (1993).

It was noted that at very low velocities detection is mediated by directional non-selective mechanisms. It was also proposed that opponency occurs between local directional signals. How then is it possible at low velocities for opponent processes to produce any meaningful output if there are no directional signals to go on ? This problem may be countered. It has been suggested that the non-directional mechanisms have some residual directional sensitivity (Thompson 1984), although at a single unit level this is ambiguous in signalling the direction of motion. Further, opponency occurs not just between two opposed local mechanisms but is based upon interactions between several such mechanisms (Nawrot and Sekuler, 1989). If signals from a large number of these non-directional mechanisms are averaged together as is proposed, then the ambiguity in the signals can effectively be reduced. Opponency effectively increases the signal to noise ratio of the local noisy directional units, by averaging the outputs of several local motion mechanisms. Thus pure unambiguous direction signals are not required for opponent processing, and thus for the effects of opponency to be evidenced.

Thus detection of the stimuli is mediated by directionally selective mechanisms that respond to one direction of motion only. The outputs from these mechanisms are subjected to some form of centre surround opponency which can either be due to interactions between local motion mechanisms or by these mechanisms feeding into a higher level centre surround mechanism. Opponency is less likely to occur at detection threshold contrasts and therefore a certain level of contrast is required in order for opponency effects to be evidenced. At threshold contrasts where the opponent mechanisms do not function, discrimination of stimuli is carried out by high level global shear and linear mechanisms, whereas at suprathreshold contrasts discrimination is mediated by the opponent processes which give rise to the observed greater sensitivity to shearing and compression than to linear motion.

Following the rejection of local shear and compressive sensitive mechanisms as an explanation of shear and compression sensitivity, we will go on to examine the effects of manipulations of various stimulus characteristics (spatial frequency and grating orientation) upon the sensitivity of observers to shear and compressive motion. On the basis of these experiments it was hoped that this opponent process model would be further characterised in terms of the level of processing that opponency occurs.

Chapter 4: Effect of different spatial frequency components on shear and compression processing

The experiment reported in this chapter investigated the effect of components of different spatial frequency upon the perception of shear, compression and linear motion. The results were discussed in terms of the opponent process model proposed in the previous chapter.

Experiment 4

4.1 Introduction

Previous work with shearing and compressive type motions has thus far failed to examine the effects of defining the motion with two different spatial frequencies. This is not surprising given the fact that most previous work with shear and compression has been done using random dot stimuli e.g. Richards and Lieberman (1982), Regan (1986), Van Doorn and Koenderink (1983), Nakayama (1981).

In contrast to these previous experiments, sinusoidal grating stimuli were used in this experiment. Sinusoidal grating stimuli were used as the spatial frequency content of sinusoidal gratings may be controlled very easily, allowing simple shearing and compressive displays to be created from components differing in spatial frequency.

This experiment is of some theoretical interest. It is generally accepted that the initial stages of visual perception involves spatial filtering of the visual image with bandpass filters e.g. Campbell and Robson (1968). These spatial filters are thought to have spatial frequency bandwidths of approximately one octave. Thus all visual processing proceeds, initially within a number of parallel spatial frequency sensitive channels. In view of this it is interesting to find out if sensitivity to shear and compression occurs within spatial frequency channels i.e. is the sensitivity to shear and compression maximal when the components making up the motion are within the same spatial frequency channel (within one octave of each other) or is sensitivity not effected by differences in spatial frequency between components.

Current theories of motion perception (Fennema and Thompson, 1979; Adelson and Movshon, 1982; Movshon, Adelson, Gizzi and Newsome,1986) involve a two stage process (see figure 15). The first stage involves local decomposition of the image into one dimensional spatial components of various orientations and in directions of motion perpendicular to the component orientation. The second stage involves the recombination of all the local motion signals found at a given spatial location. The aim of this is to find a single direction and speed defining the motion at a particular location in the visual image with which all the component motions are consistent. This is done over

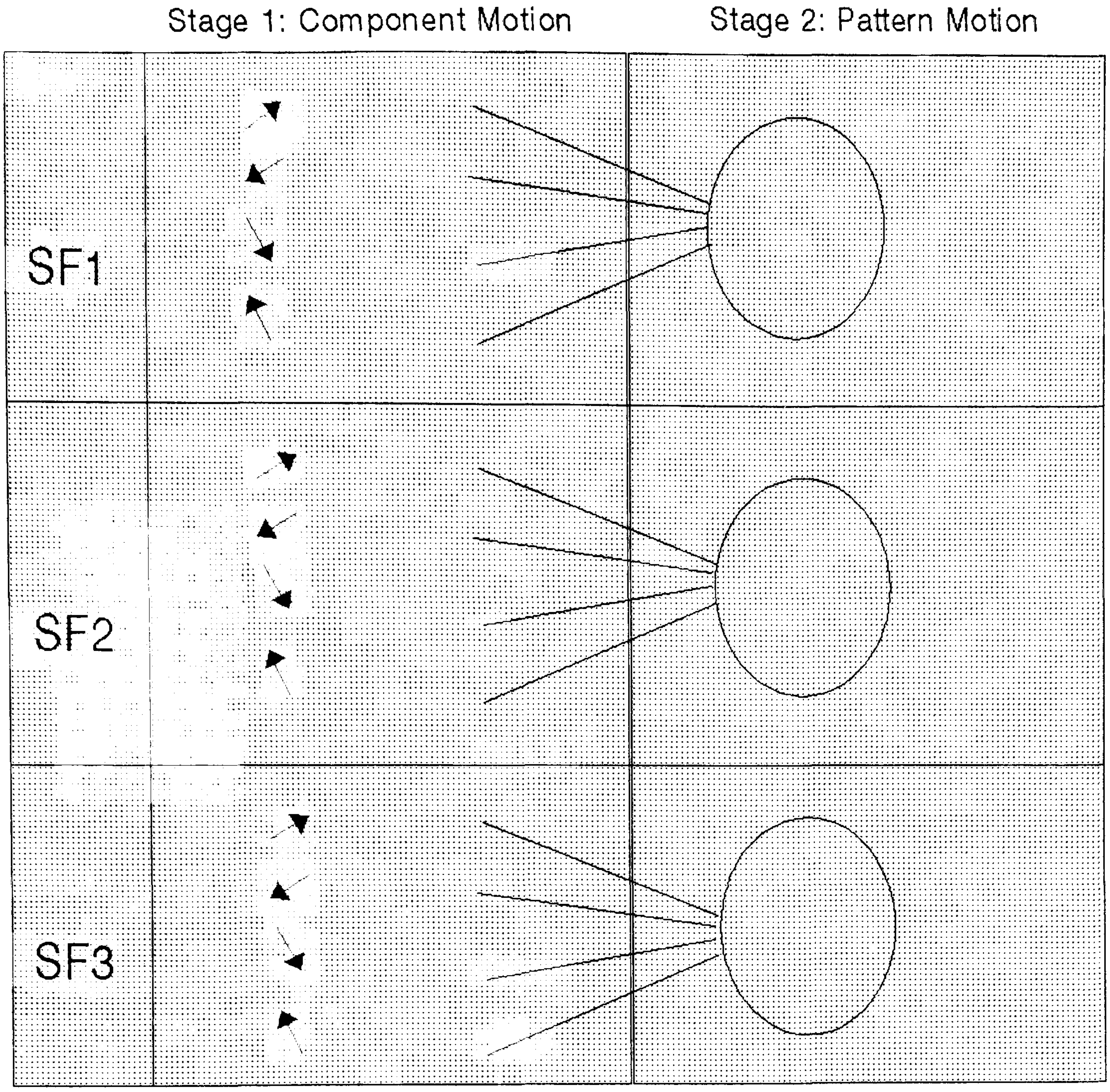


Figure 15: Schematic diagram to illustrate main features of Two Stage Models of Motion Perception.

each spatial range (spatial frequency band). The second stage is essentially processing two dimensional pattern motion. Smith (1992) (see figure 16) has recently modified the above two stage models in the light of new data. When exploring two stage models of motion perception a convenient stimulus is a plaid which comprises two sinusoidal gratings of different orientations each moving in a direction perpendicular to its orientation. The two gratings are superimposed onto each other. The resulting percept is one of a rigid plaid motion moving coherently in a new direction. The perceived direction of motion of the plaid is normally that predicted by the stage two of the above models. It is generally held that coherent motion is only observed when the two components are of similar contrast and of similar spatial frequency i.e. within one octave of spatial frequency of each other (Adelson and Movshon, 1982). Smith sought to examine the limits of coherent motion of plaids in terms of the spatial frequencies of the plaid components. For a variety of contrasts (5% to 60%) and a range of speeds of component motion, Smith obtained estimates of the coherence of the plaids, using plaids made up of different spatial frequency components. He found that for the higher contrasts coherence was obtained when the spatial frequencies of the components differed greatly, the maximum difference being between three and four octaves of spatial frequency. This result was clearly contrary to the expectations of the two stage models. Two stage models (eg Adelson and Movshon, 1982) propose that coherence should not be obtained for such large differences in spatial frequency as there is no pooling across spatial frequency channels of component motion information. Smith (1992) proposed that his results could be explained by modifying the two stage models. He suggested

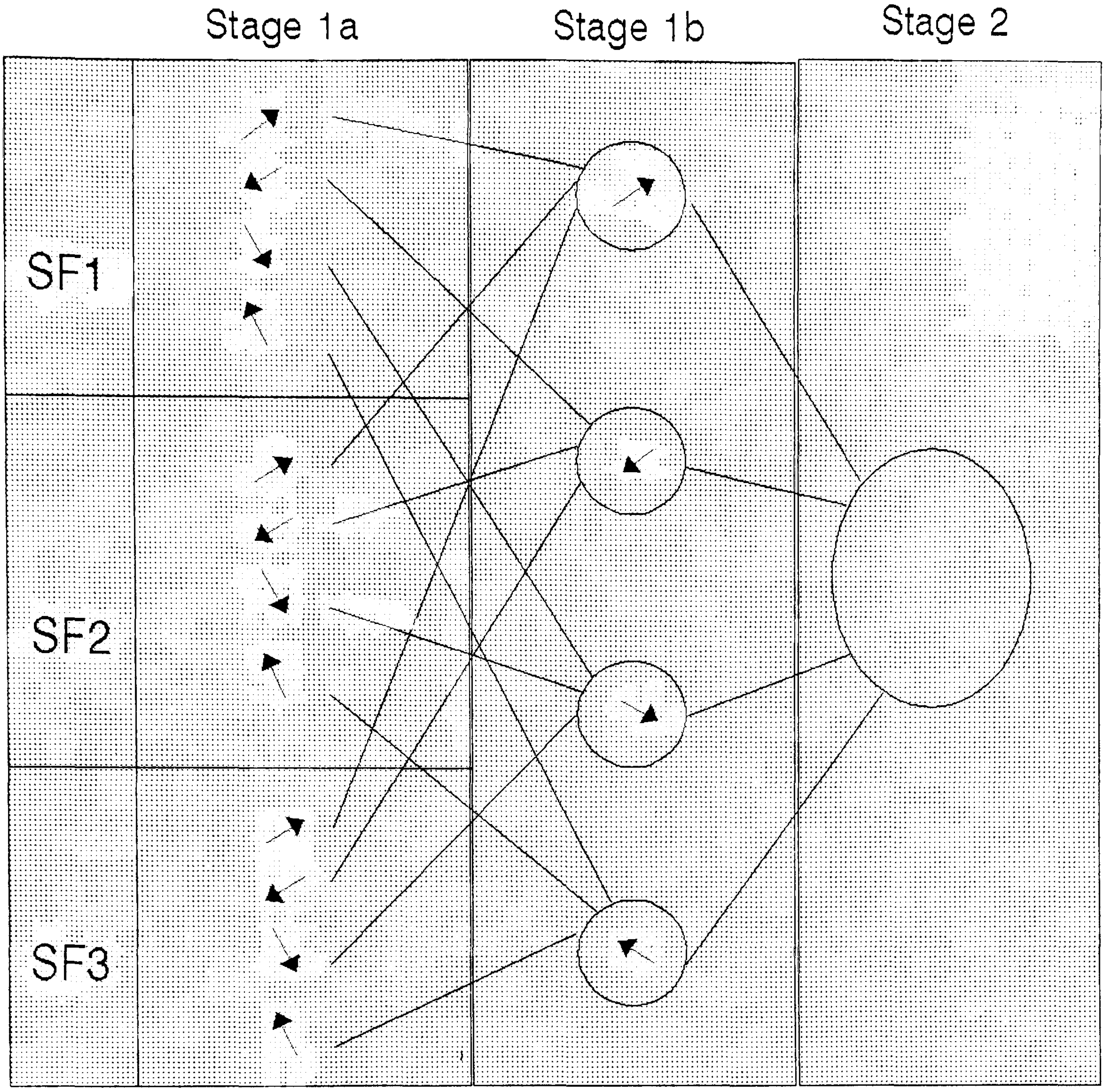


Figure 16: Diagram of Smith's Model (Smith, 1992). This model repreesents motion processing at a single retinal location. (For explanation see text).

incorporating a stage 1b between stage 1a, (the first stage in the above models computation of component motion) and stage 2. Stage 1b features pooling across spatial frequencies of outputs from stage 1a which have a common direction of motion. This gives rise to a spatially broad band signal, encoded in terms of direction. It also predicts that coherence should be observed between components of different spatial frequency.

Our previous experiments (expts 1 to 3) have indicated that the sensitivity to shear and compression is constrained by the visual systems ability to detect local directions of image motion. Further our results have shown that it is unlikely that there exists specific shear and compression sensitive mechanisms in the visual system. The upshot of this is that before shear or compression can be signalled, the visual image has to be analysed into its local directions of motion. The implication of this in terms of two stage models is that shear and compression are processed at some stage after stage 1, i.e. after local component directions of motion have been obtained.

In experiments 1 to 3, it was observed that at high contrasts there is a difference in the way that shear or compression and linear motions were processed. It was suggested that this reflected some sort of directional opponency effect which gives rise to greater responses to opposed motion than to linear motion. It was decided to carry out this experiment at the same high contrast levels as experiment 1 (50% contrast), as it appears that at such contrast levels there is a real difference between responses to the two types of motion.

If opponency effects are responsible for the suprathreshold differences in the responses to shear and compression, and linear motion, it is interesting to speculate as to the pattern of results that would be expected from this experiment, with particular reference to the two stage models described above. Within the two stage model framework, and accepting Smith's (1992) modification of these models, the results of this experiment could be used to give clues as to the location of the hypothesised opponency effects, (in terms of the level of processing), in the visual system.

Smith's modification (Smith 1992) of the two stage model will be used as the theoretical framework for this experiment. It is believed that this is valid given that Smith based his conclusions upon the higher than expected coherence ratings obtained at high contrasts (40% to 60%). These contrast levels are of the order of those used in our experiment 1, where evidence for directional opponency was found, and are of the order of those to be used in this experiment (50%). Thus if it is the case that the kind of processing occurring at Smith's hypothesised level 1b were contrast specific and only operating at higher contrasts, the processing of level 1b would still be in operation at the contrast levels used in this experiment. Hence it is argued that statements about processing levels made with reference to Smith's model are valid.

In Smith's formulation, stage 1a involves computation of component motions which are computed within spatial frequency bands. At Stage 1b information signalling common direction of motion is pooled across spatial frequency. If it is the case that the perception of shear and compression is affected by a difference between the spatial frequency of the components then the results would be expected to show it becoming increasingly more difficult to discriminate shear and compression respectively, from linear motion. As a result the lower thresholds of motion for shear and compression would be expected to increases as the difference between the spatial frequency components increased. Also there would no longer be any advantage in terms of velocity threshold (shear and compression lower than linear) of shear and compression over linear motion. Such a finding would imply that the directionally opponent interactions hypothesised to underlie shear and compression processing, would be located at a stage before Smith's stage 1b and after stage 1a. This is because it has already been established (expts 1 to 3) that shear processing is constrained by the ability to detect local directions of motion (as happens within spatial frequency bands at stage 1a). An effect of spatial frequency as described above would indicate that at the stage when the opponency effects occur, the visual system has not pooled spatial frequency responses and is operating within spatial frequency bands. Thus the two opposed directions of motion will not be expected to interact with each other as they are created by two different spatial frequencies and are as it were trapped within independent spatial frequency.

If on the other hand no effect of spatial frequency is observed, in which case results similar to those found in experiment 1 would be obtained. It may be suggested that the opponency effects would occur at a level either at or after Smith's stage 1b. This is because at stage 1b the visual system now has a broad band directional signal to work with. This would mean that in the case of a shear or a compression composed of two different spatial frequencies, the two local directions would have been computed at stage 1a and then the stage 1b processing would effectively remove the, 'split,' between the two directional signals in terms of spatial frequency. This would then leave the visual system with two opposed motion directions irrespective of the spatial frequency of the components. Thus stage 1b processing allows the two opposed motion directions to interact with each other. Opponent effects could then operate upon the two opposed directions of motion giving rise to greater responses to shear and compression than to linear motion, as found in experiment 1.

4.2 Method

Apparatus

Patterns were generated for this experiment by an Innisfree Picasso under microcomputer control, using a CED 1708 interface. They were displayed on a Tektronix 608 monitor with a P31 phosphor. Each frame in the display could be specified independently. The frame rate was 202 Hz. Responses were obtained using a two button response key.

Display

The basic displays for these experiments were identical to those of experiment 3, consisting of 2 suprathreshold vertical sinewave gratings displayed on screen so that one was vertically above the other. The two gratings were separated by a vertical distance of 0.8 cm. The gratings filled the screen from left to right, each grating covering an equal area of the screen. The display subtended a visual angle of 1.9 degrees at the viewing distance of 300 cm. The drift rate of the grating was used to define the velocities of the gratings. This was controlled by phase control giving 7 bit resolution of spatial phase per frame.

As for experiment 1, four types of display were defined. Shearing motion, compression motion, linear motion and a stationary grating display. These were as described for experiments 1 to 3.

The starting phase of each grating was randomised from trial to trial as a control against the subject using vernier acuity cues to detect and identify the motion types. The directions of motion of the gratings were varied from trial to trial as for experiment 3.

In this experiment the two gratings which define the displays were each of different spatial frequency. A standard spatial frequency of 1 cycle per degree was defined. The second spatial frequency which was kept constant over each trial within an experimental run and varied between experimental runs. The spatial frequencies used gave differences in spatial frequency between the two gratings of 0, 0.8, 1, 2, 3 and 4 octaves for experiment 4a, the spatial frequencies defining these differences being all relative to the standard (1c/deg) spatial frequency and were 1 c/deg, 1.5 c/deg, 2 c/deg, 4 c/deg, 8 c/deg and 16 c/deg respectively.

For experiment 4b the spatial frequency differences were 0,0.8,1,2 and 3 octaves, corresponding to spatial frequencies of 1 c/deg, 1.5 c/deg, 2 c/deg, 4 c/deg and 8 c/deg relative to the constant spatial frequency of 1 c/deg.

The position of the variable and standard grating in the display was randomly varied from trial to trial for both static and moving displays, such that one of them was the upper and one was the lower grating. The position of the variable and standard grating was kept constant for the stationary display relative to the moving display on a given trial. Thus, for example if on a given trial, the upper grating was the variable grating for the moving display, then it would also be the upper grating in the stationary display. All gratings in this experiment were displayed at 50% contrast.

As in experiments 1b, 2b and 3b an expansion motion control stimulus was generated for experiment 4b, again no data was collected for this expanding motion.

All the moving gratings moved with the same speed, 0.1 deg/sec.

Procedure

Experiment 4 consisted of two sub-experiments. One was concerned with shearing motion (experiment 4a) and the other was concerned with compressive motion (experiment 4b).

A two alternative forced choice procedure was used. Each experimental run was separated into a series of trials. On any given trial the type of motion (linear or shear for experiment 4a / linear or compression for experiment 4b) to be shown was randomly selected. The moving stimuli could be placed into one or other of two time intervals each of which was 100 msec in duration. There was an inter stimulus interval of 100 msec duration where the screen was left at mean luminance. Into the other time interval was placed the stationary stimulus. An experimental run was initiated by the observer depressing one of the response keys.

On any given trial the observer was presented with two types of grating pattern. One moving the other stationary. For experiment 4a the moving pattern could be linear or shearing motion. For experiment 4b the moving pattern could be either linear or compressive motion. The task of the subject for both experiments was after presentation of the second interval to make two key press responses. The first was to indicate in which interval he had seen a moving stimulus (discrimination of motion from stationary) and the second response was to indicate which moving stimulus type he had seen (Experiment 4a linear or shear/ experiment 4b linear or compression), this second response constituted identification of stimulus type.

Thus for experiment 4a lower thresholds of motion were obtained for discriminating shear and linear type motion from stationary and for the identification of shear and linear motion. For experiment 4b, lower thresholds of motion were obtained for the discrimination of compression and linear motion from stationary motion and for the identification of compression and linear motion. Thus for each experiment four thresholds were obtained from any given experimental run. The thresholds were in terms of velocity i.e. the lowest velocity at which the task could be performed : lower thresholds of motion. A staircase procedure was used. The velocity at which the subject was 75% correct for each judgement was recorded as the threshold for that particular judgement.

The reported thresholds are the result of at least three experimental runs. The thresholds reported have standard errors of a maximum of ten percent.

For experiment 4b no data was collected for the control expanding motion type and the subject responded if he considered this motion to be present as in experiments 1b, 2b and 3b by pressing the third response key.

Subjects

The subjects for this experiment were the author KAR and VJH a subject who was naive to the aims of the experiment. KAR was male, was 26 years old with normal uncorrected vision and was an experienced psychophysical observer. VJH was female, 24 years old, has normal uncorrected vision and is inexperienced as a psychophysical observer.

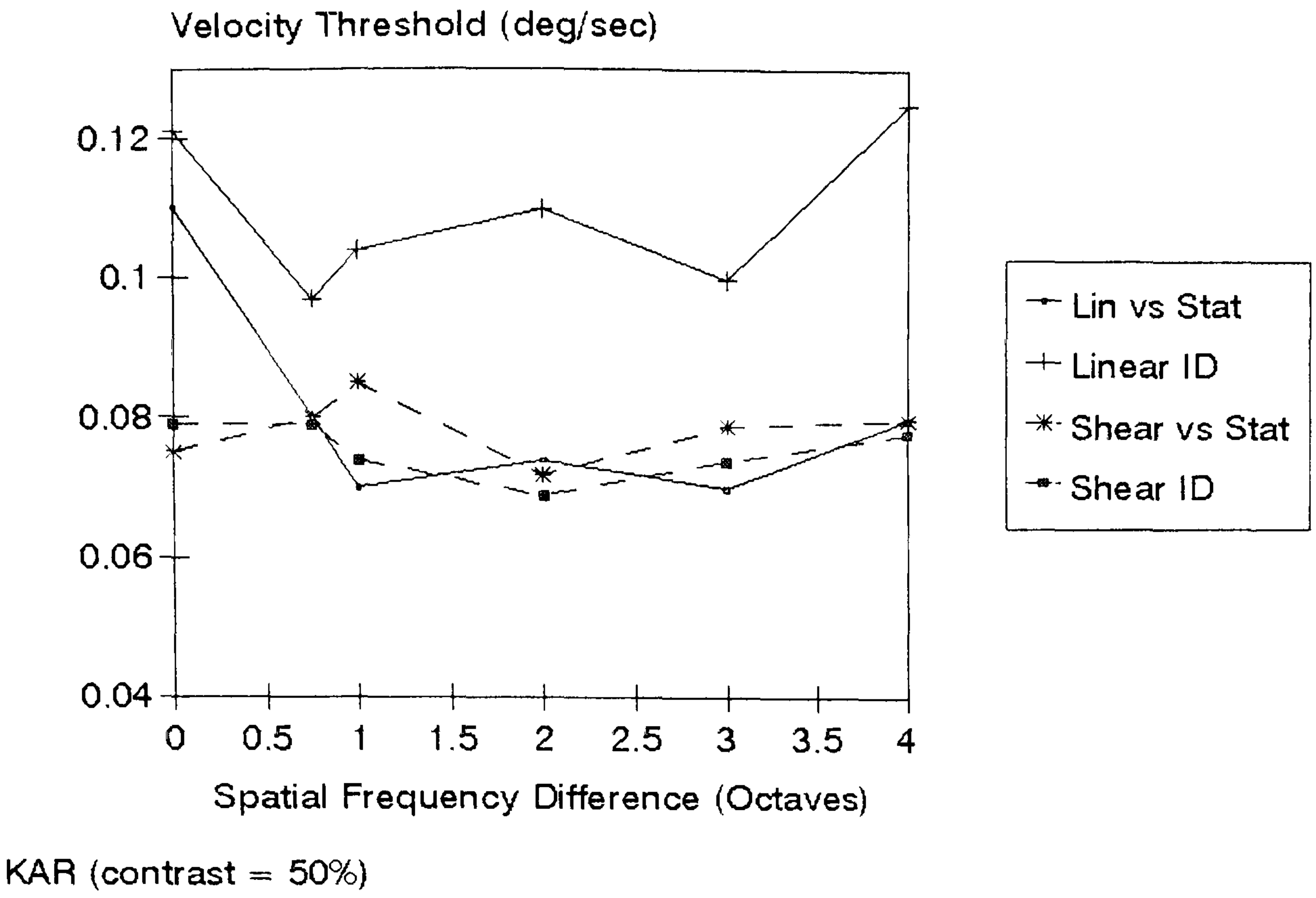
4.3 Results

Experiment 4a

(See fig 17a) Firstly examine the results of experiment 4a (shearing motion). It may be seen that the general trend of the data is for the shearing motion type to have lower motion thresholds than the linear as observed for experiment 1, over all the spatial frequency difference range. Statistical testing of the data confirmed this observation i.e. there was a significant effect of the type of motion ($F=47.593$; $df=1$; $p<0.001$).

The thresholds for shear discrimination from stationary, shear identification and linear identification can be seen to be reasonably invariant with increased spatial frequency difference. The threshold for the discrimination of linear motion from stationary for both subjects, can be seen to reduce from a velocity of the order of that for linear identification, with increasing difference between the two spatial frequencies. Analysis of variance revealed that there was a significant effect of the task i.e. ($F=21.025$; $df=1$; $p<0.001$). In addition there was also a significant effect of the spatial frequency difference, ($F=3.909$; $df=5$; $p<0.01$). These significances, are probably reflecting the relatively great decrease in thresholds for the linear discrimination from stationary result over the first octave.

It is noteworthy that there was no significant interaction between the spatial frequency difference and the type of task i.e. ($F=0.825$; $df=5$; $p>0.05$). There



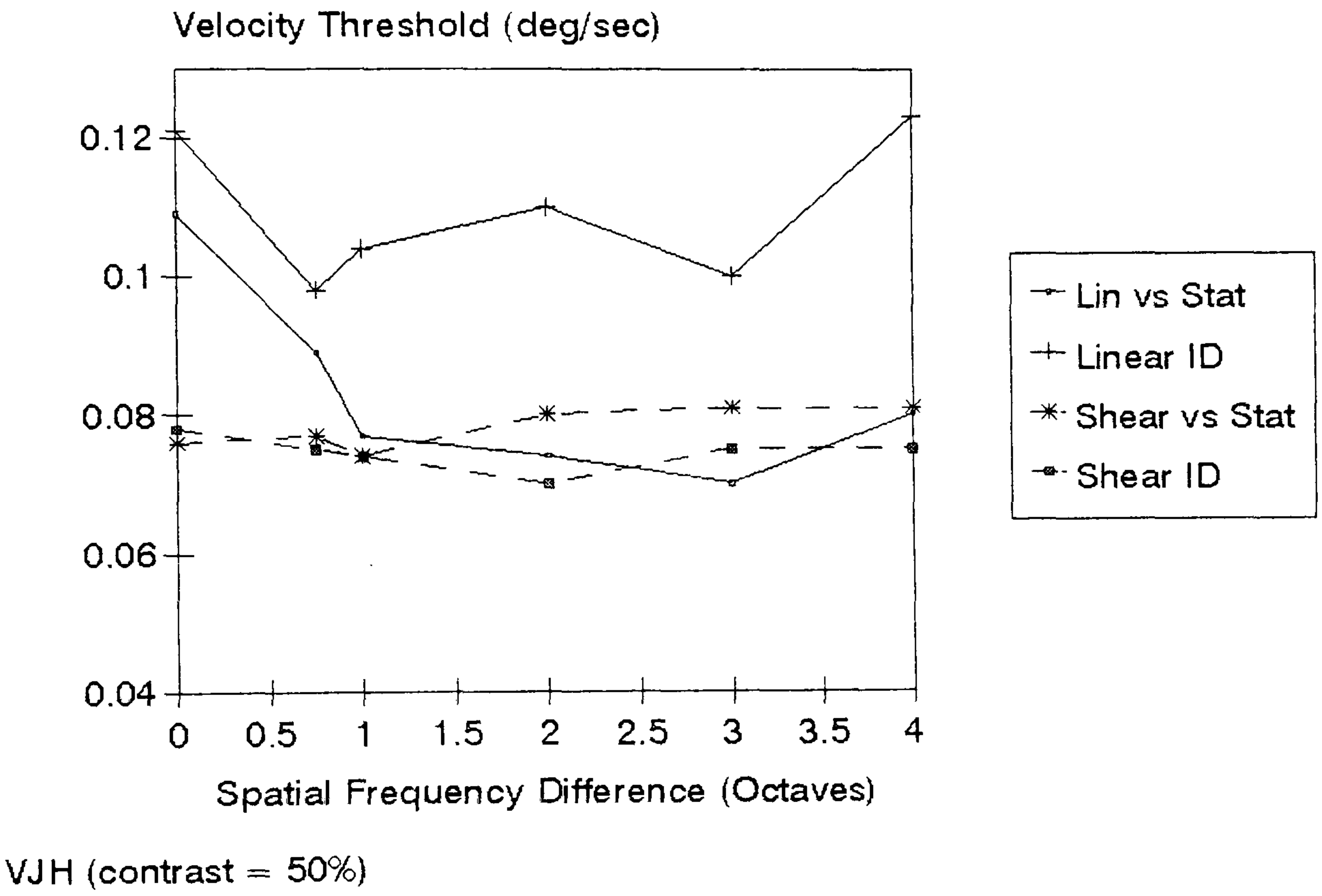


Figure 17a: Lower thresholds of motion for shear made up of two different spatial frequencies. Experiment 4a.

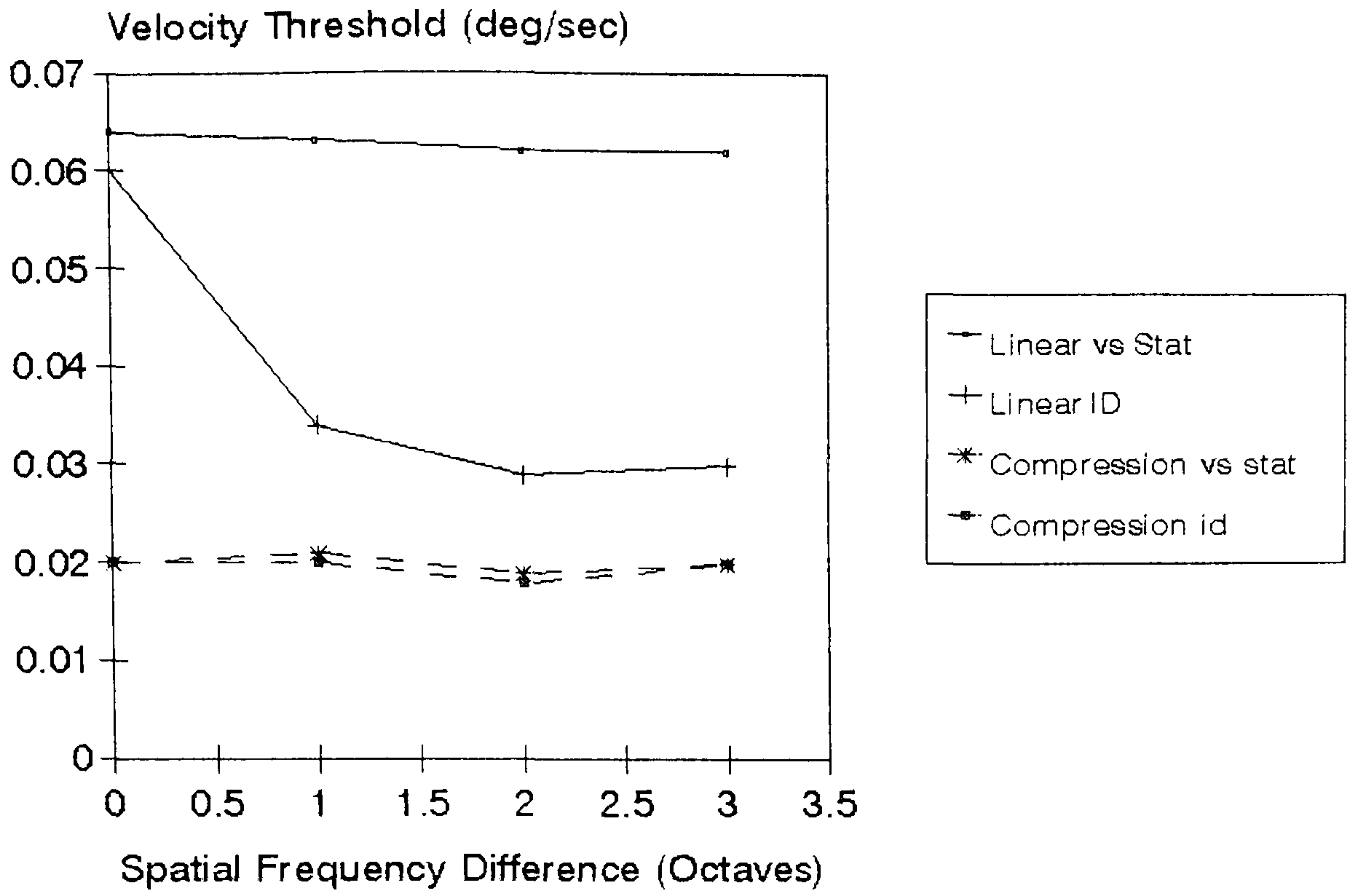
were significant interactions between, the spatial frequency difference and the type of stimulus (F=4.588; df=5; $p<0.01$), and between the task and the stimulus type i.e. (F=42.237; df=1; $p<0.000$) it is argued that these significant interactions are the product of the significant effect of the type of stimulus such that shear has lower thresholds than linear motion and the reduction in the linear discrimination threshold with increasing spatial frequency difference.

Experiment 4b

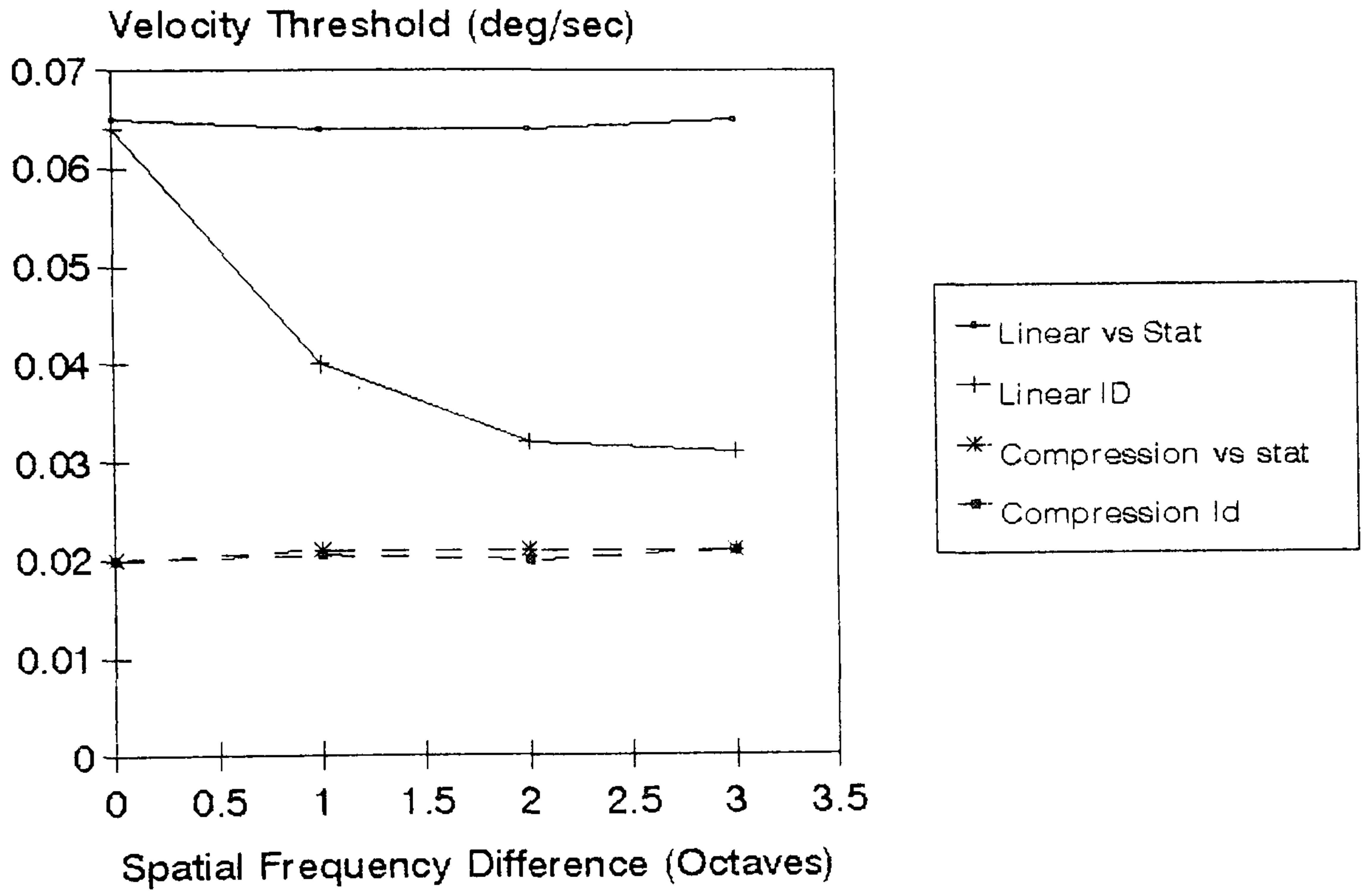
Examining now the results for experiment 4b (compression) (figure 17b). It can be seen that the results for this experiment are similar to those obtained for experiment 4a. Compressive motion has been found to have lower motion thresholds than linear motion over the entire range of spatial frequency differences used. These results are also consistent with those obtained for experiment 1b (compression, same spatial frequency components) i.e. compression had lower velocity thresholds than linear motion for all spatial frequency differences. Statistical testing of the data revealed that there was a significant effect of the type of motion (df=1; F=23.279; p=0.001).

The thresholds for compression discrimination from stationary, compression identification and linear identification can be seen to be reasonably invariant with increasing spatial frequency difference for both subjects.

The threshold for the discrimination of linear motion from stationary can be seen to decrease with increasing spatial frequency difference for both subjects. Analysis of variance revealed a significant effect of the task (df=1; F=5.637; p=0.001). There was also a significant effect of the spatial frequency difference



KAR (cont = 50%)



VJH (cont = 50%)

Figure 17b: Lower thresholds of motion for compression made up of two different spatial frequencies. Experiment 4b (df=4; F=4.036; p=0.008). As for the shear experiment (experiment 4a) it is argued that these significances reflect the relatively great decrease in the threshold for the linear/stationary discrimination.

Again there was no significant effect of the interaction between spatial frequency difference and task type for both subjects. There were significant interactions between the task and the stimulus type (df=1; F=32.717; p=0.001), and between the spatial frequency difference and the stimulus type (df=4; F=9.105; p=0.001). Again it is argued that as was the case for the shear experiment, these significant interactions reflect the significant effect of the stimulus type as compression has lower thresholds than linear motion and the linear/stationary discrimination threshold reduces with increasing spatial frequency difference.

4.4 Discussion

The results of this experiment indicate that a difference between the component spatial frequencies making up the shear and compression motions has little effect upon the relative sensitivity of the visual system to the two types of motion i.e. broadly similar results were obtained for this experiment as were obtained for experiments 3a and 3b.

It was noted for both experiments 4a and 4b and for both subjects, that the velocity thresholds for the discrimination of the linear type motion from the stationary display were different to the results of experiments 3a and 3b, i.e. the thresholds were not equal to those for the identification of linear. Indeed these results showed improved performance with increasing difference between the two spatial frequency components. It is possible to explain this finding by suggesting that what is being detected in this situation is the motion of the higher spatial frequency component. It is known that the visual system responds well to high spatial frequencies moving at slow velocities (Robson, 1966; Koenderink and van - Doorn, 1979; Kelly, 1972). The linear/stationary discrimination task of experiments 4a and 4b, merely requires the observer to state in which interval he saw motion without any requirement to say what that motion was. Consequently due to the greater sensitivity of the observer to high spatial frequencies, it would be possible for the observer to detect a moving high spatial frequency at a lower velocity than the lower spatial frequency (1c/deg for this experiment), and thus to carry out the discrimination of linear from stationary at a lower velocity of stimulus motion. Thus the observed reduction in threshold with increasing spatial frequency difference.

It was also observed that this improvement in the discrimination threshold for linear verse stationary displays, seems to reach a ceiling (in terms of sensitivity) when the threshold reaches the level of the shear and compression thresholds. This suggests that shear and compression sensitivity is equivalent to the maximal sensitivity to a single moving grating.

Within our theoretical framework, these results indicate that the opponent processes suggested to underlie the suprathreshold processing of shearing and compressive motion, are responsive to opposed motions of different spatial frequency. As a result of this it may be suggested that these opponent processes occur after stage 1a and either at or after stage 1b of Smith's model (Smith 1992) of motion processing.

It thus appears that what is important in the processing of shearing and compressive motion is the broad band direction of motion signalled as a result of stage 1b processing as opposed to the directions of motion signalled within spatial frequency bands.

Adding these findings to the suggested model of shear and compressive processing. It was argued that shear processing is constrained by the ability to detect local directions of motion. Opponent interactions then operate upon these local motion direction signals giving rise to greater responses to opposed motions such as shear and compression than non-opposed motions such as linear motion. It appears that these opponent interactions occur across spatial frequency and not within spatial frequency bands or channels. Thus it can be suggested that the opponent interactions occur between spatially broad band local directional signals. We thus have a model in which a suprathreshold shearing or compressive motion stimulus is firstly analysed into local directions of motion via local directional mechanisms within spatial frequency bands. Similar local directions of motion are then pooled across spatial frequency to produce a broad band local directional signal. Local broad band directional signals from different parts of the visual field are then subjected to opponent interactions which give rise to greater responses to opposed motions such as shearing and compressive motion than to linear motion. It is possible that the processing of the spatial frequency specific component motion signals could be being pooled at the same time as opponency effects are in operation, and so the pooling and opponency effects do not constitute separate stages of processing, but are part of the same stage. It is not possible from these findings to choose between these two possibilities.

An interesting question is to consider if there exists any physiological correlate of the kind of processes detailed here to account for the results of this experiment. Studies of area MT (an extra striate cortical area thought to be involved in motion processing, Newsome and Pare, 1988) in primate brain using plaid type stimuli have revealed that in addition to neurons that respond to pattern motion (tentatively identified with stage 2 processing in the two stage models) the majority of the MT neurons respond to motion of one or other of the plaids components (Gizzi et al 1983). It has also been noted that MT neurons are much more broadly tuned for spatial frequency than neurons in earlier stages of visual processing e.g. area V1 (primary visual cortex). Indeed many of these MT neurons had spatial frequency bandwidths of greater than 4 octaves and few of them had bandwidths of less than two octaves (Newsome, Gizzi and Movshon, 1983). Allman et al (1985) further found that some neurons in MT responded to a favoured direction of motion when the motion fell within the classical receptive field of the cell, however when that same motion was presented so that it did not fall into the cells receptive field, but fell into some surrounding region, it was noted that the cell was inhibited. When the opposite direction of motion to that favoured by the cell was presented to the cells surround then it was noted that the cell was excited. When this opposite direction of motion was presented to the cells classical receptive field the cell was inhibited. This opponency effect between the cell centre and surround resulted in the optimum stimulus type for cells with this kind of responsivity being two opposed directions of motion in the visual field, with the cells preferred direction of motion placed in the classical receptive field of the cell and the opposite direction of motion placed in the cell surround.

The suggestion of the neurophysiological work done on MT neurons is that there seems to exist some kind of pooling in the cells responses to spatial frequency before the pattern motion is computed. In addition to this there seems to be some opponent type interactions occurring within some of the MT mechanisms which could be used to carry out the processes suggested to account for this data.

Chapter 5: Effect of oriented components on shear and compression processing.

This chapter reports a series of experiments which sought to examine the effects of oriented grating components upon the perception of shear and compression. The results of this were applied to the opponent process model described previously.

Experiment 5

Effect of Oriented Grating Components on the perception of shear and compression

5.1 Introduction

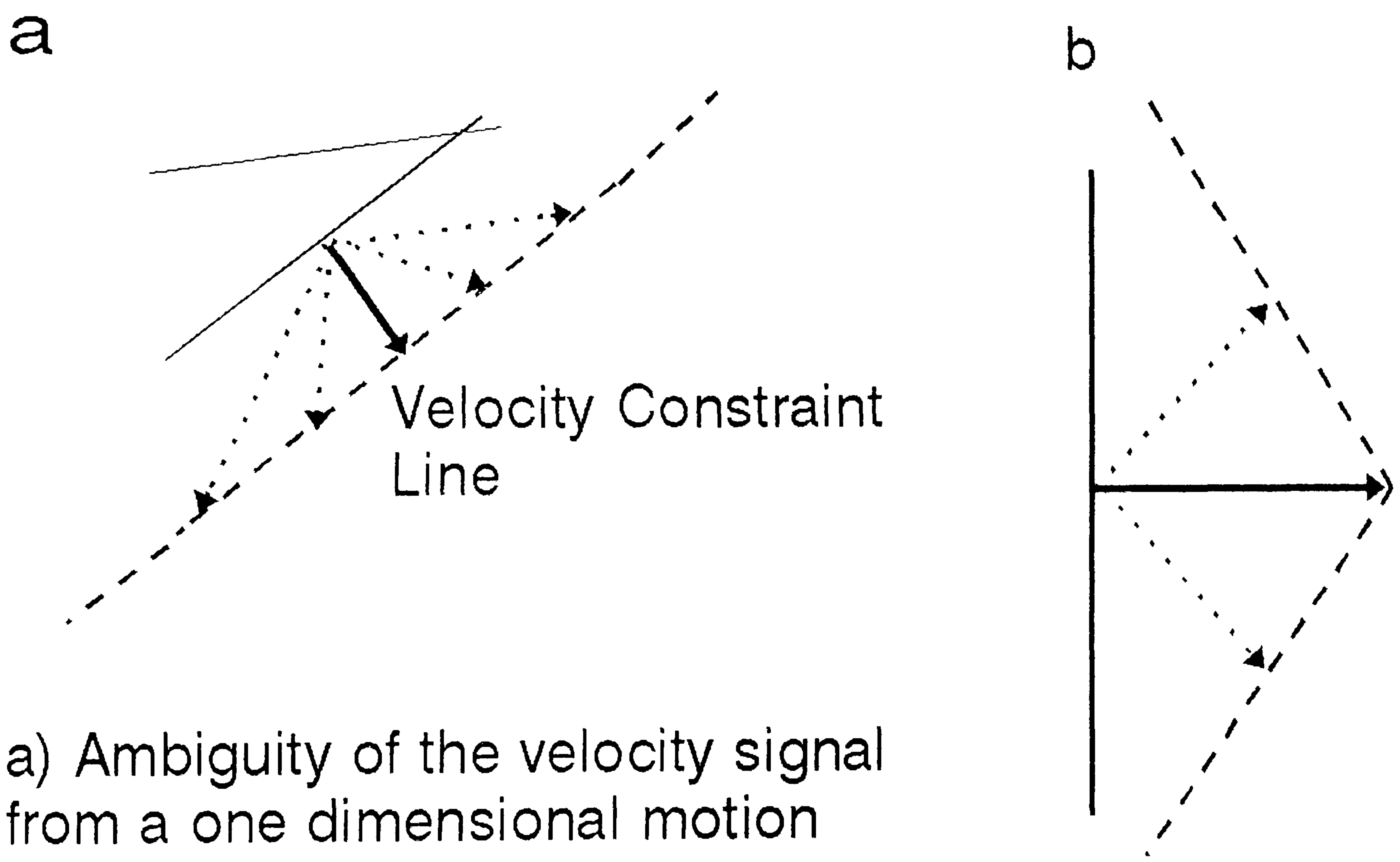
Previous work with shearing and compressive motions (eg Richards and Lieberman, 1982; Regan, 1986; Van Doorn and Koenderink, 1983; Nakayama, 1981) has not given consideration to the effects of oriented gratings. This is not surprising, given the almost exclusive use of random dot stimuli in these previous experiments, which do not readily allow manipulations of stimulus orientation.

This experiment utilised sinusoidal grating displays. Such displays were used as they allow easy control over the orientation of the gratings making up the stimuli.

Adelson and Movshon (1982) in their two stage model of motion perception (see figure 15), proposed that in the first stage the local velocities of oriented spatial frequency components are estimated. Thus a moving visual image is initially analysed into its one dimensional spatial components of various orientations. The speed of each of these are computed in a direction perpendicular to the orientation of the component. Smith (see figure 16) has recently modified the Adelson and Movshon model (Smith, 1992). At Smith's stage 1a, the moving visual image is subject to bandpass spatial filtering. Each of these spatial frequency channels contains subunits tuned to different orientations, each of which is responsible for the detection of motion in a direction perpendicular to its preferred orientation. At Smith's stage 1b outputs from stage 1a signalling motion in common directions, are pooled across spatial frequency to produce broadband directional signals. In both models there exists a stage 2 in which the motion of the stimulus pattern is computed on the basis of directional signals from previous processing. This pattern motion stage computes the direction of pattern motion by utilising, an intersection of perpendicular velocity constraints (IOC) algorithm (Fennema and Thompson, 1979; Adelson and Movshon,1982). Within this IOC scheme the possible motion vectors for each of the component motions are constrained by 'lines of constraint'. It is the single point in velocity space where these lines intersect which gives the direction of motion and the speed of the pattern motion (see figure 18).

In our previous experiments (expts 1 to 3) it was argued that there was no evidence for low level local mechanisms dedicated to signalling the presence of shear or compression in moving visual images. It was argued that the limiting

Figure 18: Intersection of Velocity Constraints



a) Ambiguity of the velocity signal from a one dimensional motion detector. Solid arrow is objects true speed and direction, dashed line shows constraint line associated with that motion. Any motion vector which ends on this line could give rise to the same detector signal.

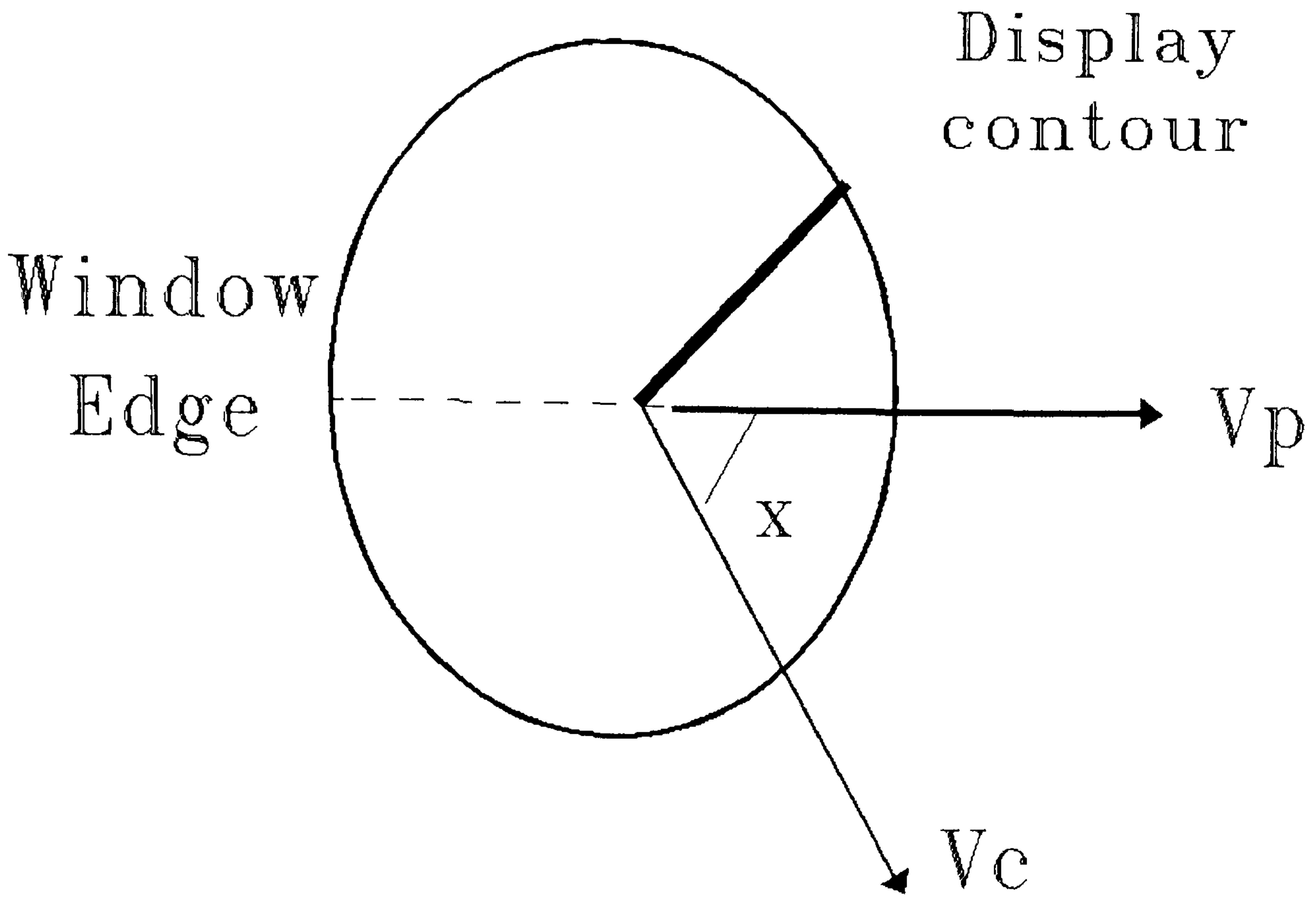
b) Solution of ambiguity. Two one dimensional signals are combined (dotted lines). Only motion that is consistent with both of them is one that runs to the constraint intersection point.

factor in the perception of shear and compression was the initial signalling of the local component directions of motion that make up the particular image motion. These processes can be thought of as occurring at stage 1 in the model of Adelson and Movshon (Adelson and Movshon, 1982) and stage 1a in Smith's model (Smith, 1992).

If it is the case that shear and compression processing is constrained by the initial signalling of local direction, then the orientation of the components making up the shear should be very important in determining the sensitivity of the visual system to shear and compression.

The thresholds of motion that were obtained in this experiment, were thresholds for directions of component motion that were perpendicular to the component orientation (as moving oriented components speeds are signalled by the visual system in directions perpendicular to the orientation i.e. Adelson and Movshon (1982). It was of interest also to examine the thresholds of motion that resulted from considering the pattern motion of resolved component motions parallel to the motion boundary as for the conditions that define pure shear or perpendicular to the motion boundary as for the conditions that define pure compression. The suggestion being that if over some range of orientations the visual system resolves the oriented components of motion along the motion boundary, then it would be expected that the motion thresholds should not only resemble the thresholds obtained for zero orientation, but should over this range of orientations, be invariant with component orientation. Vp is defined in terms of Vc by the following equation :

$$Vc / Vp = \mathrm{Cos}\,(x)$$



$$Vp/Vc = \cos(x)$$

Figure 19: Relationship Between Vc and Vp. An oriented moving contour is viewed through a circular aperture. The dotted line represents the edge of the display. Note how Vp (pattern velocity) is directed along the edge of the display.

where Vc is the component velocity threshold (the threshold obtained from the experiments), Vp is the pattern threshold (threshold result when the direction of motion is resolved parallel to the motion boundary) and x, is the orientation angle with respect to the vertical (see figure 19).

The results of this experiment are also of interest, in that when related to the two stage models of motion processing e.g. Adelson and Movshon (1992), clues as to the level, in the order of processing, of shearing and compressive motion may be determined.

5.2 Method

Apparatus

Patterns were generated, using a Cambridge Research System Visual Stimulus Generator. The patterns were displayed on a Tektronix 608 monitor of P31 phosphor. The frame rate used was 150 Hz. Responses were obtained using a Cambridge Research Systems CB1 three switch response box, only two of the switches were used here.

Display

The display of this experiment consisted of two sinewave gratings displayed on screen, one vertically above the other in the case of the shear display (experiment 5a : see figure 20a) and in the case of the compression display one grating to the left and one to the right of the display screen (experiment 5b : see figure 20b). Each grating was placed into one of two on screen windows that were defined using the VSG framestore. The windows were separated by an on screen

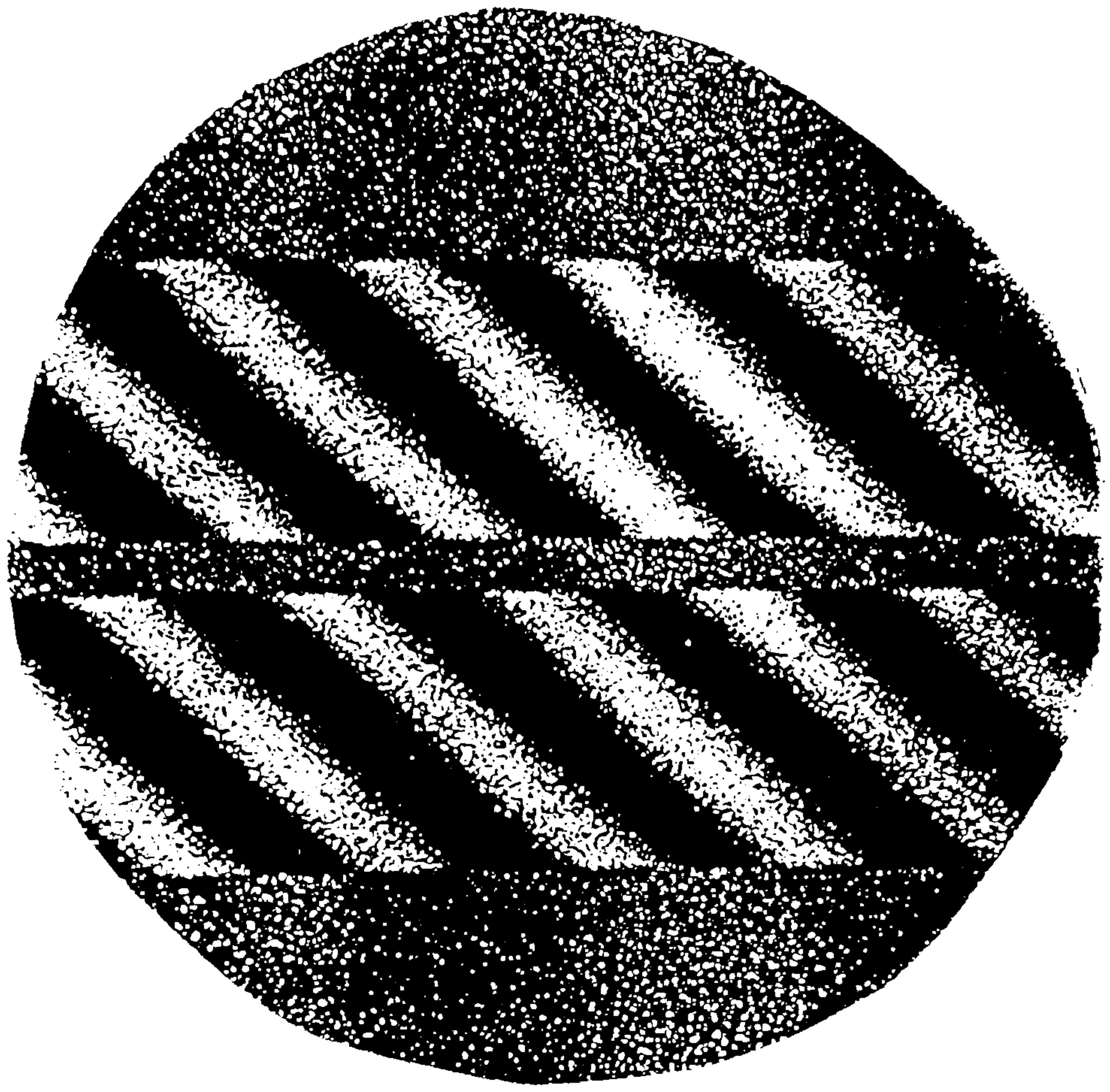


Figure 20a: Oriented Shear Display

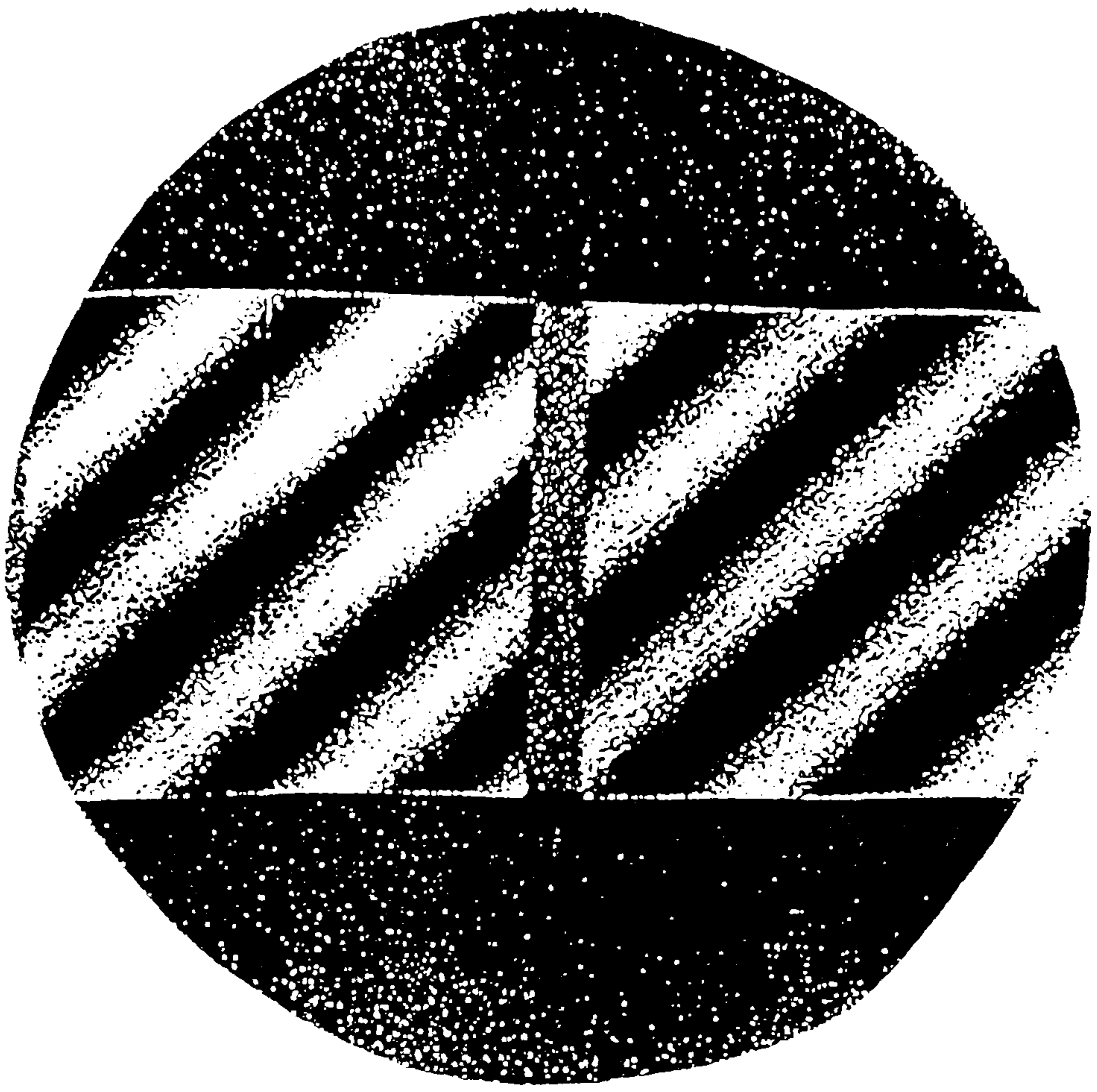


Figure 20b: Oriented Compression Display

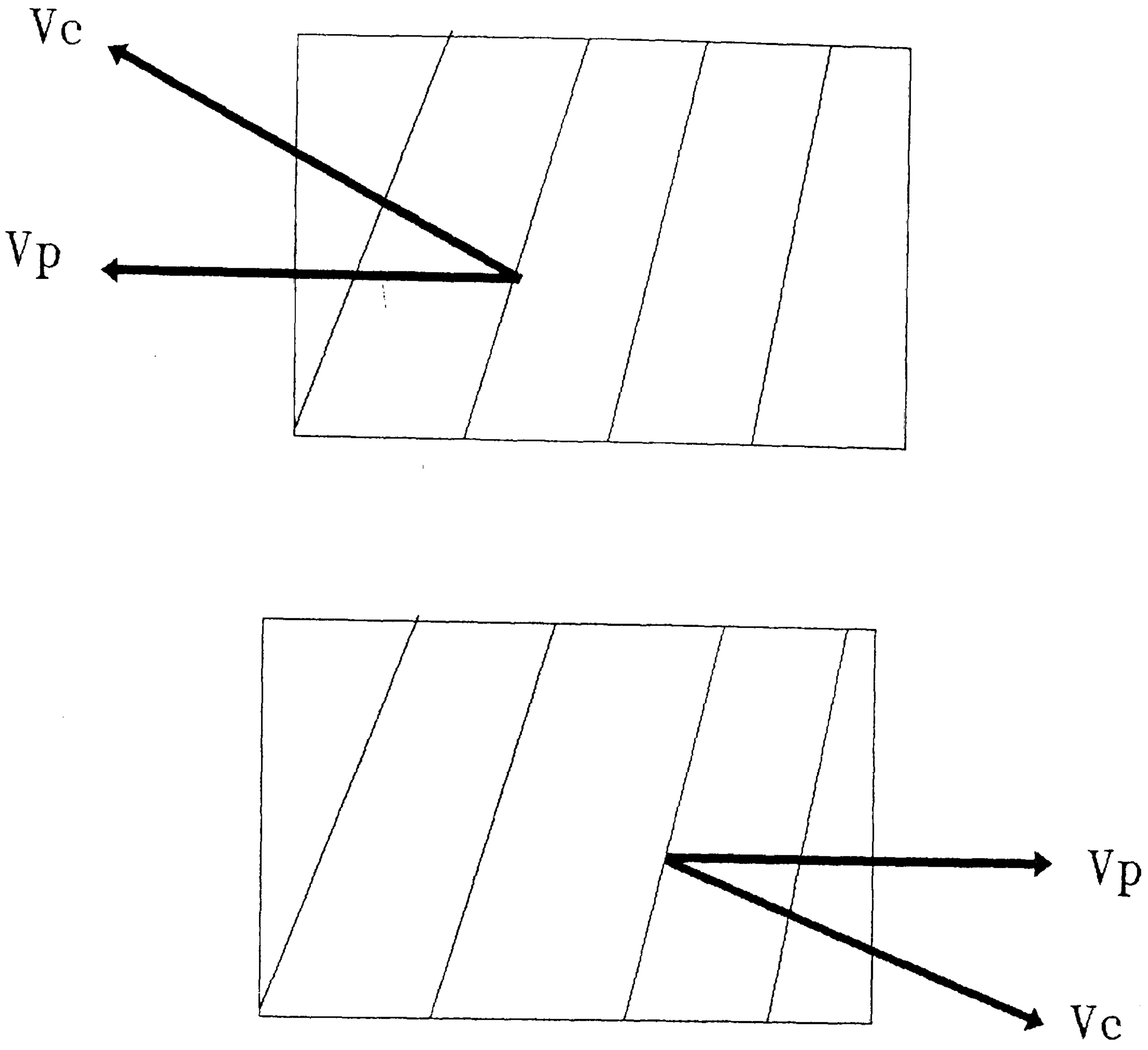


Figure 21a: Vp and Vc for shearing gratings.

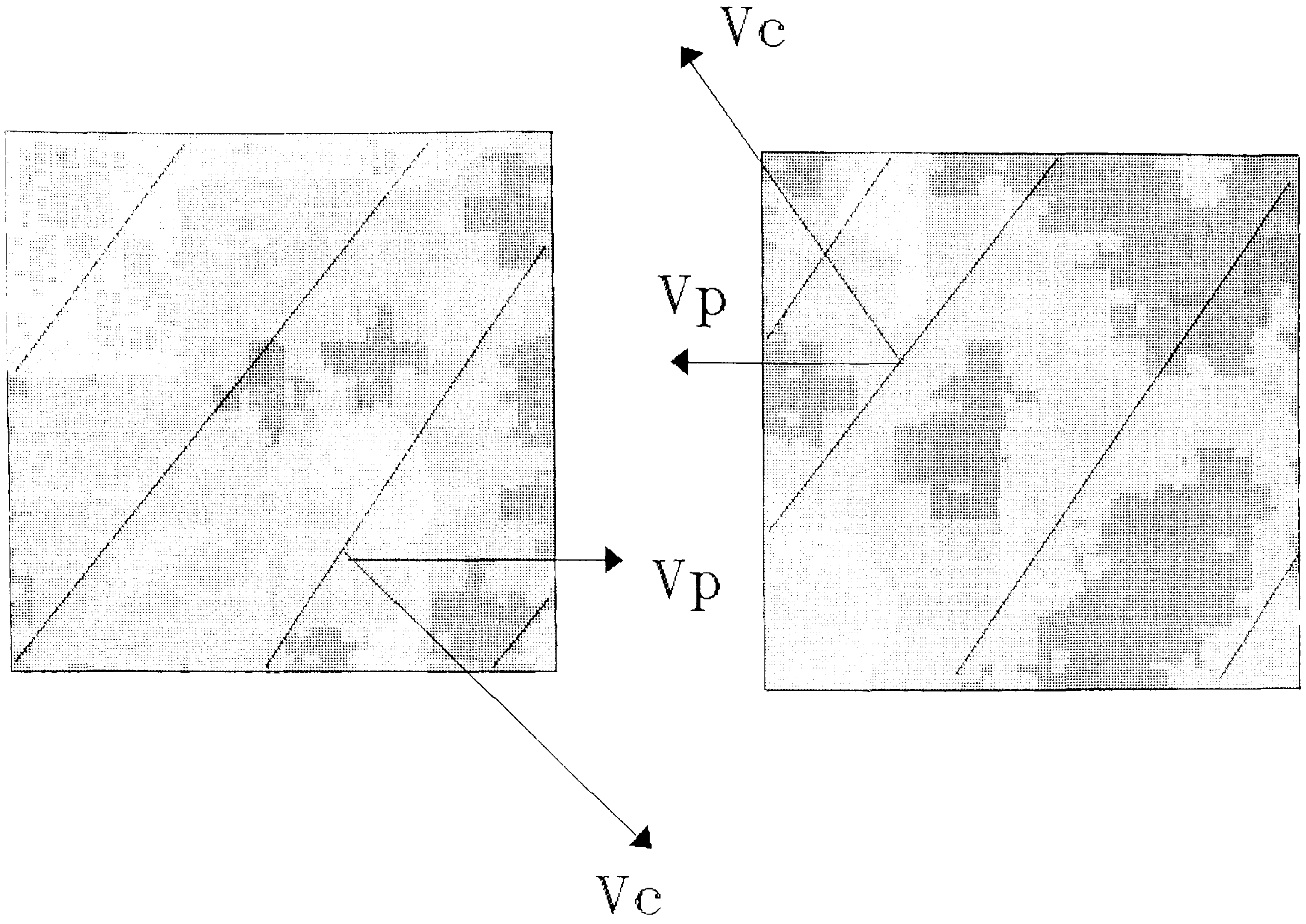


Figure 21b: Vc and Vp for Compressive Gratings

distance of 0.8 cm. The display screen subtended a visual angle of 1.97 degrees at the viewing distance of 290 cms. The two windows containing the component gratings covered equal areas of the screen and filled the screen from left to right. Several types of motion were defined for each of the experiments: for experiment 5a. Shearing, linear and stationary displays and for experiment 5b compression, linear and stationary displays.

The Shearing and compressive display consisted of two gratings moving in opposite directions of motion, linear motion displays consisted of the two gratings moving in the same direction (as for experiments 1 to 4 the direction of motion of each grating was randomised from trial to trial so as to maintain the stimulus type) and stationary displays were made of two gratings with zero velocity. The starting phase of each grating was randomised so as to control for the use of vernier cues in detecting and identifying the motion type.

The orientation of each grating was decided prior to the start of an experimental run. Each of the two gratings defining the displays was given the same orientation. All orientations were expressed with respect to the vertical. Within a given experimental run the grating orientation was kept constant. Six orientations were used for experiment 5a, 10, 20, 30, 45, 60 and 80 degrees. Five orientations were used for experiment 5b, 10, 30, 45, 60, 80 degrees. Each oriented grating was placed into one of the windows so that it filled the window completely.

As in experiments 1b, 2b and 3b an expansion motion control stimulus was generated for experiment 5b, again no data was collected for this expanding motion.

Procedure

A two alternative forced choice PEST procedure was used. Each experimental run was separated into a series of trials. On any given trial the type of motion (linear or shear: experiment 5a/linear or compression: experiment 5b) to be shown was randomly selected. The moving stimuli (linear or shear or compression) could be placed randomly into one or other of two time intervals each of 100 msec duration. There was an inter stimulus interval where the screen was left at mean luminance of 100 msec. Into the other time interval was placed the stationary stimulus. An experimental run was initiated by the observer depressing one of the response keys. On any given trial the observer was presented with two types of grating pattern. One moving the other stationary. The task of the subject was after presentation of the second interval to make two key press responses. The first was to indicate in which interval he had seen a moving stimulus and the second response was to indicate which moving stimulus type he had seen (linear or shear: experiment 5a; linear or compression:experiment 5b). The first response constituted discrimination of a moving from the stationary stimulus. The second response constituted identification of the moving stimulus type.

Velocity threshold data was obtained for experiment 5a: discriminating a moving shear and a moving linear type motion from stationary and also threshold data was obtained for the identification of shear and linear motion, and for experiment 5b: discriminating a moving compression and a moving linear motion from stationary and identifying a compression and linear motion. Thus four thresholds were obtained in any given experimental run. The thresholds were in terms of velocity i.e. the lowest velocity at which the task could be performed (lower thresholds of motion).

The reported thresholds are the result of at least three experimental runs. The thresholds reported have standard errors of ten percent or less.

For experiment no data was collected for the control expanding motion type, the subject responded if he considered this motion to be present as in experiments 1b, 2b and 3b by pressing the third response key.

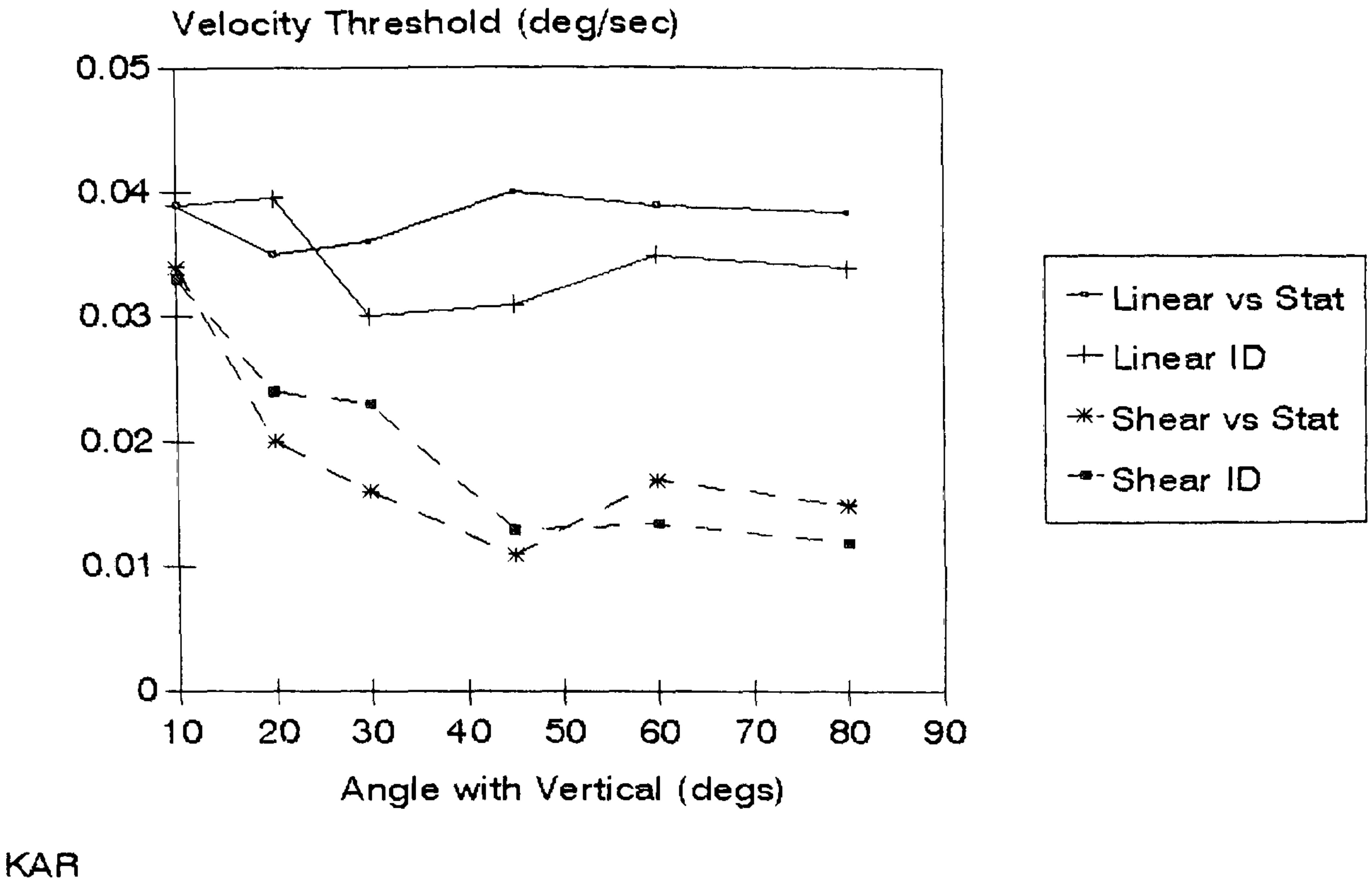
Subjects

The subjects for this experiment were the author KR, who was 26 years old, is male, has normal vision and is an experienced psychophysical observer and VJH who was 25 years old, is female, has normal vision and was naive to the aims of the experiment.

5.3 Results

Experiment 5a

First consider the results of experiment 5a (figures 22a and 22b). Results generally consistent with those of experiment 3 were obtained for all orientations when considering the pattern motion thresholds: Vp (figure 22b) i.e. lower thresholds when the directions of motion in each window were opposite to each other. Analysis of variance results for the pattern motion thresholds revealed that there was no significant effect of the task type i.e. ($F=0.031;df=1;p>0.05$). There were significant effects of the type of stimulus ($F=84.650;df=1;p<0.001$) and of orientation ($F=1154.703;df=5;p<0.001$) and a significant interaction between the orientation and the type of stimulus ($F=4.981;df=5;p<0.01$). This



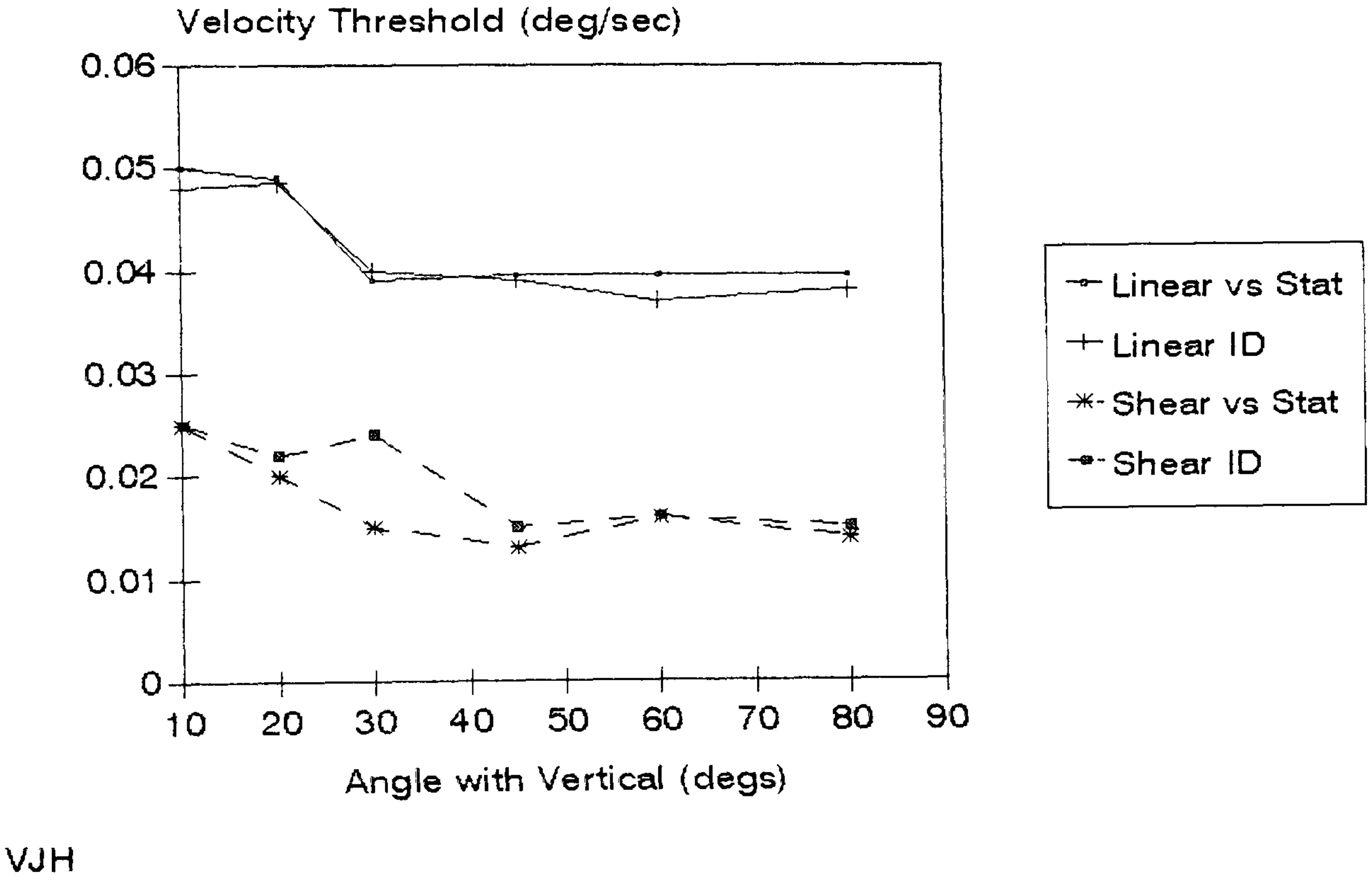
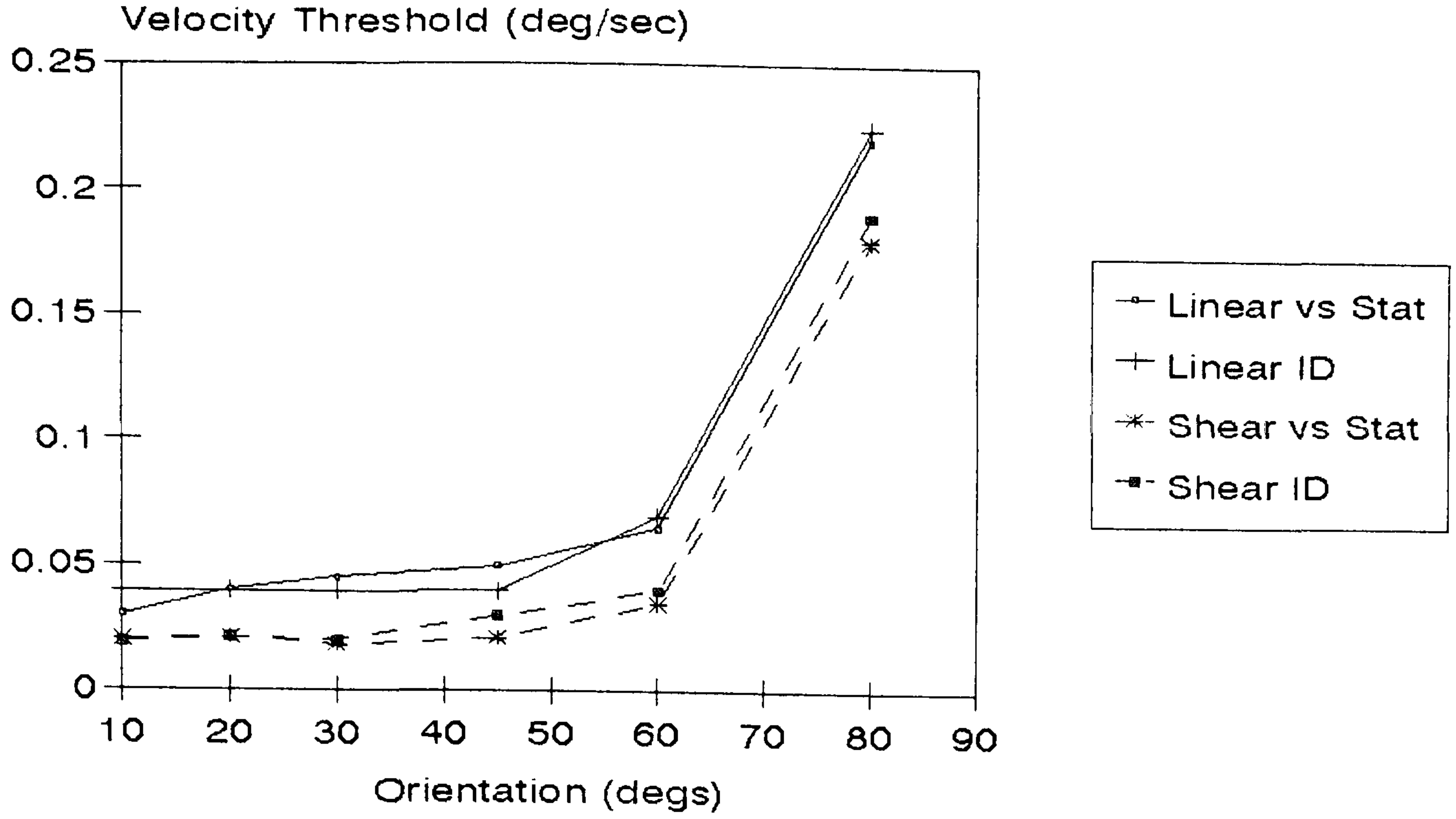


Figure 22a: Experiment 5a, Shear Component Thresholds Vc. Lower thresholds of motion. Lines represent thresholds for the four types of task.



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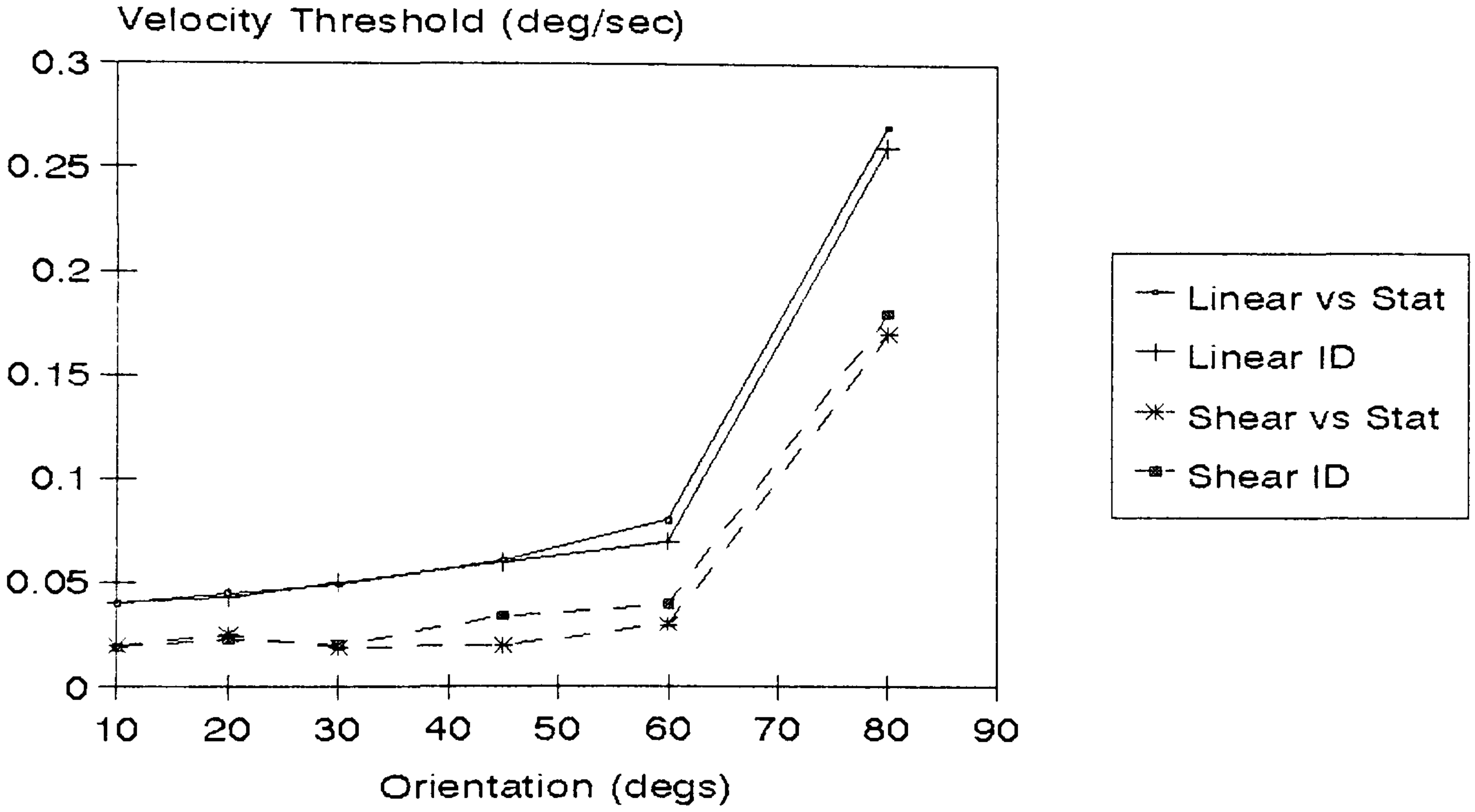


VJH

Figure 22b: Experiment 5a, Shear Pattern Thresholds Vp. Lower thresholds of motion. Lines represent thresholds for the four task types.

indicates that the pattern of the results was due to the stimulus type and the orientation, the task type was not an important factor in determining the results.

The pattern thresholds (Vp) for shearing motion appear to increase with orientation indeed they appear to be dependent upon the orientation of the components.

The component motion threshold, Vc, (figure 22a) results show a similar pattern to that obtained for the pattern thresholds, Vp, i.e. lower thresholds over all orientations for the opposed motion displays.

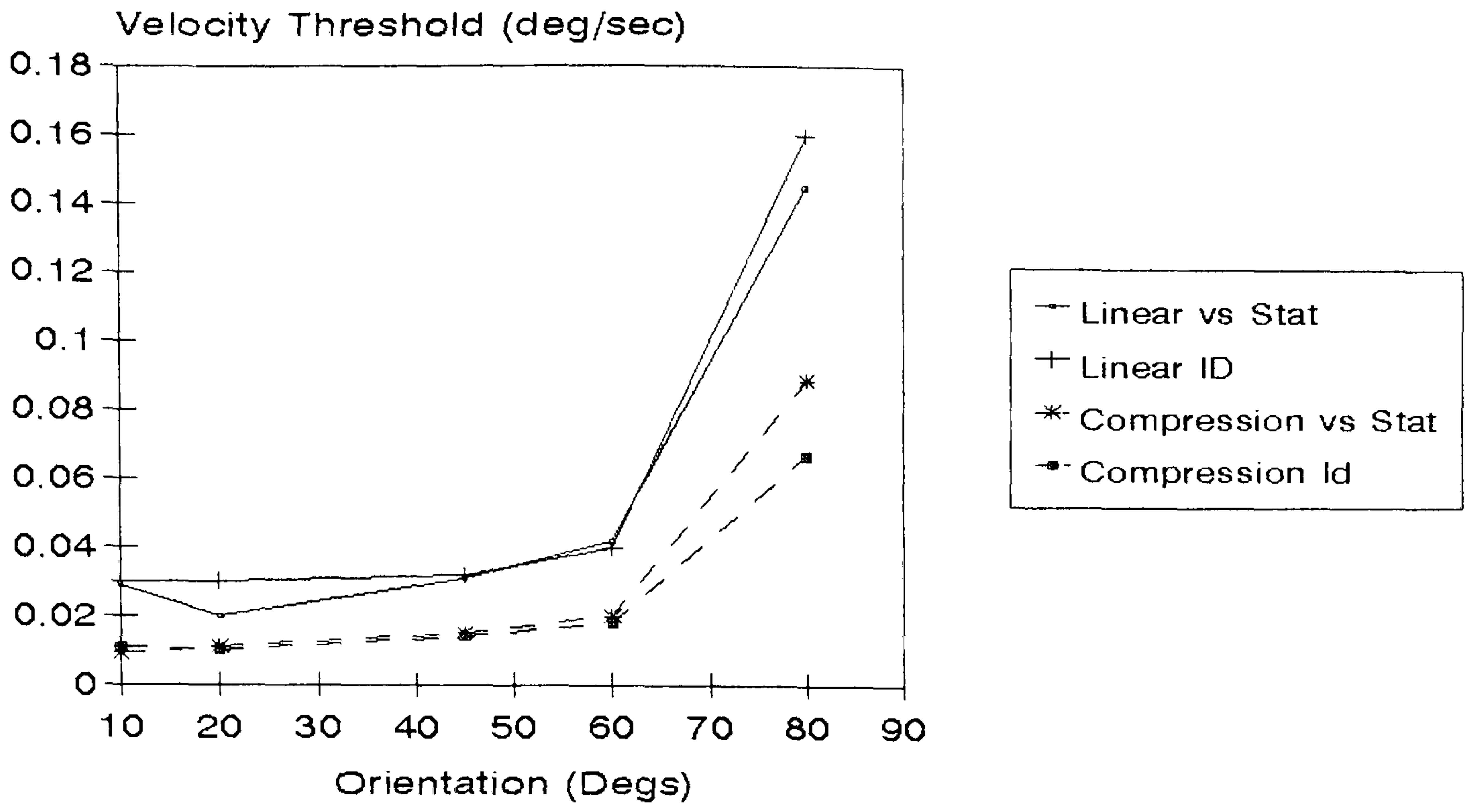
The component thresholds, Vc, are very much less dependent upon the orientation than the pattern thresholds. However there is a detectable reduction in threshold with increasing orientation.

Analysis of variance revealed a similar pattern for component thresholds Vc to that obtained for the pattern thresholds Vp i.e. significant effects of orientation ($F=13.348;df=5;p<0.001$), stimulus type ($F=121.198;df=1;p<0.001$) and for the interaction between the stimulus type and the orientation task type ($F=0.943;df=1;p>0.05$). This again illustrates that the pattern of results is determined by the orientation and the stimulus type.

For both sets of results (pattern and component) there were significant interactions between the stimulus type and the task. It is argued that these significant interactions due to the type of stimulus, given the significance of the stimulus type and the insignificance of the task type for both sets of results.

Experiment 5b

Examining the results of experiment 5b (figure 23a: pattern motion thresholds:



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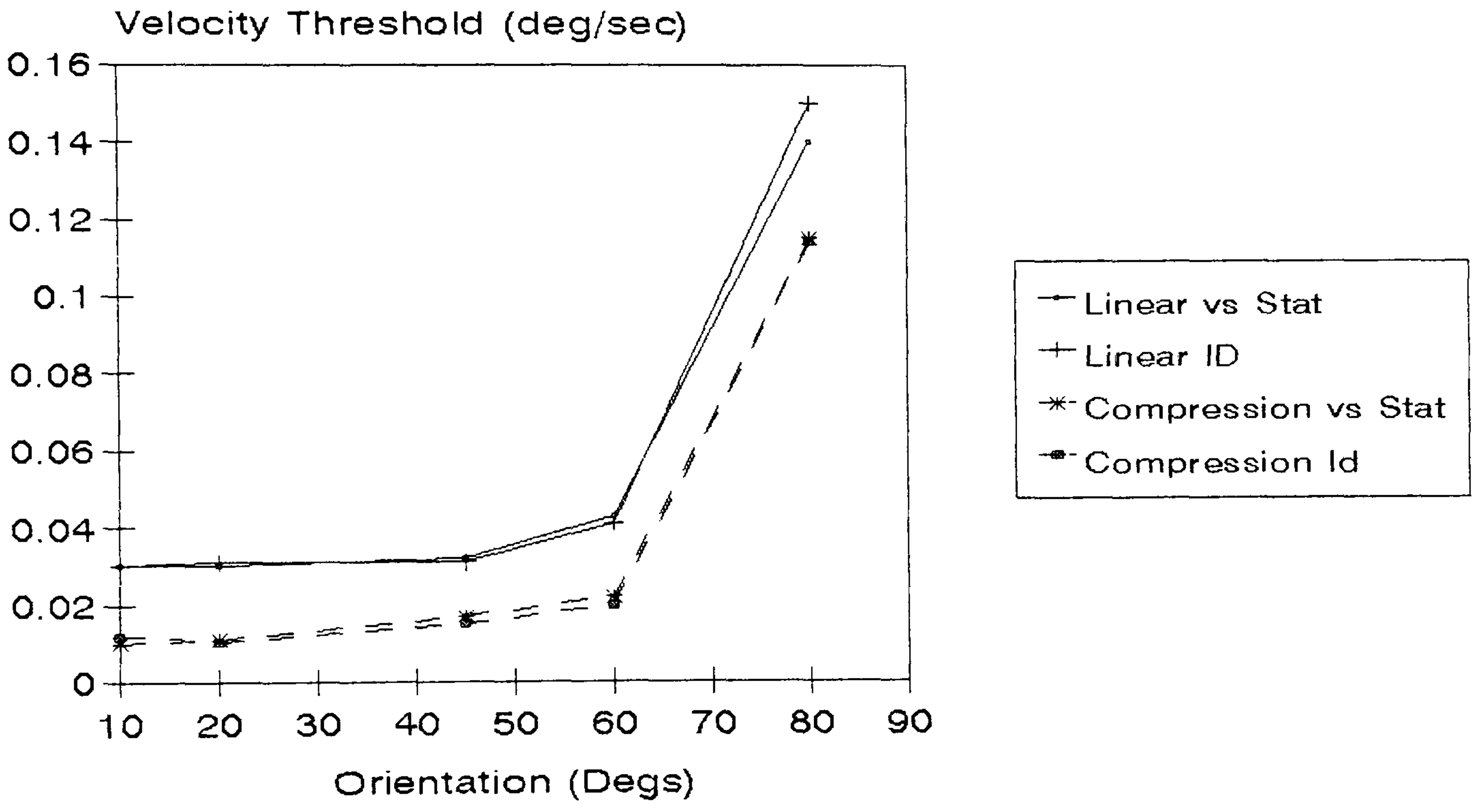

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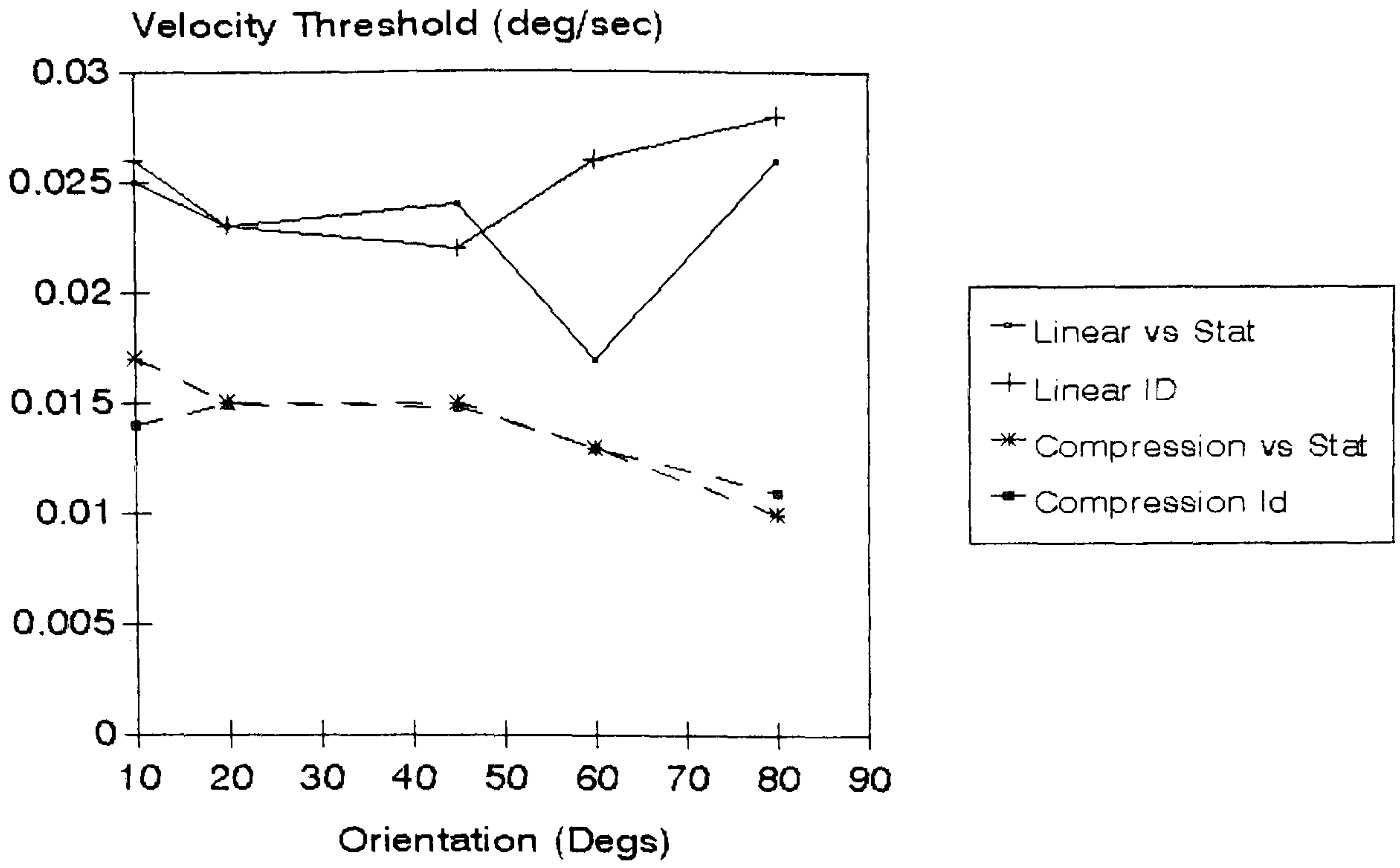
Figure 23a: Experiment 5b, Compression Pattern Thresholds Vp. Lower thresholds of motion.



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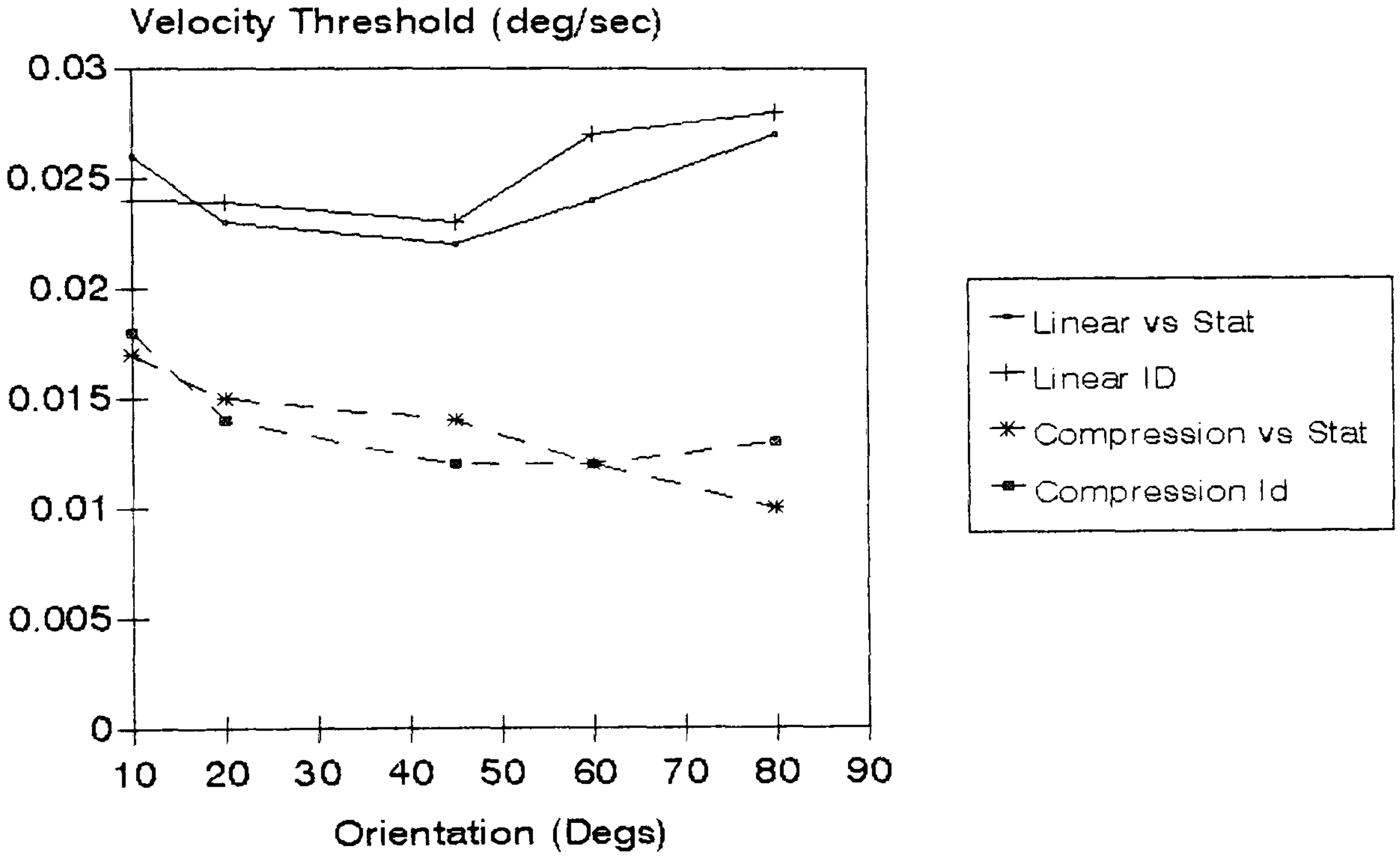


VJH

Figure 23b: Experiment 5b, Compression Component Thresholds Vc. Lower thresholds of motion

Vp and 23b: component motion thresholds: Vc). Firstly the general pattern of results for both the component and the pattern thresholds is similar to those for experiment 5a.

As in experiment 5a, results generally consistent with those of experiment 3 were obtained over all orientations.

Analysis of variance results for the pattern motion thresholds revealed that there was no significant effect of the task type. There were significant effects of the type of stimulus (df=1;F=93.305.364;p<0.001) and of orientation (df=4;F=12.406;p<0.001) and a significant interaction between the orientation and the type of stimulus (df=4;F=7.687p<0.01). This indicates that as with experiment 5a the pattern of the results was due to the stimulus type and the orientation, the task type was not an important factor in determining the results.

Again the component thresholds appeared to be much less dependent upon orientation than the pattern motion thresholds.

Analysis of variance for the component thresholds, Vc, revealed a similar pattern to that for the pattern thresholds, Vp, with significant effects of orientation (df=4;F=14.958;p<0.001), stimulus type (df=1;F=116.364;p<0.001) and for the interaction between the stimulus type and the orientation task type (df=4;F=9.518;p>0.001). This again illustrates that the pattern of results is determined by the orientation and the stimulus type.

For both sets of results (pattern and component) there were significant interactions between the stimulus type and the task. It is argued that these significant interactions are the result of the type of stimulus given the significance of the stimulus type and the insignificance of the task type for both sets of results.

5.4 Discussion

It appears that evidence for opponency was obtained over the full range of orientations used. It was also observed that the component motion thresholds are very much less dependent upon orientation than were the pattern motion thresholds. The pattern thresholds demonstrated a large noticeable increase with increasing orientation. The subjective reports indicated that the observer's ability to perceive the motion type e.g. shear (experiment 5a) or compression (experiment 5b) reduced with increasing orientation. Observers reported that particularly with orientations of over 45 degrees it was very hard to see the particular opposed motion (shear or compression) type. Typically for experiment 5a they reported the opposed motion percept for the larger orientations was compression and not shear, while for experiment 5b the percept was shear and not compression. It seems therefore that shear shaded into compression (experiment 5a) and compression shaded into shear (experiment 5b) with increasing component orientation. As a result of this observation it could be that in this experiment, the pattern of results are the product of measuring the two lower motion thresholds (for shear and compression) simultaneously, i.e. as the orientation of components change resulting in a change from a pure shear or pure compression, both types of motion are present simultaneously.

The finding that the pattern motion thresholds were greatly dependent upon the orientation whilst the component motion thresholds showed a much weaker dependence is further evidence for the idea (experiment 1; Wright and Gurney, 1992) that the sensitivity to shear and compression is constrained by sensitivity to the direction of motion of the components making up the shear or compression.

The suggestion is that the direction of motion of the components is firstly analysed from the display and then the presence of shear or compression is indicated by later processing of the component directions. This suggestion follows from two stage models of motion perception (eg Adelson and Movshon, 1982; Smith, 1992).

The results of this experiment are consistent with those of Wright and Gurney (1992). In common with their results the current results are consistent with what would be predicted by two stage models of motion perception i.e. the component motion thresholds have less variation with orientation than pattern motion thresholds. Wright and Gurney (1992) found that plaid motion thresholds (pattern motion) showed a greater dependence upon the relative direction (orientation) of the components making up the plaid pattern than was found for the component motion thresholds. They argued that this was evidence that components of a plaid are detected independently prior to pattern direction. Wright and Gurney also found that the component motion thresholds showed a weak dependence upon the component orientation. They argued that this was the result of processing of the stage one signals by stage 2 mechanisms. They suggested that a flat function of component motion thresholds with orientation would be expected if the grating components were not subject to stage 2 processing. As this was not the case then it was argued that noise added to the stage 1 signals by stage 2 processes accounted for the small reduction in the component thresholds that they found. Following from this argument the small reduction in the component motion thresholds in our experiments can be explained as being the results of stage 2 processes of the stage 1 signals generated for each of the display windows.

The stimuli used in this experiments were made up of two sinusoidal grating components placed inside rectangular windows. It is the case that stage 1 and stage 2 processes will be carried out within each of the display windows. As there exists an edge i.e. the edge of the window, in the display, there are several sources of motion information present in the display. Two of these are the motion due to the components (signalled by stage 1) and motion at the edge of the window. The motion signal at the edge of the window is assumed to result from stationary oriented components (Wright and Gurney, 1992). Thus stage 2 processes have two motion signals present with which to compute an IOC. Solution of the intersection of constraints algorithm gives rise to a pattern motion signal which is parallel to the longest edge of the window (see figure 24a : shear type display and figure 24b : compression type display).

In experiment 3 it was suggested that the lower motion thresholds obtained for shear and compression at suprathreshold contrasts as compared with linear motion indicate the operation of opponent interactions between spatially separated motion mechanisms. The results of the current experiment found that for both experiment 5a and experiment 5b lower pattern and component thresholds than linear motion were obtained for all orientations when two opposed directions of motion were present in the display. This result suggests that opponent interactions occur regardless of the component orientation.

It is interesting to consider the location of these opponent processes within the motion perception system. Two stage models of motion perception will be the framework within which this will be considered (see figures 15 and 16).

It was argued that these results provide evidence that shear and compression

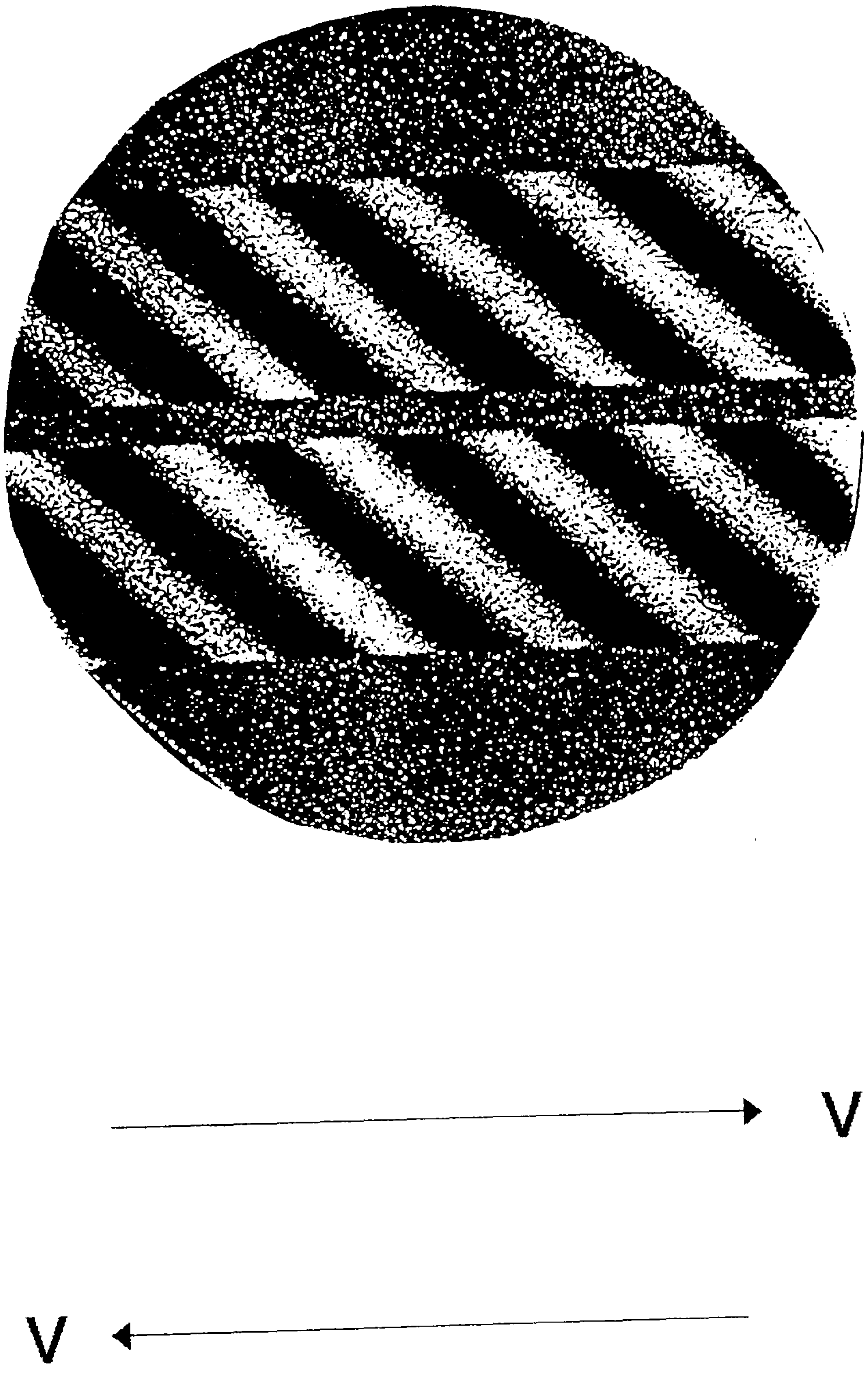


Figure 24a: IOC solution for oriented shear display

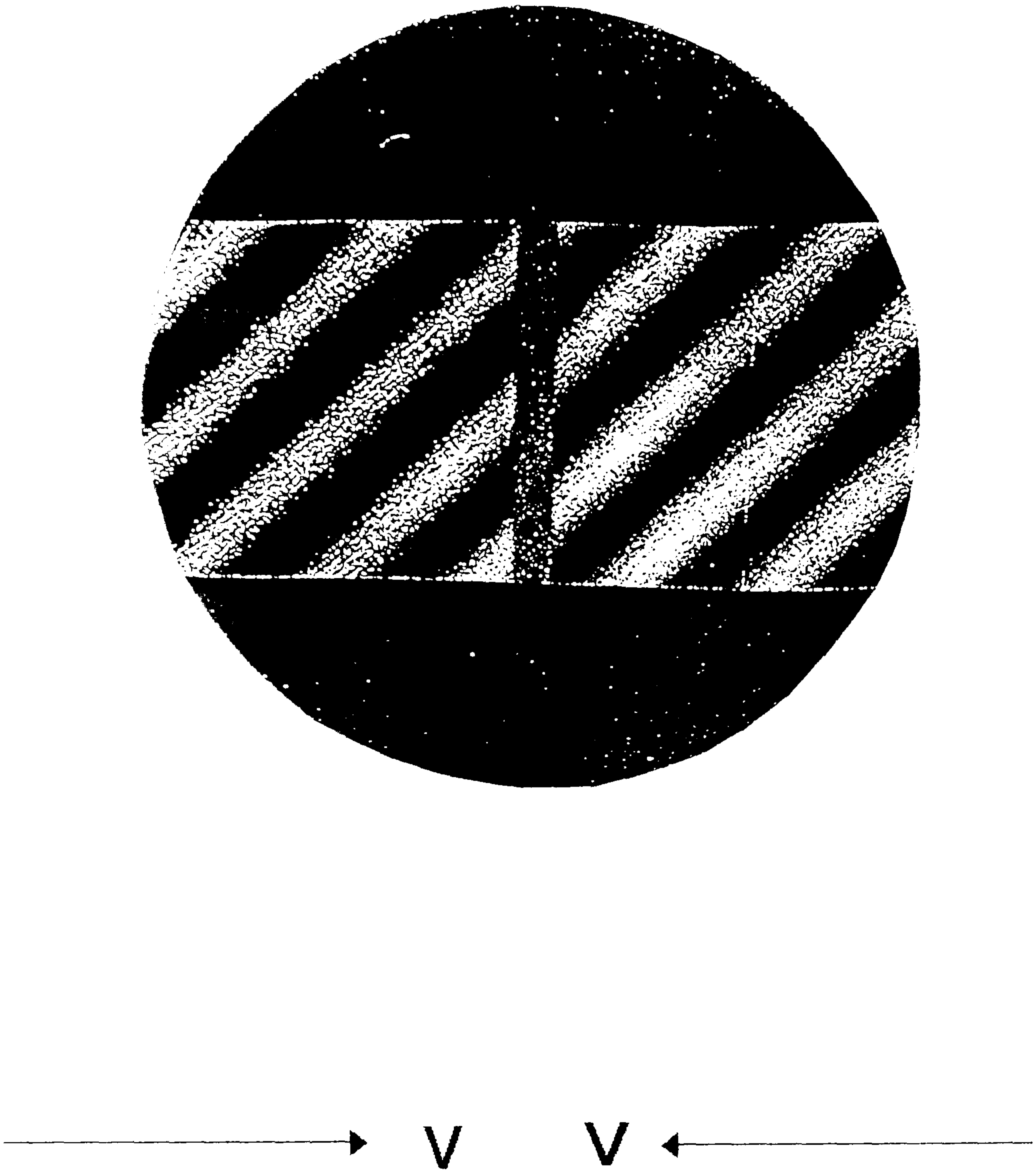


Figure 24b: IOC solution for oriented Compression display

sensitivity is constrained by the sensitivity of stage 1 processes to component motion. Further that the results of stage 1 processes are subjected to processing by stage 2 mechanisms and as such noise is added to the stage 1 signal by stage 2 processing. The evidence for opponency irrespective of the orientation of the components is suggestive of the fact that opponent interactions occur after stage 1 processing. It was suggested from experiment 4 that the probable location of this opponency is at or after Smith's (Smith, 1992) stage 1b. The location of these opponent interactions relative to stage 2 processes will now be considered. Several possibilities exist. Each will be discussed in turn in relation to the results of this experiment.

One possible explanation is one in which opponent processing occurs after the processing of component direction and in parallel with the computation of stage 2 intersection of constraints (see figure 25,A). If the opponent processes take place after stage 1 and in parallel with stage 2 processing, these opponent interactions would be responding to the directions of motion of the components i.e. would respond to the outputs of stage 1 processes. This leads to the prediction that lower component motion thresholds than linear motion would be expected for all cases of opposed component motion irrespective of, and for all component orientations. This was found in this experiment. However this scheme also predicts that as the opponent interactions occur in parallel to stage 2 processes the results of opponent processing will not be subjected to later stage 2 processing. This leads to the prediction that the component thresholds would have no dependence upon component orientation i.e. a flat component motion threshold with orientation function should be obtained. This was not observed, there was

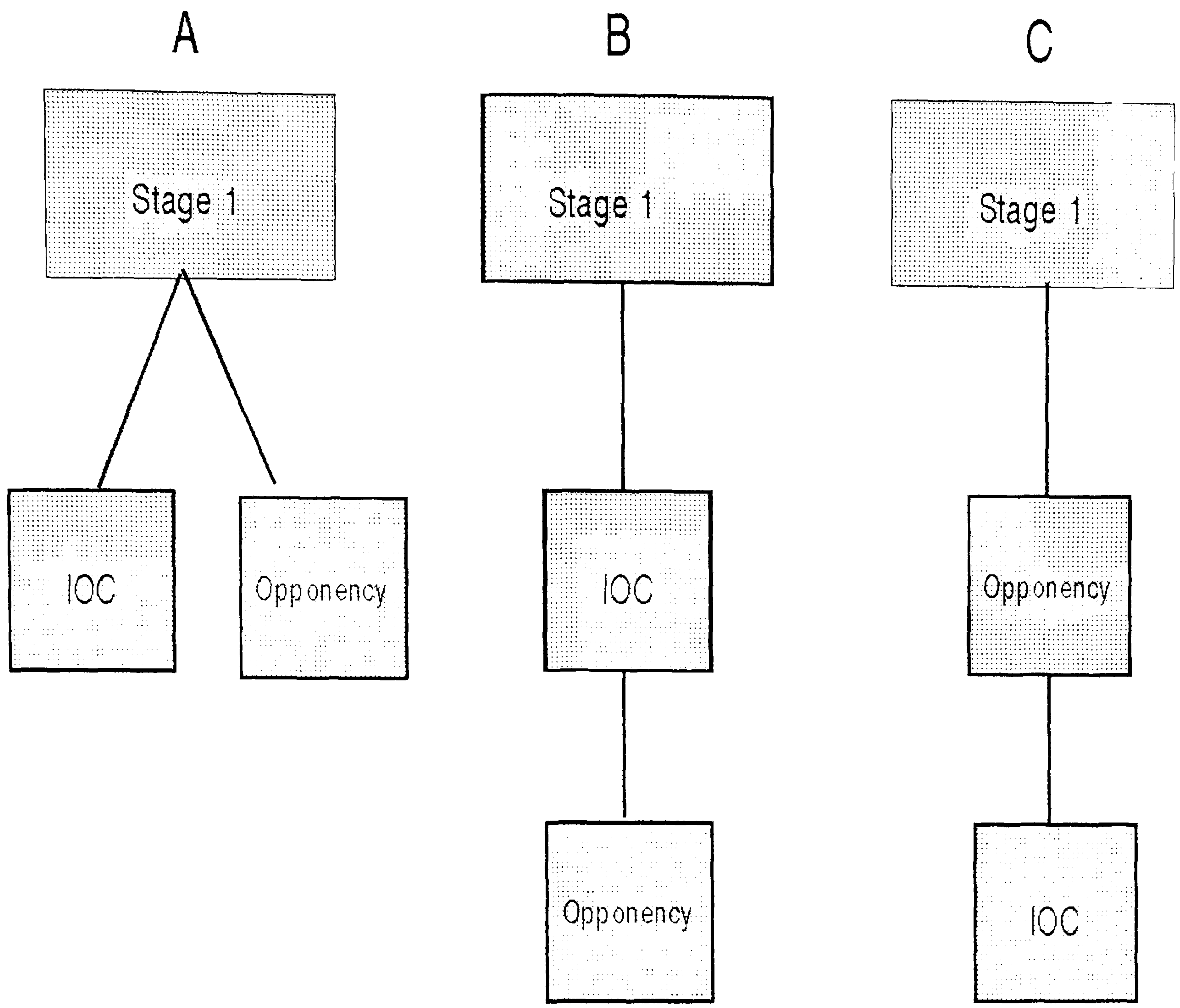


Figure 25: Three Models for level of Opponency. (For explanation see text).

a slight increase in the component thresholds with increasing orientation indicating the effects of stage 2 processes (Wright and Gurney, 1992). Thus as this model does not account for all aspects of the data it is rejected as a possible explanation of shear and compression processing.

Another possibility is that opponent processes occur after processing at stage two in two stage models (see figure 25,B). Thus within this scheme stage 1 processes would be carried out for each of the display windows. Stage 2 processes would then be carried out upon the stage 1 outputs again for each window. The stage 2 outputs would then be subjected to opponent interactions across space i.e. the stage 2 signals generated for each window would interact. This model makes the prediction that evidence for opponency should be obtained for all component orientations when there exists an opposed component motion signal in the display. The data reveals this to be the case. The opponent processes within this scheme would essentially be occurring between the outputs of stage 2 (IOC) processes. The effect of stage 2 noise according to Wright and Gurney (1992) is to decrease the component motion thresholds. Thus this model predicts that the component motion thresholds for opposed motion displays should decrease with increasing orientation. This was found by these experiments. It seems that this model does predict the results of this experiment and as such could be a good model of the processes involved in the perception of shear and compression.

A third possibility is that opponent interactions occur prior to stage two processes (see figure 25,C). That is they occur after stage 1 and before stage 2 processes. Due to the occurrence of opponent interactions between stage 1 mechanisms sensitive to opposed directions of motion, when the stimulus consists of two oppositely moving components, greater activity is engendered in the motion mechanisms responding than when a linear stimulus is presented. The resultant motion signals are then subjected to stage two processes. This suggestion explicitly states that stage 1 signals should be affected by stage 2 processes as they occur prior to and in series with stage 2 processes. This model therefore predicts the observation that the component motion thresholds showed a slight decrease with component orientation. Further this model also predicts that as opposed component motion was present for each orientation in experiments 5a and 5b evidence for opponency should be obtained for all component orientations (as was observed by the experiment). Thus this model also appears to fit the data of this experiment and so may also be a good model of shear and compression processing.

To summarise, the pattern of these results give clues as to the level at which processes responsible for the perception of shear and compression occur within the visual system. The evidence tends to favour an interpretation of shear and compression sensitivity based upon the detection of component directions of motion, to be identified with stage 1 processes in two stage models (eg Adelson and Movshon, 1982). The greater sensitivity to shear and compression is given by the functioning of directional opponent mechanisms which give greater responses to opposed directions of motion. The question of the location of these opponent processes within current two stage motion processing models (Adelson and Movshon, 1992) has not been resolved by this experiment. The results suggest that opponent process do not occur in parallel to stage 2 processes. The results favour some kind of serial processing with either opponent processes occurring after stage 1 and before stage 2 processes or alternatively after stage 1 and stage 2 processes. Experiments 6 and 7 attempted to further clarify the level of processing at which these opponent processes occurred.

Experiment 6

Effect of Terminator Motion on Shear and Compression Processing

5.5 Introduction

The displays used in experiments 5a and 5b contained other motion signals as well as those due to motion of the oriented components. These motion signals are produced by line terminators at the edges of the display windows. It could be that the results of experiments reflect the operation of processes sensitive to terminator motion as well as component motion signals. It was therefore decided to carry out an experiment to see the effects of terminators upon the perception of shear and compression.

It has been shown that when objects are occluded two kinds of boundaries are intermingled in the visual image, real object boundaries i.e. the physical edge of the object (Intrinsic boundaries) and boundaries due to another object occluding which is in front of the first object (Extrinsic boundaries) (Nakayama et al, 1987, 1989). These authors argued that it is the location of intrinsic boundaries that is critical to object recognition whereas extrinsic boundaries, which result from accidental occlusions, are not. They suggested that the two kinds of boundary need to be distinguished in order for objects to be recognised. In windowed grating displays the boundaries are defined by the ends of the bright and dark lines of the sinusoidal gratings (if the grating stimulus is thought of as a series of bright and dark lines) it is suggested that the boundaries are intrinsic boundaries. The ends of the grating are the line terminators. Nakayama et al (1989), and Shimojo et al (1989) suggest that the same distinction can be made between two types of line terminators as can be made between object boundaries, namely intrinsic terminators and extrinsic terminators. Intrinsic terminators are associated with intrinsic boundaries and are associated with the physical edge of the display. Conversely, extrinsic terminators are associated with extrinsic boundaries and are the result of occlusion of an object. Intrinsic terminators are suggested to be of greatest importance in object recognition and motion perception etc. (Nakayama et al, 1989; Vallortigara and Bressan, 1991). It is argued that provided the grating is perceived to be of equal stereoscopic disparity i.e. in the same depth plane, as the aperture window the terminators present in windowed gratings are intrinsic terminators (Shimojo et al, 1989). The barber pole effect (Wallach, 1935) provides a good example of the effects of line terminators upon motion perception and is also an illustration of the solution of the aperture problem (Wallach, 1935; Fennema and Thompson, 1979; Adelson and Movshon, 1982; Hildreth, 1984; Shimojo and Richards, 1986; Nakayama and Silverman, 1988; Mussap and Crassini, 1993).

The aperture problem can be described by considering the following. When an oriented moving grating is placed within a circular window, its direction of motion is ambiguous. The perceived direction is usually perpendicular to the oriented lines. If an oriented moving grating is placed inside a rectangular aperture, then the perceived direction of motion is always in a direction along the longest side of the aperture. For a vertical window the perceived direction is in a vertical direction, a horizontal window produces horizontal motion. This shows that the shape of the window is crucial to the solution of the aperture problem. Hildreth (1984), and Nakayama and Silverman (1988) suggest that the perceived direction of motion in the barber pole effect is the result of the detection of the unambiguous motion of line terminators at the edges of the aperture. These are propagated out along the oriented stripes of the grating towards the centre of the window. The reason that the motion is seen along the longest edge of the window is (within this framework) due to the relatively greater number of terminators along the longer edges as compared to the shorter edges. Thus for a horizontal window (as used in our experiments) there will be more terminators unambiguously moving in a horizontal direction than vertically. The ambiguity of the circular aperture is due to the lack of any edges in the display. Shimojo et al (1989) showed that the barber pole effect is abolished if the bars of the grating were made to appear behind the aperture (the grating pattern was in uncrossed disparity relative to the aperture plane). This finding suggested that the bars of the grating in the barber pole effect are seen as stopping at the aperture edge and as such illustrates the importance of intrinsic terminators as opposed to extrinsic terminators (when the bars appeared behind the aperture). It may be seen that if line terminator motion predicts motion along the longest edge for all windowed gratings, then the conditions for shear and compression would always be met and so would always be present in the display regardless of the grating orientation. As stated this experiment was carried out in order to examine the effects of terminator motion upon shear and compression perception.

If terminator motion was not an important determinant of the results of experiment 5, then it would be expected that the results of the current experiment should be different. Such a pattern of results would lend support to the models described above in the sense that sensitivity to terminator motion would be unlikely to give a satisfactory explanation of the experiment 5 data. Clearly similar results to experiment 5 would indicate a major role for terminator motion in determining the results of that experiment.

5.6 Method

Apparatus

Patterns were generated using a Cambridge Research System Visual Stimulus Generator. The patterns were displayed on a Tektronix 608 monitor of P31 phosphor. The frame rate used was 150 Hz. Responses were obtained using a Cambridge Research Systems CB1 three switch response box, only two of the switches were used here.

Display

The displays of this experiment emphasised line terminators. The displays thus consisted of the edges of the rectangular windowed displays from experiment 5.

The framestore of the VSG controls the shape of the display window on the display screen. The grating is then displayed within this display window. The display window can be open selectively to show the grating and has a resolution down to the level of what is conventionally called a pixel. Thus in producing the displays of this experiment sinusoidal gratings were displayed within predefined grating windows. Thus the 'edges' used in this experiment were created by producing windows within the VSG framestore with reference to a raised cosine probability function. The probability of finding a pixel on the display was greatest when the pixel coincided with the edge of one of the rectangular windows of experiment. The probability reduced to zero over a limited spatial extent of 0.15 degrees of visual angle. The display windows when created were filled with gratings of each of the orientations used in experiment. This was in order to make the experimental results comparable with those of experiment 5. It also allowed that any effects upon terminator motion signals of the oriented grating components in experiment 5 would also be present in this experiment. As the display windows of this experiment were essentially narrow attenuated bands of varying pixel drawing probabilities the appearance of the display was of a series of dark and light blobs (see figure 26a and 26b). The presence of the oriented gratings filling the windows was not apparent.

The edges were separated by an on screen distance of 0.8 cm. The display screen subtended a visual angle of 1.97 degrees at the viewing distance of 290 cms. The edges covered equal areas of the screen and filled the screen from left to right. Moving displays were created by giving motion signals to the gratings which filled the windows. The orientations of the boundaries between the edges for experiment 6a were as for experiment 5a (shearing experiment) i.e. boundaries parallel to the direction of motion of the edges (see figure 26a). The orientations of the boundaries between the edges for experiment 6b were as for experiment 5b

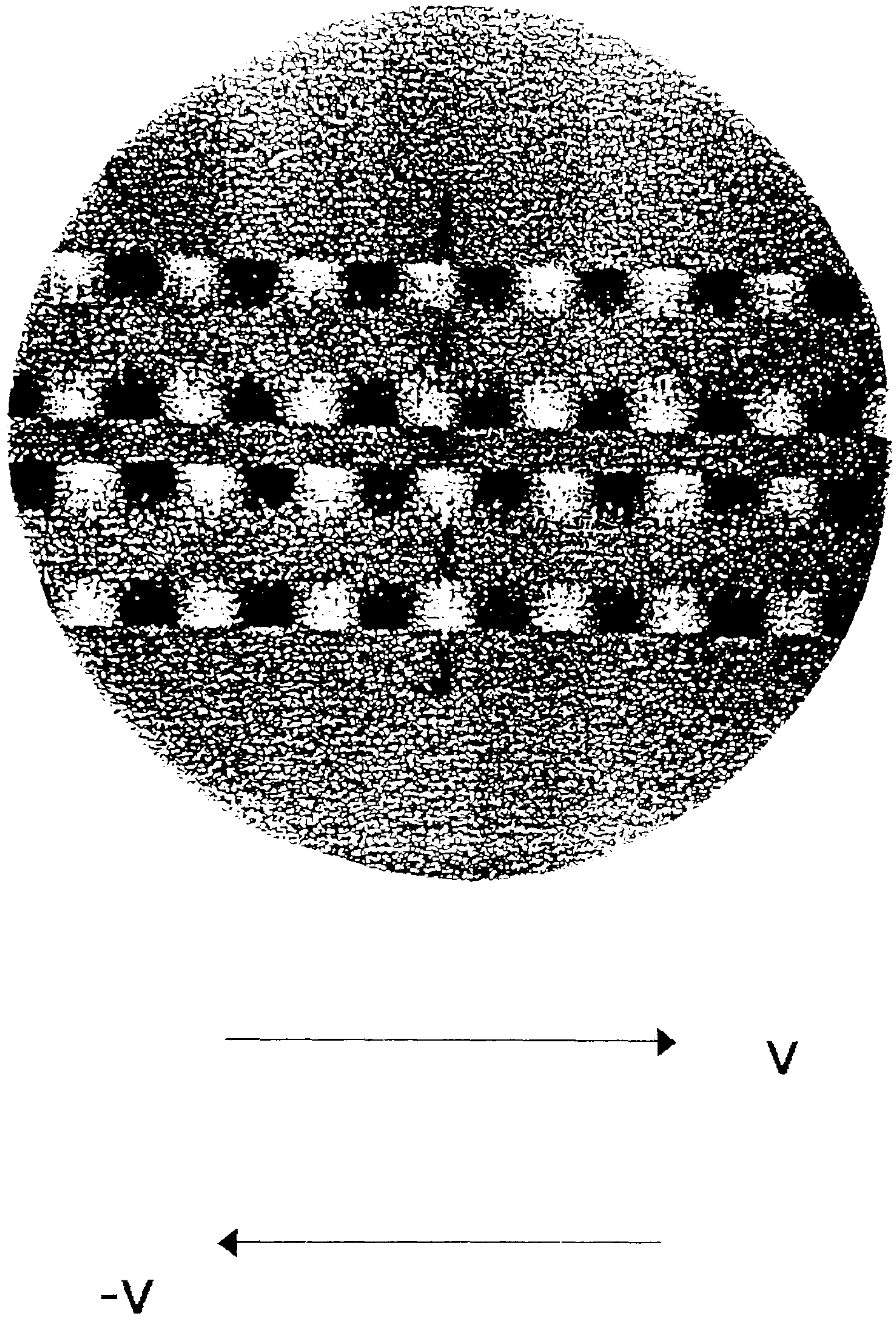


Figure 26a: Shear Terminators display. Note that this display made use of raised cosine edges.

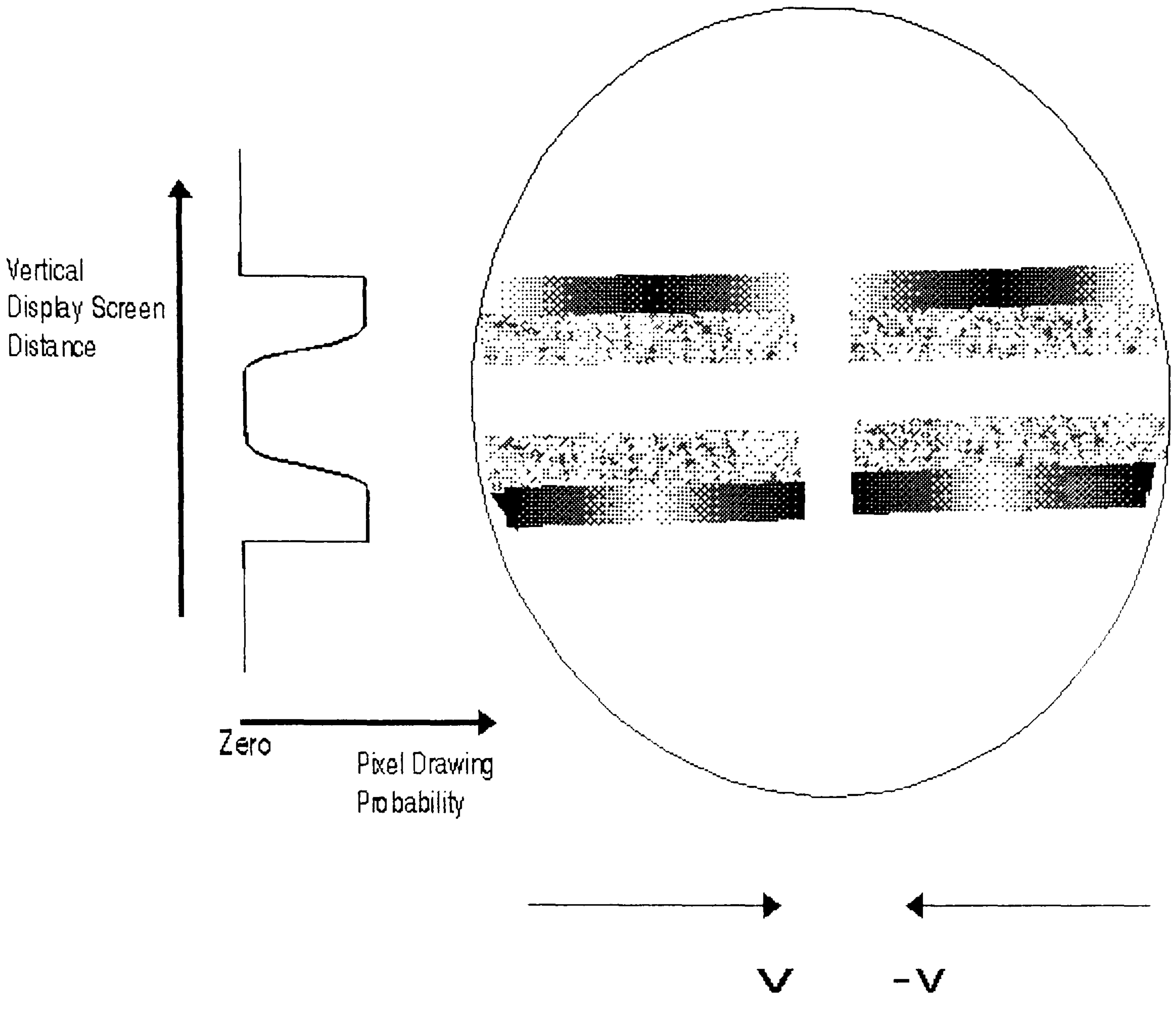


Figure 26b: Schematic diagram of the display for experiment 6b (compression). Note the raised cosine pixel drawing probability for the grating edges.

(compression experiment) i.e. boundaries perpendicular to the direction of motion of the edges (see figure 26b). Shearing motion displays and compressive motion displays were generated by giving opposite directions and linear displays were created by giving the same direction of motion to the gratings that filled the display windows as shown in figures 26a and 26b.

As in experiments 1b, 2b and 3b an expansion motion control stimulus was generated for experiment 6b, again no data was collected for this expanding motion.

Procedure

The procedure for this experiment was as for experiment 5. The subjects task in these experiments being to report in which interval he observed motion and what type of motion was present. The motion thresholds reported for this experiment are the velocities of the terminators along the edges of the display windows and correspond to the velocities given to the gratings that filled the windows. As there was no oriented grating components in the display there was no pattern or component motion signals associated with the displays.

For experiment 6b no data was collected for the control expanding motion type, the subject responded if he considered this motion to be present as in experiments 1b, 2b and 3b by pressing the third response key.

Subjects

The subjects for this experiment were the author KR, who was 26 years old, is male, has normal vision and is an experienced psychophysical observer and VJH who was 25 years old, is female, has normal vision and was naive to the aims of the experiment.

5.7 Results

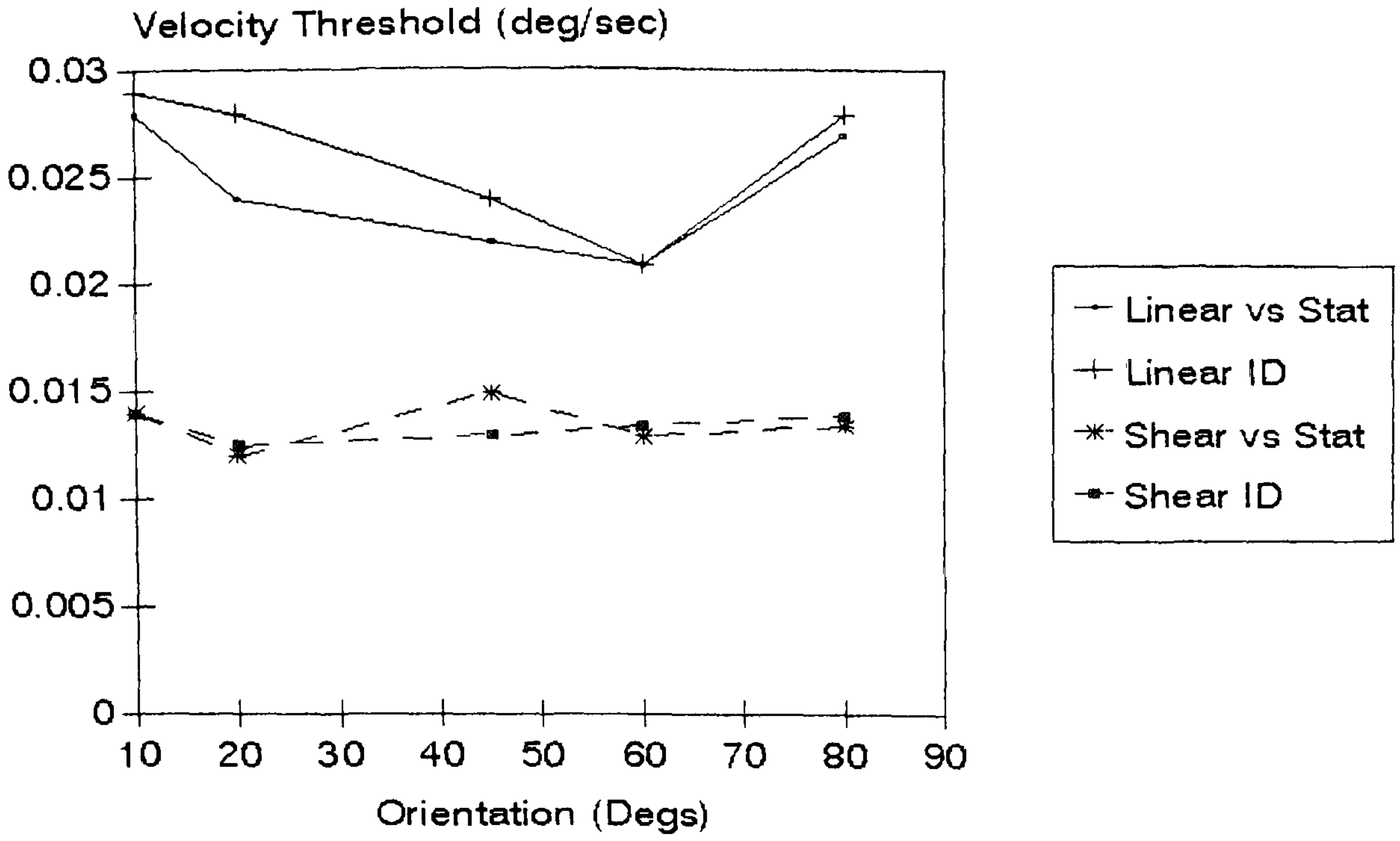
Results for experiment 6a can be seen with reference to figure 27a. Results for experiment 6b can be seen with reference to figure 27b.

The results for both experiment 6a and 6b are very similar. Evidence for opponency was obtained for both these experiments i.e. lower thresholds were obtained when the displays contained opposed (either compression or shear) rather than linear motion. It was also the case that a flat function of motion threshold with respect to orientation was obtained for linear and opposed motion in both experiments. This indicates that the thresholds obtained were independent of the orientation of the gratings that filled the display windows.

The reports of the observers indicated that for experiment 6a shear was observed and for experiment 6b compression was observed whenever there was an opposed motion signal present in the display. This indicates that the type of motion observed when presented with a display depended only upon the orientation of the edges with respect to the boundary between them. These results clearly differ from those of experiment 5.

5.8 Discussion

The flat functions relating motion thresholds to orientation clearly differ from those of experiments 5a and 5b. This suggests that the results of experiment 5 were independent of the effects of terminator motion.



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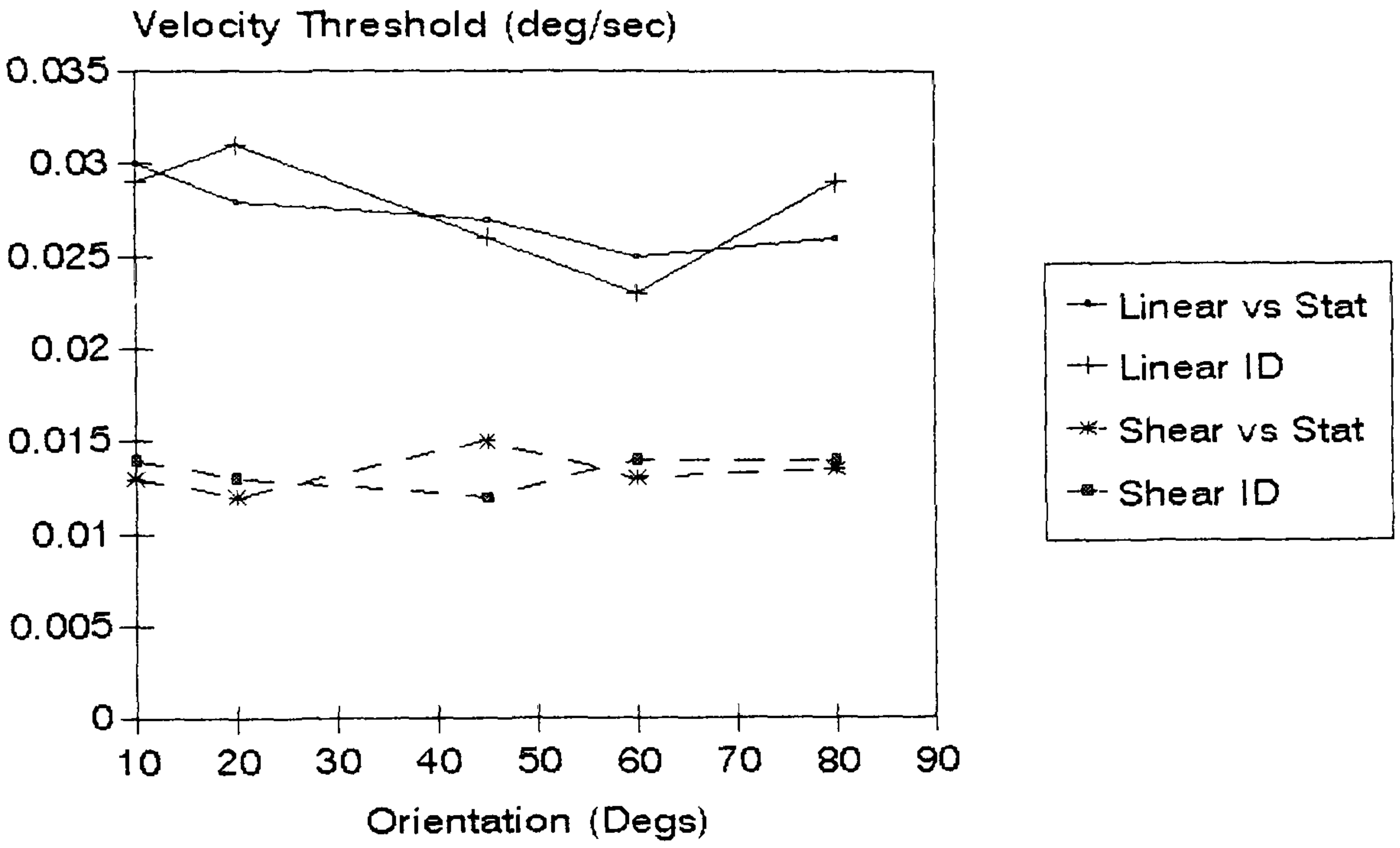

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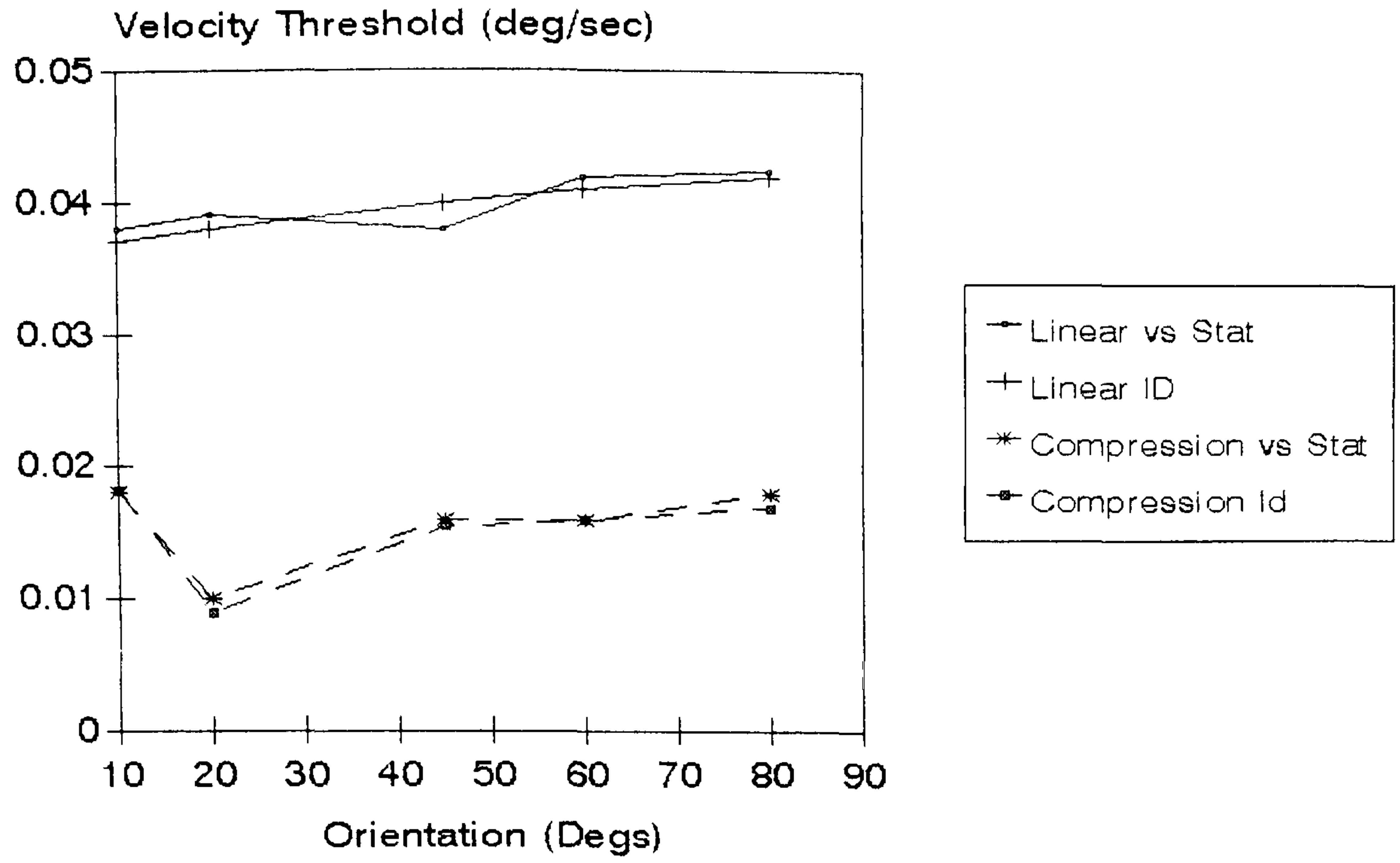
Figure 27a: Experiment 6a, Edges Shear Thresholds



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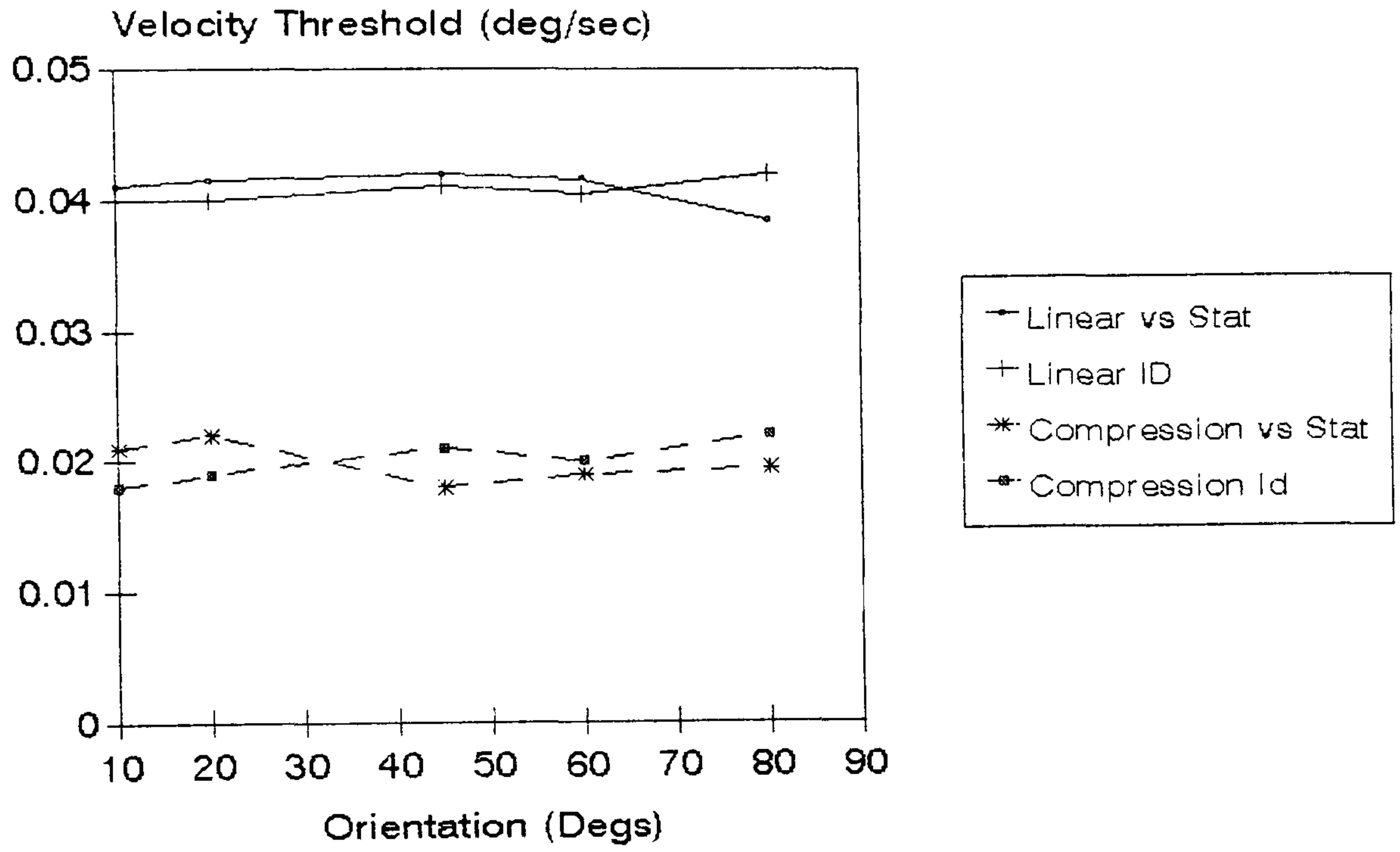


VJH

Figure 27b: Experiment 6b, Edges Compression Thresholds

The subjective reports that shear and compression were seen whenever there was an opposed motion signal present suggest that if observers were using terminator motion in experiment 5 then shear and compression would also be seen for all orientations. As this was not the case then it may be concluded that the results of experiment 5 were not determined by terminator motion effects.

The results of this experiment also indicate the occurrence of opponent processes whenever there was an opposed motion signal present. This suggests that opponent processes can occur between terminator motion signals as well as between grating motion signals.

It is interesting to consider why it was the case that the terminators that were present in the displays of experiment 5 did not give rise to similar results as this experiment. One possible explanation could be that in the displays of experiment 5 the terminators were not intrinsic terminators but were instead extrinsic terminators. Extrinsic terminators are regarded as being of little importance in motion perception (Vallortigara and Bressan, 1991). Thus if the terminators present in the displays of experiments 5a and 5b were of this type then it would be expected that they would have little effect upon the pattern of results of the experiment.

For single windowed grating displays the terminators present in the display are intrinsic, that is they are associated with the physical edge of the display grating. Lorenceau and Shiffrar (1992) suggest that if the aperture window is clearly outlined then the terminators will be regarded as extrinsic rather than intrinsic. This is due to the presence of strong monocular occlusion cues within a clearly defined aperture. These monocular occlusion cues are in the form of T-junctions

(Lorenceau and Shiffrar, 1992; Shimojo et al, 1989). T-junctions occur at the edges of gratings which have been occluded by another object, they are in the shape of a letter 'T' the flat part coinciding with the edge of the window or the boundary between the grating and the occluder (see figure 28). It could be that the small on screen gap between the two windowed gratings in experiments 5a and 5b, gives rise to these strong monocular occlusion cues at the edges of the display windows that would not be present with a single isolated grating. This could thus result in the two windowed gratings being perceived as occluded gratings rather than as single independent gratings. If this was the case in experiment 5, then as described the terminators would be regarded by the visual system as extrinsic terminators (the result of occlusion) and as such would have no effect upon the perception of motion. In such a case as extrinsic terminator motion signals contribute little to the perception of motion, then the dominant motion signals would be associated with the oriented grating components and so these would determine the percept and the thresholds for experiment 5.

This is further support for the notion (Shimojo et al, 1989) that the process by which occlusion is detected and terminators are labelled as extrinsic or extrinsic occurs prior to the attribution of motion signals to the display. This is because if the type of terminator effects motion perception as previous research indicates (Shimojo et al, 1989; Nakayama et al, 1989; Lorenceau and Shiffrar, 1992; Vallortigara and Bressan, 1991) then the type of terminators present must be decided prior to motion interpretation.

It is interesting to ask where sensitivity to terminator motion fits into models of motion perception and specifically models of shear and compression sensitivity.

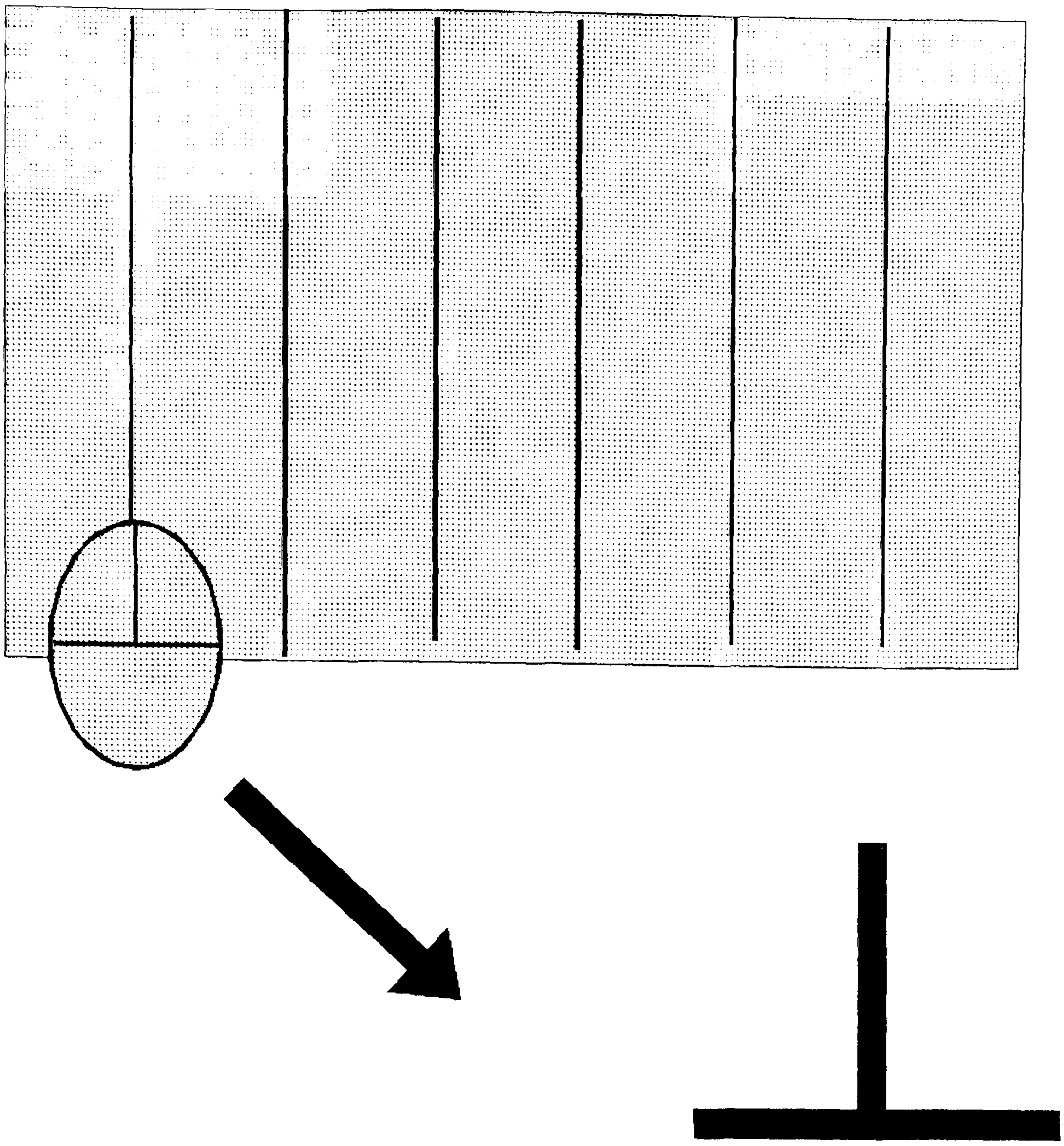


Figure 28: 'T' Junctions at Window Edge

The results of this experiment indicate that motion signals that are generated by terminator motion are subject to opponent interactions as are motion signals generated by sinusoidal component motion. They further show that terminator motion signals alone are enough to allow the perception of shear or compression. If the argument is accepted that only extrinsic terminator motion signals were available to the observer in experiments 5a and 5b then it is possible to say only that extrinsic terminator motion signals do not contribute to the perception of shear and compressive motion. This would be expected given the suggestion (Vallortigara and Bressan, 1991) that extrinsic terminator motion signals contribute little to the perception of object motion. The role of intrinsic terminators on the other hand is an open question and is one that the current study does not fully address. It may be assumed that the terminator motion signals generated in the current experiment (experiment 6) were intrinsic terminator motion signals, as the terminators seem to have had some effect upon the motion percept. If this is so then the evidence for opponency can be considered to be opponency between intrinsic terminator motion signals.

Thus when intrinsic terminator motion signals are available they do contribute to the perception of shear and compression and indeed to motion perception generally.

An unresolved question concerning terminator motion is how the motion signals generated interact with motion signals generated by oriented sinusoidal components. This is an issue within the wider context of motion perception and is one that is beyond the scope of the current study. All that is to be noted here is that terminator more specifically intrinsic terminator motion can contribute to the perception of shear and compression and the motion signals generated are subject to opponent interactions.

Experiment 7

Effects of oriented components upon shear and compression sensitivity: Removing Motion Cues at Window Edges.

5.9 Introduction

The purpose of this experiment was to examine the effects upon the perception of shear and compression of removing motion cues associated with the edges of the display window.

It can be seen that if the boundary of a window is attenuated, so that it is no longer a horizontal straight line, then the ability to compute unambiguously an intersection of constraints is also attenuated. There is no longer a single boundary component but several oriented components (see figures 29b and 29c). The result of this is that it is no longer possible to predict a stage 2 motion signal that is parallel to the edge of the display window.

The motion of the edge terminators would also be made ambiguous, as again there is no longer a single straight line of terminators in the display. The result of this is that the terminator motion signal would not be parallel to the edges of the display window, but would be in a number of directions associated with the attenuated window edges.

Opponent interactions occur between opposed directions of motion. If computation of IOC gives rise to ambiguous directions of motion for each of the display windows it is likely that the conditions for opponency would not be met i.e. two non opposed or similar directions of motion could be signalled by the IOC process due to the presence of ambiguous motion signals associated with the window edges.

Given that attenuation of motion signals at window edges may effect the computation of an IOC and effects the salience of terminator motion, it may be seen how this can be used to test the different predictions of the models detailed to account for shear and compression processing (figure 25).

The first model postulating that opponent processes occur after stage 1 processes and in parallel to stage 2 processes (figure 25a) was discounted by the results of experiment 5 on the grounds that this model predicts no effect of orientation upon component motion thresholds. If such a system were to be presented with a stimulus with attenuated edges then this model would again predict the presence of opponency (lower thresholds for shear and compression than for linear motion) and also that the component thresholds would be independent of the orientation. This model thus predicts lower thresholds for shear and compression than for linear motion over all orientations and no dependence of the component thresholds with orientation.

If opponent processes occur after stage 2 (IOC) processes (see figure 25b) then for the type of displays used in this experiment any benefits in terms of motion thresholds of opposed motion over linear motion displays (lower thresholds for the compressive or shearing displays relative to the linear displays) would be abolished or at least attenuated. This would be because such a system would require unambiguous stage 2 outputs signalling motion in two opposite directions in order

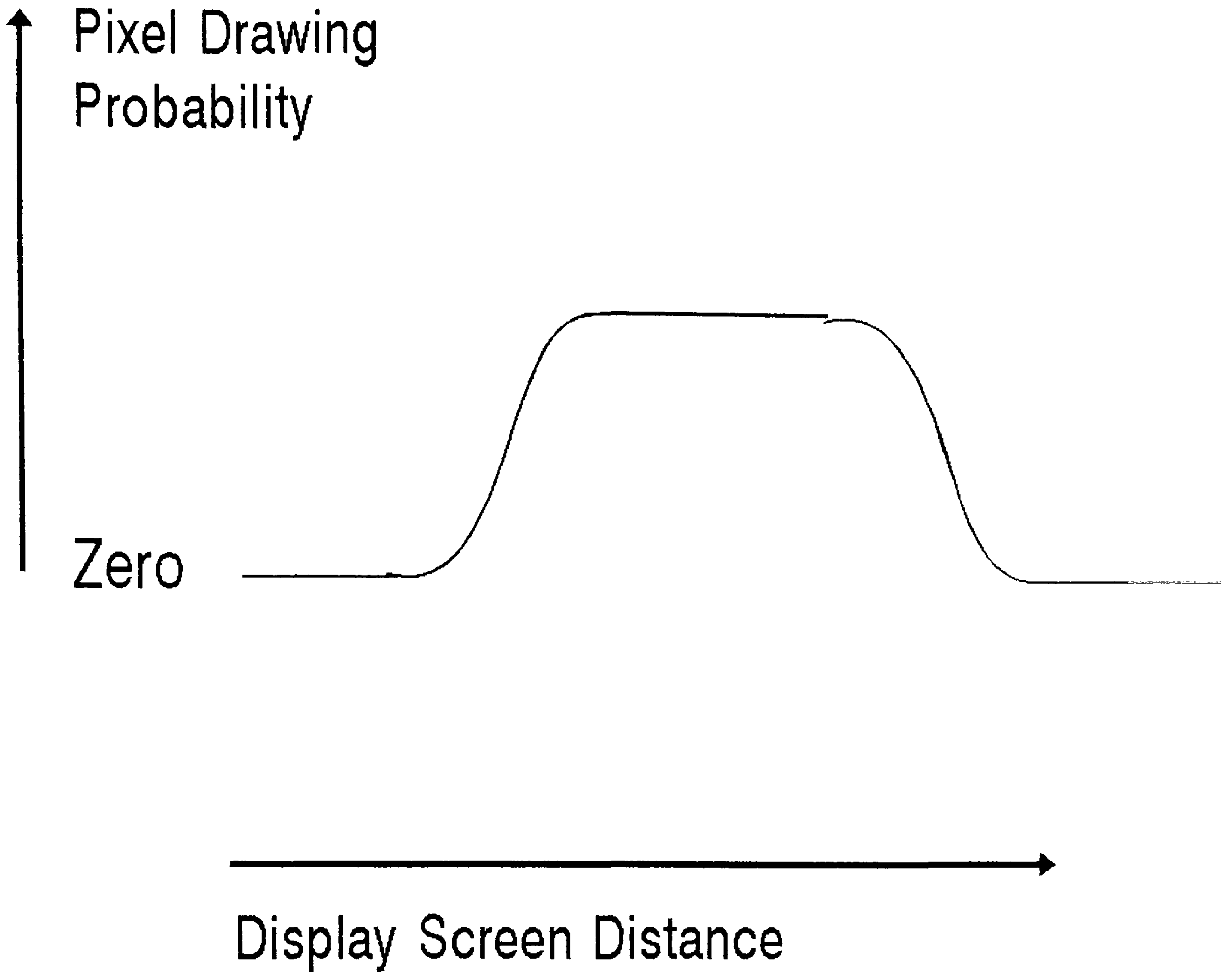


Figure 29a: Raised Cosine Windows Pixel Drawing Probability

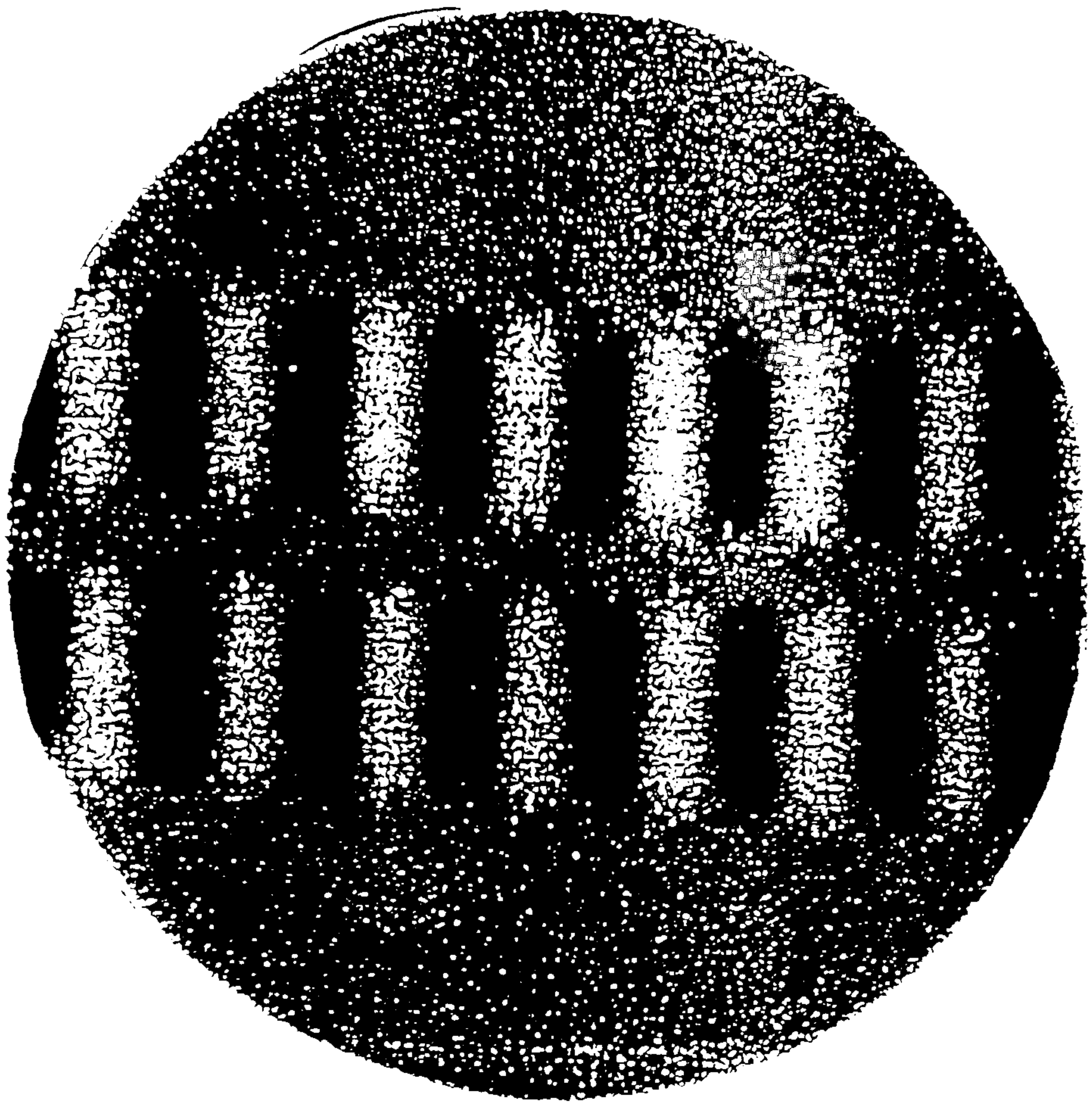


Figure 29b: Shear Raised Cosine Display

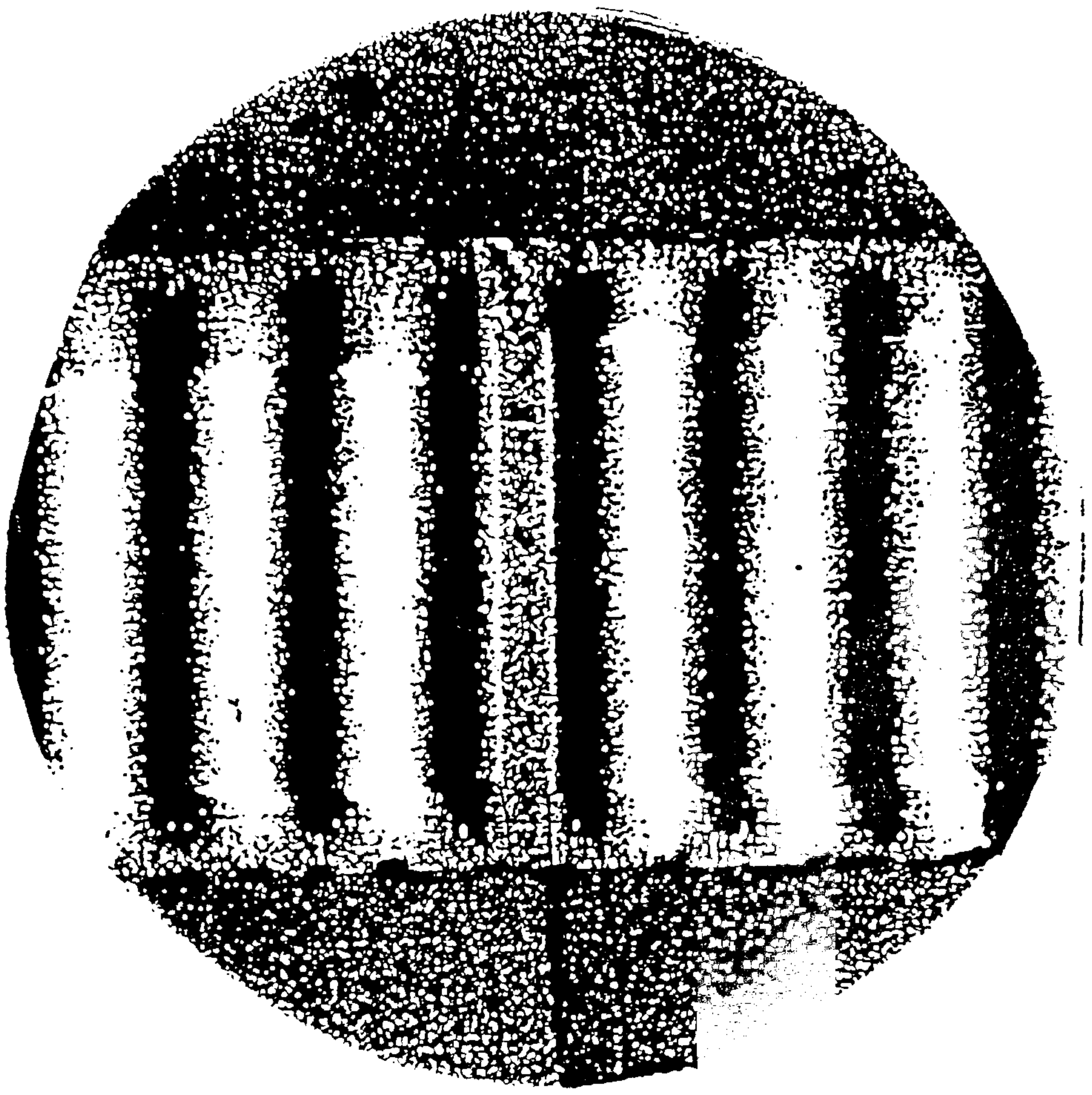


Figure 29c: Compression Raised Cosine Display

to give rise to opponency. Clearly with attenuated window edges the stage 2 outputs would be very likely to be ambiguous, with a range of possible solutions of IOC for each window. Thus it would be expected that the results of this experiment would differ substantially from those of experiments 5a and 5b, with equivalence or at least reduced differences between the shear or compression thresholds and the linear thresholds.

If the opponent processes occurred after stage 1 processes but prior to stage 2 processes (see figure 25c), the fact that the stage 2 processes produce ambiguous signals would not effect the opponent processes. This would mean that a similar set of results to those of experiments 5a and 5b should be obtained i.e. lower thresholds for shear and linear motion over all orientations. This model differs from the parallel process model described in figure 25a in its prediction that component motion thresholds would show some dependence upon orientation, due to the effects of stage 2 noise (Wright and Gurney 1992).

Essentially then this experiment allows comparisons to be drawn between the predictions of the models proposed to account for the results of experiment 5a and 5b.

The method of attenuation of the window edge was to vary the display screen pixel drawing probability across a region bounding the edges of the windows. The probability function used was a raised cosine function (see method).

It was suggested in the discussion to experiment 6 that the results of that experiment differed from those of experiment 5 as the terminator motion present in the displays of experiment 5 was of the extrinsic type. Another aim of this experiment was to test this suggestion i.e. by removing all terminator motion signals from the displays of experiment 5. Clearly if the experiment 5 displays contained only extrinsic terminators, and as these are thought not to play a part in motion perception, then if terminator motion is removed the results should resemble those of experiments 5a and 5b. If on the other hand the terminator motion of experiments 5a and 5b did play a part in the perception of motion then the results of this experiment would be expected to differ substantially from those of experiment 5.

Again as for experiments 5a and 5b data are presented as component and pattern lower thresholds of motion.

5.10 Method

Apparatus

Patterns were generated using a Cambridge Research System Visual Stimulus Generator. The patterns were displayed on a Tektronix 608 monitor of p31 phosphor. The frame rate used was 150 hz. Responses were obtained using a cambridge research systems cb1 three switch response box, only two of the switches were used here.

Display

The display of this experiment consisted of two sinewave gratings displayed on screen, one vertically above the other in the case of the shear display (experiment 7a : see figure 29b) and in the case of the compression display one grating to the left and one to the right of the display screen (experiment 7b : see figure 29c). Each grating was placed into one of two on screen windows that were defined using the VSG framestore. The windows were separated by an on screen distance of 0.8 cm. The display screen subtended a visual angle of 1.97 degrees at the viewing distance of 290 cms. The two windows containing the component gratings covered equal areas of the screen and filled the screen from left to right.

The probability of finding a pixel on the display was calculated for both the windows using a raised cosine function so that there was a 50% chance of a pixel appearing at points in the display coinciding with the edges of the windows, reducing to zero at points along the centre of the display and to the top of the top window and bottom of the lower window (see figure 29a). Maximum pixel probability occurred for all other regions of the display. The effect of this was to give the edges of the display something of a frosted glass appearance, with no definite edges.

Three types of motion were defined for each of the experiments: for experiment 7a. Shearing, linear and stationary displays and for experiment 7b compression, linear and stationary displays.

The shearing and compressive display consisted of two gratings moving in opposite directions of motion, linear motion displays consisted of the two gratings moving in the same direction (the direction of motion of each grating was randomised from trial to trial so as to maintain the stimulus type) and stationary displays were made of two gratings with zero velocity.

The starting phase of each grating was randomised so as to control for the use of vernier cues in detecting and identifying the motion type.

The orientation of each grating was decided prior to the start of an experimental run. Each of the two gratings defining the displays was given the same orientation. All orientations were expressed with respect to the vertical. Within a given experimental run the grating orientation was kept constant. Six orientations were used, 0, 10, 20, 30, 45, 60 and 80 degrees. Each oriented grating was placed into one of the windows so that it filled the window completely.

As in experiments 1b, 2b and 3b an expansion motion control stimulus was generated for experiment, again no data was collected for this expanding motion.

Procedure

A two alternative forced choice PEST procedure was used. Each experimental run was separated into a series of trials. On any given trial the type of motion (linear or shear: experiment 7a)/(linear or compression: experiment 7b) to be shown was randomly selected. The moving stimuli (linear or shear or compression) could be placed randomly into one or other of two time intervals each of 100 msec duration. There was an inter stimulus interval where the screen was left at mean luminance of 100 msec. Into the other time interval was placed the stationary stimulus. An experimental run was initiated by the observer depressing one of the response keys. On any given trial the observer was presented with two types of grating pattern. One moving the other stationary. The task of the subject was after presentation of the second interval to make two key press responses. The first was to indicate in which interval he had seen a moving stimulus and the second response was to indicate which moving stimulus type he had seen (linear or shear: experiment 7a; linear or compression:experiment 7b). The first response constituted discrimination of a moving from the stationary stimulus. The second response constituted identification of the moving stimulus type.

Velocity threshold data was obtained for experiment 7a: discriminating a moving shear and a moving linear type motion from stationary and also threshold data was obtained for the identification of shear and linear motion, and for experiment 7b: discriminating a moving compression and a moving linear motion from stationary and identifying a compression and linear motion. Thus four thresholds were obtained in any given experimental run. The thresholds were in terms of velocity i.e. the lowest velocity at which the task could be performed (lower thresholds of motion).

The reported thresholds are the result of at least three experimental runs. The thresholds reported have standard errors of ten percent or less.

For experiment 7b no data was collected for the control expanding motion type, the subject responded if he considered this motion to be present as in experiments 1b, 2b and 3b by pressing the third response key.

Subjects

The subjects for this experiment were the author KR, who was 26 years old, is male, has normal vision and is an experienced psychophysical observer and VJH who was 25 years old, is female, has normal vision and was naive to the aims of the experiment.

5.11 Results

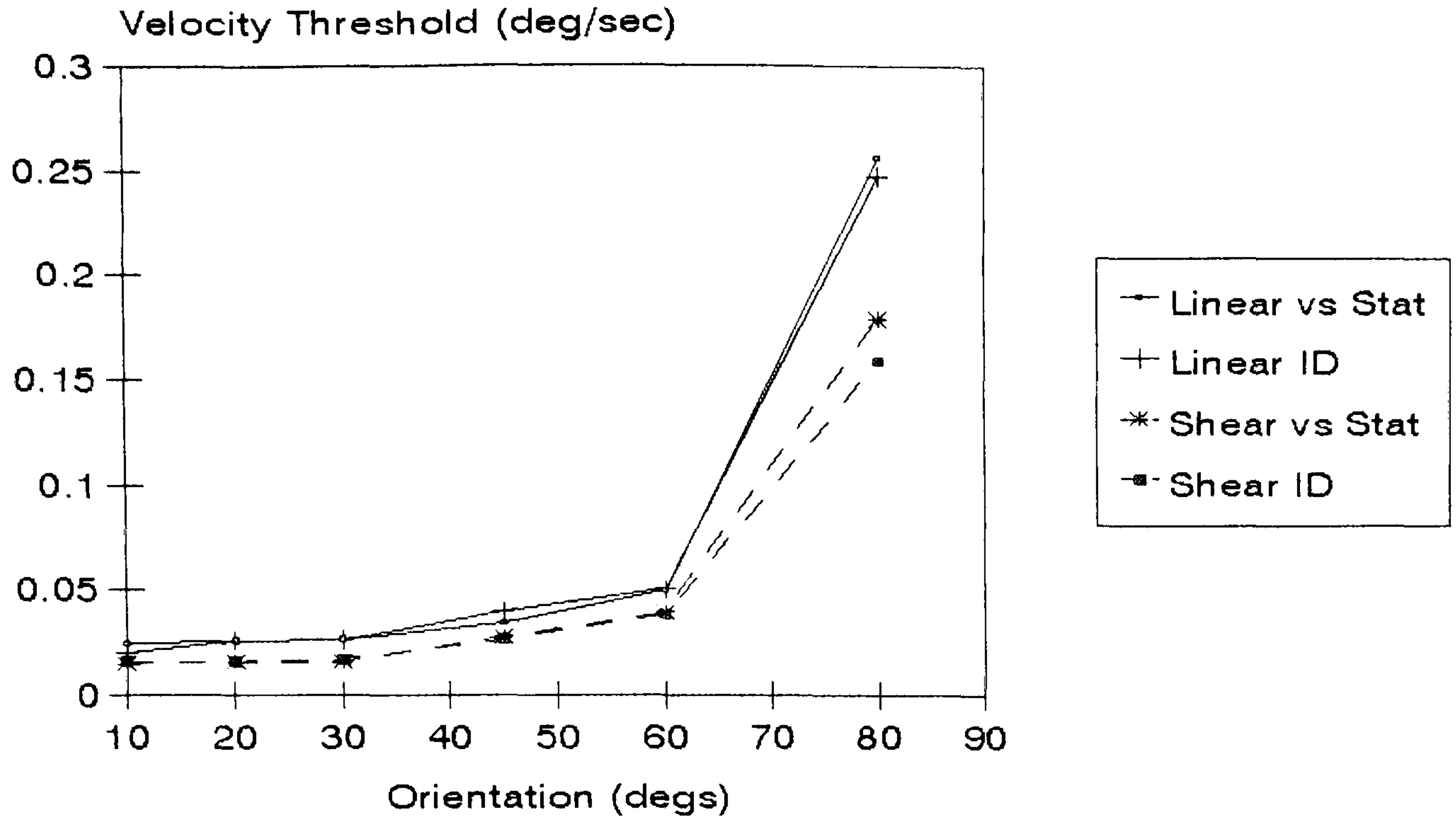
Experiment 7a

First consider the results of experiment 7a (figures 30a and 30b). Results generally consistent with those of experiment 5a were obtained for all orientations when considering both the pattern motion (figure 30a) and component motion (figure 30b) thresholds.

Analysis of variance results for the pattern motion thresholds revealed that there was no significant effect of the task type i.e. $(f=0.031;df=1;p>0.05)$. There were significant effects of the type of stimulus $(f=84.650;df=1;p<0.001)$ and of orientation $(F=1154.703;df=5;p<0.001)$ and a significant interaction between the orientation and the type of stimulus $(F=4.981;df=5;p<0.01)$. This indicates that the pattern of the results was due to the stimulus type and the orientation, the task type was not an important factor in determining the results.

The pattern thresholds, Vp, for shearing motion appear to increase with orientation. The shearing motion thresholds always remaining less than those for linear motion.

The component threshold, Vc, (figure 30b) results show a similar pattern to those obtained in experiment 5a. There is a slight dependence (reduction) of the shear threshold upon the orientation of the sinusoidal components, shear thresholds always being less than those for linear motion. The linear thresholds show little dependence upon orientation. It is apparent from a comparison of the shear pattern and shear component results that the component thresholds like those of experiment 5a are very much less dependent upon orientation than the pattern thresholds. Analysis of variance revealed a similar pattern to that for the pattern



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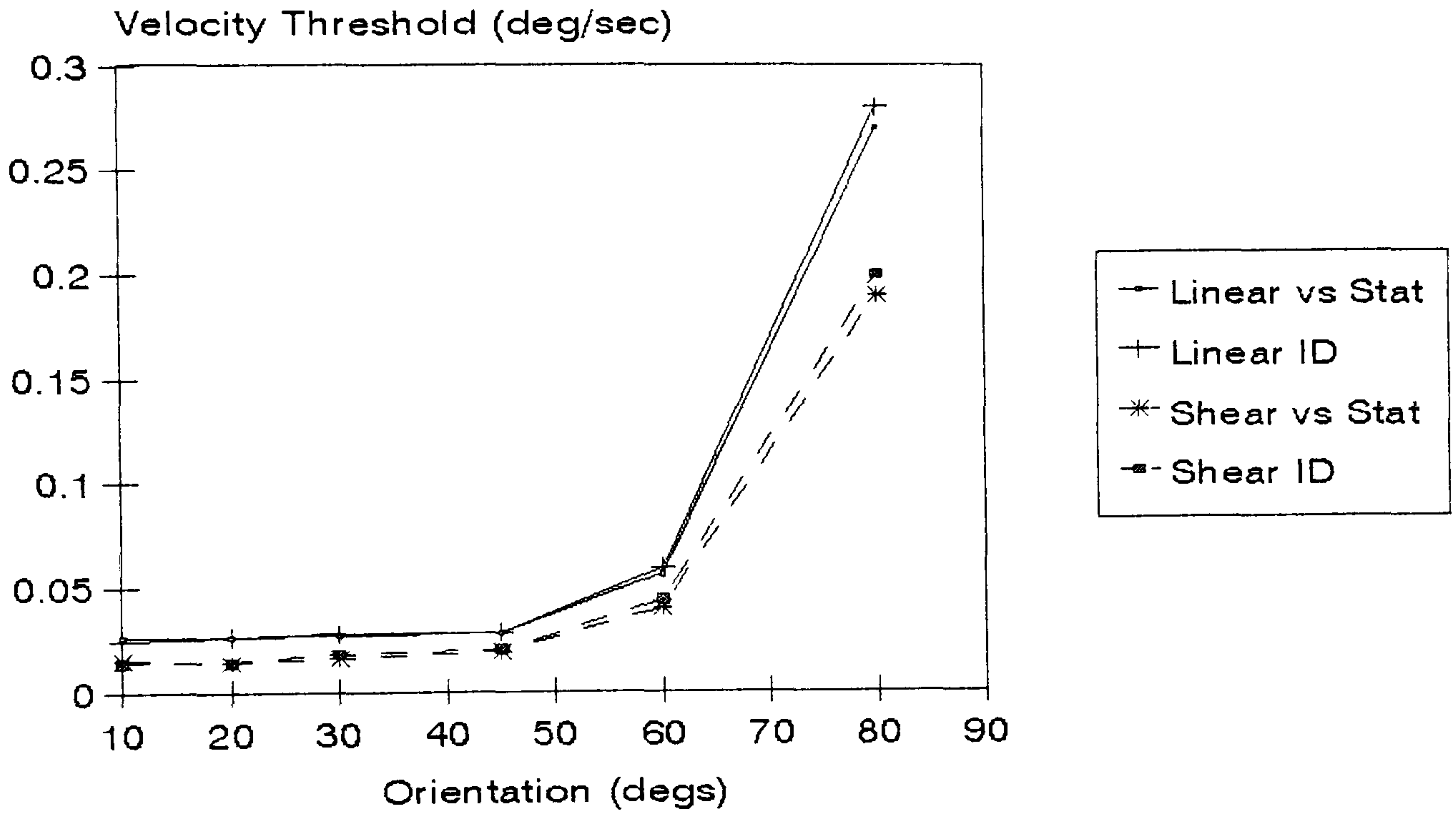
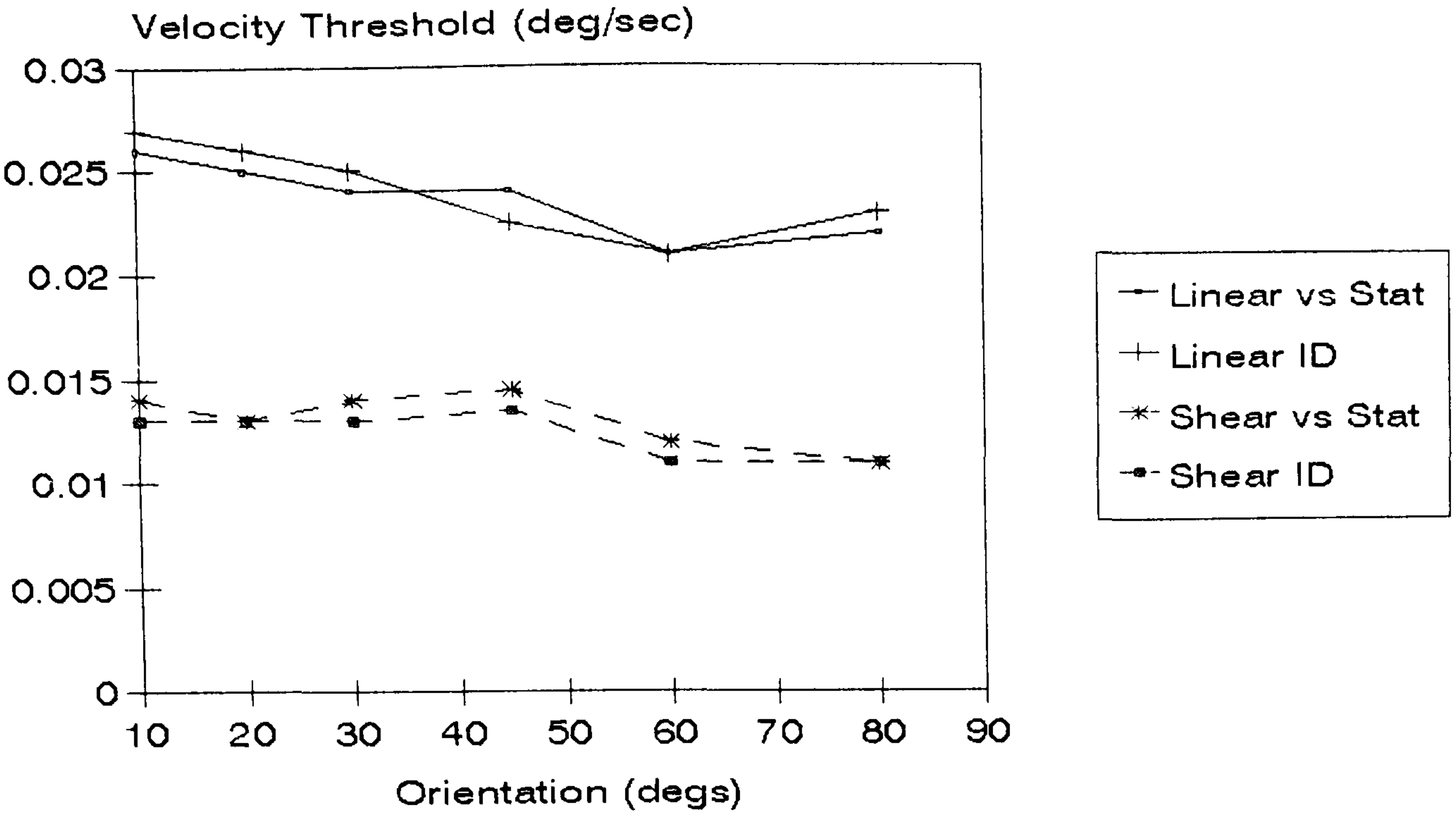


VJH

Figure 30a: Experiment 7a, Shear Pattern Thresholds Raised Cosine Gratings. Lower thresholds of motion



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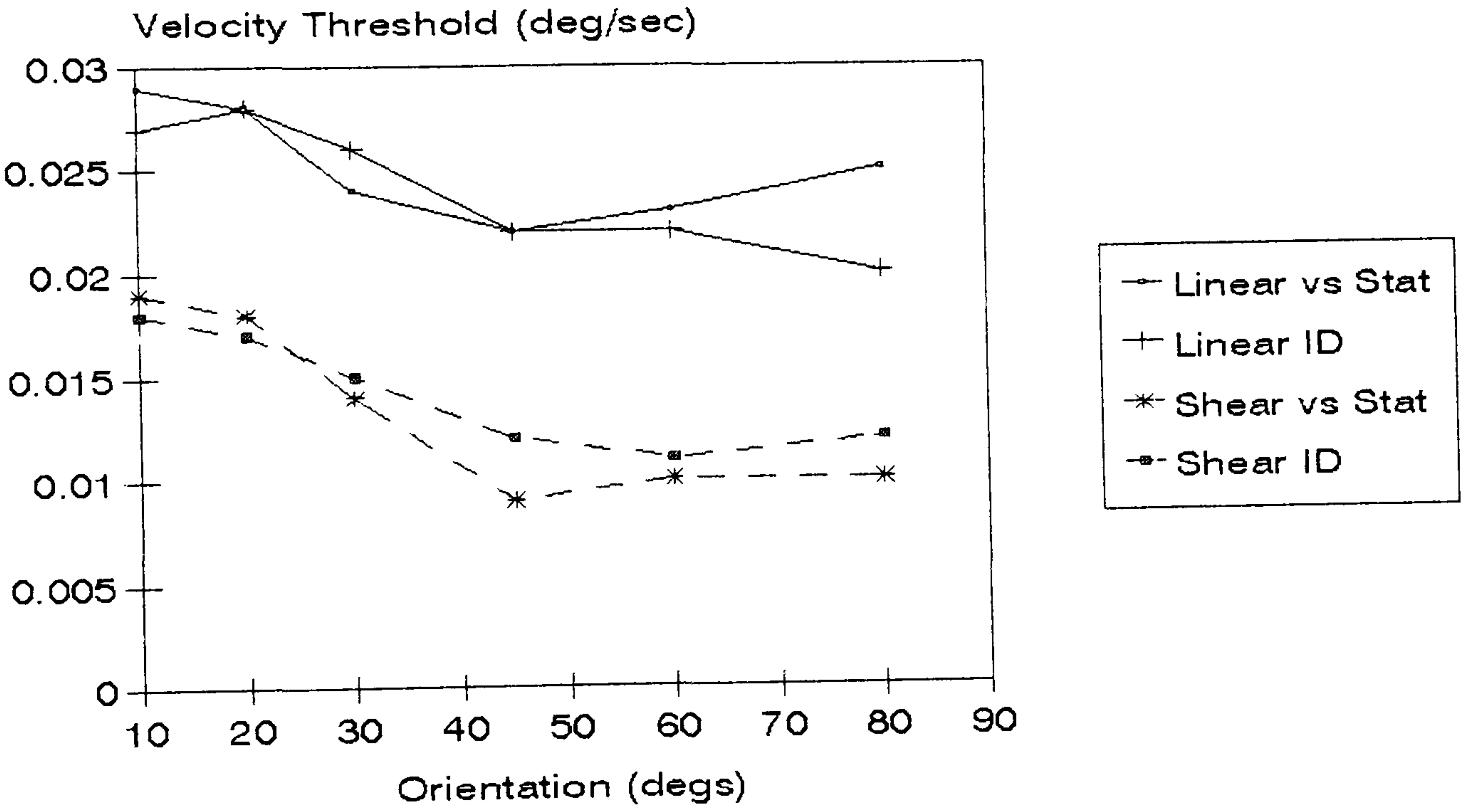


VJH

Figure 30b: Experiment 7a, Shear Component Thresholds Raised Cosine Gratings. Lower thresholds of motion thresholds with significant effects of orientation ($f=13.348;df=5;p<0.001$), stimulus type ($F=121.198;df=1;p<0.001$) and for the interaction between the stimulus type and the orientation task type ($F=0.943;df=1;p>0.05$). This again illustrates that the pattern of results is determined by the orientation and the stimulus type.

For both sets of results (pattern and component) there were significant interactions between the stimulus type and the task. It is argued that these significant interactions are the result of the type of stimulus given the significance of the stimulus type and the insignificance of the task type for both sets of results.

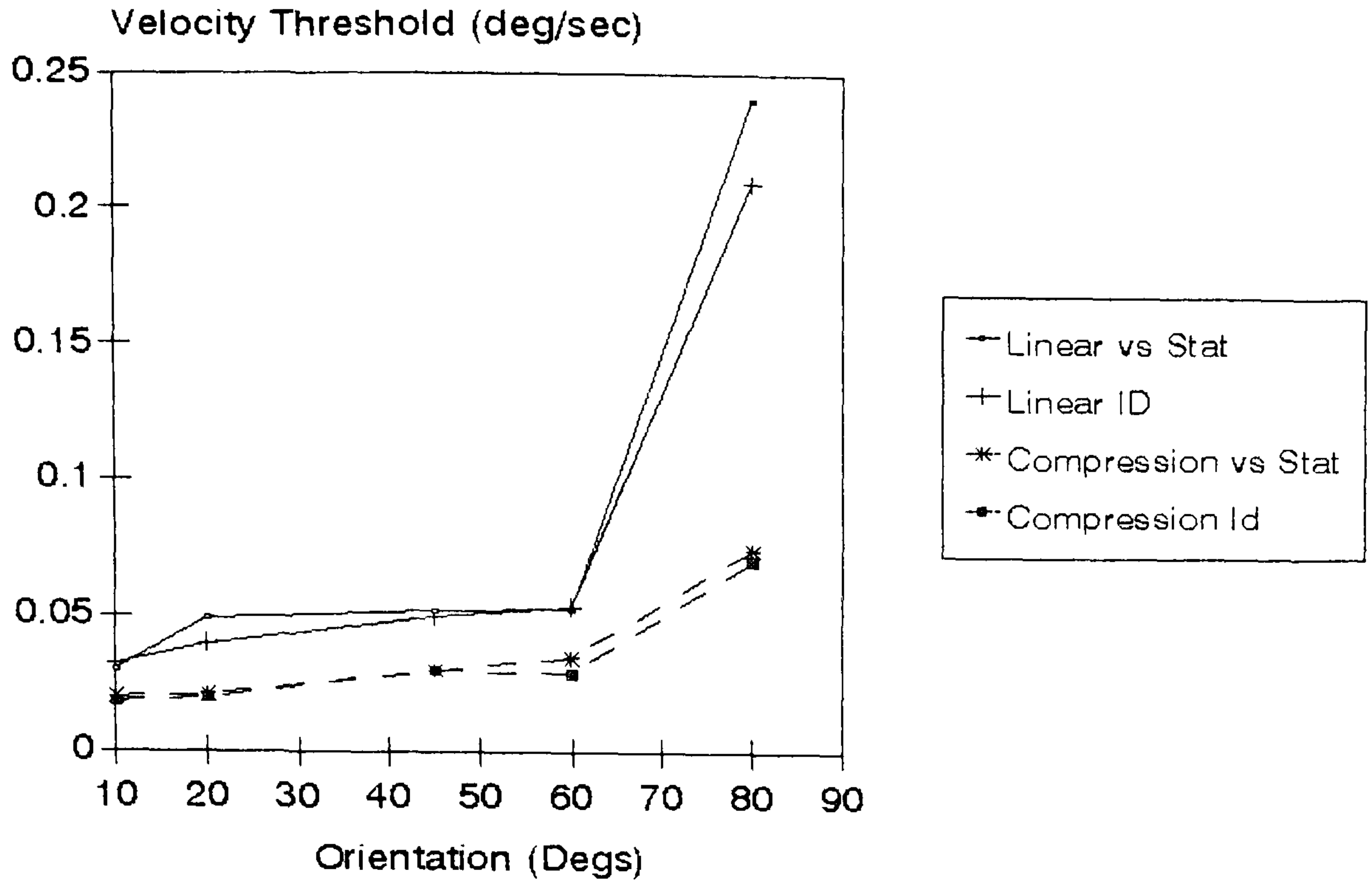
Experiment 7b

Examining the results of experiment 7b (figures 31a and 31b). Firstly the general pattern of results is similar to those for experiment 5a for both subjects.

As in experiment 5a, results generally consistent with those of experiment 3 were obtained i.e. lower thresholds for compression than for linear motion. When considering the pattern motion thresholds (figure 31a) it may be seen that the pattern of results is very similar to those of experiment 7a (figure 30a).

Compressive motion pattern thresholds show a great dependence upon the orientation, while linear pattern thresholds show somewhat less dependence. It is also the case that the results of this experiment for pattern motion are very similar to those of experiment 5b.

Analysis of variance results for the pattern motion thresholds revealed that there was no significant effect of the task type. There were significant effects of the type of stimulus ($df=1;F=92.294;p<0.001$) and of orientation



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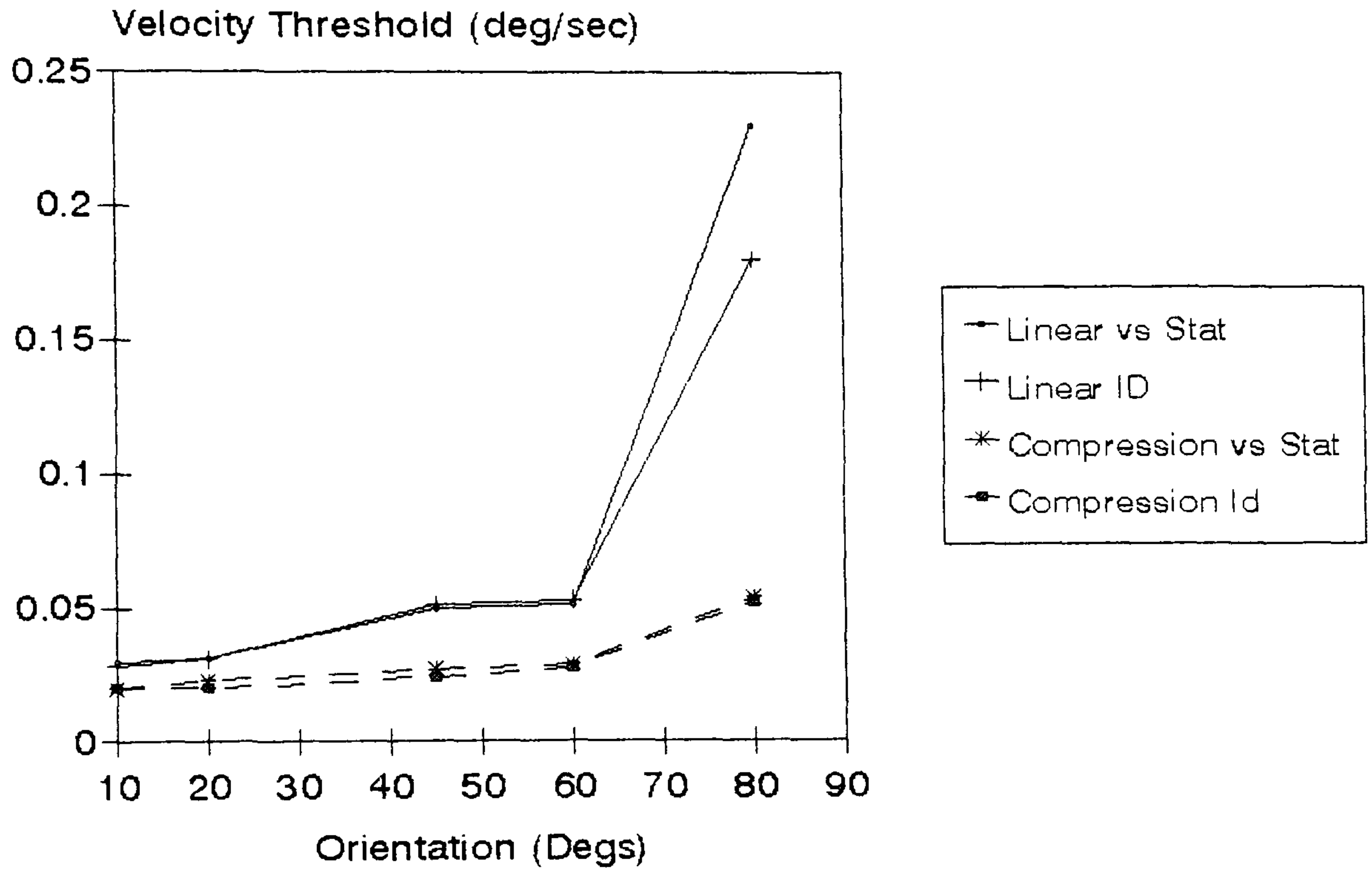
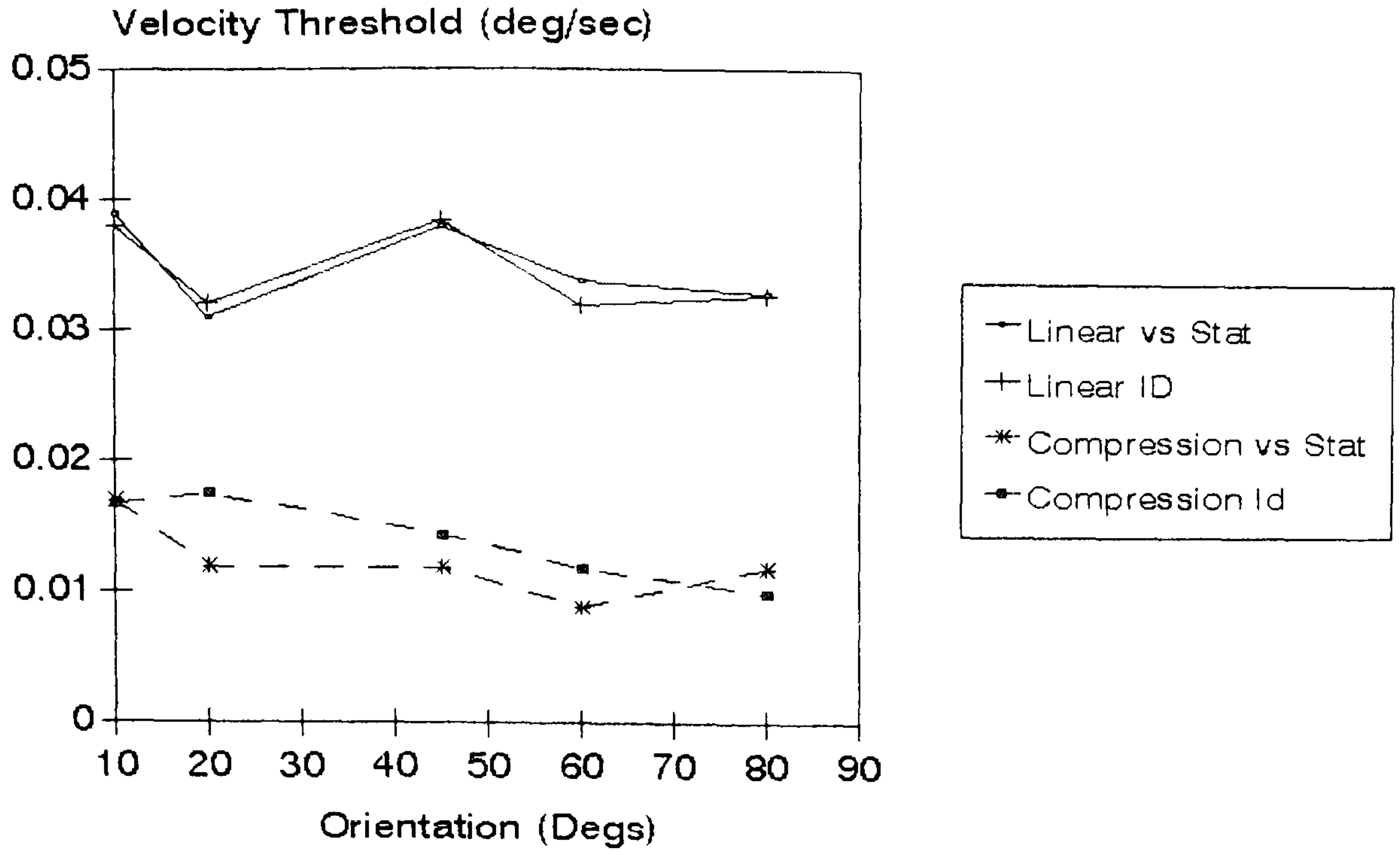


VJH

Figure 31a: Experiment 7b, Compression Pattern Thresholds Vp. Lower Thresholds of motion



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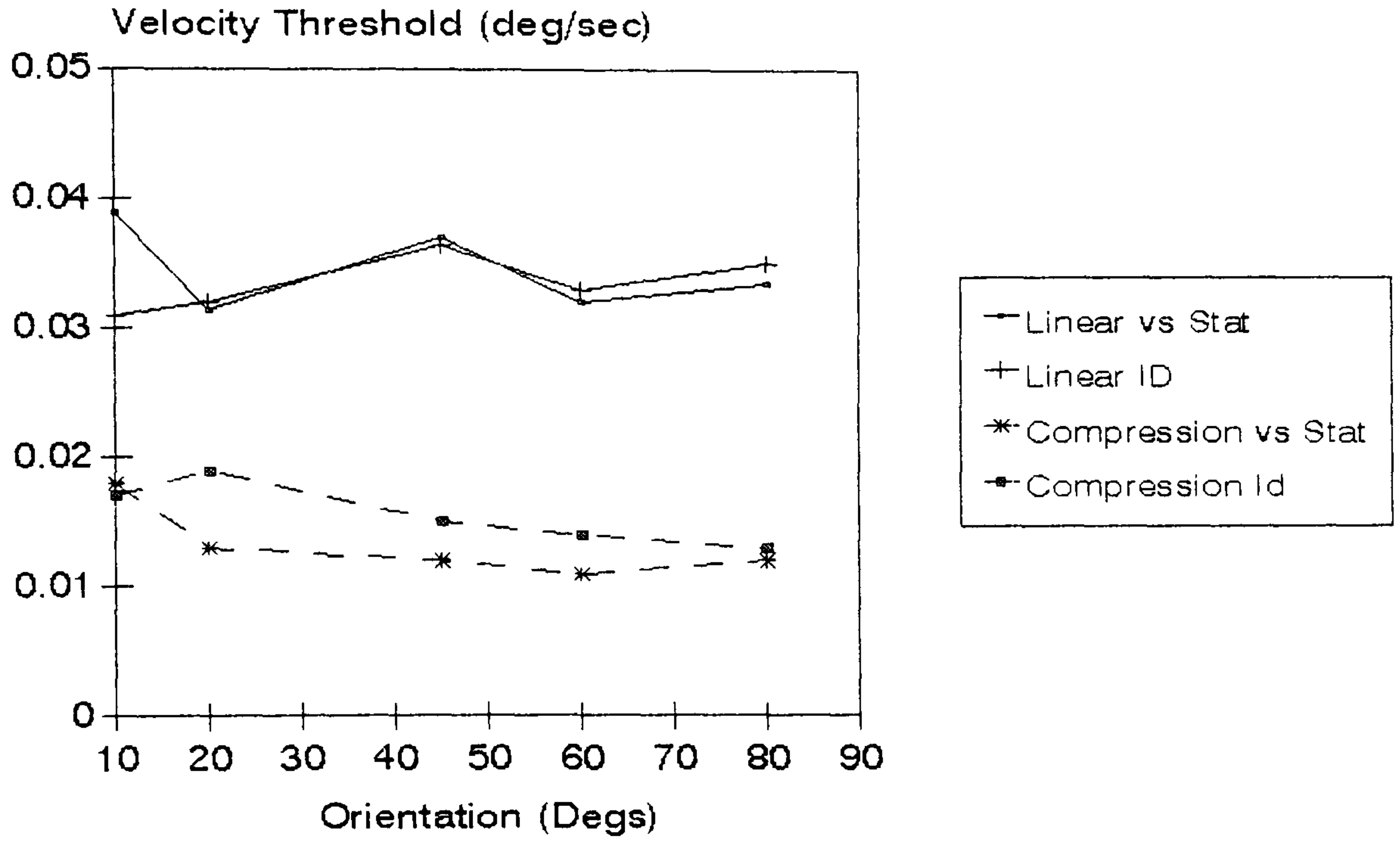

VJH

Figure 31b: Experiment 7b, Compression Component Thresholds Vc. Lower thresholds of motion.

(df=4;F=12.462;p<0.001) and a significant interaction between the orientation and the type of stimulus (df=4;F=7.759;p<0.01). This indicates that as with experiment 5a the pattern of the results was due to the stimulus type and the orientation, the task type was not an important factor in determining the results.

The component threshold (figure 31b) results for compression show a similar pattern as those found in experiment 5b. Compression has lower component thresholds than linear motion. Compression component thresholds show a dependence upon the orientation not shown by the linear thresholds, however comparing this to the compression pattern results it is apparent that the pattern results are much more dependent upon the orientation than the component results.

Analysis of variance revealed a similar pattern to that for the pattern thresholds with significant effects of orientation (df=4;F=10.98;p<0.001), stimulus type (df=1;F=1186.532;p<0.001) and for the interaction between the stimulus type and the orientation task type (df=4;F=9.217;p>0.001). This again illustrates that the pattern of results is determined by the orientation and the stimulus type.

For both sets of results (pattern and component) there were significant interactions between the stimulus type and the task. It is argued that these significant interactions are the result of the type of stimulus given the significance of the stimulus type and the insignificance of the task type for both sets of results.

5.12 Discussion

The results of this experiment were strikingly similar to those of experiments 5a and 5b. The component motion thresholds for both shear and compression were more consistent over the range of orientations than were the corresponding pattern thresholds. Secondly evidence for opponency was obtained with the opposed motion stimuli for both experiments 7a and 7b. Finally the observers reported that it became increasingly harder to perceive shear or compression with increasing orientation of the components.

As evidence for opponency was obtained for all stimulus orientations when the components moved in opposite directions, it appears that an unambiguous intersection of constraints need not be carried out in order for opponent interactions to take place. This coupled with the similarity between the current results and those of experiment 5 , suggests that opponent processes are occurring prior to stage 2 processes.

Thus the model proposing opponency between stage 1 processes outputs which is then fed into stage 2 (see figure 25c) is supported by these data.

The addition of stage 2 noise to stage 1 signals suggestion (Wright and Gurney, 1992) received further support from this data i.e. the observed slight decrease in the component thresholds with respect to increasing orientation.
The flatter function of the component thresholds with respect to orientation as compared with the pattern thresholds lends further support to the notion that thresholds are limited by stage 1 processing and that stage 1 processes occur firstly.

In this experiment terminator motion cues were removed. The fact that these results were similar to those of experiments 5a and 5b and different from those of experiments 6a and 6b (where terminator motion cues were present) is further support for the suggestion that it was unlikely that terminator motion signals were being used by the observers in experiment 5. As terminators were present in the displays of experiment 5 this finding may be taken as some support for the suggestion that the terminators present in the displays of experiments 5a and 5b were extrinsic as opposed to intrinsic (see discussion experiment 6).

The observers experience suggested that it became increasingly harder to perceive the presence of shear or compression with increasing component orientation. This was a similar finding to experiment 5. This leads to the suggestion that what was most important in the determination of the percept for both these experiments was the component directions of motion relative to the boundary between the display windows and is again further support for the idea that the terminators in experiments 5a and 5b were of the extrinsic type.

This is not to rule out any possible influence of the motion of intrinsic terminators upon the percept. Experiments 6a and 6b clearly show that when intrinsic terminators are present in the display then their motion does influence the percept. An interesting point to consider is where terminator motion cues fit into our model. No suggestion was made regarding this in the discussion of experiment 6. However in the light of the current experiments this may be considered. If opponent processes occur prior to stage 2 processes and between the outputs from stage 1 processing as our results suggest, and as it was shown (experiment 6) that terminator motion is subjected to opponent processes then it is likely that intrinsic terminator motion signals are processed at stage 1. This is a reasonable suggestion as it has been argued that attribution of terminator type is made very early on in terms of the level of visual processing possibly at level V1 or V2 (Shimojo et al, 1989). This would mean that whether a moving terminator was extrinsic or intrinsic would be available at the stage 1 level of processing. As to whether terminator motion signals are processed by the same stage 1 mechanisms as component motion signals is another question which is beyond the scope of this study.

Thus to summarise experiment 7. It was argued that the results of the experiment indicate that the probable location of the opponent motion processes suggested to underlie suprathreshold shear and compressive motion processing (experiment 3) is after stage 1 processing and prior to stage 2 processing in two stage models of motion perception (Adelson and Movshon, 1982). It was further suggested that the results of this experiment support the suggestion that the terminator motion cues present in the displays of experiment 5 were due to the presence of extrinsic terminators and so did not contribute to the motion percept of experiment 5.

5.13 Summary of Experiments 5,6 and 7

The results of these experiments support the notion that the sensitivity to shear and compressive motion is limited by the ability to detect local oriented component motions i.e. is limited by the sensitivity of stage 1 processes in two stage models of motion perception (Adelson and Movshon, 1982). The suggestion of Wright and Gurney (1992) that stage 1 motion signals are subjected to noise from stage 2 processes was also supported by these experiments.

Evidence was obtained supporting the notion of opponent processing in motion perception and the notion that the greater sensitivity to shear and compression is the result of such processes. It was suggested that in mechanistic terms these opponent interactions are likely to occur between stage 1 component motion signals prior to stage 2 processes. Thus a model was proposed which suggests serial processing of motion information from stage 1 through opponent processes feeding into stage 2 processes (see figure 25c).

These experiments illustrated that the type of motion seen by the observer depends upon the directions of motion of the sinusoidal grating components and the intrinsic terminators in the display relative to the boundary between the display windows. It was also found that opponency occurred irrespective of the orientation of the components and irrespective of the type of motion reported by the observer, provided that the components were moving in opposed directions.

The motion signals produced by terminator motion or more specifically intrinsic terminator motion (Shimojo et al, 1989) are also subjected to opponent processes. It was suggested that the motion signals generated by intrinsic terminators is processed at a level prior to stage 2 and possibly at stage 1.

It is interesting to ask whether the data of these experiments are consistent with known neurophysiology.

The data suggest a heirachy of processing from stage 1 through opponency to stage 2. It has been found that the neurophysiological conditions do exist for such a heirachy. Movshon et al (1986) found that some 20% of primate area MT neurons responded to the direction of a plaid (pattern motion sensitive) whereas V1 neurons responded to the direction of motion of the grating components of the plaid. Other studies have obtained similar results (Albright et al, 1984; Maunsell and Newsome,1987). Movshon et al (1985) found that some MT cells which responded to plaid motion were also sensitive to the direction of motion of gratings which moved in the same direction as the plaid, while other MT cells responded only to grating direction. This further supports the notion of heirachical processing with the grating direction MT cells representing a lower level of processing than MT pattern cells. MT pattern cells can thus be equated with stage 2 processes while V1 or MT grating cell may be equated with stage 1 in two stage process models.

Allman et al (1985) found evidence in MT cells for opponent type processing. It is unclear from their data whether these cells were MT pattern sensitive or MT grating direction sensitive cells hence the results do not necessarily support our model. However they do show that stage 1 processing at least must have taken place given that stage 1 processes could be occurring at V1 or within the MT grating direction cells.

Thus our suggested models is consistent with the known neurophysiology particularly in its insistence in heirachical processing and the occurrence of opponent processes after stage 1 processes have been carried out.

Chapter 6

A Model of Shear and Compression Processing: Implications of Experiments 1 to 7.

The results of these experiments indicate that shear and compression are not processed by local shear and compression sensitive mechanisms.

It is likely that the sensitivity to shear and compression is constrained by the ability to detect the local directions of motion. This means that the sensitivity to these differential invariants is constrained by the sensitivity of local directionally selective mechanisms (Adelson and Bergen, 1985; Reichardt, 1961).

At suprathreshold contrasts it appears that the visual system has greater sensitivity to shear and compression than to linear motion. It was proposed that this reflects the operation of spatially determined centre surround opponent processes. The input to these opponent processes is the direction signals generated by the local directional mechanisms. These opponent processes do however not appear to function at low (detection threshold) contrasts.

A model was suggested (see figure 32). The first stage of motion processing is carried out by local directional motion mechanisms. This first stage is to be

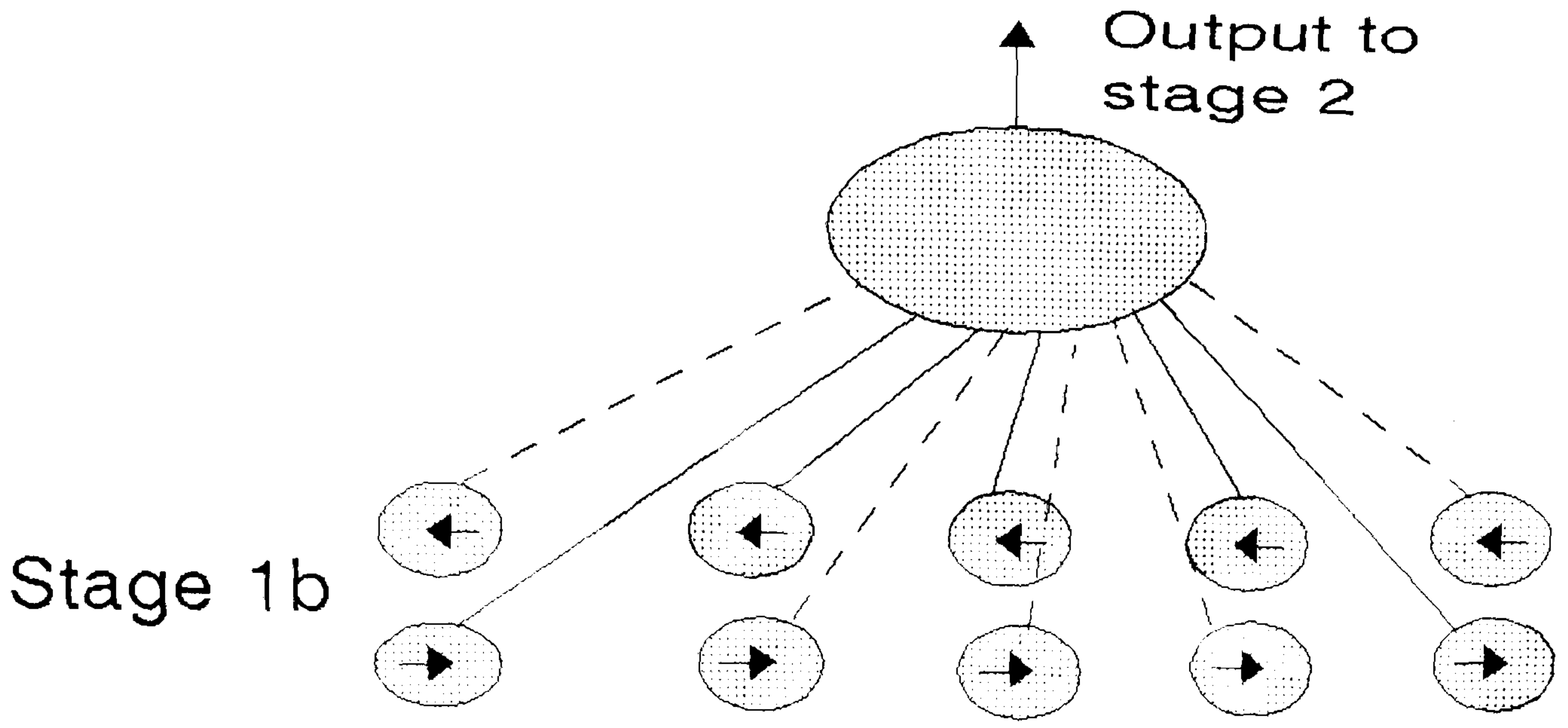

Figure 32a: Oponency occurring after stage 1b and before stage 2, via opponent units. The outputs of each subunit feed into higher level opponent units. Stage 2 processes would then operate on the outputs of the opponent units. Dotted lines indicate inhibitory connections, undotted lines indicate facilitatory connections.

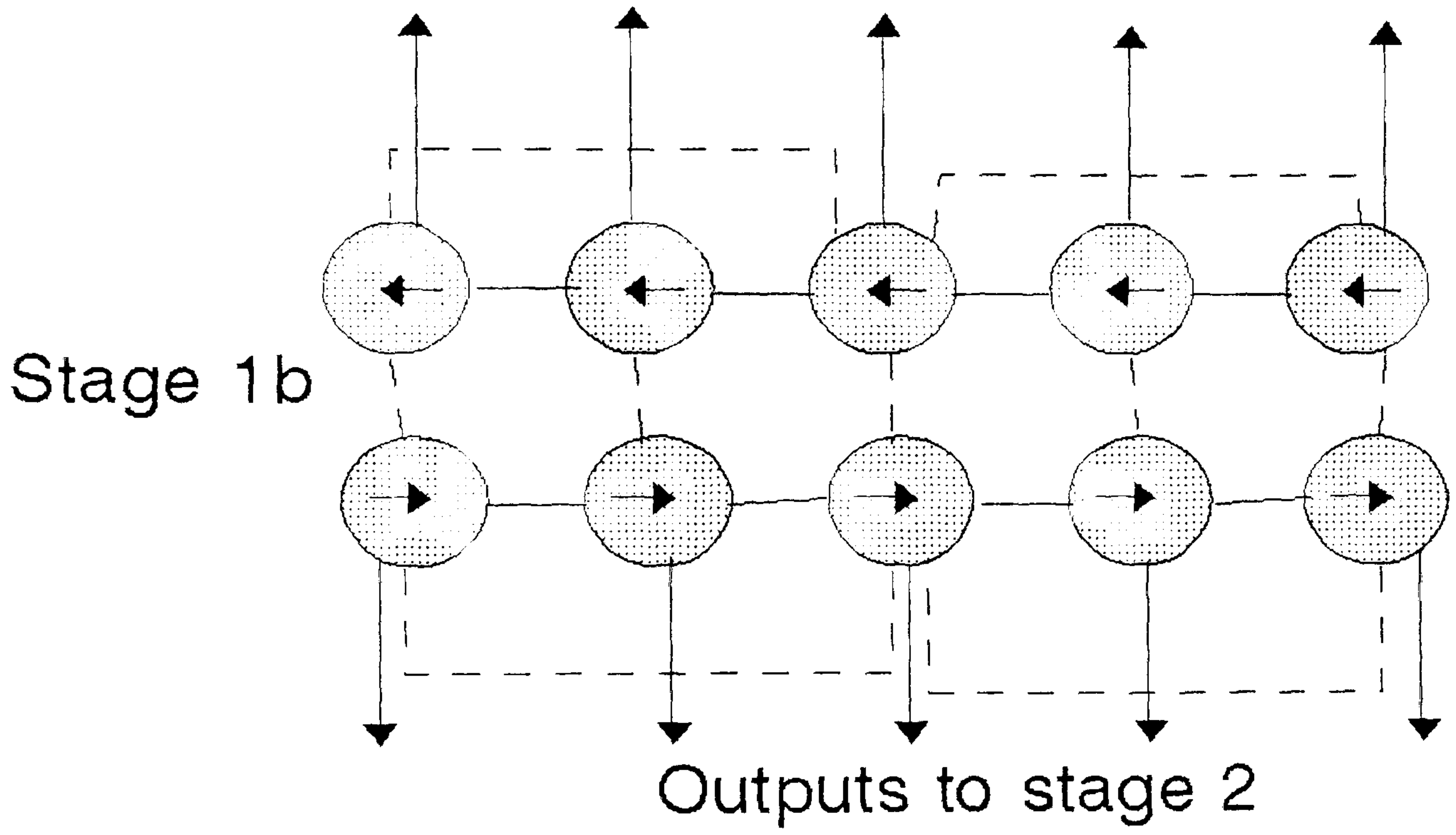

Figure 32b: Diagram showing oponency at stage 1b. Each subunit has an output to stage 2 mechanisms. Dotted lines indicate inhibitory connections undotted lines indicate facilitatory connections

Note. in each diagram retinotropic distance changes from left to right. Units drawn above each other would respond to motion in the same part of the visual field..

identified with stage 1 processes in two stage models of motion perception (Adelson and Movshon, 1982; Smith, 1992). Following from Smith (1992), these stage 1 signals are subjected to pooling across spatial frequency channels (stage 1b, Smith, 1992) to produce broad band spatial frequency motion signals. These broad band motion signals are then subjected to opponent processes, provided that the contrast of the stimulus is of a great enough magnitude. It was proposed that one reason for the dependence of opponency upon stimulus contrast is the probability of two local motion mechanisms with opposed directional sensitivities firing. For opponency to occur two local motion mechanisms must signal the presence of motion. The probability of any one mechanism firing depends upon the contrast. At low contrasts this probability is low as compared with higher contrasts and so opponency effects will be less likely to occur.

The outputs of these opponent processes are subjected to further processing to be identified with stage 2 processes in two stage models of motion perception (Adelson and Movshon, 1982).

Thus a heirachy of motion processing is suggested, with opponency between opposed directions of motion at suprathreshold contrasts accounting for shear and compression processing. The location of opponency is to be identified either at or immediately after Smith's stage 1b. Hence opponency may occur either between mechanisms located at stage 1b i.e. a line element explanation of opponency effects (Nawrot and Sekuler, 1989) or due to the action of a higher level opponent mechanism located after stage 1b and before stage 2.

Part Two

Motion Capture and Induced Motion

Chapter 7

7.1 General Introduction

Motion in one part of the visual field is able to induce motion in other parts of the visual field. Two general categories of motion induction have been identified. The first of these is when motion in one part of the visual field induces motion in the opposite direction in another part of the visual field. An example of this is the well known illusory perception of motion of the moon in a cloudy night sky; the moon appears to move in the opposite direction to the direction of motion of the clouds (Porterfield, 1759). Another example is when a moving outline of a rectangle causes a stationary dot, which is inside the rectangle to appear to move in the opposite direction (Dunker, 1938). The second type of motion induction, is when motion in one part of the visual field induces the same direction of motion in another part of the visual field. This was first described by MacKay (1961) and by several authors since using a variety of stimulus materials e.g. using random dots (Chang and Julesz, 1984; Nawrot and Sekuler, 1990) and with grating displays (Ramachandran and Cavanagh, 1987; Murakami and Shimojo, 1991,1992,1993).

These two types of motion induction give rise to two distinct perceptual experiences. Rather than refer to both effects as motion induction, which would lead to confusion, many authors have given descriptive labels to them. Historically, the first to be identified and the most studied is that of opposite induced motion. This has been referred to in the literature as Induced Motion e.g. Wade and Swanston (1987), and as Motion Contrast eg Nawrot and Sekuler, (1990); Zhang, Yeh and De Valois, (1993). Same direction induction, has received more recent interest being refered to variously as Motion Capture eg Ramachandran (1981), and Motion Assimilation eg Nawrot and Sekuler, (1990). Hereafter, the term "induced motion" will describe situations where the motion from one part of the visual field induces motion in the opposite direction and the term "motion capture" will describe situations in which motion from one part of the visual field induces motion in the same direction.[3]

7.2 Previous Research on Motion Capture

Much work has been carried out in order to identify the precise conditions under which motion capture occurs. Ramachandran and Cavanagh (1987) demonstrated that when a low spatial frequency sinusoidal grating was superimposed upon a random dot dynamic noise pattern, the percept was of the

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[3] Motion capture within the terms of this study is slightly different to motion capture as scribed by Ramachandran (1981). For Ramachandran, motion capture referred to nditions where a target appears to move in the same direction and at the same velocity as inducing motion. In this study this is not a requirement, motion capture refers here to nditions where the direction of motion of a target is changed by the motion of an inducer.

dots adhering to the grating and moving with it in the same direction. They further showed that dynamic noise which was captured by the motion of a low spatial frequency grating was indistinguishable from correlated noise patterns which moved in the same direction as the moving grating. The motion capture effect was not however as strong if the random dots moved in a direction that was orthogonal to the direction of motion of the grating. They went on to examine the spatial frequency characteristics of the motion capture effect. Their results revealed that low spatial frequency gratings were far more capable of capturing high spatial frequency gratings than vice versa and that the lower the spatial frequency of the low frequency grating the more effective it was at capturing the higher spatial frequency grating. If, however, the high spatial frequency grating was moved in a direction that was orthogonal to that of the low spatial frequency grating direction, motion capture was almost never seen, also high spatial frequencies were easier to capture if they moved in a similar direction to the low spatial frequency grating than in the opposite direction.

Chang and Julesz (1984) and Nawrot and Sekuler (1990), have carried out similar experiments using dynamic random dot stimuli. Chang and Julesz (1984) produced displays consisting of adjoining horizontal strips of different random dot motion. In some of the strips the direction of dot motion was ambiguous, in the surrounding strips unambiguous motion was produced. It was found that the perceived direction of motion in the ambiguous strips could be biased by the unambiguous motion in the surrounding strips. Thus for example, the ambiguous motion strips might be perceived as moving left or right. The introduction of a bias e.g. rightward motion, in the surrounding strips would lead to the perception of rightward motion in all the strips over the entire display i.e. motion capture. It was found that this effect was dependent upon the width of the strips, with the effect diminishing as the width exceeded 15 min arc. With wide strips the percept changed to one of different directions of motion e.g. left and right across the display i.e. induced motion.

Nawrot and Sekuler (1990) used similar random dot displays but in contrast to the findings of Chang and Julesz, they found that the capture effect could be produced for dot strip widths of up to 45 min arc. They suggested that the difference in the spatial limit of the capture effect that they found as compared to that of Chang and Julesz was that the dot density was greater in the displays of Chang and Julesz. They also found that if one increased the width of the strips of random dots, the percept changed from one of motion capture (homokinesis in their terminology) to induced motion (heterokinesis), indicating that there is some sort of relationship between conditions favouring motion capture and induced motion which depends upon the width of the stimuli used.

Nawrot and Sekuler (1990) examined the threshold signal to noise ratio in the test strip for determining that motion was in the opposite direction to that of the biassing surround. The signal to noise ratio referred to the proportion of coherently moving dots (signal) moving amongst the randomly moving dots (noise). It was found that as the strip width was increased from conditions favouring capture to condition favouring induced motion the threshold increased i.e. more signal was required in the test strip to see the opposite direction of motion under conditions favouring capture than under conditions favouring induced motion. It appears therefore that the motion capture effect is limited in the spatial range over which it may operate and is associated with an increase in the threshold for determining the direction of motion in the test or captured region when the direction of motion in the test region is opposite that of the surround.

Chen, Yeh and Da Valois (1992) carried out experiments on motion capture and induced motion using random dot stimuli. They used square patches of random dots. Squares responsible for inducing motion contained coherently moving random dots, target squares consisted of either dynamic (where the percept was of random motion of the dots) or static random dots. The experimental display consisted of the target square being flanked by two inducing squares on opposite sides. The direction of coherent motion in the inducing squares was always along the longitudinal axis of the three squares. They found that, motion capture was always seen i.e. the direction of motion of the dots in the target square was the same as that for the two inducing squares, for all dot densities with moving dots in the target, but induced motion was seen for static target dots. Motion capture was greatly reduced if blank frames were alternated in the successive presentation of the target, this according to the authors had the effect of removing the percept of random motion in the target square and indicates that the short range motion system (Braddick, 1972) is involved in the motion capture effect. When the target and inducing patterns were subjected to bandpass filtering, an analogous result to those of Ramachandran and Cavanagh (1987) was produced, lower frequency patterns were more able to capture high frequency patterns than vice versa.

Zhang, Yeh and De Valois (1993) have examined the effects of a drifting grating within an aperture, upon the perceived motion of the aperture. Their displays consisted of sinusoidal gratings within circular apertures. The aperture could be defined either by an abrupt transition from grating to background ("hard aperture") or by a two dimensional Gaussian reduction in contrast of the grating ("soft aperture"). The motion of the grating and aperture could be controlled independently. The subjects were required to judge the direction of aperture movement. With such a stimulus arrangement these authors hoped to examine the influence of the short range motion system (Braddick, 1974) on the long range non-Fourier motion system (Braddick,1974; Chubb and Sperling, 1988). The grating would stimulate the short range system and movement of the aperture independent of the grating would stimulate the long range system. It was found that a hard aperture when presented in the fovea appeared to move in the opposite direction to the grating i.e. induced motion. A soft aperture presented in the periphery appeared to move in the same direction as the grating i.e. motion capture. When the aperture was presented in the fovea as the "softness" of the aperture was increased motion capture was favoured. Also for foveally presented stimuli, for a hard aperture induced motion was maximal if the grating's mean luminance was matched to that of the background decreasing as the mean luminance became less than that of the background. These results show that short range processes interact with long range processes giving rise to the perception of illusory motion, consistent with Nawrot and Sekuler (1990) show that there is a continuum from motion capture to induced motion.

Murakami and Shimojo (1991,1992,1993) have carried out interesting experiments that support the findings of Nawrot and Sekuler (1990) and Zhang et al (1993) that there is a continuum from motion capture to induced motion. In their experiments they have examined the conditions that favour motion capture and those that favour induced motion. They have utilised grating stimuli in their experiments. The displays used consisted of a central circular sinusoidal grating (the target) surrounded by a background of another sinusoidal grating. The results of these experiments have shown that, relative to the conditions that give rise to motion capture, motion capture changes to induced motion, with a higher luminance contrast of the central target grating; with the surround moving faster than the centre; at smaller eccentricities; with a larger background; and with a larger scale of the whole stimulus. It was further found that applying a cortical magnification factor to the results for eccentricity and stimulus size nulled the effects of eccentricity and size.

Yo and Wilson (1992) have carried out motion capture experiments using plaid type stimuli. Two oriented one dimensional sinusoidal gratings of equal spatial frequency were superimposed onto one another, forming a plaid that moved in a resultant direction consistent with the intersection of constraints (Adelson and Movshon, 1982) solution for the two component grating orientation and direction. It was found that the plaid captured the direction of motion of a third one dimensional grating superimposed onto the plaid, such that it appeared to move in the direction of motion of the plaid rather than of one of the components. The third grating was either six times higher or six times lower in spatial frequency than the plaid component spatial frequencies. The plaid was seen to be less effective at capturing the direction of the third grating when the plaid components were of higher spatial frequency than the third grating.

Scase and Braddick (1993) examined the stimulus characteristics that give rise to motion capture and induced motion. They measured the changes in motion-coherence threshold for a random dot test strip, flanked by inducing regions of moving random dots. The amount of induced motion or motion capture depended upon the degree of coherence in the inducing regions. At low coherence motion capture occurred while at high coherences induced motion occurred. If the presentation time of the stimulus was increased then induced motion occurred at a lower inducing region coherence. Motion capture was more likely when the boundary between the inducing and test areas were orthogonal to the motion axis than when they were parallel to it. These results indicated that the interactions underlying motion capture propagated most strongly in a direction parallel to the axis of motion and that motion capture and induced motion are related along a continuum.

Yuille and Grzywacz (1988), demonstrated motion capture using a display of just three dots in a two frame apparent motion display (see figure 33). They set up an apparent motion display which consisted of a central ambiguous dot motion which was presented next to a peripheral unambiguous motion. Of particular interest was the finding that the motion capture produced was critically dependent upon the proximity of the unambiguous dot motion to the ambiguous motion. In other experiments e.g. Yuille and Grzywacz (1988), showed that if a series of randomly moving dots were placed inside a moving circular the dots appeared to move in the same direction as the direction of motion of the frame.

From the experiments of Chen et al (1992) it appears that motion capture involves the short range motion system. The findings of Zhang et al (1993) also support the involvement of the short range motion system and suggest a role for

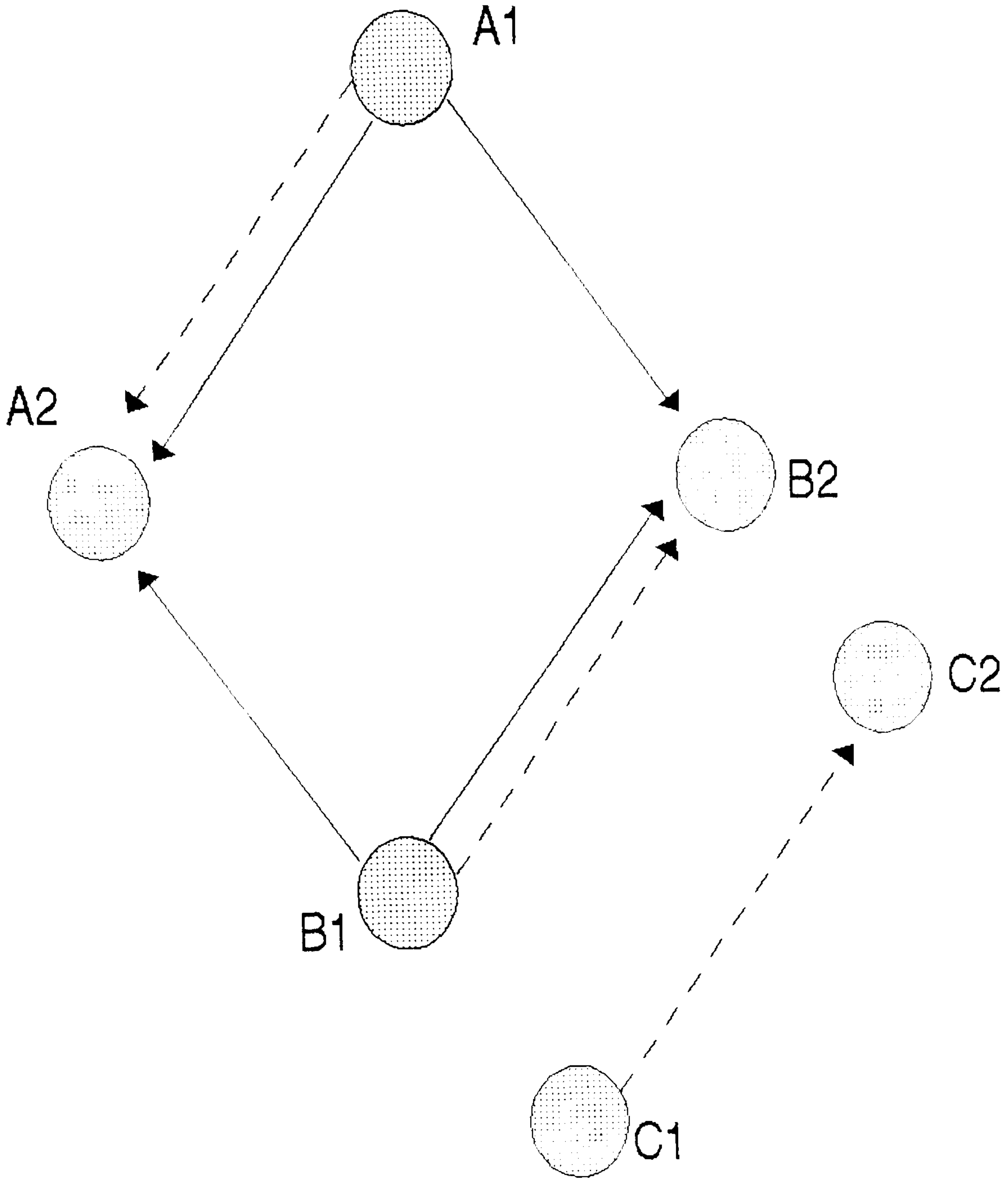


Figure 33 : Motion Capture Stimuli used by Yuille and Grzywacz (1988)

the long range (Braddick, 1974) or non-Fourrier (Chub and Sperling, 1988) motion system. The finding that induced motion and motion capture can be elicited using similar stimuli (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Scase and Braddick, 1993; Zhang et al, 1993) indicates that possibly similar neural structures could underlie both effects. The dependence of motion capture upon the proximity of the inducing field to the captured field and upon the size of the captured field (Chen et al, 1992; Nawrot and Sekuler, 1990; Chang and Julesz, 1984; Murakami and Shimojo, 1991,1992,1993) suggest the involvement of spatial interactions between these motion sensitive neurons. The fact that low spatial frequencies appear better at capturing high spatial frequencies than vice versa (Ramachandran and Cavanagh, 1987; Chen et al, 1992) indicates that low spatial frequency motion signals are, under certain conditions, capable of negating or masking those from high spatial frequencies indicating interactions featuring some form of inhibition. Models of motion capture should therefore account for these findings.

7.3 Models of Motion Capture

Ramachandran and Cavanagh (1987) explained motion capture by suggesting that firstly motion is extracted separately for different spatial frequency bands by spatially selective motion mechanisms. There is good empirical evidence to support this notion e.g. Smith (1992). If an object makes a rapid movement resulting in a large jump, according to Ramachandran and Cavanagh, motion information from the low spatial frequencies (which correspond to gross figural structures such as the object shape and other salient features of the object), will mask or inhibit motion information resulting from the high spatial frequencies (which correspond to fine image detail such as patterning of the object). This inhibition of high spatial frequencies, does not result in the high spatial frequencies appearing stationary, it is argued that they appear to move with the low spatial frequencies. It is as if the high spatial frequencies were glued to the low spatial frequencies. The upshot of this is that if high spatial frequencies have no or ambiguous motion signals of their own then the high spatial frequencies will by default be assumed to move with the low spatial frequencies. This explanation of motion capture explains the data of Ramachandran and Cavanagh reasonably successfully. For example, random dots were captured by a moving grating, the grating was of lower spatial frequency than the random dot pattern which moved ambiguously, hence the motion of the low spatial frequency becomes attributed to the dots. This explanation is however unsatisfactory for a number of reasons. As the authors explain, this is only a tentative account of the mechanism giving rise to motion capture phenomena it is by no means an exhaustive explanation of all the possible processes involved. The model does not provide any explicit account of the types of interaction that may be going on between the different spatial frequency selective motion mechanisms. Further their model is unable to account for the observation that under certain conditions high spatial frequency motion may capture low spatial frequency motion. This account explicitly states that capture involves the inhibition of high spatial frequency motion signals by those of low. Whilst low spatial frequency motion usually captures high spatial frequency motion any model must explain the opposite result. The model does not give any account of the spatial dependence of the capture effect, although it does not preclude it, any model of capture must explain this. Finally the model does not give any account of the contrast dependence of motion capture, e.g. the finding that increasing the contrast of the target pattern switches the percept from motion capture to induced motion (Murakami and Shimojo, 1991,1992,1993).

Yuille and Grzywacz (1988,1989, Grzywacz and Yuille, 1990) have produced a model of motion perception which whilst not explicitly intended as a model of motion capture, does predict the existence of such phenomena for conditions in which human observers experience them. The theory splits the computation of image motion into to two stages. The first stage is what the authors refer to as the measuring stage. This stage measures the local motion energy in the image using motion energy selective mechanisms e.g. Adelson and Bergen, (1985). The nature of the mechanisms giving rise to the output of the first stage is not important to the model, it merely assumes that local motion energy can be signalled by the visual system. The output of the first stage of the model is ambiguous. The second stage of their model is what they refer to as the smoothing stage. Here a velocity field is constructed which covers the whole visual field, including areas for which no estimates of local motion have been made. The velocity field is constrained to fit the measured motions found in the measuring stage whilst being as smooth as possible e.g. it encourages nearby motions to be similar and motion direction to be constant over time. This second smoothing stage is essentially a theory of how coherent motion might be extracted from ambiguous local motion signals. The second stage performs an integration of the local motion measures from the first stage over space and time. For example, for the three dot apparent motion display of Yuille and Grzywacz (1988) described previously, the model predicts the occurrence of motion capture and also predicts that the effect is dependent upon the proximity of the third dot to the central ambiguous motion (see figure 33). The model describes the kind of computations that a system that demonstrates motion capture phenomena should go through, implicitly suggesting that motion capture phenomena could result from processing at the models second stage, motion capture is an emergent property of the smoothing stage. This seems a sensible proposition in that the whole concept of similar directions of motion being induced in one part of the visual field from another seems to imply the smoothing of the local motion signals. As a model of motion capture phenomena the model of Yuille and Grzywacz (1988,1989) is useful as it describes the kind of computations the visual system may be doing in order to give rise to this effect. The theory is limited by the fact that it is a computational model. It does not provide an explicit account of the type of mechanisms that could be giving rise to these capture effects. Similarly the model, whilst predicting the distance dependence of the capture effect (how far the inducing and induced fields are away from each other), fails to provide any account of the reported relationship between contrast and capture or the relationship between spatial frequency and capture.

A model of motion capture phenomena that does provide a description of the mechanisms that could give rise to it is that of Murakami and Shimojo (1991,1992,1993). In their model they seek to explain motion capture and induced motion phenomena as being subserved by a set of centre-surround antagonistic motion detectors. To recapitulate the general features of antagonistic centre-surround mechanisms (see figure 13a/b), the centre of the mechanism is tuned to a particular range of velocities i.e. a range of speeds in a given direction for example rightward. The motion mechanism is excited if the centres preferred motion is presented within the receptive field of the centre, the motion mechanism is inhibited if the opposite direction of motion to the centres preferred direction is present in the centre. The motion mechanism may also be excited if motion in the opposite direction to the centre's preferred direction is present in the surround. If motion in the same direction as the centres preferred direction, is present in the surround, then the mechanism is inhibited. It may be seen that maximal activation of the motion mechanism will occur if the motion presented to the mechanism is in the preferred direction at the centre and the opposite direction in the surround. Maximal inhibition occurs if motion in the opposite direction to the centres preferred direction is present in the centre and motion in the same direction is present in the surround. These antagonistic interactions between the centre and surround operate across space, with the centre having a spatially limited receptive field size. Implicit to a model featuring these kinds of mechanism is that local directions of motion are signalled prior to the operation of these opponent mechanisms. It can be seen how such a mechanism, featuring excitatory and inhibitory interactions across space could give rise to motion capture.

Consider the experiments of Murakami and Shimojo (1991,1992,1993) described above. Their stimuli consisted of a central stationary grating surrounded by a moving grating. Capture was produced if the central grating was small relative to the surround. It may be seen that how the dependence of the capture effect upon the size of the central grating arrises. When the stimulus size is small enough, both the target centre and surround will both fall into the centre region of the mechanism. The mechanism surround will not be stimulated by the display while the mechanism centre will be stimulated by the motion in the display surround. The display centre is stationary and so will give rise to no directional signal whilst the display surround will excite mechanisms with centres tuned to its direction of motion. As a result of this the percept will be of motion in the direction of the display surround ie motion capture. In the situation where the display is large enough so that the moving display surround falls in the mechanism surround while the stationar display centre falls into the mechanism centre. The display centre gives rise to non-directional signal. Motion in the display surround will excite the surround of the mechanism. This in turn gives rise to excitation of mechanisms with centres tuned to the opposite direction of motion of the surround. Thus the percept with a larger display will be one of motion at the centre in the opposite direction to that in the surround ie induced motion. Thus this model does appear to explain the subjects perceptions. It also explains the dependence of the motion capture effect upon the distance apart of the inducing and induced fields, and it provides an attempt to describe the kind of mechanisms that could give rise to motion capture effects. The model does however have nothing explicit to say about the effects of spatial frequency upon motion capture.

Nawrot and Sekuler (1990) have produced a model which was designed to explain both motion capture and induced motion (see figure 14a/b). The model is essentially an extension of the work of Williams and colleagues (Williams, Philips and Sekuler (1986); Williams and Sekuler (1984); and Williams and Philips (1987)) which has examined and modelled cooperativity in human motion perception. In order to facilitate the description of the model of Nawrot and

Sekuler, it is firstly necessary to introduce the concept of cooperativity. A cooperative system consists of a series of local elements or subunits that interact with each other. These subunits are linked together via non-linear excitatory and inhibitory interactions. These interactions between the subunits give rise to global behaviours that would not occur if the subunits were in isolation. In addition, cooperative systems, when they have reached a stable state, have a tendency to resist change from that stable state. This tendency of a cooperative system to resist change from a stable state is called hysteresis. Hysteresis can be thought of as a form of memory and it is one of the signatures of cooperative behaviour (Williams and Philips, 1984). One of the features of cooperative systems is that they afford computational economies which increase the signal to noise ratio in the system (Davis and Rosenfeld, 1978,1981). There is good evidence that the visual system exhibits cooperative behaviour for example in stereopsis (Julesz, 1971; Sperling, 1970; Marr and Poggio, 1976; Mayhew and Frisby, 1981) and in motion perception (Williams and Sekuler, 1984, Williams and Philips, 1987; Williams et al, 1986; Nawrot and Sekuler, 1990; Snowden and Braddick, 1989a,1989b,1990; Bertenthal et al, 1993; Smith, Snowden and Milne, 1994). In order to illustrate the effects of cooperative phenomena in motion perception it is interesting to examine one of these experiments on motion cooperativity. Williams, Philips and Sekuler (1986) used random dot cinematograms in which the proportion of correlated dot motion (proportion of dots moving in the same direction) changed with respect to time. As the degree of correlation was increased from zero the percept changed from a random swirling appearance i.e. random motion or noise (uncorrelated dots), to a percept of global flow of the dots in the direction of the correlated motion. The percept of global flow was reversed to one of random noise when the proportion of correlation was reduced from some high value with respect to time. The proportion of correlated dot motion at which the percept switched from noise to global flow was found to be different from that for the percept switch from global flow to noise i.e. the point of change of percept depended upon the history of stimulation. Thus the experiment had demonstrated that the visual system, once it had reached a stable state e.g. either a percept of noise or global flow, resisted change to an alternative state. This is an example of hysteresis, and as hysteresis is one of the markers of cooperative behaviour this finding was taken by Williams Philips and Sekuler (1986) to indicate that the motion perception system exhibits cooperative behaviour.

It is of interest to note that the existence of hysteresis in the visual system, tends to argue against models such as that of Murakami and Shimojo. The reason for this is that hysteresis arises as a result of cooperative interactions between interconnected processing subunits. Antagonistic centre-surround mechanisms produce their opponent effects as a result of their receptive field organisation and not as a result of interconnectivity between subunits. The lack of interconnectivity of such mechanisms means that they are unable to predict the existence of hysterises without making additional assumptions (i.e. that antagonistic centre-surround units are themselves interconnected). We will return to this theme later on when the nature of opponent mechanisms is discussed.

Williams and his colleagues (Williams et al, 1986; Williams and Philips, 1987) modelled this cooperative behaviour of the motion perception system. The main features of their cooperative model were that it comprised of a series of directionally selective mechanisms which covered all possible 360 degrees of motion direction. The model assumed non-linear excitatory and inhibitory interactions between the directionally selective mechanisms. Excitatory interactions were between mechanisms sensitive to similar directions of motion, inhibitory interactions were between mechanisms sensitive different directions of motion. Within this model the directionally selective mechanisms represent the subunits of the cooperative mechanism. Local random motion is represented in the model as a steady state of uniform activation across all of the mechanisms; Global flow in a given direction is represented as a localization of activation in the mechanism most selective for motion in the direction in question (Williams et al, 1986).

Nawrot and Sekuler (1990) argued that whilst this model is successful in modelling interactions between motion sensitive mechanisms it is silent about the characteristics and effects of interactions between motion sensitive mechanisms across space. They pointed out that in the displays used by Williams et al (1986), every local region of the display contained a similar sample of the range of directions of motion in the display. This they suggest would serve to render any spatial interactions between motion mechanisms virtually impossible to measure. As a result they carried out a series of experiments which allowed spatial interactions to take place (Nawrot and Sekuler, 1990; see above). The findings of Nawrot and Sekuler (1990) resulted in one modification to the cooperative model of Williams et al. The modification involved hypothesising a spatial limit within which similarly directionally tuned motion mechanisms excite each other and beyond which these mechanisms inhibit each other (see figure 34).

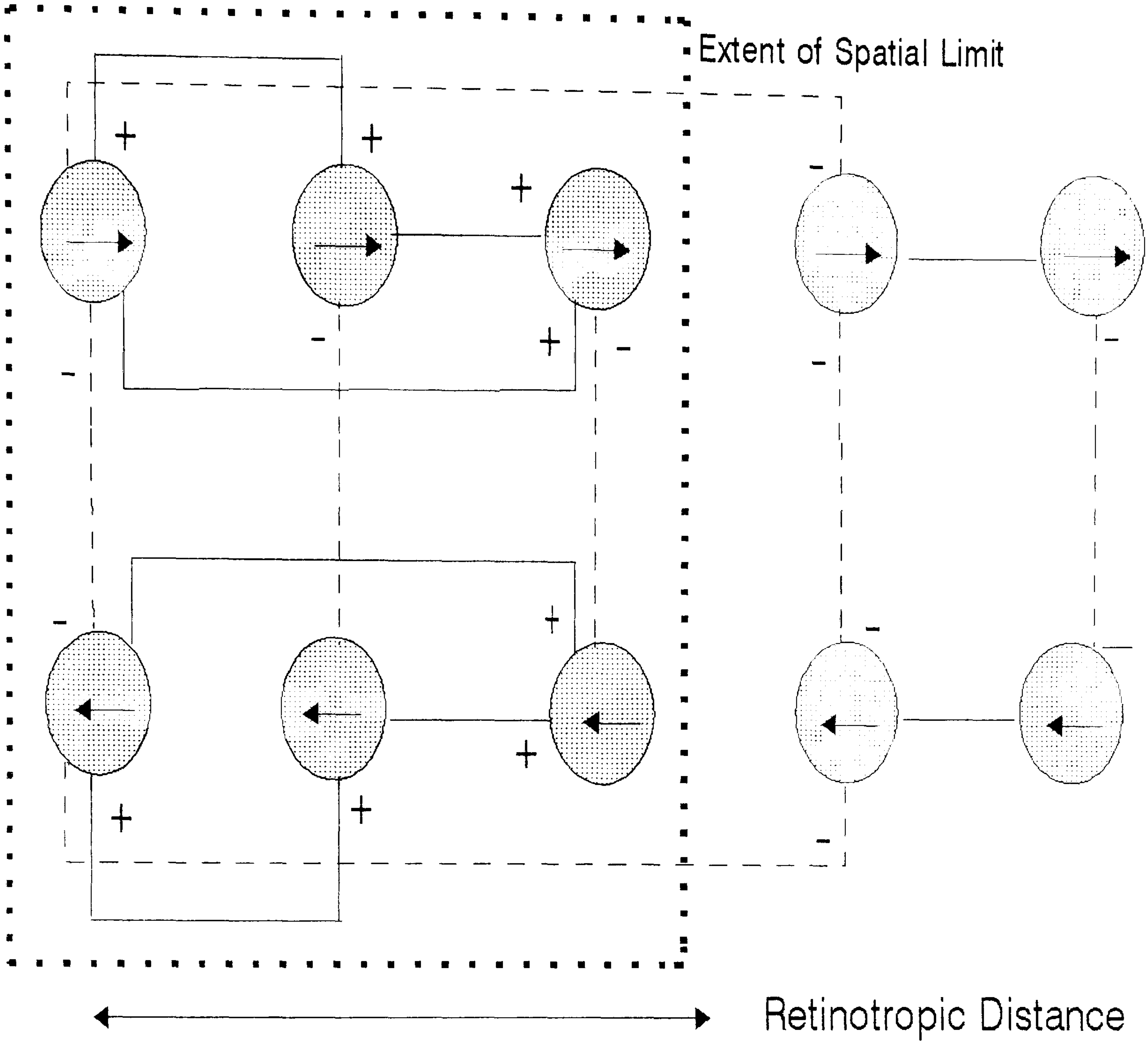


Figure 34: Line Element Model of Nawrot and Sekuler (1990) Showing the Spatial Limit. Note how units with similar directional sensitivities inhibit each other if outside the spatial limit.

In figure 34, retinotropic distance is represented by vertical distance in the diagram. Horizontally adjacent mechanism pairs have spatially overlapping receptive fields. Excitatory interactions are shown by solid lines ending with a plus sign, inhibitory interactions are shown as a dotted line ending in a minus sign. As stated above this model can explain motion capture. Consider a stimulus in which there exists a central strip of stationary random dots flanked by two inducing strips of coherently moving random dots both with the same direction of motion e.g. rightward motion. It may be seen that if the central strip was narrow enough such that motion from the flanking mechanisms was contained solely within the excitatory region, i.e. where mechanisms tuned to similar directions of motion excite each other, then all the rightward sensitive mechanisms would be excited. This would mean that mechanisms which had not been excited by a motion signal i.e. those into whose field the stationary central dot pattern had been displayed, would give out a motion signal of rightward motion. Hence the percept would be motion of the central dots in the same direction as the flanking dots - motion capture. This model explains the distance dependence of the motion capture phenomena, and also incorporates motion capture into a model of cooperative effects in motion perception. The suggestion is therefore, that motion capture could be an emergent property of the kind of a cooperative network of motion mechanisms proposed by Williams et al, provided that the cooperative network featured spatial dependence of the excitatory and inhibitory interactions between directional mechanism. The model as stated does not however, have anything to say about the effect of spatial frequency upon the motion capture effect, which clearly is a limitation.

Yo and Wilson (1992) on the basis of their motion capture experiments (see above) have proposed a modification of the cooperative motion model of Williams et al (1986). They suggest that the excitatory interactions between similarly tuned directional mechanisms, may operate between different spatial scales i.e. excitation is not limited to spatial frequency channels but may operate across them. Hence directional mechanisms tuned to the same direction but sensitive to different spatial frequencies (or spatial scales) could excite each other. If excitatory interactions occur across spatial frequency in cooperative mechanisms, then combining this notion with the motion capture model of Nawrot and Sekuler (1990), this model is able to explain some of the effects of spatial frequency upon motion capture. Consider the experiments of Chen et al (1992), where different spatial frequencies are present in the inducing and test stimulus patterns. In the model of Nawrot and Sekuler (1990), the excitatory interactions between like tuned motion mechanisms are spatially limited. If the test and inducing strips of dots are narrow enough, both the test and inducing fields will fall into the receptive fields of motion mechanisms in this excitatory region. If the excitatory interactions between the motion mechanisms exist for different moving spatial frequencies, then the model would predict that motion capture should occur i.e. the dots in the test strip will move in a similar direction to those in the inducing dot strips. Chen et al (1992) found this.

This modification does explain some of the effects of spatial frequency upon motion capture phenomena, it does however not explain the fact that motion capture is stronger for low spatial frequencies capturing high spatial frequencies and not vice versa i.e. its prediction is that capture will occur with equal strength irrespective of the spatial frequencies of the stimuli.

Zhang et al (1993) sought to explain their results in terms of the importance of boundaries in determining figure-ground relationships of motion signals. They argued that a "hard" aperture when presented to the fovea has a sharp boundary within which the grating is enclosed. This sharp transition between the drifting sinusoidal grating and the background results in a discontinuity between local motion signals near the boundary of the aperture. Thus the boundary and aperture are seen as different objects undergoing separate motion with the boundary of the aperture appearing to move against a background of a moving grating.

For the "soft" grating the boundary is not very well defined. The whole patch could be regarded as a single figure moving against a uniform background. As the fall off in luminance contrast between the grating and background is gradual the local motion signals associated with the grating change smoothly. Zhang et al (1993) suggest that in this case the motion of the grating and aperture are integrated in order to increase the strength of the figure ie the grating patch.

These authors argue that the main reason for the occurrence of motion capture and induced motion is to increase the signal strength of the figure and suppress the signal strength of the ground. The difference between the two effects being in what constitutes figure and ground in each situation. Arguing within the framework of the short and long range motion systems Zhang et al (1993) suggest that when induced motion occurs (hard aperture), the local short range motion signals (sinusoidal grating) become dissociated from the long range motion signals (aperture), while the two types of motion signals become associated when motion capture occurs. In the case of motion capture the local (Fourier) motion signals associated with the grating serve as the cause of the global motion of the stimulus.

Zhang et al (1993) also offer an explanation for the effects of mean luminance of the grating patch on the occurrence of motion capture and induced motion. The task of judging the aperture's direction of motion could be mediated by the long range motion system, which they argue is based upon computation of positional displacement of a distinct feature. As the feature becomes more salient, then the stronger will be its input to the long range system and correspondingly the weaker the influence of short range signals. Thus by changing the mean luminance of the grating patch, then the patch becomes more or less distinct from the background, hence the proportion of activation due to short and long range processes will change with more activation due to long range processes when luminance is greatest and more due to short range processes when it is lowest. Essentially this model is an explanation of the effects of "Gestalt" (global) factors for figure-ground segregation on the occurrence of motion capture and induced motion.

The explanation of motion capture and induced motion of Zhang et al (1993) offers a neat explanation of their data and emphasises the potential role of higher level factors in induced motion and motion capture. However, Murakami and Shimojo (1993) argue that Gestalt factors such as these are unlikely to be the main factors in their research. In contrast to Zhang et al (1993) their displays always appeared to be two figures (target and inducer) on a background irrespective of if induced motion or motion capture occurred. Further Murakami and Shimojo (1993) argue that while chromatic contrast is one of the primary cues for figure/ground segregation, a homochromatic target (luminance contrast only) and a heterochromatic target (both luminance and chromatic contrast) behave in the same way. The model of Zhang et al (1993) does not explain the effects of spatial frequency upon motion capture nor, in contrast to the models of Nawrot and Sekuler (1990) and Murakami and Shimojo (1991,1992,1993), does it suggest an explicit mechanism or neural organisation to account for induced motion and motion capture.

All the models described, require local motion mechanisms or subunits to analyse the motion information in the image. There appears to be two general types of motion capture model. The first type is characterised by models such as those of Murakami and Shimojo (1991,1992,1993) and Yuille and Grzywacz (1988,1989). These models essentially propose a two stage system, the first stage features extraction of local direction of motion information by motion selective subunits. It is the second stage where the processing that gives rise to the effects such as motion capture takes place, this involves some kind of processing of the local motion signals, smoothing of the motion signals or antagonistic opponency between two directions of motion.

The second type of model is characterised by that of Nawrot and Sekuler (1990) which in common with the first type of model features local processing of image motion, but unlike these models does not explicitly require that the processing that gives rise to motion capture takes place at some higher level second stage. Motion capture, according to this model is an emergent property of the interactions between the motion selective subunits.

The two mechanistic models of motion capture, that of Murakami and Shimojo (1991,1992,1993) and that of Nawrot and Sekuler (1990) can be taken as examples of two general types of mechanism that could give rise to motion capture i.e. a two stage mechanism or a single stage cooperative network of local directionally selective units.

Chapter 8

Experiments 8 to 11: Motion Capture and Induced Motion

It is the purpose of this chapter to introduce the general aims of the experiments that make up part two of this study. Further, as each of the four experiments utilised the same general methodology, this will also be described in this chapter. Experiments 8 to 11 will be described in turn in chapters 8 to 11.

8.1 General Introduction

These experiments had three principle aims. The first was to replicate some of the previous findings concerning the stimulus conditions that give rise to motion capture. The second aim was to try and extend current knowledge of the conditions giving rise to motion capture by testing for its existence under new stimulus conditions. The third aim was to try and examine the nature of the interactions between motion mechanisms that underlie motion capture.

It was decided to use sinusoidal grating stimuli in these experiments. The reason for this is that with such stimuli one has greater control over the spatial frequency characteristics of the stimulus than when one uses random dot cinematograms. The limitations of random dot stimuli in allowing experiments concerning stimulus characteristics, can be seen with reference to previous capture experiments. It has proved possible with random dots only to examine the effects of the size of the stimuli (Nawrot and Sekuler, 1990; Chen et al, 1992; Chang and Julesz, 1984) and of spatial frequency (Chen et al, 1992). Grating stimuli, on the other hand, allow variations in the size and contrast (Murakami and Shimojo, 1991,1992,1993), spatial frequency (Ramachandran and Cavanagh, 1987) and orientation, of the stimuli relatively easily, as well as allowing experimentation with more complex pattern stimuli such as plaids (Yo and Wilson, 1992).

The experiments to be reported here, utilised displays similar to those used by Murakami and Shimojo (1991,1992,1993) i.e. a centre surround arrangement of sinusoidal gratings, a central circular test grating being surrounded by an annulus containing the inducing grating(s) (see figure 35a,b and c).

The first of the experiments (experiment 8) examined the effect of the size i.e. diameter, of the central test grating; the second experiment (experiment 9) examined the effect of the contrasts of the surround and central test gratings; the third experiment (experiment 10) examined the effect of the orientation of the surround grating relative to the centre grating; the fourth experiment (experiment 11) examined the effect of different plaid patterns in the surround.

The experiments concerning the size of the central test grating (experiment 8) and the contrasts of the centre and surround (experiment 9) were intended to replicate this previous work e.g. Murakami and Shimojo (1991,1992,1993), two of the current experiments (experiments 10 and 11) were intended to extend it.

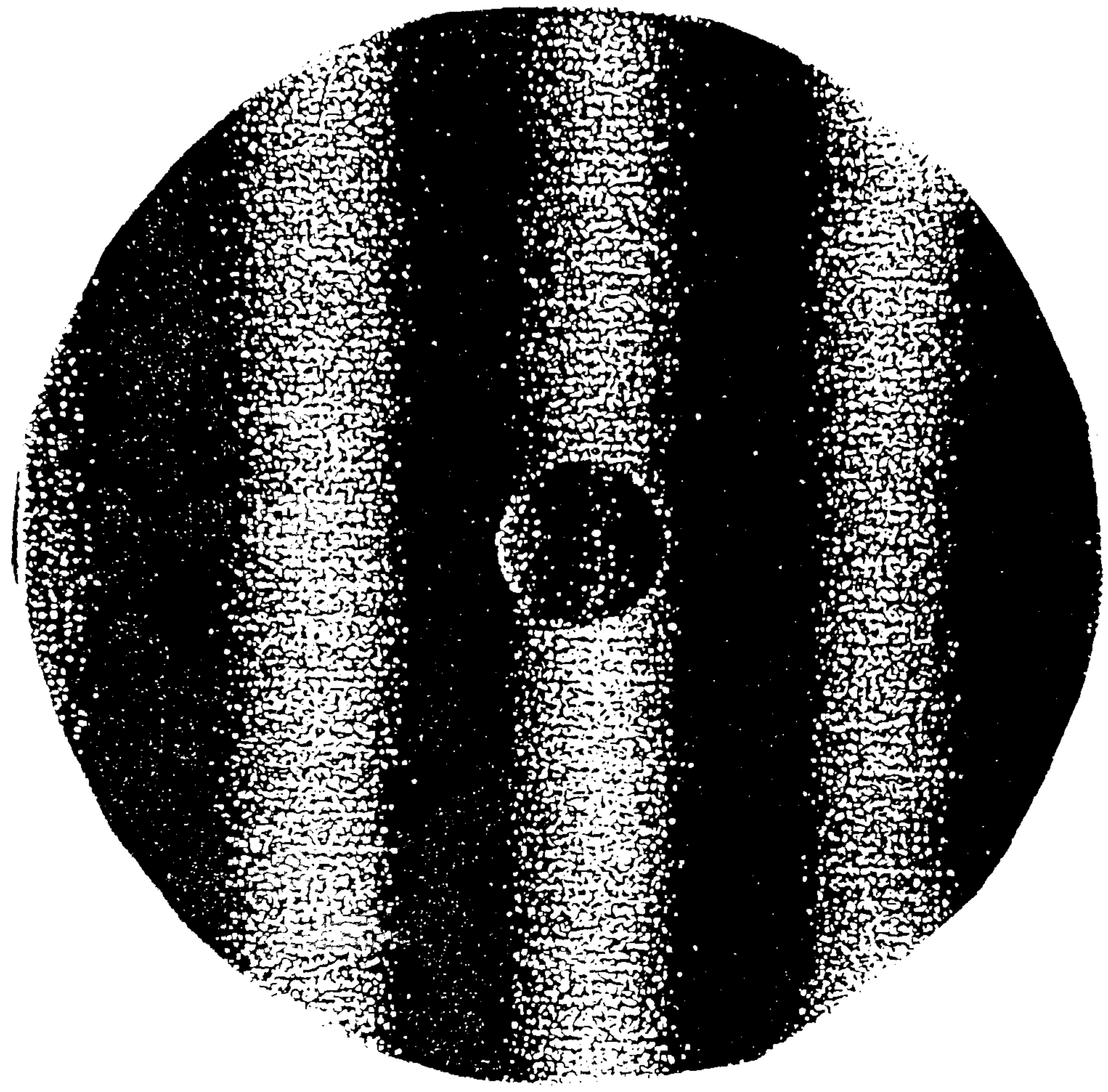


Figure 35a: Basic Centre-Surround Display

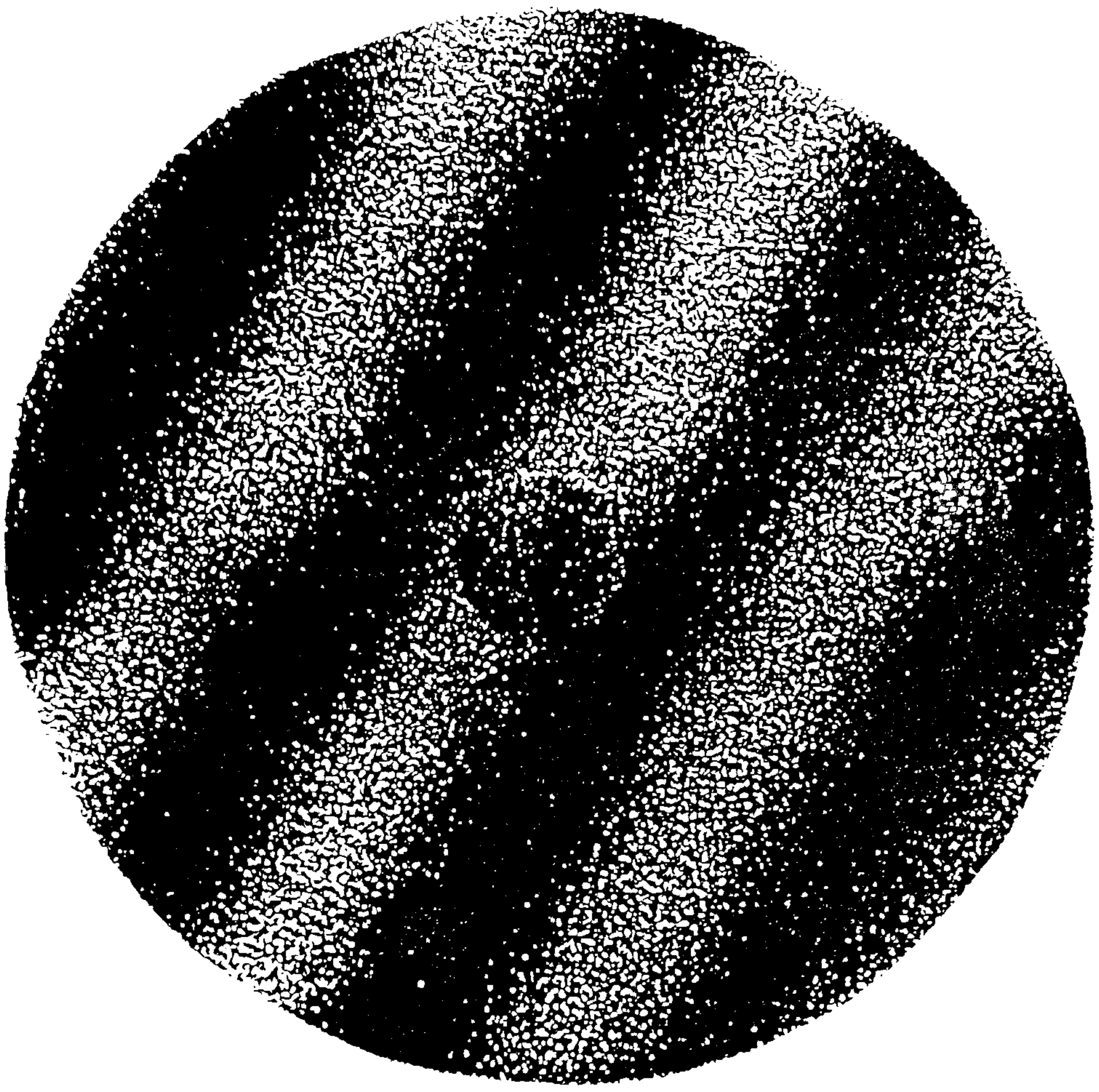


Figure 35b: Oriented Surround Display

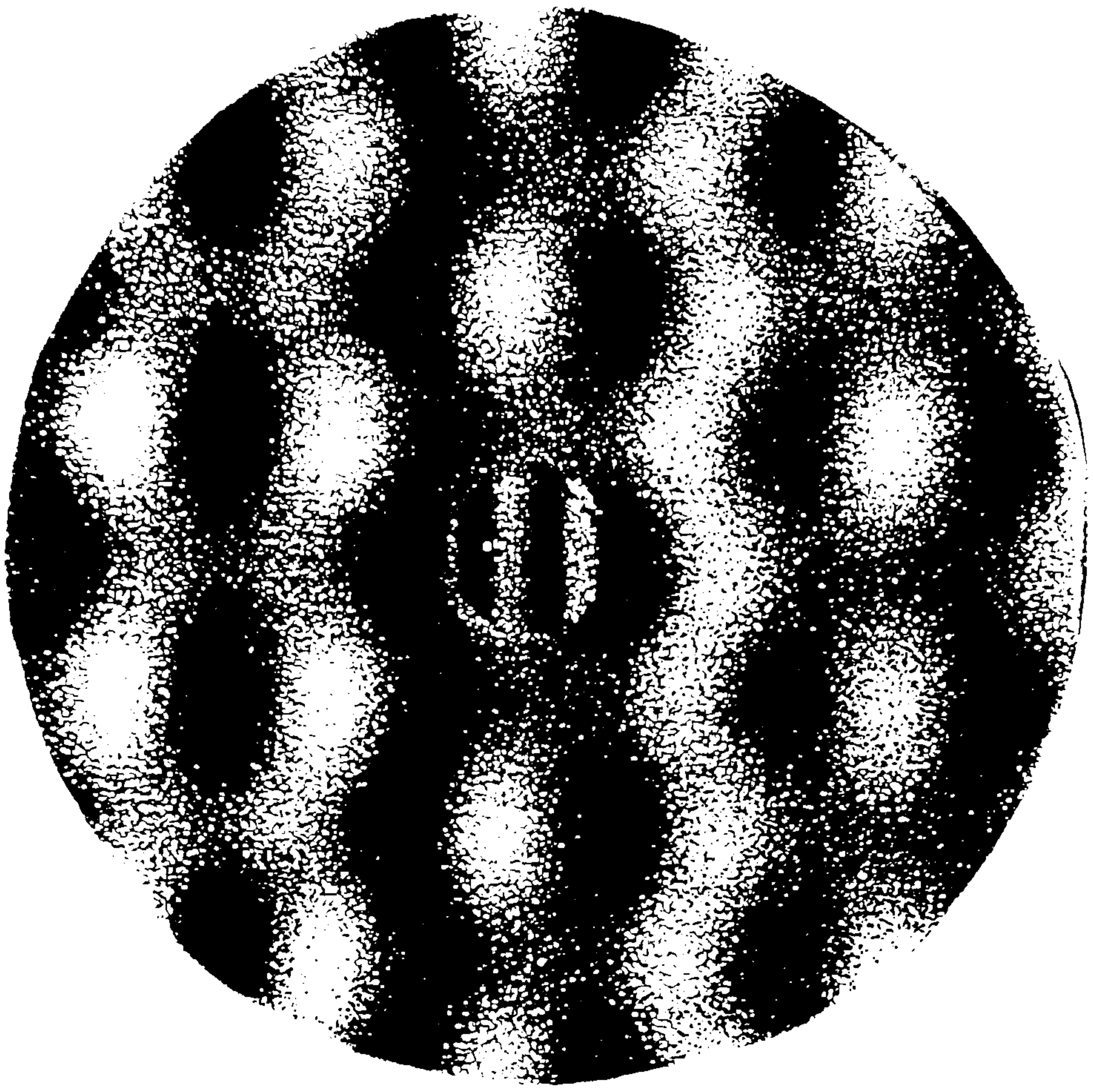


Figure 35c: Plaid Surround Display

No previous work has been done to characterise the effect of orientation between the inducing field and the test i.e. captured field, this was done in experiment 9.

Although previous work has examined the effect of a moving plaid stimuli upon motion capture (Yo and Wilson, 1992), no work has examined the effect of plaid motion in the surround upon grating motion in the centre as was done in experiment 11 (Yo and Wilson (1992) used a stimuli with the test grating superimposed upon the plaid).

It was important to know if motion capture had occurred when the subjects had been presented with a particular stimulus configuration. Rather than rely solely upon subjective reports as to what they saw during the experiments, what was required was some quantitative indicator motion capture. Such an indicator of motion capture was found to exist. This was the induced shift in motion discrimination threshold from conditions of motion capture to conditions of no capture (Nawrot and Sekuler, 1990). In their experiments, Nawrot and Sekuler (1990) found that relative to conditions of no motion capture, motion capture was associated with an increase in the threshold for reporting the direction of motion in a test strip of random dots, while induced motion was associated with a reduction in the threshold. In this study it was decided to use this threshold shift as an index of the occurrence of motion capture.

As motion capture is an illusory effect of stimulus direction such that a test stimulus appears to move in the same direction as an inducing field (Ramachandran and Cavanagh, 1987), it was decided in these experiments to obtain velocity threshold measurements for the discrimination of the direction of motion of the test field, when the test field physically moved in the opposite direction to the inducing surround. Thus for example if the surround moved to the left then these experiments were interested in the threshold for observing the opposite i.e. rightward motion in the test (centre) stimulus. As the induced shifts in the motion thresholds are between conditions of motion capture and no motion capture it was important to set up control conditions in which motion capture could not occur i.e. a no capture condition. As motion capture and induced motion occur as a result of spatial interactions between different directionally tuned motion mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993), if there is no motion signal in the inducing field (the surround in our experiments) then motion capture of the centre by the surround can not occur. Informal experiments confirmed this, no motion capture or induced motion was reported by the subjects for any speed of motion of the centre, in conditions where the inducing surround did not move. Thus a stationary surround was used as the no capture, no induced motion control condition for all the experiments of this study. (The motion thresholds obtained for the stationary surround conditions were the velocity thresholds for observing motion in the same direction as the direction for the moving surround stimulus).

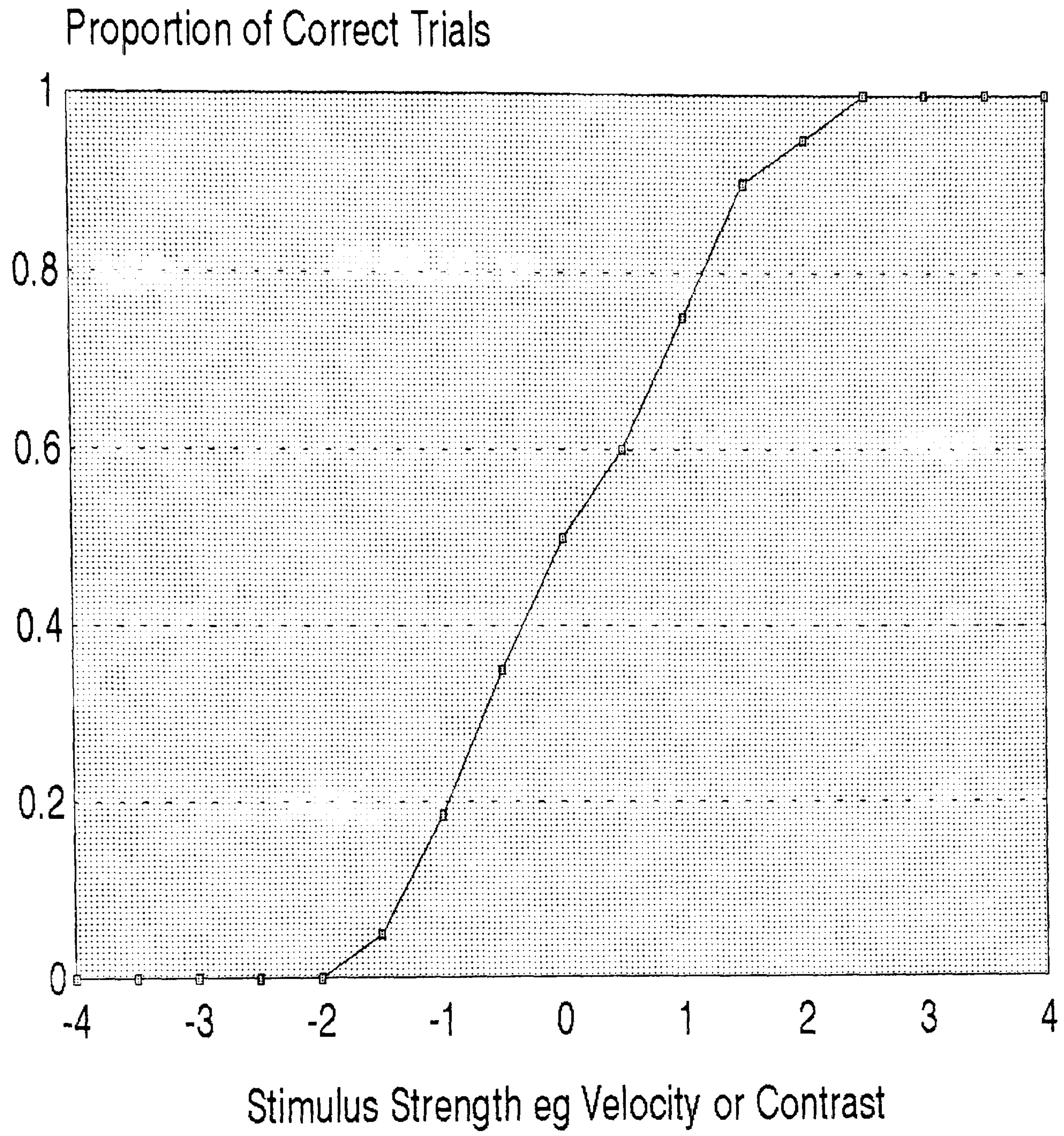
In these experiments, in order to index the occurrence of motion capture for a particular stimulus configuration, the velocity thresholds were obtained for the central test grating direction of motion, when this direction of motion was opposite that of the inducing field. These velocity thresholds were obtained for control conditions of no motion capture (stationary surround) and for conditions with moving surrounds (possible motion capture). If motion capture occurred for any of the stimulus configuration of this study, then relative to the control conditions of no motion capture, the occurrence of motion capture should be associated with an increase in the velocity threshold measure for the test direction of motion. Similarly if induced motion occurred then this should be associated with a decrease in the velocity threshold for the test field.

Another aim of this study was to examine the kind of interactions between motion mechanisms that give rise to motion capture phenomena. Of particular interest was the induced shifts in motion threshold in motion capture. The importance of the shift in threshold in motion capture, is that it may be related to the way in which motion mechanisms interact with each other. To fully understand how shifts in motion threshold can be related to possible modes of interaction between motion sensitive mechanisms, it is necessary to consider what is meant by thresholds. In order to do this it is necessary to consider the nature of the psychometric function and how the shape of this function gives rise to thresholds.

The psychometric function is the experimentally measured function which relates the probability of a subject responding with a particular response to the value of the stimulus (Watt, 1991). The psychometric function has the form of a sigmoidal curve which rises monotonically from a probability of zero to a probability of plus one. The function is at its steepest when the probability is 0.5. A typical psychometric function is illustrated in figure 36.

The shape of the psychometric function is determined by two parameters, the subject's sensitivity to the particular stimulus dimension under investigation, and any bias the subject has for a particular feature of the stimulus presented. For

Figure 36: Typical Shape of a Psychometric Function

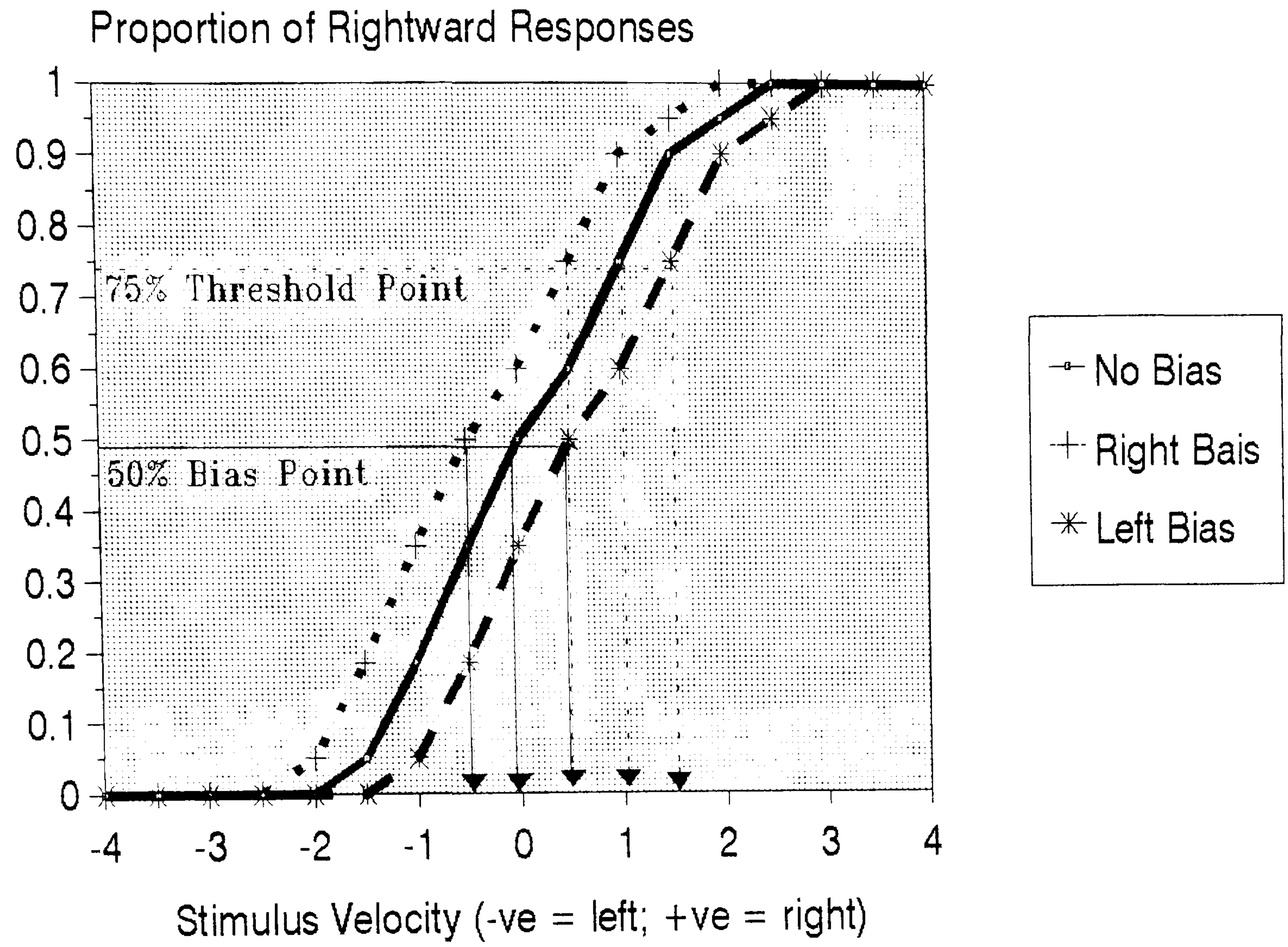


example, in an experiment where the subject has to report the direction of motion of a stimulus (either rightward or leftward) the probability that the subject will report that the stimulus moved to the right, for a particular speed of stimulus motion, will depend upon how sensitive the subject is to rightward motion, and if the subject is biassed in any way, for example to regard some rightward speeds of motion as motion in a leftward direction.

The bias and the sensitivity of the subject relate to the noise generated by the visual system when it is presented with a stimulus. The greater the noise the more unsure the subject will be as to the nature of the stimulus he has observed.
The noise in the system is normally distributed and is added to the signals transmitted by the visual system in response to a stimulus. The sensitivity of the subject relates to the standard deviation of the noise distribution, such that the greater the sensitivity the smaller the noise standard deviation. The bias of the subject relates to the mean of the noise distribution.

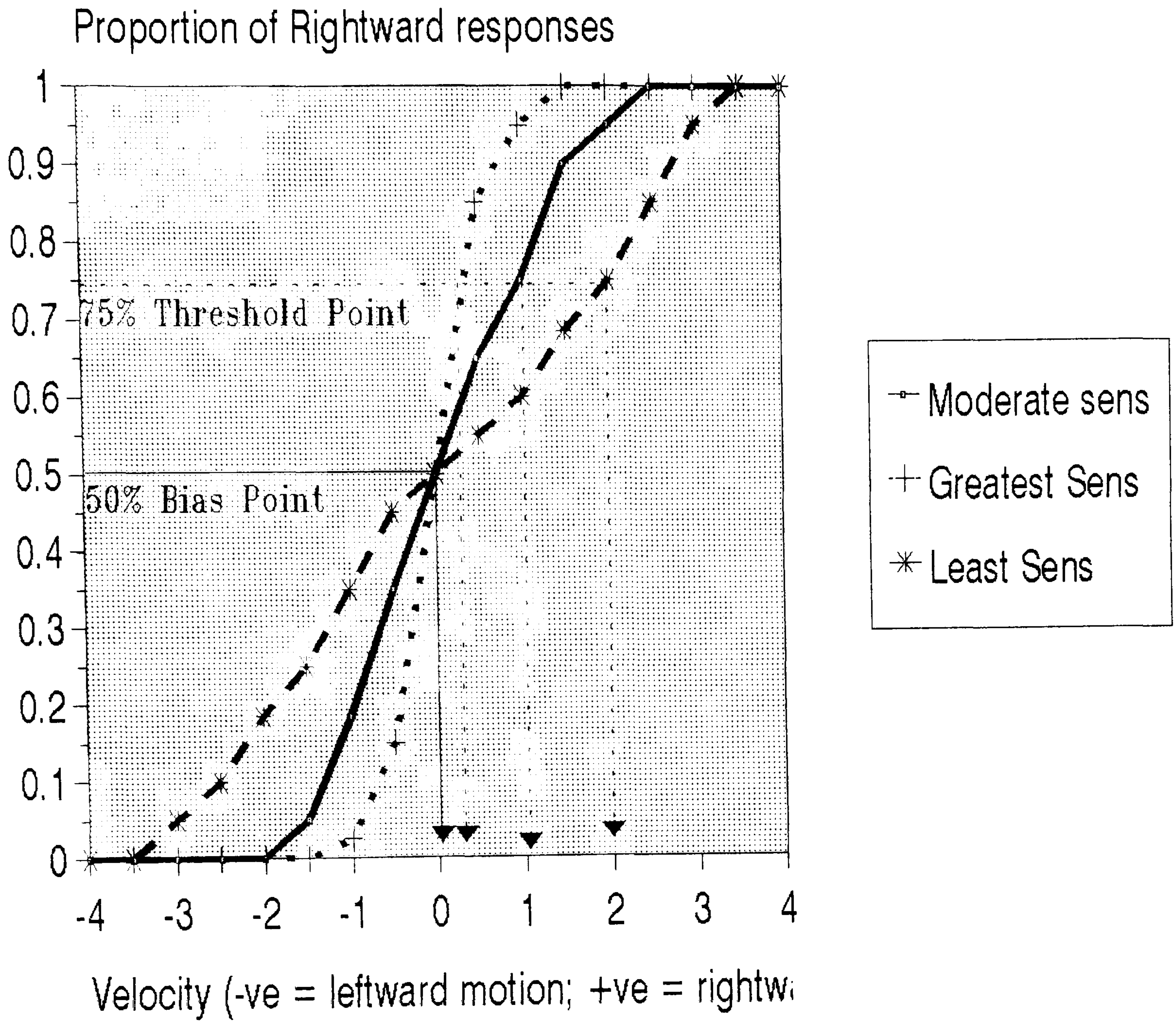
How the sensitivity and bias of the subject effect the psychometric function will be described. In order to do this it is best to consider a hypothetical experiment. Assume that the subject's ability to detect rightward motion is being assessed over a range of different speeds of motion, some to the right (a positive speed range), some to the left (a negative speed range). The percent rightward judgements are then plotted against the speed of stimulus motion (see for example figures 37 and 38). The psychometric function obtained will run from 0% the speed at which the subject never responds rightward (ie stimulus always perceived to be going leftward) through 50% the speed at which the subject respond left and right with equal probability up to 100% the speed at which the subject responds

Figure 37: Effect of Different Biases Upon Shapes of Psychometric Functions



The bias velocity and the 75% threshold velocity are indicated by the arrows. Note the shifts in these velocities with different biases.

Figure 38: Effect of Different Sensitivities upon Shapes of Psychometric Functions



Arrows indicate 75% threshold velocity for detecting rightward motion.
Note how the threshold velocity changes with changing sensitivity.

right all of the time. Assume firstly that the sensitivity of the subject to rightward motion is constant with changing experimental conditions. If the subject has no bias toward a particular direction of motion the bias point, which is the point at which the subject reports both directions of motion with equal probability i.e. the 50% point, will be at or close to a speed of zero degrees per second i.e. there is no speed so the subject will be equally likely to report right and left. If on the other hand the subject has a bias towards seeing leftward motion such that certain rightward speeds are perceived as being leftward, then the bias point between the two directions of motion, will be shifted along the speed axis of the psychometric function in the direction of increasing rightward speed (see figure 37). Similarly if the subject is biassed to see some leftward speeds as rightward then the bias speed will be shifted along the speed axis in the direction of increasing leftward speed. Hence a change in bias point, with no change in the sensitivity has the effect on the psychometric function of shifting the function along the speed axis in the direction of the bias. Considering the sensitivity to rightward motion.

In our example, if we are comparing two experimental conditions in which the subject has greater sensitivity to rightward motion in one condition as compared with the other, assuming equal bias across the two conditions. For any given speed rightward, the proportion of rightward judgements in the more sensitive condition increases relative to the conditions of less sensitivity. In our example as the bias does not change between conditions, it can be seen that with increased sensitivity the slope of the psychometric function will increase i.e. the function will become steeper. For example the speed at which 100% rightward judgements is obtained will be slower in conditions of greater sensitivity relative to lower sensitivity (see figure 38). Hence the sensitivity relates to the slope of the psychometric function, increasing sensitivity gives rise to increasing slope, while the bias relates to the position of the 50% point of the psychometric function.

The threshold for reporting, for example, the direction of motion of a stimulus depends upon the shape of the psychometric function. It is usual in psychophysics to take a particular proportion of responses as the threshold. For example the speed at which the subject judged the stimulus to be moving to the right 75% of the time might be taken as the threshold for seeing rightward motion. It can be seen how the sensitivity of the subject to rightward motion would effect this threshold measure. The sensitivity relates to the slope of the psychometric function, the lower the sensitivity, the shallower the function, hence the higher the threshold speed for rightward judgements obtained (see figure 38).

Similarly it may be seen how the bias between different directions of motion might effect this threshold. If the subject were biassed, such that he perceived some rightward speeds to be moving leftward, this would shift the psychometric function along the speed axis (see figure 37). Thus for a given sensitivity the threshold for rightward motion judgements would increase with a change in bias towards leftward motion.

Relating this back to our discussion of motion capture phenomena. It was noted previously that the threshold for a particular judgement depends upon the sensitivity and bias of the subject as regards the particular stimulus presented. This means that the shift in the motion threshold under conditions of motion capture relative to conditions of no capture (Nawrot and Sekuler, 1990) could be due to a change in the sensitivity to the particular direction of motion of the stimulus, a change in the bias point between opposite directions of motion or a combination of the two effects. From the results of Nawrot and Sekuler (1990), it is not possible to determine the cause of this threshold shift as the nature of the psychometric functions they obtained were not reported.

As the threshold shift in motion capture is relative to conditions of no motion capture, the psychometric functions for conditions of motion capture need to be compared to those for conditions of no motion capture (the no motion capture psychometric function would be for judgements of test motion in the same direction as for the capture condition). From a comparison of the two psychometric functions it would then be possible to find out if the threshold shift in motion capture is due to a sensitivity change, a change in bias or a combination of both effects.

As it was the intention to examine the nature of the threshold shift in motion capture, the psychometric functions that gave rise to these thresholds were recorded for both the control (stationary surround) and the experimental (moving surround) conditions. In order to obtain psychometric functions for the test grating direction discriminations, it was necessary to carry out direction discriminations across a wide range of velocities of the central test grating. The test field direction discrimination threshold was the velocity threshold for seeing the test grating move in the opposite direction to the surround. In order to obtain the full range of probabilities of response i.e. 0 to 100%, a negative and positive range of test grating velocities were used. Negative velocities were speeds in the opposite direction to the inducing surround, positive velocities were speeds in the same direction as the surround. Thus, in conditions where the surround field moved to the left, these experiments were concerned with obtaining the proportion of rightward motion judgements for the test stimuli over a range of both rightward (negative velocity) and leftward (positive velocity) speeds.

For conditions in which motion capture was evidenced. If the threshold shift depended solely upon the sensitivity to motion direction then it would be expected that the psychometric function corresponding to the case of no capture would be steeper than that of the motion capture function, with an equal bias (50%) point. If the threshold shift depended solely upon the bias of the subject then it would be expected that the slopes of the two curves would be equal and that the psychometric function for the capture conditions would be shifted along the speed axis relative to that for the no capture conditions. A combination of both effects would result in the two curves differing in slope and bias point.

If the probabilities of response for a particular judgement (eg percent correct), for each test field speed, are converted to z-scores and plotted against the test field speed, the theoretical fit of the resultant plot is a straight line. The important feature of this straight line plot is that the slope of the plot corresponds to the sensitivity of the visual system to the particular stimulus dimension, while the y-axis intercept is a measure of the bias of the system. Examining the z-score plots can thus allow comparisons of the relative importance of the bias and sensitivity in determining the threshold for a particular psychophysical judgement. If the threshold shift of motion capture were to be dependent upon a change of sensitivity to a particular direction of motion then it would be expected that the slope of the z-score plot would be different for capture than for no capture conditions. Further it would be possible to say whether the sensitivity to a particular direction of motion had increased (greater slope of z-score plot) or decreased (reduced slope). If on the other hand the effect is dependent upon the bias of the system then one would expect that the y-axis intercept of the z-score plots would differ between the capture and no capture plots.

A consideration of the psychometric functions relating directional discriminations of the test field to the velocity of the test field, allowed the principal aims of this study to be met. If motion capture was evidenced by any of the stimulus configurations, then it would be associated with a shift in the threshold for the direction discrimination. Thus the conditions for which capture occurs in this study may be compared with those of previous studies and other stimulus characteristics favouring capture may be found. In addition to this, the nature of the threshold shift in motion capture may be explained by referring to the slope and bias of the resultant psychometric functions obtained in this study.

It may be noted that the magnitude of any threshold shift i.e. the difference between the test grating velocity thresholds for capture motion (or induced motion) and no capture conditions, can be considered to be a measure of the strength of motion capture (or induced motion). The magnitude of the threshold shift being greater for greater motion capture.

8.2 General Methods : Experiments 8,9,10 and 11

Apparatus

Visual stimuli for all the experiments were generated using a Cambridge Research Systems Visual Stimulus Generator (VSG). Stimuli were displayed on a Tektronix 608 monitor with a P31 phosphor. The frame rate used was 150 Hz.

Subjects responses were obtained using a Cambridge Research Systems CB1 dedicated response box.

Visual Stimuli

It was found from informal experimentation, that the best display for producing motion capture effects was when the display consisted of a central circular window filled with a sinusoidal grating. This was surrounded by a moving sinusoidal grating which filled the remainder of the display screen (see figure 35). In addition it was found that the best capture effects were observed when the two gratings differed in terms of their spatial frequencies. Consistent with the findings of Ramachandran and Cavanagh (1987) the best capture effects were found when the gratings differed in terms of spatial frequency by at least a factor of three i.e. when the centre spatial frequency was at least three times that of the surround.

The visual stimuli used in these experiments made use of these findings. The general stimulus design for these experiments consisted of a central grating of high spatial frequency surrounded by a moving grating stimulus of low spatial frequency.

The display screen used in these experiments was circular and subtended a visual angle of 1.97 degrees at the viewing distance of 290 cms.

A circular window was defined at the centre of the display screen using the framestore of the VSG. Into this window was placed a vertical sinusoidal grating of 6.0 cycles/degree spatial frequency, such that it filled the entire centre window.

The remainder of the display screen was filled with a moving sinusoidal grating stimulus. Two general types of surround stimulus were used, either a single grating of 2.0 cycles per degree spatial frequency or a plaid stimulus composed of two differently oriented sinusoidal gratings each of 2.0 cycles per degree spatial frequency (see descriptions of individual experiments).

Procedure

For each experiment a single temporal interval, two alternative forced choice design was employed for each experiment, using the method of constant stimuli.

All the experiments reported utilised sixteen constant stimuli. The stimuli were defined according to the velocity of the centre grating. There were eight possible central grating speeds 0.005, 0.01, 0.02, 0.03, 0.04, 0.05, 0.06, and 0.07 degrees per second. Half of the stimuli featured the central grating moving to the right and half to the left making a total of sixteen different stimuli. Each experiment was separated into a number of experimental runs. Each run consisted of 112 individual trials. The particular stimuli to be used on a particular run were randomly selected such that, a) each run utilised of eight of the stimuli (14 trials with each stimulus); b) each run contained four left and four right moving centre grating stimuli; c) each centre left velocity selected was paired with the equal centre right velocity (ie four velocities in each direction). Thus, for example, a given run might consist of centre velocities 0.005, 0.01, 0.02, 0.03 deg/sec leftward and the equal rightward velocities e.g. 0.005, 0.01, 0.02, 0.03 deg/sec. Each run could either be an experimental or control run. In experimental runs the surround grating(s) moved with a velocity of 0.1 deg/sec. On any given trial the surround grating could move either leftward or rightward, the direction of motion being determined randomly in such a way as to ensure that for each stimulus the number of trials with a leftward moving background were equal to those with a moving rightward background. This was done to control for any possible effects of motion after effects. On control runs the surround grating(s) was stationary i.e. had zero velocity. From trial to trial the starting phase of each of the gratings used in the centre and surround was randomised.

Experimental and control runs were repeated so as to give a total of 126 trials at each centre velocity for both of the surround motion directions.

On a given trial, after being presented with the stimulus the observers task was to indicate, with the aid of a response key, the direction of motion of the centre grating either leftward or rightward. The display screen was viewed with both eyes using natural pupils under photopic conditions.

Each stimulus was presented on the display screen for a total of 400 msecs within a raised cosine temporal envelope. The attack and decay of the temporal envelope were equal and of 75 msecs duration. Thus the stimulus was visible at its maximum contrast for 250 msecs.

Stimuli were designed so that, for example, a right moving centre could be paired with either a left or right moving surround (similarly for a left moving centre) within an experimental run. Data were collected for the two possible directions of surround motion for each stimulus. Thus for a given stimulus two sets of data were obtained, when it was paired with a left or right moving surround. It was found that for all the experiments reported in part two, there was no difference in the pattern of results for experimental runs where the surround moved to the left or where it moved to the right. Thus the results reported for all the experiments are for the runs when the surround moved to the right.

Subjects

Two subjects were used in each of the experiments, the experimenter, KAR, an experienced psychophysical observer aged 27 years and VJH a subject who was naive to the aims of the experiment aged 25 years. Both subjects have normal vision.

8.3 Note on the Results of experiments 8 to 11

For each experimental condition, the results obtained were the proportion of responses where the observer reported that the centre test grating moved in a particular direction (either rightward or leftward), when the stimulus surround moved in the opposite direction. The results for each condition were subjected to probit analysis in order to determine the discrimination threshold for that direction of test grating motion. The threshold was taken as the velocity of the centre test grating for which the subject responded 75% of the time that the stimulus was moving in a particular direction. Further, from this analysis, it was possible to calculate the intercept and gradient of the associated probit plots for each experimental condition. The probit analysis was carried out using SPSS/PC version 4.0.

It was one intention of these experiments to find out the stimulus conditions under which motion capture and induced motion were evidenced. As was stated, motion capture is associated with an increase in direction discrimination threshold relative to conditions of no motion capture, whilst induced motion is associated with a reduction in discrimination threshold. Thus for all of the experiments reported here, the occurrence of motion capture or induced motion was assessed by examining the direction discrimination velocity thresholds for the central test grating both for the conditions of a moving and a stationary stimulus surround.

Another intention of this experiment was to examine the underlying cause of the changes in discrimination thresholds observed with motion capture and induced motion. As described above, this was done by examining the gradient and intercept of the probit plot.

Chapter 9

Experiment 8:

The Effects of Central Aperture Size Upon Motion Capture and Induced Motion

9.1 Introduction: Experiment 8

Previous research (see above) has shown that motion capture and induced motion effects are critically dependent upon the size of the captured field. Thus it was predicted that motion capture effects should reduce with increasing central grating size. Nawrot and Sekuler (1990); and Murakami and Shimojo (1991,1992,1993) have showed that there appears to be a link between motion capture and induced motion, such that the percept changes from one of motion capture to one of induced motion as the width of the captured field is increased. From this it was expected that in this experiment there should be a similar effect, with increasing central grating diameter.

Following from the work of Nawrot and Sekuler (1990), the speed of motion at the correct 75% point on the psychometric function was taken as the threshold for identifying the direction of motion of the central grating. It was expected that the velocity threshold for detecting this direction of motion should be higher for conditions when the subjective experience was of motion capture, than for conditions where no capture was experienced. When the subjective experience was of induced motion it was expected that the velocity threshold would be reduced as compared with conditions of no-induced motion.

The models of motion capture described previously all predict that motion capture is dependent upon the size of the captured field (centre grating) and breaks down with increasing size.

In this experiment as with all the subsequent experiments on motion capture, the resultant z-scores of the psychometric function were plotted in order to examine the cause of any motion capture induced changes of threshold. Did such changes result from a change in the sensitivity to the particular direction of motion of the central grating or from a change in the bias point between the different direction of motion in the centre and surround?

9.2 Method: Experiment 8

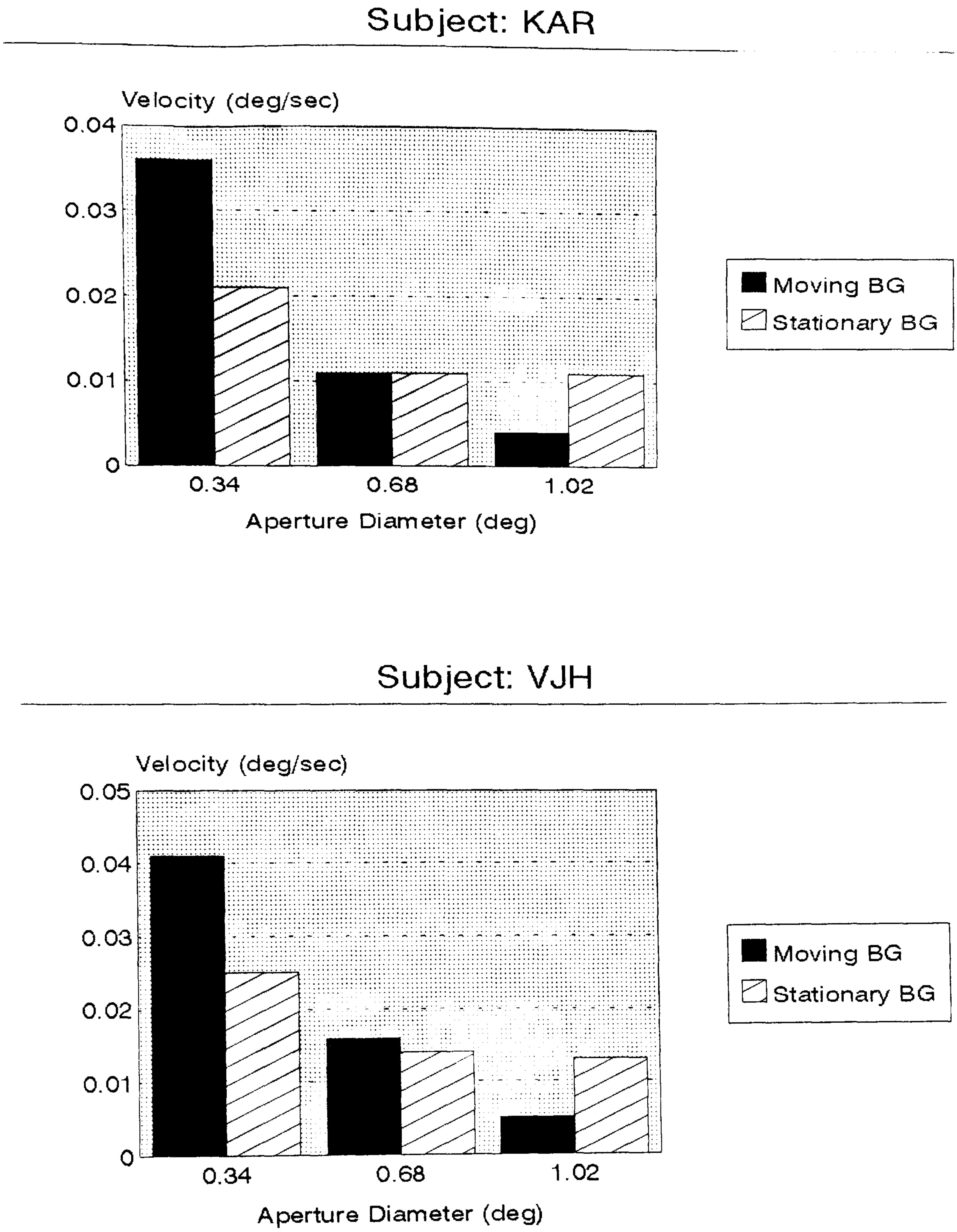
In this experiment, three central apertures were produced. The central apertures subtended visual angles of 0.34, 0.68 and 1.02 degrees at the viewing distance of 2.90 metres. The surround stimuli for this experiments consisted of a single vertical sinusoidal grating. The centre grating had a contrast of 0.15, the contrast of the surround grating was 0.5. The procedure and the display were as described in chapter 7.

9.3 Results: Experiment 8

Examining the direction discrimination thresholds (figures 39), for the smallest aperture size, the discrimination threshold with a moving surround was greater than when the surround was stationary. Thus for this condition there was evidence for the occurrence of motion capture. With the largest aperture condition, the threshold for the moving surround was less than that for the stationary surround condition. This was evidence for the occurrence of induced motion. With the intermediate aperture condition, the thresholds for both moving and stationary surround were equivalent, giving no evidence for the occurrence of either induced motion or motion capture.

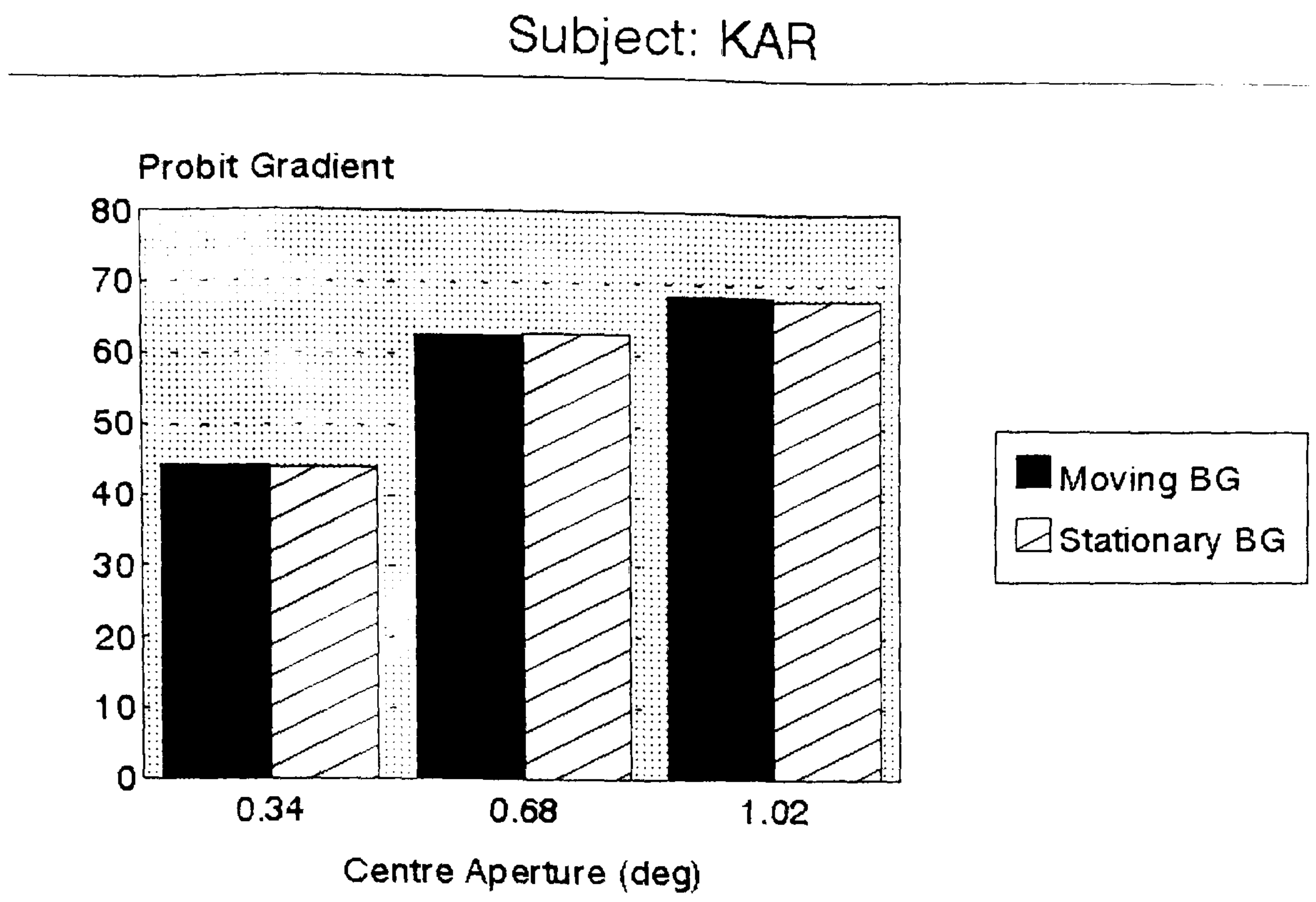
Examination of the probit gradient plots (figure 40) for this experiment revealed that for each experiment the gradients for the stationary and moving surround conditions were equal. This indicates that within each experimental condition the sensitivity of the visual system to the direction of motion of the centre test grating was equal for both the moving and stationary surround conditions. It may be seen that between experimental conditions, there was an increase in the calculated gradient with increasing central aperture size. This indicates that the sensitivity of the visual system to the direction of motion of the central test grating, increased with increasing aperture size.

Examining now the probit intercept plots for each condition (figure 41). For the smallest aperture size, the intercept was less for the moving surround than for the stationary surround. For the largest surround condition, the intercept for the moving surround was greater than for the stationary surround. For the intermediate central aperture size the intercepts were equal. The shifts in the


Subject: KAR

Subject: VJH

Figure 39: Effect of central aperture size on motion capture and induced motion. Lower thresholds of motion for three aperture sizes.



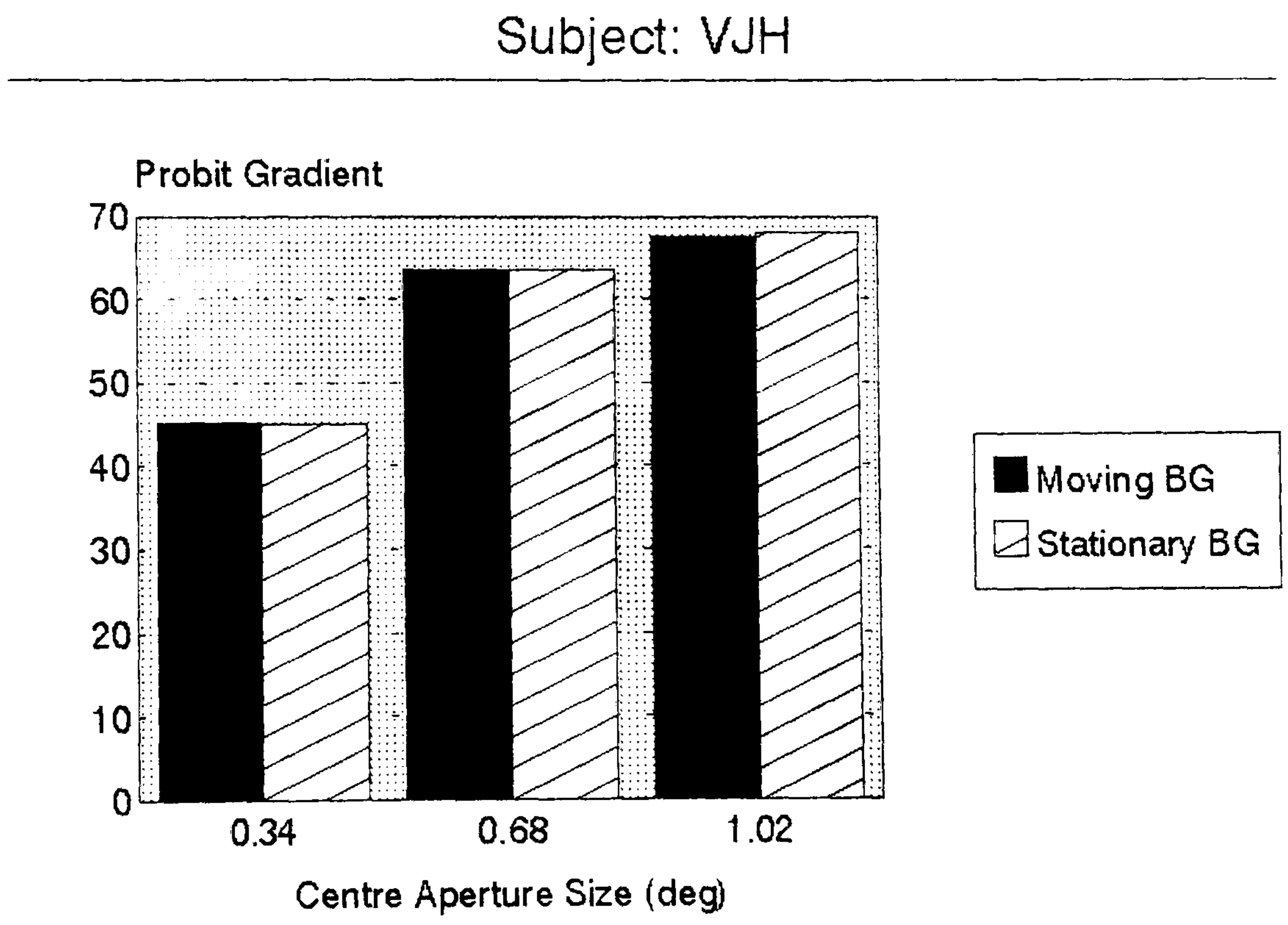
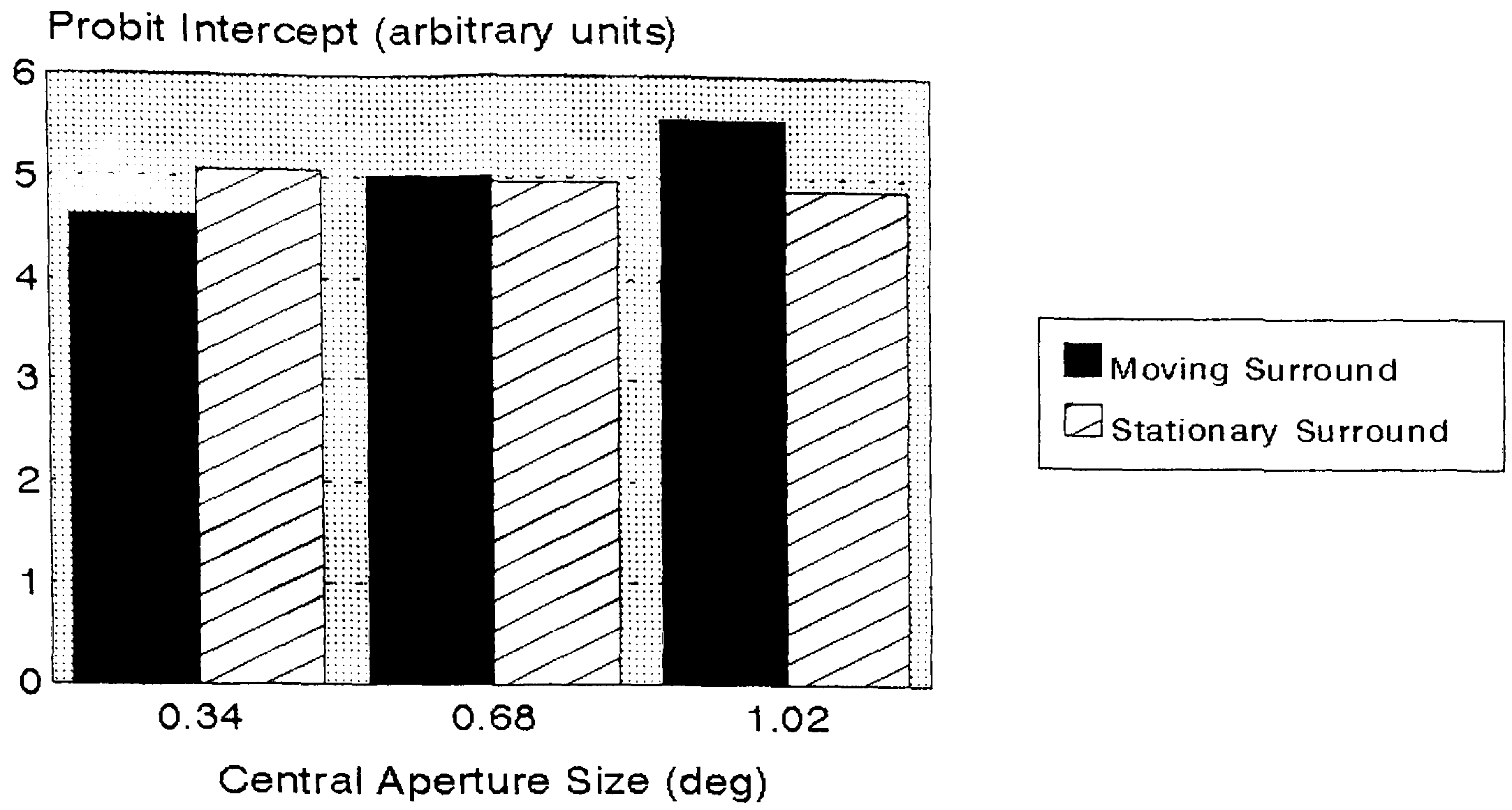


Figure 40: Gradients of the probit plots produced for the three aperture sizes of experiment 8.

Subject: KAR



Subject: VJH

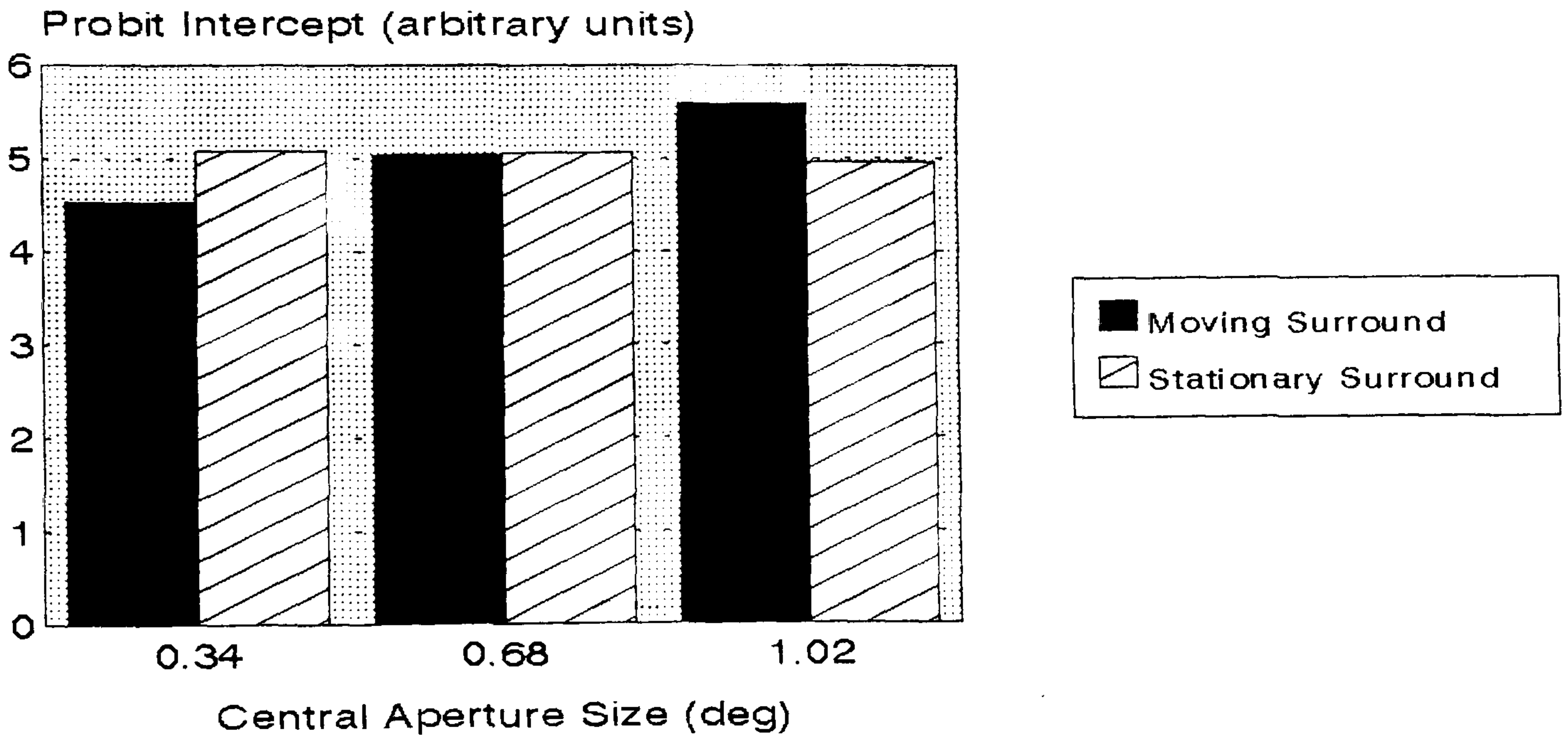


Figure 41: Intercept of probit plot produced for the three aperture sizes of experiment 8.

intercepts observed for the smallest and largest central aperture sizes suggest that under these conditions there was a shift in the bias point between opposed directions of motion for the moving relative to the stationary surround conditions.

These shifts in bias point are in opposite directions, as evidenced by the increase in intercept for the large aperture condition as compared with the decrease for the small aperture condition. It was notable that the intercepts for all aperture sizes for the stationary aperture condition were equal.

Taking these results together, evidence for motion capture was obtained for the smallest aperture condition and evidence for induced motion for the large aperture condition. As there was no change in the sensitivities to the centre test gratings direction of motion between stationary and moving surround conditions for each aperture size then the observed changes in the discrimination thresholds do not seem to be associated with changes in sensitivity. As there was a difference between the probit intercepts for stationary and surround conditions for the smallest and largest apertures it is possible to conclude that these changes in threshold are associated with shifts in the bias point between opposed directions of motion. The observed increase in sensitivity with increasing aperture size, was not related to the occurrence of motion capture or induced motion due to the equivalence of the sensitivities for the stationary and moving surround conditions.

9.4 Discussion: Experiment 8

The results of this experiment revealed that the occurrence of motion capture is dependent upon the size of the induced (test) field. Evidence for motion capture was only obtained for the smallest central test aperture size used. As the size of the central aperture increased, motion capture seemed to give way to induced motion effects. At the intermediate aperture size used there was no evidence for either motion capture or induced motion for the subjects.

The finding of a gradual change from motion capture to induced motion is consistent with the findings of Murakami and Shimojo (1991,1992,1993); Scase and Braddick (1993), Zhang et al (1993) and Nawrot and Sekuler (1990). Nawrot and Sekuler (1990) reported that as the size of the test field increases motion capture (assimilation in their terminology) shades into induced motion (contrast). Nawrot and Sekuler stated that it was possible at a certain test field diameter, the effects of motion capture and induced motion would be equal. At this point the subjective percept would be neither motion capture or induced motion. These authors suggested that this point of equivalence in the strength of the two effects would give estimates as to the spatial extent of the motion capture and induced motion effects. Their results revealed this point of equivalence to lie at a test strip diameter of 45 - 60 minutes of arc. In the current experiment, it was found that the test field diameter at which there was no evidence for motion capture or induced motion was 60 mins of arc. Assuming that this point could be equated with the point at which induced motion and motion capture strength is equal then it is interesting to note that this diameter is of the order of that found by Nawrot and Sekuler.

Accepting the above assumptions, this experiment has provided an estimate of the spatial range of motion capture in accordance with previous findings, using sinusoidal grating displays as opposed to random dots.

The results of this experiment taken together support previous findings concerning motion capture and add further weight to the argument that the occurrence of the motion capture effect is critically dependent upon the size of the captured field (Nawrot and Sekuler, 1990; Chen et al, 1992; Chang and Julesz, 1984; Murakami and Shimojo, 1991,1992,1993; Yuille and Grzywacz, 1989). Also these results lend support to all the models of motion capture and induced motion, that suggest that these perceptual effects are produced by the same underlying mechanisms, featuring excitatory and inhibitory interactions between motion sensitive mechanisms across space in the visual system (Nawrot and Sekuler, 1992; Murakami and Shimojo, 1991,1992,1993).

It was also found in this first experiment, that as the size of the central aperture increased, the threshold for the discrimination of the central grating's direction of motion decreased for both the moving and stationary surround conditions. Examination of the sensitivity to the centre's direction of motion revealed that this reduction in threshold was accompanied by an increase in the sensitivity for the central direction of motion. This increase in sensitivity was equal for both the moving and stationary surround conditions. The fact that the increase in sensitivity was equal for both the moving and stationary conditions coupled with the equivalence of the sensitivities to the central direction of motion for the moving and stationary surround for any given aperture size, indicates that this change in sensitivity is associated with the size of the stimulus aperture and not with the presence or absence of motion in the surround.

This finding is consistent with previous work concerning the size of the motion field and sensitivity to stimulus motion. For example Watamaniuk and Sekuler (1992) found that the motion thresholds to discriminate different directions of motion in a random dot display decreased as the size of the display increased. This occurred for a circular aperture diameter of up to around 9 degrees of visual angle. In the display of these experiments the maximum aperture diameter was 1.02 degrees of visual angle. This was within the spatial range reported by Watamaniuk and Sekuler and so these results support previous findings.

Chapter 10

Experiment 9:

The Effect of Centre and Surround Contrast Upon Motion Capture and Induced Motion

10.1 Introduction

The aim of this experiment was to examine the effect upon the occurrence of motion capture and induced motion of the relative contrast of the stimulus centre and surround.

Previous work, e.g. Murkami and Shimojo (1991,1992,1993), has shown that the two effects are dependent upon the contrasts of the centre and surround. As the contrast of the centre was increased the strength of motion capture was reduced and then shaded over to induced motion at high levels of central grating contrast.

Three experimental stimuli were set up. In the first a high contrast grating in the surround was paired with a low contrast grating in the centre, in the second condition a high contrast grating in the surround was paired with a high contrast grating in the centre and in the third condition a low contrast grating in the surround was paired with a low contrast grating in the centre.

Based upon the previous work on motion capture, (Murakami and Shimojo, 1991,1992,1993) it was expected that with a high contrast surround, motion capture would be evidenced for the lowest central contrast and induced motion would be evidenced for the highest centre contrast. No previous work has examined the effect upon motion capture of a low contrast inducing (the surround) and induced (the centre) field.

The models of motion capture described previously do not explicitly deal with contrast and so the results of this experiment will add to these models.

10.2 Method: Experiment 9

Three conditions were used. In the first the centre contrast was 0.15 and the surround 0.5 (low-centre, high-surround condition), in the second condition the centre and surround gratings had equal contrast of 0.5 (high-centre, high-surround condition) and in the third condition the centre and surround had equal contrasts of 0.025 (very low-centre, very low-surround condition).

The aperture size of the centre grating was 0.34 degrees. Both the gratings (centre and surround) had zero orientation with respect to the vertical.

10.3 Results: Experiment 9

Examining firstly the direction discrimination thresholds for the experimental conditions (figure 42). In the case of the high contrast surround (0.5) and medium contrast centre (0.15), the threshold velocity for the moving surround

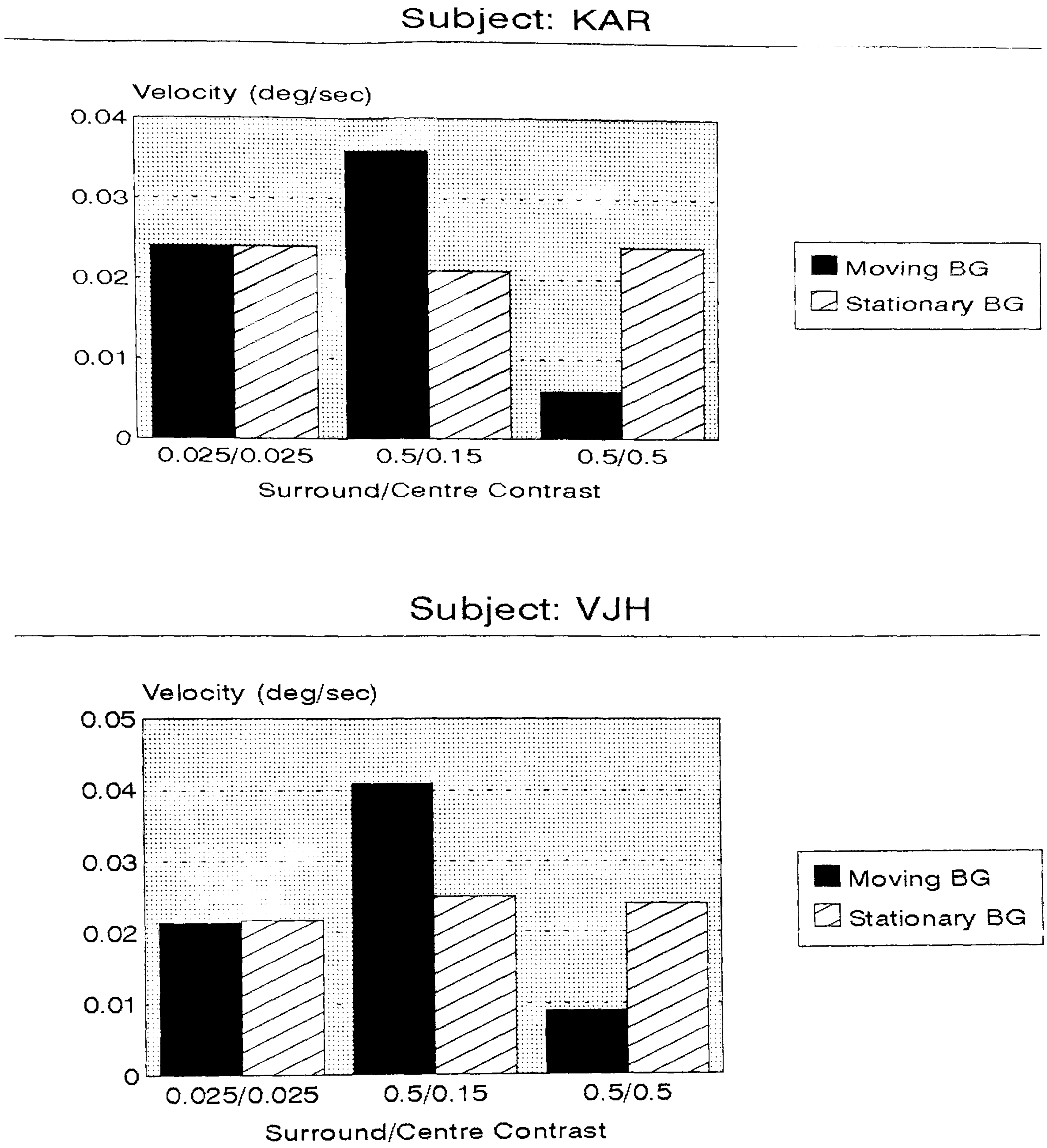


Figure 42: Effect of centre and surround grating contrast on motion capture and induced motion. Lower thresholds of motion for three pairings of centre/surround contrast.

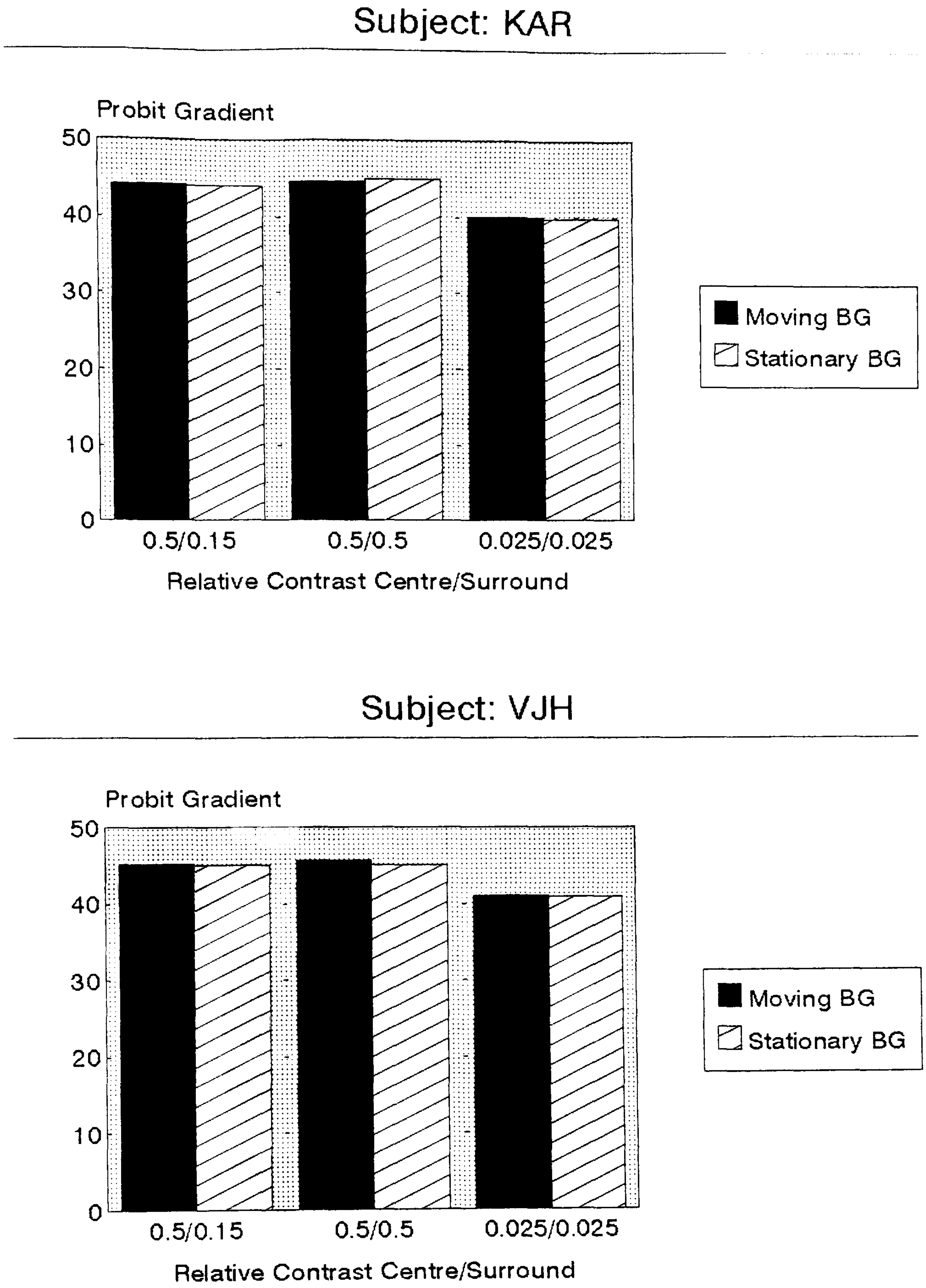
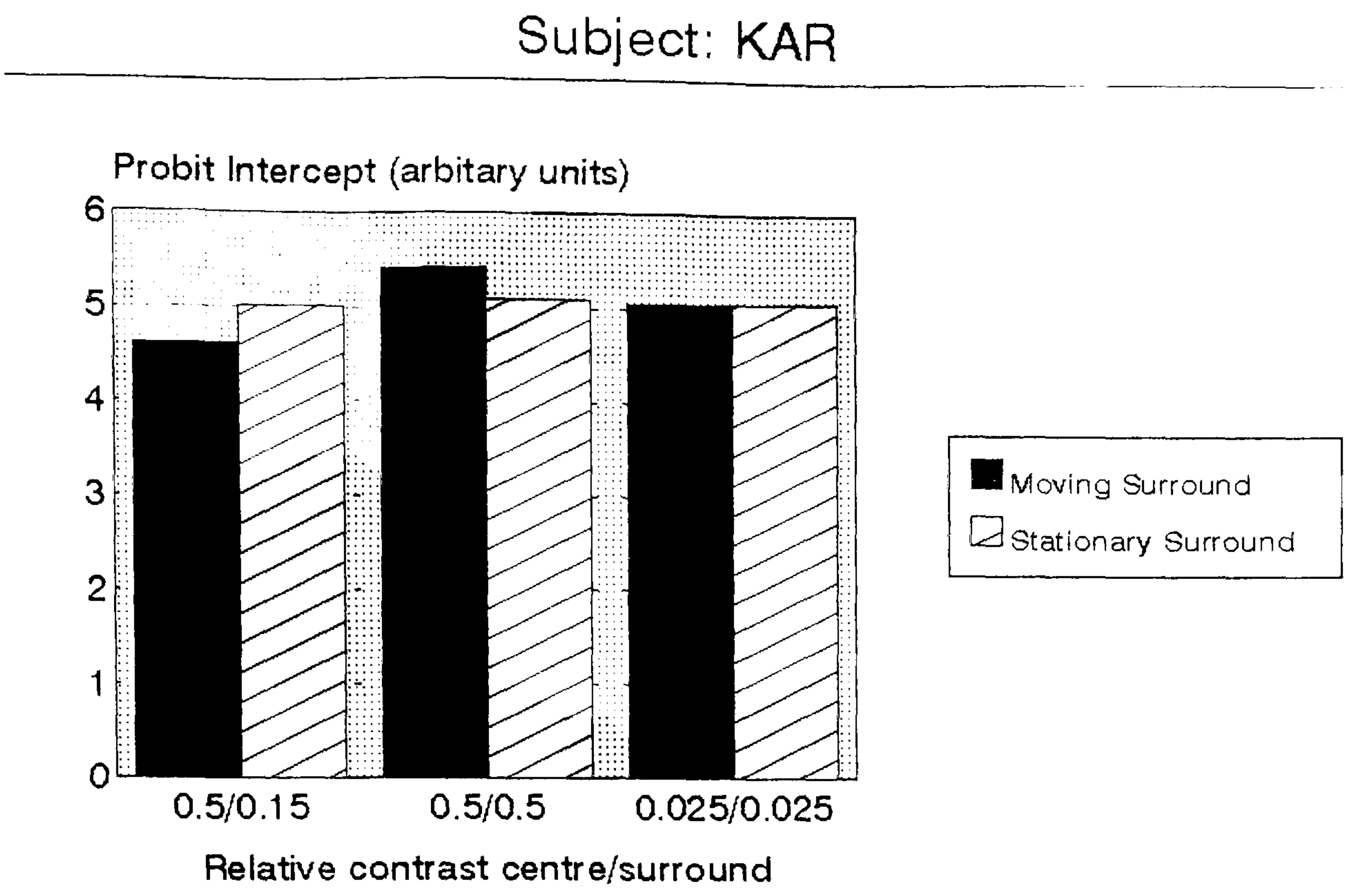


Figure 43: Gradients of the probit plots produced for the three pairings of centre/surround contrast in experiment 9.



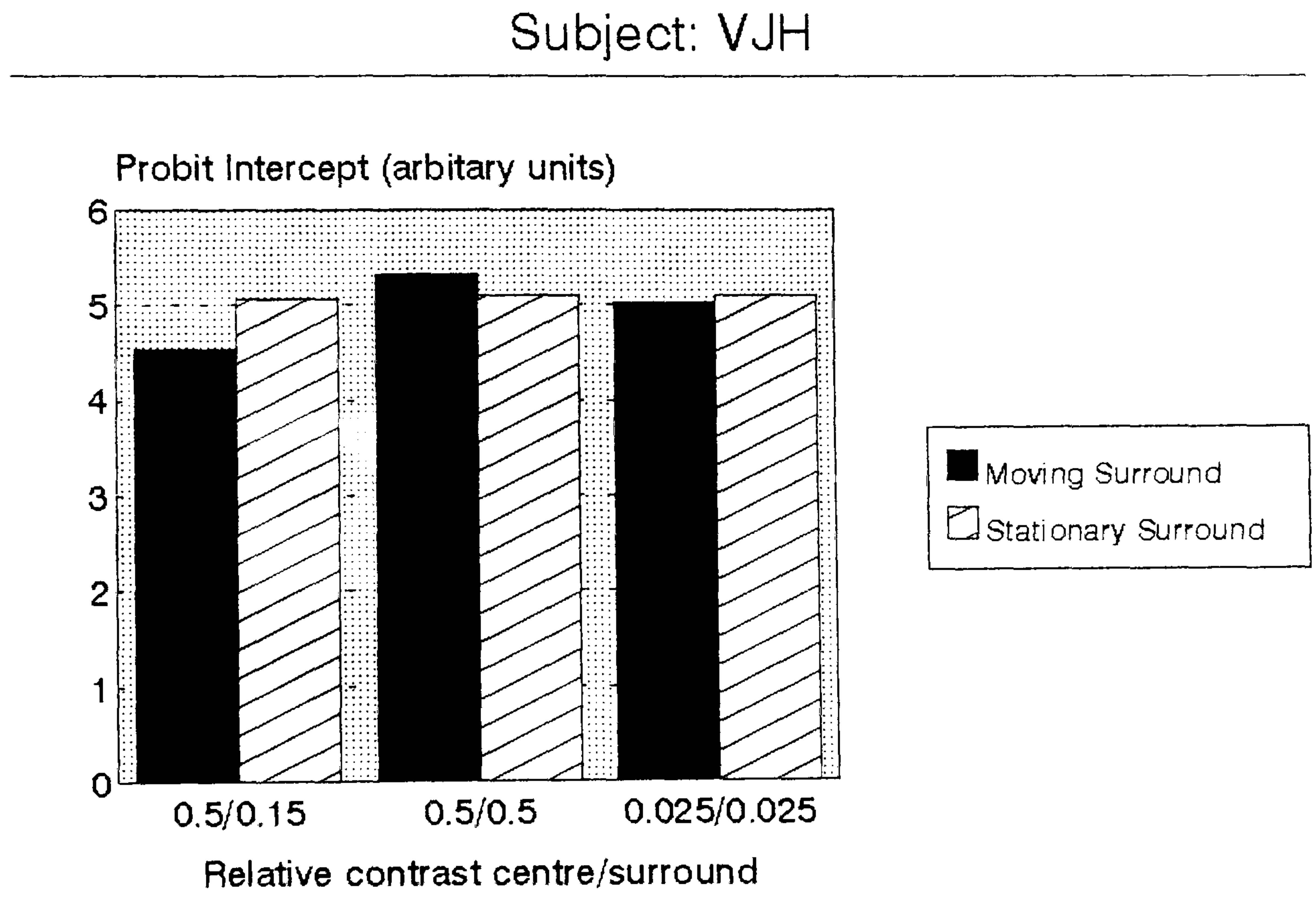


Figure 44:Intercepts of probit plots produced for the three pairings of centre/surround contrast in experiment 9.

condition was greater than that for the stationary surround. This can be taken as evidence for the occurrence of motion capture under these conditions. When the contrasts of the centre and surround were equal and both 0.5, the threshold velocity for the moving surround was less than that for the stationary surround. This was evidence for the occurrence of induced motion under these conditions. When the centre and surround contrasts were equal and both low, the velocity thresholds for both the moving and stationary condition were equal. Under these conditions therefore there was no evidence for the occurrence of induced motion or motion capture. Comparing the velocity thresholds across experimental conditions. As regards the stationary surround conditions, the thresholds were equal for the 0.5/0.5 and the 0.15/0.5 centre/surround contrast conditions, with a greater threshold for the 0.025/0.025 centre/surround contrast. The highest velocity threshold was obtained for the moving surround of the 0.15/0.5 centre/surround contrast, while the lowest velocity threshold was found for the 0.5/0.5 centre/surround contrast.

Examining the probit gradient plots (figure 43) it can be seen that for all conditions the probit gradients were equal for the stationary and moving surround conditions. This result suggests that for all the experimental conditions, there was no change in the sensitivity of the visual system to the motion of the central test grating, between the moving and stationary surround condition. It can be seen that with increasing centre test grating contrast from 0.025 to 0.15, the gradient magnitude increased. This indicated an increase in sensitivity for the centre test grating direction of motion with increasing centre contrast up to 0.15. From a centre contrast of 0.15 and 0.5 the probit gradients were equal. This indicated no change in sensitivity for the centre direction of motion with increasing contrast beyond 0.15.

The probit intercept plots (figure 44), it can be seen for the high contrast surround low contrast centre, the intercept is greater for the stationary than for the surround condition. This shift in the intercept point indicates a shift in the bias point with a moving as compared to a stationary surround. For the high centre and surround contrast condition, the intercept point is greater for the moving than for the surround condition. This result also indicates a shift in the bias point between moving and stationary surround conditions. The shift in the bias point in this case is in the opposite direction to that for the high contrast surround moderate contrast centre. For the low contrast centre and surround condition, the intercept points are equal. This indicates equal bias for the moving and stationary surround conditions.

Evidence for motion capture was obtained for the high contrast (0.5) surround moderate contrast (0.15) centre condition, while evidence for induced motion was found for the high contrast (0.5) centre and surround condition. The occurrence of motion capture and induced motion, were associated with shifts in the bias point between opposed directions of motion. The bias shifts were in opposite directions for motion capture and induced motion. There was no evidence that motion capture and induced motion were associated with any change in the sensitivity for the motion direction of the centre test grating. Increases in sensitivity were associated with increases in the contrast of the centre test grating, from a centre contrast of 0.025 to 0.15. There was no evidence for motion capture or induced motion with the lowest contrast centre and surround.

10.4 Discussion: Experiment 9

It is worth noting that the aperture size of the test grating was of the size for which motion capture was observed in experiment 8, for all the conditions of experiment 9. This means that as motion capture is obtainable with this aperture size, any evidence for other non-capture effects such as induced motion, in this experiment must be due to the experimental manipulations of the surround and test centre contrasts.

This experiment obtained evidence for motion capture only in conditions where the two gratings differed in contrast, such that the contrast of the surround was greater than the contrast of the centre test field i.e. contrasts of 0.5 in the surround and 0.15 in the centre. In the condition where the contrast of the centre and surround fields were equal and both were of contrast equal to 0.5, evidence was obtained for induced motion. These findings support the findings of Murakami and Shimojo (1991,1992,1993), that with increasing test field contrast, motion capture switches to induced motion. The further finding of experiment 9 was that in the condition where both test and surround were very low contrast (contrast equal to 0.025), there was no evidence for either induced motion or motion capture. It would be interesting to examine the effects of a high contrast centre (contrast equal to 0.5) and a low contrast surround (contrast equal to 0.15). Based upon previous work (Murakami and Shimojo, 1991,1992,1993) it would be predicted that capture of the centre grating by the surround would be unlikely.

There is general agreement in the literature (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Yuille and Grzywacz, 1989) that motion capture and induced motion result from excitatory and inhibitory interactions between differently tuned motion sensitive mechanisms across space. The results of experiment 9 indicate that the precise nature of the interactions between motion mechanisms also depends upon the contrast of the inducing and induced (test) field.

At very low contrasts of the centre and surround, the lack of evidence for motion capture or induced motion could suggest that there is no interaction between differently tuned motion mechanisms. Support for this position comes from previous research. Stromeyer et al (1984), found that at low threshold contrasts (contrasts of the order of 0.05 or less), the direction of motion of a grating, when it was presented in counterphase with another grating (two superimposed opposite directions of motion), is detected by unidirectional motion mechanisms. The response of such unidirectional mechanisms is unaffected by the presence of the opposed (superimposed) direction of motion. At high contrasts the detection of the grating's motion was strongly influenced by the presence of the oppositely moving grating, in a manner indicating directional opponency between opposite directionally tuned mechanisms. Stromeyer et al (1984) interpreted this finding as evidence for opponency between opposed directions of motion in the visual system, but that this opponency was only in operation at high suprathreshold contrasts i.e. contrasts of greater than 0.05. At low threshold contrasts oppositely tuned motion mechanisms do not interact with each other i.e. motion direction is detected independently of other motion in the visual field. Accepting this analysis, it is easy to see how, at low contrasts, effects such as motion capture and induced motion, would not be found. In the current experiment the centre grating contrast was of the order of the contrasts used by

Stromeyer et al, implying that the contrast levels in this experiment were low enough for the kind of effects described by Stromeyer et al to be evidenced. If it is assumed (as previous work suggests e.g. Murakami and Shimojo 1991,1992,1993; Nawrot and Sekuler, 1991) that the type of interactions between motion mechanisms reported by Stromeyer et al can occur between motion mechanisms from spatially separated locations i.e. between centre and surround, as well as between similarly located motion mechanisms, then at the low contrasts used in this experiment it is likely that there will be little interaction between differently tuned motion mechanisms. Due to this lack of interaction, motion capture or induced motion would not be expected to occur. This explanation is sensible, in that it allows previous results e.g. Stromeyer et al (1984), and results concerning motion capture and induced motion e.g. Murakami and Shimojo (1991,1992,1993); Nawrot and Sekuler (1990), to be reconciled.

An alternative explanation of the low contrast results is that at these low levels of contrast, the motion capture effect and the induced motion effect are of equal magnitude and so the overall effect is of no motion capture or induced motion. This second explanation is analogous to that forwarded to explain the results of experiment 8 concerning the lack of a evidence for motion capture or induced motion at the intermediate aperture size. This suggestion is rejected for reasons as set out below. If motion capture and induced motion are dependent upon interactions between directionally tuned motion mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993), then at low contrasts, if motion capture and induced motion effects are present with equal strength, there must be interactions occurring between the motion mechanism. If this is so then the findings of Stromeyer et al (1984) can not easily be reconciled within this scheme. Conversely if one wants to push this scheme by accepting that there are no interactions between motion mechanisms at low contrasts, then one is forced to reject the findings that motion capture and induced motion depend upon interactions between different motion mechanisms, a proposal which goes against the weight of evidence concerning motion capture and induced motion.

Examining now the results for the higher contrast centre (test) fields. It is interesting to ask why it should be that evidence for motion capture was found with a centre contrast of 0.15 and surround contrast of 0.5, while evidence for induced motion was found with a centre and surround contrast of 0.5. One suggestion is, that at these higher contrast levels, the contrasts of the centre and surround are now sufficiently high to allow interactions between motion mechanisms. The contrasts used of were suprathreshold for both subjects. These contrast levels were greater than the levels of contrast in which Stromeyer et al, found evidence for interactions between different motion mechanisms. This does not however explain why it is the case that evidence for motion capture was found when the centre grating had a contrast level of 0.15 while evidence for induced motion was found when the centre grating had a contrast level of 0.5. If the occurrence of motion capture depended solely upon the size of the aperture and the contrast of the centre and surround being sufficiently high for interactions to occur between differently tuned motion mechanisms, then motion capture should be evidenced for both centre contrasts (0.15 and 0.5). As this was not found by this experiment, there must be some other effect in operation that is responsible for this switch from motion capture to induced motion.

One possible explanation for this effect depends upon assumptions about the relative strength of excitation and inhibition of local motion mechanisms in response to changes in contrast. In the current experiment the subject's task was to report the direction of motion of the centre grating of the display. The direction of motion reported depends upon the relative levels of excitation and inhibition of differently tuned motion mechanisms responding to motion at the centre of the display. Motion capture will result for example, if the excitation of the left selective motion mechanisms at the 'centre' is greater than that of the right selective motion mechanisms where the physical direction of motion of the centre grating is to the right and the surround is to the left. It may be seen that in order to eliminate motion capture effects, the levels of excitation of 'centre' right selective mechanisms and the resultant inhibition of left selective mechanisms would need to be increased. Let us assume that increases in stimulus contrast give rise to greater levels of excitation and inhibition of motion mechanisms tuned to different directions of motion. Then the lower contrast (0.15) centre grating would produce less excitation and inhibition then the higher contrast (0.5) centre grating. In our example, then the excitation of right sensitive motion mechanisms and inhibition of left selective mechanisms at the 'centre' would be less for centre gratings of lower contrast as compared with those of higher contrast. The effect of the motion in the surround would be expected to be equal for both the high and low contrast centre gratings as the contrast of the surround grating (0.5) is the same for both conditions. The upshot of this is that as the contrast of the centre grating increases, it would becomes increasingly easier to perceive rightward as opposed to leftward motion, the threshold for the discrimination of rightward motion would reduce as was found by this experiment. Motion capture will shade over into induced motion.

The above hypothesis seems to explain the data of this experiment well. However if one considers previous research on the effects of stimulus contrast and motion perception, it appears at first sight that it contradicts previous observations. Most of this previous research (eg Johnston and Wright, 1985; Keck et al, 1976; Nakayama and Silverman, 1985; Derrington and Goddard, 1989) has found little evidence of a relationship between aspects of motion perception and contrast at the higher (0.15,0.5) centre contrasts used in this experiment, finding that any relationship between contrast and motion perception holds only at low (less than 0.05) contrasts. Johnston and Wright (1985) found that lower thresholds of motion for a sinusoidal grating stimuli depended upon the contrast of the stimulus only at low contrasts i.e. contrasts of less than 0.05. Above this the motion thresholds were independent of stimulus contrast. Keck et al (1976) found that the duration of the motion after effect increased with stimulus contrast, for contrasts of up to 0.06. Derrington and Goddard (1988) found that grating direction discrimination performance increases for contrasts up to 0.05 but then reduces for contrasts of greater than this magnitude. Nakayama and Silverman (1985) found that the minimum displacement for the detection of motion (dmin) improved with increasing contrast (ie reduced) up to a maximum contrast of 0.05. These previous findings have been explained by Derrington and Goddard (1988) as indicating saturation of the motion mechanisms. Derrington and Goddard proposed that the motion mechanisms can not increase in their excitation beyond a certain level which is reached at contrasts of 0.05. Thus when presented with a moving stimulus the motion mechanisms sensitive to the stimulus motion direction become increasingly more excited as the stimulus contrast is increased. At a certain contrast level, the point of saturation, there will be no further increase in excitation irrespective of further increases in contrast. This explains the finding that the lower threshold of motion for sinusoidal gratings decreased with increasing contrast only up to a contrast of 0.05 at which point it remained constant (Johnston and Wright, 1985). Following Derrington and Goddard (1988) the prediction concerning the current experiment would be that the discrimination threshold for the centre grating's direction of motion would be invariant with increasing contrast above contrast of 0.05 irrespective of the presence or absence of motion in the stimulus surround. Above this contrast motion mechanisms tuned to the direction of motion of the centre grating would be saturated. In support of Derrington and Goddard was the finding of this experiment that the centre discrimination thresholds, with a stationary surround were equal for centre contrasts of 0.5 and 0.15, with a greater threshold for the centre contrast of 0.025, indicating saturation of the motion mechanisms at some contrast of greater than 0.025 and less than 0.15. However with a moving surround it was found that the threshold depended upon the contrast of the stimulus centre. Thus the motion in the surround not only effects the threshold, but also seems to effect the observed relationship between contrast and threshold velocity. This finding is therefore inconsistent with Derrington and Goddard's position.

It is argued here, that the saturation explanation of Derrington and Goddard, whilst being an adequate explanation for the effects of contrast with single grating stimuli (as used in all the previous experiments described above), takes too simplistic a view of the situation of the current experiment.

Derrington and Goddard take account only of excitation of motion mechanisms by stimulus motion. As has been seen in previous experiments (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Chang and Julesz, 1984; Stromeyer et al, 1984; Allman et al, 1985; Snowden et al, 1992) motion mechanisms are, in addition to excitation from motion in their preferred direction, subject to inhibitory effects from opposed motion signals. Derrington and Goddard (1988) take no account of the effects of inhibition by opposite directions of motion. Hence this is an insufficient explanation of the situation of a more complex moving stimulus as in the current experiment, i.e. when two opposed directions of motion are presented simultaneously. In this case each stimulus motion direction will excite mechanisms tuned to its particular direction and will inhibit mechanisms tuned to the opposite direction (eg Nawrot and Sekuler, 1990). It is possible that for contrasts of greater than 0.05, due to the resultant inhibition by opposite directions of motion in the current displays, motion mechanisms sensitive to one of the directions of motion present would not be maximally excited. If this were so then a motion mechanism subject to inhibition would not be saturated at a contrast of 0.05 as would be the case with an uninhibited mechanism. If as is suggested the strength of the physical stimulus motion signal increases with increasing contrast (up to the point of saturation of the motion mechanism), then it would be possible that a greater contrast would be required in order to saturate a motion mechanism that was subject to inhibition. Thus saturation would occur at a higher contrast than if no inhibition was occurring. Therefore motion thresholds could continue to improve (reduce) relative to the thresholds obtained at the lower contrasts, for contrast increases above 0.05.

In the current experiment when centre and surround move in opposite directions, as there is excitation of motion mechanisms responsive to motion in the stimulus centre and surround then centre-surround interactions between motion mechanisms would be expected to occur. By contrast in a display featuring a single moving grating, only mechanisms sensitive to the direction of motion of that grating will be excited. There will be no interaction between opposed directional mechanisms. Thus when only one moving grating is presented the discrimination threshold will depend solely upon excitation of mechanisms tuned to the gratings direction of motion. If it is interactions between opposed directional mechanisms that allow contrast level to affect the discrimination thresholds, then in experiments which feature only single gratings, it would be expected that no effect of increasing contrast would be observed beyond some saturation contrast as found in previous experiments. In the case of the current experiment, the presence of the opposed stimulus motion will lead to interactions between opposed motion mechanisms. The 'centre' leftward and rightward motion mechanisms will be excited by the two directions of motion present. The leftward motion mechanisms will inhibit rightward and vice versa. Thus even if the contrast of the stimulus was great enough to saturate motion mechanisms if the direction of motion was presented alone, the resultant inhibition due to opposed motion would mean that the mechanisms would no longer be maximally excited. If the motion mechanisms are maximally excited i.e. saturated, then any increase in motion signal due to increases in the contrast will have little or no effect upon the motion threshold. If on the other hand, the mechanism is not maximally excited due to inhibition by opposed motion, then one would expect that an increase in motion signal due to increases in contrast, would further excite the motion mechanism tuned to the stimulus direction and so result in reductions in motion threshold with increasing contrast.

To account for these findings it is proposed that the strength of the stimulus motion signal increases with increasing stimulus contrast. As one increases the contrast the increasing strength of the motion signal will overcome the effects of inhibition by opposed motion signals and saturation of the motion mechanisms will occurring at a higher contrast than 0.05. The increase in the observed discrimination threshold for the moving surround condition, from a contrast of 0.025 to centre contrast of 0.15, can be explained by reference to the work of Stromeyer et al (1984). At contrasts below 0.05, directions of motion seem to be discriminated by mechanisms that are insensitive to opposed directions of motion. Above 0.05, motion discriminations are carried out by mechanisms that are affected by opposed directions of motion. Thus at the higher contrast of 0.15 interactions between motion mechanisms with opposed directional sensitivities would be expected to take place, while no such interactions take place at the lower contrast. As described above these opponent interactions would result in inhibition of motion mechanisms responding to a particular direction of motion and as such would lead to an increase in the motion threshold relative to the conditions where no such interactions took place.

Some recent work has found evidence for a link between motion processing and contrast for higher contrasts as used in the current experiment. For example, Thompson and Stone (1990) found that the perceived speed of a sinusoidal grating depended upon the contrast of the grating. The lower the contrast the lower the perceived speed of the grating as assessed by matching the speed of motion of two gratings of different contrasts presented simultaneously. Smith (1992), found that the coherence range (the range of difference in spatial frequency between two sinusoidal gratings over which the two gratings will cohere i.e. appear to move together as a single plaid pattern) depended upon the absolute contrast of the two gratings i.e. the range increased as the contrast of the two gratings was increased.

These findings have been obtained (as in this experiment) with more complex stimuli than in experiments which have found no contrast effects. Both of these experiments utilised two sinusoidal gratings presented simultaneously, as opposed to a single moving sinusoid. Thus the notion that models of the effects of contrast on motion perception do no hold for complex stimuli receives some support from this recent work.

Using sinusoidal gratings of equal high (0.4) contrast and different spatial frequency Ramachandran and Cavanagh (1987) found evidence for motion capture. This was in contrast to the results of the current experiment. The reasons for this difference in result between Ramachandran and Cavanagh (1987) and the current experiment should be examined. The two gratings used by Ramachandran and Cavanagh were superimposed while in the current experiment the gratings were spatially separated. The effect of this may be that in the current experiment, any potential interactions between oppositely tuned, spatially separated motion mechanisms would be maximised by having different motions in different parts of the visual field, whereas in Ramachandran and Cavanagh's experiment such interactions would not be favoured as both directions of motion used would occupy the same retinal areas and their stimuli would not have differently stimulated 'centre' and 'surround' regions.

The models of Nawrot and Sekuler (1990) and Murakami and Shimojo (1991,1992,1993), emphasise the importance of the size of the test field in the nature of the interactions between motion mechanisms and thus the prevalent percept, but make no statement or predictions as to the effect of stimulus contrast. It is noteworthy that the two models do not preclude the possibility of contrast related effects, they just don't make explicit predictions as to the nature of these effects. In order to account for these findings additions are required to these models. Firstly concerning the lack of evidence for motion capture or induced motion at the lowest contrasts used. This requires a reformulation of the models such that, following from the work of Stromeyer et al (1984), the interactions between directionally selective mechanisms are weak or even non-existent at the lowest contrasts. This would mean that at these contrast levels for a stimulus of the type used in these experiments, with two opposed directions of motion, the motion of the central test grating would be detected independently of the motion of the surround i.e. motion in the surround would have no influence upon the motion direction percept of the centre. Hence at these low contrasts motion capture or induced motion effects would not be found due to the lack of interaction. For higher contrast levels these models need to be modified in order that at the highest centre and surround contrasts, motion capture shades over to induced motion. This is easily possible within the framework of these models as all that is required is that the opponent interactions between motion mechanisms are able to overcome the saturation of motion mechanisms with contrast, thus increasing the contrast at which they saturate, so that increases in contrast give rise to perceptually stronger as well as physically stronger motion signals.

Chapter 11

Experiment 10:

The Effect of Surround Orientation Upon Motion Capture and Induced Motion

11.1 Introduction

The effect of orientation of the surround grating upon motion capture was assessed in this experiment. No previous work has been carried out which has examined the effect of orientation of the surround upon motion capture.

In these experiments three surround orientations were used. These were zero, ten, thirty and ninety degrees to the vertical.

It has been hypothesised (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993) that motion capture results from faciliatory and inhibitory interactions between oppositely tuned motion mechanisms. What is not known is the directional range over which these interactions operate. Utilising the results from this experiment, it will be possible to examine this and to extend the theories accordingly.

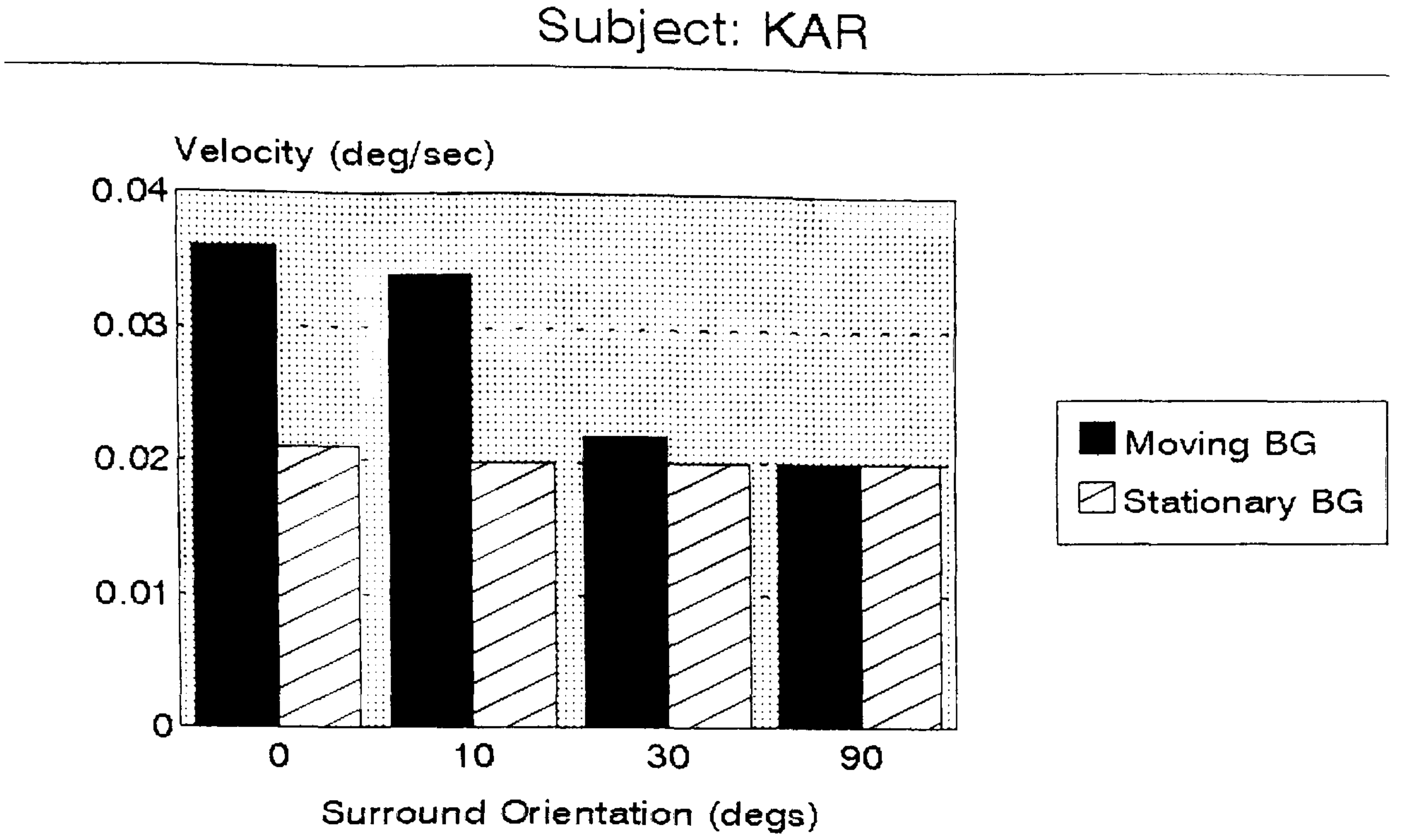
11.2 Method: Experiment 10

Three stimuli were set up (see figure 35b) which consisted of a surround made up of a single sinusoidal grating of orientations 0, 10, 30 and 90 degrees with respect to the vertical axis. The central grating was in all cases of zero degrees orientation with respect to the vertical and was housed within an aperture of 0.34 degrees. The contrasts of the centre and surround gratings were as for experiment 8.

11.3 Results: Experiment 10

Examining first the direction discrimination velocity thresholds (figure 45). It may be seen that for surround orientations of 0 to 30 degrees the velocity threshold for the moving surround was greater than that for stationary surround conditions. This was evidence for the occurrence of motion capture for surround orientations of up to 30 degrees. For the 90 degree surround orientation, the velocity thresholds for the moving and stationary surround conditions were equal. Thus no evidence was obtained for the occurrence of motion capture or induced motion with a surround orientation of 90 degrees. It was also observed that the difference between the moving and stationary surround threshold reduced with increasing surround orientation. This may be taken to suggest that the strength of motion capture reduced with increasing surround orientation.

Examination of the probit gradient plots for this experiment (figure 46) reveals that for all surround orientations, the gradients were equal for moving and stationary surround conditions. This indicates that for all orientations there was no change in the sensitivity for the direction of motion of the centre test grating



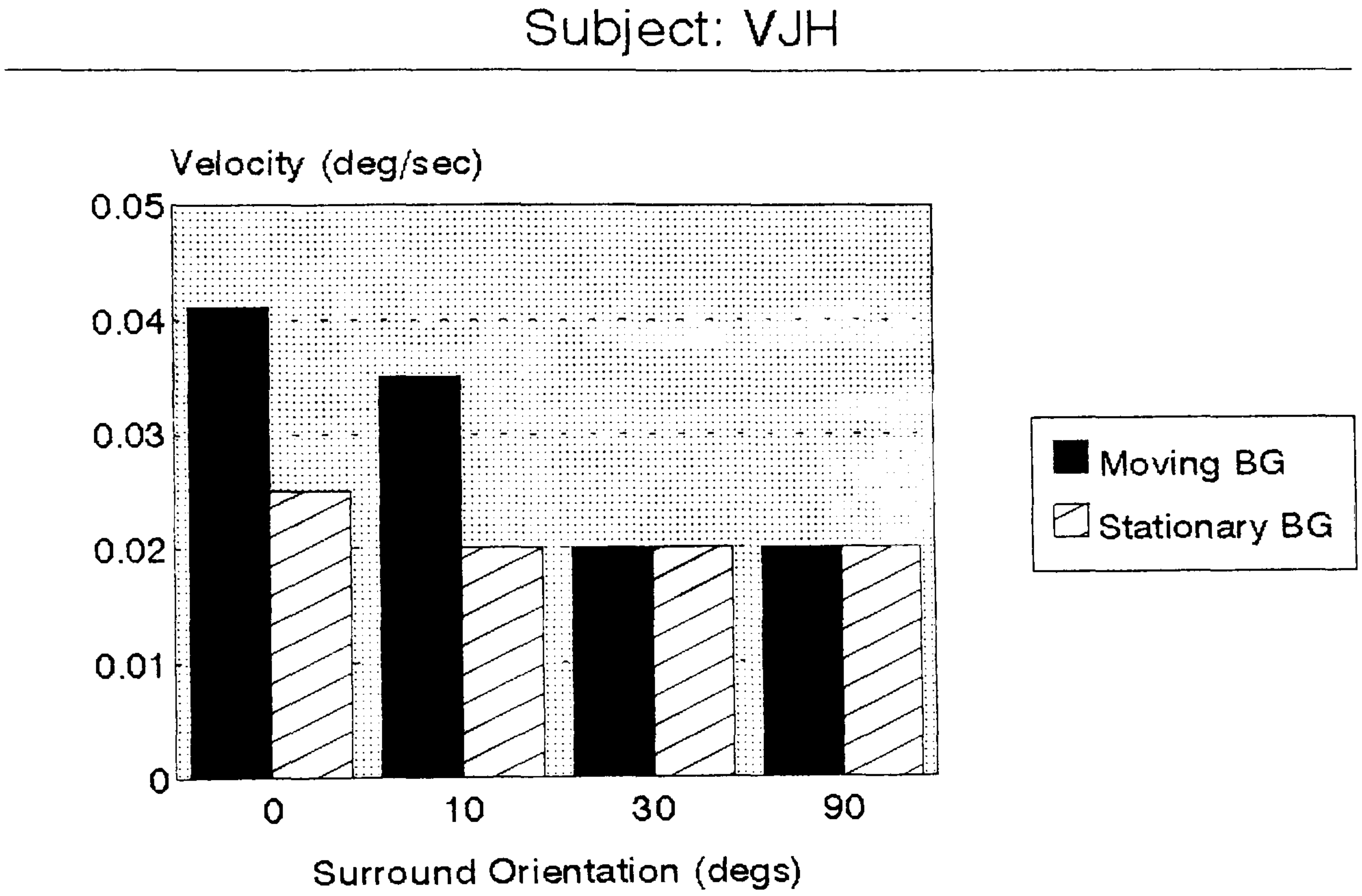


Figure 45: Effect of surround orientation on motion capture and induced motion. Lower thresholds of motion for four surround orientation (centre orientation was 0 deg)

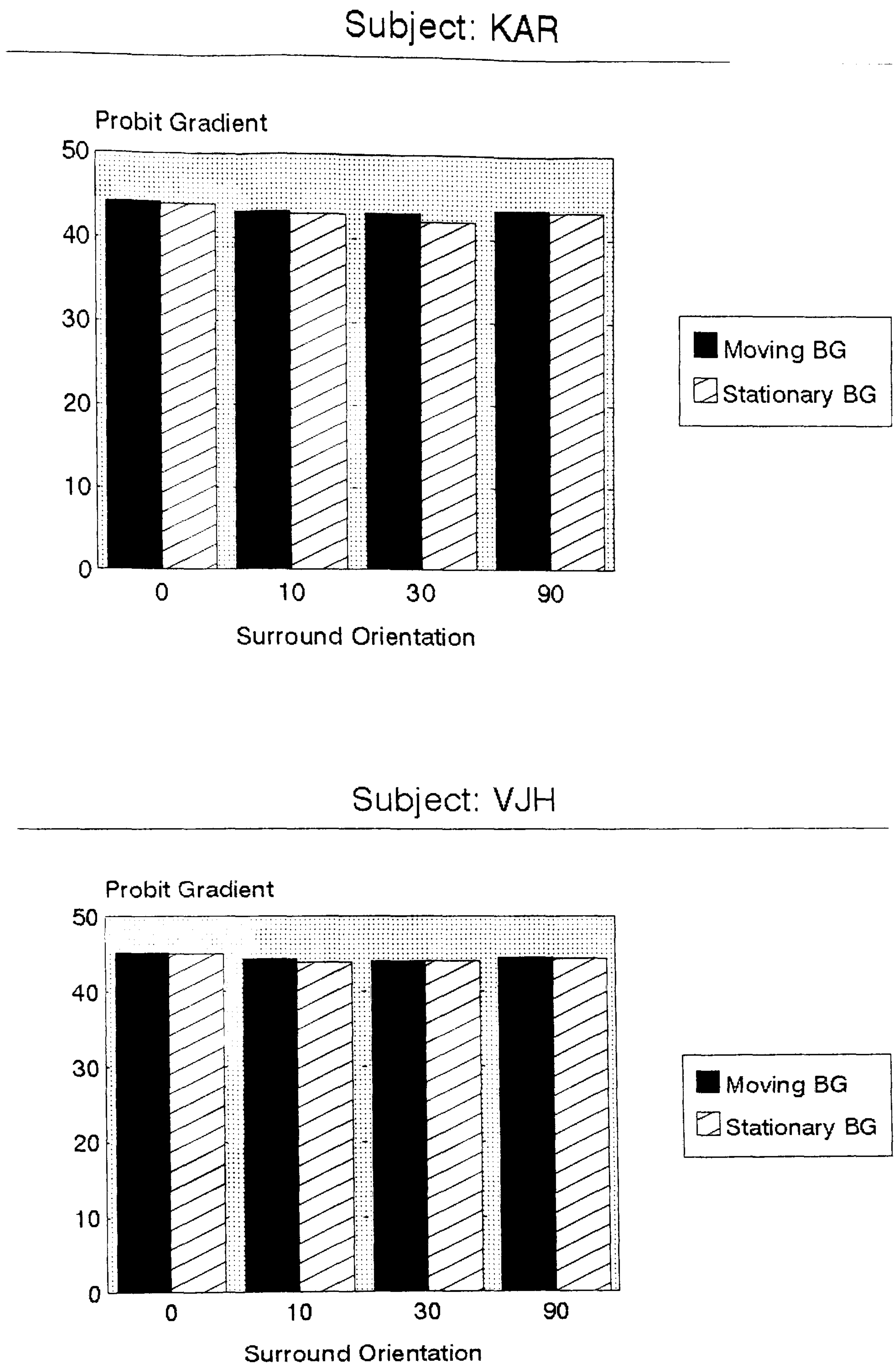
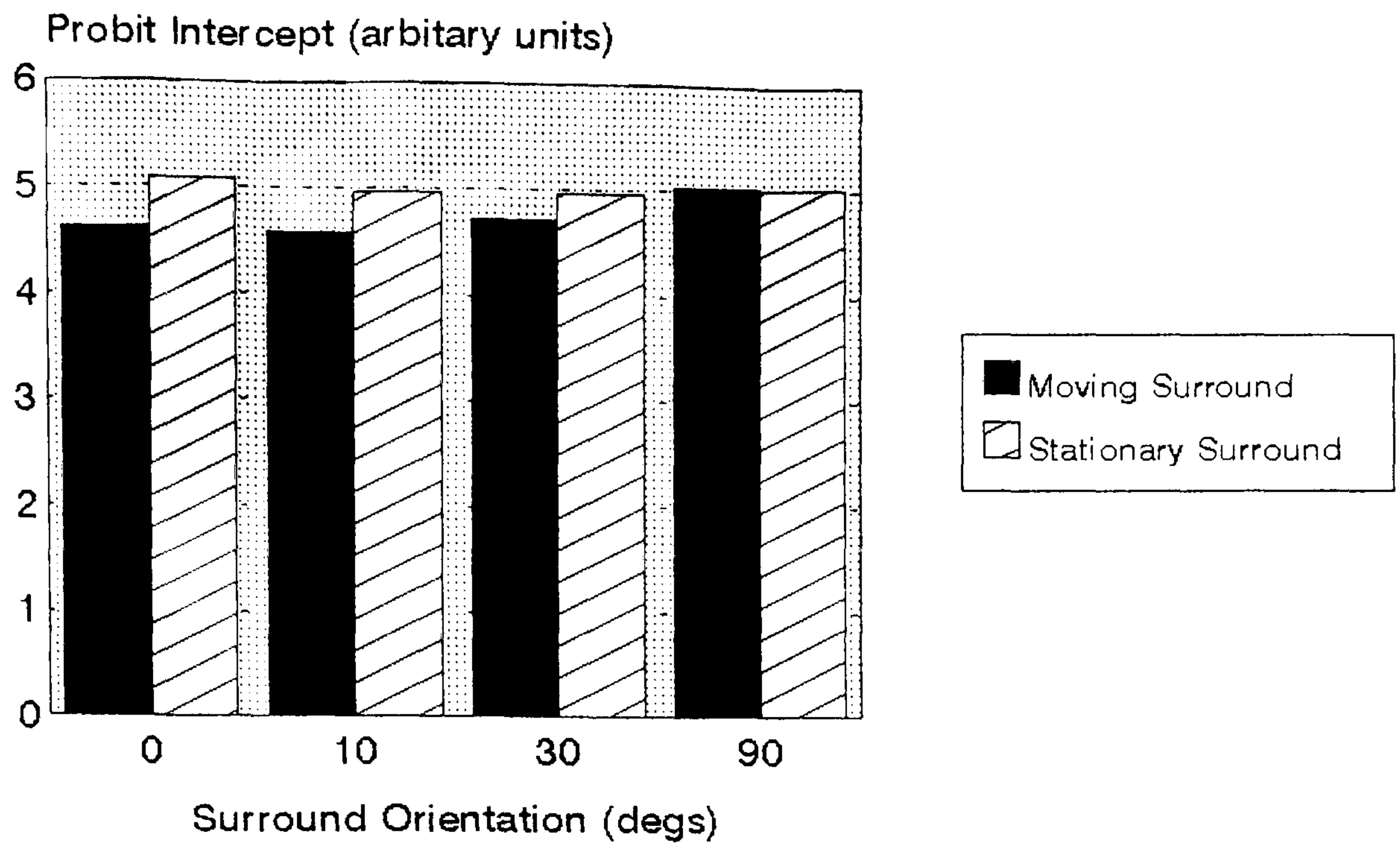


Figure 46: Gradients of probit plots produced for the four surround orientations of experiment 10.

Subject: KAR



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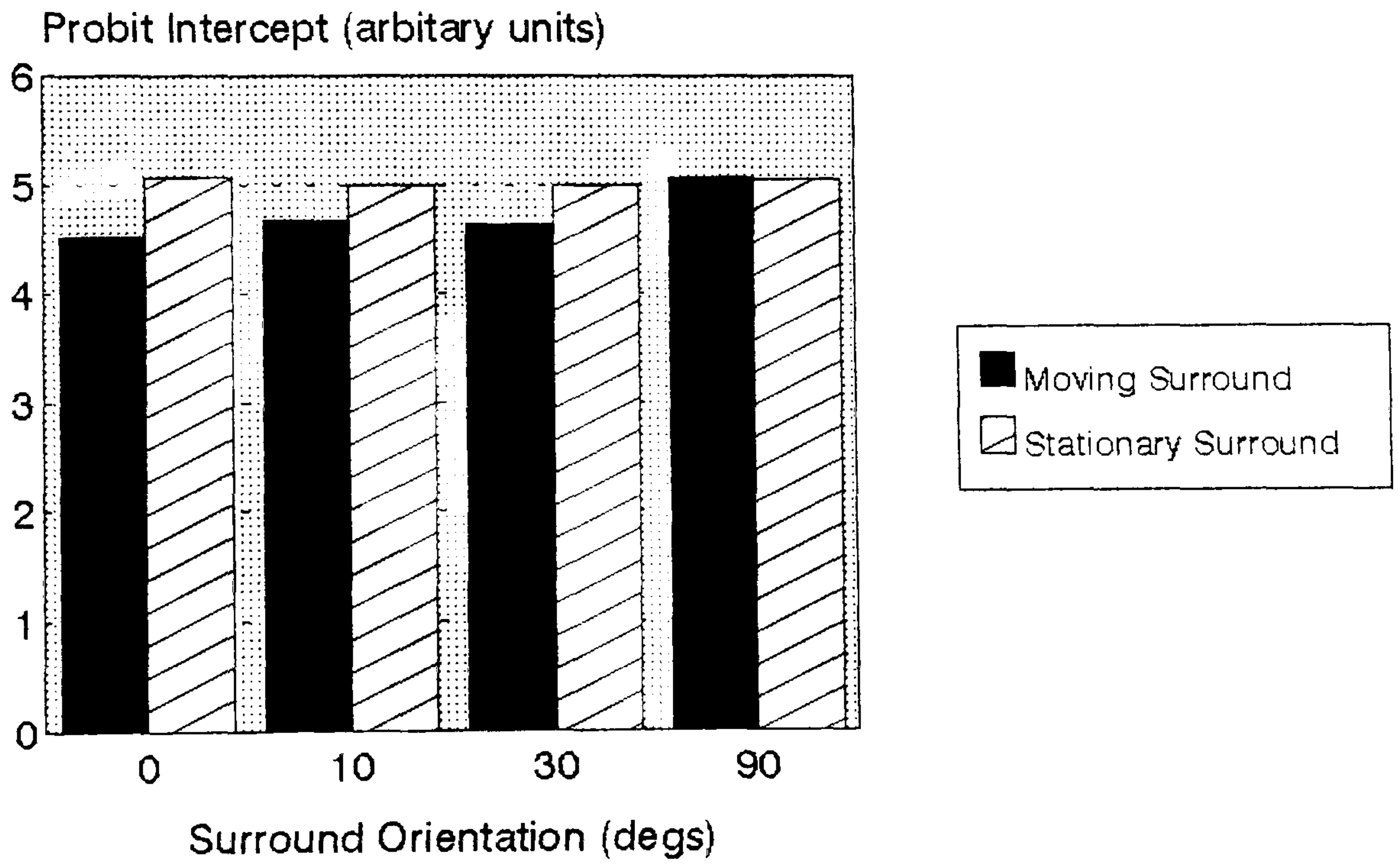


Figure 47: Intercepts of probit plots produced for the four surround orientations of experiment 10.

between moving and stationary surrounds. It may also be seen that the gradients are equal across all orientations. This indicates equal sensitivities for the direction of motion of the centre test grating regardless of the surround orientation.

Examining the probit intercept plots (figure 47), it can be seen that for surround orientations of 0 to 30 degrees, the intercepts for the moving surround conditions were less than for the stationary surround condition. This suggests a shift in bias point occurred between moving and stationary surround conditions for orientations of 0 to 30 degrees. The intercepts were equal for the 90 degree orientation condition for stationary and moving surrounds. This indicates no change in the bias at this orientation. The magnitude of the difference between intercepts reduced with increasing orientation. This could indicate a reduction in the strength of the bias shift with increasing surround orientation.

Taking these results together, evidence for the occurrence of motion capture was obtained with surround orientations of up to 30 degrees. Again the motion capture appears to be associated with a shift in the bias point between opposed directions of motion. There was no evidence for any change in sensitivity for the direction of motion of the centre test grating with increasing surround orientation, or between moving and stationary surround conditions. The strength of motion capture seemed to reduce with increasing surround orientation.

11.4 Discussion: Experiment 10

The main findings of this experiment were that motion capture was only obtained for surround orientations that were within thirty degrees of the orientation of the test grating. It was notable that the strength of motion capture reduced with increasing orientation. For orientations of greater than 30 degrees, no evidence was obtained for either motion capture or induced motion. The result with the surround grating oriented at ninety degrees to the centre grating is similar to that of Ramachandran and Cavanagh (1987) who found, using a stimulus of random dots moving at 90 degrees to a sinusoidal grating, that the strength of motion capture was very much reduced compared to the condition when the dots moved in a similar direction to the grating.

From the results it appears that the effective surround orientation that gives rise to motion capture is when the surround is within thirty degrees of the test field. It is worth considering previous work concerning orientation and motion processing.

Most models of motion perception (eg Smith, 1992; Adelson and Movshon, 1982) assume that in the initial stages, when presented with a moving stimulus the visual system analyses the signal by means of a series of bandpass spatial filters. Each of these spatial channels contains subunits which are tuned to a number of different orientations. Each of these orientation subunits detects motion in a direction which is orthogonal to its preferred orientation i.e. the subunits are directionally selective. Given this, the results of this experiment can be reinterpreted in terms of the relative directions of motion of centre and surround as opposed to their respective orientations.

If these directions of stimulus surround motion that favour motion capture are physical limits upon the motion capture effect, it is interesting to examine how these limits might operate. Consider the experimental display. As described previously, the size of the central aperture in this experiment is such that motion capture effects are favoured. Following from the models of motion capture, and assuming some kind of centre-surround opponency mechanism. Due to the size of the central aperture of the stimulus the 'centre' of the mechanism underlying the capture effect will receive stimulation from motion in both the display centre and surround. At the centre similarly tuned motion mechanisms excite each other when they are stimulated by motion signals. Our results indicate how similar two directions of motion have to be in order to give rise to excitation between motion mechanisms i.e. less than 30 degrees directional difference. Oppositely tuned motion mechanisms inhibit each other at the centre. Again our results have shown how different two directions of motion have to be in order to give rise to inhibitory effects i.e. 150 degrees directional difference. Motion mechanisms in the surround inhibit those in the centre if they have similar directional preferences, while mechanisms from the surround excite oppositely tuned mechanisms in the centre. Again our results indicate that for excitation, mechanisms in the surround have to differ from those in the centre in their directional preferences by 150, while for inhibition of the centre mechanisms by the surround the directional selectivities have to differ by less than 30 degrees.

It is interesting, to examine previous research concerning the directional preferences of motion sensitive channels. The results of such work give estimates as to what constitutes perceptually similar and dissimilar directions of motion for any given retinal location (Snowden, 1989). Ball, Sekuler and Machamer (1983) examined the ability of observers to detect and discriminate the direction of motion of random dot patterns presented in one of two time intervals. They found that the observers frequently confused the direction of motion when the directions were within thirty degrees of each other and could only correctly identify the direction of motion with total accuracy when two directions of motion differed by at least 120 degrees. These results indicate that observers are only able to perfectly discriminate two different directions of motion if those directions differ by greater than 120 degrees. If two directions of motion are detected by two different motion mechanisms then it is expected that these directions of motion can be discriminated from each other at the point of detection (Watson and Robson, 1981). If two directions can not be discriminated then it is the case that they are detected by the same motion mechanism. From the work of Ball et al (1983) it is possible to suggest that in perceptual terms motion signals within thirty degrees of each other may be considered to be motion in similar directions while motion signals differing by greater than 120 degrees may be considered to be motion in different directions. Raymond (1993) carried out similar experiments using random dot stimuli to measure the bandwidths of motion mechanisms. Shea measured coherence thresholds for test bands of random dots both with and without prior adaptation to motion. She found that the bandwidth of movement detectors was between +/-35 and +-40 degrees.

The results of this research give general support to the hypothesised directional ranges for the motion capture effect, in that they predict ranges for similar and dissimilar directions of motion that are of the order of those found in the current experiment. Thus motion mechanisms will interact in an excitatory way if their directional preferences are within 30 degrees of each other and in an inhibitory way if their preferences differ by +/- 150 degrees.

Snowden (1989) carried out experiments on motion direction discrimination using random dot displays. He found that if displays were generated which contained superimposed background motion that was in an orthogonal direction to the horizontal motion of the test pattern, the threshold for the discrimination, Dmax, declines relative to conditions where there was no orthogonally moving background. Snowden explained these results by postulating that the orthogonal motion had an inhibitory effect upon motion mechanisms tuned to the horizontal direction of motion. In his experiment, Snowden plotted psychometric functions relating the displacement of the dots in the pattern to the percentage errors in directional discrimination (Dmax was taken to be the displacement at which the subject performed with 25% errors). For all the subjects used in Snowden's experiment, the reduction in Dmax was associated with a shift in the psychometric function to toward lower displacements. It is interesting to compare the results of Snowden's experiment to those of the 90 degree oriented background condition of our experiment. The 90 degree background condition of this experiment is analogous to the orthogonal background condition of Snowden i.e. the surround in our experiment moved in a direction that was orthogonal to that of the centre. If the orthogonal motion was having a similar effect in the current experiment to that in Snowden's experiment, it would be expected that the psychometric function for the discrimination of the centre direction would be shifted in the direction of increased discrimination threshold for the orthogonal motion condition as opposed to the stationary surround condition. This would correspond to the reduction in Dmax found by Snowden, because as Dmax is thought to be a measure of the spatial range of interactions that underlie directional sensitivity (Braddick, 1974) and so the better the discrimination performance the higher observed value of

Dmax.

Comparing the current results for the moving orthogonal surround and the stationary (90 degree oriented) surround, it can be seen that no such shift in the psychometric function can be seen. The threshold for the discrimination is equal for both conditions as is the measured bias and sensitivity of the psychometric function. Thus the findings of the current experiment are not consistent with those of Snowden (1989).

Why should it be that these two experiments produce different results ? One possibility is that similar results were not obtained due to the differences in the stimuli used. In Snowden's experiment, the two directions of motion (horizontal and vertical) were superimposed upon each other. In our experiment the two different directions (eg rightward and vertical) were spatially separated. In the current experiment, if motion at 90 degrees to the preferred direction inhibits motion mechanisms, then it would be expected that the vertical motion would inhibit the motion mechanisms that are selective for rightward and leftward motion. If it is assumed that the excitatory and inhibitory interactions between motion mechanisms across space are determined by some kind of centre surround organisation (eg Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993) and that the centre is small relative to the surround (Chang and Julesz, 1984; Nawrot and Sekuler, 1990), it may be seen that in our display, motion that is horizontal e.g. to the right, and orthogonal motion are present simultaneously within the centre of the hypothesised centre surround motion mechanisms. This will result in the non-specific inhibition of the right and leftward sensitive mechanisms at the mechanism centre. Rightward horizontal motion at the centre will excite the right sensitive mechanism and inhibit the left sensitive mechanism. Comparing this to the control condition display which consists of a stationary surround, it may be seen that in this condition there is no inhibition due to orthogonal motion and so at the centre of the hypothesised centre surround mechanism, the right selective mechanisms for example will be excited by right motion and the left selective mechanisms will be inhibited. Thus as Snowden (1989) predicts, at the centre of a centre surround system in our example, there is greater activity in the right sensitive mechanisms than in the left in both the moving and stationary display surround conditions, however the activity of the right mechanism will be reduced in the moving display surround condition relative to the stationary surround condition. In terms of the 'centre' region the threshold for motion discrimination should be reduced relative to that for the stationary condition. This also predicts the shift in the psychometric function reported by Snowden. As we have seen however, motion in the surround of a centre-surround mechanism is also important in determining what occurs i.e. the levels of activity of centre mechanisms. Thus it is not enough just to consider the effects of orthogonal motion at the centre, the effects of this motion in the surround is also important. Previous psychophysical (Muarakami and Shimojo, 1991,1992,1993; Nawrot and Sekuler, 1990) and neurophysiological (Allman et al, 1985; Born and Tootell, 1992,1993) research has shown that motion in the surround has an excitatory effect upon motion mechanism with opposed directional sensitivity and an inhibitory effect upon mechanisms of the same directional sensitivity at the centre. It is here suggested that it could be that orthogonal motion in the surround has the opposite effect compared to when it is at the centre i.e. it has a non-specific excitatory effect upon centre mechanisms rather than an inhibitory effect. This suggestion has some support from neurophysiological research, Allman et al (1985) examined the response properties of cells in area Mt of the owl monkey. They found that motion in a cell's surround i.e. motion not confined to the classical receptive field of the cell (the centre in our terminology), had strong modifying effects upon the responses of the cell. The responses of one set of the cells investigated by Allman et al (type II cells in their description) was found to be strongly facilitated (excited) if motion in the surround was in a direction that was orthogonal to the preferred direction of the cells. If this is the case, and if the non-specific excitation of centre mechanisms by orthogonal motion in the surround is strong enough to overcome the inhibitory effects of orthogonal motion at the centre, it is possible to suggest that in the moving display surround condition of this experiment, the levels of activation of rightward sensitive mechanisms would be similar to those of the stationary surround condition. This would predict that there would be no change in the threshold for the motion discrimination with a moving surround compared to a stationary surround, thus no shift in the psychometric function would be found. This is the set of results obtained in this experiment. Snowden obtained different results because his display was not equipped to examine the effects of display surround motion. Thus the apparent discrepancy between the current results and those of Snowden, can be explained.

Taking our findings and those of other researchers together. In our experimental displays, leftward motion at the centre will specifically excite leftward sensitive centre mechanisms and will specifically inhibit rightward sensitive mechanisms. A rightward motion at the centre will do the exact opposite. A vertical (orthogonally directed motion) will have an inhibitory effect upon both the leftward and rightward sensitive centre mechanisms. The range of direction differences that will give rise to the excitation is +/-30 degrees and the inhibition is +/- 150 degrees. For motions in the mechanism surround, orthogonal motion will excite both left and right centre mechanisms, right motion excites leftward centre mechanisms and inhibits right centre mechanisms and left surround motion will excite centre right and inhibit centre left mechanisms.

It has been seen from previous experiments that motion capture and induced motion are related along a continuum with motion capture at one end and induced motion at the other (Murakami and Shimojo, 1991,1992,1993; Nawrot and Sekuler, 1990). Changes in the physical nature of the stimulus, are able it seems to switch the percept from motion capture to induced motion. This experiment found no evidence for such a perceptual change with surround orientation. This could mean that at least in the case of surround orientation/direction, there is no corresponding switch between the two percepts. This is an unlikely suggestion as it predicts that there is no interaction between motion in the surround and motion mechanisms at the centre for these directions of motion. As we have seen previously it is likely that even at display surround orientations of 90 degrees that there is interactions between motion mechanisms from the surround and the centre. Another and more plausible explanation is that the particular stimulus used in this experiment makes it very difficult if not impossible for induced motion to be evidenced. From experiment 8, it was found that a stimulus with the central aperture size as used in this experiment produced strong evidence for motion capture effects. Thus it could be that in this experiment, it is the size of the central aperture that ultimately determines whether evidence for motion capture or induced motion is observed. As stated above this aperture size favours motion capture effects. As one increases the orientation of the surround, the strength of the motion capture effect reduces as would be expected, but it never shades over to induced motion due to the fact that the size of the central aperture means that any excitation from the surround is never able to overcome the inhibitory effects of the display surround that are spatially located at the centre of a centre surround mechanism. This leads to a prediction that if one was to increase the central aperture size then one would, with the 90 degree orientation display obtain evidence for induced motion. This is because with a larger central aperture the hypothesised non-specific excitatory effects of the surround motion upon mechanisms at the centre would be enough to overcome the inhibitory signals at the centre of a centre surround mechanism. These findings suggest that current models of motion capture need to be reformulated in order to take account of this directional effect.

Current models of motion capture and induced motion require interactions to take place between oppositely tuned and similarly tuned directional mechanisms. However these models are silent as to the directional tolerances of these interactions i.e. how different or similar do the direction of motion have to be before they will interact in inhibitory or excitatory ways. This experiment suggests that if motion capture is explained by centre surround interactions across space, then at the centre, excitatory interactions will take place between mechanisms with directional sensitivities which are within 30 degrees of each other, inhibitory interactions will occur between mechanisms that are sensitive to directions differing by 150-210 degrees. From the surround the opposite is true. Motion orthogonal to the preferred direction of motion mechanisms, will result have inhibitory effects upon these motion mechanisms if the orthogonal motion is within the centre of centre surround mechanisms and excitatory interactions if the orthogonal motion falls in the surround.

Chapter 12

Experiment 11:

The Effects of Plaid Stimuli in The Surround Upon Motion Capture and Induced Motion

12.1 Introduction

It was the intention of this experiment to extend the findings of capture experiments to include stimuli in which a plaid was in the surround and a single test grating was at the display centre. This type of set up is similar to previous work with grating capture (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993) which has featured spatially distinct regions of different motion. Current theories of motion perception (Adelson and Movshon, 1982; Fennema and Thompson, 1979; Movshon, Adelson, Gizzi and Newsome, 1986) involve a two stage process. The first stage involves local decomposition of the image into one dimensional spatial components of various orientations and in directions of motion perpendicular to the components orientation. The second stage involves the recombination of all the local motion signals found at a given spatial location.

The aim of this is to find a single direction and speed which unambiguously defines the motion at a particular location in the visual image with which all the component motions are consistent i.e. intersection of velocity constraints. This is done for each spatial range (spatial frequency band). The second stage essentially processes two dimensional pattern motion. Smith (1992) has recently modified the two stage models, by introducing a stage termed 1b which occurs between stage 1a (the local component stage) and stage 2. Stage 1b involves pooling across spatial frequencies of stage 1a outputs having a common direction. This gives rise to a spatially broadband signal, encoded in terms of component directions, which is then subjected to stage two processing. In the case of a plaid stimulus, it may be seen that the stimulus is first analysed into its constituent components at stage one, here motion mechanisms that are sensitive to the spatial frequency and direction of motion of the components of the plaid are excited, the resulting neural signals are then subjected to stage two processes which give rise to the percept of a moving complex pattern (a plaid) with direction defined by the motion of the components. A similar process occurs for a single sinusoidal grating, however as there is only one component the stage two output is defined only by the direction of motion of the single component.

If it is accepted that motion capture is a result of interactions between different motion mechanisms across space (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993), then this experiment could determine the level (in terms of these two stage models) of these interactions in the visual system.

In this experiment three plaid stimuli were set up and placed in the display surround. As interactions between motion mechanisms are between mechanisms that are sensitive to the same direction of motion or to opposite directions of motion the plaids were set up so that either the plaid or one of the plaid components moved in the same or opposite direction of motion as the test grating. In the stimulus in which plaid motion was the key variable, the plaid was composed of gratings of orientations outside the orientation range found in experiment 10 to give rise to motion capture. In the other type of plaid stimulus where the component motion was the variable of interest the direction of the plaid was set so as to be outside the directional range found in experiment 10 to give rise to motion capture and also the orientation of the second component was set so as to be outside the orientation range for motion capture found in experiment 10.

If evidence for motion capture were to be found when the plaid direction was equal or opposite to the direction of the test grating then it would be the case that the interactions between motion mechanisms that determine motion capture would be occurring after stage two processes had been completed. This is because these stage two processes have to be completed in order to produce the plaid direction signal. If on the other hand motion capture were evidenced for the condition where component motion was in the same or opposite direction to that of the plaid then evidence would be found for these interactions occurring prior to stage two processes i.e. no need for the plaid direction to be analysed for the occurrence of motion capture.

12.2 Method: Experiment 11

In this experiment the effect a plaid stimulus was assessed. Plaids were generated and filled the surround. The plaids were made from two identical oriented sinusoidal gratings of equal spatial frequency (2.0 c/deg). All directions of motion reported were measured in a clockwise direction from vertical motion (zero degrees direction). In all conditions the orientation of the single grating filling the central aperture of the display was 0 degrees to the vertical, with direction of motion to the right (90 degrees) or to the left (270 degrees). The general stimulus may be seen with reference to figure 35c.

This experiment featured three conditions. The aim in the first condition of this experiment was to generate a plaid in which neither of the components moved with the same direction of motion as the centre grating, but in which the plaid direction of motion was either the same or opposite to that of the centre grating (along the same axis of motion). This was done in order to examine the possibility that the direction of motion of the centre gratings could be captured by the plaid direction of motion. The orientation of the gratings making up the plaid in this first condition were 45 degrees and 135 degrees to the vertical. In the second and third condition, the intention was to see if capture would be produced with a plaid in which the plaid direction of motion was not along the same axis of motion as the centre grating, but in which one of the plaid components was of the same orientation as the centre grating and thus moved along the same axis as the centre grating (either leftward or rightward). Two plaid stimuli were set up, in one the orientation of the two gratings was 90 and 0 degrees to the vertical. For the other plaid the grating orientations were 0 and 135 degrees.

The central aperture containing the single test grating subtended a visual angle of 0.34 degrees in this experiment.

12.3 Results: Experiment 11

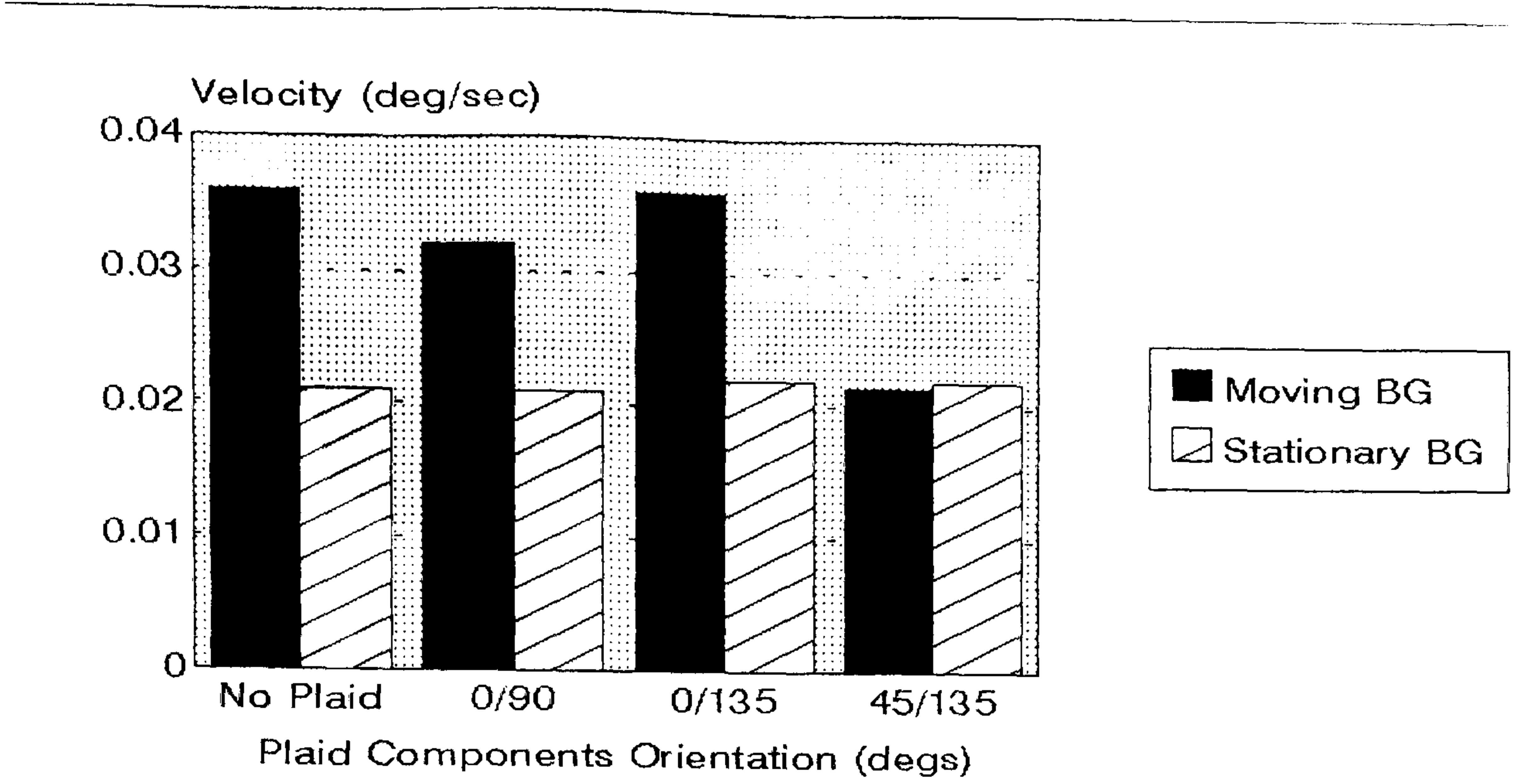
This experiment examined the effects of moving plaid patterns in the surround upon motion capture and induced motion.

Examining firstly the direction discrimination thresholds for this experiment (figure 48). For the no plaid, 0/90 degree plaid and the 0/135 degree plaid the velocity thresholds were greater for the moving than for the stationary surround condition. This is evidence for the occurrence of motion capture under these conditions. For the 45/135 degree plaid, the velocity thresholds for the moving and stationary surround were equal. This indicates no evidence for motion capture and induced motion for the 45/135 degree plaid.

Examining the probit gradient plots (figure 49), it may be seen that for all the conditions of this experiment the gradients were equal for the moving and stationary conditions, and were equal for all the conditions. This suggests that there was no change in the sensitivity for the direction of motion of the centre test grating with a moving or stationary surround, or with changes to the type of plaid in the surround.

Examining the probit intercept plots (figure 50), it may be seen that for the no plaid, 0/90 degree plaid and the 0/135 degree plaid the intercept for the moving surround was less than that for the stationary surround condition. This suggests a shift in the bias point between the moving and stationary surround conditions. For the 45/135 degree plaid condition the intercepts were equal for

Subject: KAR



Subject: VJH

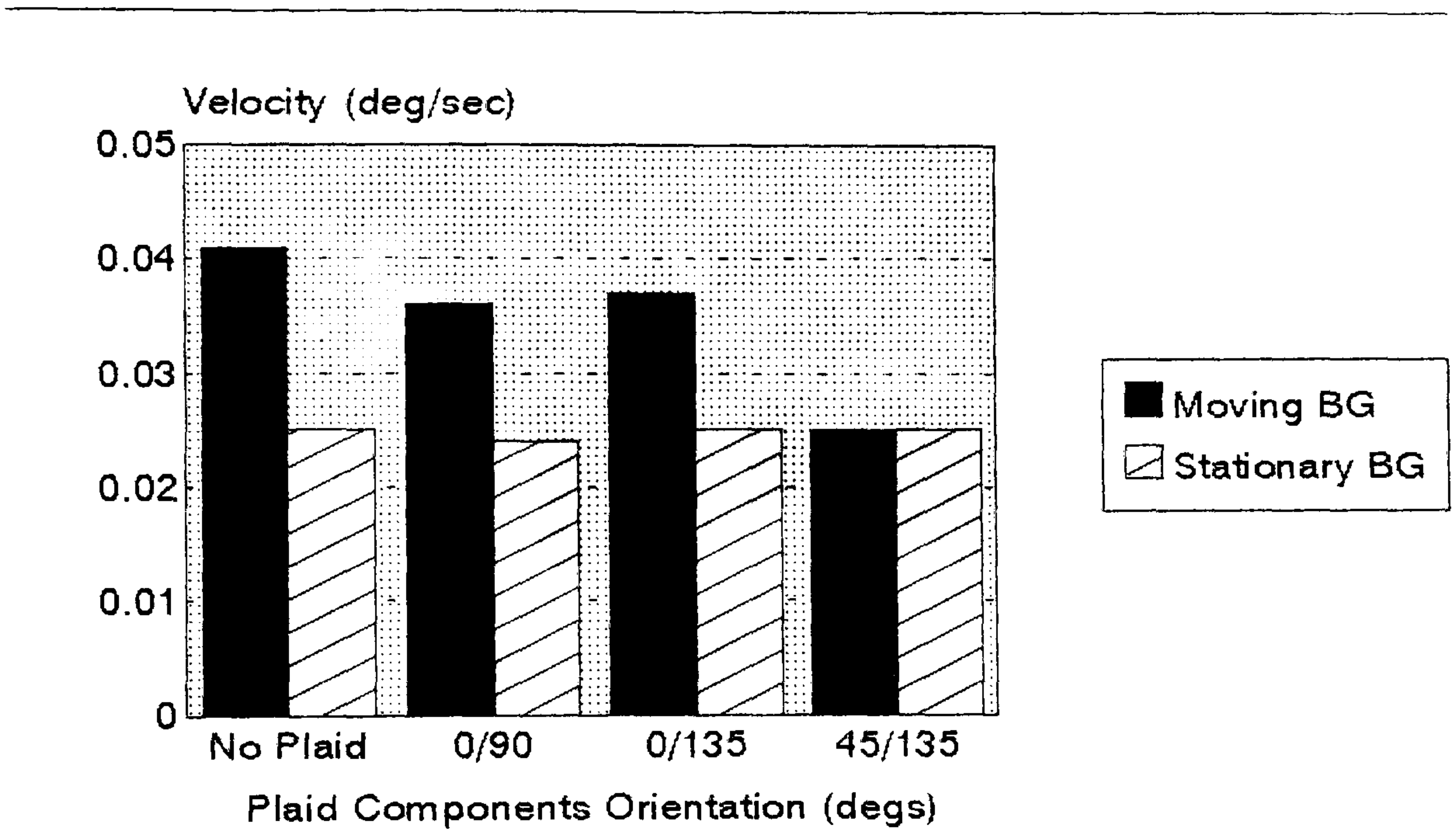


Figure 48: Effect of plaid stimuli in the surround upon motion capture and induced motion. Lower thresholds of motion for surround plaids.(Note 'NO PLAID' data is that obtained for the 0.34 deg aperture in experiment 1).

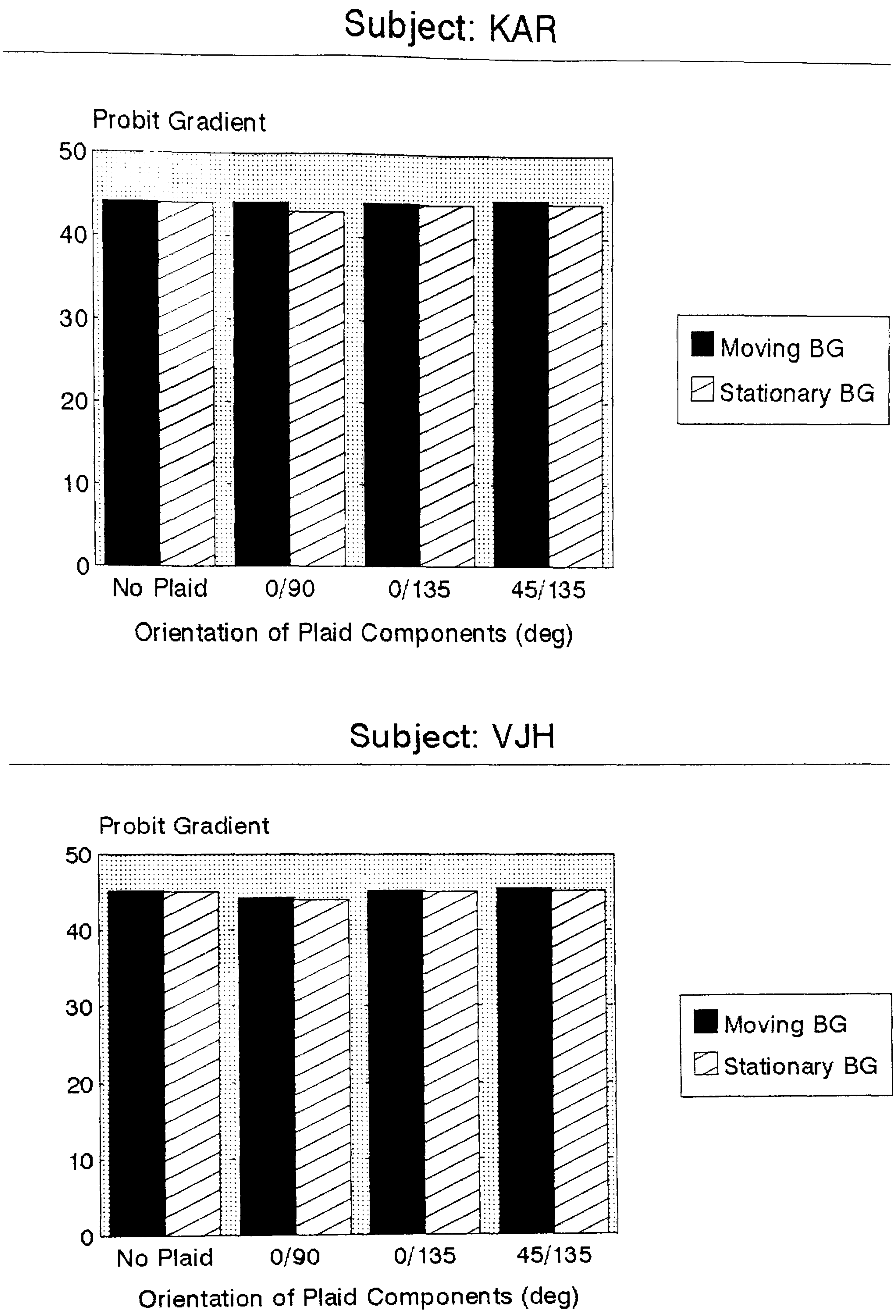


Figure 49: Gradient probit plots produced for the plaids of experiment 11.

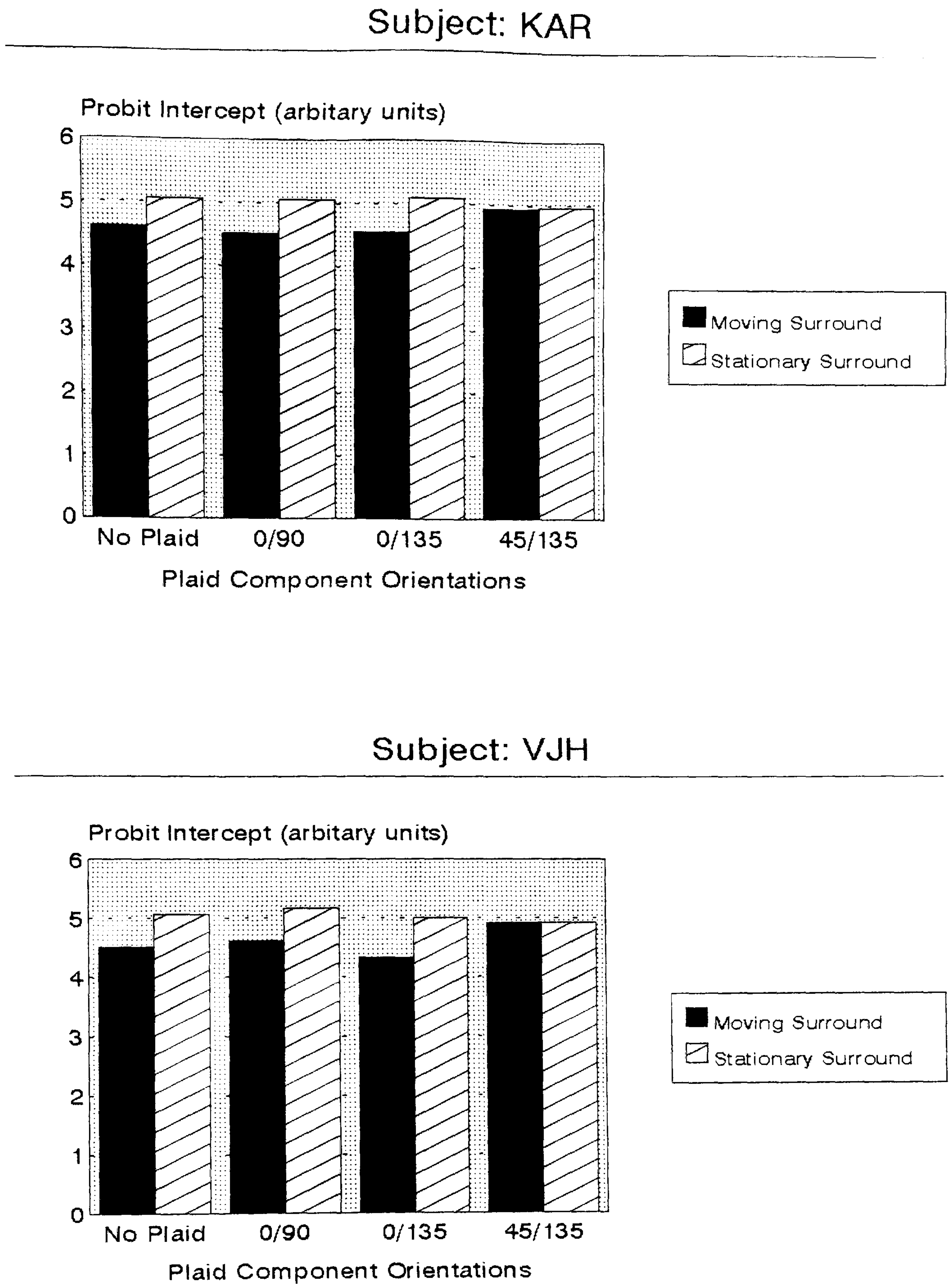


Figure 50: Intercepts of probit plots produced for the plaid surrounds of experiment 11.

the moving and stationary surround conditions. This indicates no change in bias.

Taking these results together, evidence for motion capture was obtained with no plaid, a 0/90 degree plaid and a 0/135 degree plaid. No evidence for motion capture was obtained with a 45/135 degree plaid. As the orientation of the centre was 0 degrees then it may be seen that motion capture only occurred when one of the plaid components was of the same orientation as the centre grating. Motion capture was again associated with a shift in the bias point between opposed directions of motion. There was no evidence of any change in the sensitivity to the direction of motion of the centre grating.

12.4 Discussion: Experiment 11

Evidence for motion capture was obtained only when one of the plaid components was of the same orientation (90 degrees) as the centre grating i.e. one of the components moved in the same or opposite direction as the centre grating. When the display surround contained a plaid whose direction of motion was in the same or opposite direction to that of the centre grating, but whose directions of component motion were outside the directional ranges found in experiment 10, then no evidence for motion capture or induced motion was obtained.

These results suggest the direction of motion of the plaid is not important in determining the occurrence of motion capture, what is important is the direction of motion of the plaid's components.

These findings have implications for the way in which different motion mechanisms interact with each other and the level of processing at which these interactions take place. They suggest that the interactions which give rise to motion capture effects occur at a level in two stage models (see figure 15) of motion perception (Adelson and Movshon, 1982) prior to stage two processing.

As motion capture was found in this experiment and in previous experiments (Ramachandran and Cavanagh, 1987; experiments 8,9 and 10 this study) to occur between components of different spatial frequencies then in terms of Smith's model (Smith, 1992; see figure 16) these interactions would be expected to be occurring at or after stage 1b i.e. the stage of pooling of directional signals across spatial frequencies. This suggestion is also consistent with the model proposed to account for shear and compressive motion processing in section 1 of this study (see figure 32) i.e. opponency between stage 1a signals prior to stage 2 processing.

It is argued that if there exists spatially determined centre-surround interactions between motion mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993) then these interactions occur between mechanisms tuned to the directions of motion of simple components and not to directions of motion of complex stimuli.

A related experiment has been carried out by Yo and Wilson (1992) which seemed to indicate that a plaid can capture a single sinusoidal grating, contrary to the results of our experiment. Yo and Wilson (1992) reported a phenomena that they called coherence capture. In a series of experiments they found that a plaid formed from two low spatial frequency sinusoidal gratings, could change the perceived direction of motion of the higher spatial frequency. The perceived direction of motion of the high spatial frequency was in the direction of the low spatial frequency plaid. It will be argued however that contrary to the claims of

Yo and Wilson, coherence capture is not another form of the motion capture phenomena similar to the phenomena studied in this series of experiments.

Examining the experiment of Yo and Wilson (1992) it may be seen that their experiment differs from our experiment in both the task asked of the subject and the stimuli used. In the Yo and Wilson experiment the subjects were asked to report when the stimulus appeared to move coherently i.e. when all three gratings appeared to move in the same way (plaid formation). In our experiment, the subjects were asked to report the direction of motion of the centre grating. Thus in Yo and Wilson's experiment motion capture resulted when the subjects perceived the gratings to be moving coherently as a plaid, while in our experiment motion capture occurred when the threshold for detecting a particular direction of motion was seen to be altered i.e. increased. In addition in Yo and Wilson's experiment the gratings making up the stimuli were all superimposed onto each other, where as in our experiment the plaid and the high spatial frequency grating were spatially separated. It is argued that the coherence capture phenomena is predictable from previous research on plaid formation (Smith, 1992) and does not in fact result from a plaid altering the perceived direction of a higher spatial frequency grating. Smith (1992) showed that sinusoidal gratings of different spatial frequencies could cohere to form a plaid. It is also interesting to note that in common with Yo and Wilson, Smith found that coherence likelihood increased as the contrast of the stimuli was increased. If high and low spatial frequencies can cohere to form a plaid, then it would be expected that the different spatial frequencies used in the experiment of Yo and Wilson could also cohere to form a plaid. This means that it is unlikely that the low spatial frequency plaid motion has captured the high spatial frequency grating motion, rather the coherence percept is a result of the tendency for high and low spatial frequencies to cohere to form plaids. Given this it may be seen that the coherence capture effect does not reflect the capture of a higher spatial frequency by a plaid and so the results of Yo and Wilson (1992) as they can be explained without referring to motion capture, do not contradict those of the current experiment.

These results show that with regard to two stage models of motion perception (Adelson and Movshon, 1982), the interactions between motion mechanisms thought to underlie motion capture phenomena (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993) occur at a level of processing prior to stage two. They also demonstrate that stage two motion signals (plaid direction) do not interact with motion signals from stage one at least in terms of motion capture.

This experiment allows models of motion capture to be mapped onto two stage models of motion perception. The results suggest that any model of motion capture must disallow the interaction between stage two pattern motion mechanisms and stage one component directional mechanisms.

Chapter 13

This chapter will consider the psychometric functions obtained in experiments 8 to 11 and their implications for models of motion capture and induced motion.

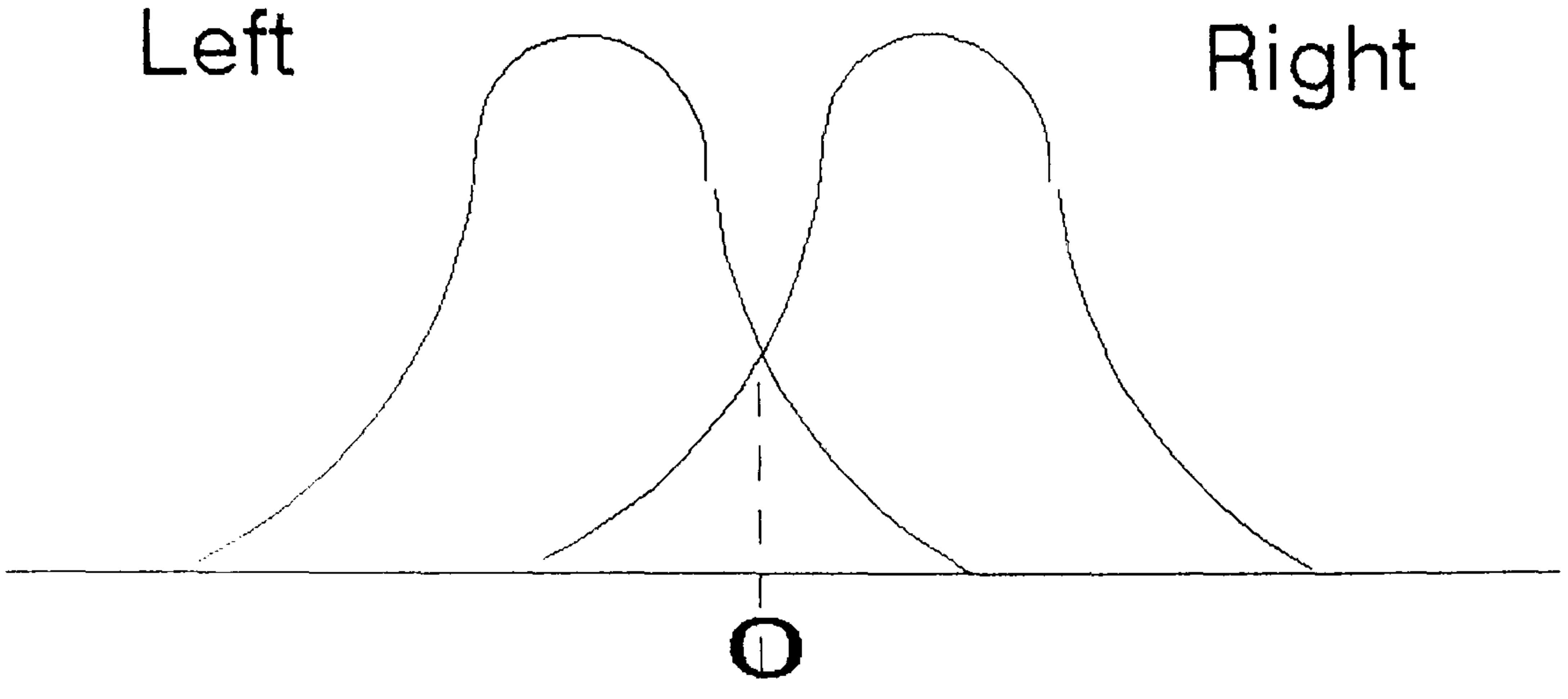
13.1 Psychometric Function Results

Another aim of the study was to examine the previously observed threshold shift in motion capture (Nawrot and Sekuler, 1990). As described this was done by examining the psychometric functions for conditions favouring motion capture (moving surround) and conditions not favouring motion capture (stationary surround).

The general finding was that in conditions where motion capture was evidenced, the shift in discrimination threshold was associated with a shift in the bias point between different directions of motion. It was also found that induced motion was associated with a shift in the discrimination threshold for the centre grating direction (in the opposite direction to the motion capture threshold shift) and this shift in threshold was also associated with a shift in the bias point. There was no evidence of any change in sensitivity for the centre grating direction of motion either for induced motion or motion capture. It was interesting that the only evidence obtained for a change in sensitivity to the centre grating's direction of motion was the observed increase with increasing centre aperture size and increasing centre grating contrast. This increase was, however, not related to the occurrence of motion capture or induced motion as the sensitivity was equal in the stationary stimulus surround (no capture or induced motion) condition to the moving surround condition. It seems that this change in sensitivity was related to the physical change in the stimulus, sensitivity being greatest with the highest contrast used (0.5) and the largest central aperture.

It is useful to consider the perceptual processes carried out by the observer in the experimental task in trying to explain the findings. Observers were required to discriminate between two possible directions of motion (left or right) of the display centre grating. Adelson and Bergen (1985) have described a scheme for the perception of stimulus velocity that is relevant to this. Velocity is computed by comparing the outputs of several local motion mechanisms which are selective for particular directions of motion (see chapter 1). Figure 51a, describes the responses of two such mechanisms (selective for leftward and rightward motion) with respect to stimulus velocity. The shape of each of the curves essentially describes the sensitivity of each mechanism to stimulus motion. As can be seen these responses are identical overlapping Gaussian curves, shifted along the velocity axis with respect to each other, each with a peak centred on the mechanism's preferred velocity. The responses of these mechanisms depend upon the velocity and the contrast of the stimulus. Thus for any given contrast, as the

Figure 51a: Overlapping Response curves of two motion mechanisms



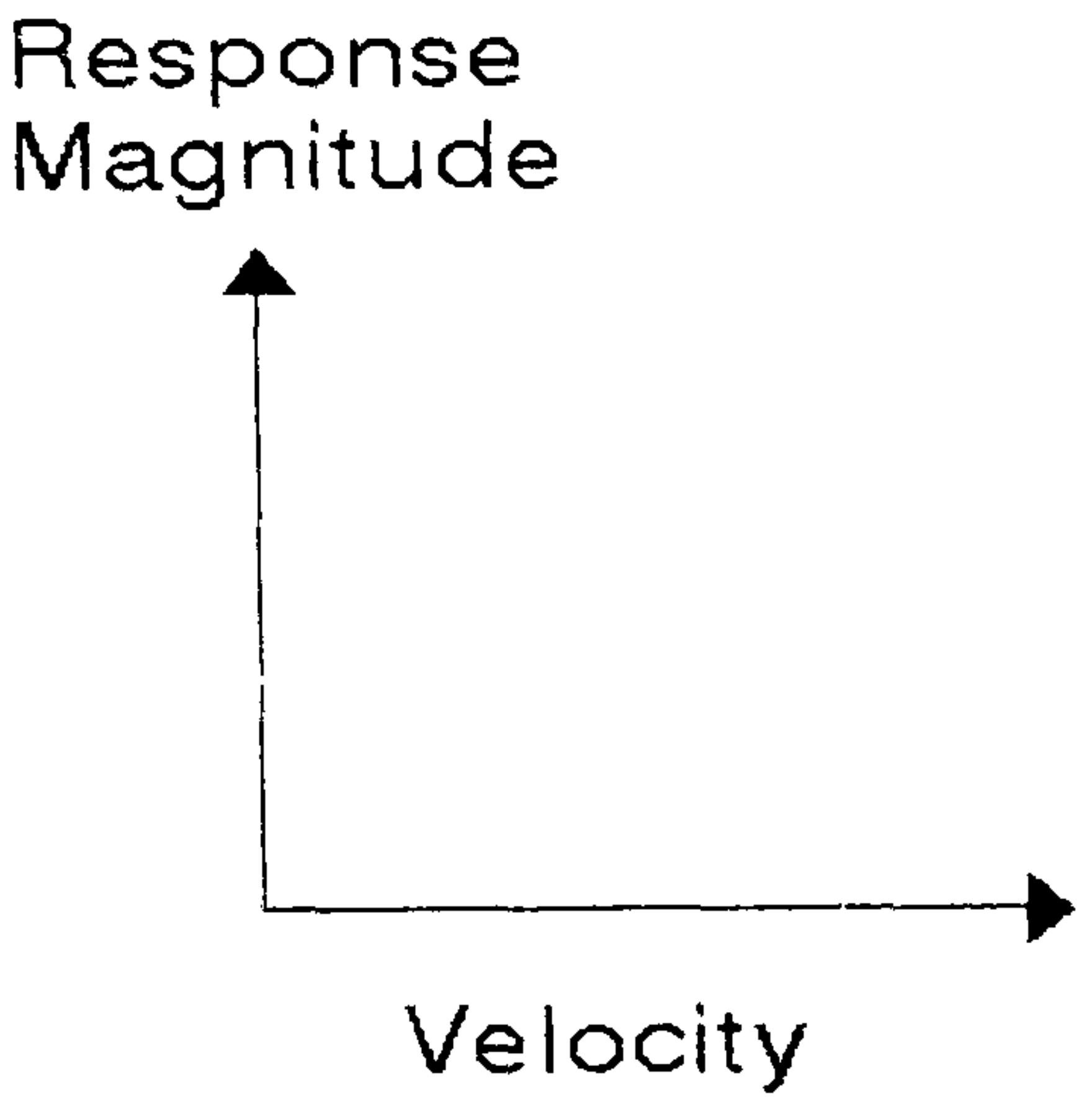
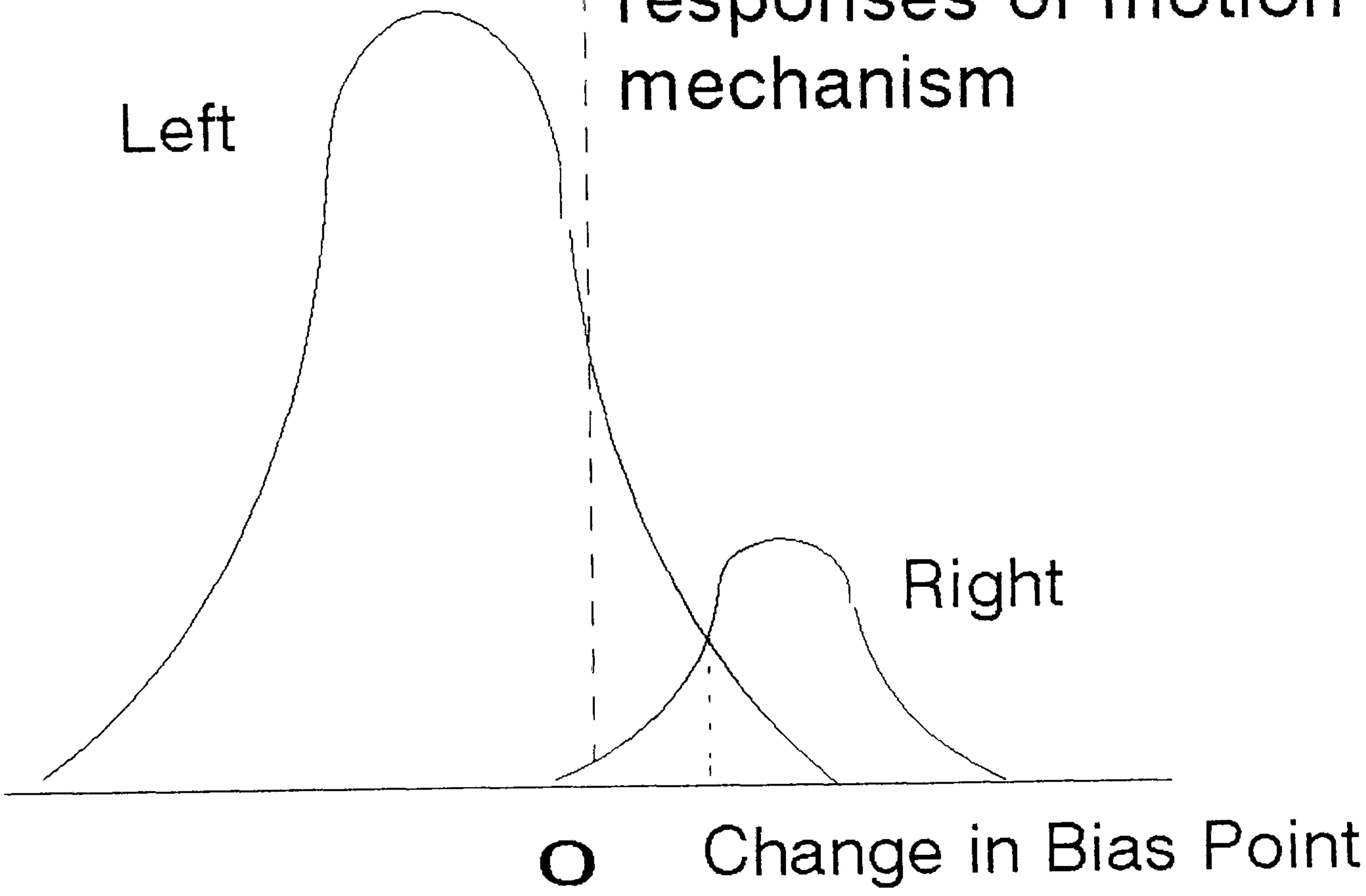


Figure 51b: Effect of inhibition and excitation on responses of motion mechanism



stimulus moves faster in a particular direction, the response magnitude of the mechanism sensitive to that direction will be greater than that of other mechanisms[4]. The perceived direction of motion at the centre of the display depends upon the relative sensitivities of all motion mechanisms with receptive fields located within this region of space.

It was argued previously that motion capture and induced motion effects can be accounted for in terms of opponent interactions between motion mechanisms. One effect of opponent interactions is to change the sensitivity of motion mechanisms to stimulus motion. Sensitivity decreases if a motion mechanism is inhibited and increases if it is excited. This may be seen by comparing figure 51a and 51b. In figure 51b the sensitivity of the rightward mechanism is increased due to excitation while the sensitivity of the leftward mechanism is decreased due to inhibition, relative to figure 51a.

When considered together the model of Adelson and Movshon (1985) and the effects of opponency upon mechanism sensitivity can explain the result that sensitivity to the centre direction of motion does not change from conditions of motion capture (or induced motion) relative to conditions of no-capture (or induced motion). Sensitivity to motion of the display centre grating is dependant upon the summated sensitivities of all motion mechanisms located in this region. Although the sensitivity to one direction of motion is reduced due to inhibition the

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[4] This will be the case provided that the velocity of motion does not increase beyond the mechanisms preferred velocity (the peak of a mechanisms curve in figure 51). If this occurs then the magnitude of the mechanisms response will reduce with increasing velocity. Similarly for any given velocity, if the contrast of the stimulus is low then the mechanisms will give out a weaker response than if the contrast is high.

sensitivity to another direction is increased due to excitation. If the magnitude of excitation and inhibition are equal, overall sensitivity to motion at the centre will remain constant from conditions of no motion capture (no induced motion) to conditions of motion capture (induced motion). Reductions in overall sensitivity due to inhibition of some motion mechanisms are effectively cancelled out by increases in sensitivity of other motion mechanisms due to excitation. This idea may be visualised by considering overall sensitivity to centre motion to be like a set of scales in which, on one side is the sensitivity to rightward motion and on one side is sensitivity to leftward motion; the sensitivity to centre motion remains constant despite changes in sensitivity to leftward or rightward motion because, as sensitivity to one direction increases sensitivity to the other decreases ie excitation and inhibition balance each other.

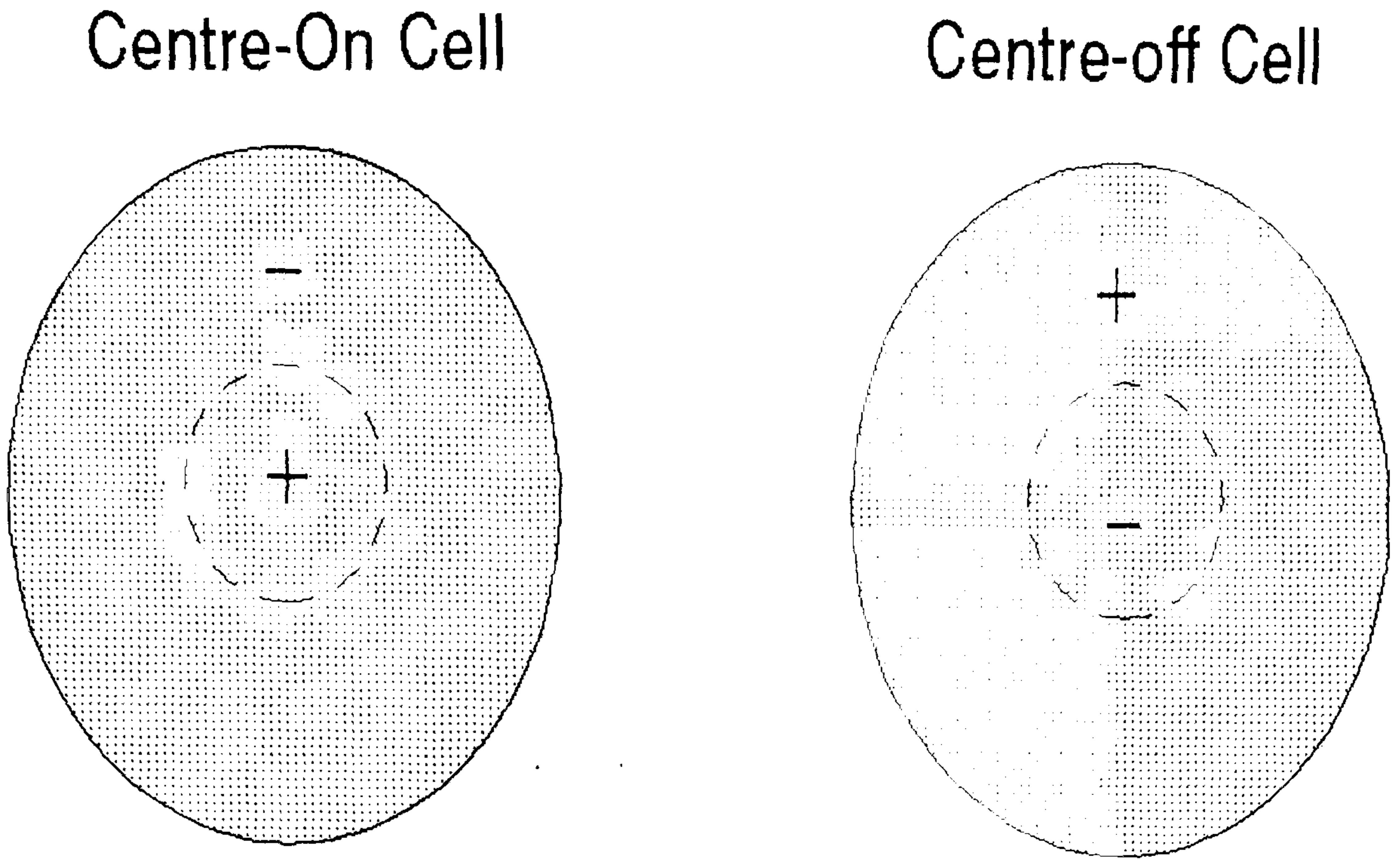
How might we explain the change in bias observed in these experiments ? By referring to figure 51a, it may be seen that as the response profiles of motion mechanisms overlap, it is therefore possible that a particular stimulus velocity could produce a similar response level in both leftward and rightward mechanisms. It would be expected that such a velocity would be very difficult for the observer to discriminate its direction of motion, and so the observer would respond with equal probability that the stimulus was moving leftward or rightward. The bias point is defined as the point at which the observer responds with equal frequency right or left, then the bias point can be seen to be this velocity at which the response of both channels is equal. As stated above, the opponent interactions thought to underlie motion capture and induced motion have the effect of changing the sensitivity of motion mechanisms either increasing it (due to excitation) or decreasing it (due to inhibition). Consider figure 51b. This figure shows two overlapping response profiles of motion mechanisms. In this example the rightward sensitive mechanism is inhibited giving rise to a reduced response profile ie a reduction in sensitivity. By contrast the leftward sensitive mechanism is excited giving rise to an increased response profile and an increased sensitivity. Comparing this diagram to figure 51a it can be seen that the rightward response profile is narrower and of lower maximum magnitude. The leftward response profile is wider and of greater maximum magnitude. (Following the suggestion made above the increase in the rightward sensitivity is exactly equal to the decrease in the leftward sensitivity). If one now examines the point of maximum overlap of the two curves in figure 51b ie the bias point, and compares it to that of figure 51a, it is apparent that this point has moved along the velocity axis. Thus the bias point has changed by altering the sensitivity to leftward and rightward motion, a greater velocity rightward is required to see rightward motion relative to that of figure 51a.

Comparing figure 51a and 51b. If it is assumed that the conditions represented in figure 51a are those when the surround of the display is stationary (no motion capture or induced motion) while those in figure 51b are conditions favouring motion capture it can be seen how the bias point has changed moving from no motion capture to motion capture. The overall sensitivity to motion at the centre would be given by the total sensitivity to both directions of motion, essentially by the area under both curves. It can be seen how this does not change for the two conditions despite changes in the sensitivity to leftward and rightward motion. Thus opponent interactions between motion mechanisms can have the result of changing the bias point whilst not changing the overall sensitivity to motion at the display centre and reflect opponent interactions between motion sensitive mechanisms.

To summarise: the observed shifts in the direction discrimination threshold, observed with motion capture and induced motion are related to shifts in the bias point (velocity) between opposed directions of motion. It is suggested that these shifts in bias would be expected from reference to, and are consistent with current theories of motion capture and induced motion that predict centre-surround, excitatory and inhibitory interactions between motion mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Yuille and Grzywacz, 1989).

Observations of a shift in the bias have been found in other psychophysical research on motion perception. Derrington and Suero (1991) carried out a series of speed discrimination experiments using sinusoidal gratings. They examined the proportion of trials on which the observer responded that a test grating appeared to move faster than a standard grating of equal spatial frequency and orientation. The responses of observers were measured for two conditions, after adapting to a similar grating moving with greater velocity (0.5 deg/sec) than the standard (0.38 deg/sec) grating and after no adaptation. They then plotted psychometric functions for both conditions. In the no adaptation condition, the proportion of trials where the test grating appeared to move faster than the standard increased as the velocity of the test grating increased. The 50% bias point was centred on a test speed of approximately 0.38 deg/sec i.e. the velocity of the standard. Thus in the absence of adaptation the perceived speed of motion of the test grating matched the actual speed of the standard grating. After adaptation, the psychometric function was shifted along the test speed axis in the direction of reduced speed (figure 2 in Derrington and Suero, 1991) relative to the psychometric function for the no adaptation condition. Thus after adaptation for a given proportion of responses, a lower speed of test motion was required. The 50% point i.e. the bias point occurred at a lower test speed than in the no adaptation condition. Hence after adaptation the apparent speed of the standard had been reduced. This finding was consistent with previous findings e.g. Thompson (1981). It was also the case in this experiment that the two psychometric functions generated were parallel, this indicated that there was no change in the slope of the psychometric functions and as such there was no change in the sensitivity to the motion of the stimulus post after adaptation. Hence, in common with our experiments, the experiment of Derrington and Suero (1991), produced evidence for a shift in the bias point with no change in the sensitivity to the motion of the stimuli. It is generally argued that the effects of adapting to a moving stimulus are the reduction in activity of motion mechanisms that are responsive to the particular stimulus i.e. its speed and direction (Braddick and Atkinson, 1982). Thus in the experiment of Derrington and Suero (1991), the adaptation to the faster moving grating would have the effect of fatiguing and thus reducing the activity of motion mechanisms responsive to velocities within the adapting range. When presented with a moving grating after adaptation, because of the adaptation of the motion mechanisms responsive to the higher velocities, their responses will be of lower magnitude than the responses of other mechanisms. Hence there will be a greater level of activity within mechanisms tuned to slower velocities. Applying the velocity perception model of Adelson and Bergen (1985), as the perceived velocity of a stimulus depends upon the relative activity of motion mechanisms tuned to different directions and speeds of motion, any stimulus velocity that is presented after adaptation, will appear to be moving slower than if no adaptation had taken place. On the basis of this it is possible that the results of Derrington and Suero, i.e. the change in bias velocity after adaptation, can be explained in a similar way to the results of our experiments: in terms of changes in the relative responses of motion mechanisms. In our experiments this results from interactions between motion mechanisms. In the experiments of Derrington and Suero, this results from the adaptation of motion mechanisms. The results of Derrington and Suero (1991), can therefore be considered to be consistent with our suggestion, that alterations in the relative responses of motion mechanisms not only alters the motion percept, but can also give rise to shifts in the bias velocity with no attendant change in sensitivity.

It is interesting to consider other research on cells known to feature centre-surround opponency and to compare these results to those of our experiments. The intention here is that any similarity between the functions obtained with known centre-surround opponent mechanisms, and our experiments would lend at least notional support to our model. Let us consider experiments on the responses of two types of retinal ganglion cells, on-centre and off-centre cells. Both types of cell feature concentric receptive fields which are arranged in a centre-surround manner such that maximal cell response of on-centre cells occurs when the centre is stimulated by light and the surround is in darkness and the opposite arrangement pertains for off-centre cells (reviewed in Sekuler and Blake, 1984). Figure 52



The cell on the left is excited by light falling into its centre and is inhibited by light falling in the surround, this is a centre-on cell. The opposite is true of the cell on the right, it is excited by light in the surround and inhibited by light in the centre, this is a centre-off cell.

Figure 52: Receptive Field Layout of Centre-on and Centre-off Retinal Ganglion Cells

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shows the receptive field lay outs for two both types of cell. Sekuler and Blake (1994) describe an experiment which examined the responses of retinal ganglion cells to light stimulation. In this experiment the centre of an on-centre retinal ganglion cell is stimulated by light of different intensities while the surround is in turn subjected to no illumination, moderate illumination and finally intense illumination. The results of such an experiment are presented in figure 53. The vertical axis represents the number of impulses per second of the cell in response to the stimulus, the horizontal axis represents the light intensity falling on the centre of the receptive field. Three lines A,B and C show the plots obtained for each level of surround illumination, A is no illumination, B moderate illumination and C intense illumination. The first thing that may be noticed is that there appears to be a shift in the graphs relative to the x-axis as the illumination of the surround increases. Therefore it would appear that the level of illumination in the surround seems to have a profound effect upon the response of the cell. Given that retinal ganglion cells feature centre-surround receptive fields, then it may be argued that the results reported by Sekuler and Blake (1994) may be used as a model for the effects of centre surround interactions. Consider the graphs presented in figure 53. If some arbitrary number of impulses per second is taken then it may be seen how, in order to obtain the same response, the magnitude of the centre stimulus has to be higher as the illumination in the surround gets higher. It may also be seen how the shapes of graphs A,B and C do not change. Thus if we consider the level of centre illumination required to produce our arbitrary number of impulses per second to be analogous to a threshold, it may be seen that there is a shift in this threshold as the strength of the surround stimulus increases. This is similar to what was found in our experiments i.e. that different levels of surround motion (stationary or moving) effect how motion at the centre of our stimulus is perceived i.e. our finding that for conditions of motion capture, the velocity threshold required to perceive the centre as moving to the right increased as the surround moved leftward relative to a stationary surround. It may also be noted that the pattern of the results represented in figure 53 looks very similar to the shift in the psychometric function plots described in chapter 7 (figure 37). It is therefore argued that given the similarity between the response functions obtained for cells known to feature centre-surround interactions and the psychometric functions obtained in our experiments with motion capture, then one probable explanation for our results is the existence of centre-surround interactions between motion mechanisms as described by our model.

Chapter 14

14.1 Experiments 8 to 11 General Discussion. A model of Motion Capture and Induced motion

The results from these experiments will be drawn together with the aim of constructing a model for motion capture. It is useful firstly to review the findings of this part of the study.

The finding of experiment 8, that the occurrence of motion capture depends upon the size of the central aperture in the display, is consistent with explanations of motion capture phenomena in terms of spatially determined centre-surround interactions between motion sensitive mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Yuille and Grzywacz, 1989). The further finding that motion capture shades to induced motion with increasing central aperture size suggests that induced motion and motion capture can be accounted for within the same explanatory framework, i.e. centre-surround interactions across space, and agrees with previous research (Nawrot and Sekuler, 1991; Murakami and Shimojo, 1991,1992,1993).

It was found that a moving low spatial frequency could capture the direction of motion of a higher spatial frequency. This is evidence that there are interactions between motion mechanisms that are sensitive to different spatial frequencies, and confirms the findings of Ramachandran and Cavanagh (1987), Yo and Wilson (1992), and Smith (1992). This also indicates that in terms of two stage models of motion perception (Adelson and Movshon, 1982) the interactions between motion mechanisms occur at a level of processing which is after stage one of such models i.e. after the stage where motion direction is analysed within spatial frequency bands.

The results of the plaid experiment (experiment 11) when applied to two stage models of motion perception, reveal that signals from stage two motion mechanisms do not interact with stage one motion mechanisms. This indicates that the interactions which give rise to motion capture effects must occur prior to stage two processes. These findings fit in with the model of motion perception proposed by Smith (1992). This model, which whilst being based upon two stage models, includes a stage 1b where similar direction signals are pooled across spatial frequencies. Thus it is suggested that motion capture is mediated by interactions between motion mechanisms across spatial frequency.

The finding that there is an orientation/direction limit to motion capture (experiment 10), indicates which motion mechanisms will interact with each other i.e. how similar two directions of motion need to be in order to interact in an excitatory way and how different they need to be in order to interact in an inhibitory way. Experiment 10 thus reveals the directional limits of motion capture. Within the centre region of a centre surround system, excitatory interactions take place between motion mechanisms whose directional tuning is within thirty degrees of each other, whilst inhibitory interactions occur between motion mechanisms with directional tuning that differs by between 150-180 degrees. For the interactions between surround and centre motion mechanisms this is reversed.

Experiment 9 demonstrated that the contrast of the centre grating is of importance in determining the occurrence of motion capture or induced motion, with motion capture shading to induced motion with increasing centre grating contrast. At very low centre contrasts, no motion capture or induced motion occurs due to the lack of interaction between direction mechanisms at such contrast levels (Stromeyer et al, 1984). In our model of motion capture, the effect of contrast is in terms of the strength of motion signal that is provided to the motion mechanisms. A certain level of contrast is required in order to produce interactions between different motion mechanisms (Stromeyer et al, 1984). For contrasts beyond this level it is the interaction between the strength of the motion signal and the relative levels of excitation and inhibition between motion mechanisms that determines the occurrence of motion capture or induced motion. Based upon these results a model of motion capture and induced motion phenomena can be proposed.

As the results of these experiments are consistent with the expectations of current theories of motion perception, such that Motion capture (and induced motion) are the result of spatially determined centre surround interactions between differently tuned motion mechanisms (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993), then it is the case that the proposed model of motion capture would feature such spatially determined interactions. In terms of two stage models of motion perception (eg Adelson and Movshon, 1982). These interactions would occur at a level of processing which is after the analysis of directional signals within spatial frequency channels i.e. after stage one in two stage models. Also these interactions appear to occur prior to the analysis of pattern motion at stage two. Therefore these interactions occur at a level akin to Smith's (Smith, 1992) level 1b, where motion signals are pooled across spatial frequencies. It is argued that the observed shift in the bias between opposed directions of motion under conditions of motion capture and induced motion, is consistent with the expectations of a model featuring excitatory and inhibitory interactions between motion mechanisms and is also consistent with the model proposed in section 1.

It is interesting to consider how the results of this experiment bear upon the model of Zhang et al (1993). It is suggested that similar arguments apply to this study as those forwarded by Murakami and Shimojo (1993). In common with these authors it was found that both the central grating and surround grating appeared as two distinct figure moving on the background. Thus whilst it is accepted that there is an interaction between short and long range processes that can give rise to motion capture and induced motion effects it is argued that this does not account for the results of these experiments and it is instead bottom up processes akin to those described by Nawrot and Sekuler (1990) or Murakami and Shimojo (1991,1992,1993).

14.2 Conclusions Experiments 8 to 11

It was concluded that the results of these experiments give support to theories of motion capture and induced motion that propose centre surround interactions between motion mechanisms across space (Nawrot and Sekuler, 1990; Murakami and Shimojo, 1991,1992,1993; Yuille and Grzywacz, 1989).

Further, these results suggest that the level at which such interactions take place in the processing of motion information is after processing by stage 1 component mechanisms and prior to stage two pattern processing in two stage theories of motion perception (Adelson and Movshon, 1982). As motion capture and induced motion were seen to occur between different spatial frequency stimuli, it was concluded that these interactions occur after pooling of motion signals across spatial frequency. This would suggest that the interactions occur at or after stage 1b in Smith's model of motion perception (Smith, 1992).

The observed shift in the direction discrimination thresholds in motion capture and induced motion (Nawrot and Sekuler, 1990) was found to be associated with a shift in the bias point between opposed directions of motion, with no associated change in the sensitivity of motion mechanisms to the motion of the stimulus. It was argued that this finding is consistent with explanations of motion capture in terms of spatially determined excitatory and inhibitory interactions between mention mechanisms.

This is essentially the same model as that described in figure 32 to account for the results of part 1, shear and compression processing.

Part 3

General Discussion of Parts 1 and 2

Chapter 15

15.1 Summary and Conclusions from Section 1 and Section 2

Taking the results of both sets of experiments together. It seems that there is strong evidence for the existence of directional opponency accross space in the visual system. Little support was obtained for the existence of local shear and compression sensitive mechanisms.

The results supported the notion that opponency is the product of excitatory and inhibitory interactions between motion mechanisms. These interactions are spatially determined according to a centre-surround arrangement.

It was suggested that in terms of the level of processing in the visual system, opponent processes would be expected to occur before stage 2 processes in two stage models of perception (Adelson and Movshon, 1982) and after stage 1a (Smith, 1992) processes. It was suggested that opponent processing occur either at or after stage 1b processing (Smith, 1992).

The results support a first stage of motion processing featuring local directionally selective mechanisms. Indeed the results indicate that the sensitivity to differential invariants such as shear and compression is constrained by the sensitivity of these mechanisms. Further these results imply that opponency occurs only at higher suprathreshold contrasts.

15.2 Relationship to Neurophysiology

An examination neurophysiologically research reveals the existence of neuronal mechanisms that could in principle, carry out the computations required by our model.

Our model predicts that it is interactions between motion mechanisms that underlie shear and compression sensitivity and motion capture and induced motion. Further, that these interactions occur according to a centre surround spatial arrangement.

Allman et al (1985) examined the responses of neurones in the middle temporal visual area or MT (an area of brain cortex thought to be associated with the perception of motion, due to the preponderance of direction selective cells: Albright et al, 1984; Newsome et al, 1985; Newsome and Pare, 1988) of the owl monkey. They found that the responses of the neurons were influenced not only by the presence of motion within the classical receptive fields of the neurons (this refers to the discrete portion of visual field that gives rise to a response of the neurone if a moving stimulus is placed within this region: Hartline, 1938), but also by motion falling into surrounding regions. If the classical receptive field of the neurones is considered to be analogous to the centre regions of our model then this is evidence for a centre surround arrangement of neuronal motion mechanisms in area MT. Other researchers have found similar results which indicate the presence of antagonistic surrounds around the classical receptive fields of motion selective cells (Born and Tootell, 1992,1993; Sterling and Wickelgren, 1969; Frost et al, 1981; Von Grunau and Frost, 1983). Tanaka et al (1986) found similar results to those of Allman et al (1985) when examining responses of MT cells in the macaque and Hammond and Mackay (1981), and Hammond and Smith (1983) found similar results working with cells in the cat striate cortex thought to be equivallent to primate MT cells.

Our model further proposes that motion mechanisms located in surrounding regions will have inhibitory effects upon mechanisms with similar directional sensitivities located in centre regions, and excitatory effects upon centre mechanisms with opposite directional sensitivities. Allman et al (1985) found evidence that the level of activation of some of the owl monkey MT neurons recorded, was reduced when the same direction of motion was presented both to regions of the visual field corresponding to the classical receptive field of the neurone and to surrounding regions. Conversely the neurone's level of activity was facilitated by surround motion that was opposed to the direction of motion presented to the classical receptive field. Tanaka et al (1986) found similar results working in area MT of the Macaque. Again these findings are consistent with our model.

The model suggests that interactions can occur between motion mechanisms across spatial frequency. Newsome, Gizzi and Movshon (1983) recording from macaque monkey area MT found that these neurones were broadly tuned for spatial frequency, few of the neurones had spatial frequency bandwidths of less than two octaves and some had bandwidths of in excess of four octaves. The suggestion of this research is that there is (as required by our model), some pooling across spatial frequency of motion information in primate area MT.

It is interesting to consider the level of processing in the visual system in which the observed effects of opposed directions of motion occur. Snowden et al (1991) found that if both preferred and anti-preferred directions of motion were presented to the classical receptive field of MT cells then the firing rate of the cells was suppressed relative to presentation of preferred direction to the cell. For V1 cells this effect was not found. Snowden et al interpret their findings as indicating that inhibitory interactions between opposed directions of motion occur in area MT. Mikami et al (1986) found evidence for inhibitory interactions in every MT neuron that they tested and facilitatory interactions in most of them. Foster et al (1985) found that the responses of cells in areas V1 and V2 were spatially localised, indicating that broad band motion signals (required by our model) would not be available in V1 and V2. These findings may be compared with those of Newsome et al (1983) who found broad band spatial frequency responses of MT neurons. Taking these results together it appears that the most likely location for the hypothesised interactions between opposed directions of motion to occur is primate area MT and not V1 or V2, a position that is supported by other authors (Snowden et al, 1991; Zhang et al, 1993; Murakami and Shimojo, 1993).

Gizzi, Newsome and Movshon (1983) report data which indicate that of the neurons in primate area MT, most of them respond to the motion of components of complex patterns like plaids, while only a relatively small number respond to the motion of patterns for example plaids. This finding coupled with that of broad spatial frequency tuning of the MT neurones indicates that the component MT neurones could in principle be associated with Smith's stage 1b in his model of motion perception (Smith, 1992). If this is so, and as our model suggests that interactions occur at or after Smith's level 1b, then it is possible that these interactions could occur either between these component MT neurones or within a centre surround mechanism which received inputs from these component MT neurones. Thus the interactions between the different motion signals occur prior to processing by MT pattern motion neurones.

Snowden et al (1991) in reviewing the literature suggest that the inhibition effects noted between opposed directions of motion could be accounted for by competitive interactions between neurons with different preferred directions of motion, a position which supports models such as those of Nawrot and Sekuler (1990).

Thus it appears that the visual system contains neuronal units that could in principle carry out the computations required by our model. It is a highly speculative suggestion, but it is possible given the neurophysiological evidence that the kinds of interactions between motion mechanisms described in previous chapters, could occur within the human equivalent of the primate area MT. This possition is therefore in agreement with Murakami and Shimojo (1993) and Zhang et al (1993).

15.3 How Are The Opponent Interactions Realised ?: Deciding between the two models of opponency

Two possible architectures have been proposed. The first (see figure 13a and 13b) involves a higher level mechanisms that received directional signals from motion mechanisms at lower levels and has a receptive field organisation that is centre surround in nature as favoured by Murakami and Shimojo (1993). In such a framework there would be little interaction between the lower level motion subunits, their outputs would be directed to the higher level mechanism.

The second mechanistic framework (see figure 14a and 14b) does not require a higher level centre surround mechanisms. In this framework directional motion mechanisms would be connected to each other in the form of a network. The centre surround interactions would be achieved by different connections between motion mechanisms. This second possible architecture is characterised by the model of Nawrot and Sekuler (1990).

The present experiments do not give any evidence as to which of the above two possibilities is to be preferred, however it is possible to consider the most likely architecture on the basis of previous research.

It will be argued here that the preferred architecture for the opponent process is that described by Nawrot and Sekuler (1990). It is assumed that the goal of an evolving system (the visual system) is to find stable and economical strategies to carry out its processing tasks. It is generally argued that a cooperative network of processing elements, connected by non-linear excitatory and inhibitory interactions, affords many computational economies that will boost the effective signal to noise ratio in the overall system (Feldman and Ballard, 1982). As described in chapter 7 there is much evidence that the visual system demonstrates properties that are consistent with such a cooperative mechanism (Williams and Sekuler, 1984; Williams and Phillips, 1987; Williams et al, 1986; Nawrot and Sekuler, 1990; Snowden and Braddick, 1989a,1989b,1990; Snowden, 1989; Bertenthal et al, 1993; Smith, Snowden and Milne, 1994). Thus, because it features a cooperative network of processing elements and spatially determined opponent interactions that account for our results, the model of Nawrot and Sekuler (1990) is the favoured mechanism.

The other possible mechanism for opponency (specific opponent units), it is argued, is less economical in processing terms. If the visual system demonstrates cooperative phenomena then the idea of specific opponent units must be made to fit in with this. Two possible architectures can be proposed. In the first, these dedicated opponent units would receive inputs from neurons that were part of the cooperative network. In the second these opponent units would themselves be part of the cooperative network. Following the arguemnt of processing economy, then both of these schemes may be rejected as the processing required to explain our results could be done more efficiently and ecconomically with a cooperative network featuring spatially determined opponent interactions, with out the need of higher level specialised units or units with complex receptive fields connected into the network.

It would be possible to test directly which of these two mechanistic frameworks is to be preferred as they make different predictions as to the effects of increasing the distance between the centre and surround motion. For a model such as that of Murakami and Shimojo (1991,1992,1993) featuring a higher level centre surround mechanisms, it is the case that the mechanism is of finite size. Hence motion in an area of the visual field that is not within the receptive field of such a mechanism will not have any effect upon the particular mechanism. Thus if a display was presented in which motion in the surround was in the same direction as motion in the centre and in which the distance between the surround motion and the centre motion was gradually increased, there would be over a range of distances inhibition of the centre of the mechanism by the surround. For surround motion outside this distance range then it would be expected that the surround motion would not effect the particular mechanism being stimulated by the centre motion. The effect of this would be that at a certain distance between the centre and surround motion, there would be a release of inhibition of the centre. This release of inhibition would be evidenced by a decrease in the threshold for the detection of the centre direction of motion. By contrast the line element type model proposed by Nawrot and Sekuler (1991) does not make such a strong prediction. In such models the interactions proposed are between local direction of motion mechanisms and do not necessarily require a finite receptive field. Hence if in such an experiment as described above were to be carried out and a release of inhibition were to be found this would, whilst not totally ruling out line element type models, favour higher level mechanism interpretations whilst a finding of no release of inhibition would discount such interpretations.

Having given support to the model of Nawrot and Sekuler, it is worth considering where in terms of two stage process models of motion perception (Adelson and Movshon, 1982; Smith, 1992) these interactions occur.

It has been proposed in previous sections that these interactions may occur either at or after stage 1b (Smith, 1992) but before stage 2 (Adelson and Movshon, 1982). Following the theme of greatest processing economy, the most likely location would seem to be at stage 1b i.e. between 1b motion mechanisms. Greatest processing economy is obtained by such an arrangement because there is no requirement for an extra processing stage after stage 1b. The neurophysiological evidence reviewed above (section 14.2) is consistent with this interpretation i.e interactions occurring between MT neurons which are directionally selective, are broad band in spatial frequency terms and demonstrate spatially determined excitatory and inhibitory interaction effects.

15.4 Proposed Model

The findings of these experiments imply that the same model can be used to account for shear and compression sensitivity and motion capture and induced motion. The main feature of the model are summarised in figure 54.

This model features spatially determined centre surround interactions between local motion sensitive mechanisms. These interactions are excitatory and inhibitory interactions, and may be described as opponent processes. It is suggested that a heirachy of processing exists. Local directional mechanisms signal local directions of motion. Their outputs are subjected to pooling across spatial frequency to give rise to local broad band motion signals. These signals are then subjected to opponent processes. It is argued that these opponent processes are excitatory and inhibitory interactions between motion mechanisms at Smith's stage 1b (spatial broad band motion signals. Smith, 1992). The most likely architecture for these opponent processes being the line element model of

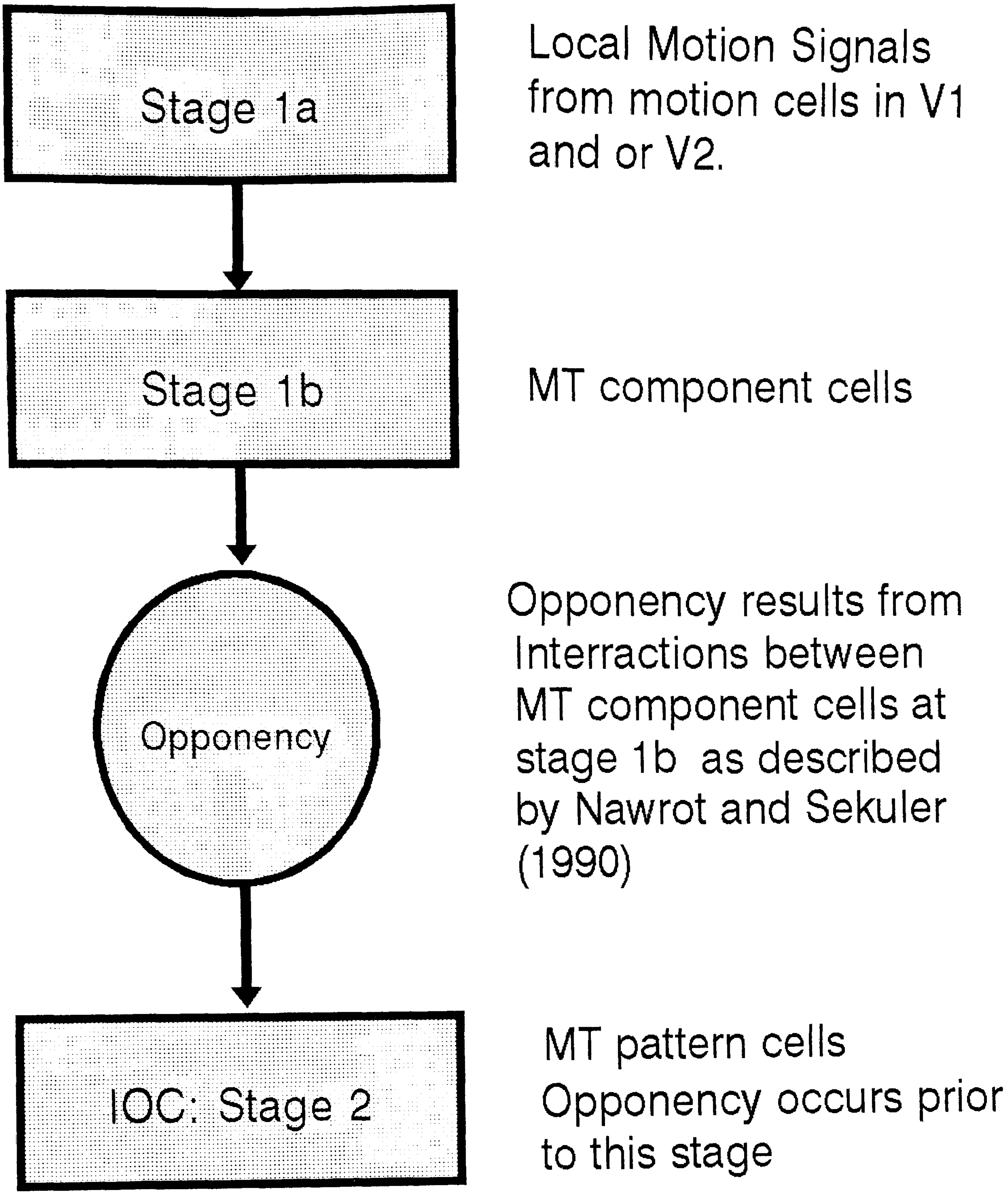

Figure 54: Proposed Opponent Model and Possible Neural Realisation. See text for explanation.

Nawrot and Sekuler (1990). Thus it is proposed that opponency is realised by excitatory and inhibitory interactions between stage 1b neurons, connected to each other in the form of a cooperative network as described by Nawrot and Sekuler (1990). It is important to note that circular symmetry is not implied for the centre-surround interactions of this model.

In neurophysiological terms it appears that stage 1a (Smith, 1992) processes could be identified with processes that occur within area V1 and V2 of the primate striate cortex. It has been shown that motion sensitive neurons in these areas are very narrow band in their spatial frequency responses (Forster et al, 1985) and these neurons do not appear to interact together to any great extent (Snowden et al, 1991). Stage 1b, the probable site of the opponent interactions between motion mechanisms, it is proposed is located within primate area MT. Here the observation of great interactivity between motion sensitive mechanisms (Snowden et al, 1991), broad band spatial frequency responses of MT neurons (Newsome et al, 1983) and spatially determined opponent interactions (Allman et al, 1985) are consistent with the processing requirements of our model. It is proposed that it is the component sensitive cells of area MT (Gizzi et al, 1983) that are involved in the cooperative network (Nawrot and Sekuler, 1990) that gives rise to the observed opponent effects.

The outputs from the opponent processes would then be processed by stage 2 processes. The location of this processing would probably be primate area MT, and it is most likely that pattern cells of MT (Gizzi et al, 1983) would be responsible for this processing.

Our results indicate that the results of stage 2 processes do not have any input into earlier opponent or other processing i.e. the lack of evidence for induced motion or motion capture when using the plaid surround in experiment 11. It is an interesting question as to if pattern cells are involved in opponent interactions at stage 2. This would seem unlikely. This is because, following from Wright and Gurney (1993), the eventual motion percept of the observer is one that has undergone processing at both stage 1(a and b) and stage 2. In our experiment 11 a single grating was surrounded by a plaid. Both stimuli would therefore have been subject to stage 2 processes. The direction of motion of the plaid would be determined as a result of stage 2 processing (Adelson and Movshon, 1982). The results of this experiment showed that motion capture was only observed when one of the gratings making up the plaid had the same orientation as the centre grating. Thus motion capture was determined by the direction of motion of components not of the plaid. If opponent interactions had occurred between stage 2 processes then it would have been expected that motion capture would have occurred for all plaid component orientations. This was not the case, hence the conclusion that opponency is unlikely to occur at stage 2.

15.5 Proposed Further Research

It would be interesting to carry out experiments in order to test which of the two competing models of the opponent interactions, the line element model of Nawrot and Sekuler (1990) or the centre-surround unit model (Murakami and Shimojo, 1991,1992,1993) is the most suitable. As described earlier each makes different predictions as to the results expected when the distance between the centre and surround of a circular centre surround display is increased. The centre surround unit model predicts that there would be a release of inhibition at a certain distance, resulting in a decrease in the motion threshold for the centre direction of motion. The line element model does not make such a strong prediction. Thus the finding of no evidence for a release of inhibition would be evidence on favour of the line element model, evidence for the inhibition release would favour the centre surround unit model.

Another interesting set of experiments could examine the effects of terminator motion upon both motion capture and induced motion. No such work has previously been carried out. It would be predicted that if terminator motion signals did effect motion capture and induced motion then it would probably be intrinsic terminator motion that would have the main effect as it is this type of terminator motion that has the greatest effect upon motion perception (Shimojo et al, 1989). Experiments revealed that intrinsic terminator motion undergoes opponent processing. It would thus further be expected that if terminator motion signals are subject to opponency (excitatory and inhibitory interactions) then motion capture and induced motion should be seen with displays made up exclusively of intrinsic terminator motion.

Our results indicated that intrinsic terminator motion signals are available at the level at which opponent processes occur i.e. stage 1b in our model. It would be interesting to examine at what level terminator motion signals are generated. The evidence would suggest that they are probably processed at stage 1 in two stage motion models. As to whether terminator motion is detected by stage 1 mechanisms is an open question which should also be considered.

Experiments could also be carried out to examine the effects of two plaid stimuli used to make up a shear or compressive motion. If opponent processes occur only prior to stage 2 processes as our model suggests, then no evidence for opponency should be obtained with a shearing or compressive plaid stimulus. Clearly if evidence for opponency was obtained this would suggest opponent processing after stage 2 processes. Obviously with such an experiment care would need to be taken in order to generate plaid stimuli that were made up of components that were not moving in opposition in the two parts of the visual field as such signals would be expected to produce opponency between the component motion signals.

15.6 Concluding Remarks

It is suggested that the results of these experiments and the model produced are consistent with previous research and are also consistent with the known neurophysiology.

The results do not lend support to notions of shear and compression processing being the result of specific sensitivities to these motion types. As such they suggest, at least with respect to deformation sensitivity, that models of motion perception suggesting specific sensitivities to all differential invariants in the retinal flow field are not satisfactory models.

Induced motion and motion capture appear to be related along a continuum and seem to be manifestations of the same underlying spatially determined opponent processing. This opponent processing also appears to provides the explanation for shear and compression sensitivity.

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