An Experimental Study of Fine-Grain Motion Perception in the Human Visual System

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Dedicated to my father and mother,

Giuseppe and Giuseppina Gravano

University of Keele

Thesis for Degree of Ph.D

Title: **An Experimental Study of Fine-Grain Motion Perception in the Human Visual System**

I certify:

(1) That the greater portion of the work submitted in the above thesis has been done subsequent to my registration for the degree of Ph.D

(11) That the above thesis is my own account of my own research.

(111) That no part of the work incorporated in the above thesis has been previously incorporated in a thesis submitted by me for a Higher Degree at any university.

Date: 15th February 1985 Signature: S. Grassano

Abstract

This thesis explores the characteristics of motion perception in the peripheral field of the human visual system as revealed by the fine-grain movement illusion, in which the sequential flashing of two spatially unresolved dot flashes results in the vivid perception of a single dot moving over a considerable distance.

A series of experiments is described in which consideration is given to the spatial and temporal dependence of the fine-grain movement illusion under different experimental conditions. Temporal response characteristics of the fine-grain movement illusion are determined, as a function of eccentricity, under conditions of photopic and scotopic adaptation. The temporal response characteristics of the illusion, which are determined using an objective measure of performance, are compared with temporal response characteristics obtained with a subjective measure of the illusion, in which subjects are required to rate the "strength" of the perceived illusion. Measurements are made of the minimum spatial separation required for two dot flashes to generate a fine-grain movement illusion. The minimum dot separation required for the fine-grain movement illusion is compared with the minimum dot separation required for spatial resolution; and the results are discussed in terms of possible motion- and form- detecting systems. Previous work has shown that fine-grain movement illusions may be made to interact with each other, so that two illusions generated sufficiently close together will, under appropriate conditions, destroy each other. Interaction thresholds, that is the minimum distance by which two illusions have to be separated so that they do not interfere in this way, are determined as a function of retinal eccentricity for different stimulus configurations. Measurements are made of the

perceived extent of the illusion and its dependence on stimulus intensity and dot separation are determined. Two further experiments are described which consider extrapolations in classical apparent motion and these results are compared with the extents obtained for the fine-grain movement illusion.

Finally the implications of the experiments described in this thesis on visual motion perception and other areas of visual perception are considered.

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Chapter 1

Introduction

Chapter 1: Introduction

1.1 Visual motion perception

One of the most basic and primitive properties of the human visual system is its capacity to detect moving objects. Unlike other visual functions motion detection is likely to have developed at an early stage in the evolution of the visual system, along with the detection of spatially distributed light patterns (i.e. form perception). Other visual functions, for example colour vision and stereovision, are likely to have developed at late evolutionary stages.

The study of motion perception has concentrated not on the perception of objects moving in the visual field (real motion) but instead on the perception of illusory motion generated by stationary stimuli (apparent motion). This is evident in that the existing literature on apparent motion greatly exceeds that concerned with real motion perception. There are many examples of apparent motion generated by stationary stimuli. For example, an isolated light in an otherwise dark visual field appears to wander (autokinesis) or a sudden change in the brightness of a pattern often gives rise to an apparent contraction or expansion of the pattern. The class of apparent motion that is of most concern in this thesis is that associated with the sequential presentation of two stationary visual stimuli. The presentation of one of the stimuli, followed by a blank interval and then the second stimulus gives rise, under appropriate spatial and temporal conditions, to the perception of motion from the first stimulus to the second stimulus. The two stimuli used to generate the illusory motion are typically spatially resolved, so that if they were presented simultaneously they would be seen as two distinct stimuli.

Studies of real-motion perception have traditionally involved the continuous motion of objects in the visual field. The object's motion is continuous in the sense that it may be considered as an infinitely large number of displacements, each displacement of an infinitesimally small spatial and temporal extent.

The two types of perceived motion, apparent and real, are based on two different classes of stimuli and as such have usually been dealt with separately in studies of motion perception. It would be reasonable, though not necessarily correct, to suppose that two motion detecting systems, each stimulated by its own class of visual stimuli, subserve the two types of perceptions. The two types of perceived motion, however, need not be considered as being mutually exclusive. The continuous motion of an object could be replaced by a series of finite and discrete stages (with no movement between each stage), and still result in the perception of continuous motion, providing the spatial and temporal step sizes fall within some spatio-temporal integration interval of the visual system. Upper limits to this integration interval might be provided by the spatial and temporal values required such that any two adjacent stages would be spatially and temporally unresolved. The resulting perceived motion could be referred to as real motion, for it would be perceptually indistinguishable from real motion, and referred to as apparent motion since there is no movement of the stimulus.

The study of movement between such stimuli which fall within spatial and temporal integration limits of the visual system may provide the means by which the gap between apparent motion and real motion can be bridged. One possible visual phenomenon that is a natural candidate for helping bridge this gap is the fine-grain movement illusion, first demonstrated by Thorson, Lange and Biederman-Thorson (1969). They showed that the sequential presentation of two peripheral spatially unresolved dot flashes can give rise to a vivid illusion of a single dot moving in the direction defined by the onset of the dot flashes. The perceived motion falls under the category of apparent motion in that the stimuli are stationary and spatially and temporally discrete. It could be argued, however, that it is the real motion detecting system that is activated by the stimuli falling within its spatio-temporal input tolerance (since the stimuli are spatially unresolved). The fine-grain movement illusion therefore has characteristics which allow it to be categorised as either apparent motion or real motion. The next section describes more of the basic characteristics of the illusion.

1.2 The fine-grain movement illusion

As noted above, the direction of the fine-grain movement illusion was found to be in the direction defined by the onset of the dot flashes. This property was made use of in an objective measure of the characteristics of the illusion in the following way. Two small sequential dot flashes were presented at an eccentricity of 22^{o}. The subject was required to indicate the sequential order of the two dot flashes, typically by using the direction of the resulting illusory motion. Subject's performance, as defined by the percentage of correct responses, were measured over a range of interstimulus intervals. Typical results of such an experiment are illustrated in Figure 1.1. At sufficiently short interstimulus intervals, subjects reported seeing a single flash, whereas at sufficiently long interstimulus intervals two sequential flashes, spatially superimposed, were seen. At both these extremes no motion was perceived and performance was, as anticipated, approximately at chance level (50% correct).

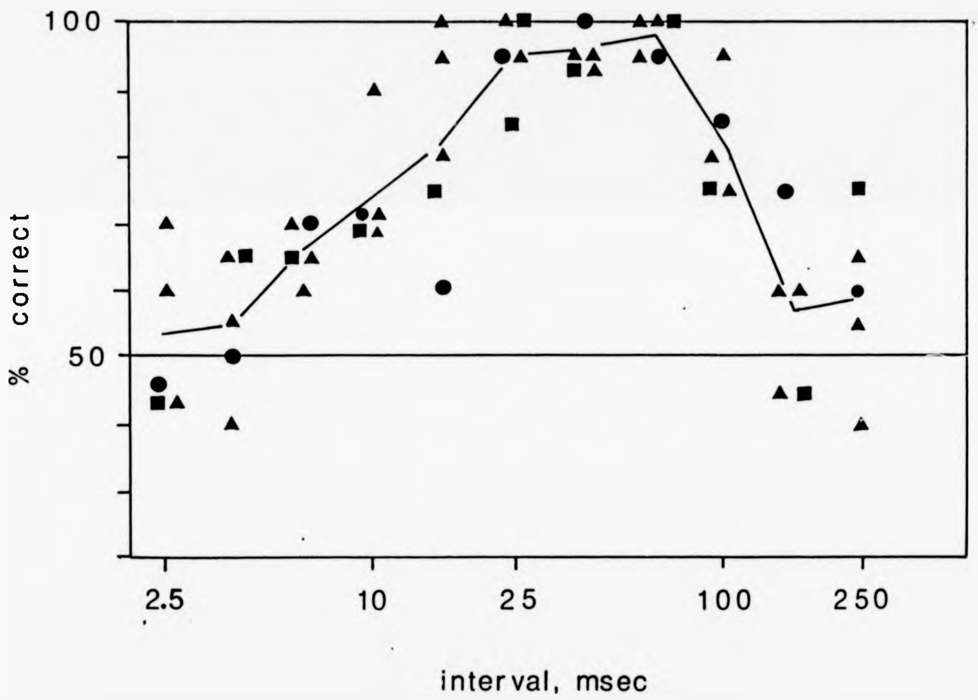

Figure 1.1 Temporal tuning characteristics of the fine-grain movement illusion (figure taken from Thorson, Lange and Biederman-Thorson, 1969).

At intermediate interstimulus intervals, however, subjects perceived a strong motion effect and were able to judge the direction and hence the order of the stimuli reliably. The dot flashes were certainly spatially unresolved as they were presented at 22^0 eccentricity and were separated by 7 min arc. Furthermore, the finding that for long interstimulus intervals the percentage of correct responses were at chance level confirms that the dots flashes were spatially unresolved. The inverted U-shaped dependence of performance levels on interstimulus interval (see Figure 1.1) is referred to, in this thesis, as the <u>temporal tuning characteristics</u> of the fine-grain movement illusion.

Thorson, Lange and Biederman-Thorson (1969) and Biederman-Thorson, Thorson and Lange (1971) conducted a series of experimental investigations relating to the fine-grain movement illusion. The experiments described in this thesis serve to confirm, elucidate and extend their findings; and to consider the implications of the fine-grain movement illusion on visual motion perception and other areas of visual perception.

1.3 Outline of thesis

A review of literature relating to visual motion perception is presented in **Chapter 2.** The main areas covered are real and apparent motion. To provide the necessary background to the study of visual motion perception requires consideration of other areas of visual perception, including peripheral vision, acuity and cortical magnification factor. The literature review is not intended to be exhaustive but rather to be representative of areas germane to this thesis.

Details of experimental methods used in the present investigation are given in **Chapter 3.** The experimental apparatus, computer programs and procedures are described, along with an explanation of the statistical methods used for data analysis.

The first set of experiments is described in **Chapter 4.** Here the dependence of the temporal response characteristics of the fine-grain movement illusion on retinal eccentricity, adaptation level (scotopic and photopic) and dot flash duration is considered. The experiments described measure subjects' performance objectively, as determined by the correctness of reports indicating the temporal order of stimulation in generating the illusion. A separate experiment considers the issue from a subjective point of view, by using a rating procedure (as used in many studies of apparent motion). The results of this experiment, on the apparent "strength" of the illusion, are compared with data derived from the objective paradigm.

Two dot flashes used to generate fine-grain motion should, by definition, be spatially unresolved. The extent to which the dot separation can be reduced and still generate a fine-grain movement illusion is considered in **Chapter 5.** Measurements are also made of an appropriately matched, spatial acuity performance. The minimum dot separation required for the fine-grain movement illusion and for spatial resolution are discussed in terms of underlying motion- and form-detection mechanisms. Two experiments are described which consider temporal aspects of the minimum separations described above; and a final experiment considers the fine-grain movement illusion under dichogeniculate presentation of the dot flashes.

The experiments described in Chapters 4 and 5 consider characteristics of a single fine-grain movement illusion. The simultaneous presentation of two fine-grain movement illusions can, under certain conditions, result in a mutually destructive interference of the two illusions. **Chapter 6** investigates the interaction of two fine-grain movement illusions by determining the minimum distance by which they have to be separated in order not to destroy each other. Interaction thresholds are determined using two different stimulus configurations: the one in which the fine-grain movement illusions are generated with their directions of motion collinear, and the other in which they are parallel (but not collinear). Consideration is also given to interaction thresholds obtained solely with two inward moving fine-grain movement illusions and two outward moving illusions. The last experiment in this chapter considers the dependence of the interaction threshold on dot separation.

In **Chapter 7** five experiments are described which consider extrapolations in illusory motion. The first three of these experiments investigate the perceived extent of the fine-grain movement illusion as a function of stimulus eccentricity, dot flash separation and increasing stimulus intensity. The last two experiments consider extrapolations in classical apparent motion.

Finally **Chapter 8** provides a review of the main experimental findings and their implications to visual motion perception and other areas of visual perception.

Chapter 2

Review of Literature

Chapter 2: Review of Literature

2.1 Perception of real motion

2.1.1 Motion acuity

A measure of the ability of the visual system to detect motion is provided by velocity thresholds. Such thresholds have been defined as the minimum detectable velocity, while the distance traversed by the moving object and all other factors are kept constant. Aubert (1886) found velocity thresholds of approximately 1 min-arc.sec^{-1} for long vertical lines viewed in the presence of a clearly visible surround. (Spatial extents or dimensions of stimuli are expressed here in degrees or minutes of arc visual angle, and velocity in minutes of arc per second, abbreviated to min-arc.sec^{-1}). If, however, the same moving stimulus was viewed in the absence of the surround, velocity thresholds rose by an order of magnitude to 10-20 min-arc.sec^{-1}. Similar values were obtained by Brown (1931a, 1931b) who found velocity thresholds of 2-6 min-arc.sec^{-1} using moving spatially periodic gratings. Leibowitz (1955b) confirmed these results and further showed that for short stimulus durations velocity thresholds were unaffected by the presence, or absence, of stationary background cues. For long stimulus durations, however, the introduction of a stationary surround reduced the velocity thresholds by about 48%. From these findings Leibowitz (1955a, 1955b) suggested that for short stimulus durations motion is processed by a low-level mechanism, whereas for long stimulus durations the processing occurs more centrally in the visual system.

The concept of two different motion-detecting mechanisms at different stages in the visual pathway may be compared with recent studies of low-level and high-level motion-detecting processes (Braddick, 1980).

Changes in a visual stimulus occurring over a small spatial and temporal range may be processed by a low-level motion-detecting mechanism, whereas large global changes may be subserved by a high-level mechanism. The idea of low-level and high-level motion-detecting mechanisms is discussed further in section 2.3.

Gordon (1947) examined the relation between velocity thresholds and spatial (acuity) thresholds. Spatial thresholds were obtained by requiring subjects to detect gaps in a stationary Landolt ring (consisting of nine equidistant gaps as opposed to the normal single gap). Velocity thresholds were obtained using the same Landolt ring, but rotating, with subjects required to set the speed of rotation such that rotary motion could just be observed. This procedure, as used by Gordon (1947), was designed to determine velocity thresholds and spatial thresholds which could be directly compared since the same type of stimulus was used. The resulting velocity thresholds were found to be approximately proportional to the corresponding spatial thresholds (the value of the proportionality constant was not given).

The minimum distance over which motion may be detected is referred to as the <u>displacement threshold</u>. Velocity thresholds differ from displacement thresholds in that the former require an object to be seen in motion whereas the latter only require the detection of a change in an object's position.

The earliest experimental data relating to displacement thresholds were provided by Exner (1875) whose results indicated that displacement thresholds were smaller than spatial thresholds. Basler (1906) obtained displacement thresholds of 20 min arc in photopic illumination, an angle less than that required for two-dot resolution (see section 2.5). The findings of Exner (1875) and Basler (1906) seem to suggest that the detection of motion, as quantified by displacement thresholds, is finer than the spatial resolution of the visual system. In contrast to this, evidence exists that the two thresholds, displacement threshold and spatial threshold, are of similar magnitude (Stern, 1894; Stratton, 1902; Gordon, 1947). Stern (1894), Stratton (1902) and Gordon (1947) all found displacement thresholds to be of the same order of magnitude as some measure of spatial acuity. Stratton (1902) used a vertically moving point of light to determine displacement thresholds, and two stationary points of light presented in succession to measure the corresponding spatial acuity. He claimed that the sequentially presented light points did not give rise to apparent motion. Measurements were made at 5^{o} and 30^{o} and the resulting displacement thresholds and spatial thresholds were found to be equal. A further experiment by Stratton (1902) using horizontally moving vertical lines to measure displacement thresholds, and two vertical lines placed end-to-end to measure vernier acuity, resulted in similarly matched thresholds. Gordon (1947) obtained indirect estimates of displacement thresholds from measurements of velocity thresholds, as discussed on the previous page, and like Stratton (1902) he found that displacement thresholds and spatial acuity were approximately matched.

More recently Scobey and Horowitz (1976) have obtained experimental data which suggest that displacement thresholds are significantly smaller than two-dot spatial resolution. They used a two-alternative forced-choice experiment which required subjects to indicate whether two dot flashes or one stationary flashing dot was presented in the visual field. The stimuli used to determine spatial thresholds and displacement thresholds differed as follows. For spatial thresholds the two dots were switched on for a duration of 0.5 seconds and then switched off for 0.5 seconds. This was repeated for a three-second period after which the subject had to indicate whether one or two dots had been presented. For the displacement thresholds the dot remained stationary for 0.5 seconds and then was rapidly displaced to the final site, where it was held stationary for a further 0.5 seconds. This sequence was also repeated over a three-second period after which the subject indicated his response. A range of dot separations were used, including a zero dot separation, and the resolution threshold was set at 50% detection level (after correction for false indications). Measurements of both thresholds were made at retinal sites between 5^o and 40^o eccentricity. The resulting displacement thresholds were found to be consistently less than the corresponding spatial thresholds. Spatial thresholds increased monotonically from 5 min arc to 20 min arc, while the displacement thresholds were between a quarter and a fifth of the spatial thresholds. In a different set of experiments Scobey and Horowitz (1972, 1976) obtained neurophysiological data relating to displacement thresholds and spatial thresholds, which supported the psychophysical results described above.

The method used by Scobey and Horowitz (1976) compares favourably with other studies which determine some measure of motion acuity which can be reasonably compared with some spatial acuity measure. Even so, it is not evident from their experiments whether displacement thresholds were determined by measurement of responses to the detection of displacement or to the discrimination of two dots from one dot. It shown in Chapter 5 that with the fine-grain movement illusion the relationship between motion acuity and spatial acuity can be explored in a manner that is probably more appropriate than other methods used in previous studies.

Temporal response characteristics of the peripheral field were considered by Tyler and Torres (1972). They obtained measurements of motion sensitivity, as defined by the just detectable displacement of a sinusoidally moving line, as a function of the temporal frequency of the line. Motion sensitivity was found to have a bandpass dependence on the temporal frequency of the line, and these tuning curves were found to be more narrowly tuned with increases in retinal eccentricity up to 20^{o}. The narrowing of these temporal response curves, with increasing retinal eccentricity, probably reflects a decrease in the ability of the peripheral visual field to detect motion.

2.1.2 Motion aftereffects and direction-specific adaptation

The previous section was concerned mainly with the absolute detection of moving stimuli. Once a visual stimulus is above some detection level the resulting perceived motion can often differ from the object's veridical motion. For example the prolonged inspection of a continuously moving object results in a gradual reduction of the object's apparent velocity (Goldstein, 1957). This adaptation resulting from the prolonged inspection of a moving stimulus is related to two other phenomena, namely motion aftereffects and direction-specific adaptation. After prolonged inspection of a moving stimulus the transfer of gaze to a stationary stimulus results in an apparent movement of the stationary stimulus. The illusory motion is seen in the direction opposite to that of the adaptation (moving) stimulus and is referred to as a motion aftereffect.

Adaptation to a moving stimulus elevates the threshold for the subsequence detection of like stimuli moving in the same direction as the adaptation stimulus (Carlson, 1962). Sekuler and Ganz (1963) obtained contrast threshold measurements for the detection of moving gratings under two conditions, the one in which the direction of motion during the adaptation (inspection) phase was opposite to that during the test phase, and the other in which the directions of the adaptation and test stimuli were the same. For velocities between 4 $deg.sec^{-1}$ and 9 $deg.sec^{-1}$, of both the test and adaptation stimuli, the luminance threshold under the opposite condition was consistently lower than that of the same condition. Measurements of the duration of the motion aftereffect, with a stationary test stimulus, were found to have a similar dependence on velocity as the threshold elevations. From these observations Sekuler and Ganz (1963) concluded that the motion aftereffect was a consequence of direction-specific adaptation (see also Sutherland, 1961).

The speed of the adaptation stimulus and of the test stimulus were equal in the experiments conducted by Sekuler and Ganz (1963). Using adaptation and test stimuli of different velocities, threshold elevations were found to be maximum when the velocities were similar (Pantle and Sekuler, 1968a,b).

The experimental data discussed above are consistent with the notion that there are direction-sensitive and velocity-sensitive elements in the human visual system. These elements exhibit a degree of tuning, in that they respond optimally to certain ranges of stimulus velocity or orientation. Similar observations have been found for the form-detecting mechanism, for it has been reported that the human visual system may contain several different classes of size detectors, with the sensitivity of each detector maximal to visual targets with sizes within a particular range (Pantle and Sekuler, 1968a).

The basis for direction-sensitive and velocity-sensitive motion-detecting mechanisms has been explored by electrophysiological recordings of neuronal activity in the mammalian visual system. Hubel and Wiesel (1962) described cortical neurones in the cat visual system which only responded strongly to stimuli moving through the cell's receptive field in a particular direction. The continual stimulation of the receptive field resulted in a fall-off of activity in the neurone's response (Hubel and Wiesel, 1965). These direction-sensitive neurones furthermore exhibited velocity-sensitive characteristics in that a given neurone responded maximally to a particular velocity. Analogous findings in retinal ganglion cells of the rabbit have been reported by Barlow and Hill (1963, 1964).

2.1.3 Motion and flicker perception

Foster (1968) considered the perception of moving spatially-periodic patterns. He found two critical temporal frequencies which divide the visual sensation into three distinct ranges; a lower range in which there exists a well defined sensation of motion and direction sense, a middle range where the sensation of motion is present but without a well defined direction sense, and finally, an upper range where the pattern is seen to be fused and without a sensation of motion nor direction (a stationary stroboscopic effect could also be seen under some circumstances). The dependence of the two critical frequencies on the angular and spatial periodicity of the pattern was examined by Foster (1969, 1971a, 1971b). A theoretical model was proposed by Foster (1969, 1971a, 1971b) which described the response of the human visual system to certain classes of moving stimuli. The model was based on the existence of two information-processing channels; a vertical channel which dealt with local fluctuations of stimuli, and a horizontal channel concerned with the spatial distribution of fluctuations. The horizontal channel (H-unit) was identified with the Reichardt multiplier

(Reichardt and Varju, 1959) and the vertical channel (V-unit) with the de Lange filter (de Lange, 1954). It was shown that the model has implications for the interaction between receptors, the existence of the phi-phenomenon and the existence of a lower speed for motion perception.

2.1.4 Motion-sensitive and pattern-sensitive mechanisms

Experiments described in the previous sections required the absolute detection of a stimulus from a uniform field of the same average luminance. This detection could be based on either the recognition of a spatial pattern or the detection of movement. At the absolute detection level an observer may see either a stationary pattern or a moving, flickering stimulus whose spatial structure is indistinct (Van Nes et al., 1967). Thresholds for flicker detection and pattern recognition were obtained by Keesey (1972), who found them to be independent functions of spatial and temporal frequency. From these observations Keesey (1972) proposed that the two thresholds represented the activity of two independent types of detectors in the human visual system; one detector sensitive to temporally modulated stimuli, which when activated results in the perception of movement or flicker, and another detector which is sensitive to the spatial structure of the pattern. These two types of detectors may be compared with the two information processing channels described by Foster (1969, 1971a, 1971b, see section 2.1.3). The independence of flicker detection thresholds and pattern recognition thresholds was confirmed by Kulikowski and Tolhurst (1973). They further found that the pattern recognition sensitivity was greatest at low temporal frequencies and moderately high spatial frequencies, whereas flicker sensitivity was maximal at intermediate temporal frequencies and low spatial frequencies (see also Tolhurst, 1973). The neurones responsible for flicker detection they called movement-analysers, and those responsible for pattern recognition they called form-analysers.

On the basis of their findings Kulikowski and Tolhurst (1973) proposed that the movement-analysers should exhibit transient characteristics when excited and the form-analysers sustained responses. For the neural mechanisms subserving the two mechanisms they considered the X-like and Y-like cells found in cat visual system (Enroth-Cugell and Robson, 1966; Cleland et al., 1971). Similar X- and Y- like cells have been identified in the visual system of the macaque monkey (de Monasterio et al., 1976; de Monasterio, 1978) and in the retina of the rabbit (Caldwell and Daw, 1978). These cells are distinguished on several aspects, one of which is that X-cells give mainly a sustained response to prolonged stimulation whereas Y-cells respond mainly transiently. Hence the sustained and transient characteristics observed in X- and Y-like cells are similar to the characteristics of the form-analysers and movement-analysers that Kulikowski and Tolhurst (1973) expected. Further evidence of this correspondence between the psychophysical observations and the physiological data are that X-cells respond optimally to higher spatial frequencies than Y-cells (Enroth-Cugell and Robson, 1966). A linearity difference is observed between X- and Y-cells, in that X-cells exhibit linear spatial summation over their receptive fields whereas Y-cells are highly non-linear. Similar linearity characteristics have been observed in the psychophysical case, for pattern systems show linear spatial summation while the movement system exhibits non-linear summation (King-Smith and Kulikowski, 1975). These similarities between the psychophysically observed motion-sensitive and pattern-sensitive channels and the X- and Y-like cells lead Kulikowski and Tolhurst (1973) to propose that the X-like cells are the substrates of the form system and the Y-like cells of the movement system. This though need not necessarily be correct for evidence exists that Y-like cells are no less sensitive than X-like cells to stimuli of low temporal frequency (Lennie, 1980a, 1980b). Lennie (1980a) reported that cortical cells, with the exception of a few, cannot be classified into distinct groups according to their sensitivity to spatial and temporal frequency; given that the movement-analysers and form-analysers, described by Kulikowski and Tolhurst (1973), are distinguished mainly by their different sensitivity to spatial and temporal frequencies, their relation to X- and Y-like cells is indeed questionable.

2.1.5 Spatial and temporal filtering in motion perception

The approach to motion perception as described in the previous section centred on the detection of moving grating stimuli. Other studies have considered the effect of such grating stimuli on the detection of simpler moving targets. Barbur and Ruddock (1980a) considered the detection of a circular disc moving across a spatially modulated background field. They obtained measurements of the luminance detection threshold, i.e. the luminance of the target such that it could just be detected, as a function of the spatial frequency of the background field. The relation between the luminance detection threshold and the grating spatial frequency they referred to as the interaction between movement and background grating, or for short, the IMG function. The effect of different parameters, of both the test object and the background grating, on the IMG function was considered by Barbur and Ruddock (1980a, 1980b). Two classes of IMG functions for foveal vision were distinguished; the one occurring when the background illumination was below 2.2 log trolands and peaking at about 4 cycles.deg^{-1}, the other occurring under higher background illumination and peaking at about 8 cycles.deg^{-1}. The IMG function measured at 30^{o} eccentricity peaked at lower spatial frequencies than those obtained at the fovea, and furthermore exhibited a similar shift in peak towards higher spatial frequencies at high illumination levels. Calculations were made of the half-sensitivity diameter of the IMG function at the fovea and at 30° off-axis and found to be 1.8 min arc and 8 min arc respectively (Barbur, et al., 1981). These values correlate with the psychophysical data reported by Johnson and Leibowitz (1976) who obtained displacement thresholds for motion detection of 1.5 min arc and 2 min arc at the fovea and at 30° eccentricity respectively.

Using techniques similar to those described above, Holliday and Ruddock (1983) investigated the temporal dependence and the spatio-temporal dependence of the threshold detection illumination level. The temporal dependence was investigated using a temporally modulated but spatially uniform grating, while for the spatio-temporal dependence a temporally and spatially modulated background was used. Responses obtained with the temporally modulated, spatially uniform field exhibited band-pass characteristics with peaks typically at 10Hz. The spatial characteristics of this temporal filter were found to be different from those of the IMG function in that the peak occurred at 1 cycle.deg^{-1} as (opposed to at about 4 cycles.deg^{-1}). Furthermore it did not shift towards lower spatial frequencies with increasing eccentricity. Spatial characteristics similar to those observed with the IMG function were, however, obtained using two identical gratings presented in spatial and temporal antiphase; the temporal characteristics obtained with two such gratings were found to be representative of a low-pass filter (Holliday et al., 1982).

These findings lead Holliday and Ruddock (1983) to identify two spatio-temporal filters, ST1 and ST2, associated with the two different sets of data they had observed. The ST1 filter has characteristics of a spatial band-pass filter with a centre frequency of 4 or 8 cycles.deg^{-1} (depending on the mean illumination level) and a low-pass temporal filter; ST2 also consisted of a spatial band-pass filter but centred at 1 cycle.deg^{-1} and a band-pass temporal response. The ST1 spatial response was dependent on the retinal site of the stimuli (its response moved towards lower frequencies as stimulus eccentricity increased), whereas the ST2 spatial response was relatively invariant with eccentricities up to 30^{0}. They proposed that ST1 filters may be associated with X-type mechanisms, as they possess sustained temporal responses and have small receptive fields; whereas ST2 filters could be associated with Y-type mechanisms as they are associated with transient stimuli and have larger receptive fields. Finally they describe a model representing the possible organization of the two spatio-temporal classes of filters.

The ST1 and ST2 filters have characteristics similar to the two information processing channels proposed by Foster (1969, 1971a, 1971b). In the model proposed by Foster the V-units extract information about local temporal fluctuations and therefore correspond to ST1 filters. The function of the H-units are more complex than that of the ST2 filters and it is likely that these filters represent an early stage of processing within the H-units.

2.2 Classical apparent motion

2.2.1 Introduction to classical apparent motion

One of the first investigations of classical apparent motion was reported by Exner (1875) who showed that two stationary light sources could give rise to vivid illusion of movement when flashed under appropriate conditions. Three stages giving distinct perceptions were identified by Exner (1875). For interstimulus intervals less than 10 msec the two flashes appeared simultaneous, at greater intervals they appeared as a single moving object, and at even greater temporal separations they appeared as two flashes in succession. Wertheimer (1912) conducted the first systematic study of apparent motion. He showed that the perception of apparent motion depended on stimulus characteristics, such as exposure time, interstimulus interval, intensity and spatial separation, and on the subject's attitude and task. The same three stages identified by Exner (1875) were observed by Wertheimer (1912) along with an additional two stages of motion: partial motion (in which the moving illusory object disappears and reappears as it journeys from the first stimulus to the second stimulus) and phi-motion (in which a sensation of motion is perceived without a clear perception of a moving object).

The relationship between interstimulus interval, stimulus separation and intensity was examined by Korte (1915) who proposed the following relations between the above three variables for apparent motion:

1) The stimulus separation is proportional to intensity, for a fixed interstimulus interval.

2) The interstimulus interval is inversely proportional to intensity, for a fixed spatial separation.

3) The interstimulus interval is proportional to the spatial separation, for a fixed intensity.

Korte (1915) further showed that if the second stimulus was brighter than the first stimulus then reversed apparent motion was perceived (the illusory object moved from the second to the first stimulus). This reversed apparent motion can be explained by the temporal latency of the first dimmer stimulus relative to the second brighter stimulus.

Korte's laws, as defined above, were shown by Neuhaus (1930) to be an oversimplification. He showed that apparent motion could be perceived over a greater range of conditions than that defined by Korte's laws. Neuhaus (1930) further showed that the onset-to-onset temporal separation provided a more suitable description of apparent motion than the interstimulus interval.

2.2.2 Spatial distortions

The final position of an illusory moving object is often perceived differently from the veridical position of the target (second) stimulus. Scholz (1924) examined the perceived separation of two flashing lights and found that for small interstimulus separations (typically of the order of 0.3°) the apparent distance was greater than the veridical distance, but at large separations (up to 17.3°) the perceived distance was smaller than the veridical distance. The magnitudes of both the expanded and the contracted separations were found to be an inverted U-shaped function of interstimulus interval, with the maxima occurring at the same interstimulus interval that yielded optimal apparent motion. This U-shaped dependence of overshoot (expanded separation) on interstimulus interval was also observed by Neuhaus (1930) but he was unable to find any evidence for contraction. The range of stimulus separations used by Neuhaus (1930) did not extend to the large values used by Scholz (1924). Overshoots obtained by Scholz (1924) and Neuhaus (1930) were typically in the range of 17%-44% and 9%-34%

respectively.

Kolers and Touchstone (1965) investigated the perceived distance traversed by illusory motion generated by two vertical lines separated by 2.4^{0} visual angle. Subjects were required to indicate whether the perceived distance traversed by a moving illusory object was greater or less than the distance set by two markers (the markers were placed a distance of 1.5^{0} below the centre of the lines). Measurements of the perceived distance were made over a range of interstimulus intervals. The results they obtained differed from those obtained by Scholz (1924) and Neuhaus (1930) in two aspects. First, the overshoots obtained were smaller (ranging from 4 to 8%), and second the overshoots were not an inverted U-shaped function of the interstimulus interval. Kolers and Touchstone (1965) considered the possibility that the variation in the perceived distance was due to eye movements but this conjecture was not verified (Kolers, 1972).

The overshoot in perceived position or distance in apparent motion is usually associated with the sequential flashing of two points of light or two parallel lines. In this thesis an experiment is described which demonstrates the existence of a different type of overshoot that may be obtained with the sequential presentation of a curved line followed by a straight line.

The existence of position and distance overshoots in visual apparent motion present problems to many of the simpler theories of classical apparent motion (see Kolers, 1972). For example vector field theories (Brown and Voth, 1937) and explanations based on overlapping fields of excitation (Wertheimer, 1912) do not provide natural schemes within which the existence of overshoot could be incorporated. Two theories of apparent motion which are possible candidates for explaining the phenomena of overshoots are next described.

Caelli and Dodwell (1980) proposed a network model of apparent motion in which a distribution of nervous activity is generated according to an iterative process (entailing a series of weighted summations) that builds up into a smooth continuous motion. Their model was used to predict an enhancement of the Poggendorf illusion under conditions of apparent motion and this prediction was verified experimentally. Within such a scheme the existence of overshoots can be considered as a residual decay of activity beyond the final state represented by the second stimulus.

An alternative approach, developed by Foster (1975b, 1978) and more cognitive in orientation, is based on a dynamical description of apparent motion. Foster's approach supposes that apparent motion is modelled internally according to laws similar to those operating in the physical three-dimensional world. The illusory object may be assigned a mass-like attribute and the dynamics of the illusory motion are determined by a principle of least action analogous to that used in classical mechanics. Evidence that processing in the visual system behaves in such an analogous manner has been provided in studies of pattern recognition and apparent motion (see for example Shepard and Metzler, 1971; Shepard and Judd, 1976; Shepard, 1981; Farrell and Shepard, 1981). The scheme proposed by Foster (1975b, 1978) correctly predicts the non-linear paths followed by some illusory transforming objects undergoing apparent motion (see Kolers, 1972). Within such a scheme the overshoot of apparent motion may be considered to be a consequence of the momentum of the mass-like attribute carrying the illusory object beyond the final target position.

2.2.3 Figural aspects

Many of the earlier studies of classical apparent motion used identical figures such as two point sources or two straight lines. Studies which considered figurally disparate stimuli generally concluded that apparent motion between two disparate stimuli could still be perceived but was less compelling than that perceived using identical figures (Wertheimer, 1912; Van der Waals and Roelofs, 1930; Squires, 1931; Orlansky, 1940). Although these early studies showed that apparent motion between disparate figures could be obtained, the way in which the visual system resolves figural disparities and hence constructs illusory motion was not determined. The manner in which the visual system resolved figural disparities was investigated by Kolers and Pomerantz (1971). They claimed that apparent motion was just as likely to take place between two disparate figures as between two identical figures. The resolution of figural disparity was found to occur not abruptly but changed smoothly and continuously as the illusory object traversed from the first to the second stimulus. For certain classes of stimulus disparities, for example when the two figures are mirror reflections of each other, this plastic deformation was not always perceived, for subjects often reported a rigid rotation outside the plane containing the two figures. This motion in depth was found to occur predominantly at high interstimulus intervals (typically at 260 msec) while the plastic two dimensional deformation occurred maximally at low values (around 50 msec). This latency of 210 msec was attributed to the increase in path length travelled whenever motion in depth occurred (see Shepard and Judd, 1976; Foster, 1978; Farrell and Shepard, 1981).

Navon (1976) provided further experimental evidence that figural identity contributes little in the construction of apparent motion. He found similar temporal latencies but believed these to be a consequence of longer processing time required to resolve the figural disparity; arguing that at short interstimulus intervals the time available to process the figural information was insufficient and hence two dimensional plastic deformation was constructed by the visual system, whereas for sufficiently long interstimulus intervals the figural identity was possible and hence the rigid transformation could be constructed.

The irrelevance of figural identity in generating apparent motion was questioned by White et al. (1979). They argued that as Kolers and Pomerantz (1971) used spatially superimposed stimuli it was possible that contour masking suppressed the figural information of the first stimulus (see Breitmeyer et al., 1974; Breitmeyer et al., 1976). By using spatially contiguous stimuli White et al. (1979) observed that figural identity played a significant role in the construction of apparent motion between figurally disparate stimuli.

The significance, or lack of significance, of figural aspects in determining apparent motion is still the subject of much controversy (Warren, 1977; Pittenger and Shaw, 1977; Ullman, 1977; Berbaum et al., 1981). The outcome of this issue has significant implications to the field of pattern recognition (see Neisser, 1967; Sutherland, 1973). There are two main theories of pattern recognition, namely a template matching theory (in which the visual input is compared to a standard template) and feature analysis (where the presence of certain features and their relationships is decisive). An inherent problem in pattern recognition is the difficulty of categorizing characteristics of visual stimuli. Apparent motion may provide a means by which the categorization of visual stimuli could be revealed. For example, in a series of theoretical and experimental investigations Foster (1972a, 1972b, 1973a, 1973b and 1975a) examined the relationship between the recognition of identity between two visual stimuli and the perception of apparent motion between the same stimuli when appropriately flashed. The stimuli he used were always such that pairs of stimuli were related by some specific transformation. For certain classes of transformations and types of visual stimuli (such as random-dot patterns and Landolt rings) Foster showed that if apparent motion could be induced between two objects then the two objects would be recognised as being the same.

2.2.4 Auditory and tactile apparent motion

Finally, it is of interest to note that apparent motion is not a phenomenon unique to the visual system. Similar perceptual illusions have been reported in both the auditory domain (Burtt, 1917(a); Kirman, 1983) and in the tactile domain (Burtt, 1917b). The existence of such illusory motion has lead to the suggestion of the existence of a central motion-processing mechanism which has afferents from all the senses (Sherrick and Rogers, 1966). Evidence for the existence of such a mechanism was given by Kirman (1974) who found the dependence of tactile apparent motion on stimulus duration was similar to that observed in visual apparent motion. Kolers (1979), however, has found differences between auditory and visual apparent motion. Claims have been made that intermodal apparent motion (i.e. perception of apparent motion resulting from the stimulation of two different senses) can be perceived (Zapparoli and Reatto, 1969); however other studies have not been able to produce such intermodal illusions (Allen and Kolers, 1981).

2.3 Short-range apparent motion

Studies of classical apparent motion, as reviewed in section 2.2, have typically employed geometrical shapes such as circles, triangles and rectangles. In this section consideration is given to apparent motion elicited when two random-dot patterns are alternated.

Random-dot patterns have been used extensively in studies of stereoscopic vision (Julesz, 1960, 1971; Marr and Poggio, 1976). These random-dot patterns, also referred to as stereograms, usually consist of two pairs of identical patterns, except for a central region of dots which in one of the patterns is displaced relative to its position in the other pattern. When one of the patterns is presented to one eye and the other pattern to the opposite eye, the central region appears at a different depth from the rest of the pattern. These stereograms contain no form information, such as edges of recognisable objects, and the correspondence established between the central displaced regions cannot be explained by a pairing of nearest neighbours (as this would result in some of the dots standing out in depth and others as receding in depth). Instead the correspondence is believed to be a consequence of a global perceptual organisation which resolves the ambiguities of the local process acting on a nearest-dot basis (Julesz, 1971).

The alternation, at an appropriate rate, of two random-dot stereograms of the kind described above, presented to both eyes results in apparent motion of the central region (Julesz and Payne, 1968; Anstis, 1970). The region of the random-dot pattern in apparent motion is seen to oscillate backwards and forwards coherently and is perceived as being segregated from the surround by clear boundaries. Since each of the stereograms is a homogeneous random array the shape seen segregated from the surround is not perceived in either of the patterns alone and is only revealed by the relationship between the displaced regions.

The global process giving rise to perceptual segregation in depth perception in static random-dot stereograms viewed dichoptically is a natural candidate for the mechanism responsible for segregation perceived in coherent motion of two alternated stereograms. This, however, need not necessarily be true, as random-dot stereograms can be constructed which when viewed stereoscopically result in the central region been perceived in uniform depth (relative to the surround) but when exposed alternatively to both eyes do not give rise to coherent apparent motion (random local motion, referred to as incoherent motion, is instead seen, Braddick, 1974).

Braddick (1973, 1974) made use of the visibility of the segregated shape as an indicator of the operation of the mechanism constructing the coherent apparent motion. By using displaced central regions which were either vertically or horizontally orientated rectangles he was able to make an objective study of the limiting conditions for coherent apparent motion. Subjects were required to indicate the orientation of the rectangle and to give a rating on the perceived clarity of its boundaries. The success rate (per-cent correct indications) and clarity ratings were measured as a function of the dot displacement, ranging from 1 min arc to 40 min arc, and were found to decrease with increasing dot displacement. Subjects' response times were also monitored and found to increase with dot displacement. For the smallest displacement (1 min arc) per-cent correct responses reached 100% and the clarity ratings corresponded to maximum clarity. The perceptual segregation of the rectangle deteriorated at displacements of about 5 min arc and was complete at displacements of 20 min arc. It was further shown that the discriminability of the central region decreased with increasing interstimulus interval (ranging from 10 to 80 msec) and that the central region appeared stationary when the frames were viewed dichoptically, although his results do suggest that some apparent motion was obtained under dichoptic presentation of the random-dot patterns.

The limiting displacement for segregation has been shown to depend on the retinal angle and not on the number of pixels across which the region is displaced (Baker and Braddick, 1982a). Furthermore the limiting displacement depends on the absolute displacement of each region alone and not the relative displacement of neighbouring regions (Baker and Braddick, 1982b). Finally Baker and Braddick (1982b) considered the dependence of the displacement limit on eccentricity. Using a restricted range of eccentricities it was shown that the displacement limit increased with eccentricity. It is not clear from their results whether at the larger eccentricities segregation still occurred at the minimum displacement of 1 min arc. It might be expected that the minimum displacement required to perceive segregation should increase with eccentricity, as occurs with velocity thresholds and displacement thresholds (see section 2.1).

The small spatial and temporal range over which segregated coherent motion may be perceived in alternating random-dot patterns led Braddick (1974) to suggest that the visual processes were subserved by a low-level motion-detecting mechanism (by low-level it is implied that the processing occurs relatively early in the visual pathway). The failure to obtain coherent motion under dichoptic conditions is consistent with the notion that a low-level mechanism is responsible, although a monocularly driven high-level process cannot be ruled out. A second motion-detecting mechanism, occurring at a high-level in the visual pathway, may in turn be responsible for the perception of apparent motion from the succession of two widely spaced stimuli. That classical apparent motion can be obtained under dichoptic presentation (Shipley et al., 1945) adds further support to the possible existence of two separate motion detection mechanisms. Further evidence for the distinction between two types of apparent motion is given by Braddick (1980) and Braddick and Aldard (1978). The short-range apparent motion obtained with alternated random-dot patterns may be related to the fine-grain movement illusion (Foster et al., 1981). The relationship between the two types of illusory motion is discussed in section 2.4.

The existence of two different motion-detecting mechanisms, operating over different spatio-temporal scales, can however be questioned. Classical apparent motion can be generated using closely spaced stimuli (Wienke and Steedman, 1965) and the fine-grain movement illusion can be obtained under dichoptic conditions (Thorson et al., 1969). Furthermore, as noted previously, the results reported by Braddick (1974) do suggest that some degree of apparent motion could be obtained under dichoptic presentation of two alternated random-dot patterns. It is possible, therefore, that there is no clearly defined spatio-temporal range over which one motion-detecting mechanism operates at the exclusion of some other motion-detecting mechanism.

2.4 Fine-grain motion perception

In sections 1.1 and 1.2 the fine-grain movement illusion was introduced and two aspects of the illusion, the spatially unresolved dot flashes required to generate the illusion and the resulting temporal tuning characteristics, were discussed. Consideration is given next to other properties and aspects of the illusion.

The temporal tuning characteristics (see Figure 1.1) were obtained by Biederman-Thorson et al. (1971) under two different viewing conditions; a high-luminance condition and a low-luminance condition. Under the high-luminance condition the tuning curves were found to be shifted towards shorter interstimulus intervals (i.e. increasing temporal resolution). This observation was made at a single retinal site of 22° eccentricity. In Chapter 4 the temporal tuning characteristics of the illusion, under scotopic and photopic levels of adaptation, are considered as a function of eccentricity.

The possibility that the fine-grain movement illusion and its temporal tuning characteristics were an artifact of involuntary eye movements was considered by Thorson et al., (1969) and Biederman-Thorson et al. (1971). Presentation of the dot flashes under stabilized vision gave extrapolated illusions and temporal tuning characteristics similar to those obtained with normal viewing of two sequentially flashed dots. In a separate experiment recordings of eye movements were made and it was found that no saccades occurred within ±400 msec of each stimulus presentation. The results of this experiment also gave temporal tuning characteristics and it was concluded that the perceived extrapolated illusory movement and its temporal tuning characteristics were not an artifact of involuntary eye movements. Furthermore the illusion could not depend entirely on retinal interactions, as it was shown that the illusion could be elicited dichoptically, and that it was likely that the neuronal mechanisms responsible for the illusion must occur in the same hemisphere as the illusion could not be obtained with dichogeniculate presentation of the dot flashes. Dichogeniculate aspects of the fine-grain movement illusion are considered further in

Chapter 5.

Foster (1977) considered whether the two different receptor systems, rods and cones, acted independently in the production of the fine-grain movement illusion. By careful selection of the spectral composition and intensities of the dot flashes so that any single dot flash was visible to only rods or only cones, he was able to show that the illusion could be produced not only by cone-cone interaction and rod-rod interaction but also by rod-cone interaction.

The results of the simultaneous production of two fine-grain movement illusions were considered by Foster et al. (1981). They showed that, under certain spatial arrangements, two illusions could be made to interact with each other. Several different spatial arrangements of dot flashes were considered, three of which are illustrated in Figure 2.1 (the dashed arrows show the illusion that might be expected if the two illusions did not interact but simply superimposed). In Figure 2.1(a) the arrangement of dot flashes did not elicit the percept of two moving dots diverging but only a stationary blur which could not be distinguished from the percept obtained if the sequence was reversed. The interaction exhibited contrasts sharply with the split motion that can be obtained (in classical apparent motion) using a similar stimulus arrangement, but on a larger spatial scale (Kolers, 1972). Configuration 2.1(b) attempted to cross two illusory travelling dots, but this also resulted in interaction and only a "smear" moving towards the right was seen. This failure to cross two fine-grain movement illusions can be compared with the observation reported by Kolers (1972) which showed that the paths of two illusory moving lines (classical apparent motion) could not be made to cross. Figure 2.1(c) shows one of the arrangements that Foster et al. (1981) found which did give a

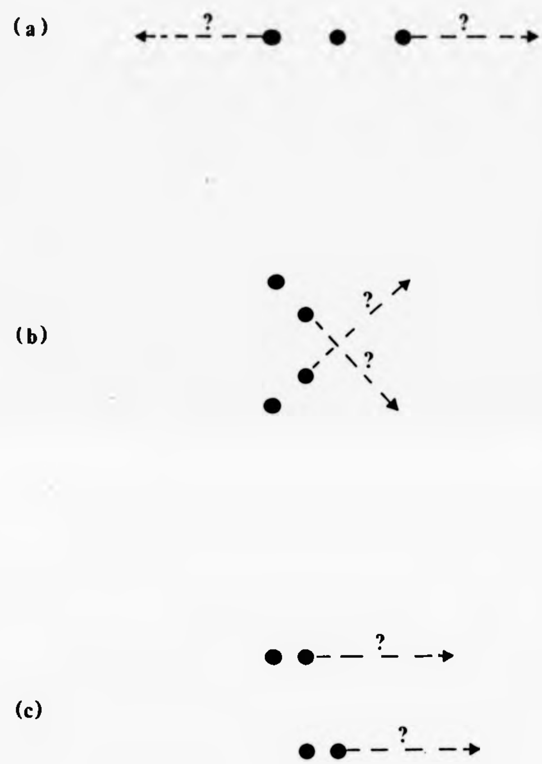

Figure 2.1 Three examples of spatial arrangements of dot flashes used by Foster *et al.* (1981) to explore the interaction that may be obtained with two closely spaced fine-grain movement illusions.

percept of two simultaneous fine-grain movement illusions. From their observations Foster et al. (1981) concluded that two fine-grain movement illusions induced within approximately a half degree of each other interfered destructively unless they were codirectional. The minimum distance by which two fine-grain movement illusions need to be separated so that they do not interact is here referred to as the interaction threshold. In Chapter 6 interaction thresholds obtained with two fine-grain movement illusions are determined for different arrangements of dot flashes.

In the fine-grain movement illusion, the perceived illusory moving dot is often seen to travel over a considerable distance. Foster et al. (1981) obtained measurements of the perceived size of the fine-grain movement illusion as a function of retinal eccentricity. They found that the size of the illusion increased from about 2.6^{o} at 9.9 degrees eccentricity to about 6.0^{o} at 23.5 degrees eccentricity. The dot separation they used was approximately 0.2^{o} and therefore these extents were over one order of magnitude greater than the actual separation of the dots giving rise to the illusion. When, however, the cortical span of the illusion was estimated, using cortical magnification factor (see section 2.6), it was found to be about 3 mm and was relatively independent of retinal eccentricity. The perceived extent of the fine-grain movement illusion is discussed further in Chapter 7.

The short-range apparent motion observed with alternated random-dot patterns (see section 2.3) may be related to the fine-grain movement illusion. Both types of illusory motion are associated with very small changes in the position of visual stimuli (typically in the order of several minutes of arc). The increase in the perceived extent of the fine-grain movement illusion can be compared with the increase in the displacement limit, obtained with random-dot patterns, with increasing eccentricity. It has been proposed (Foster et al., 1981) that the mechanism subserving the fine-grain movement illusion may be responsible for establishing the correspondence between pairs of dots in two alternated random-dot patterns. This is supported by the observation of Foster et al., (1981) that two nearby fine-grain movement illusions interfere destructively unless they are codirectional; for the correspondence could then not be based simply on a "nearest dot" principle, as this would result in a collection of closely spaced and randomly orientated fine-grain movement illusions which would destructively interfere and not give rise to coherent apparent motion. The similarities between the two types of illusory motion make it possible that they are subserved by the same motion-detecting mechanism (Foster et al., 1981; Baker and Braddick, 1982b).

A comparison of real motion perception and fine-grain motion was reported by Biederman-Thorson et al. (1971). They considered the perception of a peripherally viewed dot switched on, moved over 10 min arc and then switched off. An extrapolated movement illusion, identical to that obtained with two dot flashes, was reported. This extrapolated effect persisted even when the time taken to cover the 10 min arc distance was greater than 200 msec (a value outside the temporal tuning curves they obtained for the fine-grain movement illusion) and as large as 1 second. They noted that this result could be explained as follows; receptor pairs separated by less than 10 min arc would be stimulated within the 200 msec temporal response of the illusion and hence signal a motion response. Furthermore, they observed that if a dot was presented for some time and then moved a distance of 10 min arc and remained presented for some time, then an extrapolated illusion was not perceived. It appeared that the visual system did not construct the illusory extrapolated motion if the dot was actually seen to have stopped moving (as opposed to disappearing).

2.5 Spatial acuity

The degree to which spatial acuity operates in the visual system depends significantly on the type of visual stimulus and on the task the visual system is required to perform.

The detection of breaks (gaps) in visual stimuli is a common psychophysical measure of visual acuity. The minimum resolvable distance between two straight lines on a bright background may be as low as 0.5 min arc (Craik, 1939). Using gratings, consisting of alternating black and white strips, Frisen and Glansholm (1975) obtained values of 45 $cycles.deg^{-1}$ as the highest spatial frequency that can be resolved, corresponding to a resolution of 0.7 min arc.

The term hyperacuity is applied to any visual process in which spatial thresholds have a smaller value than the resolution limit expected from the discrete nature of the retina (Westheimer, 1979). The misalignment of two line segments can be detected for separations as small as 1-2 sec arc (Berry, 1948). Hyperacuity is observed not only with continuous lines but also with dots, for similar thresholds have been observed for the detection of misalignment of three dots (Ludvigh, 1953). Hyperacuity obviously requires some processing of the output of receptors to estimate, or interpolate, the optical image lying between centres of neighbouring receptors. Hyperacuity may be subserved by processes similar to those subserving stereoacuity, for tests in stereoacuity, in which small displacements between two stereograms presented dichoptically, give thresholds comparable with those obtained in vernier acuity (Blakemore, 1970; Snyder, 1982).

The last measure of spatial acuity considered is the contrast sensitivity function (Schade, 1956). The stimulus used is a grating whose intensity varies sinusoidally (or according to some other modulating function). The contrast of the grating is defined by the modulation ratio, m:

$$m = \frac{I_{max} - I_{min}}{I_{max} + I_{min}}$$

where I_{max} and I_{min} are the intensities of the brightest and dimmest parts of the grating. For a given spatial frequency, the contrast is adjusted such that an observer can just detect the presence of the grating. The mean intensity of the grating is kept constant so that the resulting thresholds are not confounded by changes in total intensity. Contrast sensitivity is the reciprocal of the contrast threshold. The contrast sensitivity as a function of spatial frequency is known as the contrast sensitivity function. Such functions exhibit a fall in sensitivity with low and high spatial frequencies and are maximal for intermediate values (Van Nes and Bouman, 1967; Campbell and Robson, 1968). Sensitivity is greatest at spatial frequencies of about 5 cycles.deg^{-1} and has an upper cut off value of about 60 cycles.deg^{-1} (Westheimer, 1972). The inverted U-shaped function of contrast sensitivity functions suggests the operation of high-pass and low-pass filtering in the visual system, with spatial resolution operating optimally at about 5 cycles.deg^{-1}.

The values of spatial acuity cited in the previous pages represent acuity measures obtained under optimal conditions, for example bright stimuli which are exposed for long durations and viewed foveally. As the conditions under which measurements are obtained deviate from such ideal conditions the resulting spatial thresholds tend to increase. The dependence of spatial acuity on two factors, namely stimulus duration and the position of the stimulus in the visual field, is next considered.

There is evidence that spatial acuity improves (i.e. resolution thresholds decrease) as the stimulus exposure time increases. Westheimer (1972) reported that the minimum angle of resolution is lowered considerably as the stimulus exposure is increased from 100 to 800 msec, with improvement occurring up to about 2 seconds. Increases in contrast sensitivity with increasing stimulus duration have also been reported (Schober and Hilz, 1965; Nachmias, 1967).

At photopic levels of illumination, visual acuity is highest in the foveal region and decreases rapidly with eccentricity (Ludvigh, 1941; Sloan, 1951, 1968). Using Landolt rings as test stimuli, Mandelbaum and Sloan (1947) obtained measurements of visual acuity, as a function of eccentricity, under photopic and scotopic levels of illumination (exposure time was 200 msec for all stimuli except those viewed foveally which were exposed for several seconds). At the highest level of illumination, spatial thresholds at the central region were about 0.9 min arc, and increased to 3.2 min arc and 22.7 min arc at 5° and 25° respectively. Under the lowest level of illumination thresholds were significantly higher than those obtained at the highest illumination level. Furthermore, thresholds obtained under the lowest illumination levels were almost constant with eccentricity (Mandelbaum and Sloan, 1947).

A similar fall in spatial resolution with eccentricity was demonstrated by Frisen and Glansholm (1975) using sinusoidally modulated gratings. Under photopic illumination levels they obtained values for the spatial frequency required for resolving the bars of the grating. Spatial thresholds at the fovea, 5^{o} and 25^{o} eccentricity were approximately 45 cycles.deg^{-1} (which corresponds to the bars being separated by 0.7 min arc), 15 cycles.deg^{-1} (2 min arc bar separation) and 5 cycles.deg^{-1} (6 min arc bar separation).

Next consider the dependence of hyperacuity on retinal eccentricity. Westheimer (1982) obtained measurements of two related hyperacuity thresholds (one requiring the detection of vertical alignment of two small squares, the other the detection of orientation of a straight line) along with measurements of the minimum angle of resolution (which required the detection of orientation of a grating which could be horizontally or vertically orientated). He found that thresholds for both types of hyperacuity at 10^{o} eccentricity were approximately 10 times higher than the values obtained at the foveal region, whereas the minimum angle of spatial resolution was only 4 to 5 times higher over the same range. Over the 10 degree range hyperacuity rose at least twice as fast with eccentricity as the minimum angle of resolution did.

2.6 Cortical magnification factor

The cortical magnification factor, M, is a measure of the linear extent of visual striate cortex to which each degree of the retina projects (Daniel and Whitteridge, 1959, 1961). Using neurophysiological techniques, Cowey (1964) and Rolls and Cowey (1970) obtained direct measurements of the cortical magnification factor in monkeys. They showed that it was maximal at the fovea and decreased with increasing retinal eccentricity. This implied that less striate cortex was available for the processing of visual information as retinal eccentricity increased, and was possibly one of the main factors responsible for the decrease in visual performance with eccentricity (examples of which are given later).

The direct measurement of the cortical magnification factor in man using neurophysiological techniques similar to those used in lower animals is clearly impracticable and has lead to its indirect estimation. Cowey and Rolls (1974) obtained estimates of the cortical magnification factor based on data obtained by Brindley and Lewin (1968) on the distribution of phosphenes in the lower left octant of the visual field. The values derived by Cowey and Rolls (1974) were analyzed by Foster et al. (1981) using a linear regression model. The regression equation that they obtained is used here in later chapters and was as follows:

$$M^{-1} = 0.091 + 0.067\theta$$

where M is in mm.deg^{-1}, eccentricity θ is in degrees, the correlation coefficient was 0.84.

An alternative approach to deriving estimates of the human cortical magnification factor was developed by Rovamo and Virsu (1979). They made indirect calculations based on the following three steps: first, they established the relationship between the magnification factor and retinal ganglion-cell density in primates, second, they found a plausible set of functions which described the density distribution of the human ganglion cells and third, they made use of empirical data for human visual acuity (Rolls and Cowey, 1970; Drasdo, 1977).

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Values of M derived by Cowey and Rolls (1974) are the most direct estimates available for the human visual system. Those obtained by Rovamo and Virsu (1979) are of similar form to that given by Cowey and Rolls (1974). Foster et al. (1981) used both sets of data to obtain estimates of the cortical image corresponding to the perceived extent of the fine-grain movement illusion, and found that they gave similar results. The author knows of no data on the cortical magnification factor relating to scotopic levels of adaptation, and therefore values of M had to be used which were derived from data based on photopic visual stimuli.

Next consider some applications of the cortical magnification factor. The phrase M-scaling is used to denote the transformation of spatial and temporal characteristics of a visual stimulus to the corresponding cortical image (Virsu and Rovamo, 1979). Measurements of photopic contrast sensitivity functions and the minimum angle of resolution, both as a function of retinal eccentricity, showed that after M-scaling could be made invariant with eccentricity (Virsu and Rovamo, 1979). Various critical sizes and distances, for example vernier thresholds and motion thresholds as obtained by Weymouth (1958), increase with eccentricity in a similar manner as M^{-1} and are therefore linearly related to M^{-1} (Virsu and Rovamo, 1979). The spatial sensitization phenomenon reported by Westheimer (1965, 1967) has a critical distance which, for photopic vision, increases with eccentricity in a manner almost identical to the minimum angle of resolution (Westheimer, 1982). The critical distance is defined as the size of an adaptation background field beyond which the background signal changes from being excitatory to being inhibitory. Analogous effects of M-scaling have been reported in the dependence on retinal eccentricity of spatial suppression of luminance relative to opponent-colour sensitivities (Foster, 1981).

Such examples of the dependence of visual processes on eccentricity have been taken as evidence for the existence of an invariance principle (Rovamo et al., 1978), namely that photopic visual stimuli are perceptually equally visible if the stimuli have equivalent cortical projected images, i.e. after M-scaling, irrespective of the position of the stimulus in the visual field. This invariance principle is not counter-intuitive given that M-scaling can be considered as a normalization process by which stimulation in the visual field becomes independent of the retinal location of the source of stimulation.

If all visual processes exhibited the same dependence on eccentricity as the examples given previously, then this invariance principle might be completely sufficient to explain changes in visual processing with eccentricity. One visual process, however, which does not conform to this invariance principle is the dependence of hyperacuity on eccentricity (see section 2.5). The finding by Westheimer (1982) that hyperacuity thresholds rise at least twice as fast with eccentricity as does the minimum angle of resolution is not compatible with the invariance principle. Further, of all spatial thresholds considered in this section, hyperacuity is the one most likely to be dependent on central processing and should therefore be the most likely candidate to follow such an invariance principle.

Chapter 3

Experimental Methods

Chapter 3: Experimental Methods

3.1 Apparatus

Figure 3.1 shows the apparatus used in the experiments. Experiments were run using a minicomputer to generate and display the stimuli, record the subject's response and analyse the data (during both the run-time of an experiment and for off-line analysis). The computer was a CAI (Computer Automation Incorporated) Alpha 16 bit LSI minicomputer with 64 Kbytes of RAM and dual disc drives, each with an unformatted storage capacity of 300 Kbytes.

A calligraphic interface, QVEC, linked the minicomputer to a Hewlett Packard 1321A X-Y CRT display. The phosphor, P4 sulphide, had a decay time of less than 1 msec. The transfer of data from the computer to QVEC was achieved by direct memory access, so enabling the stimulus data to be accessed, and therefore displayed, rapidly. The refresh rate of a vector displayed on the CRT was locked to the mains signal, so that a stimulus requiring a duration of say 100 msec was achieved by 6 refreshes, each refresh separated by a 20 msec blank interval. This fine temporal structure of the stimulus was not detectable by subjects. The refresh rate was locked to the mains cycle so that any possible distortion of the signal would not give rise to fluctuations in the position of flashes on the face of the CRT.

Subjects viewed the CRT through a viewing system (see Figure 3.1) which provided a dark featureless background field (for experiments conducted under scotopic conditions) and a uniform light background field (for experiments conducted under photopic conditions). The background lighting was provided by four fluorescent tubes (Thorn 'Daylight cool

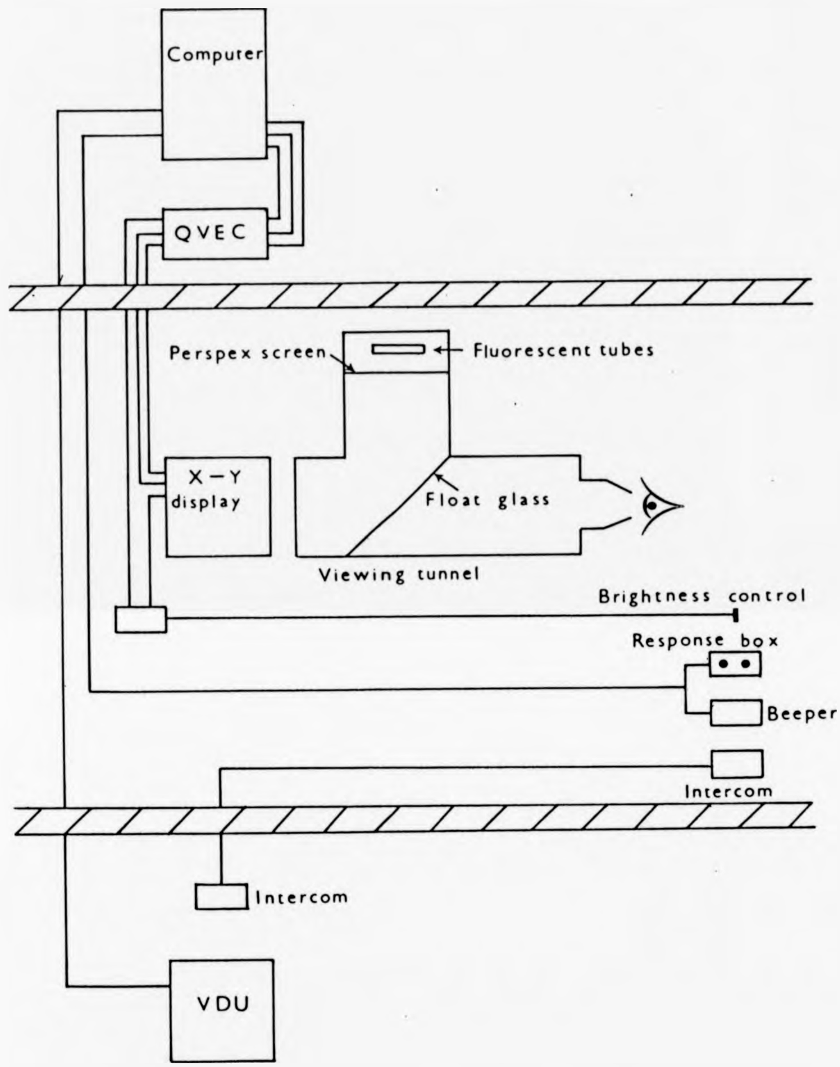


Figure 3.1 Apparatus used for experiments.

light') powered from a stabilized D.C. supply. Sheets of white perspex diffused the light, which was then reflected by a sheet of float glass. The luminance of the background field was about 30 cd m^{-2}. A viewing hood was used to steady the subject's head. Fixed to the face of the CRT was a yellow light emitting diode, used as a fixation point. The viewing distance was 75 cm.

The luminance of the CRT display could be set by the subject while viewing the display through the viewing system. A hand-held push-button box was linked to the computer. Subjects used this button box to initiate a block of trials and to indicate their response in each trial. An intercom system, linking the subject to the experimenter, was available so that any queries by the subject could be dealt with quickly.

3.2 Computer programs

The programs used to control experiments and for data analysis were written by the author in an extended version of Fortran II. Figure 3.2 illustrates the operation of the program used to control experiments. Before the start of an experiment a control file was set up, by the experimenter, containing all the necessary parameters required for the experiment. At the start of the experiment the controlling program read the control file and proceeded to run the experiment automatically. No experimenter intervention was required other than setting up the original control file. The data analysis program was used to fit a psychometric function to the response functions obtained experimentally. The method of analysis is described in section 3.6.

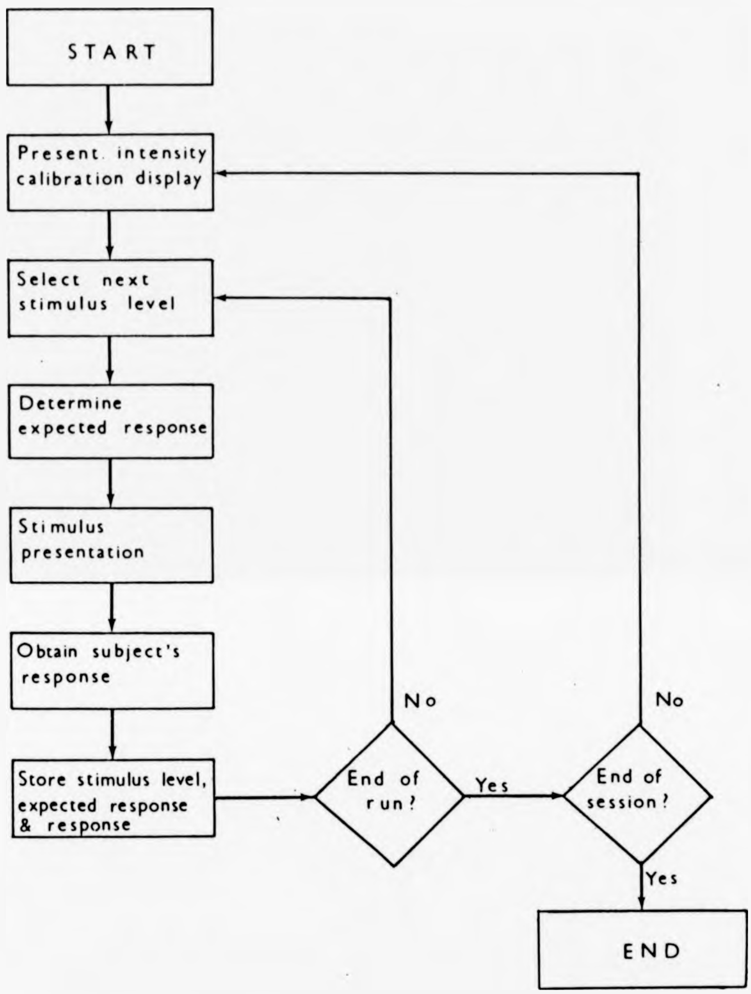


Figure 3.2 Flow chart illustrating program used to control experiments.

3.3 Stimuli used for experiments

The stimuli used were dot flashes, with each dot subtending approximately 0.04^{o} visual angle. The dot flashes were presented to the left of the fixation point. Subjects fixated the fixation point with their right eye and hence the stimuli fell on the temporal side of the retina (so avoiding the blind spot on the nasal side). The horizontal distance between the fixation point and the midpoint of the stimulus was controlled by the computer and varied as so to give the required retinal location (ranging from 5^{o} to 25^{o} eccentricity). The display was calibrated, before the start of all experimental sessions, using a transparent sheet consisting of vertical and horizontal markings identical to that used in a calibration pattern displayed on the CRT face. The resolution of the display, that is the minimum possible distance between the centres of two dots, was 0.01^{o} vertically and 0.03^{o} horizontally. This difference in resolution resulted from the requirement that a large field (25^{o}) was required horizontally, whereas vertically only a small field was required with maximum resolution.

The duration of each dot flash was, in most experiments, about 1 msec as a single painting was used with no refreshes. For experiments requiring longer dot flash durations the refresh rate was 20 msec. The interstimulus interval between two dot flashes depended upon the particular experiment and details are given later where appropriate.

The intensity of the stimuli was set by the subject to be ten times luminance increment threshold (typically 35 μcd.sec). Subjects achieved this by adjusting the luminance of a calibration display while viewing it through a 1 log unit neutral density filter placed over the screen of the CRT. The luminance calibration display consisted of a single flashing dot, of duration equal to that used in the experiment, presented at the relevant retinal site.

3.4 Experimental procedure

The majority of experiments were based on a two-interval forced-choice paradigm. The task subjects were required to perform depended on the particular experiment. Instructions to the subject were type-written, and an example set of instructions (as used for Experiment 4.1) follows.

> When you are instructed to start the experiment press button 4. This will initiate the intensity-calibration display and you may proceed to set the intensity of the display. This is achieved by first moving the filter to the far right, fixating the fixation point and adjusting the intensity such that you can just see a flashing dot. Upon completion of your setting you must move the filter back to its far left position and then press button 3. You will then hear 2 tones, indicating that the first run is about to start. At this point please fixate the fixation point. You will be presented with a visual stimulus consisting of two vertically separated dot flashes that may give rise to an appearance of motion. Upon completion of the stimulus you are required to indicate whether the upper flash or the lower flash occurred first, using, if present, any motion cues.

Your response is signalled as follows:

a) Press button 1 if the upper flash occurred first

b) Press button 2 if the lower flash occurred first

Try to respond as quickly, but also as accurately as possible. Upon indicating your decision, the next stimulus will be automatically presented after a few seconds. Please ensure that you are fixating before the onset of the next presentation.

At the end of each run you will hear 2 tones indicating a rest period. When you are suitably rested you may continue with the next run by pressing button 4; then proceed to reset the stimulus intensity and continue as described above. Upon completion of the last run you will hear several tones indicating that the session is over and you may leave.

Do you have any questions?

Subjects were required to dark adapt for 20 minutes. This was timed by the experimenter and the subject told, via the intercom, when the period was complete.

Subjects were given the option of initiating trials themselves or for the trials to follow automatically after each response. All subjects opted for the latter of these two options. No feedback, concerning the subject's performance, was given.

Each experimental session lasted between 45 minutes and 1 hour. Experiments involving threshold tracking (see section 3.6) typically required a total of 15 runs, consisting of 3 runs per retinal site and 36 trials per run. Experiments using the balanced block design (see section 3.7) typically consisted of 3 runs, that is one run at each retinal site, but each run consisting of 100 trials (instead of 36). Observations at different retinal sites were made systematically, with eccentricity either increasing (that is starting at 5^{0} and progressing to 25^{0}) or decreasing (going from 25^{0} to 5^{0}). The order of the eccentricity alternated with each experimental session.

3.5 Experimental design

In the majority of experiments the subject was presented with a stimulus (or stimuli) and was required to make a binary decision based on his perception of the stimulus (or stimuli). During a run the stimulus (or stimuli) presented to the subject differed, from trial to trial, in only one of two possible ways. First, there was the subject's required response. Each trial could be assigned an expected correct response (for example the onset sequence of two dot flashes) and according to whether the subject's response matched the expected response a correct or incorrect score could be given for that trial. Second, there was some measure of the stimulus, referred to as the stimulus level which was allowed to vary from trial to trial. The stimulus level varied either continuously or was restricted to a set of pre-determined discrete values. The expected response, however could only be one of two possible states. The subject's performance, as defined by the percentage of trials performed correctly, as a function of the stimulus level is referred to as a response function. The characteristics of the response function depend upon the nature of the experiment. Experiments described in this thesis gave rise to two different types of response function: the one in which the subject's performance increases monotonically with the stimulus level (referred to as a psychometric function), and the other in which performance levels are an inverted U-shaped function of the stimulus level. Two different experimental designs were made use of to examine the two different response functions encountered in this study. These are an adaptive threshold tracking procedure, used whenever the response function was expected to be of the type that monotonically increased, and a randomized balanced block design used for the inverted U-shaped response functions. First consider the adaptive procedure. An adaptive procedure is designed to determine, quickly and efficiently, a predefined threshold level (defined as the stimulus level at which the response function reaches some criterion level). The tracking algorithm proceeds typically as follows. The stimulus level is initially set such that the subject's task is relatively easy and hence the subject's performance is above the required level. The stimulus level is then decreased, according to a given set of rules, until the subject's performance falls below the required level. The procedure is then reversed (the exact rules and conditions that determine the reversal are given in section 3.6) so that the stimulus level begins to increase so making the subject's task easier. The adaptive procedure therefore yields information at a region about the threshold, but at the expense of the characteristics of the response function at regions remote from the threshold level. Should the performance level not be a monotonic function of the stimulus level then such an adaptive procedure cannot be used as there may not be a uniquely defined threshold level. Hence the adaptive procedure design was only used whenever there was an *a priori* reason to expect a monotonic response function and only a threshold level was required (as opposed to information about the whole function). The adaptive procedure used in this thesis is an hybrid version of PEST (Parametric Estimation by Sequential Testing) in which inferences are made about the whole response function underlying the PEST data, and is fully described in section 3.6.

Next consider the randomized balanced block design. Here the subject's immediate response history is not used to determine the next stimulus level, but a predefined set of stimulus levels are used and an equal number of tests made at each stimulus level. This procedure therefore gives more detailed information of the whole response function, within a given range of stimulus levels, but at the expense of less information at some specified point of interest. Stimulus levels are selected from a fixed set according to an algorithm which randomizes and balances the order in which the stimulus levels are selected. The use of such an experimental design does not place any requirements on the nature of the response function under investigation. This method is fully described in section 3.7.

3.6 Adaptive threshold tracking procedure

The adaptive procedure used was based upon an hybrid version of PEST as developed by Hall (1981). Hall's hybrid procedure differs from the original PEST procedure, as developed by Taylor and Creelman (1967), in that the final threshold level is not taken from the final state of the tracking but instead is interpolated from a psychometric function fitted to the data points. The rules used to select stimulus levels by Hall (1981) differ slightly from those originally developed by Taylor and Creelman (1967). The hybrid procedure used in this thesis is described next.

Figure 3.3 illustrates the operation of the adaptive procedure within the program. The software was written by Dr. G. F. Pick and consists of two subroutines WALD and PEST. The WALD routine determines whether a statistically significant decision can be made as to whether the current stimulus level is to high or to low. This decision is based on Wald's sequential probability ratio test (Wald, 1947). The WALD routine is initialized with the required per cent correct and continuously monitors the number of successes, the expected number of successes and the percentage correct. The routine PEST is initialized with the initial stimulus level, the starting step size and the maximum step allowed. After an experimental trial the result of the trial is passed to the WALD routine which exits with one of three responses: the stimulus level is too high, or too low, or no decision yet reached. The WALD response is passed to the PEST routine, which returns the next stimulus level and a flag to indicate whether or not the threshold has been reached. The rules used by PEST are as developed by Taylor and Creelman (1967) and are as follows:

1) On every reversal of step direction the step size is halved

2) If a second step is required in the same direction it is the same size as the first.

3) The fourth and subsequent steps in a given direction are each double their predecessors. This, however, is restricted by the maximum allowed step size (if one has been defined).

4) The third successive step in a given direction is either the same as or double the second depending upon the sequence of the steps leading up to the most recent reversal. The third step size was doubled if the

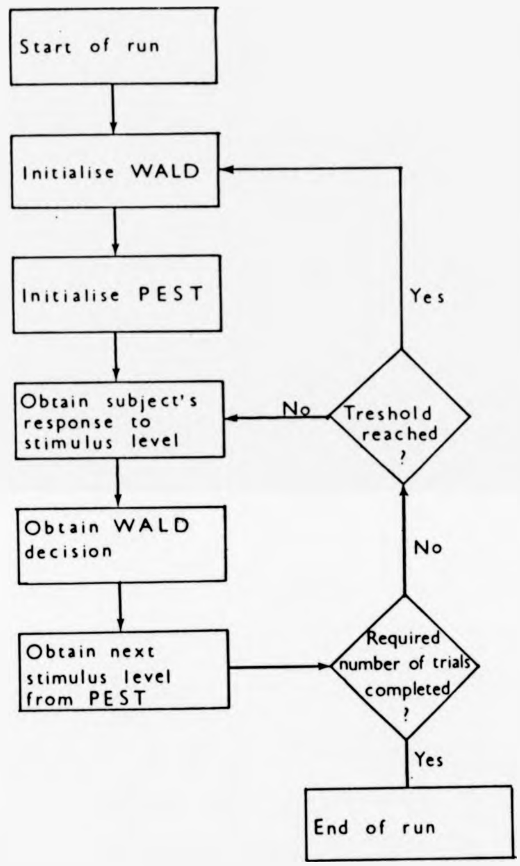


Figure 3.3 Operation of PEST.

step leading to the reversal was not the result of a doubling, while if the step size leading to the most recent reversal involved a doubling then the third step was not doubled.

This set of rules was developed by Taylor and Creelman (1967) from intuition and trial and error, using computer simulation. In their paper they give an heuristic rationale for the above set of rules.

In Taylor and Creelman's (1967) implementation the tracking procedure is halted when the step size falls below a predefined stopping step size and the threshold level is taken to be the midpoint of the last two stimulus levels. There are two main shortcomings with such a procedure. First, the number of trials required is variable. This may be advantageous in some cases where convergence is quick and hence relatively few trials are required, but it can result in very lengthy and tedious runs (for example if the subject suffers a lapse in concentration). Second, all the information obtained during a run is not fully utilized, for the estimated threshold depends mostly on the state of the tracking towards the end of the run. Trials early on in the run therefore contribute less than those towards the final stage.

A fixed number of trials per run was therefore preferred. The tracking procedure was allowed to operate normally and if a threshold was reached before the required number of trials were completed then the tracking was re-initialized and allowed to continue. After completion of all the required trials the threshold was not taken from the final state of the tracking but instead the response data and the stimulus levels were fitted with a psychometric function, from which the threshold was interpolated. Responses are assumed to be normally distributed and hence the data need to be modelled using a cumulative normal curve.

The cumulative normal curve is, however, difficult to compute and hence it was approximated by the following logistic curve (Taylor and Creelman, 1967):

$$P(x) = \left[1 + \frac{(N-1)}{1 + \exp(-(x-M)/S)}\right]\frac{1}{N}$$

where,

P(x) = Probability of a correct response at level x

x = Stimulus level

N = Number of alternative forced choices

M = Midpoint of the psychometric function

S = Spread of the psychometric function

The experiment provides a set of x and P(x) values and it is required to determine the values of M and S. This was achieved as follows. Estimates were obtained for the lower and upper limits of M and S. The lower limits for both M and S were always taken to be zero. The lower limit of zero for M was based on the fact that the stimulus levels could only assume positive values. A lower limit of zero for S was possible as the psychometric functions were always monotonically increasing functions of the stimulus level (a monotonically decreasing psychometric function would have a negative spread). The upper limit of M was taken to be twice the maximum stimulus level used. This was believed to be a conservative estimate as the tracking procedure always ensured that stimulus levels at the extreme end of the psychometric function were included. The upper limit for the spread was also taken to be twice the maximum stimulus level used.

The two dimensional space defined by the limits of M and S was divided into a 40 by 40 grid. At each point within the grid the expected psychometric function was computed, at the required stimulus levels, and a χ^2 variable was computed between the expected scores and the actual scores:

$$\chi^2 = \sum_{i=1}^{N} \left[\frac{O(x_i) - E(x_i)}{S(x_i)} \right]^2$$

where:

$E(x_i)$ = Expected score at stimulus level x_i

$O(x_i)$ = Observed score at stimulus level x_i

$S(x_i)$ = Standard error at stimulus level x_i

N = Number of stimulus levels

The standard error was computed from the observed score and the number of trials, n, as follows:

$$S(x_i) = \sqrt{\left(\frac{O(x_i).(1 - O(x_i))}{n} \right)}$$

The χ^2 statistic has N-2 degrees of freedom since two parameters, M and S, are estimated from the analysis.

The entire space was scanned for the minimum χ^2 value. On completion of this coarse search, the operation was repeated but with the grid centred at the estimated minimum, and the upper and lower values of M and S redefined as follows. If the resolution of the first scan was (d_m, d_s) and was centred at (m,s) then the grid searched was defined by $(m \pm d_m, s \pm d_s)$. This second search can be considered as a fine tuning after the first search locates the position of the minimum.

The hybrid procedure used by Hall (1981) differed from the procedure described here in that he used a maximum likelihood method to determine the psychometric function underlying the response data. In Chapter 5 some of the results of Experiment 5.1 were analysed using both methods, and it was found that there is no significant difference between the two methods of analysis. In the Appendix given at the end of the thesis the results obtained with the two different methods of fitting the psychometric function are given in tables.

Once the mean and the spread of the psychometric function were estimated, the threshold was set to be the stimulus level that corresponded to 76% correct. The 76% correct criterion level was used as this corresponds (in a two-interval forced-choice paradigm) to a discrimination index of d'=1 (Green and Swets, 1966).

Each experimental session which used the threshold tracking procedure typically consisted of 15 runs (3 runs per retinal site) with 36 trials per run. For the first run at each retinal site, the initial parameters used by PEST were selected on the basis of pilot experiments. The results of the first run were <u>not</u> included in the final analysis but were only made use of to obtain more representative initialization PEST parameters for the second and third runs. The initial stimulus level used for the second and third run (in each block of 3) was set to be twice the threshold estimated by the first run, and the initial step size was taken to be half of the value of the estimated threshold. Hence each block of three runs contributed only two threshold estimates that were used in the final analysis.

3.7 Randomized balanced block procedure

This design presents the subject with a specified set of stimulus levels. The stimulus level used for a given trial was no longer based on the subject's response to the previous trials but was selected by the following algorithm. The N stimulus levels are first randomized, and N runs performed, each run consisting of N trials (so that a total of N^2 trials are performed). The stimulus level for the i^{th} trial of the j^{th} run is taken to be the k^{th} element of the randomized list, where:

$$k = i.j \mod(N+1)$$

The value of N has to be one less than a prime number. This design has the property that order and carry-over effects are maximally balanced over the entire N^2 trials. If less than N runs are used the balancing is incomplete. Experiments using this design always consisted of 10 different stimulus levels, so that each block of runs consisted of 100 trials.

3.8 Statistical methods

3.8.1 χ^2 comparison

Given two sets of sample means (for example the minimum dot separations required for the fine-grain movement illusion) $s_1, s_2, \ldots, s_N$ and $t_1, t_2, \ldots, t_N$ with standard errors $u_1, u_2, \ldots, u_N$ and $v_1, v_2, \ldots, v_N$ respectively, then a measure of the difference between the two samples is given by the following quantity, distributed approximately as χ^2:

$$\sum_{i=1}^{N}\left(\frac{s_i - t_i}{\sqrt{\left[u_i^2 + v_i^2\right]}}\right)^2$$

with N degrees of freedom. For a continuous variate, x_i, the standard error, SE, is defined as:

$$SE = \sqrt{\left(\sum_{i=1}^{n}\frac{(x_i - \bar{x})^2}{n(n-1)}\right)}$$

where $\bar{x}$ is the mean value and n is the number of x_i values. If the variable has a binomial distribution then the standard error of the proportion p is estimated by:

$$SE = \sqrt{\left(\frac{p(1-p)}{n}\right)}$$

where p is the proportion of correct response in n trials.

3.8.2 't' Test comparison

Given two sample means, s and t, with standard errors u and v then the quotient:

$$\frac{s-t}{\sqrt{\left[u^2+v^2\right]}}$$

is distributed approximately as the normal variate z.

3.8.3 Linear regression analysis

Linear regression analysis was performed using GLIM (General Linear Interactive Model) on a GEC 4190 minicomputer. The linear regression analysis obtains estimates of not only the gradient and the y-intercept of the least squares regression line, but also estimates of the standard error of both parameters (see Green and Margerison, 1978). The ratio of the gradient of the regression line to its standard error is distributed approximately as the normal variate z. To compare whether the estimated gradients of two sets of data were significantly different or not the following ratio, which is distributed approximately as the normal variate z, was computed:

$$\frac{g_1-g_2}{\sqrt{\left[s_1^2+s_2^2\right]}}$$

where g_1 and g_2 are the gradients of the regression lines and s_1 and s_2 are estimates of the respective standard errors.

3.9 Subject details

Subjects used for experiments throughout this thesis were RSS, DHF, MJM, NJL, CJH and SG. Relevant details are as follows:

RSS: Female, experienced in psychophysical observations, unaware of purpose of experiments, 25 years of age, corrected right eye Snellen acuity 6/6.

DHF: Male, experienced in psychophysical observations, aware of purpose of experiments, 37 years of age, corrected right eye Snellen acuity 6/4.

MJM: Male, experienced in psychophysical observations, unaware of purpose of experiments, 25 years of age, right eye Snellen acuity 6/4.

NJL: Male, experienced in psychophysical observations, unaware of purpose of experiments, 24 years of age, right eye Snellen acuity 6/4.

CJH: Male, unexperienced in psychophysical observations, unaware of purpose of experiments, 21 years of age, corrected right eye Snellen acuity 6/6.

SG: Male, author, experienced in psychophysical observations, 22 years of age, right eye Snellen acuity 6/4.

Chapter 4

Temporal Response Characteristics of the Fine-Grain Movement Illusion

Chapter 4: Temporal Response Characteristics of the Fine-Grain Movement Illusion

4.1 Retinal dependence of temporal response characteristics of the fine-grain movement illusion

Thorson, Lange and Biederman-Thorson (1969) obtained measurements of the temporal response characteristics of the fine-grain movement illusion at a single retinal site 22^o from the fovea. The experiments in this chapter consider the dependence of the temporal response characteristics on retinal eccentricity. The spatial separation of the two dots flashes, used to elicit the fine-grain movement illusion, is a critical parameter which must be carefully selected. It may be set constant over the different retinal sites, or made to vary to take into consideration changes in visual performance with increasing eccentricity. The use of a constant dot separation was rejected as the results would then be confounded by changes in spatial acuity with eccentricity (see section 2.4). Two different experimental conditions, which differed in the way in which the dot separations varied with eccentricity, were considered. In Condition 1 the dot separation, at a given retinal site, was set to the midpoint of the minimum dot separation required for the fine-grain movement illusion and the minimum dot separation required for spatial resolution. Values of the minimum dot separation for the fine-grain movement illusion and the minimum dot separation for spatial resolution were determined as described in Experiment 5.1 (see Chapter 5). In Condition 2 the dot separation, at a given retinal site, was set at a fixed value above the minimum dot separation required for the fine-grain movement illusion. The first experiment considered the temporal response characteristics of the fine-grain movement illusion, as a function of retinal eccentricity, under the two different experimental conditions.

Experiment 4.1

Methods

Subjects were presented with two dot flashes, orientated vertically. The separation of the dot flashes was set to either the midpoint of the minimum dot separation required for the fine-grain movement illusion and the minimum dot separation required for spatial resolution (Condition 1) or was set to 0.02° above the minimum dot separation required for the fine-grain movement illusion (Condition 2). Ten different interstimulus intervals were used, which ranged from 20 msec to 300 msec in steps of 40 msec, and included a zero and a 500 msec interval. The horizontal distance between the centre of the dot flashes and the fixation point was varied from run to run to give the required retinal location. The onset order of the two dot flashes was determined pseudo-randomly. The subject's task was to indicate the onset sequence of the flashes (i.e. whether the upper flash or the lower flash occurred first) and they were informed that they could use the direction of any perceived motion to base their decision on.

Each dot flash subtended approximately 0.04° visual angle and had a duration of about 1 msec. The dot flashes were presented to the left of the fixation point along a horizontal meridian. Subjects viewed the fixation point with their right eye only (the left eye was covered by an eye patch) and hence the stimuli fell on the temporal side of the retina. A head rest was used to steady the subject's head. The dot flashes were presented on a dark background and were viewed through the viewing system. The intensity of each dot flash was set to 1 log unit above luminance increment threshold. The experiment was conducted under

Table 4.1

Retinal sites ......: 5^o, 15^o, and 25^o

Dot-flash separation:

		Eccentricity, degrees		
		5	15	25
Condition 1 -	SG	0.10^o	0.17^o	0.26^o
	MJM	0.12^o	0.26^o	0.32^o
Condition 2 -	SG	0.10^o	0.13^o	0.19^o
	MJM	0.08^o	0.17^o	0.14^o

ISI ....: 0, 20, 60, 100, 140, 180, 220, 260, 300, 500 msec.

Dot-flash duration .: 1 msec

Dot diameter ....: 0.04^o

Dot-flash luminance : 1 log unit above luminance increment threshold

Viewing conditions .: Scotopic (20 minutes dark adaptation)

scotopic conditions with subjects required to dark-adapt for 20 minutes at the beginning of each session.

Two subjects participated in the experiment: SG and MJM. Details of their age and visual acuity are given in section 3.9. Each subject performed ten experimental sessions per experimental condition, with each session consisting of 3 runs (1 run per retinal site). Observations were at retinal sites of 5^o, 15^o and 25^o eccentricity in either an ascending or descending order (the order was reversed from session to session). Each run consisted of 100 trials (10 trials per interstimulus interval) at a fixed retinal site. Interstimulus intervals were selected according to the randomized balanced block algorithm described in section 3.7. Relevant experimental details are summarised in Table 4.1.

Results

Figures 4.1(a) and 4.1(b) show the performance levels obtained under experimental Condition 1 for SG and MJM respectively. Figures 4.1(c) and 4.1(d) show results obtained under Condition 2 for SG and MJM respectively. Each point shows the per cent correct sequence discrimination (performance) over 100 trials. For clarity the standard error of each proportion is not shown (standard errors range from 5.0% at 50 per cent correct to 3.0% at 90 per cent correct). All four sets of results exhibit the following trend: the temporal response curves shift towards smaller interstimulus intervals as eccentricity increases. This trend is strongly evident in Figures 4.1(b), 4.1(c) and 4.1(d), but rather less so in Figure 4.1(a). The general form of the tuning characteristics does not appear to depend strongly on the spatial separation of the dot flashes. For all 12 curves sequence discrimination levels at the highest interstimulus interval (500 msec) were approximately at chance level. Both subjects reported that for a

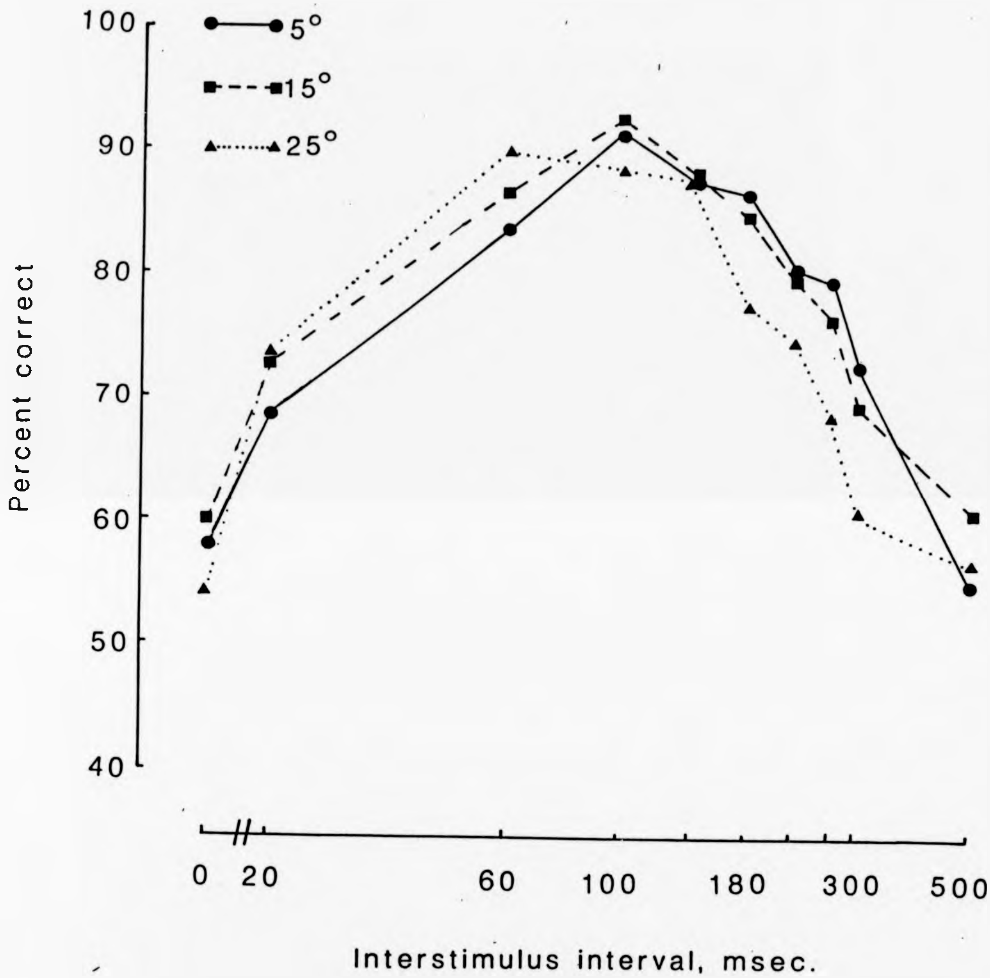


Figure 4.1(a) Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.1, Condition 1). Scotopic adaptation conditions. Subject SG.

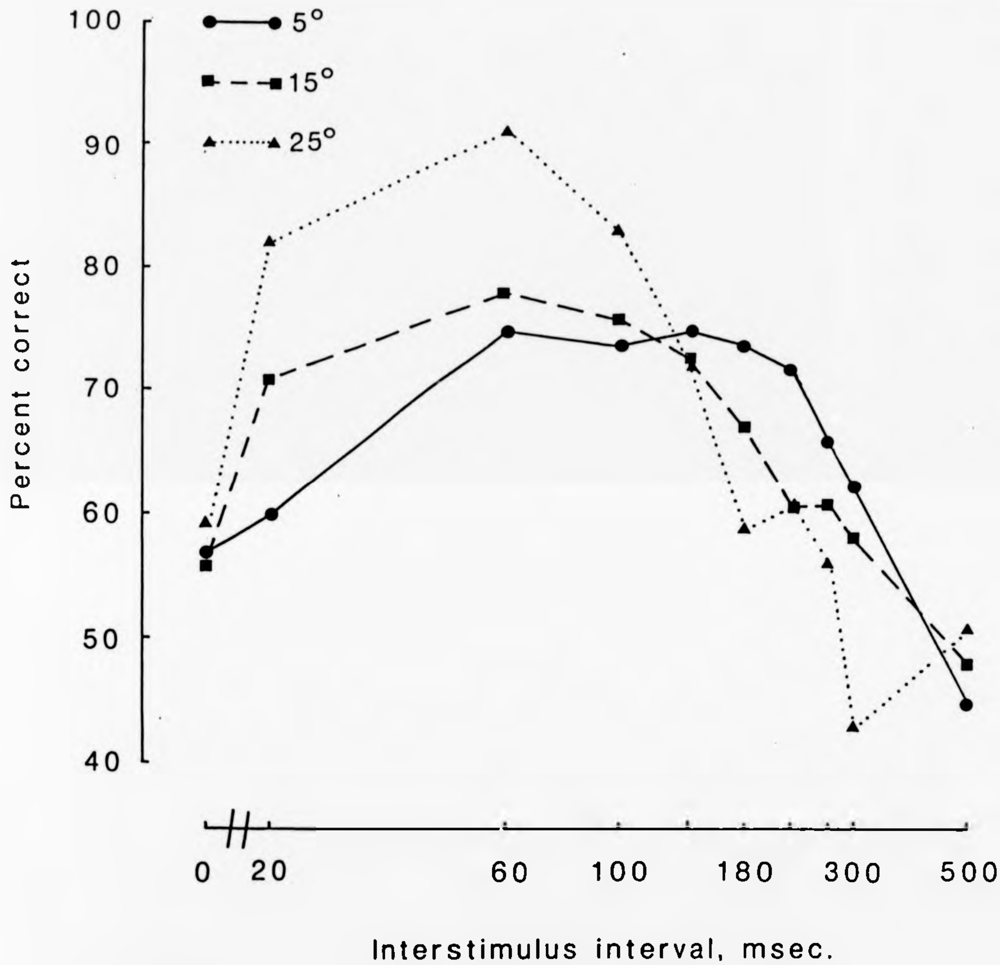


Figure 4.1(b) Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.1, Condition 1). Scotopic adaptation conditions. Subject MJM.

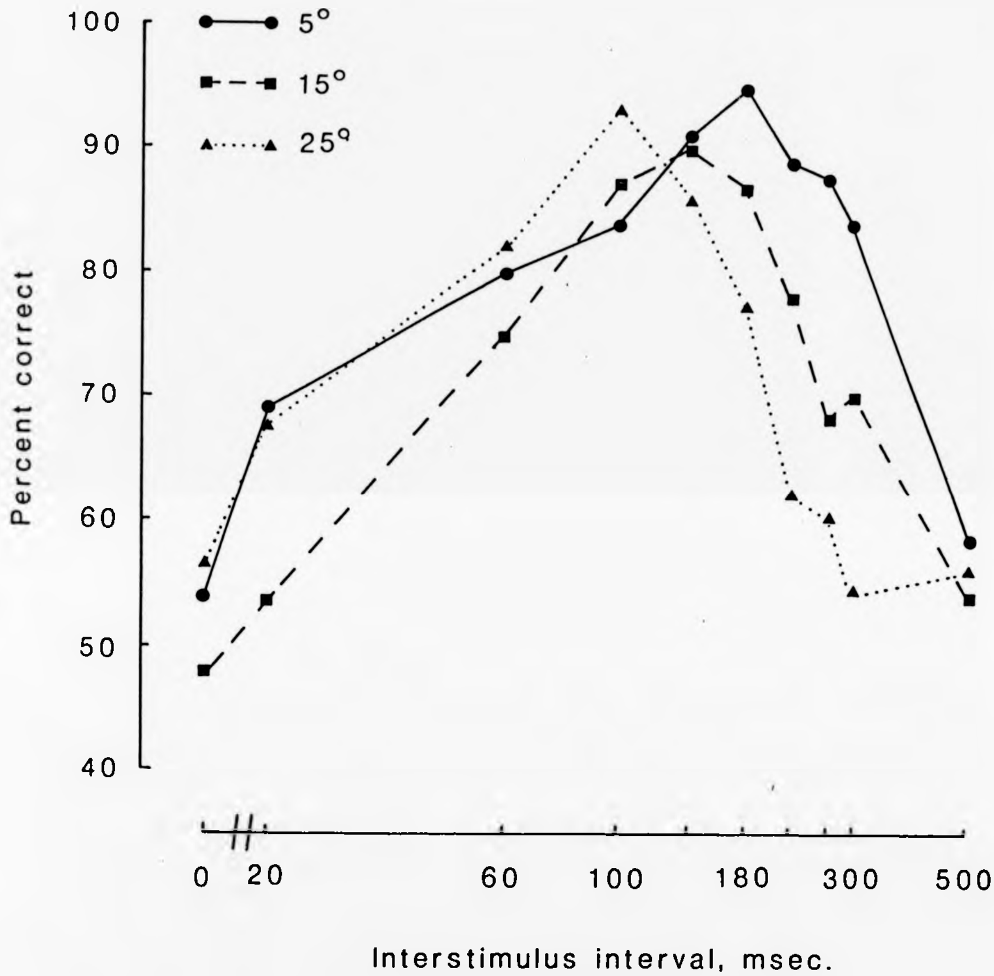


Figure 4.1(c) Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.1, Condition 2). Scotopic adaptation conditions. Subject SG.

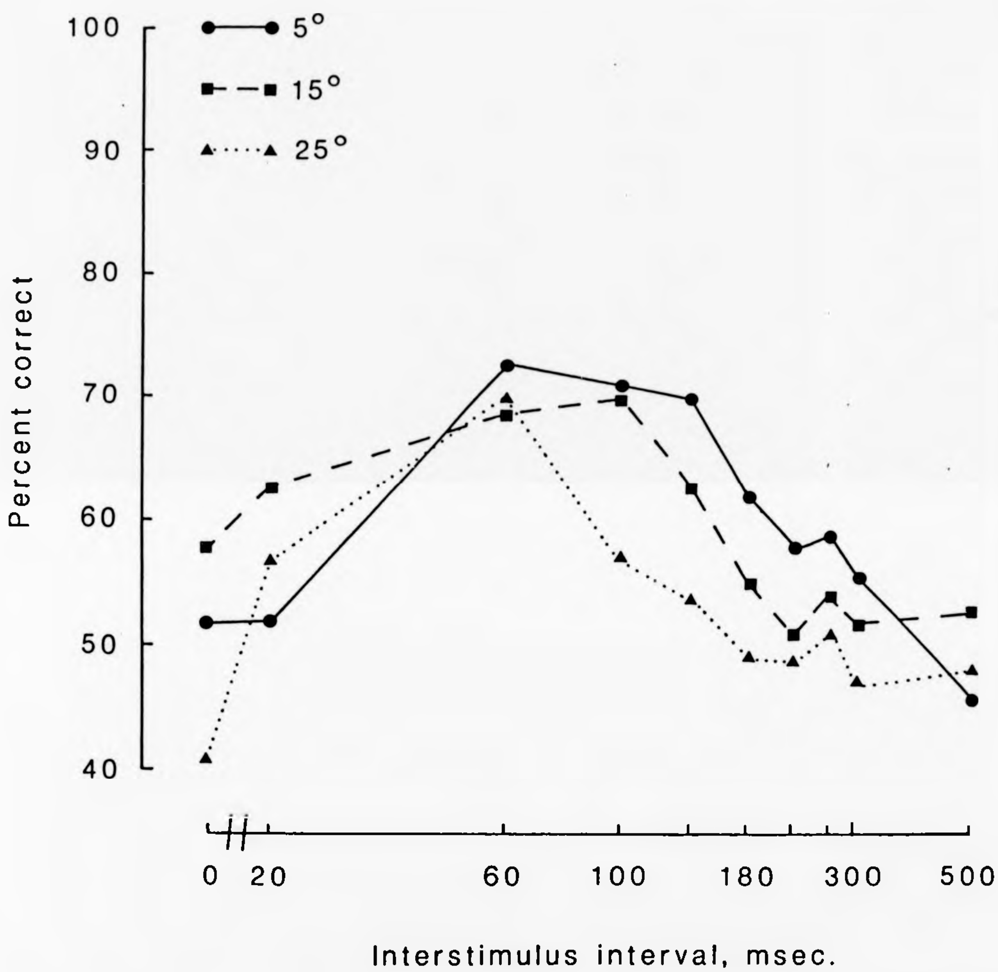


Figure 4.1(d) Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.1, Condition 2). Scotopic adaptation conditions. Subject MJM.

significant proportion of trials a single dot, moving over a considerable distance, was vividly seen.

Discussion

The results of this experiment show that the temporal tuning characteristics of the fine-grain movement illusion showing reliable sequence discrimination, as first demonstrated by Thorson et al. (1969) at a retinal site of 22^0, can be obtained at retinal sites as close as 5^0 away from the fovea. Given that dot flashes were spatially unresolved (which was confirmed by the low discrimination levels at high interstimulus intervals) it must be implied that sequence discrimination was not based on the detection of onset sequence but on the direction of perceived illusory motion.

The shift in response curves towards smaller interstimulus intervals with increasing retinal eccentricity may appear counter to the observation by Biederman-Thorson et al. (1971) that under high-luminance conditions the response curves shift towards smaller interstimulus intervals. This shift towards smaller interstimulus intervals can be explained on the basis of increases in temporal responsiveness associated with high-luminance viewing conditions. It could be argued, therefore, that the temporal response characteristics at large eccentricities should be shifted towards larger interstimulus intervals, for at larger eccentricities a greater proportion of rod receptors would be stimulated. The observed shift in temporal response characteristics towards smaller interstimulus intervals may not therefore be due to changes in the relative proportions of the two photoreceptors. Rather, it may be a consequence of increases in the density of Y-type fibres and their receptive field sizes with increasing eccentricity. Such Y-type fibres respond optimally to high temporal frequencies and therefore if the temporal response characteristics of the fine-grain movement illusion were reflecting some property of Y-type fibres, a shift towards smaller interstimulus with increasing eccentricity would be expected.

4.2 Temporal response characteristics of the fine-grain movement illusion under photopic conditions

Biederman-Thorson et al. (1971) examined the temporal response characteristics of the fine-grain movement illusion under two different conditions: a high-luminance condition (with dots at 10L and the surround at $3x10^{-3}L$) and a low-luminance condition (dots at 0.3L and the surround at $10^{-5}L$). They found that under the high-luminance condition peak performance levels occurred at smaller interstimulus intervals (25 msec) than that obtained under the low-luminance condition (which gave peak levels at approximately 63 msec). This shift in peak performance with increase in luminance of the field, towards smaller temporal intervals is consistent with increases in temporal resolution obtained under light adapted conditions. This result was demonstrated at a single retinal site of 22^{o}.

The next experiment, Experiment 4.2, considered temporal response characteristics under photopic conditions. The aim was first to replicate and hence confirm the shift in peak performance towards smaller interstimulus intervals with increase in luminance, and second to determine the dependence of the temporal response characteristics under photopic conditions as a function of retinal eccentricity.

Experiment 4.2

Methods

The method and procedure differed to that used for Experiment 4.1 (Condition 1) in only two aspects. First, the stimuli were presented on a white uniform background field (subjects were no longer required to dark-adapt). Second, subjects set the intensity of the dot flashes to 2 log units above luminance increment threshold (in contrast to the 1 log unit used in Experiment 4.1). This increase in stimulus intensity was found to be necessary, for in pilot experiments, using dot flashes set to 1 log unit above luminance increment threshold, subjects reported great difficulty in maintaining a clear image of the flashes. Subjects were SG and MJM. Each subject performed ten experimental sessions, with each session consisting of 3 runs (1 run per retinal site). Each run consisted of 100 trials (10 trials per interstimulus interval) at a fixed retinal site. Relevant experimental details are summarised in Table 4.2.

Results

Figures 4.2(a) and 4.2(b) show the results for SG and MJM respectively. Each point gives the per cent correct over 100 trials. Both results show that, at all retinal sites, peak discrimination levels occur at the smallest interstimulus interval (20 msec). At large interstimulus intervals, discrimination levels decrease with increasing eccentricity.

Discussion

The occurrence of maximum discrimination levels at the smallest interstimulus interval (20 msec) is consistent with Biederman-Thorson et al.'s (1971) finding that under high-luminance conditions maximum discrimination occurred at 25 msec. Although these photopic temporal response curves were obtained using spatial thresholds measured under scotopic conditions it is nethertheless instructive to compare the results of this experiment with the results of Experiment 4.1 (Figures

Table 4.2

Retinal sites ......: 5^{o}, 15^{o}, and 25^{o}

Dot-flash separation: Eccentricity, degrees

	5	15	25
SG	0.10^{o}	0.17^{o}	0.26^{o}
MJM	0.12^{o}	0.26^{o}	0.32^{o}

ISI ....: 0, 20, 60, 100, 140, 180, 220, 260, 300, 500 msec.

Dot-flash duration .: 1 msec

Dot diameter ....: 0.04^{o}

Dot-flash luminance : 2 log unit above luminance increment threshold

Viewing conditions .: Photopic (background field luminace 30 $cd.m^{-2}$)

Experiment 4.2

Methods

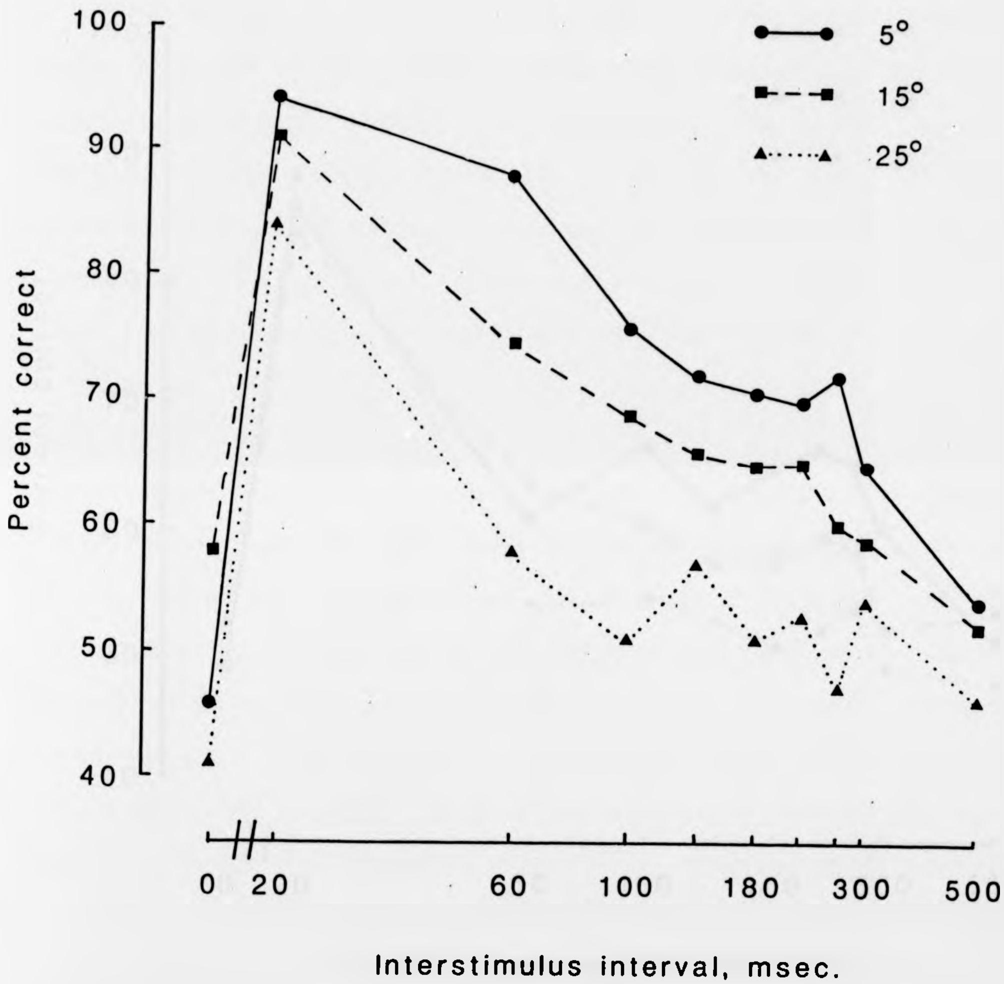
The method and procedure differed to that used for Experiment 4.1 (Condition 1) in only two aspects. First, the stimuli were presented on a white uniform background field (subjects were no longer required to dark-adapt). Second, subjects set the intensity of the dot flashes to 2 log units above luminance increment threshold (in contrast to the 1 log unit used in Experiment 4.1). This increase in stimulus intensity was found to be necessary, for in pilot experiments, using dot flashes set to 1 log unit above luminance increment threshold, subjects reported great difficulty in maintaining a clear image of the flashes. Subjects were SG and MJM. Each subject performed ten experimental sessions, with each session consisting of 3 runs (1 run per retinal site). Each run consisted of 100 trials (10 trials per interstimulus interval) at a fixed retinal site. Relevant experimental details are summarised in Table 4.2.

Results

Figures 4.2(a) and 4.2(b) show the results for SG and MJM respectively. Each point gives the per cent correct over 100 trials. Both results show that, at all retinal sites, peak discrimination levels occur at the smallest interstimulus interval (20 msec). At large interstimulus intervals, discrimination levels decrease with increasing eccentricity.

Discussion

The occurrence of maximum discrimination levels at the smallest interstimulus interval (20 msec) is consistent with Biederman-Thorson et al.'s (1971) finding that under high-luminance conditions maximum discrimination occurred at 25 msec. Although these photopic temporal response curves were obtained using spatial thresholds measured under scotopic conditions it is nethertheless instructive to compare the results of this experiment with the results of Experiment 4.1 (Figures



<u>Figure 4.2(a)</u> Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.2). Photopic adaptation conditions. Subject SG.

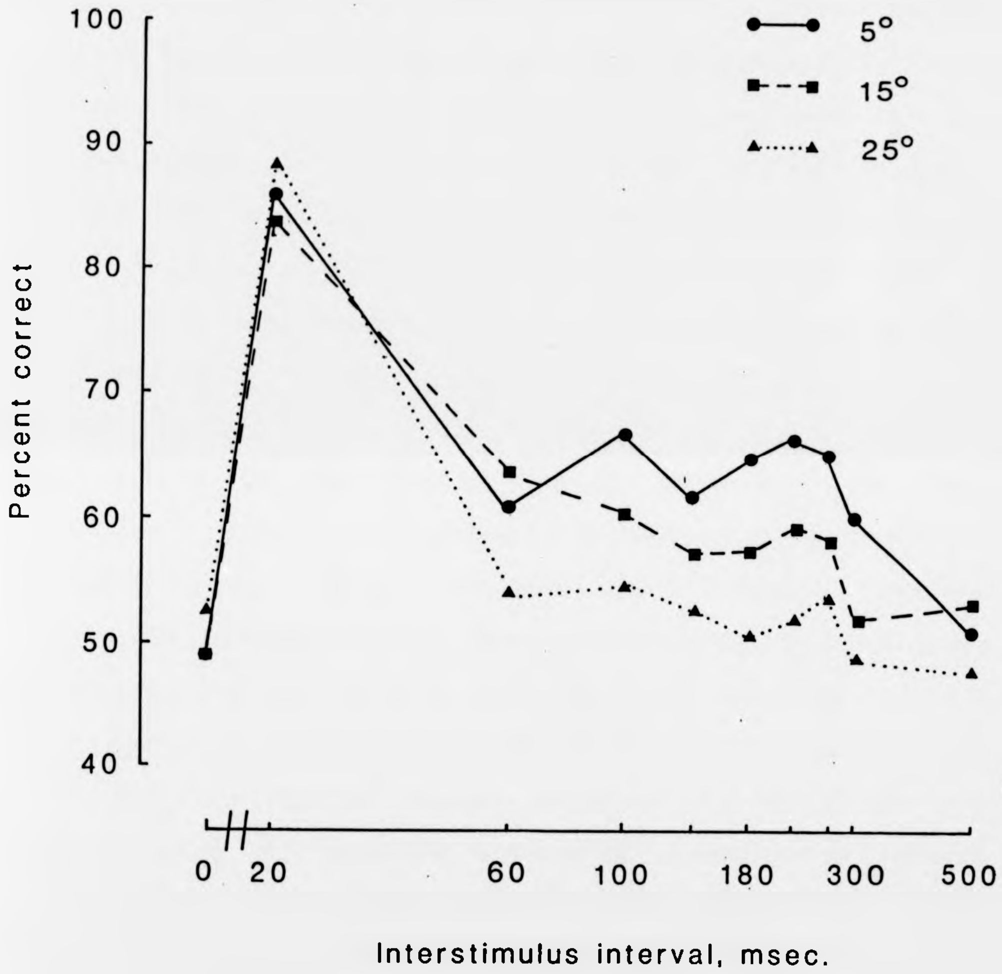


Figure 4.2(b) Temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 4.2). Photopic adaptation conditions. Subject MJM.

4.1a and 4.1b), then it can be seen that under photopic adaptation levels there is a shift in temporal response characteristics towards smaller interstimulus intervals (which is also consistent with Biederman-Thorson et al.'s (1971) observations). The shift in temporal response curves with photopic adaptation has occurred at all three retinal sites considered. At 25^0 eccentricity the shift in peak position, under photopic conditions, is 40 msec for both subjects, compared with a 38 msec shift obtained by Biederman-Thorson et al. (1971) at 22^0 eccentricity. At the other retinal sites the shift in peak position under photopic conditions is always greater than or equal to 40 msec.

The decline in sequence-discrimination performance, at large interstimulus intervals, with increasing eccentricity may be interpreted in one of two ways. It may be due to a shift in the temporal response characteristics towards smaller interstimulus intervals with increasing eccentricity (as was observed with Experiment 4.1 under scotopic conditions). Alternatively it is possible that under photopic conditions the temporal response characteristics are simply more narrowly tuned with increasing eccentricity. A narrowing of temporal response characteristics, with increasing retinal eccentricity, has been observed by Tyler and Torres (1972) using sinusoidally oscillating lines (see section 2.1). It is not possible here, however, to determine which of the explanations for the decrease of sequence discrimination with increasing eccentricity is valid, for this would require data on sequence discrimination at interstimulus intervals of less than 20 msec which were not available with the present system.

4.3 Subjective rating of the fine-grain movement illusion

The fine-grain movement illusion differs from classical apparent motion in two main aspects: the spatio-temporal range over which the illusion can be elicited and the objective way in which the illusion can be studied (Thorson *et al.*, 1969). Experiments 4.1 and 4.2 have considered some spatio-temporal aspects of the fine-grain movement illusion. Consideration is next given to the way in which the illusion can be quantified.

In the previous experiments subjects were required to indicate the onset sequence of two dot flashes. This is clearly an objective procedure in the sense that a subject's response can be compared with the actual onset sequence of the two dot flashes, and can therefore be objectively rated as being correct or incorrect. This objective procedure, by which the illusion can be quantified, contrasts sharply with the subjective procedures traditionally employed in studies of classical apparent motion. Such subjective procedures typically require subjects to rate the perceived *strength* of the illusory motion (see e.g. Kolers, 1972).

The next experiment determined temporal response characteristics of the fine-grain movement illusion using a subjective procedure similar to that typically employed in studies of classical apparent motion. The aim of the experiment was to consider how well the objective estimates of sequence discrimination fit with subjective assessments of the strength of the fine-grain movement illusion. Subjects were no longer asked to indicate the onset sequence of the two dot flashes but to report whether or not they saw a moving dot.

Experiment 4.3

Methods

The method and procedure were identical to those used in Experiment 4.1 (Condition 1) apart from the task subjects were required to perform. Subjects were no longer instructed to indicate the onset sequence of the two dot flashes but were asked to indicate whether or not they saw a moving dot. The subjects were MJM and SG. Relevant experimental details are summarised in Table 4.3.

Results

Figures 4.3(a) and 4.3(b) show per-cent responses, over 100 trials, indicating "Yes - motion seen" for SG and MJM respectively. Unlike the previous experiments, the results of this experiment can have values varying between 0% and 100% and hence they can not be directly compared with the results of Experiment 4.1 (Figures 4.1a and 4.1b). Both sets of results are similar to those obtained with the sequence discrimination procedure, in that responses are an inverted U shaped function of the interstimulus interval.

Discussion

Results for both subjects (Figures 4.3a and 4.3b) show a shift in the rating curves towards smaller interstimulus intervals with increasing retinal eccentricity. This shift is consistent with the shift in sequence discrimination curves towards smaller interstimulus intervals with increasing eccentricity, as observed in Experiment 4.1 (see Figures 4.1a and 4.1b).

To compare the rating curves with the sequence discrimination curves the percentage rating levels, r, were transformed using the following transformation $r' = 50 + r/2$. This linear transformation has no significance other than meeting the obvious requirements that the 0%

Table 4.3

Retinal sites ......:	5^o, 15^o, and 25^o			
Dot-flash separation:		Eccentricity, degrees		
		5	15	25
	SG	0.10^o	0.17^o	0.26^o
	MJM	0.12^o	0.26^o	0.32^o
ISI ....:	0, 20, 60, 100, 140, 180, 220, 260, 300, 500 msec.			
Dot-flash duration .:	1 msec			
Dot diameter ....:	0.04^o			
Dot-flash luminance :	1 log unit above luminance increment threshold			
Viewing conditions .:	Scotopic (20 minutes dark adaptation).			

Experiment 4.3

Methods

The method and procedure were identical to those used in Experiment 4.1 (Condition 1) apart from the task subjects were required to perform. Subjects were no longer instructed to indicate the onset sequence of the two dot flashes but were asked to indicate whether or not they saw a moving dot. The subjects were MJM and SG. Relevant experimental details are summarised in Table 4.3.

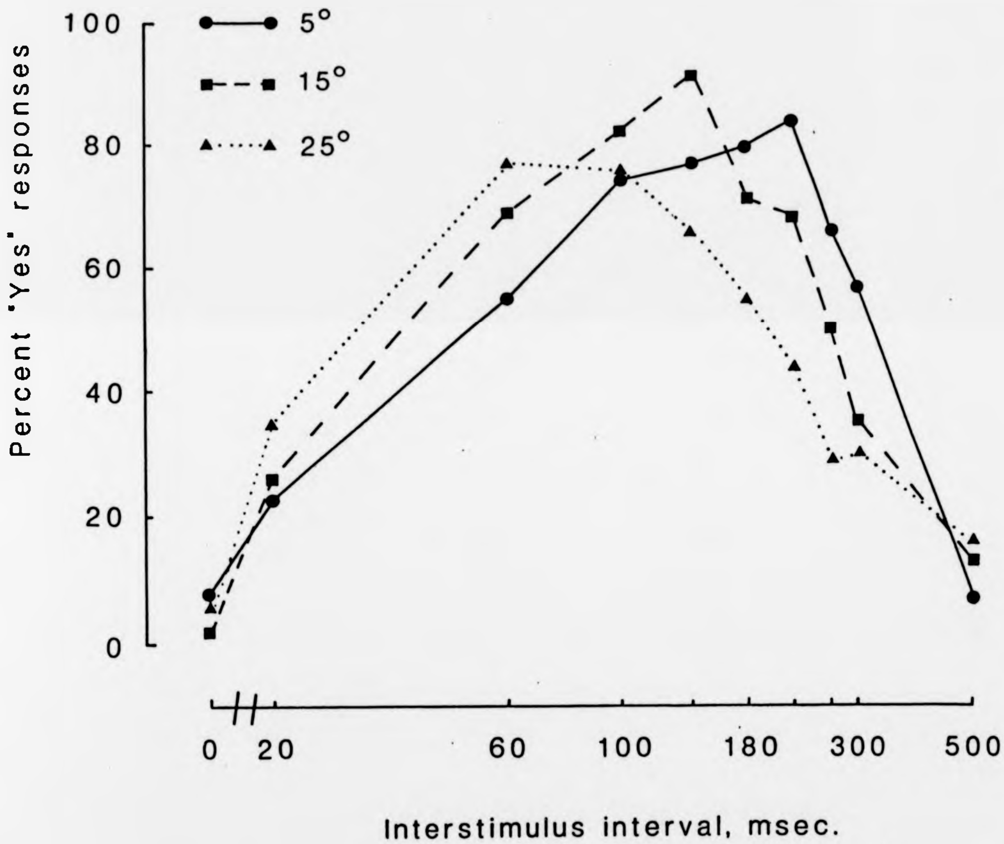
Results

Figures 4.3(a) and 4.3(b) show per-cent responses, over 100 trials, indicating "Yes - motion seen" for SG and MJM respectively. Unlike the previous experiments, the results of this experiment can have values varying between 0% and 100% and hence they can not be directly compared with the results of Experiment 4.1 (Figures 4.1a and 4.1b). Both sets of results are similar to those obtained with the sequence discrimination procedure, in that responses are an inverted U shaped function of the interstimulus interval.

Discussion

Results for both subjects (Figures 4.3a and 4.3b) show a shift in the rating curves towards smaller interstimulus intervals with increasing retinal eccentricity. This shift is consistent with the shift in sequence discrimination curves towards smaller interstimulus intervals with increasing eccentricity, as observed in Experiment 4.1 (see Figures 4.1a and 4.1b).

To compare the rating curves with the sequence discrimination curves the percentage rating levels, r, were transformed using the following transformation $r' = 50 + r/2$. This linear transformation has no significance other than meeting the obvious requirements that the 0%



<u>Figure 4.3(a)</u> Subjective rating of the fine-grain movement illusion (Experiment 4.3). Scotopic adaptation conditions. Subject SG

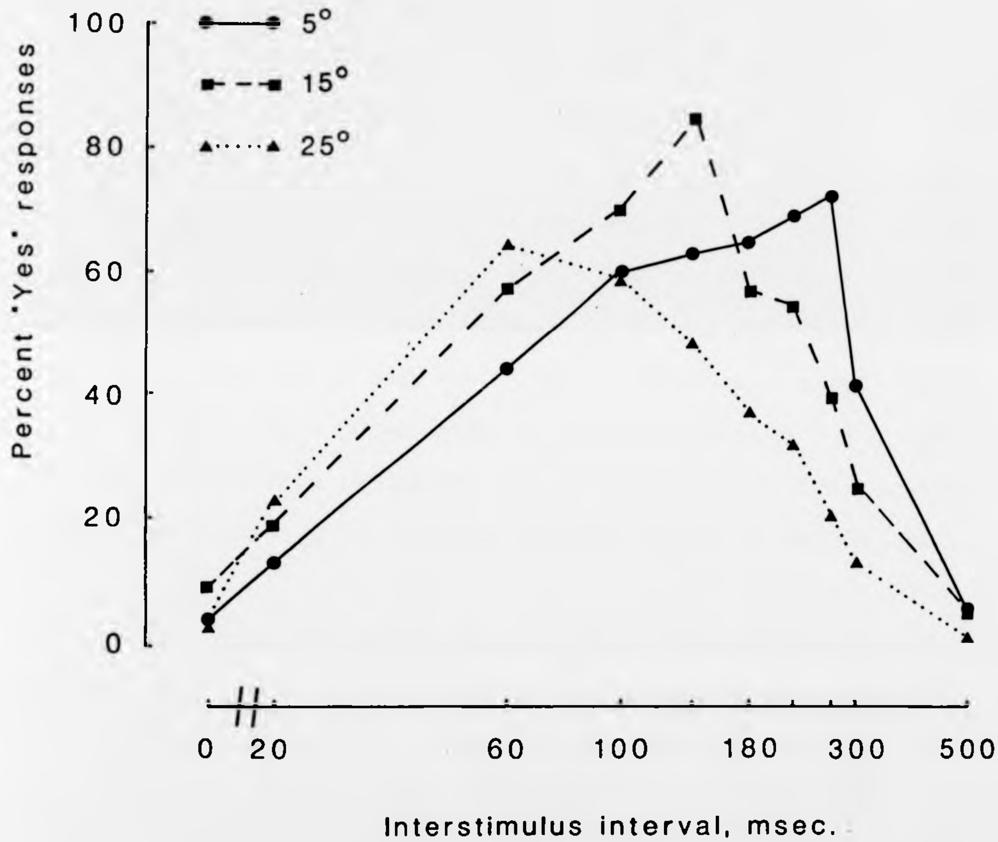


Figure 4.3(b) Subjective rating of the fine-grain movement illusion (Experiment 4.3). Scotopic adaptation conditions. Subject MJM

rating level transforms to 50% performance level and 100% rating level transforms to 100% performance level. The transformed rating levels, r', and the sequence discrimination levels (Figures 4.1a and 4.1b) are shown in Figures 4.4(a) and 4.4(b) for SG and MJM respectively. It was not expected that the transformed rating levels would correspond exactly to the sequence discrimination levels. To assess how well the objective discrimination procedure correlated with the subjective rating procedure a linear regression of the dependence of rating levels on sequence discrimination levels was performed. The resulting Pearson's product moment correlation coefficients are shown in the top right-hand corners in Figures 4.4(a) and 4.4(b). The relatively high values of the correlation coefficients indicate that when a subject was able to accurately determine the onset sequence of the two dot flashes, this would correspond to a high proportion of positive ratings. This correlation was anticipated since in practice subjects based their sequence-discrimination responses on the direction of the perceived illusory motion and not on the onset sequence to the two dot flashes.

The temporal response characteristics for rating performance can be compared with similar results obtained in classical apparent motion by Kolers and Pomerantz (1971). They considered the perception of illusory motion between geometric shapes (for example circles and squares) and required subjects to report the occurrence of smooth continuous motion between two figures. They found that rating levels were an inverted U shaped function of the interstimulus interval, much as in the present study. An objective assessment based on sequence discrimination is of course not available for classical apparent motion.

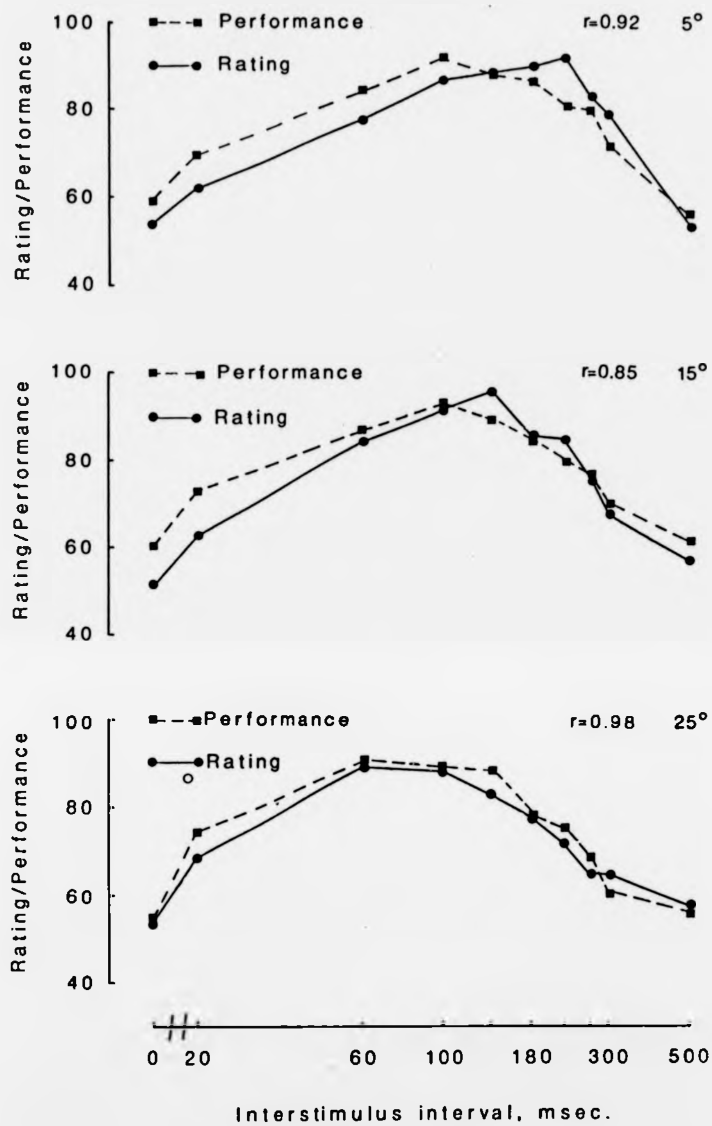


Figure 4.4(a) Comparison of transformed rating levels (obtained with the subjective rating procedure) with performance levels (obtained with the sequence discrimination procedure). Subject SG.

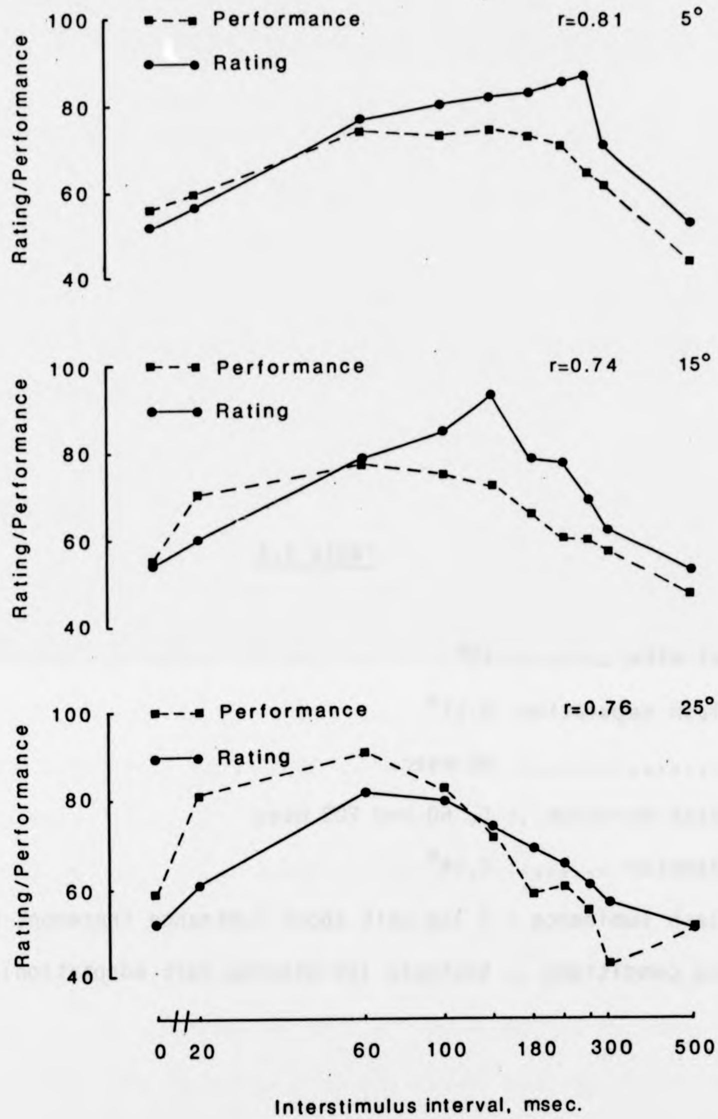


Figure 4.4(b) Comparison of transformed rating levels (obtained with the subjective rating procedure) with performance levels (obtained with the sequence discrimination procedure). Subject MJM.

Table 4.4

Retinal site	15^{o}
Dot-flash separation	0.17^{o}
ISI	80 msec.
Dot-flash duration .	1, 60 and 200 msec
Dot diameter	0.04^{o}
Dot-flash luminance	1 log unit above luminance increment threshold
Viewing conditions .	Scotopic (20 minutes dark adaptation).

4.4 Effect of stimulus duration on temporal response characteristics

The experiments described in sections 4.1, 4.2 and 4.3 provide information relating to the temporal dependence of the fine-grain movement illusion on interstimulus interval. In this section a control experiment is described which considers the effect of increasing stimulus duration on temporal response characteristics of the fine-grain movement illusion.

Experiment 4.4

Methods

The experimental method and procedure were as described for Experiment 4.1 (Condition 1) except that during an experimental session the stimulus duration, and not the retinal site, was changed from run to run. Observations were made at a single intermediate retinal site of 15^{o} eccentricity. The author acted as subject and performed ten experimental sessions. Each experimental session consisted of 3 runs (1 run per stimulus duration) and the stimulus duration was kept constant at either 1 msec (as used in previous experiments), 60 msec or 200 msec during a run. The stimulus duration varied from run to run in either a decreasing or increasing order, and the order reversed from session to session. The experiment was conducted under scotopic adaptation conditions, with a 20-minute dark-adaptation period at the start of each session. Relevant experimental details are summarised in Table 4.4.

Results

Figure 4.5 shows the results. Each point gives the per cent correct over 100 trials. Sequence discrimination at the larger stimulus durations differ mainly at the 20 msec interstimulus interval, where the performance level obtained with the 200 msec stimulus duration is significantly larger than that obtained with the 60 msec stimulus duration. At the largest interstimulus interval (500 msec) sequence discrimination levels obtained with the two larger stimulus durations were both 75%.

Discussion

The high sequence discrimination levels obtained at long interstimulus intervals with the 60 and 200 msec dot flash durations suggest that either illusory motion was seen by the subject (at interstimulus intervals that would not give rise to illusory motion with the smallest stimulus duration) or that the two dot flashes were no longer spatially unresolved and that the subject was basing his response on the detectable onset sequence of the dot flashes (as opposed to the direction of perceived illusory motion). Increases in spatial acuity with increasing stimulus duration have been reported (see section 2.5) and in section 5.2 an experiment is described which considers the minimum dot separation required for spatial resolution using a larger stimulus duration. It is shown in Experiment 5.2 that using a dot-flash duration of 500 msec the minimum dot separation required for spatial resolution is not significantly different from that obtained using a 1 msec dot-flash duration. It must therefore be concluded that in this experiment the high sequence discrimination levels obtained at long interstimulus intervals were due to the subject responding to the direction of fine-grain movement illusions and were <u>not</u> a consequence of the subject detecting the onset sequence of spatially resolved dot

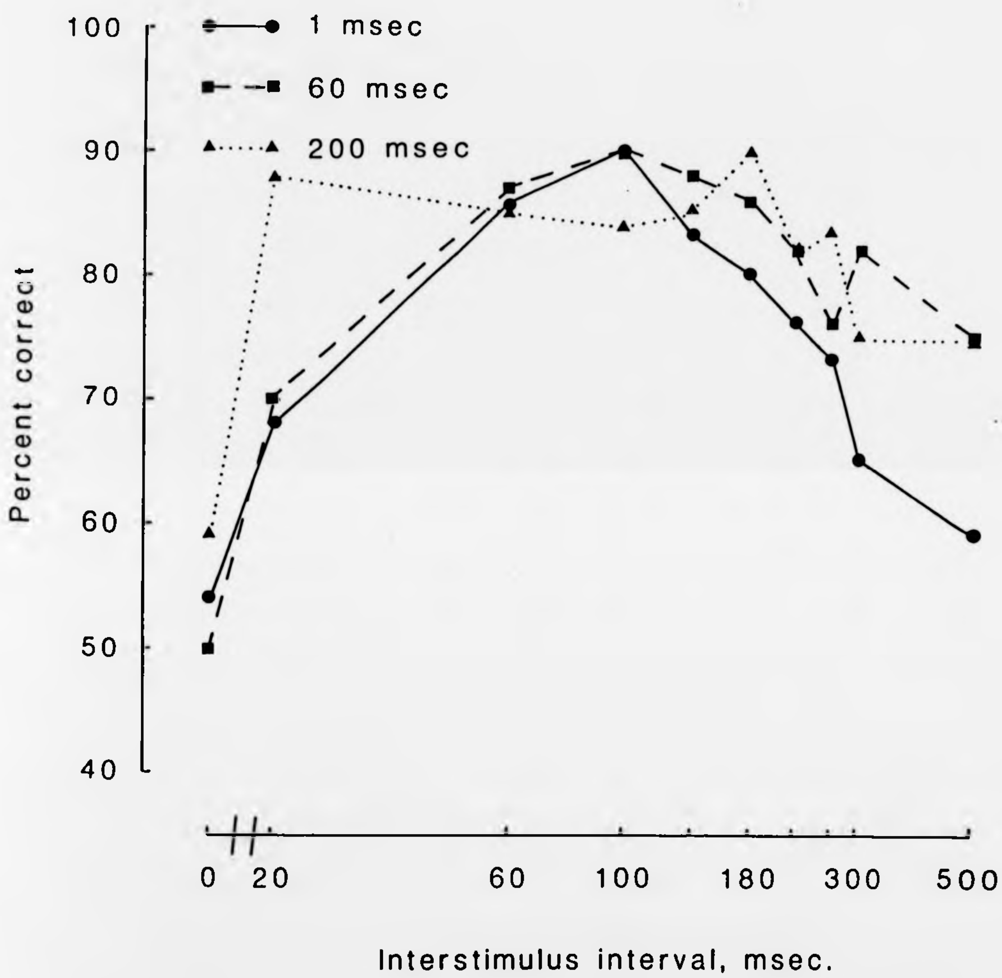


Figure 4.5 Temporal response characteristics of the fine-grain movement illusion using three different dot flash durations (Experiment 4.4). Scotopic adaptation conditions. Subject SG.

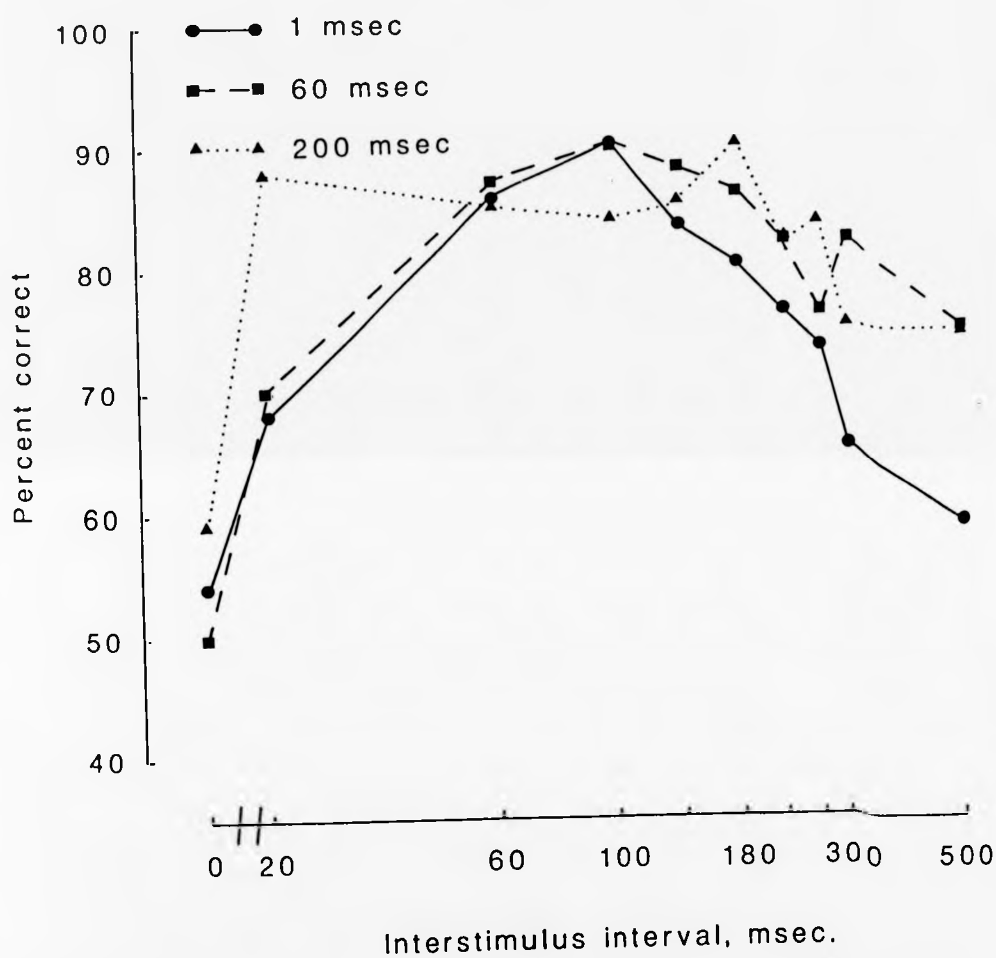


Figure 4.5 Temporal response characteristics of the fine-grain movement illusion using three different dot flash durations (Experiment 4.4). Scotopic adaptation conditions. Subject SG.

flashes.

4.5 Summary and Conclusion

Experiments have been described in this chapter which consider the temporal response characteristics of the fine-grain movement illusion as a function of retinal eccentricity. The temporal tuning characteristics first reported by Thorson et al. (1969) at a peripheral site of 22° have been shown to occur at retinal sites as close as 5° to the point of fixation. As stimulus eccentricity increases there is a shift in the temporal tuning characteristics towards smaller interstimulus intervals. This shift in the temporal response characteristics cannot be explained easily on the basis of changes in the distribution of rod and cone receptors with eccentricity, but may reflect changes in the distribution of motion-sensitive Y-type fibres and their receptive field sizes. Under photopic conditions, maximum discrimination performance occurred at the smallest interstimulus interval (20 msec) at all three retinal sites tested. For large interstimulus intervals, sequence discrimination decreased with increasing eccentricity, suggesting either that the tuning curves became more narrowly tuned or that like temporal response characteristics obtained under scotopic conditions they undergo a shift towards smaller interstimulus intervals. It was not possible here to distinguish between these two possibilities. The shift in response characteristics towards smaller interstimulus intervals under high-luminance conditions reported by Biederman-Thorson et al. (1971) was found here to occur at all three retinal sites examined.

The preceding observations were made using an objective procedure in which subjects were required to determine the onset sequence of the two dot flashes. Measurements were also made of the strength of the perceived illusory motion using a rating procedure similar to that commonly employed in studies of classical apparent motion. Rating levels exhibited temporal tuning characteristics similar to those obtained with the objective sequence discrimination procedure. Furthermore, the rating curves, like the sequence discrimination curves, showed a shift towards smaller interstimulus intervals with increasing retinal eccentricity. By using a suitable transformation of the rating levels it has been shown that sequence discrimination performance and strength rating levels show a high correlation. It may be concluded that when subjects were able to determine accurately the onset sequence of the two dot flashes this corresponded to the perception of a moving dot. The correlation between the subjective rating procedure and the objective sequence discrimination procedure may be of importance to the relationship of the fine-grain movement illusion to classical apparent motion. The use of a subjective procedure may be considered as a common link between the two types of illusions, for when used to study the fine-grain movement illusion it gives results that are similar to those obtained in classical apparent motion.

Chapter 5

Minimum Dot Separation for the Fine-Grain Movement Illusion and Minimum Dot Separation for Spatial Resolution

Chapter 5: Minimum Dot Separation for the Fine-Grain Movement Illusion and Minimum Dot Separation for Spatial Resolution

5.1 Dependence of minimum dot separation for the fine-grain movement illusion and minimum dot separation for spatial resolution on retinal eccentricity

In section 2.1 studies were reviewed which examined the ability of the peripheral field of the visual system to detect moving stimuli relative to its spatial resolution ability. Such studies tended to one of the following conclusions: that the two visual processes are evenly matched or that spatial resolution is not as good as motion detection. The experimental evidence on which such conclusions are based on is, however, inadequate. Much of the work, for example Stratton (1902), used different experimental procedures to obtain measurements of motion detection and spatial acuity. The resulting acuity measures are therefore difficult to compare directly and comparisons can lead to misleading interpretations. Other studies, for example Gordon (1947) and Scobey and Horowitz (1976), aware of the problem of inappropriate comparisons, aimed at obtaining suitably matched measures of motion detection and spatial acuity. Although these are an improvement on previous attempts, they too have their own shortcomings (see section 2.1) and it is believed that the approach described in this section provides a more satisfactory approach. It is shown in this chapter that with the fine-grain movement illusion the relationship between motion detection and spatial acuity can be examined in a more compatible manner than the procedures previously used.

The next experiment obtained measurements of two different spatial thresholds: the minimum dot separation required for two sequentially presented dot flashes to generate a fine-grain movement illusion and the minimum dot separation required to resolve two dot flashes presented simultaneously. To determine the minimum dot separation required for the fine-grain movement illusion subjects performed sequence discriminations using two sequential dot flashes.

Experiment 5.1

Methods

Minimum dot separation for spatial resolution. Each trial consisted of two intervals, in the one, two vertically orientated dot flashes were presented simultaneously and in the other a single dot flash was presented (two simultaneous superimposed dot flashes so that the stimulus intensity in both intervals was the same). The order in which either two dot flashes or a single dot flash occurred was determined pseudo-randomly. The two intervals in any one trial were separated by 1.5 seconds. In the two-dot interval the dot separation was controlled by the PEST procedure, which is fully described in section 3.6. The subject's task was to indicate in which interval two dots were present.

Minimum dot separation for sequence discrimination. Each trial consisted of two intervals both containing two vertically orientated dot flashes presented sequentially. The onset order of the dot flashes was different in both intervals and was determined pseudo-randomly. Hence if in the first interval the upper dot flash occurred first followed by the lower dot flash, then in the second interval the lower dot flash occurred first followed by the upper dot flash. The dot separation was always equal in both intervals and was controlled by the PEST procedure. The two intervals in any one trial were separated by 1.5 seconds. The

Table 5.1

Retinal sites ......:	5^o, 10^o, 15^o, 20^o and 25^o
ISI ....:	80 msec.
Dot-flash duration .:	1 msec
Dot diameter ....:	0.04^o
Dot-flash luminance :	1 log unit above luminance increment threshold
Viewing conditions .:	Scotopic (20 minutes dark adaptation).

interstimulus interval (between pairs of dot flashes) was 80 msec. The subjects's task was to indicate in which interval the upper dot flash occurred first and they were informed that they could use the direction of any perceived motion to base their decision on.

Each dot flash subtended approximately 0.04^o visual angle and had a duration of about 1 msec. The dot flashes were presented to the left of the fixation point along a horizontal meridian. Subjects viewed the fixation point with their right eye only (the left eye was covered by an eye patch) and hence the stimuli fell on the temporal side of the retina. A head rest was used to steady the subject's head. The dot flashes were presented on a dark background and were viewed through the viewing system. The intensity of each dot flash was set to 1 log unit above luminance increment threshold. The experiment was conducted under scotopic conditions with subjects required to dark-adapt for 20 minutes at the beginning of each session.

Four subjects participated in the experiment; SG, DHF, RSS and MJM. Two of the subjects, SG and DHF, performed eight sessions each (four sessions in which measurements were made of the minimum dot separation for sequence discrimination and four in which measurements were made of the minimum dot separation for spatial resolution). The other two subjects, RSS and MJM, performed four sessions each (two sessions for each type of spatial threshold). Each experimental session consisted of 15 runs (three runs per retinal site) and 36 trials per run. Observations were made at 5 retinal sites: 5^o, 10^o, 15^o, 20^o and 25^o eccentricity in either an ascending or descending order (the order was reversed from session to session). Relevant experimental details are summarised in Table 5.1.

Results

All four subjects reported that during observations, in which measurements of sequence discrimination were made, a single moving dot was seen for a substantial proportion of trials. The data for MJM and RSS were analysed using the method described in 3.6, which is now briefly restated. The first run, of each block of three runs, was not used in the analysis (for the results of the first run were used to obtain better PEST initialization parameters for runs 2 and 3). Runs 2 and 3 consisted of 36 trials each and a psychometric function was fitted to each set of 36 trials. From the psychometric function the threshold was taken to be the stimulus level that corresponded to the 76% correct discrimination level. Each experimental session therefore determined two thresholds (per retinal site) and hence a total four thresholds (per retinal site) were determined for RSS and MJM. Figures 5.1(a) and 5.1(b) show the final results for MJM and RSS respectively. Each point is the average of four thresholds.

For subjects SG and DHF the responses of runs 2 and 3 were pooled and a psychometric function was fitted to the resulting 72 trials. Each experimental session that SG and DHF performed therefore determined only one threshold per retinal site. The two subjects, however, performed a total of eight experimental sessions each (four sessions in which measurements were made of the minimum dot separation for sequence discrimination and four in which measurements were made of the minimum dot separation for spatial resolution) and hence the final results, shown in Figures 5.1(c) and 5.1(d), for SG and DHF respectively, are also the means of four thresholds per retinal site. To summarize, each point in Figure 5.1(a), 5.1(b), 5.1(c) and 5.1(d) are averages of four thresholds; for RSS and MJM each threshold was obtained from 36 trials, whereas for SG and DHF each threshold was obtained from 72 trials.

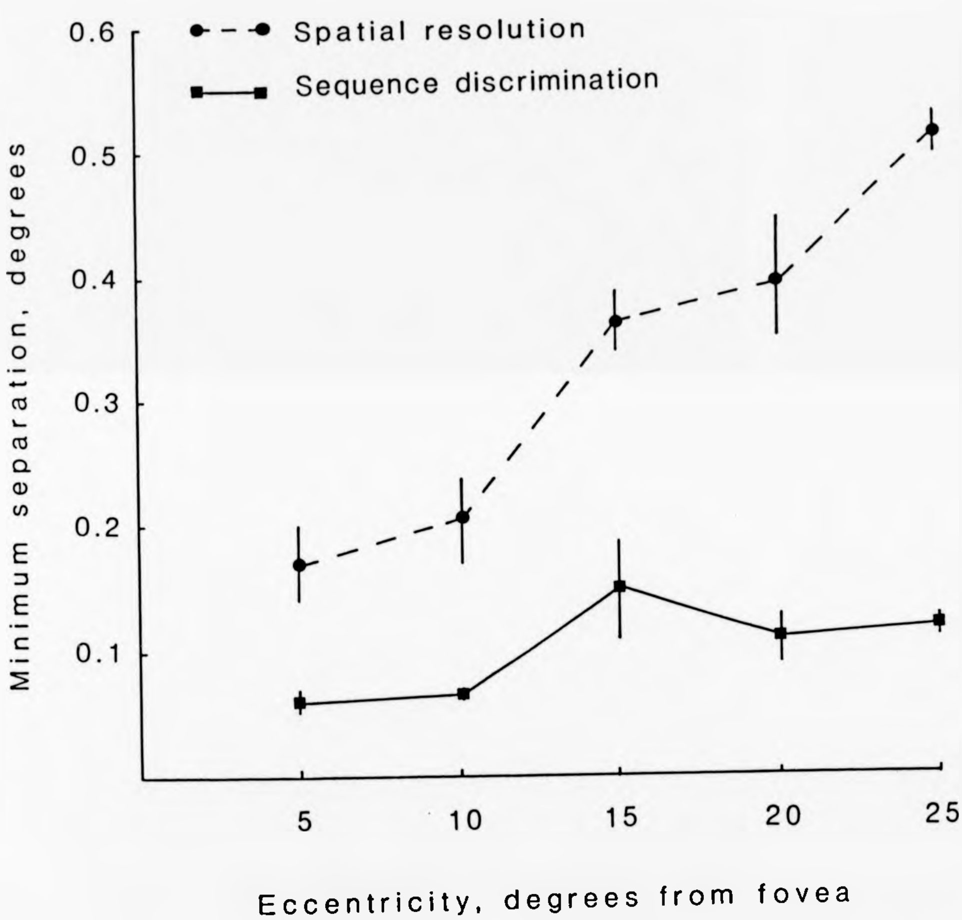


Figure 5.1(a) Minimum dot separation for sequence discrimination and minimum dot separation for spatial resolution (Experiment 5.1). Scotopic adapation conditions. Subject MJM.

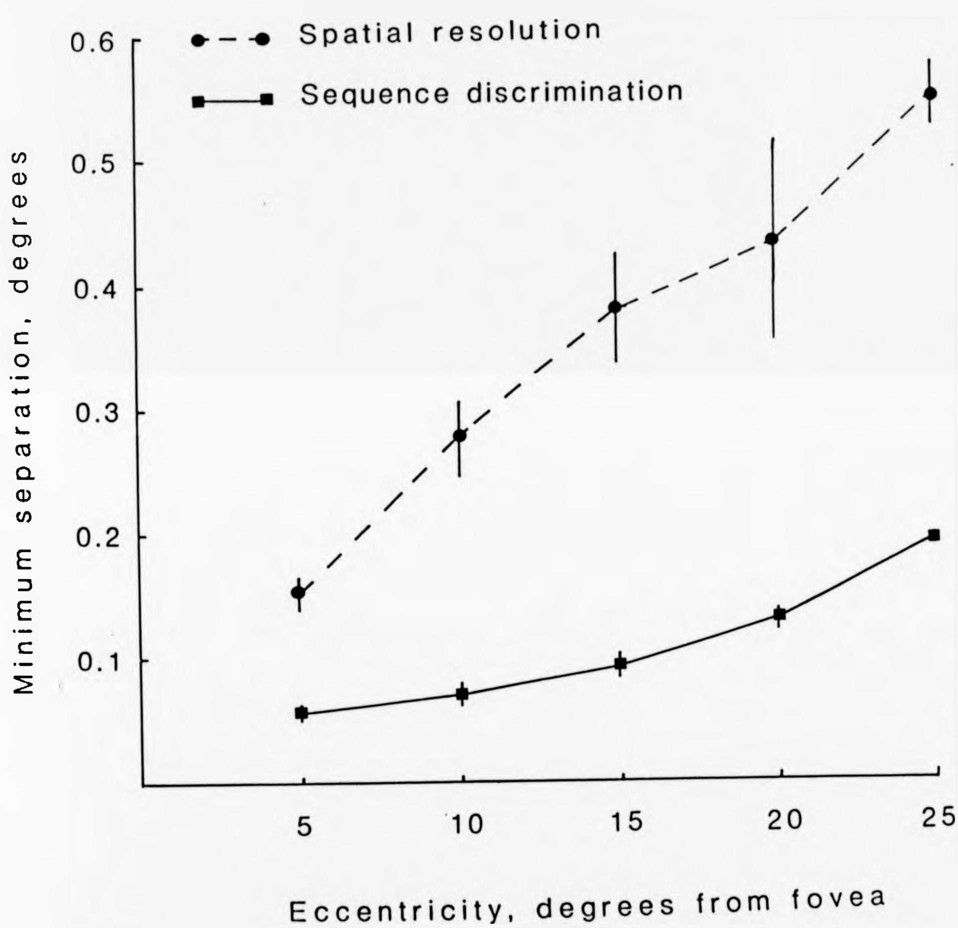


Figure 5.1(b) Minimum dot separation for sequence discrimination and minimum dot separation for spatial resolution (Experiment 5.1). Scotopic adapation conditions. Subject RSS.

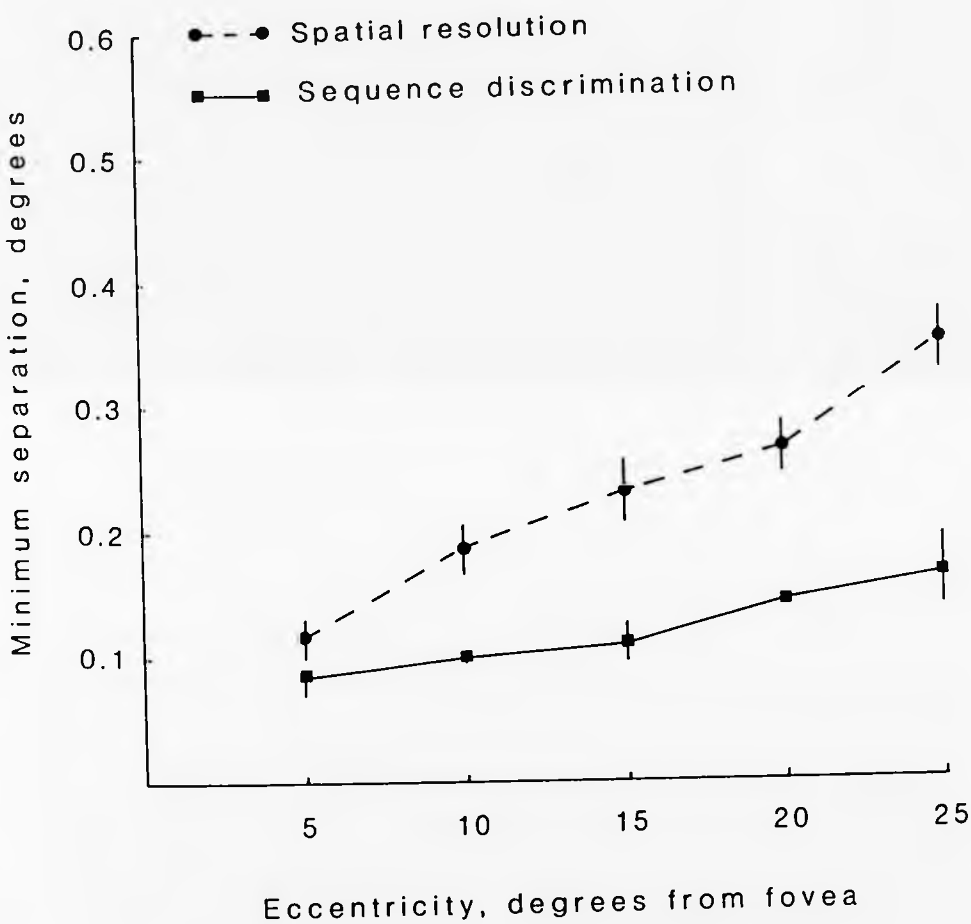


Figure 5.1(c) Minimum dot separation for sequence discrimination and minimum dot separation for spatial resolution (Experiment 5.1). Scotopic adapation conditions. Subject SG.

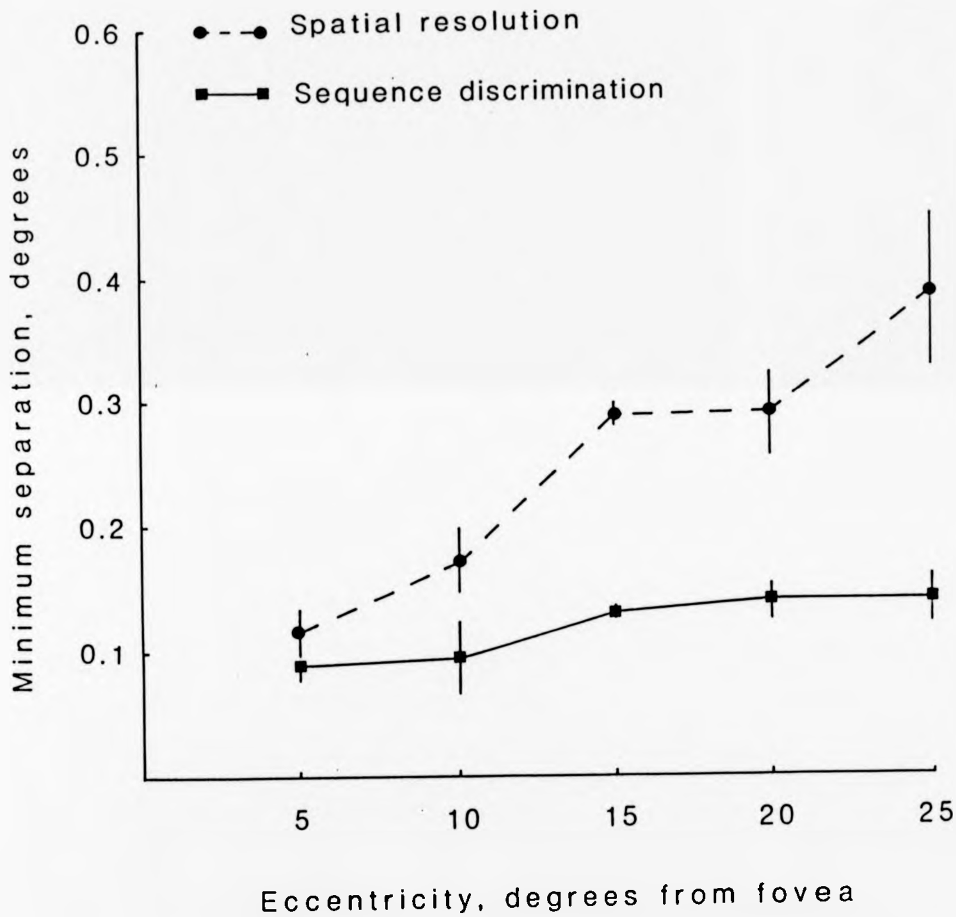


Figure 5.1(d) Minimum dot separation for sequence discrimination and minimum dot separation for spatial resolution (Experiment 5.1). Scotopic adapation conditions. Subject DHF.

The vertical bars represent ±1 standard error of the mean. The method of analysis used to analyse the data obtained with subjects RSS and MJM was used in all subsequent experiments described unless clearly stated otherwise.

As a check on the χ^2 technique used to fit psychometric functions the results obtained for SG and RSS were re-analyzed using a maximum likelihood method to fit psychometric functions (see Hall, 1981). The results of both methods of analysis are given in the appendix at the end of the thesis, and it is clear from the results that there is no significant difference between the two methods of analysis.

For all four subjects, and at all retinal sites, the minimum dot separation for sequence discrimination was smaller than the corresponding minimum dot separation for spatial resolution. The data, illustrated in Figures 5.1(a), 5.1(b), 5.1(c) and 5.1(d), were analysed using a least squares linear regression of minimum dot separation against stimulus eccentricity (see section 3.8.3). Gradients of minimum dot separation for the fine-grain movement illusion against stimulus eccentricity were 0.0034, 0.0067, 0.0030, 0.0041 for MJM, RSS, DHF and SG respectively and 0.0181, 0.0200, 0.0159, 0.0108 for the gradients of minimum dot separation for spatial resolution against stimulus eccentricity. Gradients of the minimum dot separation for spatial resolution were significantly greater than the gradients of the minimum dot separation for sequence discrimination ($p<0.001$ for all four subjects). The ratios of the gradient of the minimum dot separation for spatial resolution to the gradient of the minimum dot separation for sequence discrimination were 5.3, 3.0, 5.3 and 2.6 for MJM, RSS, DHF and SG respectively. Averaged over all four subjects the mean ratio of the gradients was 4.1.

Discussion

The minimum dot separations for sequence discrimination shown in Figures 5.1(a), 5.1(b), 5.1(c) and 5.1(d) represent the minimum dot separation for the fine-grain movement illusion, since these thresholds were below the minimum dot separation for spatial resolution and subjects therefore must have based their decisions on the direction of perceived motion and not on the spatially resolved onset sequence of the dot flashes.

In their original demonstration of the fine-grain movement illusion Thorson et al. (1969) made no formal measurements showing that the dot flashes were spatially unresolved. The dot flashes were presented at 22^o eccentricity and were separated by 7 min arc. This value is compatible with the value for the minimum dot separation for the fine-grain movement illusion obtained here at 20^o which was approximately 8.0 min arc (averaged over all four subjects).

Foster (1977) obtained direct measurements that showed that two dot flashes used to generate the fine-grain movement illusion were spatially unresolved. This was achieved by a procedure similar to that used here, in which subjects were required to indicate whether presentations consisted of two dots or a single dot. Foster (1977) used dot flash separations which varied between 4.5 min arc and 9.0 min arc, and presented 16^o from the fovea. Discrimination levels were found to be approximately at chance level. In the experiment described here the minimum dot separation required for spatial resolution at 15^o was 19.1 min arc (averaged over all four subjects). Foster's experiments were not aimed at determining the minimum separation required for the fine-grain movement illusion but at establishing that the stimuli used were indeed spatially unresolved. The results of Experiment 5.1 are therefore consistent with existing experimental data asserting that the fine-grain movement illusion is generated with spatially unresolved dot flashes. The present results, however, show not only that the fine-grain movement illusion occurs with spatially unresolved dot flashes but also that the minimum dot separation required for the fine-grain movement illusion is substantially below the minimum dot separation required for spatial resolution at retinal sites greater than 5^{o}.

The values of the minimum dot separation for the fine-grain movement illusion obtained here are larger than the displacement thresholds obtained by Scobey and Horowitz (1976). For retinal sites lying between 24^{o}-40^{o} they obtained displacement thresholds in the range of 3-4 min arc; compared to 9.3 min arc at 25^{o} obtained here. In their experiments, however, they used greater dot intensities (2 log units above luminance threshold), longer dot durations (0.5 sec) and the threshold level was taken to be 50% detection level. All these factors are likely to improve visual performance and therefore give rise to lower thresholds.

Consider next the dependence of the minimum dot separation for the fine-grain movement illusion and the minimum dot separation for spatial resolution on retinal eccentricity. The gradient of the minimum dot separation for the fine-grain movement illusion against stimulus eccentricity was, on average, 0.0043. In that this was about one quarter of the gradient of the minimum dot separation for spatial resolution against stimulus eccentricity, it may be concluded that the fine-grain movement illusion is relatively stable with changes in stimulus eccentricity.

It might be argued that the fine-grain movement illusion represents some form of motion hyper-acuity and that its comparison with the minimum dot separation for spatial resolution is inappropriate. The retinal dependence of spatial hyperacuity, however, has been shown to increase at least twice as fast with eccentricity as the minimum dot separation for spatial resolution (Westheimer, 1982). It must therefore be concluded that the fine-grain movement illusion is relatively stable with respect to eccentricity irrespective of which type of spatial acuity measure it is compared with.

In section 2.1 a review was given of experimental data relating to the ability of the visual system to detect motion relative to its ability to detect spatial structure (form). The two types of threshold determined in the present experiment clearly represent acuity measures of motion detection and form detection in the visual system. The result obtained here support the view that the peripheral field of the visual system is tuned more finely to the detection of motion than to the detection of form. Its ability to perform both types of visual function decrease with increasing eccentricity. The rate at which the decrease in the visual system's ability to detect motion with increasing eccentricity is, however, significantly less than the rate of decrease in its ability to detect spatial structure.

In section 2.6 the cortical magnification invariance principle, as proposed by Rovamo <u>et al.</u> (1978), was described. This invariance principle proposed that visual processes become invariant with eccentricity after scaling with the cortical magnification factor (M-scaling). The rapid increase of hyperacuity with eccentricity (Westheimer, 1982) is the only currently known visual process that does not conform to this invariance principle. In Figure 5.2(b) the

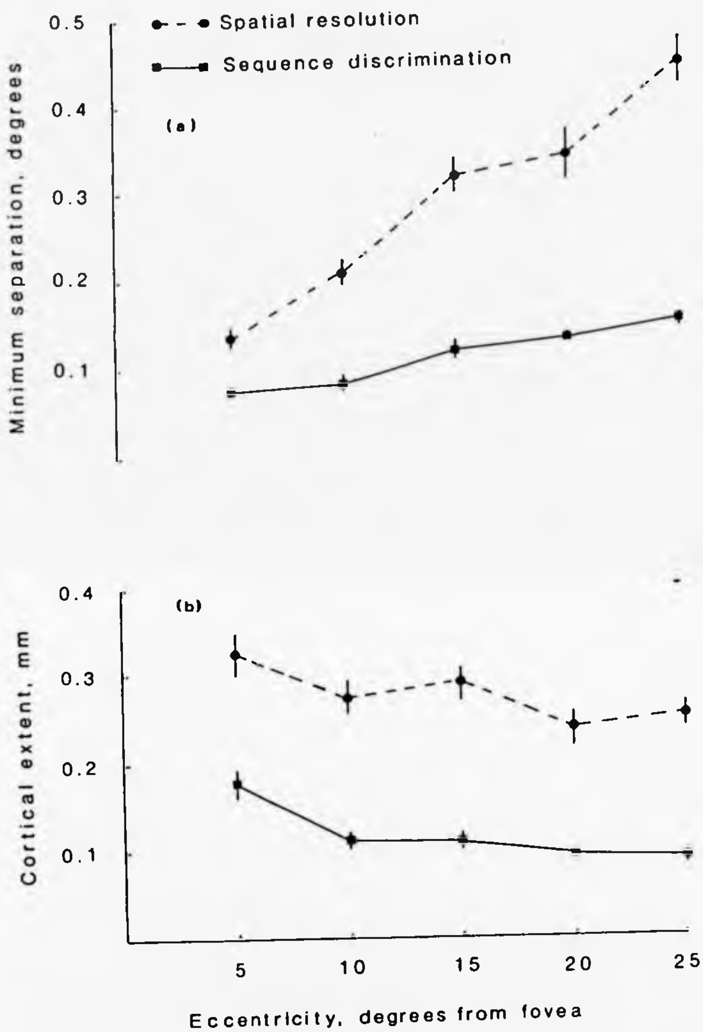


Figure 5.2 (a) Mean minimum dot separation for the fine-grain movement illusion and mean minimum dot separation for spatial resolution (averaged over four subjects). (b) Mean cortical estimates corresponding to the minimum dot separation for the fine-grain movement illusion and to the minimum dot separation for spatial resolution (averaged over four subjects).

estimated cortical distances, averaged over all four subjects, corresponding to the minimum dot separation for the fine-grain movement illusion and the minimum dot separation for spatial resolution are shown (see section 2.6 for details of the M-scaling parameters used). For comparison, Figure 5.2(a) shows the averages, taken over all four subjects, of the minimum dot separation for the fine-grain movement illusion and the minimum dot separation for spatial resolution. The average data, shown in Figure 5.2, were analysed using the least squares linear regression model described in section 3.8.3. Both curves in Figure 5.2(a) have positive gradients which are significantly greater than zero ($p<0.001$ for both gradients); the ratio of the gradient of the minimum dot separation for spatial resolution to the gradient of the minimum dot separation for the fine-grain movement illusion was about 4 and the gradients were significantly different ($p<0.001$). In Figure 5.2(b) both curves have negative gradients which are significantly different from zero ($p<0.05$ for the gradient of the cortical extents corresponding to the minimum dot separation for spatial resolution and $p<0.01$ for the gradient of the cortical extents corresponding to the minimum dot separation for the fine-grain movement illusion); the ratio of the two gradients was 0.99 and the gradients were not significantly different ($p>0.9$). It is interesting that the relationship between the two gradients changes from being significantly different to being not significantly different after M-scaling.

The finding here that under scotopic conditions cortical images of the minimum dot separation for spatial resolution decrease with increasing eccentricity was suprising, for under photopic conditions cortical images corresponding to the minimum angle of resolution have been reported to be relatively constant with stimulus eccentricity (Cowey and Rolls, 1974; Virsu and Rovamo, 1979). The possibility arises that the rate at which spatial acuity increases with increasing stimulus eccentricity decreases with decreasing levels of illumination. Evidence that such a decrease occurs is provided in reports by Mandelbaum and Sloan (1947) who observed that under high levels of illumination spatial acuity thresholds increased substantially with increasing stimulus eccentricity, whereas under much lower levels of illumination spatial acuity thresholds were almost constant with stimulus eccentricity (see section 2.5). It is likely therefore that cortical images depend on not only stimulus eccentricity but on levels of illumination. The observed decrease of the cortical images corresponding to the minimum dot separation required for the fine-grain movement illusion could likewise be reflecting the scotopic conditions under which the experiment was conducted.

5.2 Dependence of minimum dot separation for spatial resolution on stimulus duration

Studies in the field of classical apparent motion have provided experimental evidence that the processing of figural information can take longer than the processing of motion information (see section 2.2). In a similar way, it might be hypothesised that the values of the minimum dot separation for spatial resolution, obtained in the previous experiment, were higher than the minimum dot separation for the fine-grain movement illusion because of insufficient exposure duration. The total duration of the pair of dot flashes used to generate fine-grain movement illusions was approximately 80 msec, compared to 1 msec for the pair of dot flashes used to determine the minimum dot separation for spatial resolution. The differences between the minimum dot separation for spatial resolution and the minimum dot separation for the fine-grain movement illusion could therefore be an artifact of the

Table 5.2

Retinal sites ......:	5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o}
ISI ....:	80 msec.
Dot-flash duration .:	500 msec
Dot diameter ....:	0.04^{o}
Dot-flash luminance :	1 log unit above luminance increment threshold
Viewing conditions .:	Scotopic (20 minutes dark adaptation).

temporal properties of the dot flashes, and may not be reflecting fundamental differences between the form-detecting mechanism and the motion-detecting mechanism.

In Experiment 4.4 it may be recalled that using stimulus durations of 60 and 200 msec, sequence discrimination levels at large interstimulus intervals (500 msec) were significantly greater than 50% (see Figure 4.5). One possible explanation for this was that the two dot flashes were no longer spatially unresolved and that the subject was basing his decisions on the onset sequence of distinguishable dot flashes, as opposed to the direction of perceived motion. The results of Experiment 4.4 therefore could be interpreted as evidence that the minimum dot separation for spatial resolution decreases with increasing stimulus duration.

In the next experiment the minimum dot separation for spatial resolution was determined, as a function of retinal eccentricity, using a greater stimulus duration than was used in the previous experiment.

Experiment 5.2

Methods

All conditions were as described for Experiment 5.1 apart from dot-flash durations which were now 500 msec. Subjects were SG and RSS. Each subject performed four experimental sessions, with each session consisting of 15 runs (three runs per retinal site). The experiment was conducted under scotopic conditions. Relevant experimental details are summarised in Table 5.2.

Results

Figures 5.3(a) and 5.3(b) show the results for SG and RSS respectively. Each point is the mean value of eight measurements, vertical bars represent ±1 standard error of the mean. The values of the minimum dot separation for spatial resolution using the shorter stimulus duration (1 msec), as obtained in Experiment 5.1, are indicated by the broken lines. The minimum dot separations obtained with long stimulus durations and those obtained with short stimulus durations were compared using the χ^2 test, described in section 3.8.1, and were found to be not significantly different ($p>0.1$ for SG and $p>0.25$ for RSS).

Discussion

The results obtained here differ from existing experimental data suggesting that spatial acuity improves with increasing stimulus duration. Westheimer (1972) asserted that the minimum dot separation for spatial resolution decreases with increasing stimulus duration from 100 msec up to some 2 seconds. He does not, however, describe how these results were obtained and only refers to his findings informally. Other evidence that spatial acuity improves with stimulus duration derives from measurements of contrast sensitivity functions with varying stimulus duration (Nachmias, 1967).

The results of this experiment clearly suggest that, in the given experimental conditions, there was no difference in spatial acuity between a 1 msec dot flash exposure and a 500 msec exposure. This implies that differences between the minimum dot separation for the fine-grain movement illusion and the minimum dot separation for spatial resolution, observed in Experiment 5.1, are unlikely to be an artifact of the duration of pairs of dot flashes.

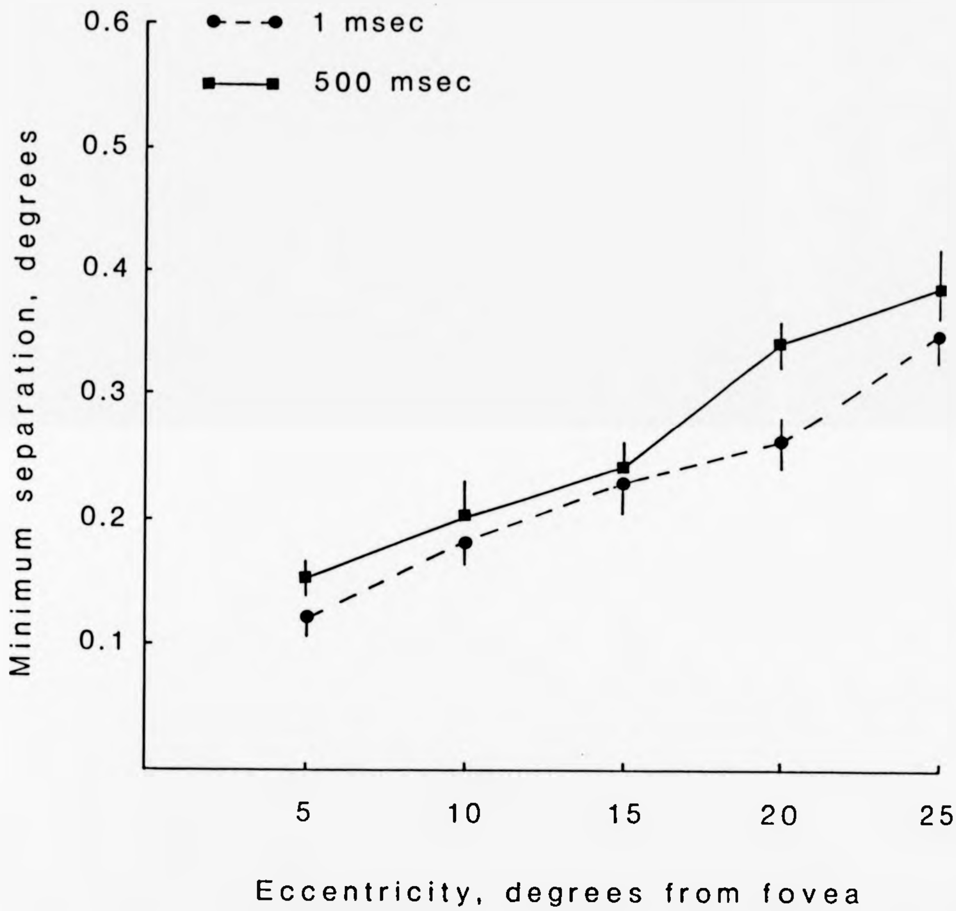


Figure 5.3(a) Minimum dot separation for spatial resolution using a 500 msec dot-flash duration (Experiment 5.2) compared with that obtained using a 1 msec dot-flash duration (Experiment 5.1). Scotopic adapation conditions. Subject SG.

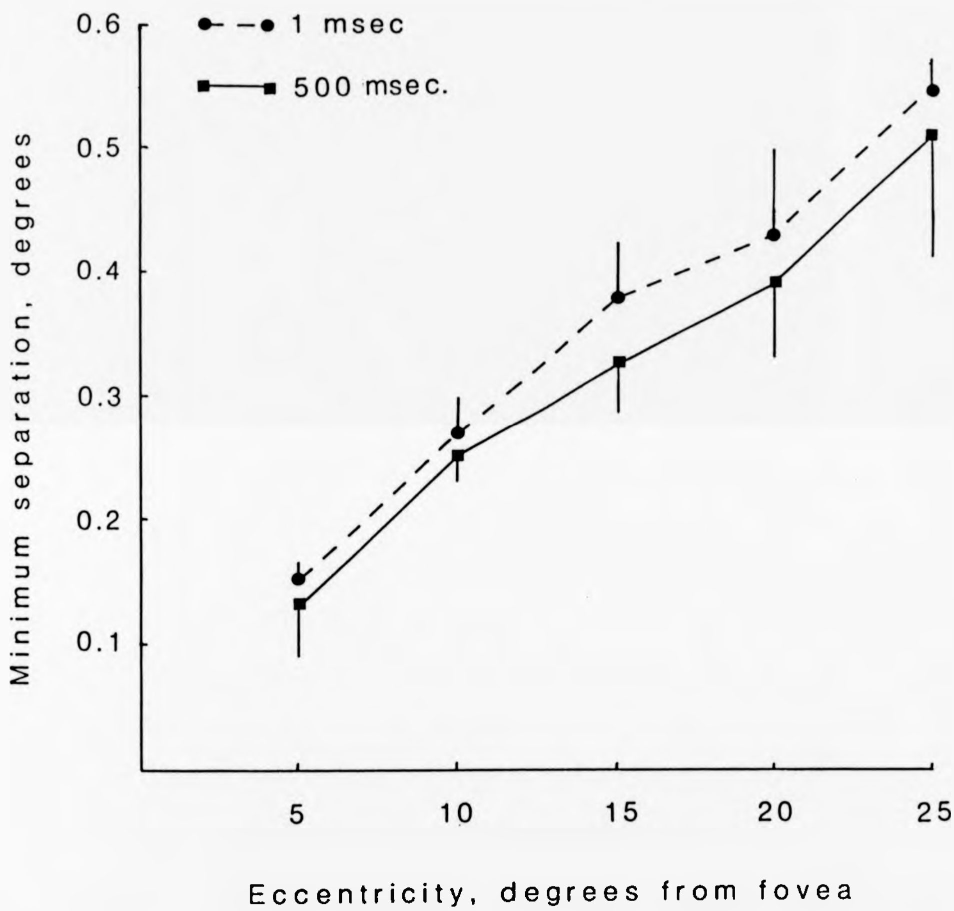


Figure 5.3(b) Minimum dot separation for spatial resolution using a 500 msec dot-flash duration (Experiment 5.2) compared with that obtained using a 1 msec dot-flash duration (Experiment 5.1). Scotopic adapation conditions. Subject RSS.

The results of this experiment also have implications for the interpretation of Experiment 4.5. In Experiment 4.5 the use of 60 and 200 msec dot-flash durations resulted in sequence discrimination levels, at long interstimulus intervals, which were greater than chance level. The hypothesis that this increase in sequence discrimination was due to the dot flashes being spatially resolved (and therefore the subject responding to the onset sequence of the dot flashes) can be rejected in the light of the outcome of the present experiment. It appears therefore that the increase in sequence discrimination, observed with long dot flash durations (see Figure 4.5), must be attributed to fine-grain motion being generated at interstimulus intervals that would not occur with smaller dot flash durations.

5.3 Effect of interstimulus interval on the minimum dot separation for the fine-grain movement illusion

In section 2.3 a review was given of short-range apparent motion that may be obtained with two alternated random-dot patterns. The perception of coherent motion, in a central region of displaced elements, in two random-dot patterns could only be obtained when the spatial displacement and the interstimulus interval between frames were relatively small (typically a displacement of 15 min arc and interstimulus interval of 10 msec). The perceptual segregation of the central region was shown to decrease as the limiting displacement increased and as the interstimulus interval increased. Similarities between short-range apparent motion in random-dot patterns and the fine-grain movement illusion suggest that two processes reflect the operation of the same motion-detecting mechanism (see section 2.4 for a discussion of the relationship between the fine-grain movement illusion and short-range apparent motion in random-dot patterns). Should the two types of illusory motion be

Table 5.3

Retinal sites ......:	25^o
ISI ....:	60, 100, 140, 180 and 220 msec.
Dot-flash duration .:	1 msec
Dot diameter ....:	0.04^o
Dot-flash luminance :	1 log unit above luminance increment threshold
Viewing conditions .:	Scotopic (20 minutes dark adaptation).

subserved by the same motion-detecting mechanism then they might be expected to exhibit a similar dependence on interstimulus interval. Experiments described in Chapter 4 have already considered one aspect of the dependence of the fine-grain movement illusion on interstimulus interval (i.e. its temporal tuning characteristics). The next experiment considers this dependence further by determining the minimum dot separation required for the fine-grain movement illusion as a function of interstimulus interval.

Experiment 5.3

Methods

The method and procedure were similar to that used for Experiment 5.1, and differed only in the following aspects. Observations were made at a single retinal site of 25^o eccentricity. The interstimulus intervals used ranged from 60 msec to 220 msec in steps of 40 msec. The experiment consisted of four experimental sessions for each subject. Each session consisted of a block of 15 runs (three runs per interstimulus interval). During any one session the interstimulus interval was systematically changed in an increasing or decreasing order, and the order reversed from session to session. The subjects were SG and MJM. The experiment was conducted under scotopic conditions. Relevant experimental details are summarised in Table 5.3.

Results

Both subjects reported that at all interstimulus intervals a single moving dot could be seen for a substantial proportion of trials. Results on the minimum dot separation for sequence discrimination are shown in Figure 5.4. Each point is the mean value of eight measurements; vertical bars represent ±1 standard error of the mean.

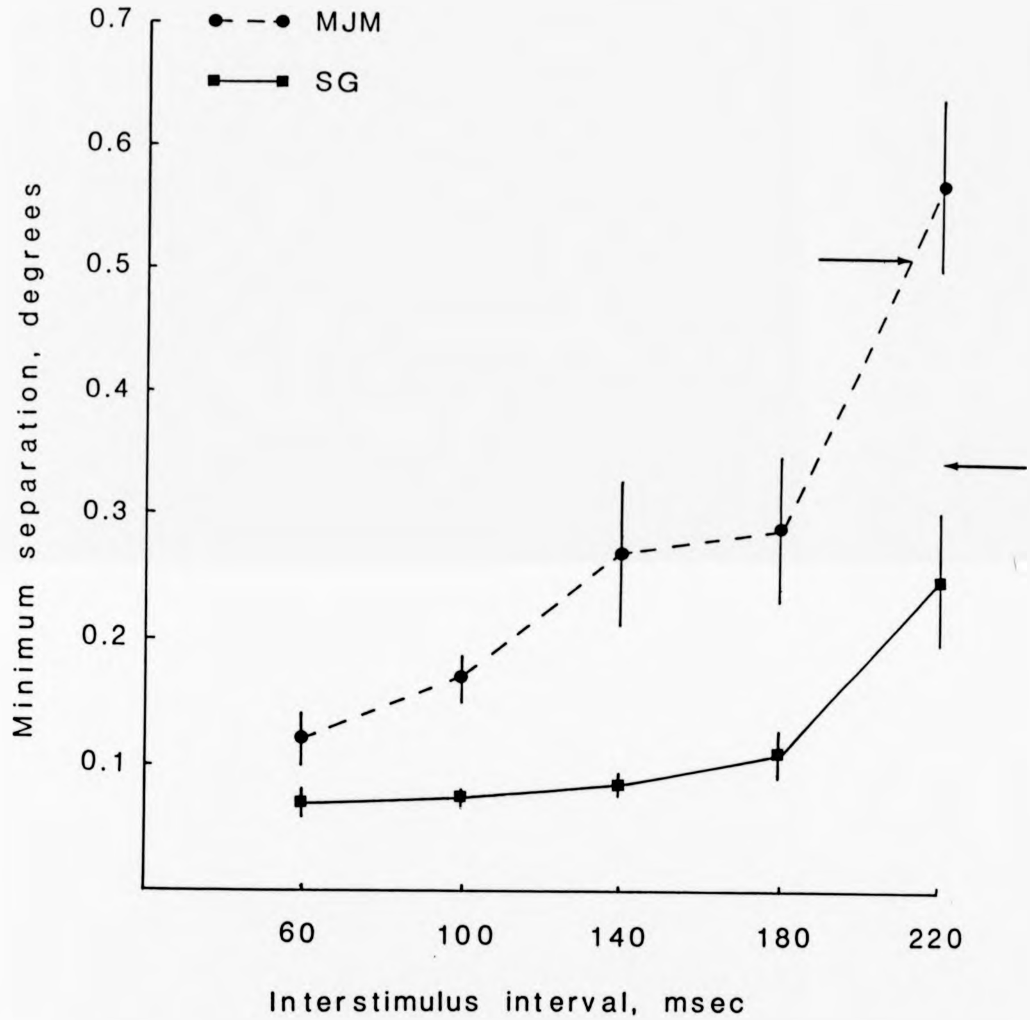


Figure 5.4 Minimum dot separation for sequence discrimination as a function of interstimulus interval (Experiment 5.3). Scotopic adapation conditions. Subjects SG and MJM.

For both sets of data, the minimum dot separation for sequence discrimination increased with increasing interstimulus interval. The horizontal arrows indicate the minimum dot separation for spatial resolution for each subject (as obtained in Experiment 5.1). The minimum dot separation for sequence discrimination lies below the minimum dot separation for spatial resolution at all interstimulus intervals except at 220 msec for MJM.

Discussion

Apart from the value obtained at 220 msec for MJM, all sequence discrimination thresholds lie below their respective minimum dot separation for spatial resolution, and hence it may be assumed that subjects were basing their decisions on the direction of perceived motion and not on the onset sequence of spatially resolved dot flashes. It may therefore be assumed that the minimum dot separation required for the fine-grain movement illusion increases monotonically with increasing interstimulus interval.

An upper limit on the interstimulus interval for short-range apparent motion, obtained with random-dot patterns, was given by Braddick to be between 80-100 msec. The experiment described here, however, suggests that the fine-grain movement illusion may be generated with interstimulus intervals of up to 180-220 msec. Although the results obtained here were at a retinal site of 25^{o} it is unlikely that at smaller retinal sites this 180-220 msec range would change much given that the minimum dot separation required for the fine-grain movement illusion changes only slightly with eccentricity (see section 5.1). Stimulus durations used by Braddick (1974) were 75 msec, hence in terms of the stimulus onset asynchrony Braddick's range was approximately 155-175 msec. In the experiment described here the stimulus onset asynchrony was approximately equal to the interstimulus interval, since the duration of each dot flash was substantially smaller than the interstimulus interval. It appears therefore that the temporal dependence of the minimum dot separation required for the fine-grain movement illusion and short-range apparent motion, obtained with random-dot patterns, are similar if temporal intervals are expressed in terms of stimulus onset asynchronies as opposed to interstimulus intervals.

5.4 Minimum dot separation for sequence discrimination with dichogeniculate presentation of two dot flashes

Thorson et al. (1969) presented two horizontally orientated dot flashes, several degrees below a fixation point, near the vertical midline that separates the nasal and temporal sides of the retina. The fixation point was shifted laterally so that the image of the dot flashes scanned the region around the vertical midline. For all subjects tested a movement blind spot was located in which subjects did not perceive a strong extrapolated movement illusion. The region of the retina at which an extrapolated movement illusion was not obtained was assumed to correspond to when the dot flashes straddled the vertical midline (i.e. dichogeniculate presentation of the two dot flashes). The failure to obtain the fine-grain movement illusion under dichogeniculate conditions has lead to the suggestion that the illusion could be used clinically to locate the meridian of the nasotemporal division of the retina (McIlwain, 1972; Foster et al., 1981).

The final experiment described in this chapter determined the minimum dot separation required for sequence discrimination at retinal sites near to the vertical midline of the retina. Several retinal locations were considered, including a retinal site such that two dot flashes presumably fell on different sides of the retina. On the basis of Thorson et al.'s findings it was expected that the minimum dot separation required for sequence discrimination would be greatest at retinal sites at which dot flashes straddled the vertical midline.

Experiment 5.4

Methods

The method and procedure were similar to those used in Experiment 5.1 apart from the following aspects. Pairs of dot flashes were orientated horizontally (as opposed to orientated vertically as used in previous experiments). Dot flashes were presented at either 5^o or 10^o below the fixation point. The vertical position below the fixation point was located by allowing the subject to adjust, by using the push button box, the horizontal position of a test dot flash, located at either 5^o or 10^o below the fixation point, such that the test dot flash appeared directly below the fixation point. Dot flashes were presented at horizontal distances of $\pm 4^o$, $\pm 2^o$, $\pm 0.4^o$, $\pm 0.2^o$ and 0.0^o away from the vertical midline (negative values indicate that the centre of dot flashes fell on the nasal side of the retina, and positive values indicate that the centre of dot flashes fell on the temporal side of the retina). Each trial consisted of a single interval in which two dot flashes were presented sequentially. The interstimulus interval was 80 msec. The subjects task was to indicate the onset sequence of the two dot flashes. A bite-bar was used to steady the subjects head during observations.

The author acted as subject and performed a total of 12 experimental sessions. The 12 sessions consisted of (i) four sessions in which dot flashes were presented 5^o below the fixation point and their centre was a horizontal distance of $\pm 0.4^o$, $\pm 0.2^o$ and 0.0^o away from the vertical midline; (ii) four sessions in which dot flashes were 10^o below the

Table 5.4

Retinal sites ......:	5^{0} and 10^{0} vertically below the fixation point
ISI ....:	80 msec.
Dot-flash duration .:	1 msec
Dot diameter ....:	0.04^{0}
Dot-flash luminance :	1 log unit above luminance increment threshold
Viewing conditions .:	Scotopic (20 minutes dark adaptation).

fixation point and their centre was $\pm 0.4^{0}$, $\pm 0.2^{0}$ and 0.0^{0} away from the vertical midline; (iii) two sessions in which dot flashes were 5^{0} below the fixation point and their centre a horizontal distance of $\pm 4^{0}$ and $\pm 2^{0}$ away from the vertical midline (iv) two sessions in which dot flashes were 10^{0} below the fixation point and a horizontal distance of $\pm 4^{0}$ and $\pm 2^{0}$ away from the vertical midline. The experiment was conducted under scotopic conditions. Relevant experimental details are summarised in Table 5.4.

Results

The author noted that for a significant proportion of trials an extrapolated movement illusion could be seen. Figure 5.5 shows the results. Each value obtained at horizontal distances of $\pm 0.4^{0}$, $\pm 0.2^{0}$ and 0.0^{0} away from the vertical midline were averages of eight measurements. Values at $\pm 4^{0}$ and $\pm 2^{0}$ away from the vertical midline were averages of four measurements each. Vertical bars represent ±1 standard error of the mean. The highest value of the minimum dot separation for sequence discrimination occurred when the centre of dot flashes fell on the vertical midline (which presumably corresponded to dichogeniculate presentation of the dot flashes). The minimum dot separations for sequence discrimination obtained with dot flashes 10^{0} below the fixation point were compared, using the χ^2 test described in section 3.8.1, with values obtained with dot flashes 5^{0} below the fixation point and found to be significantly different ($p<0.05$).

Discussion

Two aspects of the results of this experiment support the suggestion (McIlwain, 1972; Foster et al., 1981) that the fine-grain movement illusion could be used clinically to locate the vertical midline of the human retina. First, that the highest values of the minimum dot separation for sequence discrimination occurred when the dot flashes

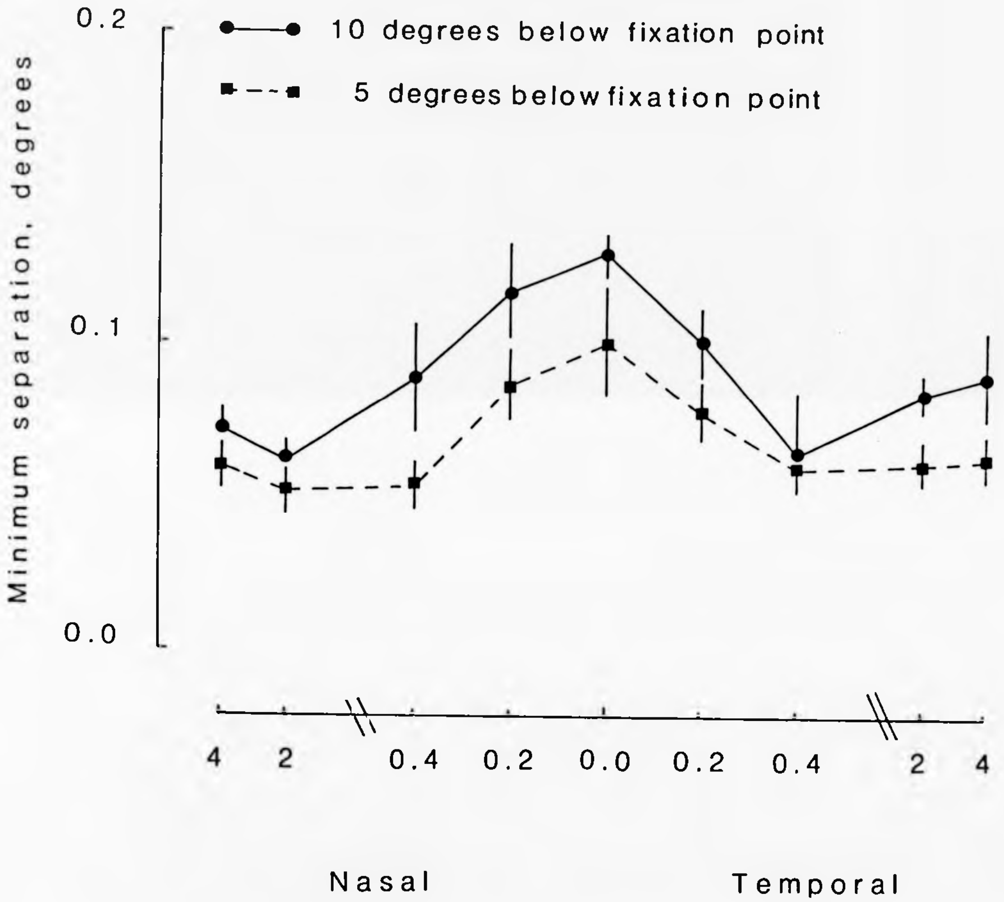


Figure 5.5 Minimum dot separation for sequence discrimination at retinal sites near to the vertical midline separating the nasal side of the retina from the temporal side (Experiment 5.4). Scotopic adapation conditions. Subjects SG.

were presented under conditions which were presumably dichogeniculate. Second, that this observation occurred both with dot flashes at 5^o and 10^o below the fixation point. Hence it seems possible that the locus of the peak value, of the minimum separation for sequence discrimination, maps out the position of the vertical midline. It is not possible to conclude from this experiment that the minimum dot separations, obtained for sequence discrimination, correspond to minimum dot separations for the fine-grain movement illusion, for no measurements were made of the corresponding minimum separation for spatial resolution. Minimum separations were comparable to those measured along the horizontal meridian (see Figure 5.1a) and hence the existence of the peak around 0^o implies a weakening of the effect but not sufficient to eliminate a movement illusion.

5.5 Summary and Conclusion

It has been shown explicitly that the minimum distance by which two dot flashes have to be separated to elicit a fine-grain movement illusion is substantially smaller than the minimum dot separation for spatial resolution. This difference between the two type of spatial thresholds is unlikely to be an artifact of the duration of dot flashes.

Both the minimum dot separation for spatial resolution and the minimum dot separation for the fine-grain movement illusion were found to increase with retinal eccentricity. The increase in the minimum dot separation for the fine-grain movement illusion occurred at approximately one quarter of the rate at which the minimum dot separation for spatial resolution increased with retinal eccentricity. This suggests that the motion-detecting mechanism is relatively stable with retinal eccentricity when compared to the form-detecting mechanism.

In this sense it could be argued that the peripheral field of the visual system is specialized for motion detection.

The experiments described in this chapter have implications for the cortical magnification scaling principle asserting that spatial extents of photopic visual processes become invariant with retinal eccentricity after multiplication by the cortical magnification factor M. Estimates of the cortical extent corresponding to the minimum dot separation for spatial resolution exhibited a slight decrease with retinal eccentricity. Although this decrease was gradual, it was however significantly different from zero. This finding can be compared to previous reports that cortical images corresponding to photopic spatial acuity are relatively constant with stimulus eccentricity. Furthermore, cortical extents corresponding to the minimum dot separation for the fine-grain movement illusion also exhibited a gradual, but again significant, decrease with eccentricity. The differences between the retinal dependence of cortical images observed here and those previously reported are possibly reflecting the use of different adaptation states (Mandelbaum and Sloan, 1947).

It has been suggested that the fine-grain movement illusion may be related to the coherent short-range apparent motion that can be obtained with random-dot patterns. Braddick (1974) showed that the coherent motion obtained with random-dot patterns decreases with increases in interstimulus interval. Measurements of the minimum dot separation for the fine-grain movement illusion have shown it to increase with increasing interstimulus interval, hence providing further evidence that the two type of illusions may be related. The range of temporal intervals over which the two types of illusions may be elicited are similar when temporal intervals are expressed in terms of stimulus onset asynchronies as opposed to interstimulus intervals. This suggests that the stimulus onset asynchrony may be a more appropriate way of describing temporal characteristics of visual stimuli giving rise to apparent motion, than the interstimulus interval.

Finally the suggestion that the fine-grain movement illusion could be used to locate the vertical midline, dividing the nasal and temporal side of the retina, was tested. The minimum dot separation for sequence discrimination was determined over a range of retinal locations near the vertical midline of the eye. The resulting minimum dot separations were found to be highest when the dot flashes straddled the vertical midline (presumably under dichogeniculate conditions). These findings add support to Thorson <u>et al.'s</u> (1969) and Biederman-Thorson <u>et al.'s</u> finding that the fine-grain movement illusion cannot be obtained under dichogeniculate conditions and that the illusion could therefore be used to locate the vertical midline that separates the nasal and temporal sides of the retina.

Chapter 6

Spatial Interaction Thresholds obtained with Two Fine-Grain Movement Illusions

Chapter 6: Spatial Interaction Thresholds obtained with Two Fine-Grain Movement Illusions

6.1 Spatial interaction thresholds of two collinear fine-grain movement illusions as a function of retinal eccentricity

The previous two chapters have considered various aspects of a single fine-grain movement illusion. In this chapter the perception of two fine-grain movement illusions, generated close to each other, is considered. Foster et al. (1981) described the effects of pitting two illusions against each other and a summary of their observations was given in section 2.4. Several different stimulus configurations were investigated and it was found that two fine-grain movement illusions elicited within 0.5^{0} of each other destructively interfered unless they were codirectional. When these conditions were not met the resulting perception was of a smeared or blurred image, sometimes in motion, as opposed to two distinct fine-grain movement illusions. The destructive interference of two fine-grain movement illusions has no analogy in the field of classical apparent motion. For example two apparently moving straight lines can be brought as close together as required without the illusions destructively interfering with each other (providing the paths taken by the illusory objects are not made to cross, Kolers, 1972). The minimum distance that two fine-grain movement illusions can be brought together without destroying each other is referred to here as the spatial interaction threshold.

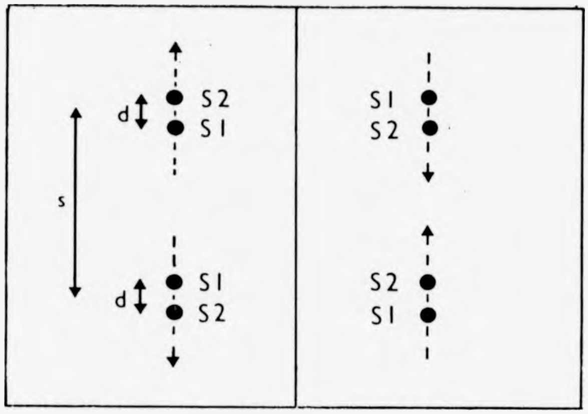
In the experiment described in this section, spatial interaction thresholds were measured as a function of eccentricity.

Experiment 6.1

Methods

Figure 6.1(a) shows the stimulus configuration used to measure spatial interaction thresholds obtained with two collinear fine-grain movement illusions. The onset sequence of dot flashes is denoted by S1 and S2, where S1 preceded S2. The broken arrows indicate the direction in which fine-grain movement illusions would be generated if no interactions occurred. Each trial consisted of two intervals, with each interval consisting of two pairs of vertically orientated dot flashes, sequentially flashed so that, under appropriate conditions, two collinear fine-grain movement illusions, moving in opposite directions, were generated. The onset order of dot flashes in the second interval was always the reverse of the onset order of dot flashes in the first interval, so that if two inward (see right-hand side of Figure 6.1a) moving fine-grain movement illusions were generated in the first interval, then in the second interval two outward (see left-hand side of Figure 6.1a) moving fine-grain movement illusions were generated. The onset order of dot flashes in the first interval was determined pseudo-randomly. The two intervals in a given trial were separated by 1.5 seconds. The dot separation, d, was kept constant during a run and was set at the midpoint of the minimum dot separation required for the fine-grain movement illusion and the minimum dot separation required for spatial resolution (see section 5.1). The centre-to-centre separation of pairs of dot flashes, s, was controlled by PEST (see section 3.6) and hence varied during a run. The subject's task was to indicate in which interval the outer dot flashes occurred first; they were informed that they could use the direction of any perceived motion to base their decision on.

(a) Collinear



(b) Parallel

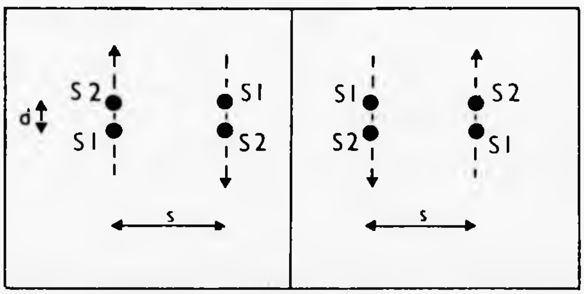


Figure 6.1 Spatial arrangement of dot flashes used to generate (a) two collinear fine-grain movement illusions (used in Experiments 6.1, 6.3 and 6.4) and (b) two parallel fine-grain movement illusions (used in Experiment 6.2).

Table 6.1

Retinal sites ......: 5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o}

Dot-flash separation:

	Eccentricity, degrees				
	5	10	15	20	25
SG	0.10^{o}	0.14^{o}	0.17^{o}	0.21^{o}	0.26^{o}
RSS	0.10^{o}	0.17^{o}	0.24^{o}	0.28^{o}	0.37^{o}

ISI ....: 80 msec.

Dot-flash duration .: 1 msec

Dot diameter ....: 0.04^{o}

Dot-flash luminance : 1 log unit above luminance increment threshold

Viewing conditions .: Scotopic (20 minutes dark adaptation).

Each dot flash subtended approximately 0.04^{o} visual angle and had a duration of about 1 msec. The dot flashes were presented to the left of the fixation point along a horizontal meridian. Subjects viewed the fixation point with their right eye only (the left eye was covered by an eye patch) and hence the stimuli fell on the temporal side of the retina. A head rest was used to steady the subject's head. The dot flashes were presented on a dark background and were viewed through the viewing system. The intensity of each dot flash was set to 1 log unit above luminance increment threshold. The experiment was conducted under scotopic conditions with subjects required to dark-adapt for 20 minutes at the beginning of each session.

Subjects were SG and RSS. Each subject performed two experimental sessions, with each session consisting of 15 runs (three runs per retinal site) and 36 trials per run. The retinal sites considered were 5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o} eccentricity in either an ascending or descending order (the order was reversed from session to session). Relevant experimental details are summarised in Table 6.1.

Results

The resulting interaction thresholds are shown in Figure 6.2. Each point is the mean of four values; vertical bars represent ±1 standard error of the mean. Spatial interaction thresholds were an increasing function of eccentricity.

Discussion

At 10^{o} eccentricity, spatial interaction thresholds were 0.75^{o} and 0.38^{o} for SG and RSS respectively; compared with Foster et al.'s (1981) finding that two fine-grain movement illusions, viewed at 10^{o} eccentricity, had to be separated by about 0.5^{o} for the illusions not to destructively interfere.

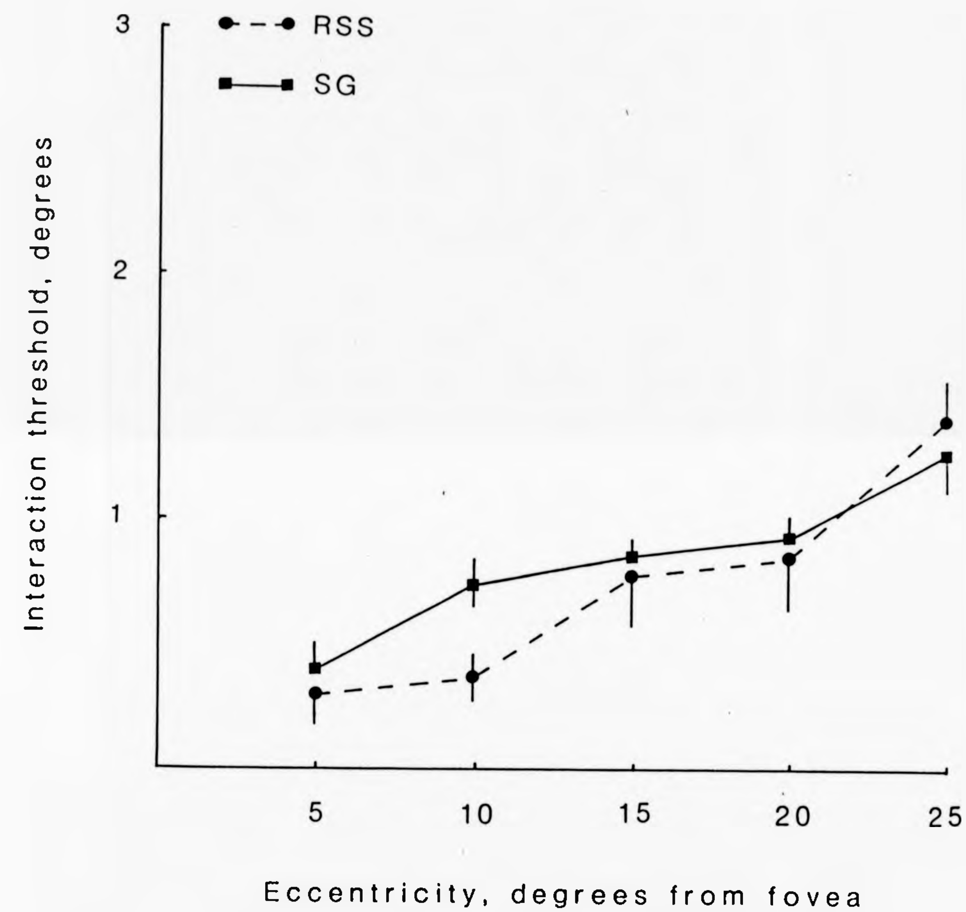


Figure 6.2 Spatial interaction thresholds obtained with two collinear fine-grain movement illusions (Experiment 6.1). Scotopic adaptation conditions. Subjects SG and RSS.

The increase of spatial interaction thresholds with eccentricity suggests that estimates of the cortical distances corresponding to the thresholds might be roughly constant with eccentricity. Figure 6.3 shows the cortical distances, as a function of eccentricity, that correspond to the spatial interaction thresholds (see section 2.6 for details of the cortical magnification factor). Both curves in Figure 6.3 were analysed using the least squares linear regression model described in 3.8.3. Neither gradient was significantly different from zero ($p>0.1$ for SG and $p>0.3$ for RSS). Averaged over all retinal sites the cortical estimates, corresponding to the spatial interaction thresholds, were 0.82 mm for SG and 0.66 mm for RSS. Spatial interaction thresholds, unlike the minimum dot separation required for the fine-grain movement illusion, therefore give cortical images which are relatively invariant with retinal site. This difference in the retinal dependence of the two cortical images suggests that the mechanism responsible for the generation of the fine-grain movement illusion may be different from that which controls the interaction of two illusions.

A possible cause of the interaction of two fine-grain movement illusions is that the visual system attempts, and fails, to construct two fine-grain movement illusions with partially overlapping extents. The perceptual size of the illusion is significantly greater than the separation of the dots used to generate the illusory motion (Foster et al., 1981). For example, at 10^{o} eccentricity Foster et al. (1981) found the extent of the illusion was 2.6^{o}. This value is much larger than interaction thresholds obtained in the experiment described here. Clearly if the size of the fine-grain movement illusions, typically generated in the experimental conditions used in this thesis, were of similar size to the illusions generated in Foster et al.'s (1981)

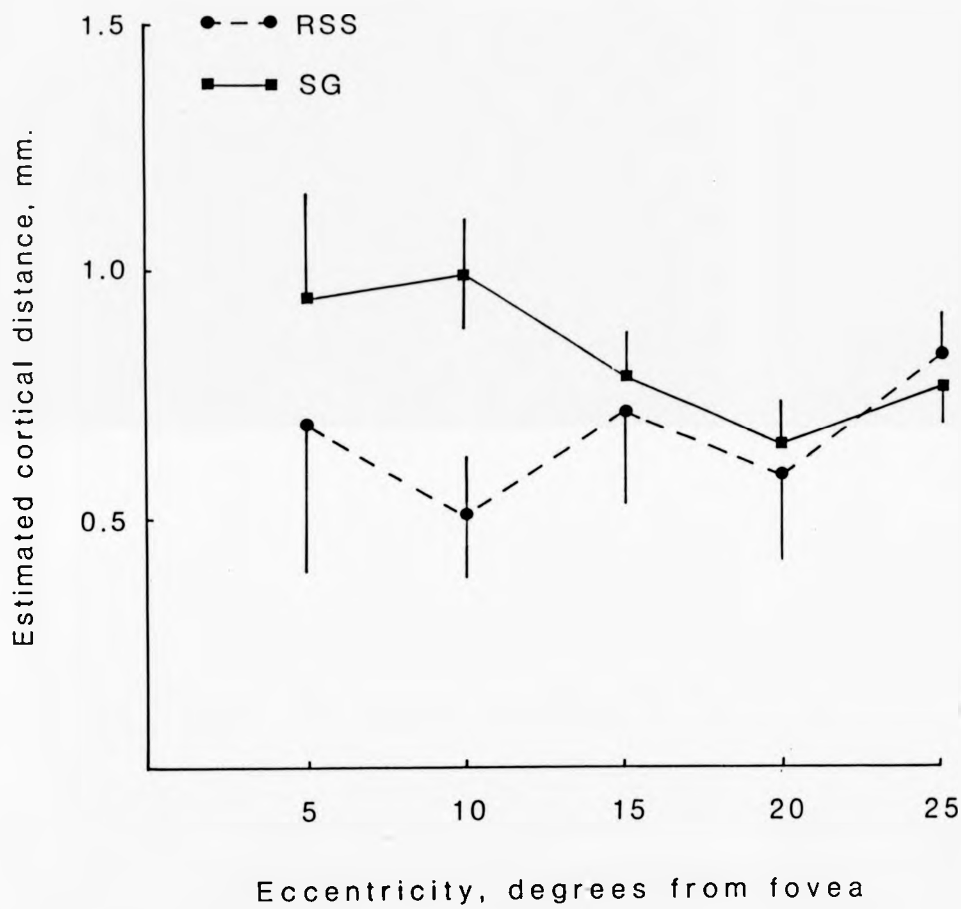


Figure 6.3 Estimated cortical distances corresponding to spatial interaction thresholds obtained with two collinear fine-grain movement illusions. Subjects SG and RSS.

experimental conditions, then the destruction of two illusions could be a trivial consequence of overlapping spatial extents. The perceived extent of the fine-grain movement illusion increases with increasing eccentricity (Foster et al., 1981), adding support to the possibility that the interaction of two illusions is related to the extent of the illusion. If the hypothesis that the interaction of two illusions is due to the visual system attempting to construct two overlapping fine-grain movement illusions is correct, then it would be expected that two parallel, but not collinear, fine-grain movement illusions should give rise to significantly lower spatial interaction thresholds than those obtained with two collinear illusions. Spatial interaction thresholds obtained with two parallel, but not collinear, fine-grain movement illusions are considered in the next section.

6.2 Spatial interaction thresholds obtained with two parallel fine-grain movement illusions

The next experiment considered spatial interaction thresholds obtained with two parallel, but not collinear, fine-grain movement illusions. Codirectional fine-grain movement illusions were not considered as these would have given zero spatial interaction thresholds (Foster et al., 1981). The spatial arrangement of dot flashes is shown in Figure 6.1(b). Under appropriate conditions two parallel fine-grain movement illusions, moving in opposite directions, would be generated. If the hypothesis that the interaction of two fine-grain movement illusions is a trivial consequence of the visual system attempting to construct two overlapping fine-grain movement illusions is correct, then it should be possible to bring two parallel fine-grain movement illusions arbitrarily close together without the illusions interacting with each other.

Table 6.2

Retinal sites ......:	5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o}					
Dot-flash separation:		Eccentricity, degrees				
		5	10	15	20	25
	SG	0.10^{o}	0.14^{o}	0.17^{o}	0.21^{o}	0.26^{o}
	RSS	0.10^{o}	0.17^{o}	0.24^{o}	0.28^{o}	0.37^{o}
ISI ....:	80 msec.					
Dot-flash duration .:	1 msec					
Dot diameter ....:	0.04^{o}					
Dot-flash luminance :	1 log unit above luminance increment threshold					
Viewing conditions .:	Scotopic (20 minutes dark adaptation).					

Experiment 6.2

Methods

The method and procedure were identical to that used in Experiment 6.1 apart from the arrangement of dot flashes and the task that subjects were required to perform. Figure 6.1(b) shows the arrangement of dot flashes. The dot flashes were now arranged so that under appropriate conditions two parallel fine-grain movement illusions, moving in opposite directions, would be generated. The onset order of dot flashes in the second interval was always the reverse of the onset order in the first interval. Hence, for example, if in the first interval the pair of dot flashes nearest to the fixation point generated a downward moving fine-grain movement illusion (see left-hand side of Figure 6.1b) then in the second interval the same pair of dot flashes would generate an upwards moving illusion (see right-hand side of Figure 6.1b). Subjects were asked to indicate in which interval the upper dot flash, of the two dot flashes nearest to the fixation point, occurred first and were informed that they could base their decision on the direction of any motion they perceived. Two subjects, SG and RSS, participated in the experiment. Each subject participated in two experimental sessions, with each session consisting of 15 runs (three runs per retinal site). Relevant experimental details are summarised in Table 6.2.

Results

Results are shown in Figures 6.4. Each point is the mean of four values; vertical bars represent ±1 standard error of the mean. For both subjects spatial interaction thresholds obtained with two parallel fine-grain movement illusions were higher than spatial interaction thresholds obtained with two collinear fine-grain movement illusions. The two different types of interaction thresholds are significantly different ($p<0.005$ for both subjects, see section 3.8.1 for χ^2 test).

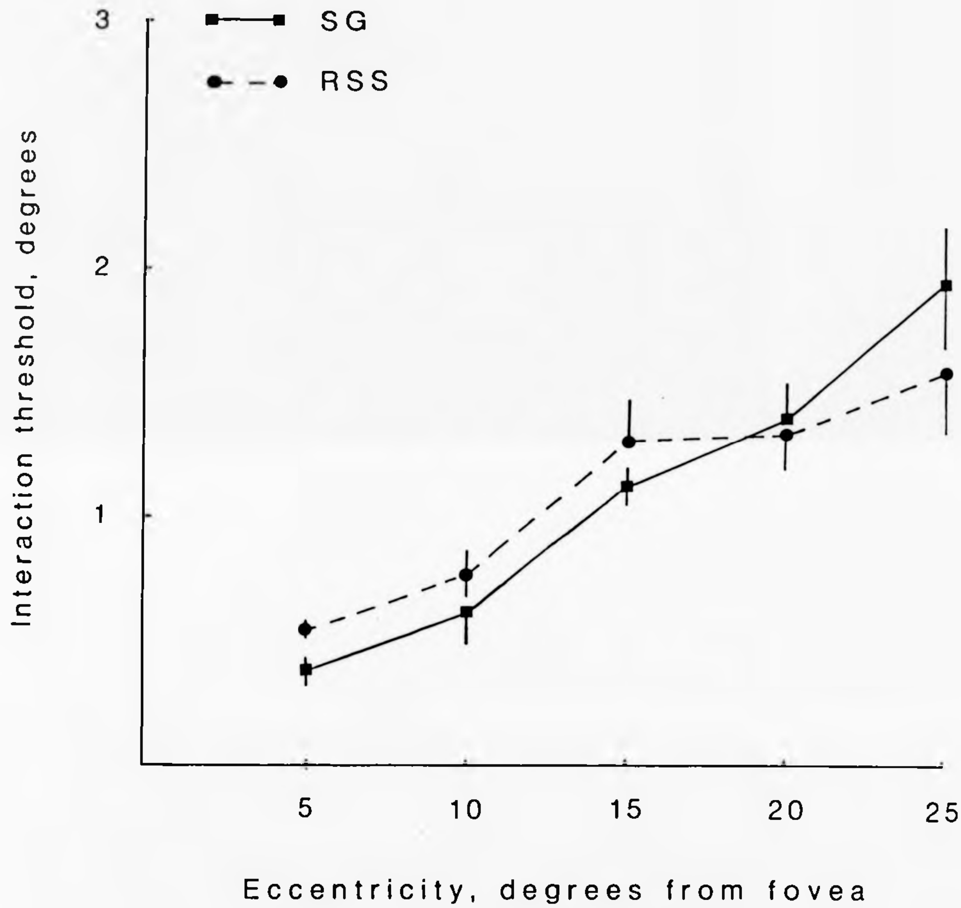


Figure 6.4 Spatial interaction thresholds obtained with two parallel fine-grain movement illusions (Experiment 6.2). Scotopic adaptation conditions. Subjects SG and RSS.

Discussion

The results of this experiment clearly indicate the incorrectness of the hypothesis that the interaction of two fine-grain movement illusions is a consequence of the visual system attempting to construct partially overlapping illusions. The parallel fine-grain movement illusions generated in this experiment could not have had overlapping extents and therefore on the basis of the above hypothesis should have given rise to significantly smaller, and possibly zero, interaction thresholds than those obtained with two collinear illusions.

The dependence of the interaction of two fine-grain movement illusions on the spatial arrangement of the illusions has implications for whether the interaction occurs before or after the illusions are generated and on the patterns of neural activity underlying the illusion. Foster et al.'s (1981) observations, relating to the interaction of two illusions under different spatial arrangements (see section 2.4), suggest that the interaction of two illusions occurs prior to the construction of the illusions. For if the interaction occurred after the construction of the illusions, then it would be expected that interactions would have a greater dependence on spatial arrangement than was observed. The results of Experiments 6.1 and 6.2 strengthen the hypothesis that the interaction of two fine-grain movement illusions occurs before the construction of the illusions.

6.3 Spatial interaction thresholds of two inward moving and two outward moving collinear fine-grain movement illusions

The third experiment described in this chapter is a control experiment that considers the spatial interaction thresholds that correspond solely to two inward moving fine-grain movement illusions and solely to two outward moving illusions. The aim of the experiment was to see if there was an asymmetry in the spatial interaction threshold for the two different spatial arrangements of illusions. In Experiment 6.1 the spatial interaction thresholds corresponding solely to two inward or to two outward moving illusions could not be determined. For in that experiment each trial consisted of two intervals in which pairs of dot flashes could generate both inward moving fine-grain movement illusions and outward moving illusions. In Experiment 6.3 each trial consisted of a single interval with dot flashes that could generate either two inward or two outward moving fine-grain movement illusions. With such an experimental paradigm the results of the experiment could be analysed to determine the spatial interaction thresholds that correspond solely to two inward moving fine-grain movement illusions and solely to two outward moving illusions.

Experiment 6.3

Methods

The method and procedure were similar to those used for Experiment 6.1 apart from the task the subject was required to perform and each trial consisting of only one interval. The arrangement of dot flashes was the same as that used in Experiment 6.1 (see Figure 6.1a). Each trial, however, consisted of only one interval with two pairs of dot flashes which, under appropriate conditions, generated either two inward moving

Table 6.3

Retinal sites ......:	5°, 10°, 15°, 20° and 25°				
Dot-flash separation:	Eccentricity, degrees				
	5	10	15	20	25
	0.10°	0.14°	0.17°	0.21°	0.26°
ISI ....:	80 msec.				
Dot-flash duration .:	1 msec				
Dot diameter ....:	0.04°				
Dot-flash luminance :	1 log unit above luminance increment threshold				
Viewing conditions .:	Scotopic (20 minutes dark adaptation).				

fine-grain movement illusions or two outward moving illusions. The onset order of dot flashes was determined pseudo-randomly. The subject's task was to indicate whether the inner pair of dot flashes or the outer pair of dot flashes occurred first, and that he could base his decision on the direction of any perceived motion. The author acted as subject and performed a total of four experimental sessions. Each experimental session consisted of 15 runs (three runs per retinal site). The experiment was conducted under scotopic conditions. Relevant experimental details are summarised in Table 6.3.

Results

The data were analysed in three different ways. First, all responses obtained during a single run (i.e. all 36) were analysed by the usual procedure whereby a psychometric function was fitted to all the 36 responses (i.e. responses to inward moving illusions and to outward moving illusions were pooled). Second, only responses to inward moving fine-grain movement illusions were taken into consideration and a psychometric function fitted to these points (which averaged out at 18 responses per run). Finally only responses to outward moving illusions were pooled together and analysed. At each retinal site the experiment therefore gave three spatial interaction thresholds. The results are shown in Figure 6.5. Each point is the mean of eight values; vertical bars represent ±1 standard error of the mean. The three sets of results were compared, pairwise, using the χ^2 test, described in section 3.8.1, and were found to be not significantly different ($p>0.5$ for results obtained with combined inward and outward moving illusions compared with results obtained with inward moving illusions, $p>0.5$ for results obtained with combined inward and outward moving illusions compared with results obtained with outward moving illusions and $p>0.9$ for results obtained with outward moving illusions compared with results obtained with inward moving illusions).

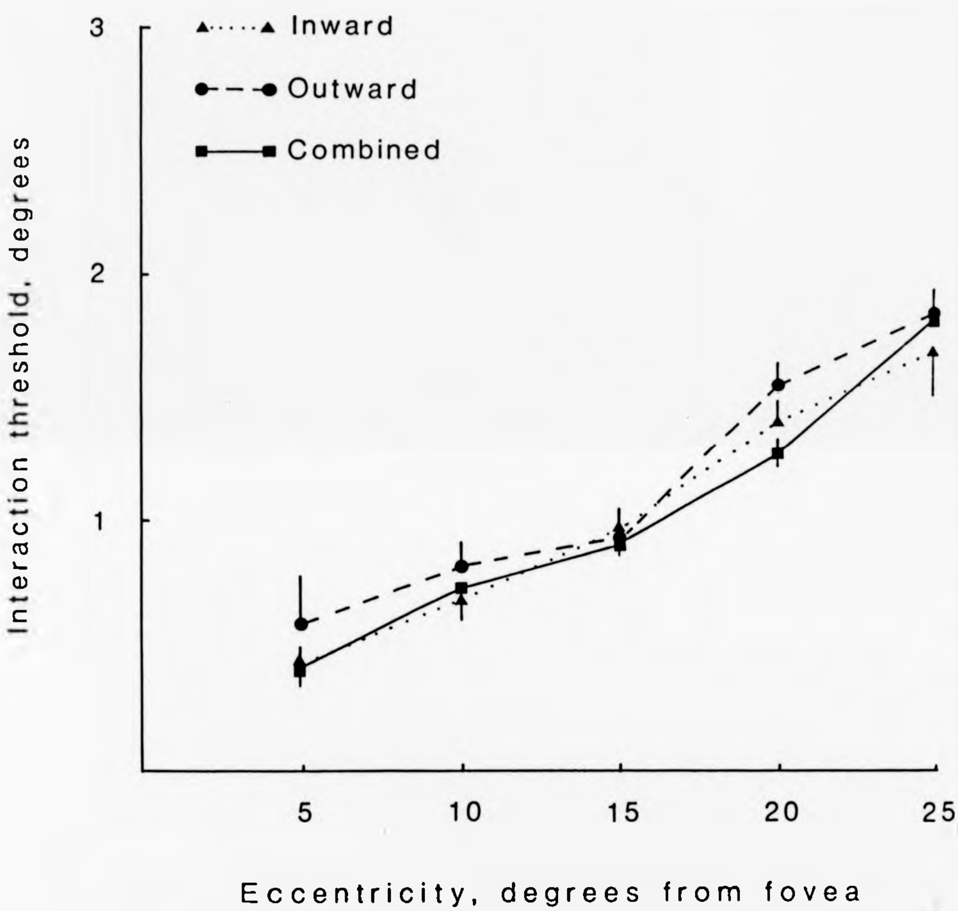


Figure 6.5 Spatial interaction thresholds determined separately for two inward moving fine-grain movement illusions; two outward moving collinear fine-grain movement illusions and combined inward and outward moving illusions (Experiment 6.3). Scotopic adaptation conditions. Subject SG.

Discussion

Spatial interaction thresholds obtained with two inward moving fine-grain movement illusions have been shown to be not significantly different from spatial interaction thresholds obtained with two outward moving illusions. This finding that spatial interaction thresholds obtained with two collinear fine-grain movement illusions is independent of whether the two illusions are moving away from or towards each other supports the hypothesis advanced in the previous section, namely, that the interaction of two fine-grain movement illusions occurs before the illusions are constructed.

6.4 Dependence of spatial interaction threshold on dot flash separation

The final experiment in this chapter considered the dependence of spatial interaction thresholds on the separation of dot flashes used to generate fine-grain movement illusions. The aim of the experiment was to consider spatial interaction thresholds obtained with stimuli generating classical apparent motion. The strong degree of destructive interference obtained with two fine-grain movement illusions cannot be observed with classical apparent motion. For example consider the arrangement of dot flashes shown in Figure 2.1(a). When the separation of dot flashes is sufficiently small, typically several minutes of arc, the visual system attempts to construct two diverging fine-grain movement illusions but fails due to interactions. If, however, the dot flashes were separated by a significantly larger distance, typically several degrees, then the centre dot can be seen to move, smoothly and continuously, in opposite directions towards the two outer dot flashes (this is often referred to as "split motion"). Under appropriate spatial arrangement of the stimuli the visual system is therefore capable of constructing classical apparent motion and is not subject to strong destructive interference. In the example cited, the difference between the two experimental conditions is only one of spatial scale, the stimuli used to generate illusory motion are identical in both cases. The question arises whether interactions are an all-or-nothing mechanism, which can be observed with closely spaced dot flashes but not with widely spaced dot flashes. Alternatively, the mechanism responsible for interactions could operate on a graded basis, with interactions gradually decreasing with increasing spatial extents. To examine whether interactions operate on an all-or-nothing basis or are graded the next experiment considered spatial interactions as a function of the separation of dot flashes used to generate illusory motion. A range of dot separations was used such that some dot flashes were spatially resolved and others were spatially unresolved. Illusory motion generated with spatially resolved dot flashes would be categorised formally as classical apparent motion, whereas illusory motion generated with two spatially unresolved dot flashes would be categorised formally as fine-grain motion.

Experiment 6.4

Methods

The method and procedure were similar to that used in Experiment 6.1, apart from the dot-flash separation, d, which was altered from run to run (instead of the retinal site varying from run to run). The collinear stimulus configuration was used (see Figure 6.1a). Observations were made at a single retinal site of 25° eccentricity. The separation of dot flashes, used to generate illusory motion, was kept constant during a run but varied systematically from run to run between 0.1° and 0.7° in steps of 0.1°. The author, SG, acted as subject and performed a total of four experimental sessions. Each

Table 6.4

Retinal sites ......: 25^o

Dot-flash separation: 0.1, 0.2, 0.3, 0.4, 0.5, 0.6 and 0.7 degrees

ISI ....: 80 msec.

Dot-flash duration .: 1 msec

Dot diameter ....: 0.04^o

Dot-flash luminance : 1 log unit above luminance increment threshold

Viewing conditions .: Scotopic (20 minutes dark adaptation).

session consisted of 21 runs (three runs per dot-flash separation). The experiment was conducted under scotopic conditions. Relevant experimental details are summarised in Table 6.4.

Results

In the previous three experiments spatial interaction thresholds were defined according to the centre-to-centre separation of pairs of dot flashes. This may not be appropriate in this experiment since the separation of dot flashes was not constant. The results were therefore expressed in three different forms, one in which separations were taken from the centre-to-centre of pairs of dot flashes (as used in Experiments 6.1, 6.2 and 6.3) and the other two in which separations were taken from the nearest two dot flashes and the outer two dot flashes. Figure 6.6 shows the results expressed in both forms. Each point is the mean of eight values; vertical bars represent ±1 standard error of the mean. The vertical arrows indicate the minimum dot separation for spatial resolution at 25^o eccentricity for SG, as obtained in Experiment 5.1. The spatial interaction thresholds are a decreasing function of the separation of dot flashes.

Discussion

Points to the left of the vertical arrows correspond to spatial interaction thresholds obtained with two spatially unresolved dot flashes, whereas points to the right of the vertical arrow correspond to spatial interaction thresholds obtained with two spatially resolved dot flashes. The left side of Figure 6.6 therefore shows spatial interaction thresholds obtained with two fine-grain movement illusions, whereas the right side shows spatial interaction thresholds obtained with two dot flashes undergoing classical apparent motion. The monotonic fall of interaction thresholds, with increasing dot separation, clearly shows that interaction is not an all-or-nothing

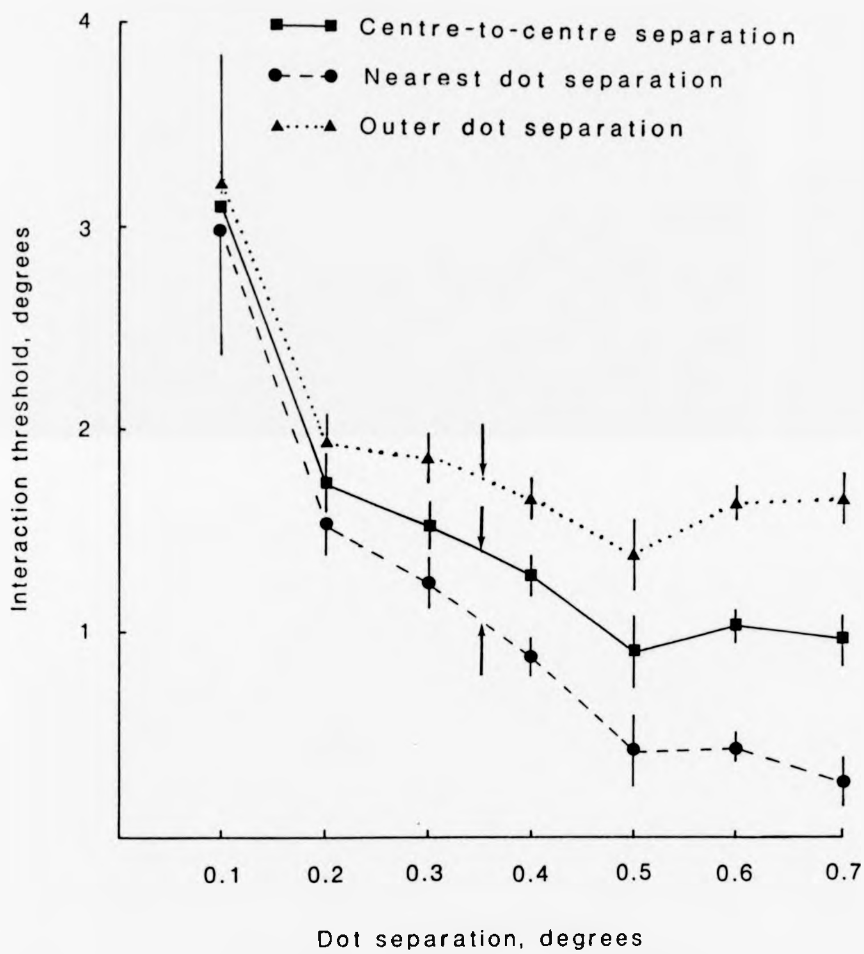


Figure 6.6 Spatial interaction thresholds obtained with two collinear fine-grain movement illusions as a function of the separation of dot flashes used to generate the illusion (Experiment 6.4). Scotopic adaptation conditions. Subject SG.

mechanism, but is a graded according to spatial extents. These results can be interpreted as evidence that classical apparent motion can, under certain conditions, exhibit destructive interaction. One possible objection to this interpretation is that two dot flashes with a separation just above the minimum dot separation for spatial resolution may not generate classical apparent motion but result in a fine-grain movement illusion.

In Figure 6.7 the ratio of spatial interaction thresholds to the separation of dot flashes is shown. At the smallest dot separations, 0.1^o, the spatial interaction threshold is about 30 times larger than the dot separation, while at the largest dot separation, 0.7^o, the interaction threshold is only 1.5 times the dot separation.

In section 1.2 it was mentioned that the fine-grain movement illusion may be an ideal candidate for bridging the gap between the perception of real motion and apparent motion. The experiment described in this section provides an example of how this might be achieved. It is possible that the real-motion detecting mechanism is responsible for the construction of the fine-grain movement illusion since dot flashes, used to generate the illusion, are spatially unresolved. Hence by determining characteristics of some attribute of illusory motion, over a range of dot separations which include spatially resolved dot flashes and spatially unresolved dot flashes, the results reflect the operation of mechanisms responsible for real-motion perception and apparent-motion perception.

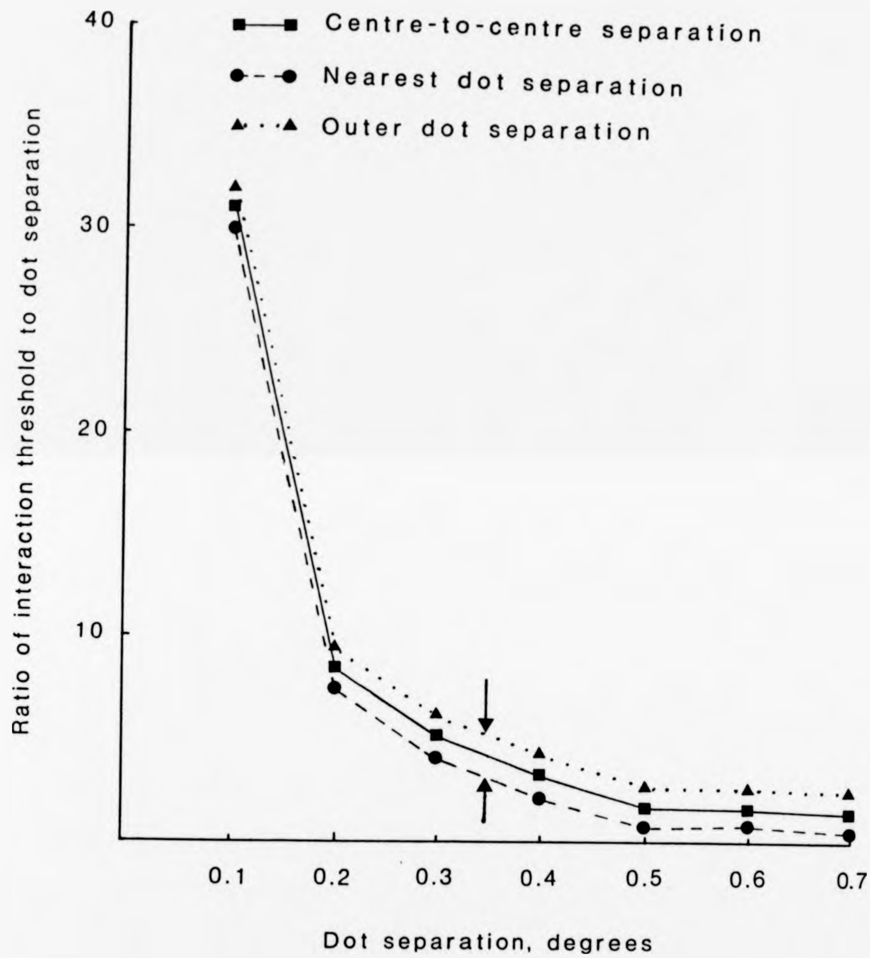


Figure 6.7 Ratio of spatial interaction thresholds, obtained with two collinear fine-grain movement illusions, to the separation of dot flashes used to generate illusory motion.

6.5 Summary and conclusion

It has been shown that the minimum distance by which two fine-grain movement illusions have to be separated so as not to destructively interact with each other increases with retinal eccentricity. Two different spatial arrangements of two fine-grain movement illusions were considered, one in which two illusions were collinear and the other in which they were parallel, but not collinear. Spatial interaction thresholds obtained with the parallel fine-grain movement illusions were found to be significantly greater than spatial interaction thresholds obtained with two collinear fine-grain movement illusions. This observation has two implications. First, that the interaction of two fine-grain movement illusions cannot be explained on the basis that the visual system attempts, and fails, to construct two partially overlapping fine-grain movement illusions. For under such an hypothesis spatial interaction thresholds obtained with two parallel fine-grain movement illusions would be expected to be smaller than spatial interaction thresholds obtained with two collinear fine-grain movement illusions. Second, that the interaction of two fine-grain movement illusions takes place before the construction of the two illusions. Should the interaction take place after the two illusions are constructed then, again, it would be expected that parallel fine-grain movement interaction thresholds would be significantly smaller than collinear fine-grain movement illusion interaction thresholds. It may furthermore be assumed that the neural activity responsible for the fine-grain movement illusion occurs after the occurrence of interactions.

Cortical estimates of spatial interaction thresholds were found to be roughly constant with retinal eccentricity. This contrast with the finding in Chapter 5, that cortical images corresponding to the minimum dot separation required for the fine-grain movement illusion decreased with increasing eccentricity. This difference in the retinal dependence of cortical images may suggest that the mechanism responsible for the construction of the fine-grain movement illusion could be different from the mechanism that controls the interaction of two illusions.

Finally spatial interaction thresholds have been determined as a function of the separation of dot flashes used to generate illusory motion. A range of dot-flash separations were considered, which included values below the minimum dot separation for spatial resolution and values above it. Spatial interaction thresholds were found to decrease with increasing dot-flash separation. Spatial interaction thresholds obtained with two spatially resolved dot flashes, represent the interaction of two objects undergoing classical apparent motion. The results therefore show that the destructive interaction that can be observed with two fine-grain movement illusions, under appropriate conditions, is not restricted to the fine-grain movement illusion but can also be observed in classical apparent motion, although to a much lesser extent.

An alternative interpretation of the dependence of interation thresholds on dot-flash separation is based on the finding that over dot-flash separations of between 0.2^o and 0.7^o interaction thresholds were approximately constant (when measured in terms of the distance between the outer two dot flashes). This sugests that it is the total extent of the illusion that is responsible for interactions; which could be reflecting the existence of a receptive field, of constant dimension, subserving the interaction.

Chapter 7

Perceived Extent of Illusory Motion

Chapter 7: Perceived Extent of Illusory Motion

7.1 Extent of the fine-grain movement illusion as a function of eccentricity

The perceived extent of the fine-grain movement illusion was shown by Foster et al. (1981) to be significantly larger than the physical separation of the dot flashes used to generate the illusion. Measurements of the extent of the illusion were made over a range of retinal sites, and it was found to be as large as 6^{o} at 24^{o} eccentricity. The separation of the dot flashes was about 0.2^{o} and hence the perceived size of the illusion was some 30 times greater than the dot-flash separation. The extent of the illusion was shown to increase with increasing eccentricity. The length of the path traversed by an object undergoing classical apparent motion is also perceived as being different from the veridical distance between the two relevant visual stimuli; but this difference is significantly less than that observed in fine-grain motion (see section 2.2.2). The first experiment in this chapter determined the perceived extent of fine-grain movement illusions typically generated in the experimental conditions employed in this thesis. Measurements of the extent of the illusion were made over a range of retinal sites.

Experiment 7.1

Methods

The technique described in this section, to measure the extent of the fine-grain movement illusion, is based on the method employed by Foster et al. (1981). Figure 7.1 shows the arrangement of dot flashes used to obtain measurements of the extent. Each pair of dot flashes was

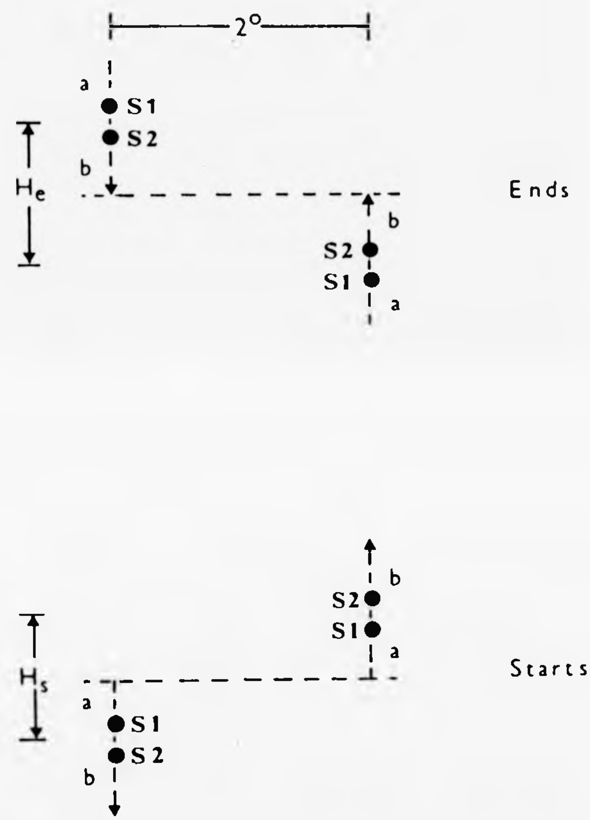


Figure 7.1 Spatial arrangement of dot flashes used to measure the extent of the fine-grain movement illusion (used in Experiments 7.1, 7.2 and 7.3).

orientated vertically. The two pairs of dot flashes were parallel, but not collinear, and had a horizontal separation of 2^{0}. The onset order of dot flashes is indicated in Figure 7.1 by S1 and S2, where S1 always preceded S2. The onset order of dot flashes was fixed during any one run, such that if each pair of dot flashes generated a fine-grain movement illusion then the two illusions would be either travelling towards each other (i.e. the ends, denoted by arrowheads in Figure 7.1, were nearest to each other) or moving away from each other (i.e. the starts of the illusions were nearest to each other). The extent of each fine-grain movement illusion was represented as the sum of a part *a*, which was taken to be the distance between the start of an illusion and the two dot flashes, and a part *b*, which was the distance between the end of an illusion and the two dot flashes. Measurements were made of H_s the vertical centre-to-centre separation, of the pairs of dot flashes, at which subjects perceived the starts of two illusions to be just horizontally aligned, and H_e the vertical separation at which the ends of two illusions were just horizontally aligned. Assuming that two illusions had identical shapes then the extent of the illusion L was given by $a + b = (H_e + H_s)/2$. The centre-to-centre separation, *s*, of the pair of dot flashes was controlled by the PEST procedure (see section 3.6).

All experiments described so far in this thesis were based on a two-alternative forced choice procedure. A subject's response in these experiments (with the exception of Experiment 4.3) could always be compared to the required response and hence evaluated to have been correct or incorrect. Experiments were designed such that at sufficiently small stimulus levels a subject's score would be at chance level, and hence the psychometric function used to analyse responses ranged from 0.5 (50% correct) at the zero stimulus level and approached

1.0 (100% correct) with increasing stimulus level. Here, however, responses could vary between 0% and 100% and therefore a different psychometric function was required. An appropriate form of the psychometric function was obtained by letting the number of alternative force choices, N in the formula given in section 3.6 (see page 56), tend to infinity. The resulting psychometric function is given by:

$$P(x) = \frac{1}{1 + \exp(-(x-M)/S)}$$

This has the desired property that as the stimulus level, x, varies between ±infinity then p(x) varies between 0 and 1 (i.e. 0 and 100%). The threshold was now taken to be the stimulus level that corresponded to the 50% correct level (Taylor and Creelman, 1967). Apart from the use of a different form of the psychometric function the curve fitting procedure was as described in section 3.6.

Each dot flash subtended approximately 0.04° visual angle and had a duration of about 1 msec. The dot flashes were presented to the left of the fixation point along a horizontal meridian. Subjects viewed the fixation point with their right eye only (the left eye was covered by an eye patch) and hence the stimuli fell on the temporal side of the retina. A head rest was used to steady the subject's head. The dot flashes were presented on a dark background and were viewed through the viewing system. The intensity of each dot flash was set to 1 log unit above luminance increment threshold. The experiment was conducted under scotopic conditions with subjects required to dark-adapt for 20 minutes at the beginning of each session.

The interstimulus interval (i.e. the time interval between S1 and S2, see Figure 7.1) was 80 msec. The subject's task was to indicate whether

Table 7.1

Retinal sites ......: 5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o}

Dot-flash separation:

	Eccentricity, degrees				
	5	10	15	20	25
SG	0.10^{o}	0.14^{o}	0.17^{o}	0.21^{o}	0.26^{o}
MJM	0.12^{o}	0.14^{o}	0.26^{o}	0.26^{o}	0.32^{o}

ISI ....: 80 msec.

Dot-flash duration .: 1 msec

Dot diameter ....: 0.04^{o}

Dot-flash luminance : 1 log unit above luminance increment threshold

Viewing conditions .: Scotopic (20 minutes dark adaptation).

or not the two illusions overlapped. Two subjects, SG and MJM, participated in the experiment. Subjects made separate measurements for the starts and the ends of the illusions. Each subject performed a total of four experimental sessions; two in which measurements were made of the starts and two in which measurements were made of the ends of the illusions. Observations were made at retinal sites of 5^{o}, 10^{o}, 15^{o}, 20^{o} and 25^{o} eccentricity in either an ascending or descending order (the order was reversed from session to session). Each session consisted of 15 runs (three runs per retinal site) and 36 trials per run. Relevant experimental details are summarised in Table 7.1.

Results

Figure 7.2 shows results for SG and MJM for the combined start and end extents. Each point is the mean value of four readings; vertical lines represent ±1 standard error of the mean. For both subjects the perceived extent of the fine-grain movement illusion increased with increasing eccentricity. At all retinal sites the start extents were greater than the corresponding ends of the illusion (for SG the starts averaged out to be about 37% greater than the ends; for MJM they were about 40% greater).

Discussion

Values of the extent of the fine-grain movement illusion were significantly lower than those obtained by Foster et al. (1981); they found that the extent varied from approximately 2^{o} to 6^{o} as the stimulus eccentricity increased from about 10^{o} to about 24^{o}; compared with increases of approximately 1^{o} to 2^{o} between 10^{o} and 25^{o} obtained here. There are, however, several differences between the experimental methods and procedures used by Foster et al. (1981) and those used here. In sections 7.2 and 7.3 the dependence of extent on two parameters is considered in an attempt to reconcile the observed differences.

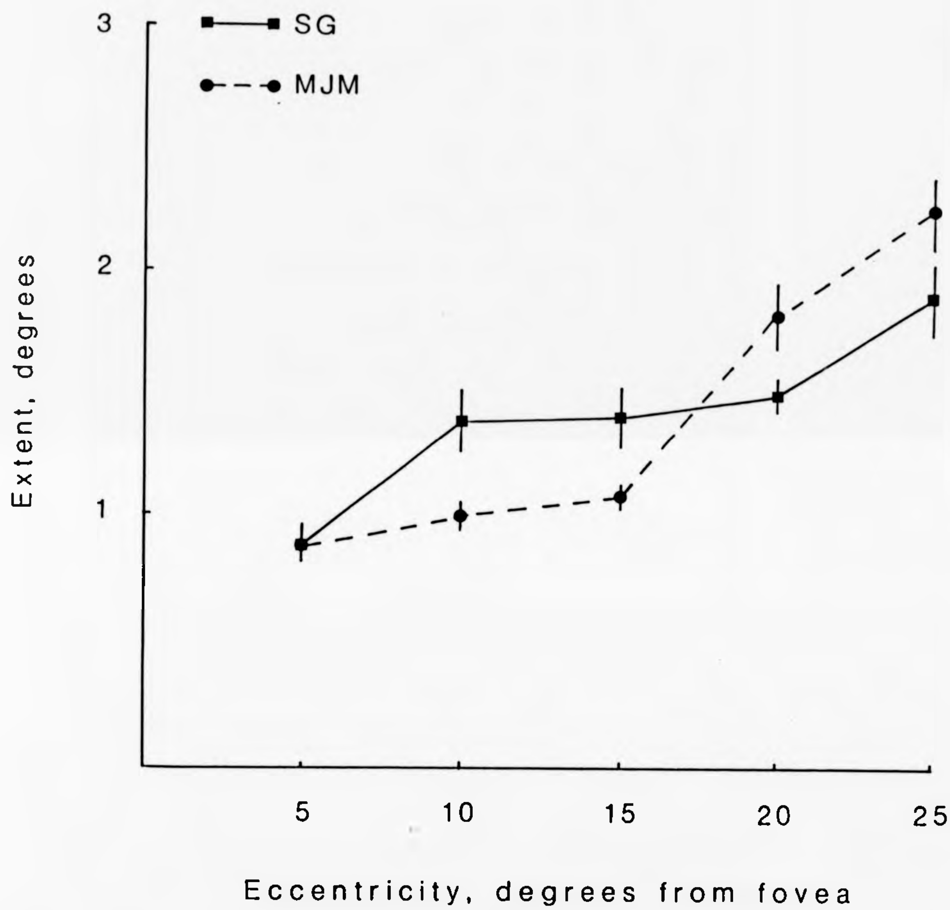


Figure 7.2 Extent of the fine-grain movement illusion as a function of retinal eccentricity (Experiment 7.1). Scotopic adaptation conditions. Subjects SG and MJM.

The finding that the starts of the illusions were greater than the ends indicate that the perceived extent of the illusion is not symmetrically located about the two dot flashes.

Estimates of cortical distances corresponding to the extent of the fine-grain movement illusion were obtained using the cortical magnification factor described in section 2.6. The cortical distances corresponding to the extent of the illusion are shown in Figure 7.3. For both subjects the estimated cortical distance decreases with eccentricity. The data shown in Figure 7.3 were analysed using the least squares linear regression model, described in section 3.8.3, and the gradient of each curve was found to be significantly different from zero ($p<0.01$ and $p<0.05$ for SG and MJM respectively). These results differ from Foster et al.'s (1981) finding that the cortical distance corresponding to the extent of the fine-grain movement illusion is relatively constant with eccentricity and has a mean value of approximately 3 mm. The maximum cortical distance obtained here was at 5^{o} eccentricity and had a value of just under 3 mm. One possible explanation for the observed difference in the retinal dependence of cortical distances is that Foster et al. (1981) used a constant dot separation of 0.2^{o} at all retinal sites; whereas here the dot separation increased with increasing eccentricity (for both subjects the dot separations used to determine extents increased from approximately 0.1^{o} to 0.3^{o} as eccentricity increased from 5^{o} to 25^{o} away from the fovea). If the extent of the fine-grain movement illusion decreases with increasing dot separation, then using a dot separation which increases with eccentricity a smaller gradient might be obtained than if the dot separation were kept constant over different retinal sites. Note that interaction thresholds were shown to exhibit a decrease with increasing dot separation (see section 6.4). In section 7.3 extents of the

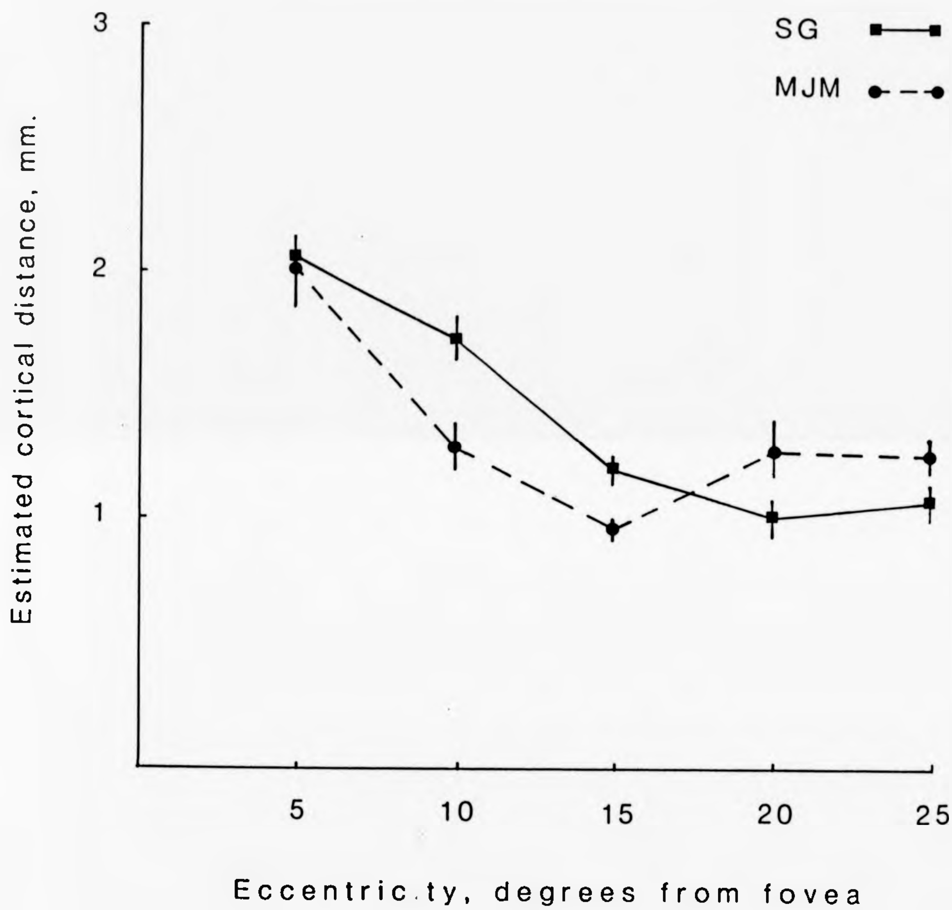


Figure 7.3 Estimated cortical distances corresponding to the extent of the fine-grain movement illusion. Subjects SG and MJM.

fine-grain movement illusion were measured over a range of dot separations (varying from 0.1^o to 0.5^o) and it was found that the extent of the illusion did not decrease with increasing dot separation over the range of values considered. This implies that the difference in the retinal dependence of cortical distances, corresponding to the extent of the fine-grain movement illusion, observed here and that observed by Foster et al. (1981) is not an artifact of the separation of dot flashes.

Next consider the relation between the extent of the fine-grain movement illusion and the interaction of two illusions. Extents of the fine-grain movement illusion, observed in this experiment, are larger than the interaction thresholds obtained in sections 6.1 and 6.2. This appears to be somewhat contradictory, for it implies that it is possible for two non-interacting illusions to overlap. Clearly this is impossible, and hence it can only be assumed that extents of fine-grain movement illusions generated with the arrangement of dot flashes used to determine extents (see Figure 7.1) were larger than the extents of illusions generated with the arrangement of dot flashes used to determine spatial interaction thresholds (see Figure 6.1). The pairs of dot flashes used to obtain extent measurements were vertically and horizontally separated (see Figure 7.1) as opposed to just vertically separated (as used to obtain collinear fine-grain movement illusion interaction thresholds) or just horizontally separated (as used to obtained parallel fine-grain movement illusion interaction thresholds). Hence the overall degree of destructive interaction was probably less in the stimulus configuration used to determine extent measurements than in those used to determine spatial interaction thresholds. It can therefore be concluded that the perceived extent of two fine-grain movement illusions decreases as the degree of interaction between the illusions increases.

7.2 Dependence of the extent of the fine-grain movement illusion on stimulus intensity

Values of the extent of the fine-grain movement illusion obtained in the previous section were between 2 and 3 times smaller than those obtained by Foster et al. (1981). There are several differences between the experimental conditions used by Foster et al. (1981) and those described here. Biederman-Thorson et al. (1971) found that the luminance of dot flashes and of the background field had the largest systematic effect on the fine-grain movement illusion. In the previous experiments the intensity of dot flashes were set to 1 log unit above luminance increment threshold, whereas in the experiment reported by Foster et al. (1981) flashes were set between 2.5 and 3 log units above luminance increment threshold. In both experiments (i.e. those described here and those conducted by Foster et al., 1981) observations were made under scotopic conditions with subjects requiring to dark adapt for 20 minutes. It was therefore decided to consider the extent of the fine-grain movement illusion using a higher stimulus intensity. The next experiment, Experiment 7.2, considers the extent of the fine-grain movement illusion obtained with dot flashes with intensities set at 2 log units above luminance increment threshold.

Table 7.2

Retinal sites ......:	5^{o}, 15^{o}, and 25^{o}			
Dot-flash separation:		Eccentricity, degrees		
		5	15	25
	SG	0.10^{o}	0.17^{o}	0.26^{o}
	MJM	0.12^{o}	0.26^{o}	0.32^{o}
ISI ....:	80 msec.			
Dot-flash duration .:	1 msec			
Dot diameter ....:	0.04^{o}			
Dot-flash luminance :	2 log unit above luminance increment threshold			
Viewing conditions .:	Scotopic (20 minutes dark adaptation).			

Experiment 7.2

Methods

The method and procedure were similar to those used in Experiment 7.1, apart from stimulus intensities which were now set 2 log units above luminance increment threshold. The maximum luminance of the stimuli presented on the face of the CRT was not sufficiently great for 2.5-3.0 log units suprathreshold levels to be reached. Observations were made at three retinal sites: 5^{o}, 15^{o} and 25^{o} eccentricity in either an ascending or descending order (the order was reversed from session to session). Subjects were SG and MJM. Each subject participated in four sessions (two in which measurements of starts were made and two in which measurements of ends were made). Relevant experimental details are summarised in Table 7.2.

Results

The resulting extents are shown by the unfilled bars in Figures 7.4(a) and 7.4(b) for SG and MJM respectively. Each threshold is the mean of four values, vertical lines represent ±1 standard error of the mean. Filled bars indicate extents obtained with the lower dot-flash intensities (i.e. 1 log unit above luminance increment threshold, as obtained in Experiment 7.1). There is a clear increase of perceived extent obtained with the higher stimulus intensity. At all retinal sites, and for both subjects, extents obtained with the higher dot-flash intensity were significantly greater than those obtained with the lower intensity ($p<0.01$ at all retinal sites and for both subjects, see section 3.8.2 for t-test).

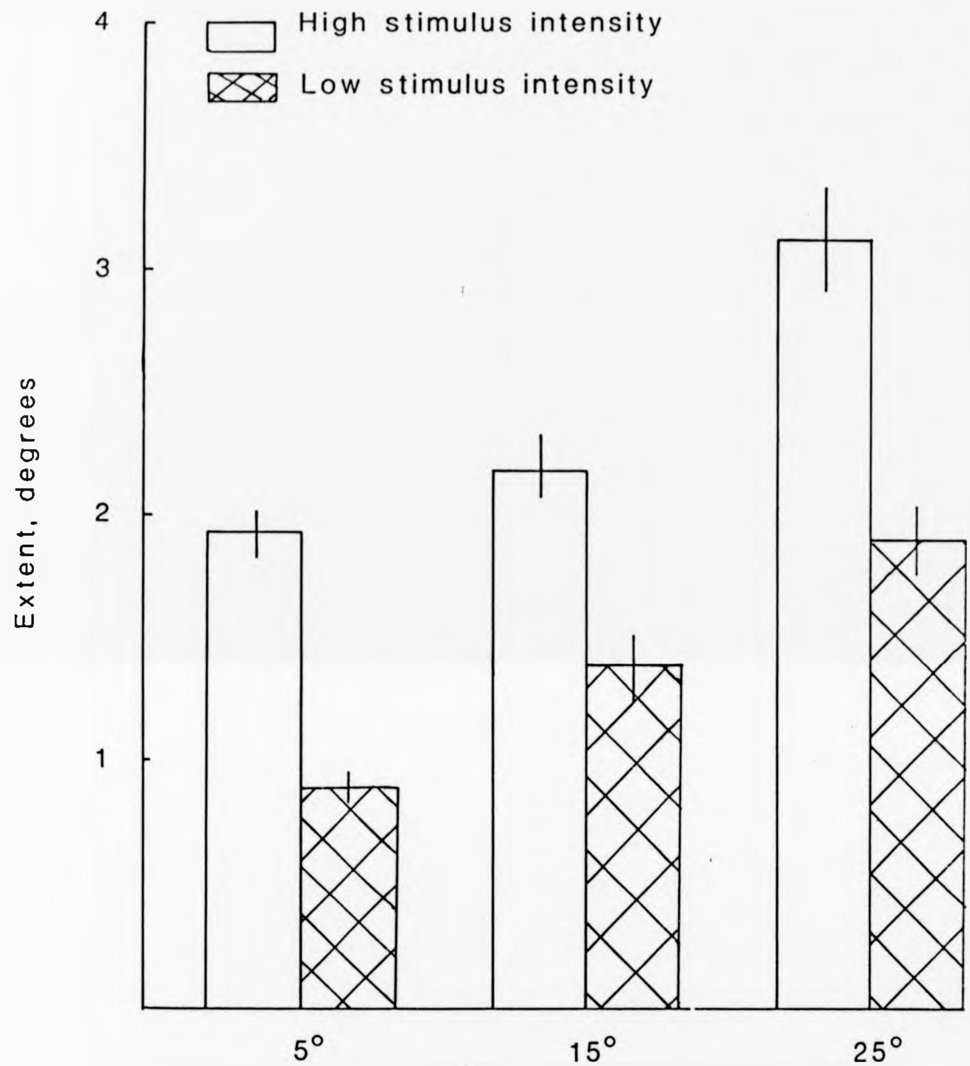


Figure 7.4(a) Extent of the fine-grain movement illusion obtained with dot flashes set at 2 log units above luminance increment threshold (unfilled bars, Experiment 7.2), compared with extents obtained with dot flashes set at 1 log unit above luminance increment threshold (filled bars, Experiment 7.3). Subject SG.

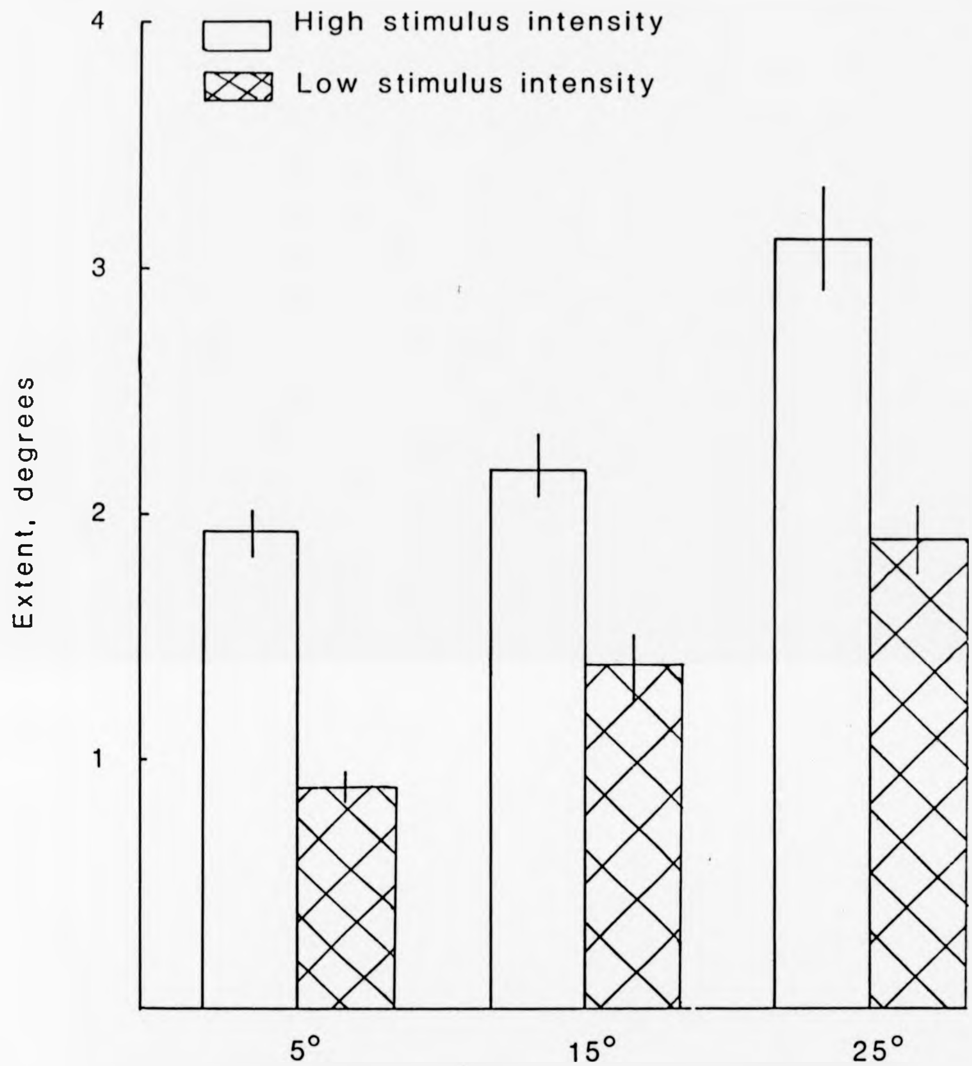


Figure 7.4(a) Extent of the fine-grain movement illusion obtained with dot flashes set at 2 log units above luminance increment threshold (unfilled bars, Experiment 7.2), compared with extents obtained with dot flashes set at 1 log unit above luminance increment threshold (filled bars, Experiment 7.3). Subject SG.

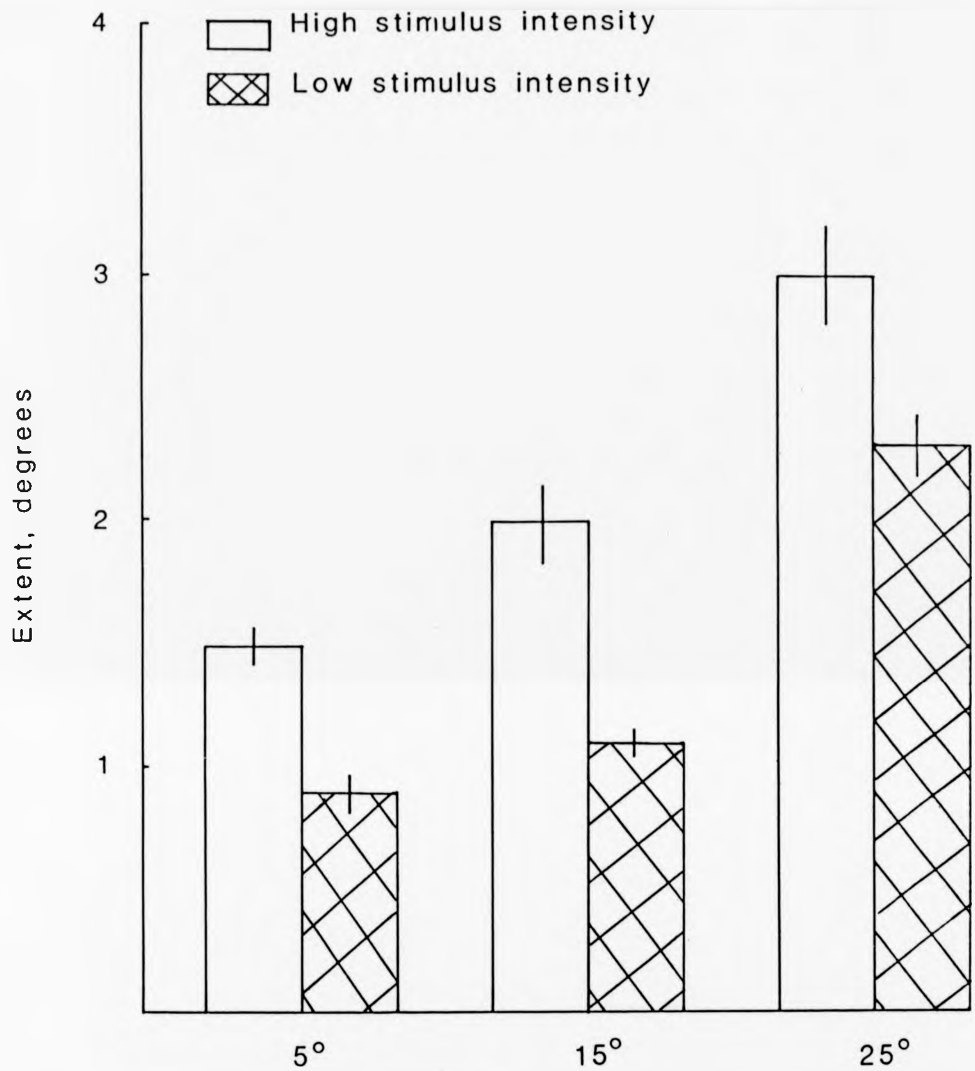


Figure 7.4(b) Extent of the fine-grain movement illusion obtained with dot flashes set at 2 log units above luminance increment threshold (unfilled bars, Experiment 7.2), compared with extents obtained with dot flashes set at 1 log unit above luminance increment threshold (filled bars, Experiment 7.3). Subject MJM.

Discussion

It has been shown that by increasing the intensity of dot flashes the perceived extent of the fine-grain movement illusion increases significantly. Extents measured with the higher dot-flash intensity were about 83% (for SG) and 62% (for MJM) greater than those obtained with the lower intensity (averages taken over the three retinal sites considered). Despite this increase in the extent of the fine-grain movement illusion, obtained by increasing the intensity of dot flashes, the resulting extents were still lower than those obtained by Foster et al. (1981). It must be recalled, however, that Foster et al. (1981) used dot-flash intensities that were between 2.5 and 3.0 log units above luminance increment threshold, compared to 2 log units used in this experiment. It is possible that further increases in stimulus intensity gives rise to further increases in extent.

7.3 Effect of dot separation on the extent of the fine-grain movement illusion

The dependence of the extent of the fine-grain movement illusion on dot separation is of interest for two reasons. The first reason is based on the difference between the degree of extrapolation observed in the fine-grain movement illusion compared to that typically obtained in classical apparent motion (see section 2.2.2 for a discussion of the perceived extent obtained in classical apparent motion). Extents, of the fine-grain movement illusion, obtained in the previous two sections were between 9 and 20 times greater than the separation of dot flashes used to generate the illusory motion. In classical apparent motion, however, differences between the perceived extent travelled by an illusory moving object and the physical separation of the stimuli, giving rise to the illusory motion, is typically only a few per cent of the spatial separation of the stimuli and at most about 40 per cent (see section 2.2.2). It was therefore decided to consider the dependence of extent over a range of dot separations which included both spatially resolved and spatially unresolved dot flashes. Extents measured with two spatially unresolved dot flashes should be about an order of magnitude larger than the separation of the dot flashes, since the two dot flashes would elicit a fine-grain movement illusion, whereas extents obtained with two spatially resolved dot flashes would be expected to be significantly smaller since the resulting illusory motion could be formally categorised as classical apparent motion.

The second reason for examining the dependence of extent on dot separation is that the differences in gradients observed between Foster et al.'s (1981) results and those of Experiment 7.1 could be resolved if the extent, of the fine-grain movement illusion, decreases with increasing dot separation. In Experiment 7.3 the extent of perceived illusory motion was determined over a range of dot separations which included spatially resolved and spatially unresolved dot flashes.

Experiment 7.3

Method

The method and procedure differed from that used in Experiment 7.1 in only the following aspects. Observations were made at a single retinal site of 15^{o} eccentricity. During any one run the dot separation, d, was kept constant; but its value was varied systematically (i.e. either increasing or decreasing) from run to run. The range of dot separations used was 0.1^{o} to 0.5^{o}, and varied in steps of 0.1^{o}. Stimulus intensities were set at 1 log unit above luminance increment threshold. Two subjects, SG and MJM, performed the experiment. Each subject

Table 7.3

Retinal site ......:	15°
Dot-flash separation:	0.1, 0.2, 0.3, 0.4 and 0.5°
ISI ....:	80 msec.
Dot-flash duration .:	1 msec
Dot diameter ....:	0.04°
Dot-flash luminance :	1 log unit above luminance increment threshold
Viewing conditions .:	Scotopic (20 minutes dark adaptation).

performed a total of four experimental sessions, two in which measurements were made of H_s (i.e. the starts of the illusion) and two in which measurements were made of H_e (i.e. the ends of the illusion). The experiment was conducted under scotopic conditions, with subjects requiring to dark adapt for 20 minutes at the beginning of each experimental session. Relevant experimental details are summarised in Table 7.3

Results

Figure 7.5 shows the results. Each point is the mean of four values; vertical bars represent ±1 standard error of the mean. The two vertical arrows indicate the minimum dot separation for spatial resolution, at 15° eccentricity, as obtained in Experiment 5.1. Both curves appear to exhibit a gradual increase of extent with increasing dot separation, the gradient obtained for SG was however not significantly different from zero ($p>0.05$) whereas for MJM the gradient was significantly different from zero ($p<0.01$, see section 3.8.3 on linear regression).

Discussion

That extents did not exhibit a decrease with increasing dot separation implies that the difference between the gradient of extent as a function of eccentricity, obtained in Experiment 7.1 (see Figure 7.2) and that obtained by Foster et al. (1981, see Figure 3ii) cannot be an artifact of the different ways in which dot separations were varied with stimulus eccentricity.

In Figure 7.5 symbols to the right of the vertical arrows represent extents of illusory motion between two spatially resolved dot flashes, and the resulting illusory motion was therefore formally classical apparent motion. At the largest dot separation considered, extents were over 240% greater than the separation of the two dot flashes. This

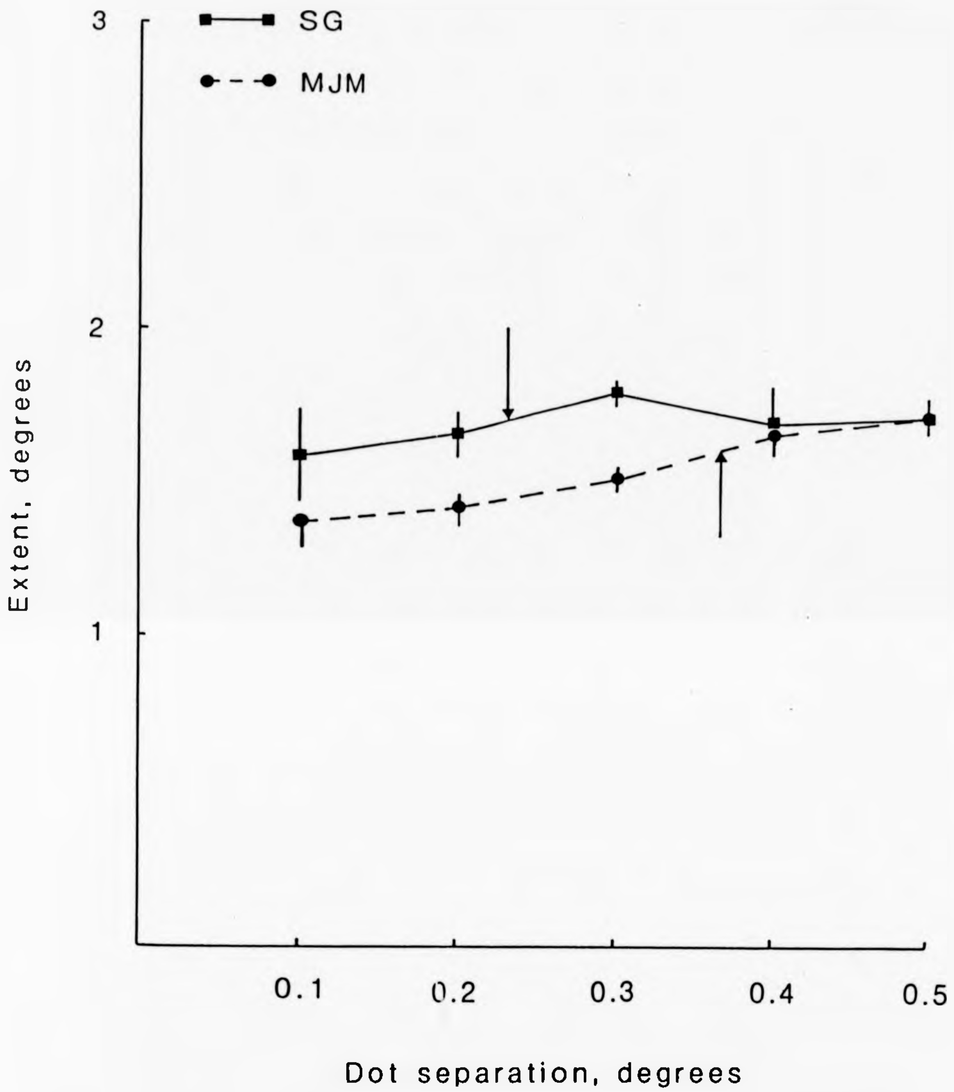


Figure 7.5 Extent of illusory motion as a function of dot separation (Experiment 7.3). Vertical arrows indicate the minimum dot separation required for spatial resolution. Scotopic adaptation conditions. Subjects SG and MJM.

value is much larger than previously reported distance overshoots, which are typically only several per cent of the stimulus separation and at most some 40% (Scholz, 1924; Neuhaus, 1930; Kolers and Touchstone, 1965). If differences between the perceived extent and the actual dot separation are considered, then we find that for the 0.5^{o} dot separation the difference here is approximately 1.5^{o}, whereas, for example, Kolers and Touchstone (1965) observed differences of about $0.1\text{-}0.15^{o}$ (they used two flashing lights separated by approximately 2.4^{o}).

Hence it is reasonable to assume that these results show that classical apparent motion can give rise to extrapolations of similar magnitudes to those obtained in the fine-grain movement illusion. This interpretation is however subject to the same objection offered in section 6.4: the minimum dot separation required for spatial resolution may not be an appropriate demarcator of the fine-grain movement illusion and classical apparent motion, for two dot flashes with a separation just above the minimum dot separation for spatial resolution may generate a fine-grain movement illusion and not classical apparent motion.

Despite this possible objection it can only be assumed that for two spatially resolved dot flashes the resulting illusory motion is classical apparent motion, and that this experiment therefore shows that with classical apparent motion relatively large extrapolations can be obtained. This finding differs from existing findings which report much smaller extrapolations in classical apparent motion (Scholz, 1924; Neuhaus, 1930; Kolers and Touchstone, 1964). It was decided therefore to examine extrapolations that can be observed with classical apparent-motion stimuli, using more traditional methods of assessment. The final two sections here differ from previous material in this thesis in that they were not directly concerned with the fine-grain movement illusion but rather with classical apparent motion proper.

7.4 Position overshoots in classical apparent motion

As noted in the previous section, it was of interest to consider extrapolations using visual stimuli and methods traditionally employed in studies of classical apparent motion. In the next experiment measurements were made of position overshoots obtained with two sequentially presented line segments presented foveally and under photopic conditions. Values of position overshoots were determined as a function of the spatial separation of the two line segments. Rating data on the "goodness" of the apparent motion were also recorded as a control.

Methods

The stimulus display is illustrated to scale in Figure 7.6. Each line segment subtended 0.125^{o} at the eye. The two line segments on the left side of the display were each presented for 50 msec. The upper segment always preceded the lower segment and the stimulus onset asynchrony was fixed at 50 msec. The vertical separation of the two line segments was varied from 0.4 to 0.8^{o} (the position of the lower segment remained fixed). The vertical position of the right hand line segment could be varied continuously.

The stimuli were produced by an on-line computer and displayed on the screen of a X-Y display oscilloscope (Hewlett-Packard, HP1317A, similar to that used in previous experiments) with P31 phosphor (decay time less than 50 μsec). The display was viewed at a distance 1.7 m through a view tunnel and optical system which provided a uniform background field (white, luminance 30 cd m^{-2}) on which the stimulus line segments were

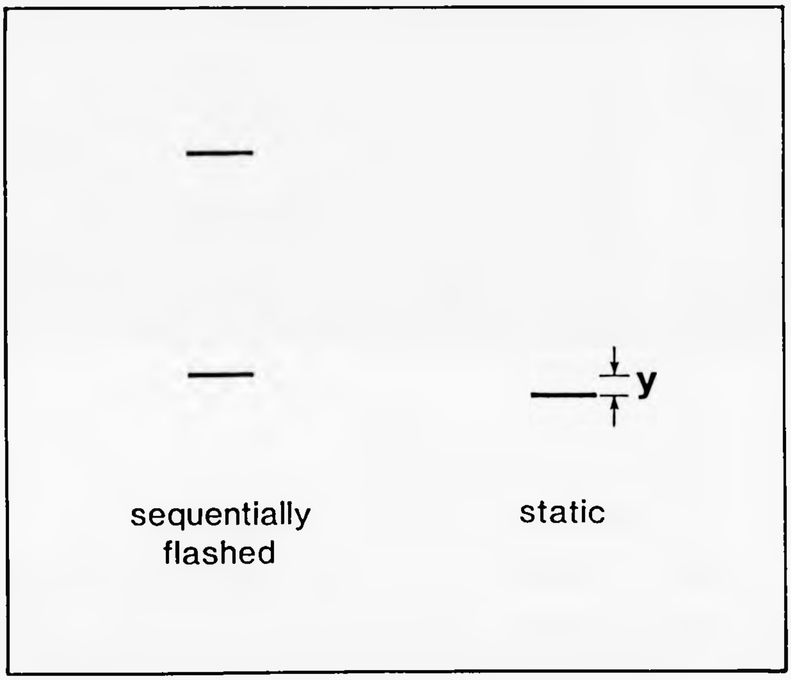


Figure 7.6 Stimulus configuration used to determine position overshoots between two straight line segments (Experiment 7.4). Display to scale.

Table 7.4

Retinal site ......:	Fovea
Line separation ....:	0.40, 0.47, 0.55, 0.63 0.72 and 0.78 degrees
SOA ....:	50 msec.
Duration of lines ..:	50 msec
Line length ....:	0.125^{0}
Stimulus intensity .:	2 log unit above luminance increment threshold
Viewing conditions .:	Photopic (background field luminance 30 $cd.m^{-2}$)

superimposed. The intensity of the lines was set at the beginning of each experimental session so that each line was approximately 2 log units above luminance increment threshold.

Subjects were instructed to adjust (by means of a rotary control) the vertical position of the right-side line segment so that it appeared to be vertically in line with the left-side lower segment. In making a position match, subjects were instructed to alternate fixation from the centre of the left-side lower line segment to the centre of the right-side line segment. After a position match had been made subjects were asked to report the "goodness" of apparent motion on the left-side of the display using one of the following three category ratings: 0--there was no apparent motion; 1--some apparent motion was evident but not as marked as in category 2; 2--one line appeared to move smoothly and continuously into the other (beta motion). After a match had been made and the rating of the apparent motion recorded a new vertical separation was selected (using the randomised balanced block procedure described in section 3.7). The previous setting of the rotary control was spoiled by the subject before a new match was begun.

Each experimental run consisted of six position matches, each with a different vertical separation of the left-side line segments. Each subject participated in one experimental session comprising six runs. Subjects received no information concerning their performance. Five subjects performed the experiment; NJL, CJH, RSS, DHF and SG. Observations were made binocularly and each subject had normal or corrected-to-normal vision (Snellen acuities each not worse than 6/6). Relevant experimental details are summarised in Table 7.4

Results

Individual results were similar, and in Figure 7.7 the pooled data are shown along with the data for individual subjects. Each point in Figure 7.7 is the mean of 30 position matches, vertical bars represent ±1 standard error of the mean. In Figure 7.7(a) the apparent vertical position, expressed in minutes of arc visual angle measured from its true position, is plotted as a function of the vertical separation of the left-side line segments (see Figure 7.6). In Figure 7.7(b) the mean "goodness" of apparent motion is illustrated, where 2.0 corresponds to beta motion and 0 to no apparent motion. The curve in Figure 7.7(a) was analysed using the least squares linear regression model, see section 3.8.3, and its gradient was found to be not significantly different from zero ($p>0.2$). Note that the apparent motion rating was substantially independent of the separation of line segments.

Discussion

The finding in this section, that position overshoots in classical apparent motion paradigms are relatively constant with respect to spatial separation, and the finding in section 7.3 that extents obtained in fine-grain motion paradigms are also relatively constant with respect to dot-flash separation suggest that the spatial separation of visual stimuli may not be responsible for the large differences in extrapolations that can be observed between the two types of illusory motion.

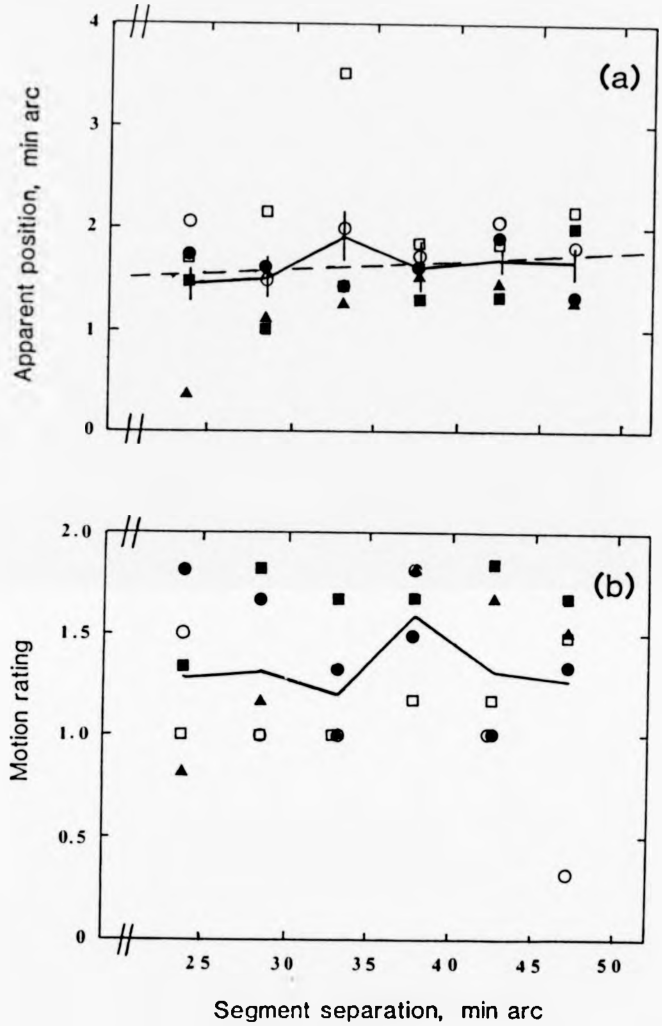


Figure 7.7 (a) Position overshoots obtained with two straight line segments, as a function of the spatial separation of the segments (Experiment 7.4). (b) Motion rating corresponding to the apparent motion generated between the two line segments.

The following factors are probable contributors to the differences in extrapolations that have been observed here: the different methods of measurement (the use of adjustable markers can alter subjective estimates of illusory motion, Foster et al., 1981), the failure to include estimates of the perceived start position in the classical apparent motion paradigm, the line rather than the spot character of the stimuli, the retinal location of stimuli and the adaptation state of the eye.

The existence of extrapolations obtained with two sequentially flashed straight lines or dots has been long established in the field of classical apparent motion, in the next section an experiment is described which demonstrates the existence of a different type of overshoot that can be obtained with curved lines.

7.5 Curvature overshoot in classical apparent motion

In the course of exploratory experiments relating to classical apparent motion and the magnitude of overshoot effects, it was noticed that the alternation of a briefly presented square and a briefly presented overlapping circle (as described by Kolers and Pomerantz, 1971) did not give rise to the illusory movement of a circle changing into a square but rather of a circle changing into a pincushion figure. The observed effect was as if the illusory figure overshoots the second figure. With respect to the previously discussed extrapolation phenomena in illusory motion it was of interest to investigate this figure overshoot and to attempt to identify the mechanism responsible for its construction. Two hypotheses were considered to explain the observed figural overshoot. First, that the pincushion shape of the target square could be a trivial consequence of classical curvature-contrast effects (Imai, 1956; Gibson, 1933 & 1937; Orbison, 1939; Oyama, 1960). Such contrast effects are typically illustrated by a square superimposed on a background of concentric circles; the edges of the square are not perceived as straight lines but rather appear curved in the direction opposite to the curvature of the circles. Second, that the visual system constructs apparent motion between the two alternated figures and that the pincushion shape of the target figure is a consequence of a genuine motion. The apparent curvature described above, involving the sequential presentation of a circle and a square, may also be observed by sequentially presenting a straight line and a curved line. This reduced stimulus configuration was used in the next experiment to determine the degree of apparent curvature obtained with a straight line and a curved line. The aim of the experiment was to determine which of the two above hypothesis was appropriate in explaining the apparent curvature. To achieve this it was necessary to determine the degree of apparent curvature using two different stimulus configurations; the one in which apparent motion occurred between the straight line and the curved line, and the other in which apparent motion between the straight line and the curved line was suppressed but the operation of any curvature-contrast effects was unimpaired. The two different stimulus configurations are shown in Figure 7.8. In Figure 7.8(a) visual apparent motion could occur between the curved line and the straight line (under appropriate temporal conditions). In Figure 7.8(b), however, the inclusion of a second horizontal straight line tangential to the curved line would give rise to apparent motion between the left-side curved line and the straight line above it and hence suppress any apparent motion between the left-side curved line and the straight line below it.

Experiment 7.5

Methods

The stimulus display illustrated in Figure 7.8 is to scale; the horizontal extent of each of the lines in the display subtended 2.0^{o} at the eye. The spatially fixed straight and curved lines on the left side of the display were each presented for 50 msec; the SOA could be either positive or negative (positive values signified that the curved line preceded the straight line). In Figure 7.8(b) the upper straight line on the left side of the display could be presented in synchrony with the lower straight line. The static curve on the right side of the display had a smoothly adjustable curvature and was presented continuously during the sequential presentation of the lines on the left side of the display. Both fixed and adjustable curved lines were arcs of a circle, and the curvature of each was specified by the angle α shown in Figure 7.8. For the left side curved line the magnitude of α was 45.0^{o}.

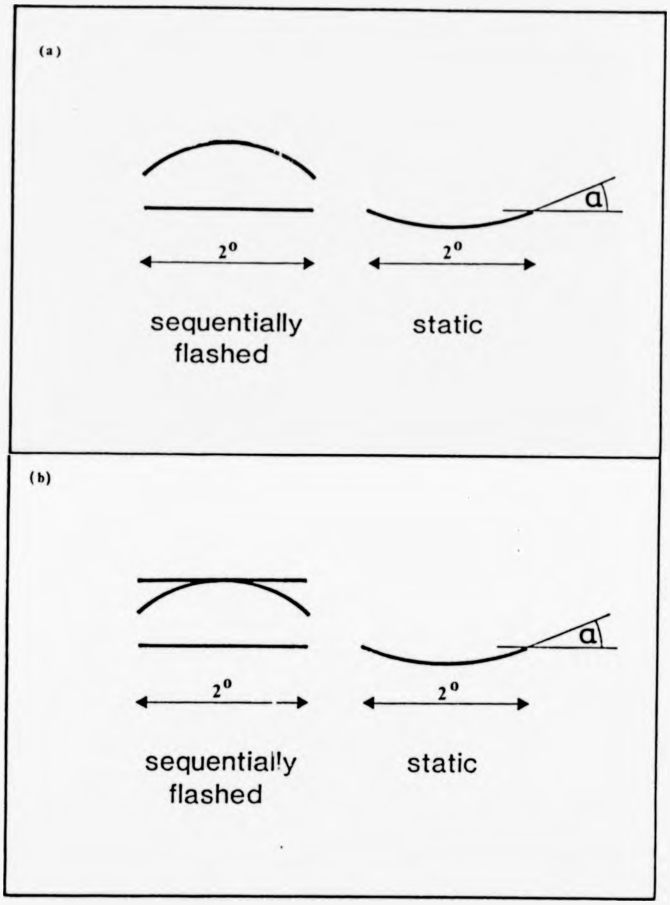


Figure 7.8 (a) Stimulus configuration used to determine apparent curvature of the lower straight line (Experiment 7.5). Display to scale. (b) Inclusion of an upper straight line, on the left side of the display, to prevent apparent motion taking place between the left-side curved line and the lower straight line (Experiment 7.5). Display to scale.

Subjects were informed that there were two types of runs; those in which the upper straight line was present and those in which it was absent. For both types of runs they were instructed to adjust (by means of the rotary control) the curvature of the line on the right side of the display so that it appeared identical to the lower line on the left side of the display. When the match appeared satisfactory they were to indicate this and, as a control, the "goodness" of apparent motion between the left side curved line and the lower line on the left side of the display, using the 0, 1, 2 category rating described in the previous section. It was stressed to subjects that they should ignore any apparent motion between the curved line and the upper straight line on those trials in which the latter was present.

The timing of presentations was as follows. For each fixed SOA the straight and curved lines on the left side of the display were presented, in the prescribed order, three times at intervals of 2 seconds. This sequence of presentations could be repeatedly initiated by the subject pressing a switch on the pushbutton box. The curvature of the line on the right side of the display could be altered only in the period between these sequences. In making a curvature match subjects were instructed to alternate fixation from the centre of the left-side lower line to the centre of the right-side line (Figure 7.8). After a match had been made, and the rating of apparent motion recorded, a new SOA was automatically selected (according to the randomized balanced block algorithm described in section 3.7). The previous setting of the adjustable right-side line was spoiled by the subject before a new match was begun.

Each experimental run consisted of 10 such curvature matches and apparent-motion ratings, with stimulus onset asynchronies rating from

-200 to 250 msec. Each experimental session consisted of a block of five runs, and each subject participated in two sessions. Runs with and without the upper straight line, on the left side of the display, were alternated and the same sequence of SOAs used in each pair.

All other aspects of the method and procedure were as described in the previous section. Relevant experimental details are summarised in Table 7.5

Results

Individual subjects' results were similar, and Figure 7.9 shows the pooled data along with individual subjects' data. In Figure 7.9(a) apparent curvature is plotted as a function of the SOA. Each point is the mean value of 50 curvature matches, vertical bars represent ±1 standard error of the mean. In Figure 7.9(b) the mean rating of the "goodness" of apparent motion, between the left-side curved line and the lower straight line, is plotted against SOA. Each point is based on 50 ratings, where 2.0 corresponds to beta motion and 0 to no apparent motion. For those runs in which the the upper straight line was presented (Figures 7.9, filled circles) apparent curvature at negative and zero SOAs was not significantly different from that for runs in which the upper straight line was absent ($F[5,245]=0.29$, $p>0.5$), but was highly significantly different at positive SOAs ($F[5,245]=24.93$, $p<0.001$). Furthermore the "goodness" of the apparent motion rating between the left-side curved line and the lower straight line was markedly reduced over all SOAs when the upper line was presented; mean rating over all SOAs was reduced to 0.20 of the rating obtained when the upper straight line was absent (a highly significant reduction, $z=6.07$, $p<0.001$).

Table 7.5

Retinal site ......:	Fovea
Line separation ....:	0.40 to 0.78 degrees
SOA ....:	0, ±50, ±100, ±150, ±200 and 250 msec
Duration of lines ..:	50 msec
Line length ....:	Horizontal extent of 2^{o}
Stimulus intensity .:	2 log unit above luminance increment threshold
Viewing conditions .:	Photopic (background field luminance 30 $cd.m^{-2}$

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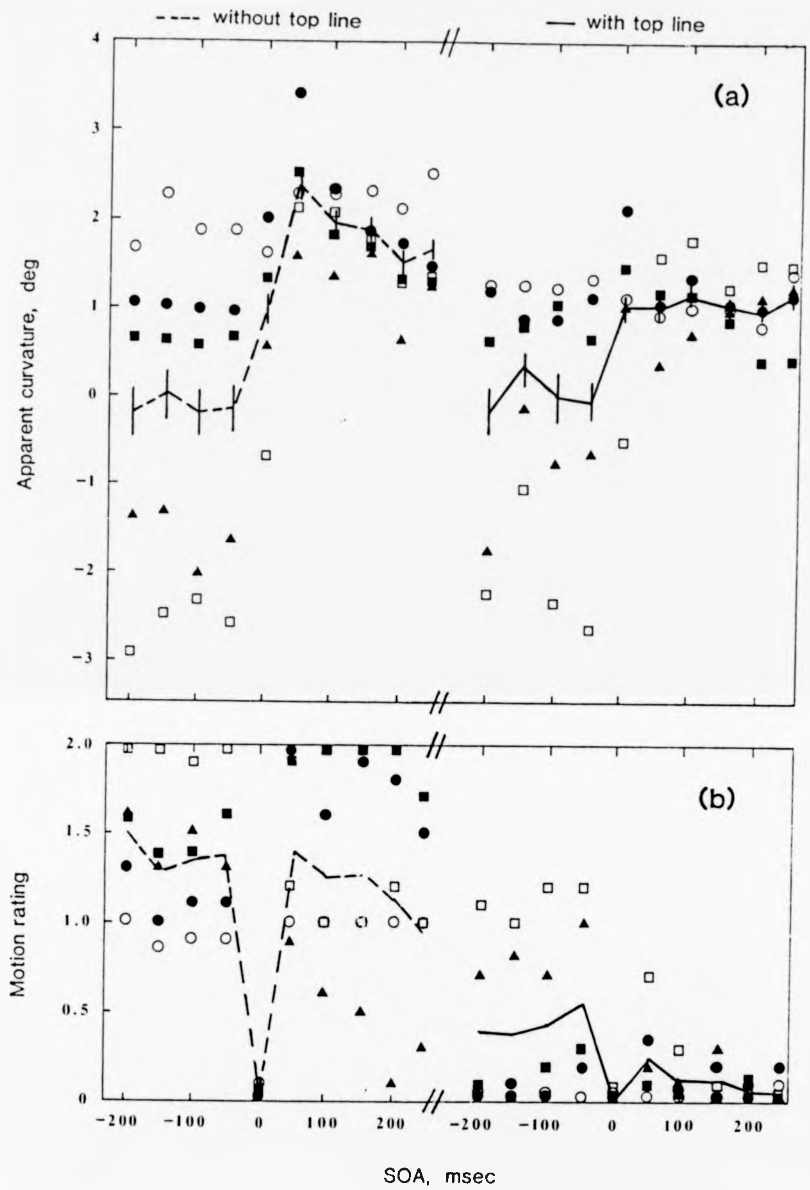

Figure 7.9 (a) Apparent curvature of lower straight obtained without upper straight line and with upper straight line (Experiment 7.5). Negative SOAs signify that the left-side curved line succeeded the lower straight line (and the upper straight line, when presented). (b) Motion rating corresponding to apparent motion between the left-side curved line and the lower straight line.

Discussion

The aim of this experiment was to determine whether the apparent curvature of the left-side lower straight line was a consequence of curvature contrast effects or was due to apparent motion between the left-side curved line and the lower line. The results illustrated in Figure 7.9(b) clearly indicated that the presence of the upper straight line greatly reduced apparent motion between the left-side curved line and the lower straight line and in addition significantly reduced the apparent curvature at positive SOAs. Note that the apparent curvature at zero SOA was not significantly altered by the presence of the upper straight line ($p>0.2$, t-test, see section 3.8.2), and it may therefore be assumed that the results obtained with the upper straight line represent curvature-contrast effects alone. Apparent curvature obtained without the upper straight line is likely to have contributions from curvature-contrast effects and from apparent motion. Although there is no a priori reason to suppose that these two contributions are simply additive, it is instructive to take differences between the sets of data in Figure 7.9(a) and of the set in Figure 7.9(b) to obtain an indication of the apparent curvature resulting from apparent motion alone. Figure 7.10 shows these differences. In Figure 7.10(a) the net apparent curvature, at negative and zero SOAs, is not significantly different from zero ($F[5,245]=0.66$, $p>0.5$); it is, however, highly significantly different from zero at positive SOAs ($F[5,245]=24.34$, $p<0.001$). At negative SOAs the straight line preceded the curved line and hence any apparent motion was from the straight line to the curved line; therefore the observed absence of apparent curvature at negative SOAs is consistent with the interpretation that the apparent curvature was due to apparent motion of the curved line to the straight lower line. Motion ratings for apparent motion are relative high at both negative and positive SOAs, and zero at zero SOA. To summarize, the results

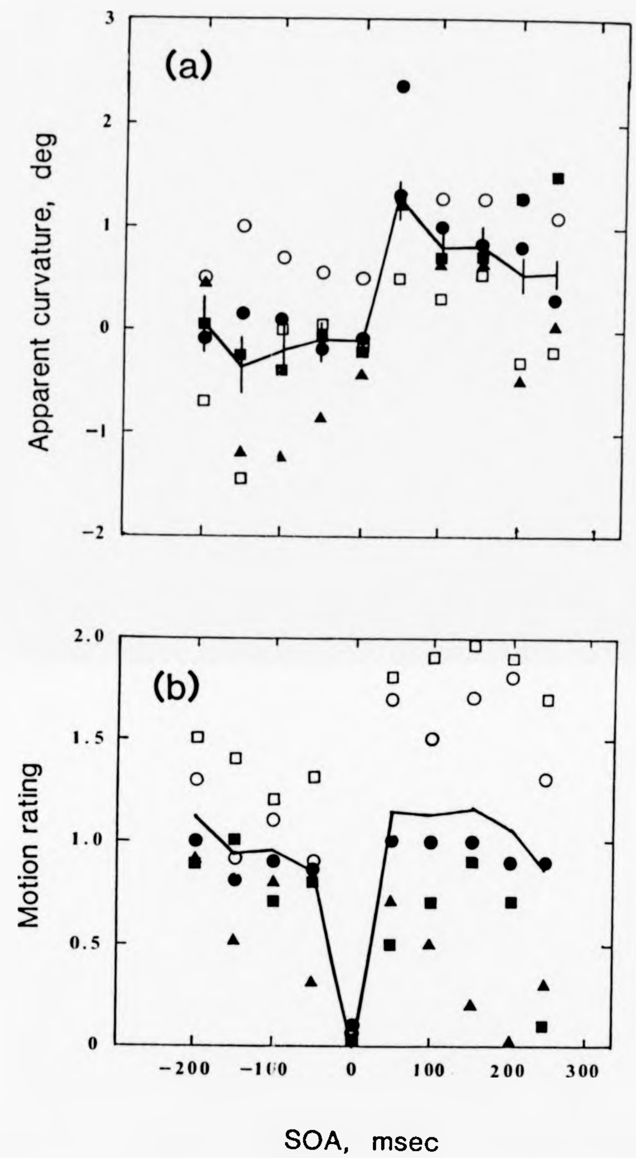

Figure 7.10 (a) Difference between apparent curvature obtained without the upper straight line and that obtained with the upper straight line. (b) Difference between motion rating obtained without the upper straight line and that obtained with the upper straight line.

shown in Figure 7.10(a) represent apparent curvature resulting solely from the apparent motion of a curved line to a straight line and any contributions due to curvature contrast effects have been removed.

Having established that the apparent curvature observed is a consequence of apparent motion, it can now be asked whether it can be explained by considering the straight line and the curved line to be decomposed into vertically aligned pairs of points, with apparent motion taking place between each pair of points. In this decomposition hypothesis the resulting apparent curvature can be considered to be a consequence of "linear" apparent-motion position overshoots between pairs of vertically aligned points. Points on the curved line near its ends have less vertical distance to travel than points near to the centre of the curved line. If the amount of position overshoot of these points increased with the vertical distance covered, then points near the centre of the curved line would overshoot more than those points near to the end of the curved line; this would clearly give rise to an apparent curvature of the straight line. The gradient of the increase in position overshoot, as a function of separation, required to give the maximum apparent curvature observed was calculated to be 0.0029. This value is approximately three times greater than the gradient of the position overshoots obtained in the previous section (see Figure 7.7a); and the difference between the two gradients is significantly different ($p<0.02$). Note that the range of line-segment separations used in Experiment 7.4 corresponded to the minimum and maximum distance between the curved line (on the left side of the display in Figure 7.8a) and the lower straight line. It can therefore be concluded that the apparent curvature observed between a briefly presented curved line followed by a briefly presented straight cannot be explained in terms of a decomposition into linear position overshoots.

The apparent curvature observed in the experiment described in this section has implications to existing theories of classical apparent motion. In section 2.2.2 two models were briefly described which provide schemes in which the existence of overshoots in visual apparent motion can be naturally explained. In the network model proposed by Caelli and Dodwell (1980) apparent motion is considered to be a consequence of nervous activity that builds up into smooth continuous motion by a series of iterative processes. Within such a scheme apparent curvature, due to the sequential presentation of a curved line followed by a straight line, could be interpreted as follows. The iterative process provides a mechanism by which the initial state (i.e. a distribution of nervous activity representing the curved line) transforms into the final state (i.e a distribution of nervous activity representing a straight line). At the end of the iterative process the decay of residual activity would take the neural activity beyond the final state defined by the target (second) form and in the current example would therefore give rise to an apparent curvature in the direction opposite to the curvature of the curved line. In the scheme proposed by Foster (1975b, 1978) apparent motion is modelled internally according to laws similar to those operating in the physical three-dimensional world. In such a scheme beta motion is represented as a trajectory within some internal space of geometrical transformations according to a principle of "least energy" and a mass-like attribute may be assigned to the motion in the space of transformations. The mass-like attribute of the moving illusory object may take the illusory object beyond the final state defined by the target (second) visual stimulus. If the initial visual stimulus is a curved line and the second stimulus a straight line, then the illusory object may be considered to result from a sequence of curvature transformations taking the curved line into a straight line; the mass-like attribute of the illusory object then takes the final state beyond the state of the second stimulus giving rise to an apparent curvature in the direction opposite to the curvature of the initial stimulus. Hence both models proposed by Caelli and Dodwell (1980) and Foster (1975b, 1978) could qualitatively explain the existence of curvature overshoots in visual apparent motion.

7.6 Summary and conclusion

The perceived extent of the fine-grain movement illusion has been shown to increase with increasing retinal eccentricity in a manner as previously demonstrated by Foster et al. (1981). The extents obtained here were smaller than those obtained by Foster et al. (1981); but there were several differences between the two experimental methods, one of which was that Foster et al. (1981) used higher stimulus intensities. By increasing the intensity of dot flashes it was shown that the perceived extent of the fine-grain movement illusion increased significantly. The gradient of extent with eccentricity was too small to give rise to cortical distances (corresponding to the extent of the fine-grain movement illusion) constant with eccentricity. Instead the cortical distances were found to decrease with eccentricity, which contrasts with Foster et al.'s (1981) finding that such cortical distances are relatively invariant of eccentricity.

The extent of perceived illusory motion was determined over a range of dot separations which included spatially resolved and unresolved dot flashes. With two spatially unresolved dot flashes a fine-grain movement illusion would be generated (under appropriate conditions), whereas with two spatially resolved dot flashes the resulting illusory motion would be formally described as classical apparent motion. It was expected that the perceived extent of the illusory motion would decrease significantly as the dot separation increased, since extrapolations in the fine-grain movement illusion are significantly larger than those obtained with classical apparent motion. No such decrease of extent over the range of dot separations was observed. One possible explanation for this is that the two-dot spatial resolution limit may not necessarily demarcate the perception of fine-grain motion from classical apparent motion (it is possible that two just resolvable dot flashes generate a fine-grain movement illusion and not classical apparent motion).

As a check on extrapolations obtained with classical apparent motion, measurements were made on position overshoots between two straight line segments. These measurements were made under conditions that are typically employed in the study of classical apparent motion; namely foveal presentation of stimuli, light-adapted conditions and relatively large stimulus extents. The results obtained were consistent with existing experimental data on overshoots in classical apparent motion: typically several per cent of the spatial separation of the stimuli.

It was further demonstrated that a different type of overshoot may be obtained in classical apparent motion using a briefly presented curved line followed by a briefly presented straight line. The resulting curvature overshoot was shown not to be attributable to static curvature-contrast effects nor the result of a simple summation of linear position overshoots. In summary, there appear to be three types of apparent-motion overshoot possibly involving progressively more central parts of the visual system: (1) linear overshoot in the fine-grain movement illusion, (2) linear overshoot in classical apparent motion, and (3) curvature overshoot in classical apparent motion.

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Chapter 8

Conclusion

Chapter 8: Conclusion

A discussion of individual experiments was given in the previous chapters. In this chapter, some final comments are made on the main implications of the experimental findings and some suggestions offered on possible further relevant work.

The shift in temporal response characteristics towards smaller interstimulus intervals with increasing retinal eccentricity (see Figures 4.1a,b) is consistent with the existence of a Y-like motion detecting channel, with a fast temporal response, that dominates performance in the peripheral field (Kulikowski and Tolhurst, 1973). This shift in temporal response cannot be explained in terms of the relative distributions of rod and cone receptors with changing eccentricity; for this would have required a shift towards larger interstimulus intervals with increasing distance from the fovea. These receptors, however, or at least their adaptational state, does influence the fine-grain movement illusion, for it has been confirmed that under photopic adaptation conditions there is a sharpening in temporal response curves accompanied with a shift towards smaller temporal intervals (see Figures 4.2a,b). In order to establish the contribution to the fine-grain movement illusion of rod and cone receptors and of X- and Y-type mechanisms it would be of interest to determine characteristics of the illusion when mediated solely by rod receptors and solely by cone receptors (it has already been reported that the illusion can be obtained with each of the two dot flashes stimulating different receptor types, Foster 1977). By careful selection of the intensity and spectral components of dot flashes it should be possible to determine temporal response curves (and other characteristics of the illusion) when the illusion is mediated only by rod receptors and then only by cone receptors. Given an understanding of the contribution made by rod and cone receptors to the illusion, it could be easier to determine the separate possible contributions of the underlying putative Y-type and X-type mechanisms.

The finding that the minimum dot separation required for the fine-grain movement illusion increases significantly more slowly than the minimum dot separation required for spatial resolution (see Figures 5.1a,b,c,d) provides strong evidence that the periphery of the visual field is more finely tuned to motion detection than it is to form detection. This observation adds further support to existence of peripherally distributed Y-type mechanisms which mediate motion detection. The comparatively fast increase in spatial acuity could be reflecting the decrease in "form-detecting" X-type mechanisms, whereas the relative stability of spatial acuity of the fine-grain movement illusion could be due to the mainly peripherally distributed Y-type mechanisms.

This question of the ability of the peripheral visual field to respond to motion relative to its ability to detect form has attracted much interest and experimental consideration in the past (see for example Sekuler, 1975). Despite this, however, experimental studies addressing this issue have generally failed to obtain suitably matched measures for spatial and motion acuity, leading sometimes to inappropriate comparisons. It is proposed that with the fine-grain movement illusion an objective measure of the ability of the visual system to detect motion can be made that can be compared to a suitably matched measure of spatial acuity; and hence provide a more accurate means of comparing the underlying form- and motion- detecting systems.

Experiments described within this thesis have implications for the cortical magnification invariance principle: that spatial characteristics of photopic visual stimuli are invariant of retinal site when expressed in terms of the corresponding cortical distance (Rovamo and Virsu, 1979; Virsu and Rovamo, 1979). Two spatial characteristics of the fine-grain movement illusion were found which after multiplication with the cortical magnification factor gave cortical images which decreased with stimulus eccentricity: the minimum dot separation required to generate the fine-grain movement illusion (see Figure 5.2b) and the perceived extent of the illusion (see Figure 7.3). Furthermore, cortical images corresponding to spatial acuity (obtained under scotopic adaptation) were also found to exhibit a slight, but significant, decrease with retinal eccentricity. It is proposed that the observed decreases in cortical images with stimulus eccentricity are reflecting the scotopic conditions under which the experiments were conducted. It would be of interest to determine cortical images corresponding to the minimum dot separation required for the fine-grain movement illusion under photopic conditions.

One of the properties of the illusion that distinguishes it from other aspects of apparent motion is the objective way in which the illusion can be studied. The finding that temporal response curves obtained with objective performance measures correlate with those obtained with subjective rating of the illusion (see Figures 4.4a,b) could prove useful in establishing the relationship between the illusion and other types of classical apparent motion. Classical apparent motion has traditionally been studied with foveally presented stimuli (see for example Kolers, 1972). Several of the experiments described in this thesis could be easily replicated using stimuli typically employed in classical apparent motion presented peripherally and using subjective rating paradigms. Such data would then provide a useful insight into the relationship between the fine-grain movement illusion and classical apparent motion.

Another way in which this relationship between the fine-grain movement illusion and classical apparent motion can be investigated is to determine characteristics of illusory motion resulting from two dot flashes over of range of spatial separations which straddle the minimum dot separation required for spatial resolution. Two such experiments were described in this thesis; the one in which interaction thresholds between two collinear illusions were determined as a function of the separation of dot flashes (see Figure 6.6) and the other in which the perceived extent of illusory motion was determined (see Figure 7.3). The finding that interaction thresholds decrease rapidly with increasing dot-flash separation (see Figure 6.6) suggests that destructive interference is not an all-or-nothing process that can be observed with fine-grain movement illusions but not with classical apparent motion. The results can be interpreted as suggesting that interactions are not an inherent property of the fine-grain movement illusion, but rather that it is associated with illusory motion on small spatial scales, and hence it is not readily observed in classical apparent motion because of the large spatial size of the visual stimuli used. Spatial extents, however, were found to be relatively constant with respect to dot separation (see Figure 7.3) and hence it is possible that factors other than stimulus separation are responsible for the large difference in extrapolations that can be observed between the fine-grain movement illusion and classical apparent motion.

This type of experiment, in which characteristics of illusory motion are determined over a range of dot separations straddling the spatial resolution threshold, could furthermore provide a means of bridging the gap between our understanding of apparent motion and of real motion. Studies of motion perception typically consider either perceived illusory motion or real motior and traditionally different types of visual stimuli are employed to study each type of motion perception.

This use of different visual stimuli makes the comparison of real and apparent motion difficult and subject to misinterpretations. Although the fine-grain movement illusion is formally an illusory form of perceived motion there exists strong circumstantial evidence that it is mediated by a real-motion detecting system (since the visual stimuli lie below the spatial resolution limit and could therefore fall within the input tolerance range of a real-motion detecting mechanism). Clearly the types of experiment described could prove valuable in exploring the relationship between real- and apparent- motion perception.

The relatively small spatial and temporal ranges over which coherent motion in random-dot patterns can be generated has been interpreted as evidence of the existence of a short-range motion detecting mechanism (Braddick 1974, 1980). Classical apparent motion, however, is typically generated using visual stimuli with larger spatial and temporal extents and could therefore be subserved by a separate "motion-sensitive" detecting mechanism. Because the fine-grain movement illusion has similarities with apparent motion observed with random-dot patterns and is generated using stimuli with small spatial and temporal extents it is a natural candidate for a visual phenomenon subserved by such a short-range mechanism. The proposal that the fine-grain movement illusion may be related to such short-range apparent motion is supported by the finding that the minimum dot separation required to generate the fine-grain movement illusion increases with increasing interstimulus interval (see Figure 5.4). Experiments described in this thesis considered at most two simultaneously generated fine-grain movement illusions. To establish further the relationship between the two types of illusory motion, consideration needs to be given to the simultaneous generation of large numbers of fine-grain movement illusions; these may be expected to exhibit similar properties to those observed with alternated random-dot patterns.

Of interest would be the retinal dependence of the minimum separation required for two random-dot patterns to generate coherent motion.

Finally a comment is offered concerning the possibility that the real-motion detecting system is operative in generating the fine-grain movement illusion. Under optimal conditions the perceived illusion, generated by two sequentially presented spatially unresolved dot flashes, is not of one dot flash moving towards another dot flash but of a compelling clearly defined motion of a single dot. In classical apparent motion it is the author's belief that although illusory motion can be perceived, it is at best seen as motion from one visual stimulus to another, and despite reports that under optimal conditions classical apparent motion cannot be discriminated from a real moving stimulus, this has not been the experience of the author and colleagues in this laboratory. The most plausible reason for this difference is that the fine-grain movement illusion represents the activity of a real-motion-detecting mechanism, whereas classical apparent motion has significant contributions from high-level cognitive processes.

Since the fine-grain movement illusion was first demonstrated in 1969 by Thorson, Lange and Biederman-Thorson it has attracted little experimental consideration from visual psychophysicists working in the field of motion perception. This seems surprising given the obvious relevance of the illusion to different areas of visual perception. It is hoped that the work presented in this thesis will help to establish the importance of the fine-grain movement illusion in developing our understanding of motion perception and other areas of visual perception in the human visual system.

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Appendix

Appendix

As mention in sections 3.6 and 5.1 the hybrid PEST technique used in this thesis differs from that used by Hall (1981) only in the method used to fit psychometric functions to raw data. The method used here was based on a minimum χ^2 analysis, whereas that used by Hall (1981) was based on a maximum likelihood method. Some of the raw data (i.e. responses against stimulus levels) obtained for Experiment 5.1 were re-analysed using a maximum likelihood method to fit psychometric functions. The same psychometric function was fitted (as given in section 3.6) and the threshold level was again taken to be the stimulus level corresponding to the 76% correct point. The following four tables show the results of both methods of analysis. Table 1 and 2 show the minimum dot separation required for the fine-grain movement illusion for SG and RSS respectively, and Tables 3 and 4 show the minimum dot separation required for spatial resolution for SG and RSS respectively. Each table has two sets of data, set (a) obtained with the minimum χ^2 analysis and set (b) obtained with the maximum likelihood analysis. For each set of data there are four threshold estimates, which are given in degrees and at the bottom of each column of four thresholds are given the mean and the standard error of the mean (SEM). Note that if the final mean values of thresholds obtained with the maximum likelihood method are plotted on Figures 5.1(b) and 5.1(c) then the majority of the points would be supperimposed on the corresponding thresholds obtained using the minimum χ^2 method.

Table 1 Minimum dot separation required for the fine-grain movement illusion. Subject SG.

(a) Minimum x^2 analysis

	Retinal site, degrees from fovea.				
	5	10	15	20	25
	0.1033	0.1093	0.1007	0.1448	0.0945
	0.0581	0.1239	0.0731	0.1272	0.2528
	0.0718	0.0848	0.1114	0.1473	0.1466
	0.1040	0.0921	0.1649	0.1608	0.1678
	------	------	------	------	------
Mean	0.0843	0.1025	0.1125	0.1450	0.1654
SEM	0.0115	0.0088	0.0192	0.0069	0.0329

(a) Maximum likelihood analysis.

	Retinal site, degrees from fovea.				
	5	10	15	20	25
	0.1022	0.1109	0.0985	0.1401	0.1147
	0.0599	0.1235	0.0758	0.1287	0.2629
	0.0701	0.0844	0.1089	0.1446	0.1481
	0.0986	0.0897	0.1643	0.1615	0.1642
	------	------	------	------	------
Mean	0.0827	0.1021	0.1119	0.1437	0.1725
SEM	0.0105	0.0091	0.0188	0.0068	0.0319

Table 2 Minimum dot separation required for the fine-grain movement illusion. Subject RSS.

(a) Minimum χ^2 analysis

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.0651	0.0591	0.1036	0.1183	0.1828
	0.0415	0.0444	0.1096	0.1424	0.2177
	0.0496	0.0728	0.0523	0.1604	0.1877
	0.0666	0.1020	0.1006	0.0970	0.1893
	------	------	------	------	------
Mean	0.0557	0.0696	0.0915	0.1295	0.1944
SEM	0.0061	0.0123	0.0132	0.0139	0.0079

(a) Maximum likelihood analysis.

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.0648	0.0588	0.1035	0.1166	0.1865
	0.0420	0.0440	0.1081	0.1410	0.2215
	0.0560	0.0822	0.0518	0.1568	0.1857
	0.0824	0.1025	0.1039	0.1000	0.1754
	------	------	------	------	------
Mean	0.0613	0.0719	0.0918	0.1286	0.1924
SEM	0.0085	0.0129	0.0134	0.0126	0.0100

Table 3 Minimum dot separation required for spatial resolution. Subject SG

(a) Minimum x^2 analysis

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.1035	0.2365	0.2629	0.2704	0.3183
	0.0925	0.1500	0.1596	0.2536	0.4179
	0.1729	0.2020	0.2769	0.2135	0.2902
	0.1063	0.1508	0.2319	0.3240	0.3814
	------	------	------	------	------
Mean	0.1188	0.1848	0.2328	0.2654	0.3520
SEM	0.0183	0.0211	0.0262	0.0229	0.0291

(a) Maximum likelihood analysis.

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.1213	0.2499	0.2596	0.2690	0.3195
	0.0950	0.1483	0.1587	0.2619	0.4164
	0.1722	0.1990	0.2818	0.2927	0.2884
	0.1089	0.1584	0.2383	0.3642	0.3794
	------	------	------	------	------
Mean	0.1244	0.1877	0.2346	0.2970	0.3509
SEM	0.0168	0.0220	0.0268	0.0234	0.0289

Table 4 Minimum dot separation required for spatial resoultion. Subject RSS.

(a) Minimum x^2 analysis

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.1175	0.2921	0.2897	0.0138	0.5511
	0.1630	0.1907	0.3185	0.4900	0.5133
	0.1284	0.3444	0.4662	0.5490	0.6227
	0.1990	0.2788	0.4487	0.5430	0.5243
	------	------	------	------	------
Mean	0.1520	0.2765	0.3808	0.4300	0.5529
SEM	0.0184	0.0319	0.0448	0.0982	0.0246

(a) Maximum likelihood analysis.

Retinal site, degrees from fovea.

	5	10	15	20	25
	0.1161	0.2881	0.2916	0.0578	0.5489
	0.1681	0.1975	0.3048	0.4939	0.5088
	0.1331	0.3461	0.4967	0.5491	0.6196
	0.1953	0.2789	0.4404	0.5377	0.5394
	------	------	------	------	------
Mean	0.1532	0.2777	0.3834	0.4130	0.5542
SEM	0.0177	0.0306	0.0506	0.1179	0.0234