The Visual Response to Alternating Chromatic Stimuli

BY

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SUMMARY

Sequential exposure of two adjacent stimuli fulfilling certain conditions with regard to proximity, duration and form elicits the perception of an object moving between the stimuli locations. Kenkel (1913) designated this form of motion "beta" movement. Substantial evidence indicates that activation of movement-sensitive neurones by alternating stimuli is responsible for the appearance of the phenomenon. Small alternating stimuli subtending about 2 mins. of arc, presented against a black background, are used to establish the maximum spatial threshold for beta motion. Such spatial thresholds are considered to delineate perceptive fields of movement-sensitive neurones. The perceptive field is the psychophysical equivalent of visual receptive field organisation found in man. Significant threshold variation occurs with stimulus wavelength, suggesting that spectrally opponent cells may act as inputs for movement-sensitive neurones. A direct relationship is established between stimulus duration and the perceptive field size for beta motion. Significant interaction effects between pulse duration and wavelength, resembling the Bezold - Brucke hue shift, are indicated. The influence of both temporal overlap and interstimulus interval upon beta motion, is related to the existence of phase differences between excitation and inhibition. A linear increase in perceptive field size for beta motion is found with increasing eccentricity up to 10°. Rod activity is considered responsible for the increased sensitivity to short wavelength stimuli occurring with eccentricity in excess of 4°.

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CHAPTER I

Introduction

The present project has developed from interest surrounding the functional inter-relationships of "colour-specific" receptors and their behaviour, particularly as illustrated in the phenomenon of "beta" apparent motion.

Sequential exposure of two adjacent stimuli fulfilling certain conditions with regard to proximity, duration and form, elicit the perception of an object which moves between the stimuli locations. The moving object appears to be single and clearly defined. The first experimental description of the phenomenon was made by Exner (1875) and the work elaborated by Wertheimer (1912). Kenkel (1913) designated this form of apparent motion "beta" movement and it is clearly distinguished from the objectless sensation of motion termed "phi" by Wertheimer. Categorising the appearance of apparent movement, therefore, has been one of the first tasks undertaken. Increasing the spatial separation of asynchronous stimuli leads to the breakdown of beta motion, suggesting that its underlying mechanism has very definite spatial characteristics.

In 1915 Korte formulated laws relating four factors to apparent motion; spatial separation of stimuli, luminance, stimuli duration, and temporal pause. These laws were questioned, since Neuhaus (1930) found apparent movement to occur over a wide range of interstimulus intervals for any stimulus duration and spatial separation. Koffka (1935) also regarded Kortes laws to be of limited value. A systematic examination of the effects produced upon beta motion by some of the factors outlined by Korte has been made. This may provide an insight into the mechanism by which it is processed in the visual system. Movement-sensitive neurones, discussed in Chapter IV, have recently been advocated as a basis for such a mechanism. It would be necessary for two alternating spots to impinge upon the excitatory receptive field of the cell in order to produce optimal apparent motion. The response continues as the spatial separation of the stimuli is increased, until only one remains incident upon the excitatory receptive field. The receptive field characteristics of movement-sensitive neurones may, therefore, be determined by the visual response to alternating chromatic stimuli.

In early studies of receptive fields, Hartline (1938, 1940) found their size to depend upon the intensity of an exploring spot. More recently, a concentric overlapping distribution of excitatory and inhibitory receptive fields has been clearly demonstrated (Barlow, 1953; Kuffler, 1953; Wagner et al., 1963). The current concept is to regard excitatory and inhibitory receptive fields as overlapping Gaussian sensitivity distributions (Rodieck and Stone, 1965). If similar characteristics apply to movement-sensitive neurones, response differences may be demonstrated under certain conditions.

Light pulses have generally been used as stimuli for apparent movement. One of the initial questions posed is whether movement-sensitive neurones respond differently depending upon stimulus wavelength, or is the response merely dependent upon a luminance change. If the response is in some way wavelength dependent, the input mechanism to movement-sensitive neurones may be revealed. Accordingly, the mechanisms of spatial and spectral opponency have been reviewed in Chapter III.

Many of the earlier workers, whose work is reviewed in Chapter II, became absorbed with ascertaining the optimum interstimulus interval for apparent movement. This, however, is not critical since optimal apparent motion is seen over a wide range of values, although the phenomenon is not seen with synchronous stimuli. The extent to which stimuli must be asynchronous may provide an insight into the behaviour of inhibitory mechanisms, essential to movement-sensitive neurones and without which they could not function. This may be ascertained from the apparent movement response produced by varying the temporal overlap or interstimulus interval of the stimuli.

The relationship existing between stimulus intensity and receptive field size has been referred to earlier. The investigation of such a relationship requires a very powerful source, maintaining a constant colour temperature, which must be used to provide a stimulus intensity range spanning several logarithmic units. This poses a number of difficulties especially in the spectral extremes. A relatively simple method is necessary to investigate changes occurring in the receptive field size of movement-sensitive neurones, in response to differing stimulus characteristics. Since the visual response to a stimulus may be defined by both stimulus intensity as well as its duration, the changes occurring in the apparent movement response with stimulus duration provides a useful method.

Receptive field size has been found to increase with retinal eccentricity (Wiesel, 1960; Enroth - Cugell and Robson, 1966; Ikeda and Wright, 1972), and it is generally held that the peripheral retina has a higher motion sensitivity than does the fovea. Changes in the maximum spatial threshold for optimal apparent motion with retinal location may, therefore, be anticipated.

These factors of principal interest have been selected for investigation in this project, which looks at the visual response to alternating chromatic stimuli and the insight into visual processing offered by this response.

CHAPTER II

Apparent Movement Phenomenon : A Literature Survey

The problems posed to nineteenth century workers, which arose when excitation and experience failed to agree, were both new and difficult. Apparent movement of the environment or of a stationary object challenged existing concepts that the eye presented to the mind a true and accurate picture of the external world. The apparent rotation of the environment when a subject is spun around was noted as early as 1801 by Erasmus Darwin. This was similarly noted by Purkinje writing about Vertigo, over the period 1820 to 1827, incorrectly suggesting that it arose from the soft pliable brain lagging behind the hard skull.

In the early nineteenth century Roget noted how the spokes of rotating carriage wheels appeared curved when seen through the vertical apertures of a garden fence. This provided the first introduction to the stroboscopic phenomenon in which successive images, differing slightly in form or spatial location, are seen to change shape or move. One of the first experimental demonstrations was given by Michael Faraday in 1831, in which two counter-rotating spoked wheels produced the appearance of a single wheel having twice the number of spokes. Earlier, in November 1830, the Belgian scientist Plateau constructed a disc having sixteen images of a dancer who appears to move continuously as the disc is rotated. He called his device an "eye-deceiver" or phenakistoscope, and gave it to a fellow Belgian Quentelet, so that he might pass it on to Faraday. Later, however, in January 1833 Quentelet published an account of the instrument and the phenomenon under his own name. In July of the same year Stampfer described a similar device which he termed a "visual whirler" or "stroboscope". The development of these devices, and Addams' (1834) account of the waterfall illusion, provided the foundations upon which nineteenth century research into movement perception was built.

Over the following years the view emerged that movement was perceived by the mind, resulting from "sensations" received by the eye. The question arose as to whether movement should be regarded as a central "perception" or as a peripheral "sensation".

In 1875 Exner found that two closely-situated electric sparks, when illuminated successively, gave the appearance of a single moving spot. If the stimuli were synchronous the appearance was described as "simultaneity", whilst asynchronous stimuli produced succession. A slight temporal overlap of stimuli, however, gave the illusion of movement. Exner argued that motion could not be an inferred attribute of objects perceived in different places; because the timing of events was so rapid, and the perception of motion so immediate, that memory could not be its source. Experimental work led him to conclude that movement perception involved a special process in its own right. This, he regarded as one of the basic constituents of perception and not a derived or computed one. Hence, Exner regarded the appearance of movement as a sensation. Exner's conclusions agreed with those of contemporary theorists. Dvorak supported Mach's (1870) concept that movement relied upon an independent simple retinal process, and was not a space-time complex.

Support came for Exner's view from Vierordt (1876) who regarded movement as both nativistic and primary, concluding in his paper, "Nihil est in intellectu, quod non antea fuerit in sensu". (nothing exists in the intellect which has not previously existed in the senses) Movement is a sensation in itself, Vierordt asserted - "like time in the Zeitsinn". Schneider (1878) also considered movement to be "biologically prior" to other conditions of sensation, observing that some faint or small objects were only perceived when they move.

A general law of "subjective complementary motion" was advanced by Thompson (1880) to account for the waterfall illusion described some forty-six years earlier. He suggested that continued motion resulted in retinal adaptation and that this "contrasts" with the field-surround which is seen to move in the opposite direction. A similar principle was propounded at the same time by Helmholtz and Hering to account for simultaneous colour contrast.

Later years, however, saw a change in viewpoint. The school of Gestaltqualitat (von Ehrenfels, 1890) considered perceived movement as a form-quality, associated with location changes of the stimulus with time. Exner's assertions were fiercely challenged by Stern (1894) who considered movement to be a perception. Marbe (1898) also held this view, regarding seen movement as a phenomenon resulting from fusion of successive periodic retinal excitations and subscribing therefore to Talbot's Laws of Fusion. Marbe was greatly influenced by his mentor Wundt who had originally suggested that stroboscopic movement resulted from fusion and eye movements. Following Marbe's work, the perception of movement was generally considered to be a wholly - or partly - central phenomenon and no longer a "sensation". One last attempt, however, was made by Dürr (1900) to base a theory on purely peripheral mechanisms. If an apparently moving spot is fixated, rather than a stationary target, good movement is obtained. Dürr therefore suggested, as did Wundt, that the phenomenon depends upon eye movements. Numerous workers were later to discount this theory.

It was thirty-seven years after Exner's work before the next major contribution on apparent movement was made by Wertheimer (1912). During this period both the motion-picture camera and projector were invented. The delay may be partly ascribed to technological reasons: it was difficult to obtain a suitable stimulus - the electric sparks used by Exner being rather impractical. The predominant reason was probably that the study of illusions - regarded as "subjective perversions of the contents of objective perception" (Külpe 1893) - was not very respectable in the scientific and intellectual environment of the time, which emphasised the veridicality of perception. Throughout this period Wundtian and Tichnerian elementarism was at its height.

Following Exner's initial classification, Wertheimer attempted to clarify the emergence of optimal apparent motion from simultaneity of the stimuli. Wertheimer studied the epistomological and perceptual states of the illusory object by interposing other stimuli into regions through which the object moved. He was also interested in the influence of subject attitude upon the illusion, as well as after-effects.

Wertheimer's contribution included the description of partial motion and phi or "objectless" motion. Partial motion occurred when the moving spot traversing the screen disappeared, before reaching the location of the second stimulus. Phi motion denoted the stage at which the object moved so rapidly between the points of appearance and disappearance that no details of its shape or appearance could be ascertained. Objectless movement - a sense of motion without a concomitant perception of a moving object, analogous to the very rapid passage of a real object - was of great theoretical importance to Wertheimer. The occurrence of phi was taken to prove conclusively that motion was not, as many contemporary psychologists believed, a complex perception built up from a sense of temporal order and memory of an object's location. Movement was therefore perceived in the absence of line, colour or any visible characteristics of the object. Object and motion were, therefore, distinguishably different aspects of perception, either existing without the other. Wertheimer wrote:

> "The sense of motion is not constructed in any material way from the subjective filling-in of objects in the intervening spaces (between the flashes) . . . . the phi phenomenon (is) separable from the (process mediating the) appearance of the two stimulus objects".

Wertheimer initiated the comparison between real and apparent movement asserting that they were indistinguishable. He also demonstrated that apparent motion could not be attributable to eye movements, since it could be induced in opposite directions simultaneously. Wertheimer suggested that the perception of motion was "behind the eye" since apparent motion could also be obtained when one stimulus was presented to each eye separately. The optimal inter-stimulus interval was found to vary with spatial separation of stimuli and some temporal overlap was possible whilst movement was still seen. With coloured stimuli the spot was observed to change colour in flight.

Wertheimer revised Exner's (1875) classification by describing a progressive series starting from simultaneity of stimuli, then optimal movement, partial movement, pure movement (phi) and finally ending with succession. Phi was seen only in the phase just prior to succession when all apparent movement, even partial movement, had ceased. The term phi is used only to describe the "sensation" of movement linking the separate stimuli, and not the apparent movement of a single, clearly defined spot, which was earlier seen. It has been pointed out (Neff, 1936) that Wertheimer's "Stadien" should not be regarded as types or stages of movement. Rather, they should be regarded as parts of the phenomena other than movement, which attend the successive presentation of visual stimuli. Apparent movement and phi have been phenomena frequently confused although to Wertheimer they were significantly different. Although apparent movement had been described by Exner, objectless movement was regarded as something new and important - an experience of movement "sui generis" which could be analysed no further, nor described in terms of quality, intensity or extent.

Much work has been undertaken describing the conditions under which apparent motion may be viewed, but few workers have elaborated upon the appearance of "objectless movement". Difficulty is encountered in considering a mechanism within the visual system, triggered by stationary stimuli, which results in a sensation of motion although movement is not perceived. Undoubtedly the appearance of phi was crucial to Wertheimer's theory, and speculation must arise that its appearance was an artefact in subjects having previously viewed apparent movement. Wertheimer actually observes that motion could be seen with only one stimulus, if this follows previous apparent motion stimulation.

Following Wertheimer's work Kenkel (1913) classified three types of apparent movement as alpha, beta, or gamma. It is beta movement, analogous to optimal apparent movement, with which the present work is most concerned. Using identical methods and apparatus, Kenkel confirmed Wertheimer's results for these new apparent movement forms.

Three years later, Korte (1915) investigated whether the direction of phi movement was dependent upon the order of presentation of stimuli. He determined whether reversal was possible by increased emphasis on the second stimulus in terms of greater intensity, direction of attention, fixation or other factors. Korte successfully obtained reversal of phi movement which he termed delta movement. Laws were formulated relating apparent movement to four factors, namely, spatial disparity of stimuli, luminance, stimulus duration and temporal pause. These have become known as Kortes Laws, although they were first postulated by Koffka.

The existence of phi was not universally accepted. In a series of papers during the period 1912 to 1918, Benussi emphasised the importance of distinguishing the "seen" from the "experienced". In 1913 he demonstrated tactually perceived apparent motion and later compared this with visually perceived apparent motion. Benussi's subjects, however, were unable to report Wertheimer's objectless movement and doubt was therefore cast upon its existence.

The comparison of real and phenomenal movement instituted by Wertheimer was not of major importance to Linke (1918). He was concerned only with movement perception itself: the way in which a single separately - perceived object taken in combination with a similar object appears to move. Movement perception may be resolved into two contrasted divisions: that which is actually perceived - the initial and final positions of the object; secondly that which is perceived by "assimilative supplementation" - the moving object seen in the intervening field. Linke regarded the "concept of identity" as a predominant factor in movement perception since a certain "something"must exist which undergoes change in colour, form or position. His analysis of movement in these terms indicates the influence of Wundt upon his work. Linke considered movement perception possible only if the two stimuli are similar, in order that they may be referred to one object. Predisposition and attitude on the part of the observer were also regarded as important.

Support for the classical ideas of "filling-in" or "assimilative supplementation" proposed by Linke, Benussi and Wittman came from Dimmick (1920). Observers noted a flash of grey occurring between the stimuli locations which was thought to give rise to the appearance of the moving spot. This supported Dimmick's view that phi could be analysed and was not, therefore, a new sensation as Wertheimer had believed. Blug, however, claimed this to be an artefact arising from Dimmick's dark intervening field, since it was not seen when stimuli and field were of approximately equal intensity. Observer attitudes were also considered important by Wittman (1921). He distinguished between analytic and synthetic observer attitudes, considering the former inhibiting and the latter facilitating movement perception. Wertheimer (1912) had described three intermediate stages between simultaneity and succession of stimuli, but Wittman described eight stages. Arising from subdivisions of the existing classification by Wertheimer, the eight stages offered no new insight into the phenomenon. Wittman does agree with Benussi in denying the existence of Wertheimer's phi, describing it as an absurdity since he considers movement perception as an experienced relationship between two objects.

Hillebrand (1922) was foremost in considering that factors other than retinal must contribute to movement perception. For support he noted that movement was not seen when the eyes were swept over a stationary object, despite movement of the retinal image; secondly movement is observed when pursuit eye movements are made, in the absence of retinal shift. Central involvement in movement perception was therefore implicated, as it also must be for phi which occurred in the absence of both retinal shift and eye movements. Hillebrand therefore developed the concept of absolute localisation first suggested by Hering. Motion was not perceived until a second stimulus impinged upon a second retinal point. He therefore proposed that the whole area underwent gradual re-evaluation of its space value influenced by absolute localisation. The visual field therefore becomes centred around the second stimulus location and this corresponds to the perception of movement. Hillebrand was one of the first to propose a mechanism for motion perception.

Later, in 1923, Wertheimer proposed that stimulation of a retinal region induced a circle of excitation in a corresponding cortical region. If two such circles of excitation occurred within the proper temporal interval of fusion a "short-circuit" occurred between them corresponding to apparent movement. The mechanism was supposed to be photochemical at very short exposure durations, whereas for longer durations inference was proposed. The present work, however, is concerned only with optimal apparent movement and the insight this provides into the visual response to chromatic stimuli.

In the same year, Köhler (1923) attempted to extend and elaborate Wertheimer's work to produce a common theory applicable to both real and apparent motion. Regarding the brain as a volume conductor he attempted to relate visual phenomena to late nineteenth century electrodynamics. Hebb (1948) contended that Köhler regarded the brain as having, "all the fine structure of a bowlful of porridge".

Further doubt was cast upon retinal theories of apparent motion by Stern (1926), whose subjects often reported apparent motion when stimuli were applied either side of the blind spot.

Temporal relationships of stimuli eliciting apparent movement had been considered important by Wertheimer, who had sought to establish the optimal inter-stimulus interval. Movement perception, and the other phenomena reported by Wertheimer, were found to be independent of inter-stimulus intervals over a wide range (45 to 225 m.sec) by Higginson (1926). He considered the work indicated an influence attributable to "predisposition" of the observer towards apparent movement. The transition from optimal to non-optimal movement may be regarded as a threshold. The effect of observer "predisposition", or prior instructions given to the observer, upon the threshold are predictable. Higginson's work led him to state that "we have here clearly demonstrated the remarkable facility of the organism whereby it may attain a functional end under extreme poverty of the experiential resources".

McConnell (1927) continued Higginson's work, obtaining apparent motion with temporal overlap of stimuli. The frequency with which movement was reported increased rapidly as the degree of overlap increased, reaching a maximum about one third of the way through the range. The maximum was maintained with occasional inversions up to an extreme temporal overlap. Higginson had shown that the length of the temporal interval between stimuli did not influence apparent movement. McConnell demonstrated that apparent movement could be seen in the absence of an inter-stimulus interval, and even with temporal overlap of stimuli. The temporal coefficient, serving as an extra organic condition of movement perception, is therefore regarded as a complex variable. The question arises as to whether motion perception is generated equally by interaction of the onsets of two flashes, their offsets, or by a combination of the onset of one and the offset of another.

Similar attempts were made to ascertain the factors affecting apparent movement by De Silva (1926). He described factors such as repetition, fatigue, background, position, form of stimulus, meaningfulness of stimulus, fixation point, and various sorts of predisposition. While probably unaware of Higginson's (1926) work, he regarded an exposure time of 65 m.sec and a temporal interval of 60 m.sec as necessary to produce optimal movement. De Silva found meaningful stimuli gave rise to apparent movement more readily than did random figures. This was later confirmed by Steinig (1929). He also found subject attitude to be important: the quiet, passive, object-orientated attitude helped apparent movement perception compared to an active, analytical, stimulus-orientated attitude. Later, Schnorr (1937) obtained evidence suggesting that extroverts reached the upper limit of apparent motion at considerably lower cycle time than did introverts.

In later work, De Silva (1928) found the first flash radically affected the likelihood of seeing apparent movement, whereas the second flash seemed to have no effect as long as it was visible. A strong first flash produced a strong illusion of movement and vice versa. The likelihood of seeing apparent motion was found to fall with prolonged testing (although such threshold changes occur commonly in psychophysical measurements).

In his final paper, De Silva (1929), analysing the visual perception of movement argues that apparent movement arises from a "filling-in" process taking place in the highest centres of the response arc. Apparent movement, he suggests, involves a sensory overlapping or succession of "clearing-up" processes on neighbouring retinal areas. These would be associated with contemporaneous integration of similar, spatially-differentiated central processes. De Silva noted that the greatest confusion of real and apparent movement occurred with fast moving objects traversing small distances.

The suggestion that other sense modalities could influence motion perception came from Werner and Zeitz (1928). Stimuli flashed at temporal intervals normally too great to produce apparent movement, did so when accompanied by faster, rhythmic auditory or kinesthetic impulses. The mechanism associated with this was not postulated.

Galli (1932) also suggested movement perception could occur following successive stimulation of different sense fields. Presenting a random sequence of optical, tactual, or auditory stimuli, remarkable apparent movements were described in which objects moved in the direction of a pressure, or a pressure moved in the direction of a sound.

Movement is not seen in isolation, and Duncker (1929) considered that the frame of reference conditions the perception of an object's motion. Earlier, De Silva (1926) described the effect of displacing a target relative to a larger framework. When flashed stroboscopically the small target is always seen to move whether or not the larger framework does. The suggestion arising from Duncker and De Silva's work was that an object or event acts as a frame of reference, against which the action of other objects or events take place. Subjects interpret the relationship between object and framework although their identity varies with the level of analysis performed by the observer.

The relationships embodied in Korte's Laws had remained uninvestigated since 1915, until Neuhaus (1930) adopted a more refined technique than his predecessor in determining the effects of stimulus duration and inter-stimulus interval. Increasing the stimulus duration resulted in a fall in the inter-stimulus interval at which motion was first seen and the interval at which it gives way to succession. This was implied in Korte's Laws, but Neuhaus found apparent movement over a wide range of inter-stimulus intervals for any stimulus duration and spatial separation. This clearly demonstrated that no fixed inter-stimulus interval existed as had been suggested earlier by Wertheimer (1912) and Higginson (1926). Apparent movement appeared to be unaffected by stimulus intensity but could possess a third dimension so that it might be seen moving in depth. Neuhaus agreed with De Silva (1928) that the duration of the first stimulus was more significant for apparent movement perception than that of the second.

Van der Waals and Roelofs (1930), using dissimilar figures, observed them to change form and colour in flight. The gradual change in form took place as one figure "grew" into another as described by Dimmick and Sanders (1929). It was argued by Van der Waals and Roelofs, that the visual system cannot know how to transform the stimuli until the second one is seen; thus the entire percept is delayed in its construction until the second flash is presented and registered in the consciousness.

Von Schiller (1933) questioned whether the flashes themselves could induce a force strong enough to bind together spatially - and temporally - disparate shapes into a gestalt unity.

Some earlier workers (De Silva, 1928; Neuhaus, 1930) had regarded the second flash as relatively unimportant, by providing merely a terminus for apparent movement. Koffka (1935), however, observed that, occasionally, attributes of the second flash affected the entire perception of motion. He also regarded Korte's Laws to be of limited value. Korte's data had indicated that a trebling of spatial separation required less than a doubling of temporal separation to maintain the perception of movement.

Ogasawara (1936) showed that the apparent separation of stimulus lights rather than the physical one determined the time interval between stimuli. Brown (1931) had earlier noted that perceived velocity, like physical velocity, depended upon two factors: perceived distance and perceived time. Brown's ideas have been dismissed as mere isomorphism and Cartwright (1942) suggested that he had misinterpreted his own data. Cartwright suggested that movement threshold and spatial thresholds are closely related. Brown, who had worked in Köhler's laboratory, was to have his theory rejected by Köhler, Wallach and Cartwright (1942).

A functional association between mechanisms responsible for the perception of light intensity and movement perception was suggested by Hovey (1936). He noted a similarity of magnitude between the thresholds for apparent movement perception and difference-thresholds for light intensity.

A timely and useful contribution to the prevailing debate was made by Bartley (1936). Apart from instances when alternate use of the two eyes produced apparent motion, it had been suggested that synaptic layers of the retina or thalamus were responsible for this fusion. Hence, a unitary, properly differentiated pattern would reach the cortex resulting in the perception of a single moving object. Bartley felt that the level at which fusion took place could not be ascertained with current knowledge about the visual system.

A theory of learning has been used to describe, but not explain, apparent movement by Ryans (1937). A formerly stationary stimulus may be observed in movement to change its position successively. Two adjacent stimuli observed successively resemble the single moving stimulus, and hence the perceptual response of apparent movement is seen early in life. Ryans suggests that increased age, accompanied by improved discrimination in adult life reduces the ability to see apparent motion, although some may persist. The theoretical issues of learning such as drive reduction and reinforcement are not considered by Ryans. Some support did come from Gantenbein (1952) who found children aged between five and thirteen saw apparent movement more easily than adults. He agreed this was due to a biological maturation factor.

A novel theory of apparent motion, regarded as predictive, was proposed by Brown and Voth (1937). It was suggested that a visual figure can be characterised by two kinds of forces: namely restraining forces, which account for stability of contour and position, figural properties and boundary phenomena, and cohesive forces which attract visual objects toward each other. These forces were alleged to behave as simple vectors. The cohesive force between stimuli increased with a fall in inter-stimulus time, resulting in optimal apparent motion when this is maximal. A further increase in inter-stimulus time results in a reduction in the cohesive vector which eventually equals the restraining forces at the moment when simultaneity occurs. Although claimed to be a predictive model, its results have not always been found to be correct (Sylvester, 1960).

It would appear that the ghost of eye-movements in respect of apparent motion was not fully laid. Hartson (1937) observed that temporal factors conducive to apparent motion corresponded with stimuli capable of initiating ballistic saccades, but which were too brief for fixation. The phi phenomenon was inhibited by fixating a stationary point and had a sweeping motion whose duration appeared independent of distance. Hartson suggested that saccadic eye movements occurred when apparent motion is experienced. This had already been disproved.

The effects of hetero-modal stimulation shown by Werner and Zeitz (1928) and Galli (1932) were confirmed by Gilbert (1939) although considerable individual differences were observed. Increases in apparent movement ranges with accompanying sound stimuli varied from no change to a 60% increase. Gilbert suggested a diurnal fluctuation in apparent movement frequency although this could be ascribed to factors affecting subject fatigue.

Similarity of form between stimuli triggering apparent movement was regarded as more important than differences in area, spatial separation, or plane of spatial orientation of stimuli by Orlanski (1940). The range of apparent movement declined with increased differences in stimuli form. This suggests that it is necessary for the visual system to assess the form disparity before resolving the stimuli. It is only when the requirements exceed the figure-resolving capabilities of the visual system that the motion illusion is impaired. Stimuli of very different form did not produce apparent motion.

The theory for apparent movement proposed by Wertheimer (1923) was considered unlikely by Verhoeff (1940). Strabismic subjects, having anomalous projection, but good visual acuity in each eye observed apparent movement arising from contra-ocular, macular stimulation. Therefore the mechanism for contra-ocular apparent motion cannot, as Wertheimer suggested, involve cortical points which bear a fixed functional relationship to the retina. Animal studies on the guinea pig suggested that apparent movement was a function of sub-cortical reflex systems (Smith, 1940). Similarly, work on the cat by Smith and Kappauf (1940) indicated that apparent movement responses were mediated by superior colliculi or pretectal nuclei of the midbrain. The value of such results was later challenged by Shapiro (1954), arguing that visual functions in lower vertebrates were administered by mesencephalic centres whilst the cortex assumed all optic functions in man with the exception of the pupillary light reflex. It is worth mentioning that brain-damaged children failed to perceive apparent motion although reduced flicker perception was present (Werner and Thuma, 1942 (b)). The conclusion was that space-time integration for flicker fusion and apparent movement processes were not identical.

Purely cortical theories of apparent motion had begun to be discredited. Shipley, Kenney and King (1945) found that under favourable conditions equally good apparent motion was obtained from interocular and monocular stimuli. This suggested that lateral neurones in the retina may not be essential for the perception of beta apparent movement.

Contemporary theories of apparent motion were brought together by Bridgeman and Smith (1945). Almost all subjects, with a complete section of the corpus callosum, perceived apparent movement resulting from contra-ocular stimulation. Similarly apparent motion is perceived from stimulation of nasal and temporal hemiretinae, eliminating the possibility of retinal interaction. Thus visual fusion occurs independently of bilateral cortical integration and sub-cortical levels are therefore implicated. It seems relevant that Hyndman (1939) found central vision was represented anterior to the accepted visual cortex and not bilaterally. Gengerelli (1948) observed that the visual system created apparent motion more readily from signals occurring within the same cerebral hemisphere.

Objectless phi motion was obtained by Smith (1948) using stimuli positioned in the temporal extremities of heteronymous fields. He concluded that neural interaction was absent from the perception of phi, so discounting Wertheimer's (1923) theory, as Verhoeff (1940) had done. It is important to stress, however, the essential difference between the sensation of motion occurring with the objectless phi phenomenon, and the perception of a distinct, moving object occurring with optimal or beta motion. Teuber and Bender (1950) failed to draw this distinction when reporting that apparent movement could be seen with flashes up to 22° apart. Neuhaus (1930), however, who had been similarly vague found that apparent movement ceased with flashes greater than 4.5° apart.

The homogenous brain field theory of apparent movement was regarded as too general and oversimplified by Ammons and Weitz (1951). They observed that phi perception appeared greater with monocular than binocular stimulation, and suggested that retinal or sub-cortical factors were important. Spatial summation occurring at the level of the second and third order of retinal neurones is considered the basis for the fusion occurring during apparent movement.

Further doubt was cast on the short circuit theory by Deatherage and Bitterman (1952). A figure flashed in the path of apparent motion resulted in its displacement in depth. Since depth was constructed as an alternative to crossed motion, the short circuit theory of apparent motion cannot be sustained. Further support for Deatherage and Bitterman came from Shapiro (1954). He found that the threshold of optimal motion seen in one eye increased when an inspection figure was viewed by the other eye.

The average duration of beta apparent motion was found to be a function of dark adaptation time by Horne and Saucer (1952). Increased dark adaptation resulted in a fall in the duration of beta movement. This may be associated either with increased rod activity or subject fatigue.

Although considerable evidence exists against eye movements as a basis for apparent motion, the question arises as to the role played by eye movements as initiators of "phase-sequences" in the occipital cortex. A close correlation between eye-movement inception and the alpha rhythm led to Meister (1951) proposing a "neuronic shutter mechanism" responsible for the apparent movement phenomenon. A similar mechanism which increased visual efficiency by suppressing retinal signals during eye movements was proposed by Hansel (1953). He suggested that apparent movement cues could not, therefore, be differentiated from those of real movement. Walsh (1952) examining such a scanning hypothesis found no correlation between visual reaction time and the alpha rhythm. He therefore opposed both the conclusions of Meister and Hansel.

Heteromodal influences were considered by Werner and Zeitz (1928), Galli (1932) and Gilbert (1939). Brenner (1953) used four types of continuous stimulation: vision, audition, voluntary motor activity, and mental arithmetic; each of which significantly reduced the apparent movement range. The range was regarded as the difference in time interval rates between succession and simultaneity. Brenner concluded that the underlying process must be localised in a part of the visual system served by all sense modalities, and having a problem-solving capability. He nominated Brodmann area 19. Brenner's conclusions have been questioned (Kolers, 1972), and it has been noted that it is possible to eat whilst doing mental arithmetic as well as whistle whilst reading (Huey, 1968). Alternative stimuli may simply affect subject attention which is said to influence the perception of apparent motion (Wittman, 1921; De Silva, 1926; Schnorr, 1937).

A theory of retinal induction was proposed by Motokawa and Ebe (1953), in which it was suggested that stroboscopic stimuli induce a state similar to the retinal trace existing behind a moving retinal image. The first stimulus produces a spreading wave of retinal induction which is terminated by the onset of the second complementary stimulus. Fusion is supposed, therefore, to occur at a retinal level. Retinal induction would leave unexplained the appearance of apparent movement for contra-ocular stimulation (Bridgeman and Smith, 1945; Smith, 1948) as well as subjective factors and heteromodal influences (Werner and Zeitz, 1928). It should be mentioned that the work of Werner and Zeitz (1928) was not confirmed by Hall and Earle (1954) who obtained identical results for apparent movement with and without the use of an audible metronome. They did, however, find all forms of motion perception to be reduced when an illuminated pendulum was placed next to the display. It has been suggested (Wilcott, 1955) that basic differences exist between the mechanisms of visual and auditory space perception.

Saucer (1953) suggested motion perception was due to a mechanism having a statistically uniform matrix structure regulated by both classical nerve conduction (axon-to-dendrite) and field forces arising from conduction occurring between adjacent axons. It was postulated that the matrix decay time correlated with the stimulation rate necessary for optimal motion. Saucer found evidence for beta movement being optimal with a stimulus repetition rate between four and twelve cycles per second, a range which contains the alpha rhythm. Saucer (1954) regarded the matrix theory as a basis for the perception of real and apparent motion. He suggested separate mechanisms existed for form and motion detection.

Form recognition and apparent movement rates were found to be positively correlated with the alpha rhythm by Murphree (1954). Such evidence, however, could not be interpreted as implying a direct link between form and motion perception. Murphree used a cybernetic "nerve-net" model similar to the scanning hypothesis investigated and rejected, by Walsh (1952). He concluded that the alpha rhythm played an important role in apparent movement, supporting the views of Meister (1951) and Hansel (1953).

Like earlier workers (De Silva, 1926; Orlanski, 1940; Jones and Bruner, 1954) Jeeves and Bruner (1956) emphasised the importance of figure in motion perception. They observed differences between thresholds established using ascending and descending methods of limits. This was ascribed to expectation since subjects shown apparent motion continue to see it for some time. Expectation plays little role in subjects who first view succession.

Train and Walthall (1958) noted that the occurrence of figural after-effect, a central perceptual process, had been reported for apparent motion by Christman (1953) and Deatherage (1954). Apparent motion appears identical to real motion, which Köhler and Held (1949) had regarded as a central phenomenon. They regarded this as being supportive of Wertheimer's view that apparent movement was itself a central phenomenon. The classical theory of apparent movement has, however, frequently been opposed. It has been suggested that disparity of retinal stimulation, although stimulation rate necessary for optimal motion. Saucer found evidence for beta movement being optimal with a stimulus repetition rate between four and twelve cycles per second, a range which contains the alpha rhythm. Saucer (1954) regarded the matrix theory as a basis for the perception of real and apparent motion. He suggested separate mechanisms existed for form and motion detection.

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Later, Rock, Tauber and Heller (1965) drew parallels between the temporal characteristics of stimuli yielding good apparent movement in man and those producing real movement in lower animals. They suggested that apparent movement was innate and functionally equivalent with real movement. Toch and Ittleson (1956) had earlier suggested movement perception to be genetically a primary category and had emphasised that apparent movement thresholds were considerably lower for children than adults (Meili and Tobler, 1931; Gantenbein, 1952).

Many workers had considered real and apparent motion to be mediated by identical mechanisms. Kolers (1963) highlighted some differences between real and apparent movement and asserted that since the stimulus conditions producing real and apparent motion are different, the mechanisms must be also. Kolers argued that to suggest identical mechanisms are responsible implies that the perception of movement is determined only by the points of onset and offset of stimulation and the temporal relations between them. The stimulation provided by a physically moving image between the stimuli may then be regarded as irrelevant. Frisby (1969, 1972) rebutts Kolers suggestions, regarding his definition as being too narrow. Stimuli used to produce apparent movement may fall within the input tolerance of a real movement mechanism. The differences found by Kolers between real and apparent movement merely reflect the mode of operation of a single real/apparent movement mechanism when receiving stimuli close to its limit of tolerance. Although Kolers (1964) found apparent movement to break down with prolonged viewing, this fails to occur when such movement is seen with cinematographic presentations. Frisby cites Graham (1965) who pointed out that real movement must reduce conceptually to apparent movement since the retina consists of a mosaic of elements. Further, it is unlikely that a second mechanism should be specially developed to detect apparent motion. Frisby mentions that movement detectors have been observed (Grüsser - Cornehls et al., 1963) which respond equally well to both real and apparent movement stimulation, a very significant statement.

Over this period a distinct concept of apparent motion emerges based on movement sensitive cells. Electrophysiological evidence produced rapid changes in the concept of visual physiology and movement sensitive cells provided a basis for the theory of apparent movement, which was considered to arise due to paradoxical activation of such cells.

The first response to apparent movement had been one of horror - since 'the real' and 'the perceived' failed to agree. A practical application of apparent movement preceded the theory for its appearance, which Wertheimer (1923), had been the first to propose. Over the following fifty years, debate had been centred around the location of the mechanism for apparent motion or factors which influence its appearance. Only recently has some insight been given into the mechanism by which it is seen.

CHAPTER III

Spatial and Spectral Opponency in Visual Processing

1. The Role of Opponent Processes in Visual Perception

"The single most important finding of twentieth-century sensory physiology is that every neuron in the sensory pathways has a combination of excitatory and inhibitory influences playing on it". DeValois and DeValois (1975). The role played by opponent mechanisms is important increasing the efficiency of neuronal systems by rapid adaptational changes occurring in both directions. Similarly the information range is increased below the zero position by inhibitory mechanisms allowing the facilitation of finer gradations between the extremes of white and black. An increased firing rate is produced in light : dark opponent mechanisms signalling a reduction in luminance, which is a far more positive response to black than simply a fall in firing rate of a light sensitive cell. Such mechanisms allow black to attain the specific nature of a colour, since it produces a finite response in an opponent cell. Two specific opponent mechanisms have been extensively investigated, mediating two principal interactions occurring before the cortex in the primate visual system. These systems have been designated:

(a) The spatially opponent organisation relating receptor activity in different spatial locations independent of colour.

(b) The spectrally opponent organisation comparing the output of different cone types.

2. Spatially Opponent Organisation

The spatially opponent organisation was first observed by Kuffler (1953) and Barlow (1953) from single ganglion cell responses in cat and rabbit respectively. Three groups had earlier been distinguished giving on, off and on-off responses (Hartline, 1938; Granit, 1950) but now only two classes were distinguished. The first responds to incremental stimuli impinging upon the receptor field centre with excitation (an increased firing rate) and inhibition when the stimulus impinges anywhere upon an annular surround. Reversed responses arise from a dark spot on a light background. In view of this, the use of their original description of on-centre cells (Kuffler, 1953) has been deprecated. These cells have since been designated + Wh - Bl cells (DeValois, 1972). Conversely the second group respond to incremental light stimuli with inhibition centrally and excitation in their surrounds. Once termed off-centre cells (Kuffler, 1953) they have been more accurately termed + Bl - Wh cells (DeValois, 1972). Other nomenclature has been employed in describing the contribution made by these cells in processing achromatic brightness information. Accordingly the two subsystems originally termed on and off-centre cells, have been designated B and D mechanisms respectively (Jung, 1973). Although placing the subsystems a little more into their visual context, arguments applied to the on and off-centre classification are similarly applicable to such terminology. Further, there exists no equivalent nomenclature applicable for opponent mechanisms engaged in the processing of colour information. It is therefore proposed, to adopt the terminology suggested by DeValois (1972) when referring to spatially opponent mechanisms.

At the ganglion cell level the two systems are clearly separated and form two populations of approximately equal numbers (Jung, 1961; DeValois, Jacobs and Jones, 1962; Jacobs, 1965). Whilst these cell types constitute virtually all cat ganglion or lateral geniculate cells, they make up less than 30% of the total in the macaque (DeValois, Abramov, and Jacobs, 1966; Wiesel and Hubel; 1966). The approximately circular concentric field configuration found at retinal and lateral geniculate levels gives way to a variety of specialised neurones, often possessing highly selective receptive fields, at cortical levels.

Reciprocal activity of the two systems is not always symmetrical. It has been suggested that inhibition in the Bl + Wh - system may have shorter latencies than that of the Wh + Bl - system at retinal (Steinberg, 1969) and lateral geniculate levels (Freund and Baumgartner, 1969; Freund, Wita and Brüstle, 1972). It is therefore possible for the Wh + Bl - system to be triggered by transient inhibition of the Bl + Wh - system.

A light effect common to both systems is the dependence of antagonistic field effects upon some illumination localised within the field centre. The inhibitory surround disappears in Wh + Bl - neurones when light is occluded from the field centre (Maffei and Fiorentini, 1972). Further work has established that surround effects in both systems depend upon centre illumination (Enroth-Cugell and Pinto, 1972; Fischer and Krüger, 1972). The Wh + Bl - system is therefore excited by stimuli which are either brighter than the surround, seen in simultaneous contrast, or else brighter than the previous sensation with successive stimulation. The converse is true for Bl + Wh - cells.

Information processing in the lower visual system is therefore considered to be based on two neuronal mechanisms. The first, regarded essentially as a retinal mechanism (Wagner, MacNichol, and Wolbarsht, 1963), consists of the antagonistic field organisation of the Wh + Bl - and Bl + Wh - systems. The second suggested by Jung (1961) consists of a mechanism with reciprocal inhibition between the two neuronal channels involving mainly central relays in the lateral geniculate and visual cortex.

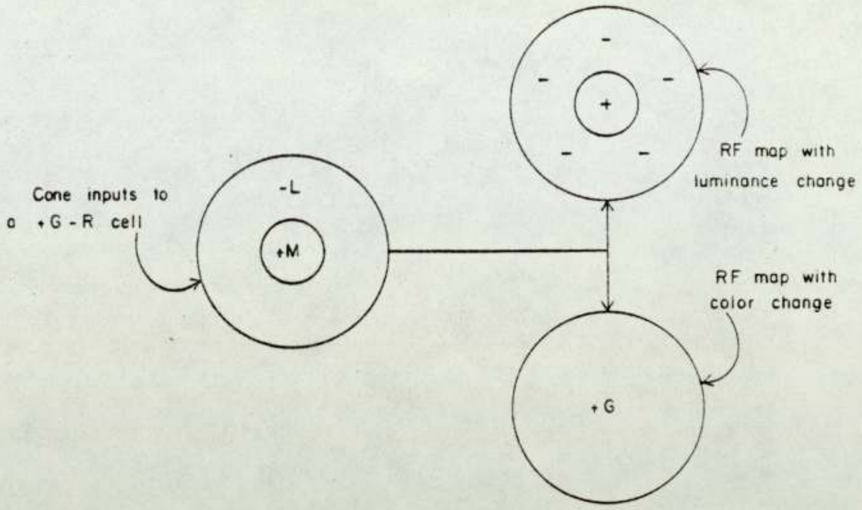


Fig. 1 Receptive field map for a spectrally opponent cell that also shows spatial opponency. Such a cell responds to both luminance changes and colour changes, but with entirely different receptive field maps for the two types of stimuli. When mapped with a luminance change, the cell shows a spatial antagonism and a RF like a +Wh -Bl cell; when mapped with a colour change the RF is uniform in sign, the cell firing to a shift toward green (and inhibiting to red) anywhere in the field.

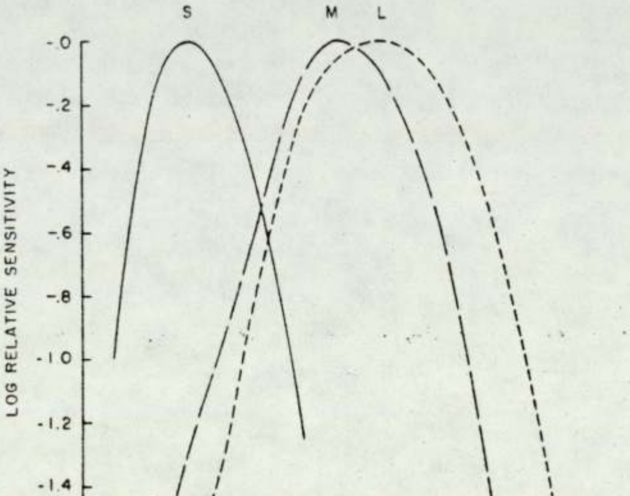


Fig. 2 Normalized absorption curves for the three cone pigments in the macaque monkey (and human) eye. Based on spectrophotometric, physiological, and psychophysical evidence.

3. Spectrally Opponent Organisation

At least two different receptor types containing pigment of different spectral sensitivity are necessary as a primary requisite of colour vision. A photon of light, which isomerises a pigment molecule, initiates the chemical events leading to neural activity. The degree of isomerisation depends upon light intensity, but is completely independent of its wavelength. A photopigment can only signal the number of photons captured, but information regarding the wavelength of light may only be obtained by comparing the activity of two or more receptor types. A neurological system facilitating such comparison is also essential.

Cells found to exhibit differential spectral sensitivity are not immediately identified as responsible for mediating colour vision responses because many animal and plant cells demonstrate such characteristics. Obviously identical responses for different wavelengths may be produced by adjusting their intensities. Cells may only be distinguished as responding to colour if response differences for specific wavelengths are maintained with a change in intensity. Similarly a multiple cone input to a single cell, viewed in isolation, does not suggest that the cell is involved in colour processing. Spectrally non-opponent cells (spatially opponent cells) is the macaque although completely colour blind (DeValois and Jacobs, 1968) demonstrate a spectral sensitivity shift following chromatic adaptation (Wiesel and Hubel, 1966). This merely indicates that at least two cone types have inputs to the cells. A cell involved in extracting movement information would also be expected to have a multiple cone input.

The discovery of midget miniature bipolar cells linking each individual cone to a single ganglion cell by Polyak (1941) suggested the existence of an exclusive link between each foveal cone and a single cortical cell (Polyak, 1957). Recent work in visual physiology and microanatomy, including studies outlined about opponent processes, suggest that the transfer of unprocessed visual information does not occur.

3(i) Introduction

Although many animals possess excellent colour vision, particularly fish and birds, rather rudimentary colour perception is found in cats (Mello and Peterson, 1964; Sechner and Brown, 1964), rats and dogs (Daw, 1973). Since oil droplets covering the retinas of birds act as colour filters, and the retinal structure of fish also differs considerably from our own, comparisons are of limited value. Close similarities between the colour vision of macaque and that of man have been demonstrated by their performance of visual psychophysical tasks evaluating spectral sensitivity, purity discrimination, wavelength discrimination, anomaloscope tests and spatial frequency discrimination (DeValois et al., 1974; DeValois and Morgan, 1974). It would therefore appear that there are close anatomical and behavioural similarities between the mechanisms for colour perception in macaque and man. Hence the results of physiological studies carried out upon macaque may be related to the psychophysical results found in man.

3(ii) Retinal Structures

Following the proposal of the trichromaticity theory by Young (1807), colour vision in primates could be ascribed to the presence of three receptor types each containing a different photopigment. Other possibilities existed, including the concept of more than three receptor types combining to form three individual colour pathways to the brain; or that more than three pigments were present combined into three receptor types.

The situation has been clarified in the primate by Marks, Dobelle and MacNichol (1964) who, using a spectrophotometric approach, found three separate pigments having broad spectral sensitivity and peak absorptions in the region of 445, 535, and 570 n.m. Results suggested that each cone possessed only a single pigment. Later Wald and Brown

(1965) suggested that some cones may contain two long-wavelength pigments.

Selective chromatic adaptation was used by Stiles (1959) to reveal in partial isolation the activity of a single cone. This technique was used by other workers to reveal three distinct spectral sensitivity functions relating to photopigments having absorption peaks at 445, 540, and 570 n.m. respectively (Wald, 1964; DeValois, 1965; Abramov, 1968). These exhibited close similarity to three of Stile's five curves for his π_1, π_4, and π_5 mechanisms.

Reflection densitometry performed on protanopes and deuteranopes at the fovea, where few cones responding to short wavelengths are known to exist (König, 1897), enabled Rushton (1963, 1965) to ascertain the absorption maxima for two pigments. These were located at 540 and 570 n.m. and were found to have broad spectral sensitivity. High background noise levels, resulting from scattering of short wavelengths and interference from absorption by rods, prevented Rushton from using this technique for cones having a maximum absorption in the blue end of the spectrum.

Many psychophysical experiments give similar results to those already outlined (Pitt, 1944; Willmer, 1955) suggesting the existence of three cone pigments having peak absorptions at approximately 440 - 450, 530 - 540, and 560 - 570 n.m. A study has been carried out on a rare family of monochromats who appear to possess cones only sensitive to short wavelengths (Blackwell and Blackwell, 1961). Such cones have a spectral sensitivity function peaking at approximately 440 n.m. The best estimate of the absorption curves (Vos and Walraven, 1971) is given in Fig. 2.

Each cone type exhibits a broad spectral sensitivity, the absorption maxima of the so-called "red" and "green" cones being very closely situated. The "red" cone pigment actually has a maximum absorption at 570 n.m., in the green region of the spectrum.

Terminology such as "red receptor" or "green receptor" is obviously ill-defined since it implies that activation of these receptors signals "red" or "green" to successive cells in the visual system. DeValois (1973) has sensibly advocated the use of the terms "L cone" (containing long-wavelength absorbing pigment), "M cone" (medium), and "S cone" (short) to denote cone types containing 570, 540 and 445 n.m. λ max. pigment. This terminology has been suggested for receptors in primates and comparable receptors in other animals. It can be seen that these short, useful terms offer advantages over the existing imprecise and, confusing descriptions of cone types. These will, therefore, be employed in future descriptions of cone types.

3(iii) Central Structures Involved in Colour Processing

Four clearly defined pathways exist by which visual information passes from the retina to central structures : to the lateral geniculate body thence to the striate cortex; to the superior colliculus; to the pretectal area; and to the accessory optic nuclei. Only transformation of colour information occurring at the lateral geniculate has been investigated in any detail and little is known about processing beyond that level, although much of this is thought to take place before the cortex. Evidence for this is found in monkeys in which cortical lesions produce defects in colour discrimination (Klüver, 1941; Weiskrantz, 1963) and ablation of the visual cortex results in retrograde degeneration of the lateral geniculate following severance of many of its cortical axons. Destruction of the superior colliculus has not been found to cause similar loss (Anderson and Symmes, 1969). Many workers have found evidence of colour information being transmitted along the geniculo-striate pathway (DeValois et al., 1958, 1966; Lennox-Buchthal, 1961; Andersen et al., 1962; Jacobs and DeValois, 1965; Wiesel and Hubel, 1966; Hubel and Wiesel, 1968). The superior colliculus in the squirrel monkey has been reported to receive colour information (Wolin et al., 1966), and up to 14% of the cells have been found to be colour coded (Kadoya and Massopust, 1970).

3(iv) Types of Colour-Specific Cells

Svactichin (1956) using microelectrode techniques on the fish retina at the horizontal cell level, obtained responses which were dependent upon the wavelength of the incident light. The recorded potentials were designated S-potentials and were found to consist of two types depending upon the retinal depth at which they were recorded; an L-type responding equally for all wavelengths and therefore regarded as a luminosity response, and a C-type giving spectrally opponent responses, therefore regarded as transmitting a colour response (Svactichin and MacNichol, 1958). Later, using single-cell recording techniques in the lateral geniculate nucleus of macaque, DeValois et al., (1958) demonstrated the presence of spectrally opponent cells. Depending upon the cell type excitation would be obtained from red stimuli and inhibition from green. These spectrally opponent responses were maintained over broad intensity ranges, the response being totally dependent upon wavelength (DeValois, 1960, 1965; DeValois et al., 1966; Wiesel and Hubel, 1966; Gouras, 1968). DeValois et al., (1966) and Abramov (1968) presented evidence for the existence of four categories of spectrally opponent cells. The first may be described as a green excitatory red inhibitory cell, designated + G - R, displaying maximum excitation at about 500 n.m. with maximum inhibition at approximately 630 n.m. Another group described as + R - G, red excitatory and green inhibitory, gave maximum inhibition in the region of 500 n.m. whilst responding with maximum excitation in the region of 650 n.m. Two other groups of cells responded in an identical opponent manner to blue and yellow. These were accordingly designated + Y - B and + B - Y, the former responding to wavelengths in the yellow region of the spectrum with excitation, whilst inhibiting with blue. The latter responded in the opposite fashion. The results are shown in Fig. 3 . Interestingly, these mechanisms confirmed the

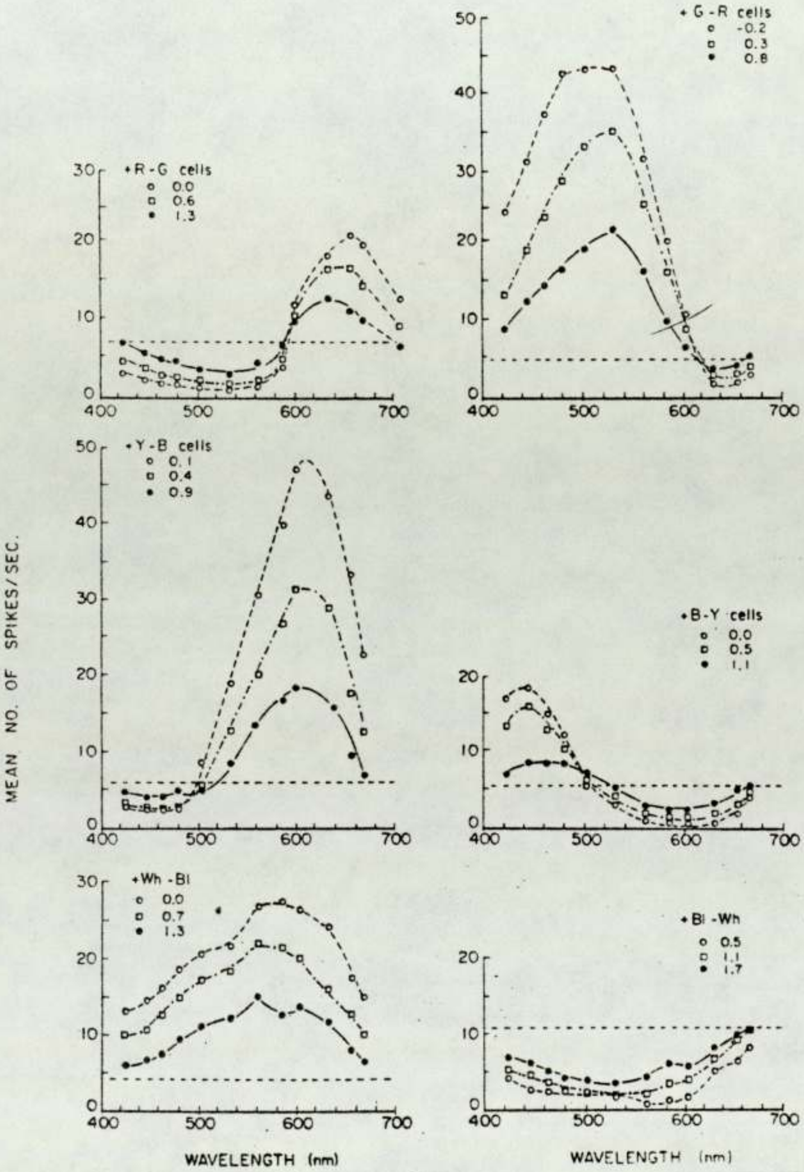


Fig. 3 Average responses of LGN cells. Plots of the average response rates of macaque LGN cells of four spectrally opponent and two non-opponent cell types. The three curves in each case are the responses to different luminance levels, the neutral densities used being indicated.

original mechanism for colour perception proposed by Hering (1878). Similarly the existence of such an opponent-process mechanism was postulated by Hurvich and Jameson (1957).

DeValois (1973) noted that in an earlier paper (DeValois et al., 1958) some cells were found responding to narrow spectral regions with excitation alone and resembled the modulators found by Granit (1947) in various animals. DeValois has ascribed this to high noise levels present in early recordings made by DeValois et al., (1958) which made the detection of inhibition difficult. It is therefore suggested that Granit's results arose in a similar manner.

The proportion of cells in the parvocellular layers related to the central retina which are spectrally opponent have been determined in the macaque as 70% by DeValois et al., (1966) and 84% by Wiesel and Hubel (1966).

Colour opponent cells in other species have been studied including the squirrel monkey (Jacobs and DeValois, 1965), spider monkey (Hubel and Wiesel, 1960), and the ground squirrel (Michael, 1968; 1971). The proportion of opponent cells (less than 25%) found in these species was much lower than that in macaque, and inferior colour vision has been advocated as a reason for these differences.

3(v) Cone Inputs to Spectrally Opponent Cells

There is general agreement that the cone inputs for the red-green spectrally opponent system (+ R - G and + G - R) arise from long and medium wavelength sensitive cones (L and M type) (DeValois et al., 1963; DeValois, 1965; Wiesel and Hubel, 1966; Abramov, 1968). The opponent cell firing rate is not dependent upon the extent of excitation provided by one cone type and the inhibition provided by the other, but upon the relative difference in the activity of the cone outputs at each spectral point. The spectrally opponent mechanism separates the maximum spectral responses of the underlying cone types. Although L and M type cones respond maximally at 570 and

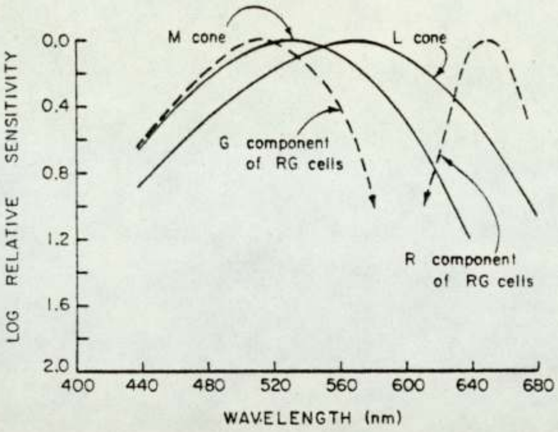


Fig. 4 Cones and opponent colour cells. The spectral absorption curves of the macaque and human L and M cones are shown in the solid lines (these curves are based on 535 and 570 peaks and fitted to the Dartnall nomogram. Other estimates would give somewhat narrower curves). The dotted lines represent the spectral sensitivity curves for the R and G components of the macaque RG opponent cells (based on the amount of light required for a certain criterion firing rate under neutral adaptation conditions). Note that the cone peaks are close together, but the peaks of the R and G functions are further apart as a result of the subtractive interactions between the cone inputs to them.

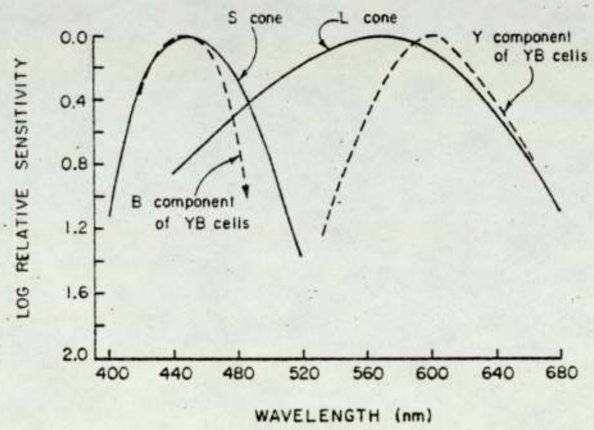


Fig. 5 Same as Fig. 4 except that the S and L cone curves are compared with the B and Y components of the YB cells. Note that since the cones which feed into the YB system lie far apart in the spectrum, the displacement of the opponent-cell peaks is not as great as that seen in the case of the RG cells.

540 n.m. respectively, the maximum responses for the red-green opponent system lie at 640 and 520 n.m. Both L and M cones are sensitive in the greenish-yellow region, but minimal differences in their spectral sensitivity make the red-green opponent system relatively insensitive to these wavelengths.

The problem of cone type input into the yellow-blue system remains unresolved. Although one is certainly from the short-wavelength sensitive (S-type) cones, the second input may be from L- or M- type cones or both.

The second input has been suggested to be an M- type cone by Wiesel and Hubel (1966). They employed a chromatic adaptation technique, coupled with the use of small monochromatic test spots, enabling the stimuli to be confined to one part of the lateral geniculate receptive field, effectively restricting it to one cone type.

DeValois (1965) and Abramov (1968), however, have argued that L-type cones provide the second input to the yellow-blue opponent system. Abramov (1968) ascertained the spectral sensitivity curve for a large sample of yellow-blue opponent cells and found a reduction in sensitivity to the long wavelengths more closely resembling the fall in sensitivity of an L-type cone pigment. Similarly the spectral responses of the yellow-blue system can be more closely predicted on a basis of S- and L- type cone type inputs.

Rod input to both spectrally opponent and non-opponent cells of the macaque lateral geniculate has been postulated (DeValois, 1965; Wiesel and Hubel, 1966). This appears consistent with both the anatomy of the visual pathway as well as psychophysical results for extrafoveal colour vision. Polyak (1957) found no separate rod pathways to the brain, but found that extrafoveal ganglion cells received inputs from both rods and cones. Clarke (1963) found extrafoveal colour vision to be tetrachromatic rather than trichromatic supporting the concept of rod involvement. Rods

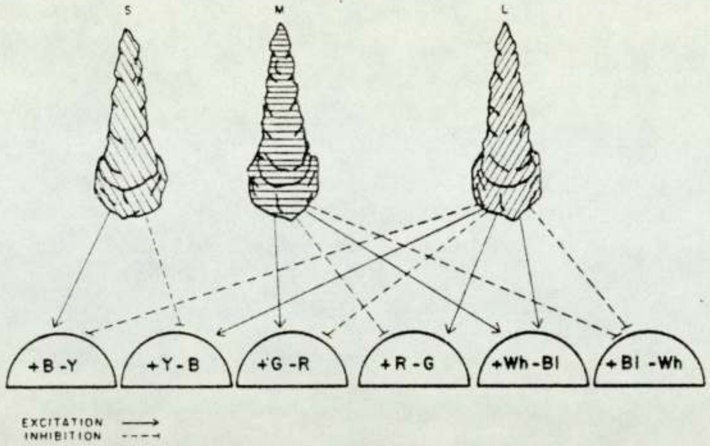


Fig. 6 A model of how the three cone types interact to form the six LGN cell types. Note that L cones feed into all pathways.

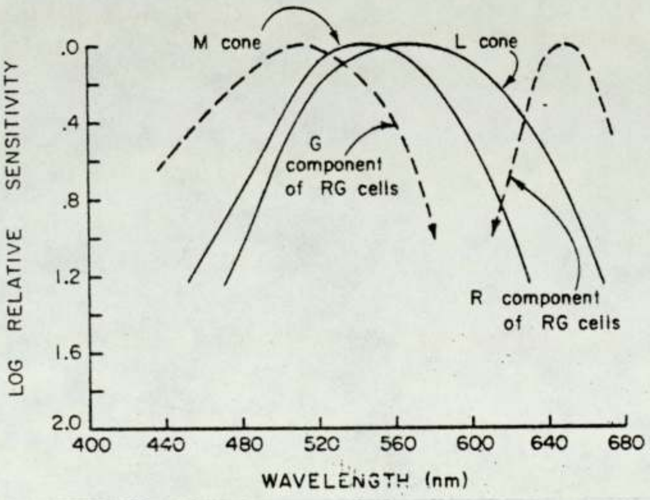


Fig. 7 An indication of how the excitatory-inhibitory interaction between L and M cones in the RG opponent cells leads to a narrowing of the spectral response curves and a shift toward the spectral extremes. The cones absorb all across the spectrum and both peak at middle wavelengths (greenish-yellow); the RG cells by differencing their outputs respond to only narrow spectral regions, peaking at 500 n.m. (green) and 640 n.m. (red).

have been found to de-saturate extrafoveal stimuli (Lie, 1963). Longer latencies for rods than cones have been found, suggesting that when activated cones may block the activity of rods. (Gouras, 1965; Gouras and Link, 1966).

3(vi) Spatial Organisation of Spectrally Opponent Receptive Fields

The receptive field characteristics of the spatially opponent mechanism have earlier been outlined. Spectrally opponent cells exhibit certain similarities in their spatial arrangement although their organisation is a little more complex.

Wiesel and Hubel (1966) found that 77% of cells in the dorsal layer were spectrally opponent, receiving an excitatory input for the cone centre and inhibitory input from the opponent cone type for the surround. Similar systems were found possessing inhibitory centres and excitatory surrounds. These receptive fields were designated Type I. The greatest number of these were red-green opponent cells. A few cells were found having a centre excited by short wavelengths and a periphery inhibited by yellow. None of the reverse systems were found.

A second type of spectrally opponent cell (Type II) was found, where the two cone inputs possessed identical spatial distribution throughout the whole receptive field. At every point in the receptive field excitation and inhibition is therefore balanced. Equal proportions of red-green and yellow-blue cells were found, the total accounting for 7% of dorsal cells. The remaining 16% of cells were found to be spectrally non-opponent.

Wiesel and Hubel (1966) considered Type I cells to receive inputs from completely discrete spatial distributions of the opponent receptor types. Overlapping distribution of receptors were considered to give rise to Type II spectrally-opponent cells. Michael (1968) working on the ground squirrel optic nerve and lateral geniculate suggested two similar divisions.

The existence of spatially discrete receptors at a retinal level, giving rise to an established centre-surround organisation found in spectrally opponent and non-opponent cells, must be questionable. Hartline (1940) demonstrated that the size of a receptor field in limulus was dependent upon the luminosity of the stimulus. A more plausible explanation, that receptors may overlap in their differential sensitivity, has been suggested.

Wagner et al., (1963), working with goldfish, found that by adapting the centre response the surround response could be recorded across the whole receptive field. The surround response appeared most sensitive at the receptive field centre.

The work of Rodieck and Stone (1965) allowed them to postulate the existence of two overlapping Gaussian spatial distributions for spectrally non-opponent cell inputs. The centre distribution was regarded as highly peaked and having a small variance, whereas the surround distribution was considered to be flatter with a much larger variance. This model therefore agrees with that for spectrally-opponent cells suggested by Wagner et al., (1963).

The work of Wagner et al. was confirmed by Mead (1967) working on lateral geniculate cells in the macaque. Also using chromatic adaptation, Mead recorded the surround response across the whole receptive field and similarly found the largest response at the centre.

Wiesel and Hubel (1966) suggested the limiting case when one cone could provide the input for the receptive field centre. DeValois (1973) pointed out, however, that the line spread function of the eye (Westheimer and Campbell, 1962) would prevent the stimulation under normal circumstances of a single cone and a functional overlap would occur.

Daw (1967) suggested that the spectrally opponent organisation was the reverse of that required to explain simultaneous colour contrast. Using very large spots and annuli Daw (1967, 1968) found evidence for surround effects which extended over a much larger retinal area than had been previously found. The far surround gave opponent colour responses which were opposite to the central stimulation. Although DeValois and Jones (1971) found a cell in the macaque lateral geniculate which displayed simultaneous colour contrast, similar cells found by other workers have been regarded as too small to produce long distance colour interactions (Hubel and Wiesel, 1968; Michael, 1973).

3(vii) Receptive Field Size of Spectrally Opponent and Non Opponent Cells

Receptive field size was found to vary by Wiesel (1960). Their size depends on retinal location increasing with distance from the fovea (Wiesel and Hubel, 1966; Mead, 1967). The total size of the receptive field is difficult to ascertain since the sensitivity of the surround falls gradually with distance from the centre. The field centre diameter is more easily measured since it has a more clearly defined cut-off point.

Determining the size of spot producing the largest centre response enabled Hubel and Wiesel (1966) to determine the receptive field centre diameter. They reported that sizes for spectrally non-opponent cells varied from 8 to 60 minutes of arc, with a median of about 30 minutes of arc. The field sizes for Type I spectrally opponent cells varied from about 2 to 60 minutes of arc, with a median of about 8 minutes of arc. Type II opponent cells appeared slightly larger, having a range of sizes between 15 and 60 minutes of arc. Mead (1967) obtained similar values to those of Hubel and Wiesel.

Parallels may be drawn between electrophysiological results for receptive field diameters and perceptive field diameters estimated in man using visual contrast phenomena. A contrast grid was first used by Baumgartner (1960) who estimated that the receptive field centre at the fovea subtended 5 minutes of arc. Later Spillman (1971) estimated a figure of 18 minutes of arc for the centre and surround of a receptive field using a Herman grid. Jung and Spillman (1970) found that in the peripheral retina perceptive fields were much larger, their mean diameters increasing linearly between 20 and 60 degrees of eccentricity. Field centres are found to double in size over this range, from 90 to 180 minutes of arc. They found no significant difference in size between Wh + Bl - and Bl + Wh - systems, although Hubel (1960) as well as Fischer and May (1970) reported slightly larger centres for Bl + Wh - cells in animals.

3(viii) The Role of Spectrally Opponent Cells in Colour Vision

Spectrally opponent cells are clearly involved in colour vision, evidence has been fully reviewed by DeValois and DeValois (1975) and may be summarised as follows:-

(i) Spectrally opponent cells in the lateral geniculate can distinguish between two different wavelengths even though luminance differences are present, although spectrally non-opponent cells distinguish only luminance differences (DeValois, 1971).

(ii) Close similarities are found between the discrimination ability of spectrally opponent cells and the typical spectral sensitivity curve as found by Judd (1932) (DeValois, Abramov and Mead, 1967).

(iii) Behavioural tests have demonstrated that the macaque has an identical purity discrimination function to that of normal human observers (DeValois and Jacobs, 1968; DeValois, Morgan and Snodderly, 1974). Single cell studies in the macaque lateral geniculate have suggested that the spectrally opponent mechanism is responsible for this (DeValois, Abramov and Jacobs, 1966; DeValois and Marrocco, 1973).

(iv) There is close agreement between the firing rates of spectrally opponent cells found by DeValois, Abramov and Jacobs (1966) and the subjective responses to monochromatic light illustrated in the colour naming techniques (Boynton

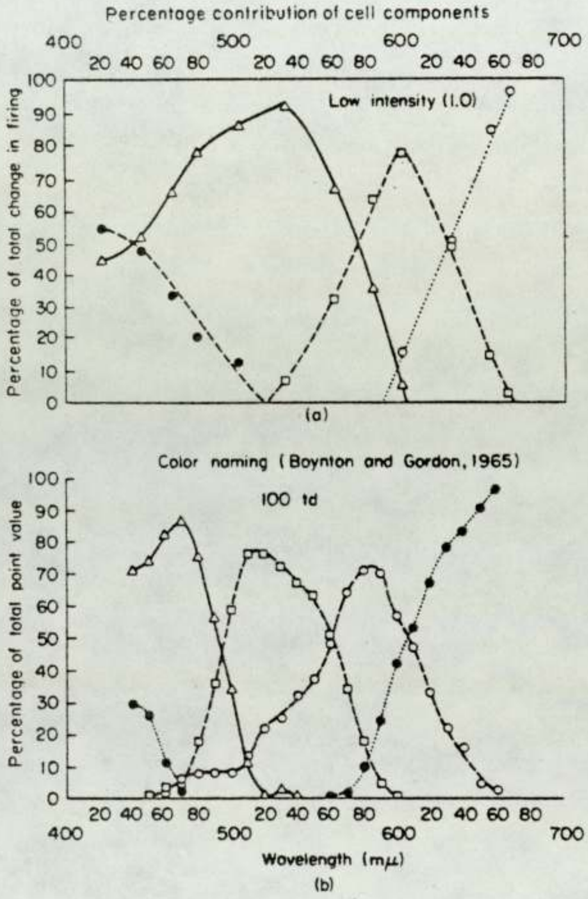


Fig. 8 Comparison of the colour names given spectral lights by human observers (bottom) with percentage of the total opponent cell firing-rate contributed by each of the four opponent cell types. At long wavelengths the agreement is good, knowing that the + R - G cells fired far more to a stimulus than any other cell type, one could predict that a human observer would see it as red, etc.

and Gordon, 1965; Jacobs and Gaylord, 1967). The colour-naming technique attempts to quantify subjective responses to wavelength, by asking subjects to describe a monochromatic wavelength using one of the four colour names; red, yellow, green, or blue. Their description may be modified by another name selected from the same group. A point system is used for scoring and plotting the results. The validity of this technique will be discussed later.

(v) Stimulus after effects are known to influence the brightness or colour of successive stimuli and are termed successive contrast effects. Recordings at the lateral geniculate have revealed such effects produced in spectrally opponent cells (DeValois and Jones, 1961).

(vi) Colour perception is influenced not only by stimulus characteristics, but also by the features of any stimulus which is simultaneously present in a surrounding region. This is termed colour contrast. Double opponent cells located in the fish retina have been suggested as a basis for colour contrast (Daw, 1968). Similar cells have been found in monkey cortex, but their small fields fail to account for the long distance colour interactions that are observed (Hubel and Wiesel, 1968; Michael, 1973). Yund (1970) has tentatively proposed a model based on coloured edge detectors, but supporting physiological evidence is, as yet, weak.

Spectrally opponent mechanisms, therefore, appear to provide the basis for colour perception, but they are not the only group of highly specialised cells to be found in the visual system. Evidence suggests that a group of cells exist possessing similar highly specialised reception fields which respond to moving stimuli. It has been further suggested that activation of these cells by alternating stimuli is responsible for the phenomenon of beta motion.

CHAPTER IV

Movement Sensitive Neurones

1. Introduction

Recent work has suggested that many cells in the mammalian visual pathway possess specialised receptive fields enabling them to detect the motion of a stimulus. When recording the activity of single cortical cells in the cat, Hubel (1959) found that a moving spot of light produced a stronger response than a stationary one. The response was sometimes greater for movement in one direction than for the opposite. Cells in the retina or lateral geniculate produced about the same response regardless of the direction in which the stimulus was moved. Optimum rates of movement varied from one cell to another, thus both the direction and rate of a moving stimulus was often critical when recording cortical cells (Hubel and Wiesel, 1959, 1962). Some of Hubel and Wiesel's "complex cells" adapted so rapidly to a stationary form that continuous movement of the stimulus proved the only way of obtaining a sustained discharge. Movement sensitive cells have been located in the rabbit retina (Barlow and Hill, 1963), a large proportion of which (about 41%) exhibit directional sensitivity (Barlow, Hill and Levick, 1964) closely resembling that found only in cortical cells of the cat (Hubel and Wiesel, 1962). Since the rabbit possesses very little binocular vision, processing for movement detection may occur earlier in the visual pathway. Discrete spot stimuli presented sequentially within the receptive field are capable of firing movement-sensitive cells (Barlow and Levick, 1965). Maturana and Frenk (1963), working on the pigeon retina, had earlier found that if a spot stimulus was flashed in one retinal position and moved to another location after

Hypercomplex cells appear as complex cells but possess some of the characteristics of simple cells. The cells had an approximately square central activation region flanked by a weak antagonistic region. The length of the line stimulus as well as other stimulus characteristics are therefore important because of the antagonistic surround to the cell (Hubel and Wiesel, 1967).

4. Classification of Movement Sensitive Neurones

4(i) Introduction

The work of Hubel and Wiesel, outlined above, suggests that complex cells in the cortex act as motion detectors. Grüsser and Grüsser - Cornehls (1973) consider that the existence of movement sensitive neurones has been established, and that activation of these by stroboscopically presented stimuli provides the basis for apparent movement. They are careful to distinguish between a movement-sensitive and a movement-specific visual neurone. A movement-sensitive visual neurone is defined as a cell which responds to a natural moving visual pattern, producing a stronger response than that for a stationary stimulus even when optimal spatial and temporal frequencies are employed. A movement specific neurone is defined as a unit which is activated or inhibited only by moving stimuli and fails to respond to a stationary stimulus.

Five main classes of movement detecting neurones may be distinguished (Grüsser and Grüsser - Cornehls, 1973) namely:

(a) Movement (M-) neurones which are movement-sensitive or specific and respond regardless of the direction in which the stimulus is moving.

(b) Movement-detecting neurones which are directionally selective (DS-neurones) exhibiting a preferred and a null direction. The cells respond optimally when a moving stimulus moves in the preferred direction, but respond minimally or not at all to stimuli which move in the null direction. Two subclasses are found . . .

(i) where the preferred and null directions are arranged at right angles to each other. (Hubel and Wiesel, 1962; Baumgartner et al., 1964, 1965; Cooper and Robson, 1968; Campbell et al., 1969).

(ii) where the null and preferred directions are separated by 180° (Guselnikov and Vodolazskij, 1968).

(c) Movement-sensitive neurones responding preferentially to moving stimulus patterns, the response depending on the spatial orientation of contrast borders relative to the visual field axis (OS-neurones). Much of the work of Hubel and Wiesel (1959, 1962, 1965, 1968) has been included in this group.

(d) Complex movement detecting neurones (CM-neurones) respond to a moving stimulus pattern impinging upon parts of its excitatory receptive field. In other sections of the same field stationary illumination elicits neuronal activation. Those movement sensitive neurones having irregularly arranged excitatory and inhibitory receptive fields would be included in this class.

(e) A group denoted as Z neurones, capable of responding to movement towards (Z+neurones) or away (Z-neurones) from the eye. Such neurones respond weakly, or not at all, to movement occurring perpendicularly to the Z axis.

Adopting this classification, it can be seen that some of the above groups are of particular interest and their characteristics will be reviewed in greater detail.

4(ii) Characteristics of Movement - and Directionally Selective-Neurones

Two classes of M-neurones were found by Humphrey (1968) in the rat superior colliculus. In the upper layer, small units having an excitatory receptive field of 2-15 degrees predominated. The optimal speed of a moving target for these was found to be 5 to 10 degrees per second. No response was obtained using faster stimuli. In the lower layer, larger excitatory receptive fields were found ranging from 30 to 90 degrees.

Similarly in the rabbit, deeper layers of the optic tectum were found to have larger excitatory receptive fields than superficial cells and these appeared to be directionally selective (Schaefer, 1966).

The excitatory receptive field size of movement-sensitive cells increases with depth in the superior colliculus of the cat (Straschill and Taghavy, 1966, 1967). The excitatory receptive field also increases with increasing distance from the area centralis in the visual field (Sterling and Wickelgren, 1969). The majority of movement-sensitive neurones (75%) in the cat are directionally selective. Movement-sensitive neurones have also been found in the tertiary visual cortex of the cat (Hubel and Wiesel, 1965, 1969; Dow and Dubner, 1969, 1971; Grüsser and Grüsser - Cornehls, 1969; Wright, 1969).

Movement-sensitive cells have been located in the primary visual cortex of monkey (Macaca mulatta) of which some have been classified as directionally selective (Wurtz, 1968, 1969, a, b, c; Hubel and Wiesel, 1968).

The spatial arrangement of the receptive field of the M-neurone is considered similar to the model outlined by Rodieck and Stone (1965) for spectrally non-opponent cells (Grüsser and Grüsser - Cornehls, 1968) (Fig. 9). Maximal excitation arises from the centre of the excitatory receptive field and falls toward the periphery. Inhibition appears greatest at the border between the excitatory

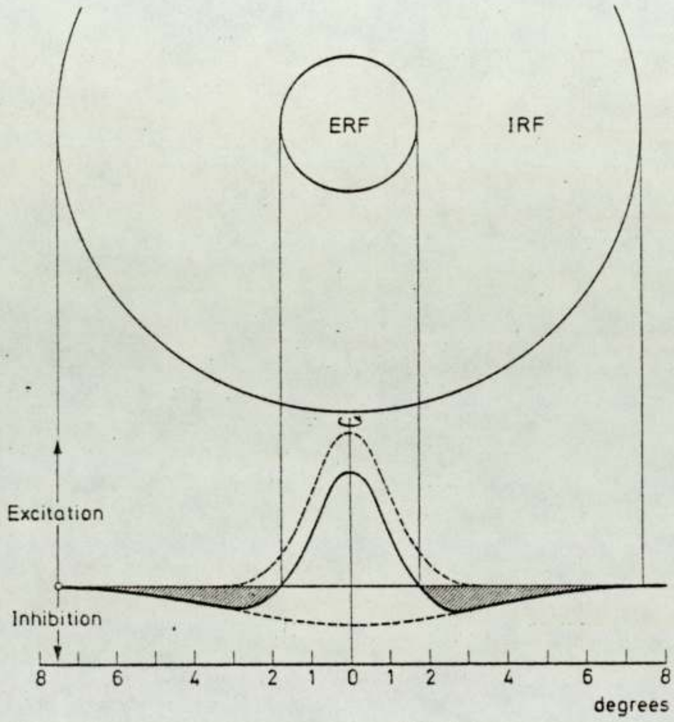


Fig. 9 Schematic representation of the distribution of excitation and inhibition elicited by stimuli moving across the ERF and IRF of movement detecting class 2 neurons in the retina of a frog.

and inhibitory receptive field and falls with increasing distance from the centre. Stationary patterns elicit no inhibition suggesting that optimal inhibition from the inhibitory receptive field arises only from a moving stimulus.

The concentric receptive field arrangement has been found to change in the cat's retina as the adaptation level shifts from the scotopic to the photopic range (Barlow et al., 1957; Domberg, 1971).

Ewert (1968) demonstrated that the toad's praycatching behaviour, normally elicited from small moving targets could also be produced when the object was illuminated stroboscopically. The work of Grüsser and Grüsser - Cornehls (1968) led them to conclude that M-sensitive neurones responded to a change in position occurring within their excitatory receptive fields. This corresponds to the apparent movement response. Some characteristics of M-neurones have been listed by Grusser and Grusser - Cornehls (1969) . . .

(a) They exhibit a short, transient response to local stimulation within their excitatory receptive field.

(b) Repetitive stimulation at the same location within the excitatory receptive field produces fast neuronal adaptation.

(c) Similar adaptation occurs when a stimulus passes repeatedly along the same path through the excitatory receptive field.

(d) They respond to stationary stimuli projected successively upon different locations within the excitatory receptive field, so producing apparent movement.

Movement-sensitive cells which are directionally sensitive have been found in all parts of the afferent visual system of mammals (Barlow and Levick, 1965; Michael, 1966, 1968; Straschill and Taghavy, 1967). Although found in restricted regions of the cat retina (Stone and Fabian, 1968) they have not been detected in the monkey retina (Hubel and Wiesel, 1968). The retina and lateral geniculate of higher mammals appears to be mainly involved with contrast and colour processing.

The importance attached to stimulus size in triggering a DS-cell indicates the presence of a strong inhibitory receptive field surrounding it. Evidence indicates that certain DS-cells lose their directional sensitivity for fast moving stimuli and exhibit a reduced sensitivity to contrast stimuli moving through the excitatory receptive field in small steps.

A positive correlation has been found in the rabbit between receptive field size for DS-neurones and the maximum stimulus velocity which elicits the greatest response (Barlow et al., 1964).

Directionally selective neurones in the rabbit and squirrel retina have been found to respond to apparent movement stimuli (Barlow and Levick, 1965; Michael, 1966, 1968). Two stimuli projected alternately onto the excitatory receptive field with a time delay interposed, produce a strong movement response. A strong response is obtained if succession of stimuli occurs in the preferred direction, and inhibition occurs with reversal. Asymmetric conduction of inhibition has been suggested to account for this, alternatively lateral excitation may be controlled by neurones which act as gates. Apparent movement therefore appears to be a sufficient stimulus to trigger both M and DS neurones.

Directional selectivity is found to disappear with low flash frequencies (less than eight per second). Thus directional selectivity depends on the angular velocity of the stimulus (Barlow et al., 1964; Oyster, 1968). The link between the spatial separation of stimuli falling within the excitatory receptive field and the inter-stimulus interval has allowed the conduction velocity and extension of unilateral inhibitory sub-units to be calculated. Values ranging from 0.8 to 2 degrees have been found (Grüsser and Grüsser - Cornehls, 1973). It is generally assumed that either DS-neurones themselves possess movement-sensitive properties, or movement-sensitive cells must exist between the level of receptors and DS-neurones.

4(iii) Additional Movement-Sensitive Neurone Types

Movement-sensitive neurones which respond to the spatial orientation of a contrast border (OS-neurones) may be mentioned since they possess many of the characteristics of M- and DS- neurones. Although responding optimally to a suitably orientated border pattern, they fail to respond to a small stationary spot projected onto their excitatory receptive field (Grüsser, 1969). It would therefore seem unlikely that stimuli used in the present study are capable of eliciting responses from OS-neurones. Similarly the highly complex movement-sensitive neurones (CM-neurones) possess far more complicated response characteristics than OS-neurones (Grüsser and Grüsser - Cornehls, 1970). Highly specific stimulus characteristics are required in order to trigger a response from the cells and it would remain impossible to guarantee that contemporaneous stimulation of cells having simple stimulus demands was not occurring. Straschill and Hoffman (1969) found evidence for the existence of Z-neurones in the cat pretectum. The existence and characteristics of such neurones does not directly impinge upon this present study, in which apparent movement occurring in the Z axis has not been investigated.

CHAPTER V

Apparatus and Method

Literature, outlined earlier, has described how apparent movement is produced when two closely situated stimuli are alternated. The following characteristics of this response were investigated. Two small alternating stimuli of similar form and colour, whose temporal characteristics could be altered, were presented to the subject against a black featureless background. This was intended to permit fine measurements of the spatial extent of optimal apparent movement over small areas of the visual field, in the absence of other complicating factors such as form or background. The maximum spatial threshold for optimal apparent motion may be determined for different pulse durations using stimuli of different monochromatic wavelengths, so investigating the role played by temporal factors as well as colour in beta motion. Hence the temporal characteristics, as well as the relative spatial location of the two stimuli, must be specified with accuracy. In addition the apparatus should facilitate temporal overlap and separation of stimuli. The apparatus was, therefore, designed with the above factors in mind.

2(i) Haploscope Construction

A specially constructed haploscope as described by Hill and Yorke (1973) provided the basis for the present apparatus (Fig. 10). This ensured complete dissociation of the stimuli so that they might be spatially separated or perfectly superimposed. Glass plates inclined at 45 degrees to each other were placed before each eye allowing stimulus to be seen binocularly, whilst stimuli A and C

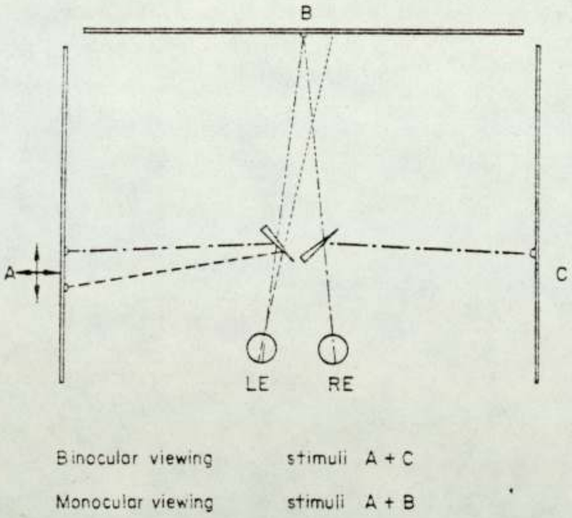


Fig. 10 The method by which the stimuli were presented to the observer is shown above. Stimuli A and B were seen by the left eye. Stimulus C consisted of a fixation spot.

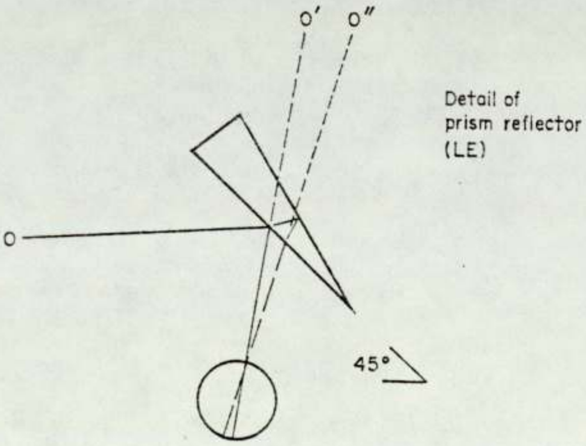


Fig. 11 The method of displacing secondary reflections is shown above.

were seen by only the left and right eyes respectively following their reflection from the plates. Stimulus C was a fixation spot used for experiments necessitating eccentric fixation. Identical stimuli A and B were therefore seen monocularly by the left eye. One prism dioptre, base down, was incorporated into each glass plate so that secondary images were displaced clear of the primary image.

A matt black background was used for all experiments, care being taken to exclude extraneous light, the whole apparatus being sited in a darkroom. It was considered important that the comparitive effects of the stimuli should be viewed in isolation without having to consider the possible effects of background luminance. Uncertainties exist in any experiment involving colour vision mechanisms about the action that background luminance has upon different receptor types. The use of a neutral grey or white background does not escape this problem. Further, in later experiments involving measurements of apparent movement eccentrically, it was considered important that the effect of any rod involvement should be seen.

A peripheral fusion lock, in the form of two white crosses situated 10° above and below stimulus B, was made available. Normally invisible, these could be made to fluoresce by illuminating them with long wavelength ultra-violet light without substantially altering the viewing conditions.

Careful manipulation of the left glass plate allowed the stimuli A and B to be perfectly superimposed, whilst two vernier gauges mounted along the X- and Y- axes were set to zero. Thereafter the location of A relative to B anywhere in the visual field could be specified in terms of its X-Y co-ordinates.

A simple chin-rest was provided for the subject, complete with forehead-bar and padded temple supports, which allowed the head to be held firmly within the apparatus. Although slight head movement was possible, this method was considered the most comfortable for use by the subject undergoing prolonged testing.

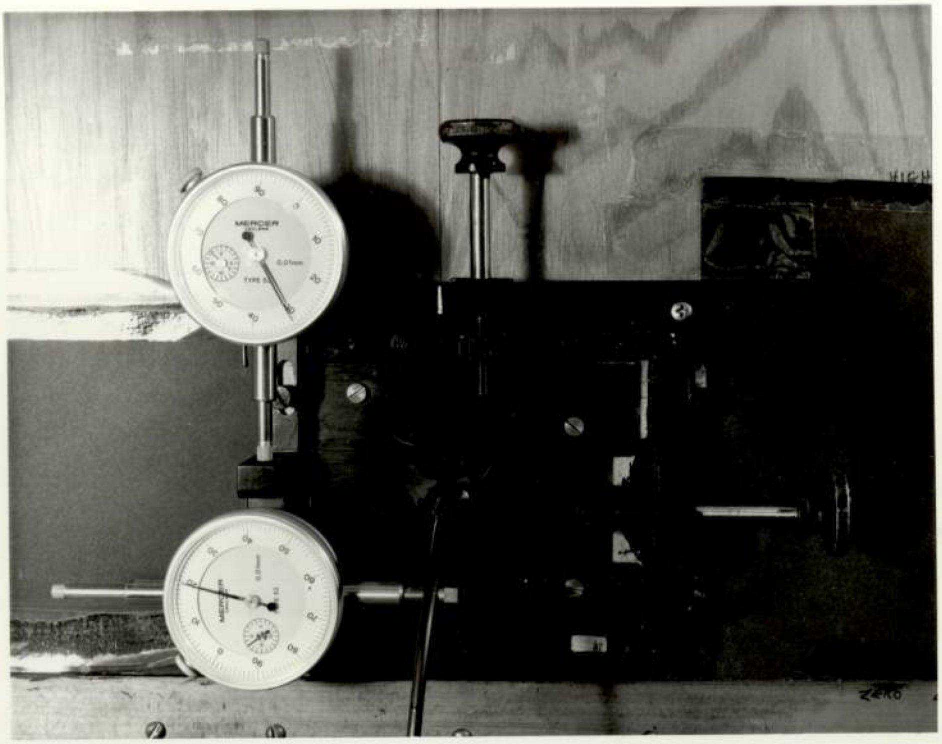


Fig. 12 The vernier gauges used to determine the spatial location of Stimulus A.

2(ii) Stimuli and Presentation

The mechanism used to produce the alternating stimuli is shown in Fig. 13. The stimuli presented to the eye are formed from the masked ends of an incoherent fibre optic bundle, which transmits light from a 12 volt, 100 watt quartz-iodine source interposed between which are a series of narrow-bandwidth interference filters.

The individual characteristics of the Grubb-Parsons (Narrow Band Type 1) filters are listed in appendix 1. The filters span the range 420 to 680 n.m. at 20 n.m. intervals, their mean bandwidth being 4.7 n.m. Heterochromatic stimuli are equated for the standard C.I.E. observer using a two log unit neutral-density wedge interposed between the interference filters and source. A calibrated "spectra" mini-spot photometer is used for this purpose and mounted a distance of 220 m.m. from the source such that its filament completely fills the central 1° ring of the photometer. Early observations had revealed slight variations in the spectral emissions of the source occurring within the first twenty minutes of running after which a steady state was arrived at. After the lamp had been allowed to run for twenty minutes, individual filters are placed before the source and the neutral-density wedge is adjusted to give a constant reading of 500 candelas per square metre. Six readings were used to establish the mean position for the neutral density wedge for each interference filter so equating them for photopic luminance. The data is listed in appendix 1. The light transmission for all the interference filters is recorded in the appendix. For filters having a maximum transmission of 460 and 480 n.m. the transmitted luminance is approximately 500 candelas per square metre. For the 440 and 680 n.m. filters the luminance of transmitted light reaches only approximately 250 candelas per square metre. The quartz-iodine source, although convenient, possesses obvious limitations

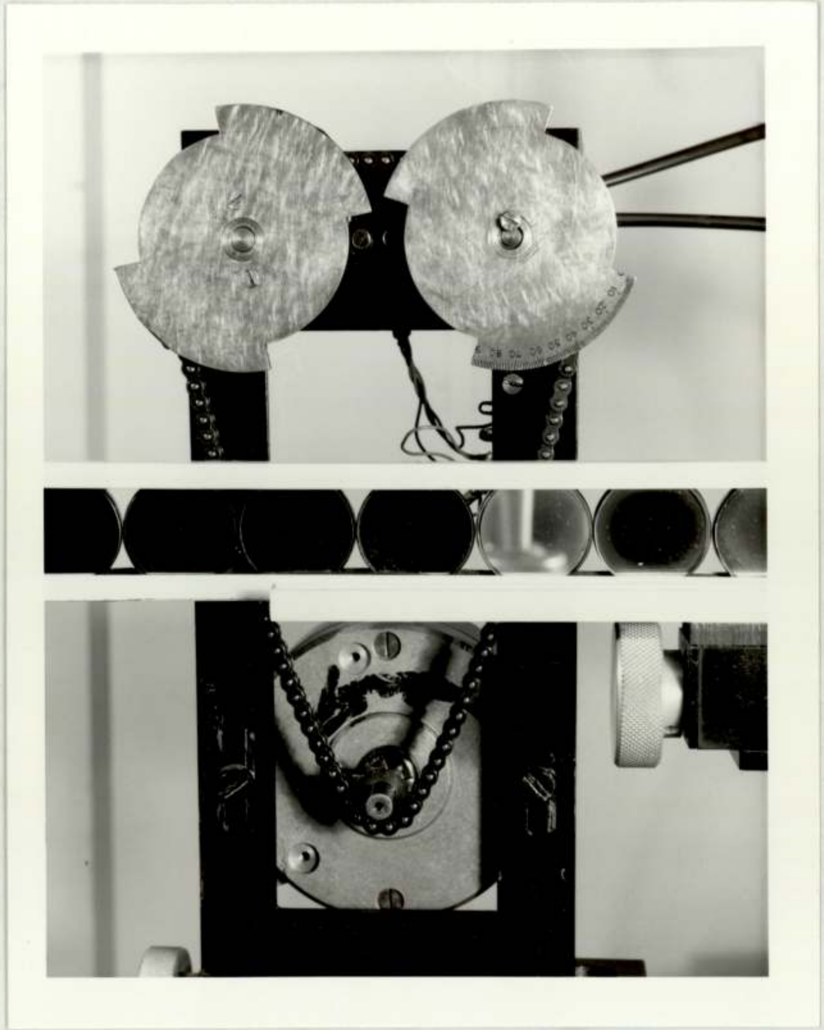


Fig. 13 The sector discs used on the apparatus and their chain drive are shown above. The ends of the two fibre optic bundles are seen behind the sector discs. The interference filters in their rack may also be seen.

in its output at spectral extremes. Increasing the brightness of stimuli restricts the spectral range over which it is possible to equate heterochromatic stimuli for luminance, and risks producing unwanted after-image effects. It was important, therefore, that stimuli should be maintained at the lowest luminance level at which they may be readily received by the subjects. This was established as being 500 candelas per square metre. A similar neutral density wedge was placed before one fibre optic bundle in order that adjacent stimuli could be subjectively equated for luminance. Two standard cobalt heat filters with a sharp cut-off point at 390 n.m. were incorporated into the apparatus.

The stimuli, seen 50 cms. from the observer's eye, consisted of a fibre optic bundle stopped-down to give an aperture of 0.3 m.m. subtending 2 minutes of arc. The 600 m.m. long fibre optic contained fibres of 50μ diameter constituting a bundle diameter of about 2.5 m.m. The transmission characteristics for a 1m. long fibre are given in Fig. 14.

Rotating sector discs, powered by a D.C. motor, generated a square stimulus waveform having a 1:1 light - dark ratio and enable alternation of the stimuli. The cycle time of the flashing stimulus, altered by adjusting the motor speed, is recorded by means of a light-sensitive diode mounted behind a single sector disc. The cycle time is then read directly from a digital display. Degree markings were engraved along one blade of the sector disc in order that relative displacement of the discs could be made, in order to alter the temporal overlap or separation of the stimuli. With the screw firmly tightened, the front plate was held firmly against the gear wheel and the roller-chain drive prevented any relative movement of the two freely rotating sector discs.

3. Subject Selection

A total of 18 university students, aged between nineteen and

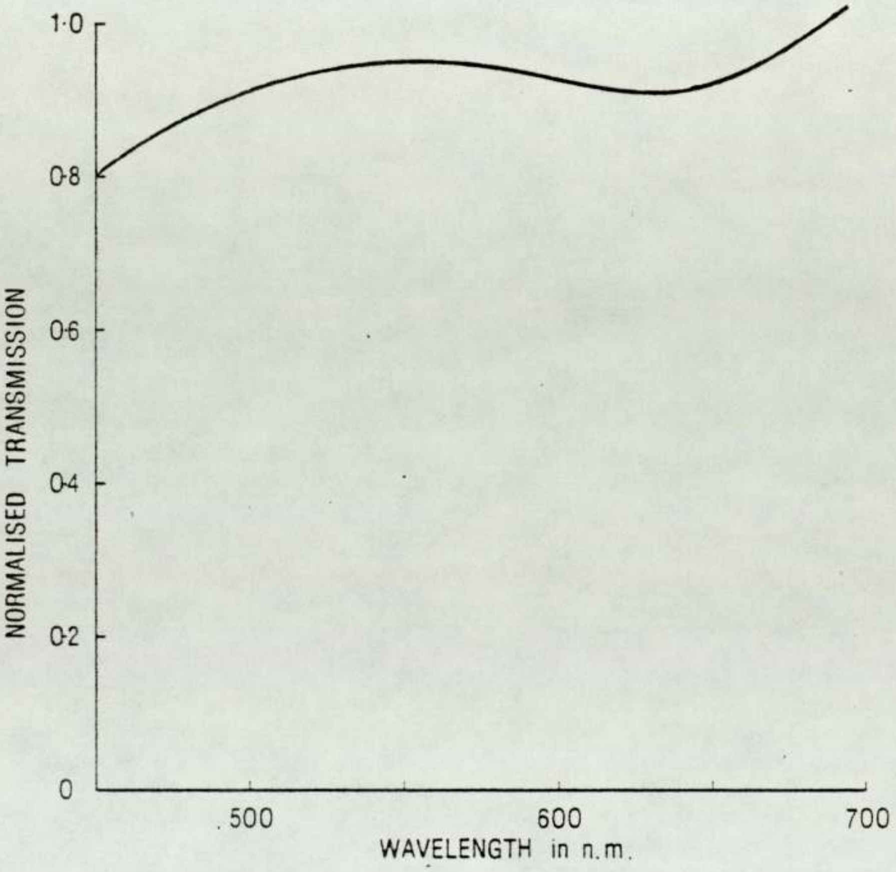


Fig. 14 Spectral transmission curve for 1m. long fibre optic light guide (Rank Optics Technical Publication).

twenty-one years, were approached to take part in the experiments. Only male subjects were used to avoid any complications which might arise being ascribed to the menstrual cycle of female subjects. Similarly, male subjects who were known to be colour defective were discarded. The following subject selection criteria were decided upon:-

(a) The presence of normal colour vision was established in subjects using both the American - Optical pseudo-isochromatic test plates and the Farnsworth-Munsell Hundred Hue test. Any subject failing to distinguish correctly a single pseudo-isochromatic plate was rejected. Similarly a subject was rejected if a significant error score was exhibited on the Hundred Hue test.

(b) Subjects should display a visual acuity of better than 6/6 each eye. If spectacles were necessary to achieve this, they were worn throughout the experiment. Subjects having tinted spectacles were rejected.

(c) The distance muscle balance was established to be within normal limits. Any subject having a horizonal heterophoria of greater than 2^{Δ} or a vertical heterophoria greater than 0.5^{Δ} was checked on a Mallet Fixation Disparity Unit. This proved necessary in only one case, for a subject having 3^{Δ} of exophoria at distance. The Fixation Disparity test revealed that the muscle imbalance was well compensated. Although working in the monocular state, stimulus B is seen by both eyes. A breakdown in fusion causes three flashing stimuli to be seen by the subject.

(d) All subjects displayed normal dark adaptation characteristics using the Goldmann adaptometer.

(e) Ophthalmoscopic examination of each subject revealed their fundi to be both normal and healthy.

The student group, although not reflecting a true cross-section of the general population, were assumed to be both intelligent and able to cope with the strenuous nature of prolonged experimental testing. It is important that subjects are fairly readily available for experimental work, particularly when large randomised block factorial designs are employed, since only a small proportion of the total number of results necessary are obtained during a single experimental session. The underlying experimental assumptions will be discussed more fully later.

4. Subject Familiarisation and Movement Criteria

As we have already noted, sequential exposure of two adjacent stimuli fulfilling certain conditions with regard to proximity, duration, and form elicit the perception of an object which moves between the stimuli locations. Initial personal observations revealed that apparent movement was seen over a wide range of stimulus cycle times ranging from 150 to 600 m.sec. With very fast cycle times (faster than 150 m.sec.) the frequency appeared to approach the critical fusion frequency so that stimuli appeared to be continuous. With very low frequencies, as the cycle time exceeded 600 m.sec., the illusion broke down. Initial observations were made with alternating stimuli having no temporal overlap or pause, so that the second stimulus could be seen instantly the first disappeared. The question of "optimal inter-stimulus interval" had dated from the time of Wertheimer (1912) and would be a factor to be considered later.

A stimulus wavelength of 620 n.m. was randomly selected. Using a cycle time of 400 m.sec. as being in the middle of the range and a horizontal spatial separation of 1.50 m.m. the illusion of apparent movement was clearly seen. After 20 minutes of dark adaptation these conditions were presented to all subjects with the following verbal instructions . . .

> "Place your head firmly in the headrest provided. Keep both eyes open and look straight ahead. You will see a specific visual stimulus which you must describe as

> fully and as accurately as you can. About 10° above this you may see some faint images which you are to ignore."

The subjects were not told that they would see a moving object since Kelly (1935) observed that apparent movement was more readily seen after it had been described. It has recently been found, however, that thresholds for distinguishing motion are unaffected when the subject is told beforehand that an illusion is being viewed (Segal and Barr, 1969).

All subjects without exception reported seeing a small, horizontally, moving stimulus. If the description was in any way ambiguous, they were asked supplementary questions as to the colour of the object or the direction of its movement. The spatial separation of the stimuli was gradually increased and the subjects were again asked to report their observations. The velocity of the apparently moving stimulus was seen to increase before the appearance suddenly changed into two separate stimuli flashing alternately.

From both personal and subject observations, three separate phases could be clearly distinguished as the spatial separation of the two alternating stimuli was increased from the zero-position of superimposition. These were designated as follows:-

(a) Optimal or Beta motion

A single clearly defined object was seen to move between the stimuli locations. This was not a sensation but the distinct appearance of an object. This persisted with increased spatial separation, the velocity of the apparently moving object increasing, until a threshold was reached resulting in . . .

(b) Non-optimal motion

The object is seen to move toward the location of the second stimulus, disappearing before reaching the point at which the second stimulus appears. The movement is described by some subjects as being "incomplete" or "broken", whilst others describe the appearance of a moving black space. The presence of a moving black space has alse been reported by Frisby (1973). Similarly, partial apparent movement was described by Wertheimer (1912). As the stimuli are further separated the extent of the partial movement diminishes until . . .

(c) No movement

The stimuli become absolutely stable and two alternating widely spaced spots are seen.

The transition from optimal to non-optimal movement, or the reverse, appears distinctly and suddenly. The transition between non-optimal and no-movement is much more gradual and the point at which this occurs is difficult to estimate. Both in describing the movement category and in result taking great care was taken to avoid giving cues (e.g. "good") to the subject. After the movement categories were clearly described by the subject, simple descriptive titles were given for experimental use. These were "smooth" - or optimal-movement, "broken" - or non-optimal movement, and no-movement.

5. Experimental Procedure

The transition point between optimal and non-optimal movement represents the maximum spatial threshold of beta motion for the specified stimulus conditions. Two closely situated alternating stimuli produce optimal motion, but when separated slightly further they no longer produce the same response. Non-optimal movement represents a totally different response, because although some movement is seen, a single clearly defined object is no longer perceived. No satisfactory explanation for this phenomenon has yet been advanced.

Any threshold must be measured repeatedly and an average found because its exact location varies with time. Random variations in sensitivity occur in every sense field. If a watch is held so that its ticking can be just heard, the sound periodically waxes and wanes. The variability theory of thresholds dates from the work of the classical psychophysicists (c.f. Fullerton and Catell, 1892; Boring, 1917; Thurstone, 1927 b; Guilford, 1927).

Of the classical psychophysical methods for threshold measurement, two have application for the outlined experiment, namely, the frequency method, and the method of limits. The frequency method involves using a convenient number of settings over the range of movement categories, from the position at which optimal movement is always seen to where it is never seen. Individual settings are presented in random order and the threshold is estimated from the 50th percentile. This method involves making a large number of individual settings, whilst the subject observes each setting and decides on the movement category. This method is very time consuming and difficult to operate when using large experimental designs. The method of limits was considered to be the method of choice. This method can be performed much more quickly since the subject reports only a change in the movement criteria. It is obviously necessary to use an equal number of ascending and descending runs. An estimate of the threshold point was quickly made by altering the second stimulus position (stimulus A) until a change in the type of movement was seen. Following this the stimulus was moved in short equal steps of 0.10 m.m. until the threshold position was reached, at which point the movement category changes. The vernier scale reading is noted before approaching the threshold from the opposite direction. This method has been termed the 'modified method of limits' approach. This method has alternatively been referred to as the 'method of serial exploration', a name characterising the descending and ascending series of results used to locate the transition point or threshold. This method is probably the one most frequently used in vision research. It assumes that the subject is capable of making a sharp distinction between the two movement types and that indecision or an "equal" situation is never reported. This is forced upon the subject by the instructions given to him to indicate when the movement category changes. The spatial threshold is therefore established as the mean of a number of individual results. This number must be as economical as possible whilst being large enough to establish an accurate mean. Early studies indicated that eight individual results were necessary to establish an accurate and reliable threshold.

To establish a threshold it is necessary to make an equal number of "ascending" and "descending" approaches to the point at which the movement category changes. Two classic errors are associated with the "method of limits" experimental approach. Errors arise due to subject hesitancy in reporting a change in the apparent movement category and is often associated with inexperience. Subject instructions can also influence this type of error, which may be increased simply by instructing the subject that he must be "absolutely sure" of a movement category change before he reports it. Another error which may occur, possibly less commonly, is when a subject anticipates a change in the apparent movement category and reports its occurrence before the threshold point.

To establish the maximum spatial threshold for a particular set of stimulus parameters the following experimental procedure was adopted:-

(a) The subject was dark adapted for twenty minutes in order to obliterate the influences of any pre-test adaptation that they may have experienced.

(b) The stimuli were illuminated continuously and the subject indicated when they appeared superimposed. The vernier scale reading was noted, this giving the "zero" position for spatial separation of stimuli.

(c) The subject placed his head in the head-rest. The spatial and temporal characteristics of the stimulus having been suitably adjusted, the subject was asked to describe the type of movement that he observed.

(d) The spatial separation of the stimuli was adjusted until the movement category changed, at which point the vernier scale reading was noted. This reading is subtracted from the first vernier scale reading to give the spatial separation of the stimuli in m.m. Two "ascending" and "descending" results are obtained, after which the subject was instructed to close his eyes. This procedure is repeated until a total of eight results are obtained from which the mean maximum spatial threshold is calculated. If a large number of repeated results are taken without a break, the subject gains some indication of the threshold location and begins to base his reports on where he believes the threshold to be rather than on pure observation.

The mean maximum spatial threshold in minutes of arc is then calculated from the spatial separation of stimuli in m.m. using the equation;

$$\text{Tan. } \theta = \frac{60\ x}{500}$$

where x is the spatial separation of stimuli in m.m.

6. Fundamental Assumptions Underlying Analysis of Variance Tests

Two types of experimental design were used, the randomised block and the randomised block factorial design. These permit statistical inference to be drawn using the F distribution, the theoretical model against which an F statistic is evaluated. To uphold the mathematical justification for hypothesis testing using the F distribution, basic assumptions about the data must be made. When some assumptions are violated the statistically powerful F distribution may still provide an adequate approximation suitable for hypothesis testing. The basic assumptions made about the data are as follows:-

(i) Observations should be drawn from a normally distributed population.

(ii) Observations should represent random samples drawn from the population.

(iii) Variances of populations should be equal, that is homogeneity of variance should be established.

(iv) Independence between the numerator and the denominator of the F ratio should similarly be established.

The mathematical derivation of the F distribution makes it very robust with respect to violation of the statistical assumptions outlined above. It is often impossible to establish with certainty that all the required assumptions are fulfilled by a set of data (Cochran, 1947).

In practice it is found that the population may depart from the normal distribution in terms of skewness, kurtosis, or both without significantly altering the F statistic. Studies by Pearson (1931) and Norton cited by Lindquist (1953) strongly support the fact that the F distribution is relatively unaffected by lack of symmetry of the treatment populations. The distribution remains unaffected by all except extreme cases of very leptokurtic or platykurtic populations. It is generally held that unless the departure from normality is so extreme that it can be easily detected from a visual inspection of the data, it will have little effect on the probability associated with the test of significance.

The F distribution is similarly robust to violation of the assumption concerning homogeneity of the population - error variances, provided that an equal number of observations are present in each

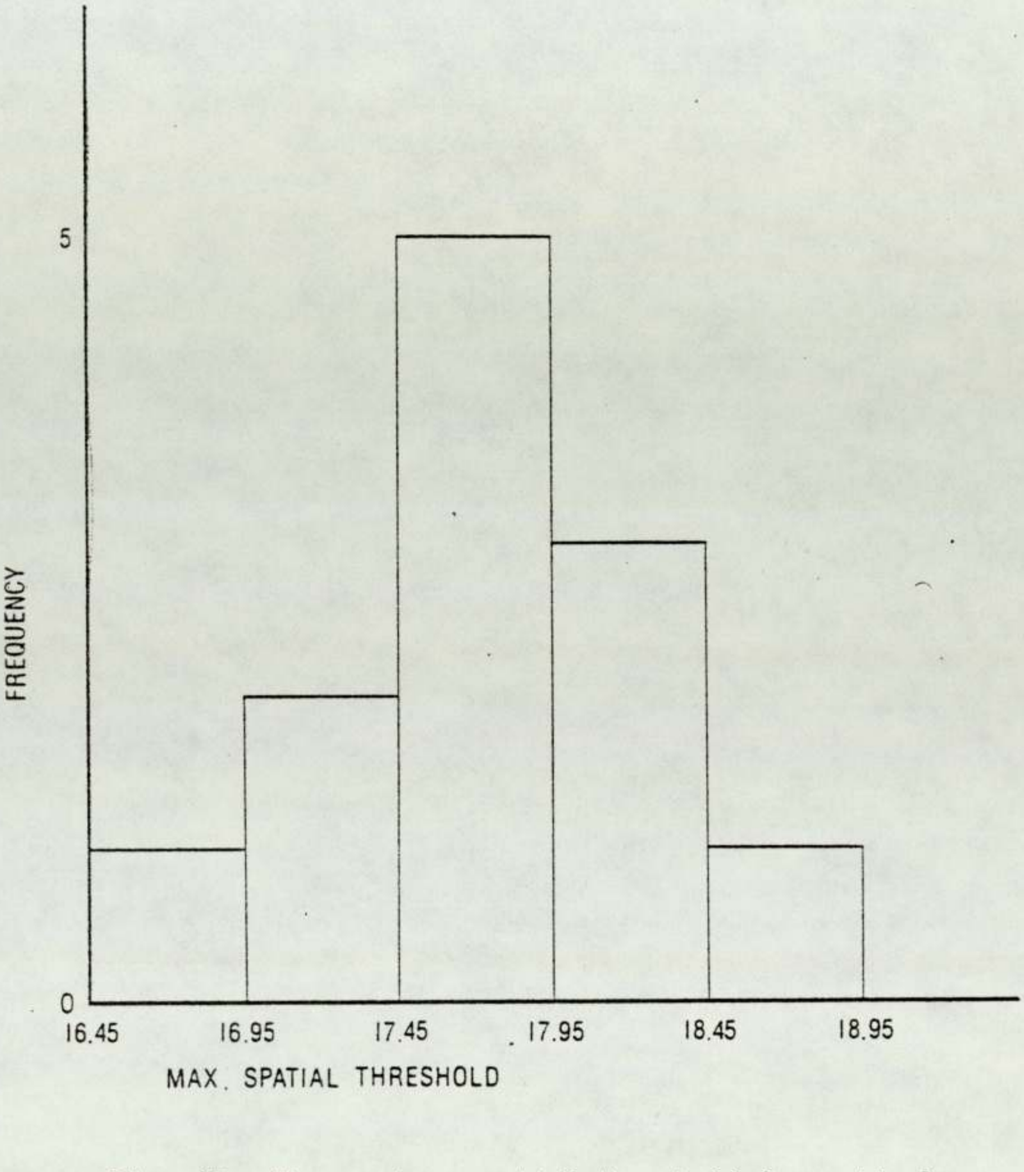


Fig. 15 The maximum spatial threshold for optimal apparent motion obtained from 12 observers using a 600 n.m. stimulus and a cycle time of 450 m.sec.

sample (Cochran, 1947; Lindquist, 1953). Heterogeneity of variance can have a marked effect on a test of significance if the test samples are of unequal size. Tests for homogeneity of variance may be made yet these have been shown to be of very little value. The simile has been made, that it is like putting out to sea in a rowing boat to see if it is safe for an ocean liner to leave port (Lindquist, 1953).

The assumption of independence between the numerator and denominator of the F ratio is sometimes difficult to cope with, but this may be assumed if random samples are drawn from a normal population.

With regard to the present experiments, the maximum spatial threshold for beta motion may be reasonably assumed to be normally distributed in the population. The sampling distribution of means appears to be normal from inspection (Fig. 15). Subjects, having normal colour vision, are selected randomly from the population, although do not reflect its age or sex distribution. In this respect our findings must be qualified, although it may be argued that the age or sex of an individual are unlikely to effect major changes in the colour vision mechanism or that responsible for beta motion. With random samples drawn from an assumed normal population, independence between the numerator and denominator of the F statistic may also be assumed. Homogeneity of variance between samples, the factor most influencing the F ratio, has been guaranteed since each subject appears at all treatment levels at which an equal number of observations have been made. It may therefore be concluded that the basic data obtained fulfills the fundamental assumptions necessary for analysis of variance.

CHAPTER VI

The Effect of Stimulus Wavelength upon Apparent Motion

Introduction

Evidence has been presented earlier which strongly suggests that apparent movement arises when two alternating stimuli impinge upon the excitatory receptive field of a movement-sensitive cell. The spatial arrangement of the two stimuli must therefore be important. It is commonly held that excitatory and inhibitory receptive fields exist as two overlapping Gaussian distributions, whose sensitivities fall with distance from this centre. It has been further suggested that the spatial extent of the excitatory receptive field is determined by the action of the inhibitory receptive field (Wagner et al., 1963; Rodieck and Stone, 1965; Mead, 1967). In an experimental situation in which background light is absent, the extent of inhibition provided by the inhibitory receptive field is minimal and may be assumed constant. If the excitatory receptive field is regarded as a sensitivity distribution, then it may be argued that the maximum spatial threshold for optimal apparent motion reflects the sensitivity response of the field. The sensitivity held by a movement sensitive neurone for a particular stimulus would determine its excitatory receptive field size, with that stimulus.

Flashing stimuli are commonly used to produce apparent movement. The response may be dependent upon the luminance change produced by a flashing spot in relation to its surroundings. If this were the sole factor, the maximum spatial threshold for optimal apparent movement would remain unaffected by the wavelength of stimuli having equal luminance. Wavelength sensitivity differences exhibited by the "inputs" to the movement sensitive excitatory receptive field may be demonstrated by establishing thresholds using stimuli of different wavelengths.

The following experiment was designed to investigate the effects of stimulus wavelength in producing optimal apparent motion.

Method

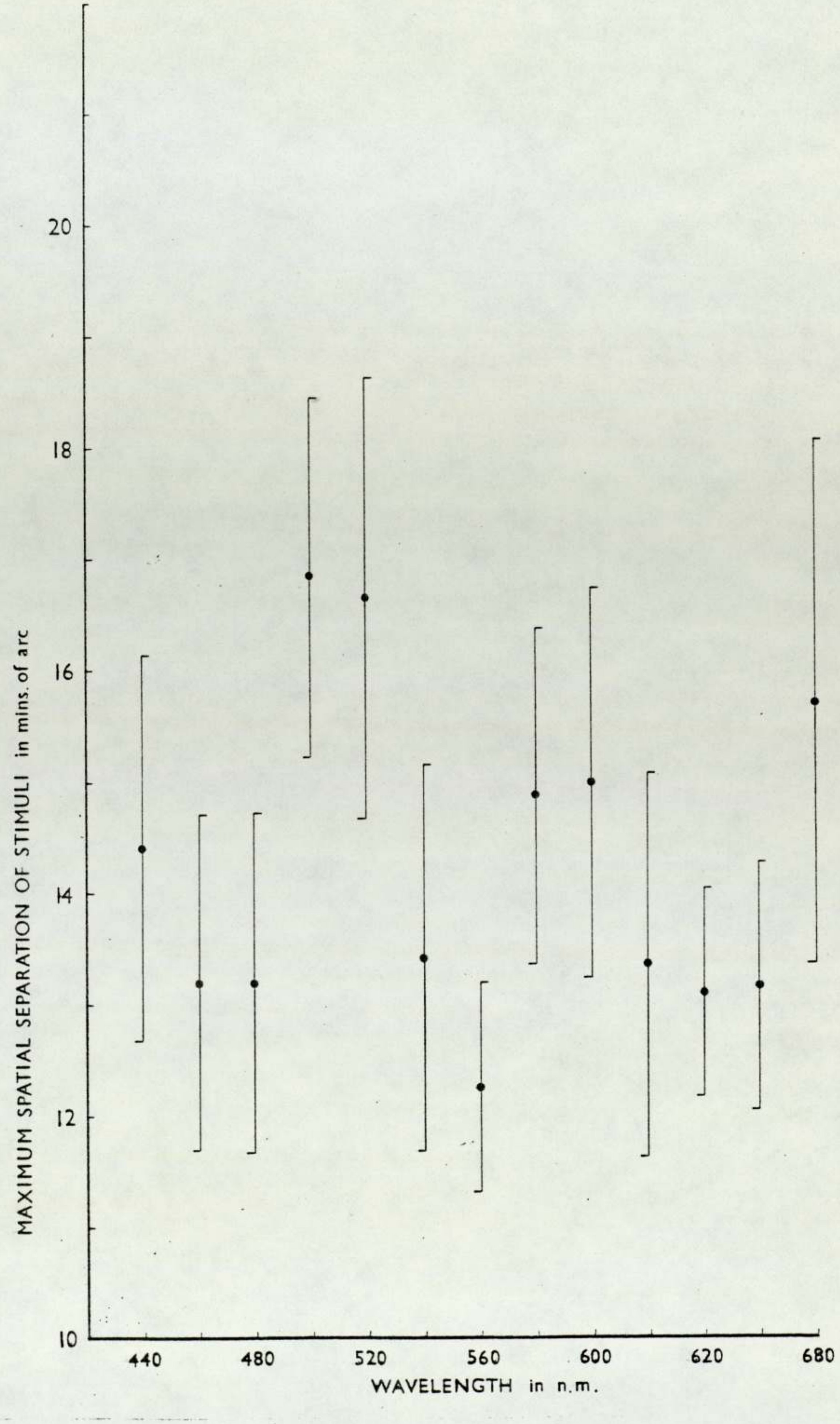
A total of eight male subjects were used to investigate the colour responses of optimal apparent motion over the range of 440 to 680 n.m. at 20 n.m. intervals. A stimulus cycle time of 400 m.sec was used as being in the middle of the established range of cycle times over which apparent movement was seen. Stimuli had a fixed 1 : 1 light : dark ratio and alternated with no temporal overlap or separation. The stimuli of different wavelengths were presented in a random order for each subject, who determined the maximum spatial threshold for horizontal optimal apparent motion using the method outlined earlier. A randomised block design was used for statistical analysis. As well as meeting the general requirements for analysis of variance, outlined earlier, the randomised block design is appropriate only for experiments fulfilling the following requirements:-

(a) Subjects must undergo one treatment at two or more levels. In this case subjects determine the mean maximum spatial threshold for beta motion at thirteen wavelength levels.

(b) Subjects must be assigned to blocks so that variability among subjects within any block is less than the variability among blocks. Minimum variability amongst subjects is ensured since each subject appears in all blocks. The number of subjects and observations within each block must be equal - a condition which has been met (in this experiment).

(c) Random assignment of treatment levels to the experimental units within each block. In this experiment one subject receives all treatment levels, i.e. views all stimulus wavelengths, in a

Graph I The Effect of Stimulus Wavelength upon the Maximum Spatial Threshold for Optimal Apparent Motion in the Horizontal Plane.



random order.

Hence the experiment fulfills the additional requirements necessary for the randomised block design.

Results

A graph of the mean maximum spatial threshold for optimal apparent motion plotted against stimulus wavelength is given (Graph I). Vertical bars represent ± 1 standard deviation from the mean. A summary table of the randomised block (RB - 13) experimental design is given below (Table 1). The formal statistical approach is as follows:-

Null Hypothesis (H_0) : The mean maximum spatial threshold for optimal apparent motion is unaffected by stimulus wavelength, that is $\mu_{440} = \mu_{460} = \dots = \mu_{680}$.

Alternative Hypothesis (H_1) : The mean maximum spatial threshold for optimal apparent motion is influenced by stimulus wavelength, that is $\mu_{440} \neq \mu_{460} \dots \neq \mu_{680}$.

Significance Level : $\alpha = 0.01$ If differences between the means exist, which are so extreme that the probability of their occurrence by chance is equal to or less than 0.01, then H_0 is rejected in favour of H_1.

Critical region for rejection of H_0 : $F \geqslant F_{(12,91)} = 2.38$.

Table 1.

source of variation	s.s.	d.f.	var. est.	F	
Between groups	206.459	12	17.205	6.039	*
Within groups	1.011	7	0.144	0.050	N.S.
Residual	239.323	84	2.849		
Total	446.793	103			

* $P < 0.01$

From the summary table it can be seen that F = 6.53. It is therefore possible to reject confidently the null hypothesis and conclude that wavelength does influence the maximum spatial threshold for optimal apparent motion. Tukey's Multiple Comparison of Means' test (HSD test) was subsequently performed (Table 2).

From Graph I it is apparent that a minimum or base threshold occurs at about 13 mins. of arc, upon which is superimposed three significant peaks or maxima. The first, and most significant of these, which occurs between 500 and 520 n.m., represents an increase in the threshold above the base level of about 30%. Stimuli of these wavelengths can be separated by about 17 minutes of arc before optimal apparent motion breaks down, compared to only 13 mins. of arc for neighbouring stimuli of 480 and 520 n.m. The second most significant peak occurs at the end of the spectral range at 680 n.m. The threshold at this point represents an increase of about 20% above the base level. A 15% increase in threshold relative to the approximate base level is found in the region of 580 to 600 n.m. forming the third peak of the distribution. Tukey's test shows this to be significantly different at the 0.05 level from the minimum threshold located at 560 n.m. A slight increase in threshold, about 10% greater than the base level, was found with stimuli of 440 n.m. although Tukey's test indicated this not to be significant.

Trends, due to the order in which the stimuli were presented, were not observed. Although accuracy might be expected to increase with practice, fatigue effects may similarly increase with time. Generally it is found that little practice is required once the subject has been familiarised with the apparatus, although prior to every experimental session each subject was allowed one practice run.

Great care was taken to avoid giving cues to the subject although the question of "demand characteristics" (Orne, 1962) is a difficult one. No pre-conceived ideas concerning the experimental outcome were held, hence it was difficult for a subject to deceive the observer. Similarly pre-conceived ideas must be present if suggestion

Table 2.

	18.86	16.66	15.71	15.01	14.88	14.42	13.43	13.38	13.21	13.20	13.17	13.11	12.27
16.86	-	N.S.	N.S.	N.S.	N.S.	0.05	0.01	0.01	0.01	0.01	0.01	0.01	0.01
16.66	-	-	N.S.	N.S.	N.S.	N.S.	0.01	0.01	0.01	0.01	0.01	0.01	0.01
15.71	-	-	-	N.S.	N.S.	N.S.	0.05	N.S.	0.05	N.S.	N.S.	N.S.	0.01
15.01	-	-	-	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.05
14.88	-	-	-	-	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	0.05
14.42	-	-	-	-	-	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
13.43	-	-	-	-	-	-	-	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
13.38	-	-	-	-	-	-	-	-	N.S.	N.S.	N.S.	N.S.	N.S.
13.21	-	-	-	-	-	-	-	-	-	N.S.	N.S.	N.S.	N.S.
13.20	-	-	-	-	-	-	-	-	-	-	N.S.	N.S.	N.S.
13.17	-	-	-	-	-	-	-	-	-	-	-	N.S.	N.S.
13.11	-	-	-	-	-	-	-	-	-	-	-	-	N.S.
12.27	-	-	-	-	-	-	-	-	-	-	-	-	-

is to be useful. Orlansky (1940) found suggestion to have little effect, although more potent form stimuli (e.g. arrows pointing in different directions) were used compared to small spots. The effects of hesitancy and expectation, as well as verbal instructions given to the subject, upon thresholds have been discussed earlier.

The manual control of spatial separation by the observer, and the pacing of the experiment, may have transmitted information unintentionally to the subject. The subject closed his eyes before each new stimulus whilst the spatial separation was set. He then described the type of motion before the threshold was determined using the standard modified method of limits. It was, therefore, difficult for the subject to infer the spatial threshold location from the preceding stimulus. This was repeated during the experimental run, to make it more difficult for the subject to guess the threshold location using time as a clue. After being shown optimal movement it takes a short space of time after which the change in motion is seen. Repetition is involved in determining the spatial threshold using a modified method of limits technique. The subject may, therefore, be given a clue that after a certain viewing time the threshold point is reached. Generally time errors or time-order effects produce a tendency to overestimate the second stimulus in relation to the first (Woodworth and Schlos berg, 1954). Series effects may also be produced, wherein a tendency is found to over or under-estimate a stimulus according to its magnitude in relation to the series as a whole. Both the randomisation of order and the break between stimuli attempted to minimise this systematic response bias.

Vertical Apparent Motion

Introduction

Having established thresholds for horizontal apparent motion, it was decided to compare thresholds for identical stimuli in the vertical plane. It has been suggested earlier that the excitatory receptive field size may vary with the sensitivity of the field inputs. If the receptive field is circular in shape identical results to those already obtained would be anticipated.

The procedure adopted was identical to that already outlined in the first experiment, except that six male subjects were used and the stimuli were arranged vertically.

Results

A graph of the mean maximum spatial threshold for vertical optimal apparent motion is given, plotted against stimulus wavelength (Graph II). The analysis of variance summary table for the RB - 13 design is given (Table 2). The statistical hypotheses, listed as follows, are similar to those proposed for the first experiment:-

H_0 : The mean maximum spatial threshold for optimal apparent motion is unaffected by stimulus wavelength, that is $\mu_{440} = \mu_{460} = \cdots = \mu_{680}$.

H_1 : The mean maximum spatial threshold for optimal apparent motion is influenced by stimulus wavelength, that is $\mu_{440} \neq \mu_{460} \neq \cdots \neq \mu_{680}$.

α : 0.01

Critical region for rejection of H_0 : $F \geqslant F_{(12,65)} = 2.50$.

Graph II The Effect of Stimulus Wavelength upon the Maximum Spatial Threshold for Optimal Apparent Motion in the Vertical Plane.

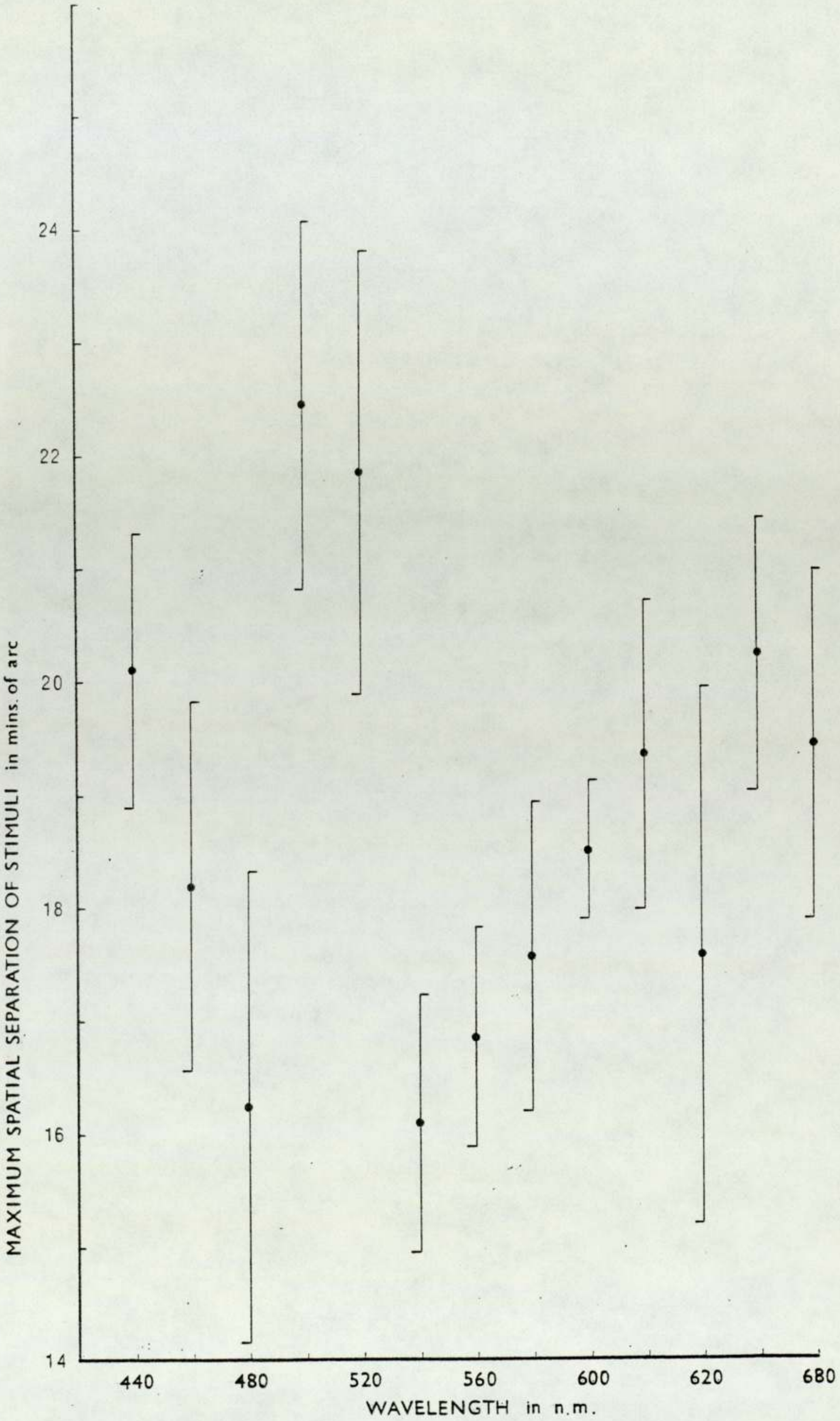


Table 3.

source of variation	s.s.	d.f.	var. est.	F
Between groups	348.97	12	29.08	4.96
Within groups	380.58	65	5.86	
Total	729.55	77		

As previously, the null hypothesis is rejected, and the results for vertical optimal apparent motion confirm that stimulus wavelength plays a significant role in apparent motion. The mean maximum spatial threshold, however, for vertical apparent motion is 18.81 mins. of arc, apparently far greater than similar thresholds recorded for horizontal apparent motion.

Horizontal thresholds, obtained for the same six subjects, were compared with the above results. This enabled statistical inference to be drawn from correlated samples. Three subjects had already provided horizontal threshold results, whilst the remainder underwent further experimentation. The experimental order in which vertical and horizontal thresholds were measured was therefore balanced, counteracting any learning or fatigue effects which might occur. The mean horizontal threshold for six subjects plotted against wavelength is given (Graph III). The problem is outlined in formal statistical terms as follows:-

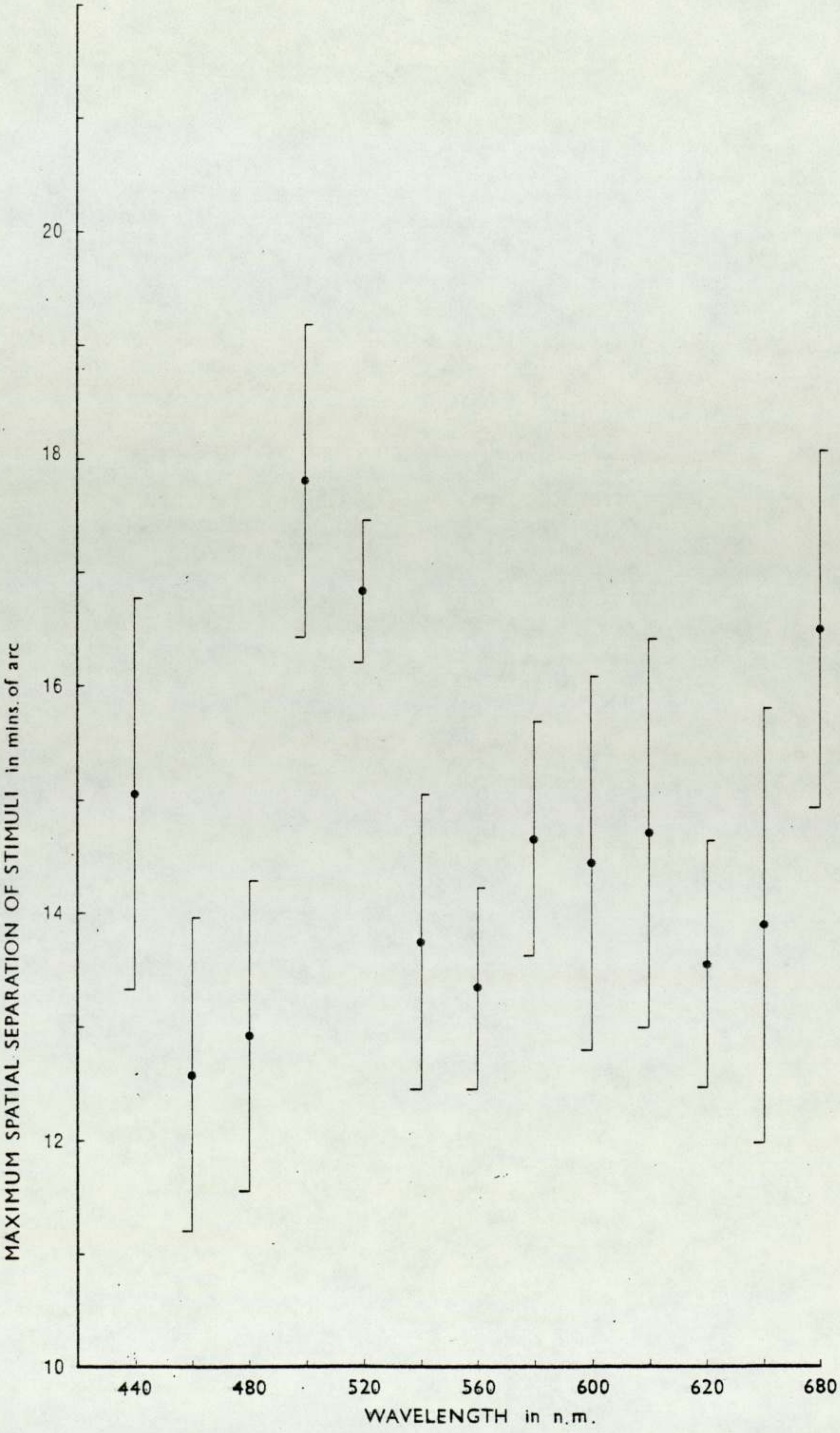
H_0 : There is no significant difference in the maximum spatial threshold between vertical and horizontal optimal apparent motion, that is, $\mu_D = 0$.

H_1 : A significant difference exists between the maximum spatial threshold for vertical and horizontal optimal apparent motion, that is, $\mu_D > 0$.

Statistical test : A 'student' t-test for the difference between correlated samples is employed.

Significance level: $\alpha = 0.01$

Graph III The Effect of Stimulus Wavelength upon the Maximum Spatial Threshold for Optimal Apparent Motion in the Horizontal Plane.



Sampling distribution: Student's t-distribution with df = 5.

Critical region: $t_{0.01} \leqslant 4.032$. Smaller probabilities, i.e. a value of t numerically greater than 4.032, will allow rejection of H_0.

The results presented (Table 3) give a value of t = 11.88 and H_0 is confidently rejected. It may be concluded that a significant difference exists between horizontal and vertical thresholds for optimal apparent motion.

The results obtained for vertical thresholds, in their response to stimuli of different wavelengths, appear very similar to those recorded horizontally. A graph of the results (Graph II) displays four peaks at 440, 500, 600 and 660 n.m. Using an assumed baseline value of 17 mins. of arc, as before, these peaks represent a proportional increase of 18, 29, 15 and 18% respectively. The peak at approximately 600 n.m. appears flattened and more difficult to detect. Similarly the peak noted at the extreme red end of the experimental range was recorded at 660 n.m. in the vertical meridian, whilst horizontal results suggested this to be at 680 n.m. Later experimental work revealed maximum spatial thresholds for long wavelength stimuli to be very susceptible to slight changes in temporal duration of the stimuli.

The overall increase in the maximum spatial threshold for beta motion in the vertical meridian is 30%.

CHAPTER VII

The Effect of Stimulus Onset-to-Onset Interval on Apparent Movement

Introduction

A number of workers have sought to ascertain the optimal inter-stimulus interval for apparent movement, although beta motion is visible over a wide range of intervals. It has been shown that the spatial threshold of the excitatory receptive field is influenced by its surrounding inhibitory receptive field (Wagner et al., 1963; Rodieck and Stone, 1965; Mead, 1967). As such the excitatory receptive field may be regarded as a dynamic rather than a fixed spatial arrangement - the extent of which depends upon its sensitivity for particular stimuli. Beta motion is seen when a second asynchronous stimulus falls within the excitatory receptive field of a movement sensitive cell, the spatial extent of which may be determined by its response to the first stimulus. The question posed is whether the onset of the second stimulus modifies the apparent movement response, since it is known that synchronous stimuli fail to produce apparent motion. The following experiment was designed to test the effect of the second stimulus of an asynchronous pair upon the beta motion threshold.

Method

Six male subjects were used to investigate the effect of temporal overlap and separation of stimuli producing horizontal beta motion on the maximum spatial threshold. The standard procedure, outlined earlier, was adopted using a single stimulus wavelength of 500 n.m. and a fixed cycle time of 450 m.sec. The stimuli had a fixed light :

dark ratio of 1 : 1. Each set of stimulus conditions was randomly presented, the degree of temporal overlap or separation varying between zero and 60° at 15° intervals. Each subject viewed all nine sets of stimulus conditions. All subjects had taken part in earlier experiments and were regarded as experienced observers.

Results

A graph of the mean maximum spatial threshold for optimal apparent motion plotted against temporal overlap/separation is given (Graph IV). Vertical bars represent ± 1 standard deviation from the mean. Temporal separation represents a delay before the second stimulus appears. Since, however, the stimuli have a light : dark ratio of 1 : 1, temporal separation of the second stimulus from the first is identical with a temporal overlap of the first stimulus with respect to the second. As with earlier experiments the apparently moving object appears to display no directional preponderance. As expected the distribution of thresholds appears symmetrical about the point of no overlap. No apparent movement is seen when the stimuli were presented only 30° out of phase, i.e., when they overlap by 60°. A randomised block design (RB - 7) was used for statistical analysis. The hypotheses were set out as follows:-

H_0 : The mean maximum spatial threshold for beta motion is unaffected by the time of onset of the second stimulus $\mu_1 = \mu_2 = \mu_3 = \dots = \mu$

H_1 : The mean maximum spatial threshold for beta motion is affected by the time of onset of the second stimulus $\mu_1 \neq \mu_2 \neq \mu_3 \neq \dots \neq \mu$

Significance level $\alpha = 0.01$. If differences between the means exist, which are so extreme that the probability of their occurrence is equal or less than 0.01, then H_0 is rejected in favour of H_1.

Statistical design : RB - 7

Critical region for rejection of H_0 : $F \geqslant F_{(6,35)} = 3.38$.

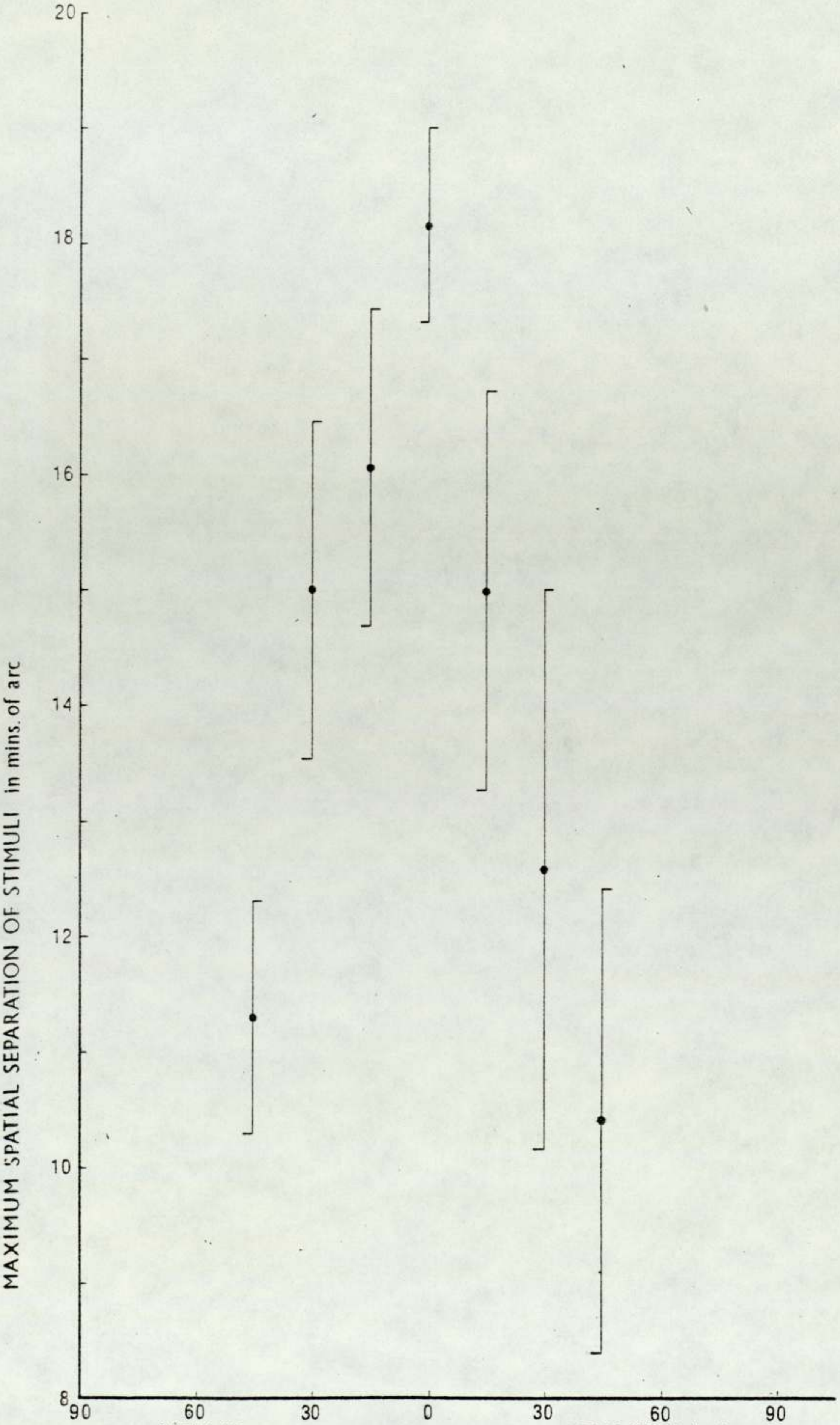
Table 4.

source of variation	s.s.	d.f.	var. est.	F
Between groups	272.975	6	45.496	14.745
Between blocks	3.095	5	0.619	0.201
Residual	92.568	30	3.086	
Total	368.638	41		

A summary of the analysis of variance table is given (Table 3) showing a value for F of 16.82, statistically confirming the conclusions apparent from the graph that onset of the second stimulus diminishes the spatial threshold for beta motion.

No apparent movement is seen with an onset-to-onset interval of 75 m.sec or less. Optimal apparent movement is seen with an interval of about 112.5 m.sec, although the maximum spatial threshold is greatly reduced compared to the threshold obtained with no temporal overlap. If the second stimulus is presented 75 m.sec or less after the onset of the first stimulus, whose duration is 225 m.sec, optimal apparent motion is inhibited by the action of the second stimulus. If the interval is longer, optimal apparent motion is clearly seen, although its spatial threshold is reduced. Thus, the inhibitory effect of the second stimulus is reduced.

Graph IV The Effect of Onset-to-Onset Interval upon the Maximum Spatial Threshold for Optimal Apparent Motion using a 1 : 1 Light : Dark Ratio.



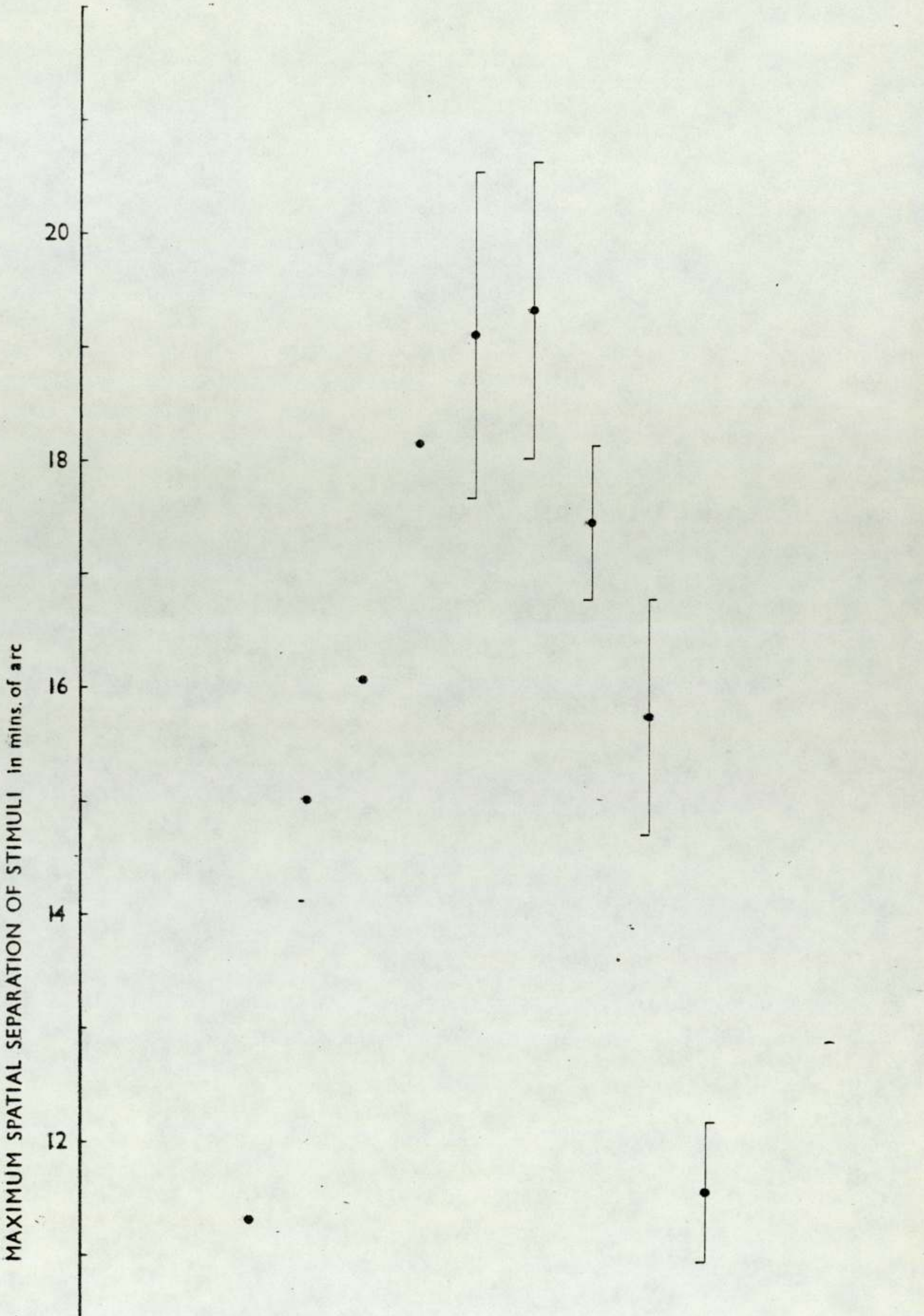
Inter-Stimulus Interval

For the reasons outlined earlier stimuli used in the apparatus, having a light : dark ratio of 1 : 1, fail to display the effects produced by temporal separation. Many early workers became absorbed with ascertaining the optimum inter-stimulus interval, although apparent movement was seen over a wide range of values. This chapter would be incomplete without an evaluation of its effects.

Modification of the sector discs used in the apparatus allowed a light : dark ratio of 1 : 3 to be produced. The additional results obtained from 4 subjects, with temporal separation of stimuli, are shown in Graph IVa.

The maximum spatial threshold for optimal apparent motion increases with a short inter-stimulus interval of up to 75 m.sec. The spatial threshold falls with inter-stimulus intervals in excess of this. With an inter-stimulus interval of 75 m.sec., values obtained for the maximum spatial threshold exceed those obtained with no interval by about 6·6%.

Graph IVa The Effect of Onset-to-Onset Interval upon the Maximum Spatial Threshold for Optimal Apparent Motion using a 1 : 3 Light : Dark Ratio.



CHAPTER VIII

The Effect of Stimulus Duration on the Maximum Spatial Threshold for Beta Motion

Introduction

Pilot studies revealed apparent motion to be seen over a wide range of stimulus cycle times from 150 to 600 m.sec. It has been suggested earlier that the response of receptors, forming the excitatory receptive field of a movement sensitive neurone, to an incident stimulus determine the spatial extent of the field. If this is so, the temporal characteristics of the visual response to a chromatic stimulus can be ascertained by observing the maximum spatial threshold for beta motion using stimuli of various duration times. It is important, therefore, to examine the interaction of both stimulus duration and wavelength upon the spatial thresholds.

The following experiment was therefore designed to evaluate the interaction of the temporal characteristics and wavelength of the stimulus.

Method

Eight male subjects participated in the experiment in which the maximum spatial threshold for beta motion was determined at 50 m.sec. intervals over the range of cycle times from 150 to 600 m.sec. This was done for all wavelengths from 440 to 680 n.m. at 20 n.m. intervals. A total of 130 different sets of stimulus parameters were therefore produced which each subject viewed in a completely random order, during the course of thirteen experimental sessions in the randomised block factorial design experiment.

A randomised block factorial design (RBF design) is a version of the completely randomised factorial design (CRF design) in which a single subject undergoes all treatment levels. Factorial experiments possess a number of major advantages:-

(i) All subjects are used in evaluating the treatment effects. Factorial experiments allow efficient use of resources since the effects of each treatment may be evaluated with identical precision as if the entire experiment were devoted singly to that treatment.

(ii) Effects may be evaluated over a wide range of experimental conditions with optimal efficiency.

(iii) Interaction effects present in the design may be evaluated.

It should also be noted that the design also possesses a number of disadvantages:-

(i) A single subject must undergo a large number of stimulus combinations. It is therefore necessary to break this down into a number of experimental sessions, during which each subject views a random selection of the total number of stimulus combinations.

(ii) Interpretation of experimental results is sometimes complex although in itself this is not a criticism of the design.

(iii) Factorial designs are often large experiments. In order to look carefully at the effects produced by both stimulus duration and wavelength a rather large design is unavoidable.

(iv) It is generally true to say that factorial designs are less efficient in determining optimum levels of treatment or treatment combinations than a sequence of small experiments. Without prior knowledge of the likely interaction effects this is not possible and some interaction effects can be missed.

The general assumptions made for the RBF-1013 design are those outlined earlier for analysis of variance. Homogeneity of variance is assumed since the subject acts as his own control, observing all stimulus conditions. Although procedures are available for determining if the variance-covariance matrices have the required symmetry, such tests are not made unless there is reason to question the respective assumptions (Kirk, 1968).

Results

The randomised block factorial design permits a number of hypotheses to be tested simultaneously. These may be set out as follows:-

$H_{0,a}$: The maximum spatial threshold for optimal apparent motion is unaffected by stimulus duration, that is $\mu_{a1} = \mu_{a2} \cdot \cdot \cdot = \mu_{am}$.

$H_{0,b}$: The maximum spatial threshold for optimal apparent motion is unaffected by stimulus wavelength, that is $\mu_{b1} = \mu_{b2} \cdot \cdot \cdot = \mu_{bm}$.

$H_{0,c}$: No significant interaction effects are observed between stimulus wavelength and duration.

$H_{0,d}$: No significant variation is observed within blocks.

(The alternative hypotheses are omitted for brevity.)

Significance level : $\alpha = 0.001$

Critical regions for the rejection of the null hypotheses are as follows:-

$H_{0,a}$: $F \geq F_{(9,903)}$ = 3.10
$H_{0,b}$: $F \geq F_{(12,903)}$ = 2.74
$H_{0,c}$: $F \geq F_{(108,903)}$ = 1.45
$H_{0,d}$: $F \geq F_{(7,903)}$ = 3.47

Table 5.

source of variation	s.s.	d.f.	var. est.	F	
Blocks	6.82	7	0.97	0.40	N.S.
Treatments	32,497.36	129			
Stimulus Duration	31,047.94	9	3,449.77	1,413.84	*
Wavelength	574.69	12	47.89	19.63	*
Interaction	874.73	108	8.10	3.32	*
Residual	2,199.87	903	2.44		
Total	34,704.05	1039			

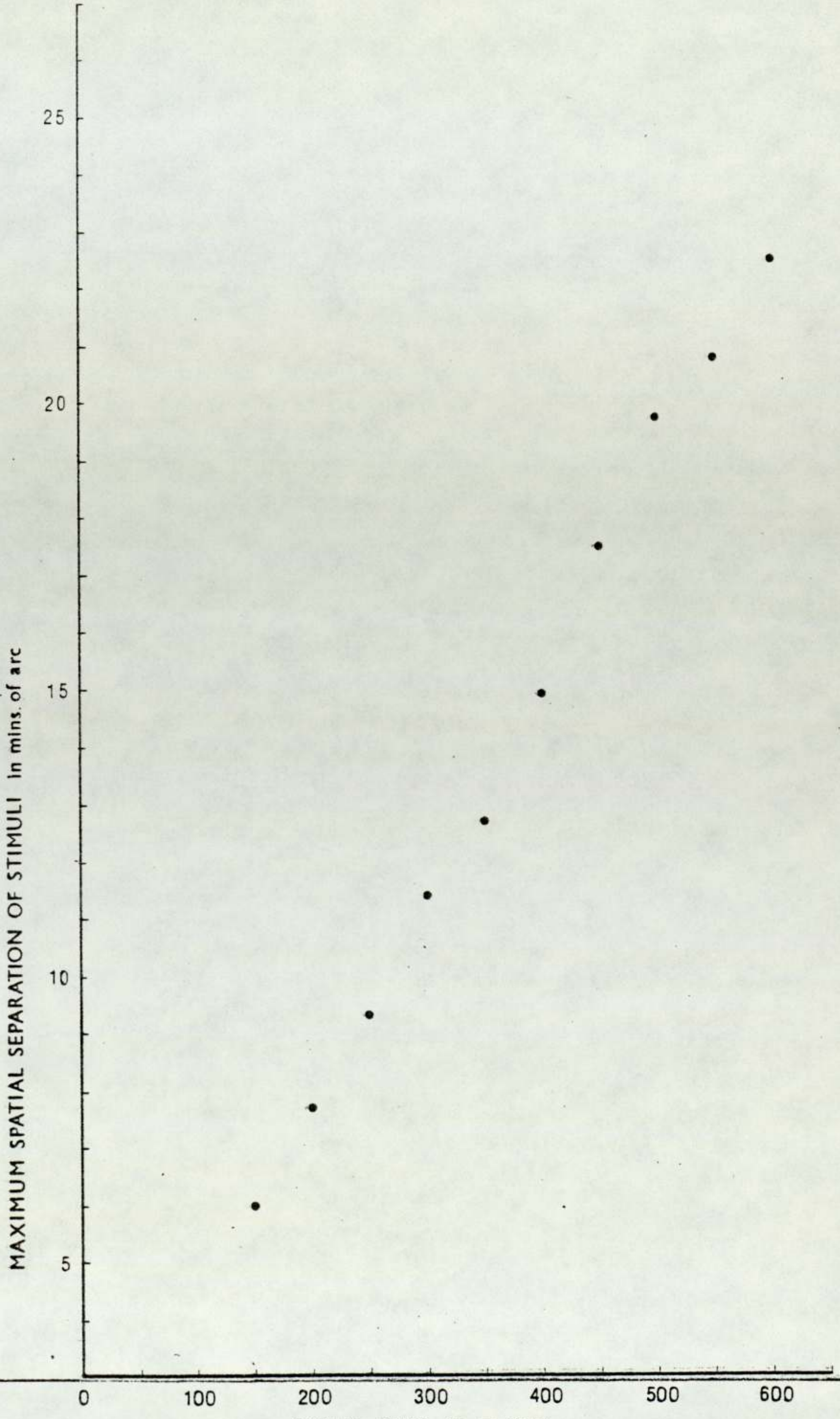
* $P < 0.001$

Results shown in the analysis of variance table (Table 4) allow confident rejection of three of the Null hypotheses outlined ($H_{0,a}$; $H_{0,b}$; $H_{0,c}$). The maximum spatial threshold for optimal apparent motion is affected by both stimulus wavelength and duration. In addition significant interaction effects are present. $H_{0,d}$ is not rejected at any significance level, indicating that no significant variation occurs within the blocks.

The maximum spatial thresholds for beta motion, with stimulus durations ranging from 75 to 300 m.sec, plotted against wavelength are shown in Graph V. For sake of clarity the usual standard deviation marks have been omitted and individual results for each cycle time have been linked with lines.

It can be seen that the spatial threshold increases with duration of the stimulus. The average result for each cycle time shows that a linear relationship exists between stimulus duration and maximum spatial threshold for beta motion (Graph VI). Thresholds were earlier noted to vary with wavelength, but the trend observed in Chapter VI clearly does not apply for all stimulus wavelengths. Generally, a linear relationship is observed between the stimulus duration and the maximum spatial threshold for optimal apparent

Graph VI The Average Change in Maximum Spatial Threshold With Increasing Stimulus Duration.



motion (Graph VI). This response appears consistant for individual wavelengths shorter than 540 n.m.

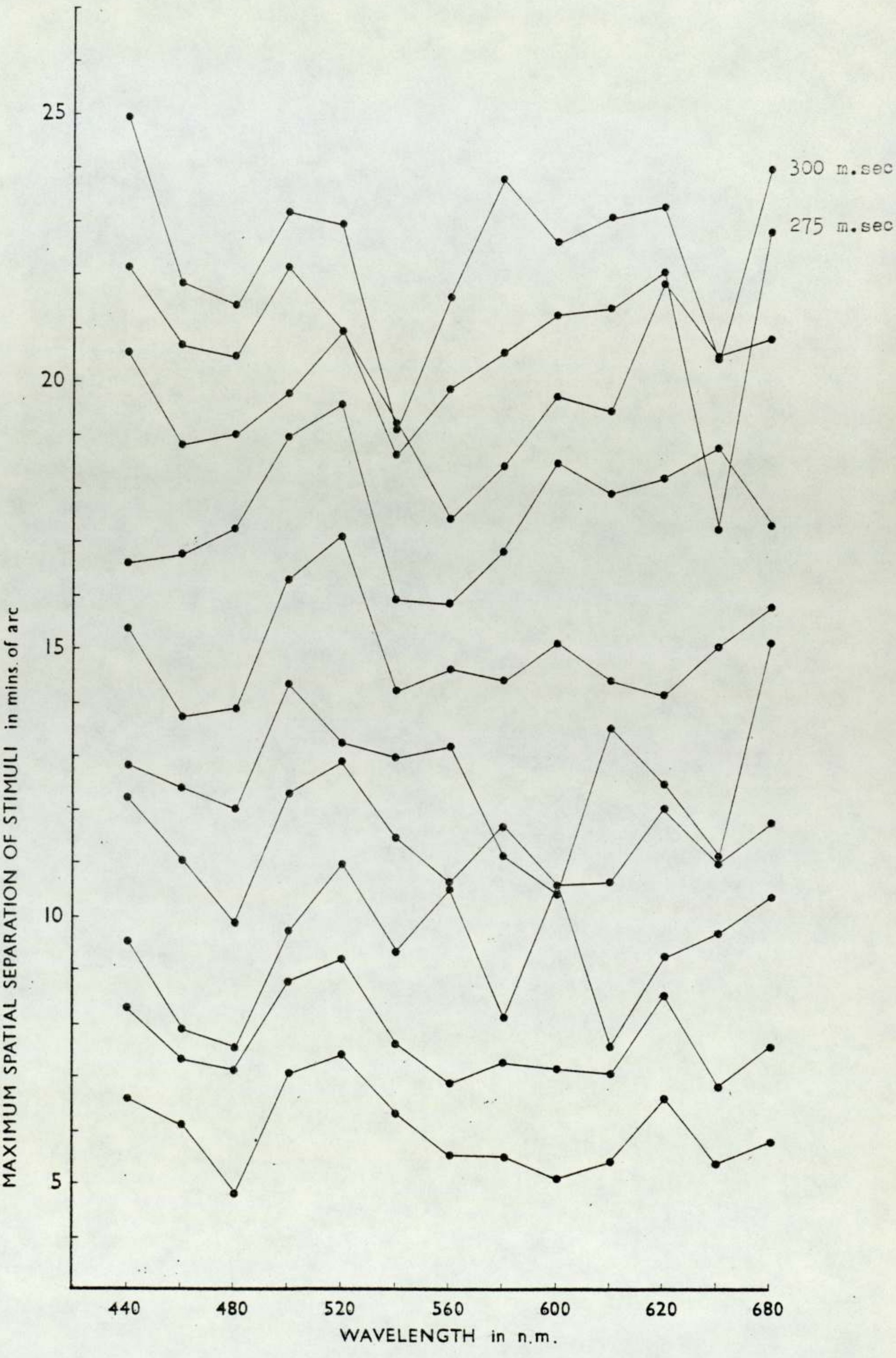
With short stimulus duration (cycle times of 150 and 200 m.sec) three distinct peaks may be observed from the graphs, at 440, 520 and 640 n.m. With longer stimulus durations peak thresholds were also observed at 440 and 520 n.m. wavelengths. The peak threshold observed at 640 n.m. appears to fall mid way between those found earlier at 600 and 680 n.m.

Results for a stimulus cycle time of 250 m.sec appear quite difficult to interpret, and will be referred to later. Results for a stimulus duration of 150 m.sec (300 m.sec cycle time) appear similar to those obtained for short cycle times of 150 and 200 m.sec. The minor peak occurring at 580 n.m. is probably insignificant. With this exception, and apart from the threshold rise due to increased cycle time, the results appear very similar.

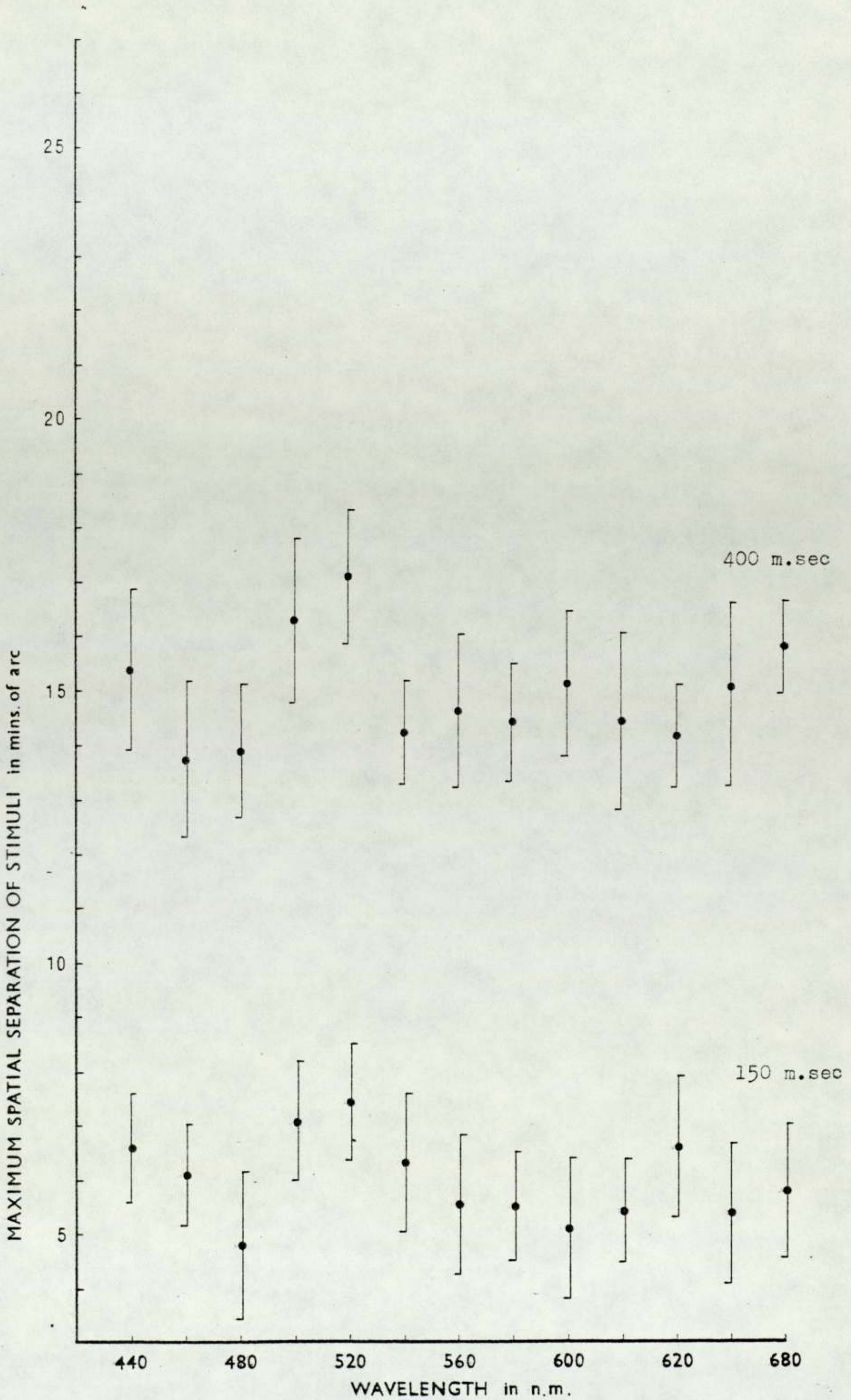
Whilst peak thresholds observed for short wavelengths remain almost unchanged with a stimulus cycle time of 350 m.sec, two other significant changes do occur. A peak threshold is noted at 620 n.m. rather than at 640 n.m. as found earlier. With a cycle time of 400 m.sec this peak appears to be located at 600 n.m. Secondly, there now appears to be a marked threshold increase at 680 n.m. compared to a neighbouring stimulus of 660 n.m. Reference has been made to the threshold pattern obtained for a cycle time of 400 m.sec earlier.

The 680 n.m. threshold peak noted for stimulus cycle times of 350 and 400 m.sec appears to move to 660 n.m. as the stimulus cycle time is increased to 450 m.sec. Further increase in the cycle time to 500 m.sec produces a further movement of the peak to 640 n.m. The threshold peak at 600 n.m. observed for cycle times of 400 m.sec remains for cycle times of 450 and 500 n.m., although not so easily distinguished.

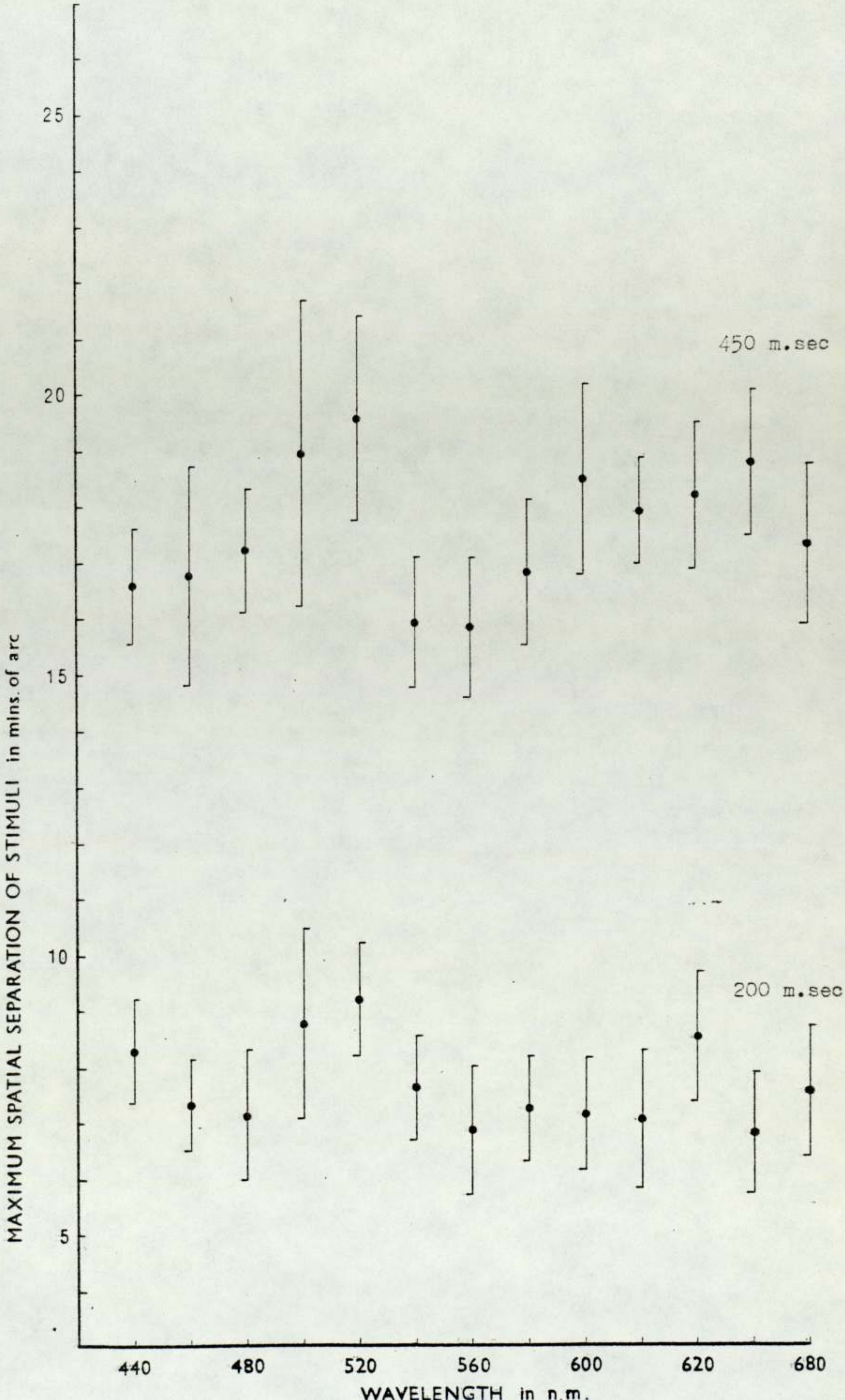
Graph V The Effect of Stimulus Duration and Wavelength upon the Maximum Spatial Threshold for Optimal Apparent Motion.



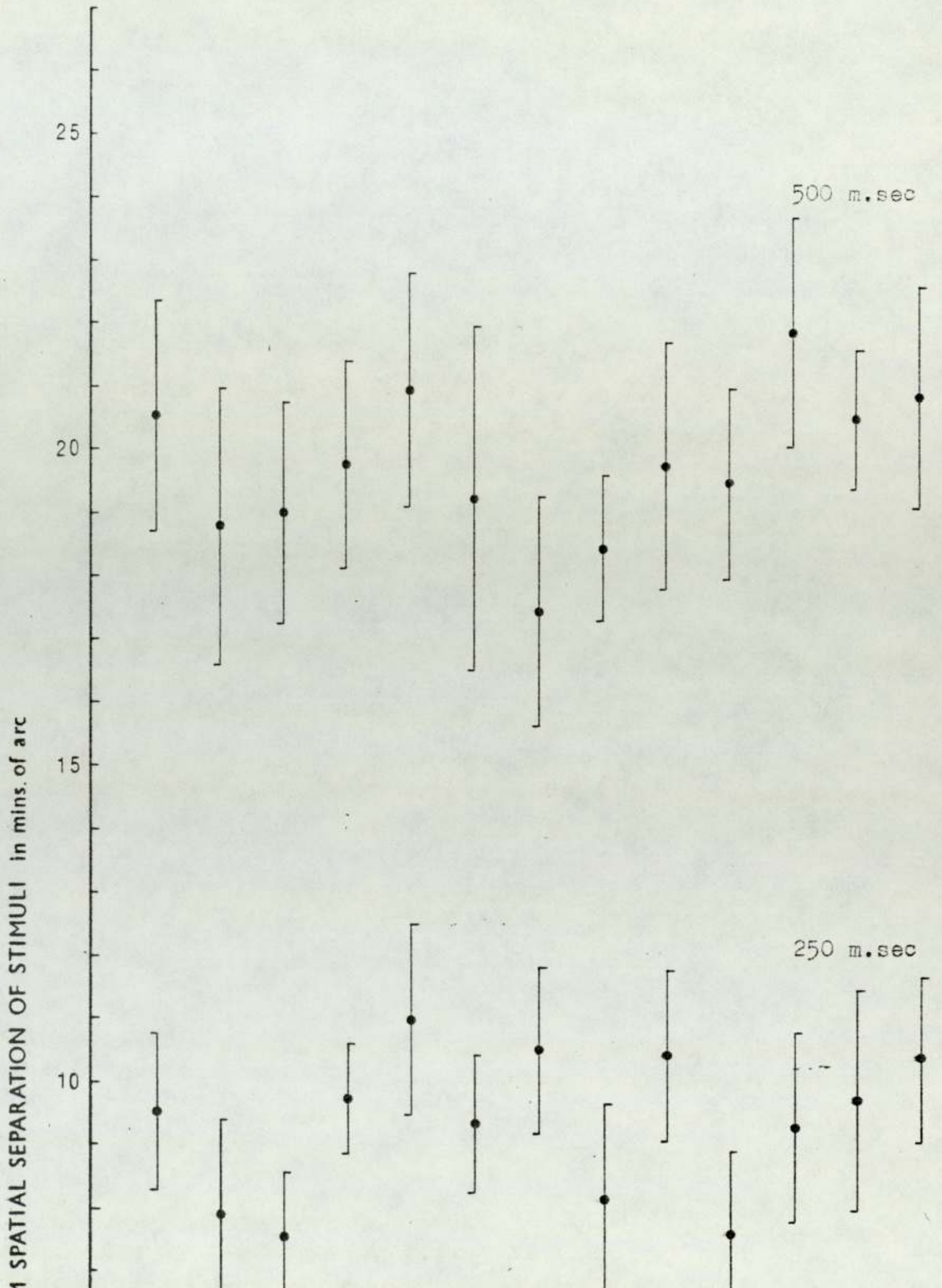
Graph Va The Maximum Spatial Threshold Plotted against Stimulus Wavelength for Cycle Times of 150 and 400 m.sec.



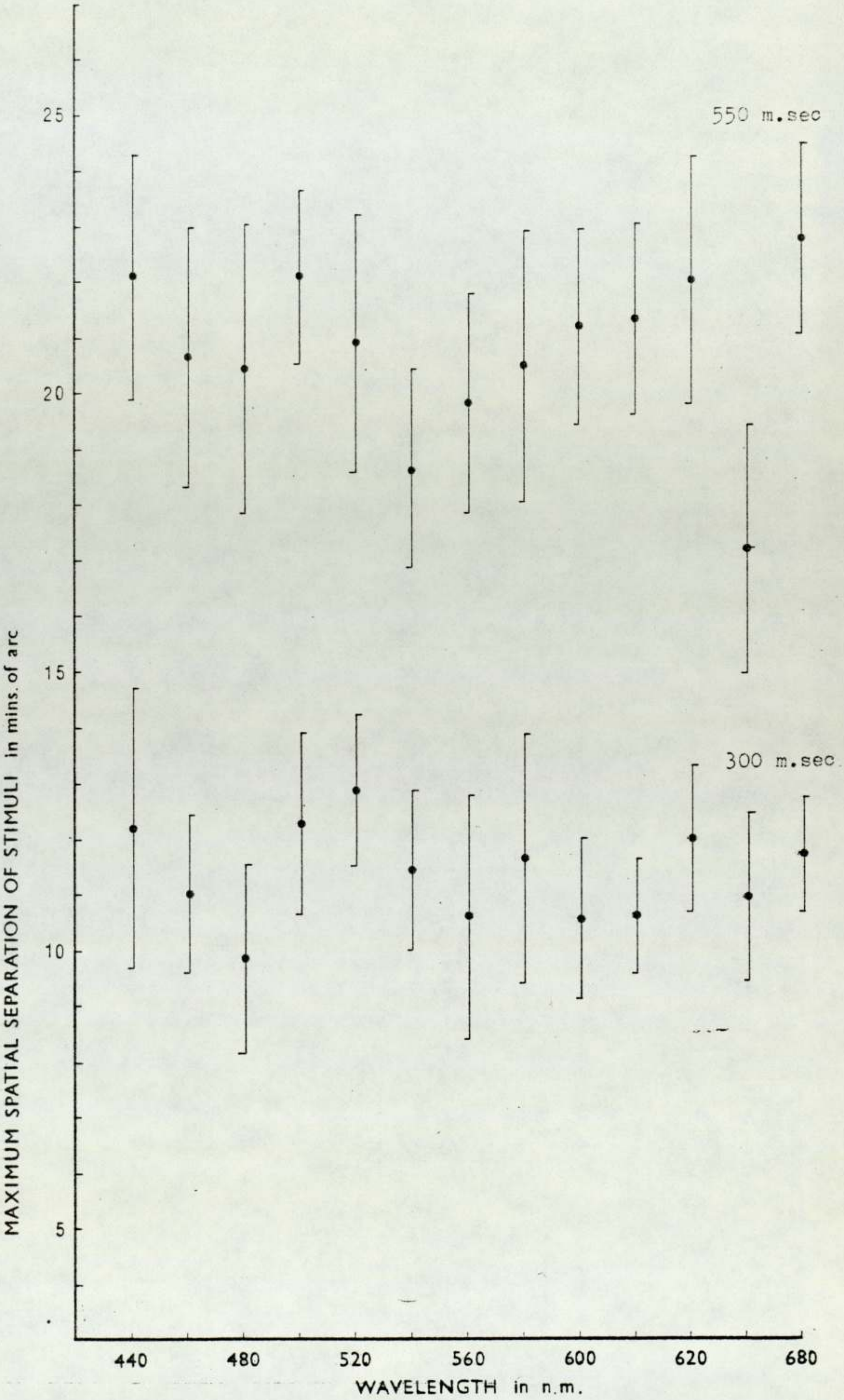
Graph Vb The Maximum Spatial Threshold Plotted against Stimulus Wavelength for Cycle Times of 200 and 450 m.sec.



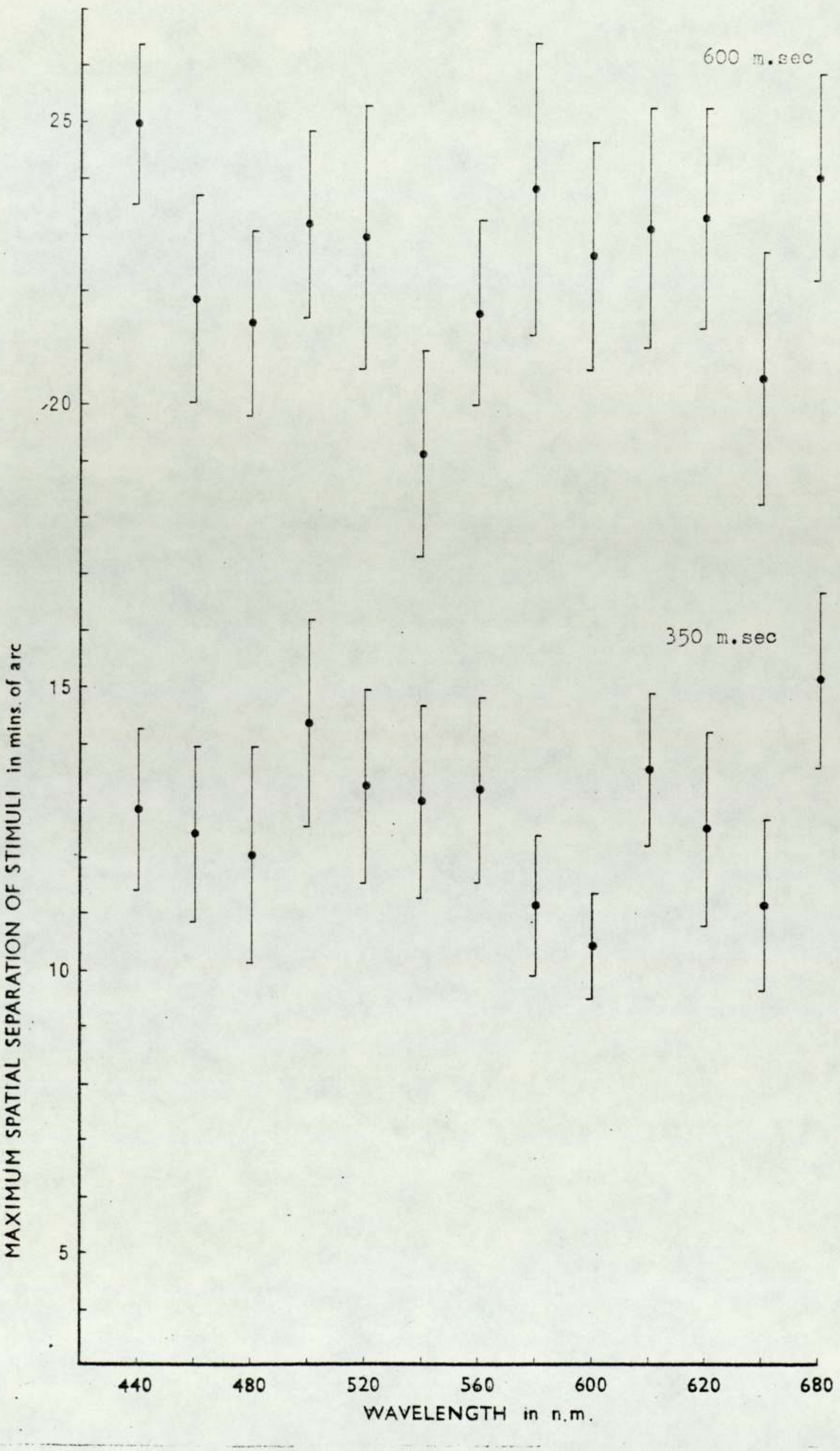
Graph Vc The Maximum Spatial Threshold Plotted against Stimulus Wavelength for Cycle Times of 250 and 500 m.sec.



Graph Vd The Maximum Spatial Threshold Plotted against Stimulus Wavelength for Cycle Times of 300 and 550 m.sec.



Graph Ve The Maximum Spatial Threshold Plotted against Stimulus Wavelength for Cycle Times of 350 and 600 m.sec.



A fairly marked increase in the threshold peak at 440 n.m. occurs with longer cycle times of 550 and 600 m.sec. Little change is noted in the second peak, found at about 560 n.m. The third peak appears in the region of 600 n.m. moving to 580 n.m., whilst the fourth peak now appears to be located at 640 n.m. At 680 n.m. there appears to be a sharp increase in threshold for these cycle times compared to those noted earlier. Generally the peaks become more pronounced with increased stimulus duration.

To summarise, the presence of four distinct peaks may be noted from the results giving the maximum spatial separation for beta motion for each stimulus cycle time. Two of these appear invariably located at 440 and 500 - 520 n.m., becoming more pronounced with increasing stimulus duration. A third peak, initially found at 640 n.m., gradually appears to move with increasing stimulus duration until it is located at 580 n.m. A fourth peak found with cycle times greater than 250 m.sec similarly appears to change with increased cycle time to be finally located at 640 n.m. This interaction effect between stimulus wavelength and duration has been shown to be very significant. With cycle times of 550 and 600 n.m. a distinct increase in the maximum spatial threshold is found in the region of 680 n.m.

It is difficult to speculate upon the threshold trends observed using a cycle time of 250 m.sec, since two results (those attained with stimulus wavelengths of 560 and 600 n.m.) appear to produce an increase in threshold inconsistant with the general trend. Such results may arise due to experimental error, although the standard duration of these points appears to be consistant with that generally observed and does not betray marked variability amongst the results. Alternatively the exaggerated results may arise because of a particular interaction between stimulus frequency and wavelength.

CHAPTER IX

The Effect of Retinal Location on Apparent Motion

It has been suggested that the maximum spatial threshold for optimal apparent motion may be linked with the sensitivity of cone inputs to the spectrally opponent mechanism. An earlier comparison of vertical and horizontal thresholds revealed a significant difference to be present. Both spectral sensitivity and distribution of cone types might play a significant role in determining the maximum spatial threshold. Having established the typical variation in threshold with wavelength for central fixation, the possible effect of cone population changes may be observed using eccentric fixation. From the time of Aubert (1886), variations in movement sensitivity with retinal location have been known. Changes in the spatial threshold for beta motion may therefore be anticipated. A typical graph of the distribution of rods and cones in the human retina is shown (Fig. 16). Marked changes occur over 10 degrees of retinal eccentricity.. The following experiment was designed to reveal changes in the maximum spatial threshold for optimal apparent motion which might occur over this region.

Method

Six male subjects were used to determine the maximum spatial threshold for optimal apparent motion for eccentric retinal areas. Horizontal thresholds were determined for stimulus wavelengths ranging from 420 to 680 n.m. at 20 n.m. intervals, and for degrees of eccentricity ranging from zero to 10 degrees at 2 degree intervals. A stimulus cycle time of 450 m.sec was employed. An adjustable fixation point was fixated by the subject allowing the stimuli to be viewed

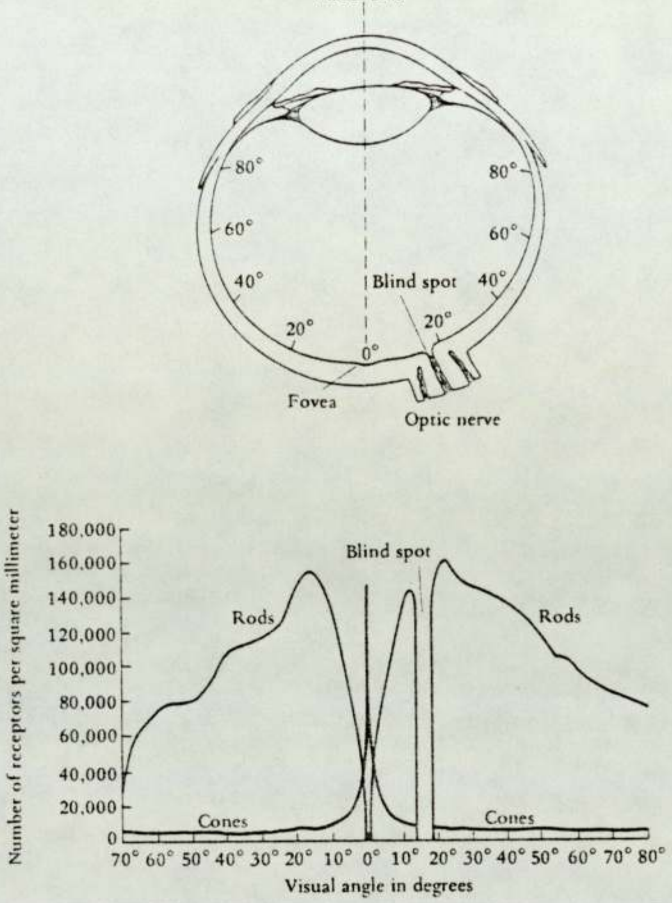
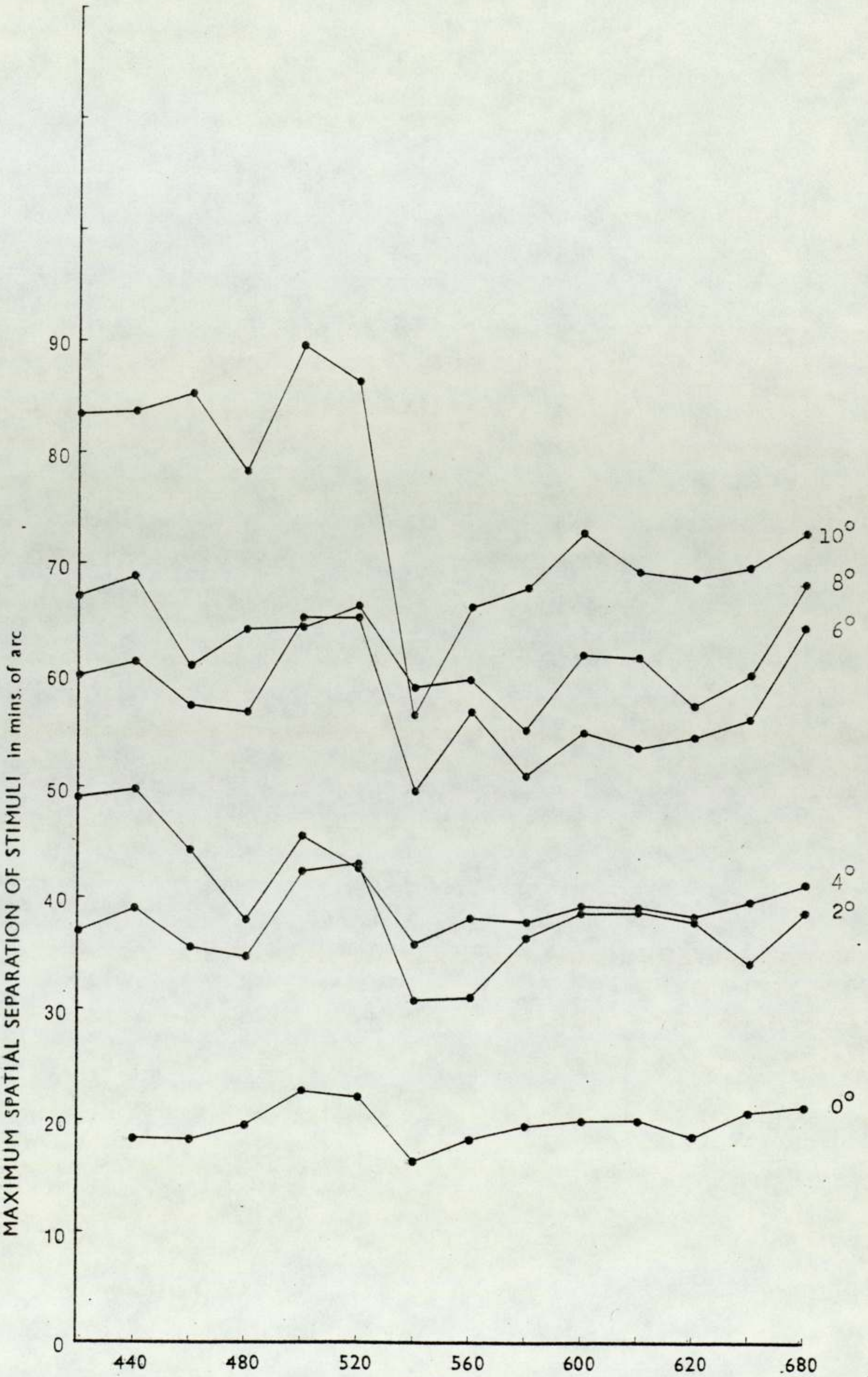


Fig. 16 Density distributions of rod and cone receptors across the retinal surface (from Pirenne, 1967).

Graph VII The Maximum Spatial Threshold for Optimal Apparent Motion plotted against Stimulus Wavelength with Increasing Retinal Eccentricity.



eccentrically. During each experimental run the subject viewed all wavelengths at one level of eccentricity in a completely randomised order. It was considered too time consuming to re-arrange the fixation point after each mean result had been obtained, thus the two factors of eccentricity and wavelength were not completely randomised. The order in which each group of eccentric stimuli were viewed was completely randomised for each subject, although results with central fixation which were obtained first acted as a training session. Thus the randomness of each result was almost certainly ensured. The remaining experimental conditions were identical to those already outlined. A randomised block factorial design (RBF - 614), the assumptions of which have already been discussed, was employed for statistical analysis.

Results

The statistical hypotheses tested by the RBF - 614 design may be listed as follows:-

$H_{0,a}$: The maximum spatial threshold for optimal movement is unaffected by retinal location.

$H_{0,b}$: The maximum spatial threshold for optimal movement is unaffected by stimulus wavelength.

$H_{0,c}$: No significant interaction effects occur between stimulus wavelength and retinal location.

$H_{0,d}$: No significant variation occurs within the blocks.

(The alternative hypotheses are omitted for brevity.)

Significance level : $\alpha = 0.001$

The critical regions for the rejection of the null hypotheses, and the acceptance of the alternative hypotheses, are as follows:-

$H_{0,a}$: $F \geqslant F_{(5,415)} = 4.10$

$H_{0,b}$: $F \geqslant F_{(13,415)} = 2.74$

$H_{0,c}$: $F \geqslant F_{(65,415)} = 1.66$

$H_{0,d}$: $F \geqslant F_{(5,415)} = 4.10$

Graph VIII The Average Increase in Maximal Spatial Threshold for Optimal Apparent Motion with Increasing Eccentricity.

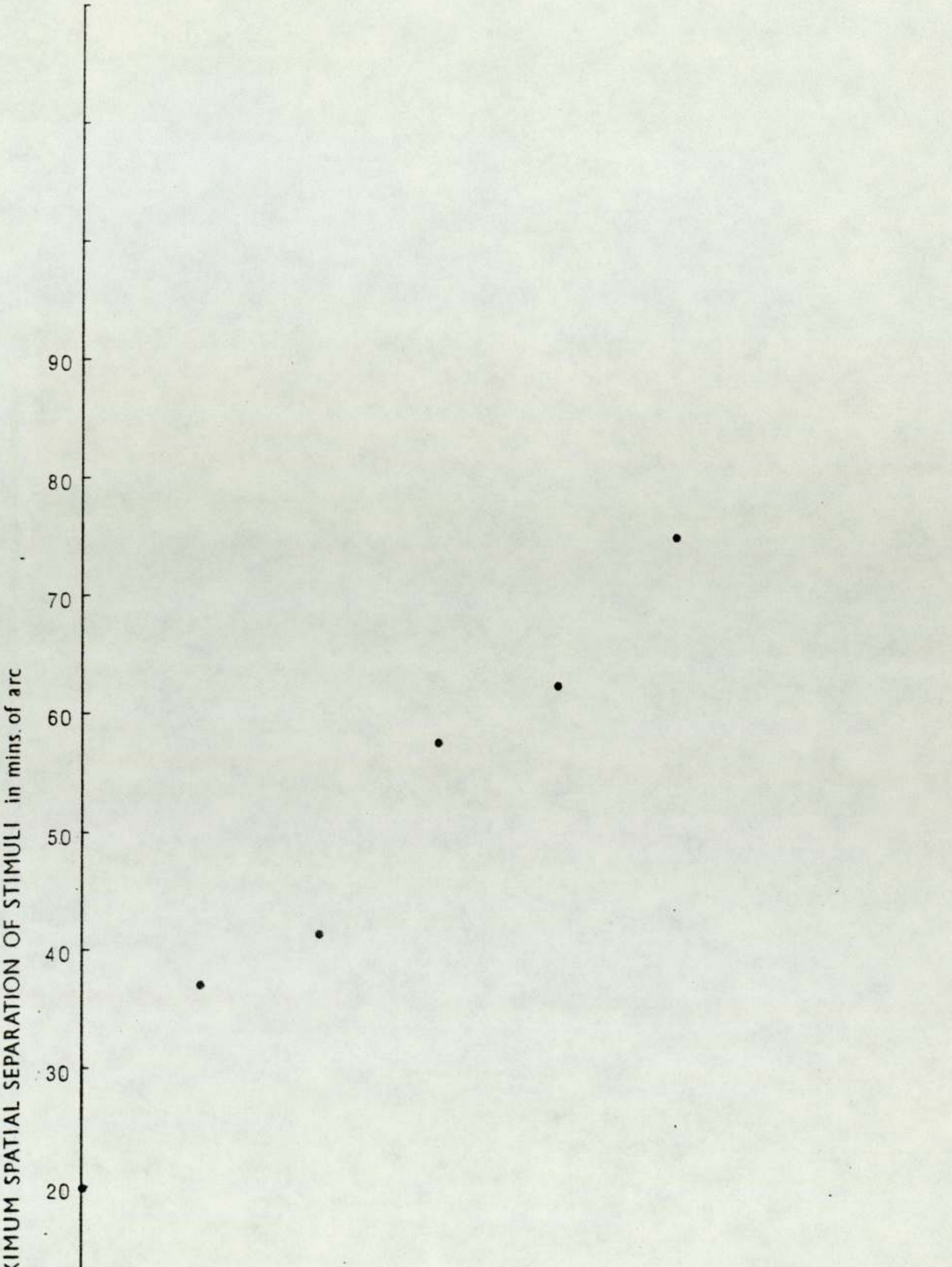


Table 6.

source of variation	s.s.	d.f.	var. est.	F	
Blocks	14.770	5	2.954	0.267	N.S.
Treatments	179,251.710	83			
Retinal Location	166,181.344	5	33,236.269	3,000.109	*
Wavelength	7,776.100	13	598.161	53.994	*
Interaction	5,294.266	65	81.450	7.352	*
Residual	4,597.516	415	11.078		
Total	183,863.996	503			

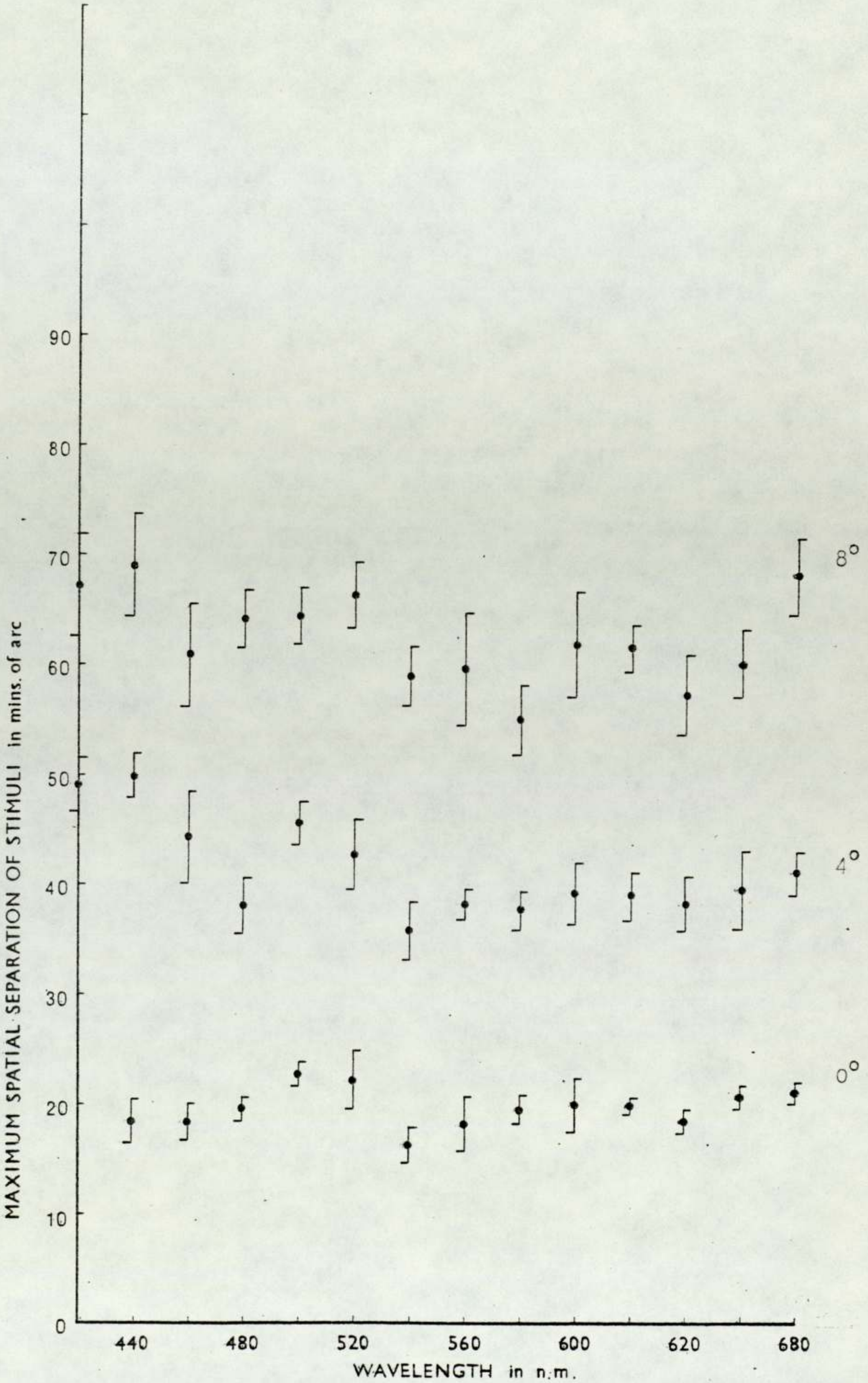
* $P < 0.001$

Three of the null hypotheses ($H_{0,a}$; $H_{0,b}$; and $H_{0,c}$) outlined earlier may be confidently rejected. The maximum spatial threshold for optimal movement is significantly influenced by both retinal location and stimulus wavelength. Significant interaction effects are also present between retinal location and stimulus wavelength. No significant variation occurs within the blocks, since $H_{0,d}$ is not rejected at any significance level. The maximum spatial threshold for beta motion, for eccentricities ranging from zero to 10 degrees, plotted against wavelength are shown in Graph VII. The usual standard deviation marks have been omitted for clarity and individual results for each cycle time have been linked with lines.

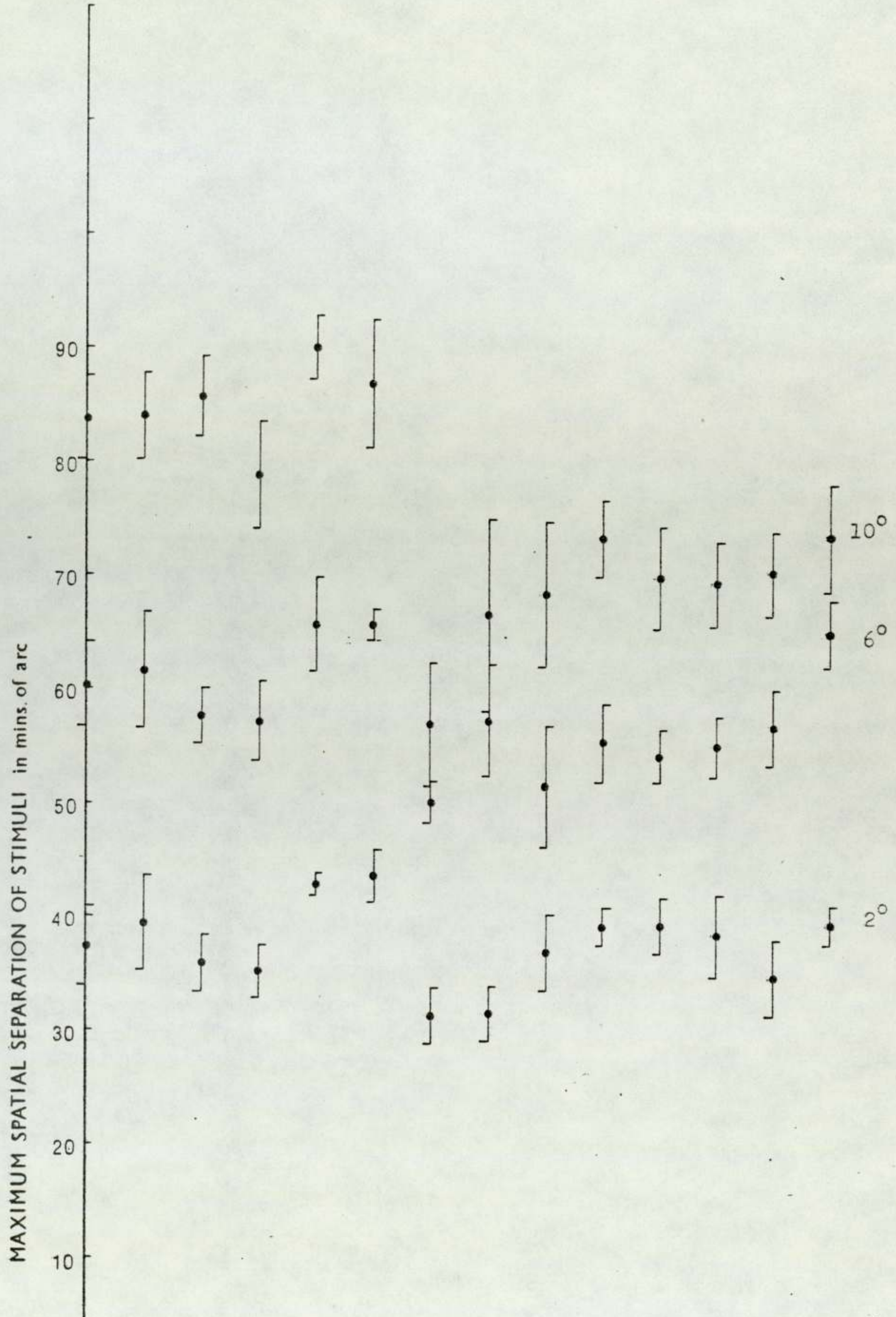
It may be seen that the variation of spatial threshold with wavelength observed foveally with a cycle time of 450 m.sec, is maintained in the peripheral field. The general trend shown in Graph VIII is for an approximately linear increase in the maximum spatial threshold with increasing eccentricity.

The threshold peaks observed foveally at 440 n.m., 500 - 520 n.m., 600 - 620 n.m., and 680 n.m. are maintained with eccentric fixation up to 10°. These peaks become more prominent with increasing eccentricity. The peak found at 440 n.m., however, becomes more

Graph VIIa The Maximum Spatial Threshold plotted against Stimulus Wavelength for Eccentricities of 0, 4 and 8 degrees.



Graph VIIb The Maximum Spatial Threshold plotted against Stimulus Wavelength for Eccentricities of 2, 6 and 10 degrees.



marked in relation to the other three with increasing eccentricity of 4° and above. Graph VII indicates that significant interaction effects which are present arise principally from spatial threshold changes occurring in the short wavelength region.

Generally, an increase in the variability of results obtained for eccentric positions produces an increase in their standard deviation. Decisions concerning movement criteria become very difficult with eccentric fixation, and the experiment becomes much more demanding. It should be mentioned that the average spatial threshold obtained with central fixation for a cycle time of 450 m.sec is about 19.6 mins. of arc. A result of 17.6 mins. of arc was the mean obtained from eight different subjects in an earlier experiment. Although inspection reveals the difference not to be statistically significant a reason for its occurrence might be postulated. In the preceding experiment eight subjects were given a complete practice run before the results were obtained. Later, this extensive training was considered unnecessary and in this experiment very little training was given. The experimental run performed with central fixation was regarded as a training session for eccentric experimental determinations. The naive subjects may not have been quite so critical or analytical in their viewing of optimal movement, and so tended to see it more readily than did experienced observers. The result would be a slight increase in the spatial threshold for optimal movement compared to that obtained earlier.

CHAPTER X

Discussion

The statistical inferences drawn from experimental work, outlined in the preceding chapters, may be summarised as follows:-

(a) The maximum spatial threshold for optimal apparent motion varies significantly with the wavelength of the stimulus.

(b) Significant differences exist between horizontal and vertical spatial thresholds for apparent movement.

(c) Significant increases in the maximum spatial threshold occur with increasing retinal eccentricity of up to 10 degrees.

Temporal characteristics of the stimulus have similarly been shown to influence the maximum spatial threshold for beta apparent movement, since . . . . .

(d) Temporal overlap of stimuli produces a significant fall in the maximum spatial threshold.

(e) Increasing the stimulus duration generally produces larger maximum spatial thresholds for optimal apparent motion, although variations occur depending upon stimulus wavelength.

The fundamental question underlying any discussion of optimal apparent motion must concern the mechanism by which it is perceived. Kolers (1963) stressed the differences between real and apparent motion, whilst Frisby (1969, 1972) argued strongly that both were perceived by identical mechanisms. These arguments were reviewed in Chapter II. Kolers (1972a) was, in a sense correct, when he stated "visual experience is not to be equated with responses from single cells in the visual cortex, however enlightening those discoveries

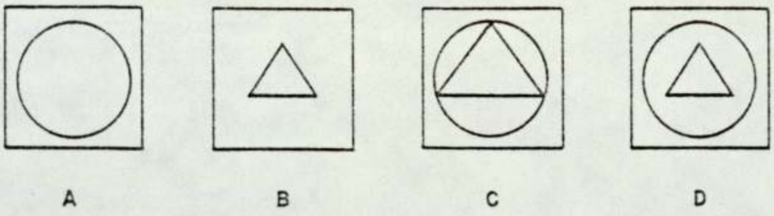


Fig. 17 Selectivity of the motion percept. When the square is alternated with the enclosed shapes in A, B or C, smooth deformation is seen; in D, however, motion is seen only between circle and square, while the triangle blinks on and off.

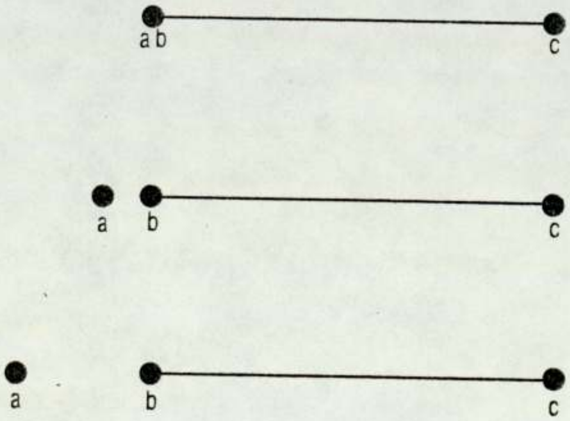


Fig. 18

may be in other respects". Although a movement sensitive cell may fire in the cortex, the process of interpretation does not end there. Such interpretive processes are difficult to speculate upon, but movement sensitive cells may subserve an identical role to that played by spectrally opponent cells in colour perception. Kolers (1972b) cites an experimental example which, he suggests, makes a theory of apparent movement based on movement-sensitive cells untenable. If in Fig. 17 the square A or B is alternated with its enclosed figure, using the "proper timing", a smooth continuous transformation occurs between them; the circle or triangle changes smoothly into the square, and vice-versa. This still occurs if a composite internal figure is used as with square C. If square D is alternated with the enclosed figure only the circle transforms into the square whilst the triangle flashes on and off. The targets are quite large, the circle subtending a diameter of 3 degrees. If movement sensitive cells are advanced as an explanation of apparent movement, then any suitable stimulus occurring within the receptive field of the cell must move. The triangle in Fig. D fails to move, although movement is observed with Fig. B, thus an explanation in terms of movement sensitive cells is impossible.

Extensive research on movement sensitive cells, reviewed earlier, has firmly established them as playing a fundamental role in movement perception. This role cannot be denied by any superficial argument, which advances a particular observation defying explanation in these terms. The question is whether the "problem for theory", outlined by Kolers, provides sufficient evidence that movement-sensitive neurones are not responsible for the perception of real or apparent movement, since no other theory has been advanced. Alternatively, can such observations be explained in terms of movement sensitive cells, and their receptive fields, acting as the building blocks of movement perception.

In the light of work on movement-sensitive neurones, for which a response to stroboscopic stimuli is considered a diagnostic test, Grüsser and Grüsser - Cornehls (1973) have asserted that they are responsible for apparent movement. The classification of these cells has already been considered in Chapter IV. It is suggested that the role played by cells having highly specific stimulus characteristics, with respect to size and orientation, may not be identical to that undertaken by more simple M- and DS- cells. These latter cells are found to respond well to apparent movement. Complex cell types appear responsible for detecting movement in large sections of the visual field. Simple cells may, therefore, be used to detect the motion of a small object traversing a stationary field, whilst complex cell types perceive movements of the field occurring when the eyes pursue a moving object. Thus, let us consider Kolers "problem" in terms of simple movement sensitive neurones and ascertain whether these could offer any explanation of his observations.

The angular subtense of Kolers' stimuli exceeded 3 degrees, far larger than the receptive field size encountered for movement sensitive cells in the central field. Although the excitatory receptive field size is dependent upon the stimulus characteristics, it may be assumed that the whole stimulus pattern does not fall within the margins of a single field. However, receptive fields generally display extensive overlapping in the retina. A smooth, continuous transformation will be observed between the alternating stimuli of figures A and B if an annular arrangement of movement sensitive neurones are suitably stimulated. Stimulus D may be similarly considered with reference to three linearly arranged stimuli (Fig. 18), two of which (a and b) alternate with the third (stimulus c). Assuming both asynchronous stimuli b and c are incident upon the excitatory receptive field of a movement sensitive neurone, optimal apparent motion would be seen. Synchronous stimuli (a and b), even when incident upon the excitatory receptive field, fail to produce apparent motion and movement between a and b will not be seen. Thus the triangle of stimulus D would not be seen to move. Apparent motion could occur between all three, using the "proper timing", so that stimuli appeared sequentially. Both temporal and spatial relationships of stimuli producing apparent motion are important. Finally, stimulus c may be considered with reference to Fig. 18 When the synchronous stimuli a and b are superimposed (as when the triangle of stimulus C touches the circle) optimal apparent motion is seen between them and the asynchronous stimulus c. When stimulus a is observed to be separate from stimulus b movement is no longer seen between them, since apparent movement does not occur between synchronous stimuli. The apices of the triangle in Kolers' stimulus C will therefore undergo optimal apparent motion together with the circle. Further, the whole triangle is obliged to undergo apparent motion avoiding the alternative, in which the figure would appear to disintegrate. Kolers (1972b), himself, noted that the visual system did not abstract out from a figure only the parts that are being alternated, allowing them to move whilst the rest remained stationary; instead the whole figure was seen to move. Kolers (1972b) conceded that the majority of examples, in which complex figures are found to undergo apparent movement, could be explained in terms of movement sensitive neurones and their receptive fields. The "problem for theory" cited above was offered by Kolers (1972a,b) as a major argument against the acceptance of theories of movement perception based on movement sensitive neurones. Clearly these arguments,. flying in the face of overwhelming evidence supporting the role played by movement sensitive neurones in real and apparent motion, cannot be sustained.

In view of their response to asynchronous or stroboscopic stimuli, movement sensitive neurones (particularly M- and DS- neurones) are strongly implicated as the mechanism by which apparent movement is seen (Grüsser and Grüsser - Cornehls, 1973). If two alternating stimuli impinge upon the excitatory receptive field of a movement sensitive neurone the illusion of a single moving stimulus is seen. This continues, as the spatial separation of stimuli is increased, until only one stimulus remains incident upon the excitatory receptive field and apparent movement immediately ceases. The maximum spatial threshold for optimal apparent motion, for specific stimulus parameters, therefore represents the perceptive field size of a movement sensitive neurone. No investigation has been carried out into the appearance of non-optimal or partial apparent movement, which has often been described as "a moving black space". It is only possible to speculate very tentatively upon the reasons for its appearance. It is known that both M- and DS- neurones respond to stroboscopic stimuli, although no estimates of their size in man have been made. Any pair of suitable stimuli are capable of firing both cell types simultaneously, but differences in their excitatory receptive field size could produce response differences as the spatial separation of the stimuli is increased. Since a DS neurone may have to sample a larger retinal area before responding to a stimulus moving in a specific direction, it may possess a relatively larger excitatory receptive field than the more simple M- neurone. Two alternating stimuli falling within or without both excitatory receptive fields pose no problem, the responses are consistent. If field size differences do occur, response inconsistencies will arise under certain conditions in which DS- nuerones signal movement whilst M- nuerones fail to respond. The problem posed to the visual system, when this is observed under experimental conditions, may be resolved as partial or non-optimal movement. Braddick (1974) has suggested the existence of two processes mediating apparent movement acting at different levels in the visual system. It should be recalled, however, that not all movement sensitive neurones respond well to alternating stimuli. Another explanation might be based on findings that off-centre cells have larger receptive fields than on-centre cells (Hubel, 1960; Fischer and May, 1970), although some workers note little difference in size (Jung and Spillman, 1970).

It has been noted that repeated stimulation of movement sensitive neurones results in a diminished response (Barlow and Hill, 1963; Hubel and Wiesel, 1965). Accordingly, optimal motion was never viewed by a subject for more than a few seconds at a time in each experimental run.

Results reviewed in Chapter VI demonstrate that the maximum spatial threshold for optimal apparent motion is influenced by stimulus wavelength. A number of workers considered the effects of colour on apparent motion (Wertheimer, 1912; van der Waals and Roelofs, 1930, 1931; Squires, 1931). All reported apparent motion between disparately coloured flashes, but did not systematically investigate the effects of colour on the phenomenon. The role played by spectrally opponent cells in processing colour information has been discussed in Chapter III. The responses given by four spectrally opponent, and two non-opponent, cell types to monochromatic light flashes are shown in Fig. 3 . Close similarities exist between those wavelengths producing maximum activity in spectrally opponent mechanisms (DeValois et al., 1966) and those giving the greatest spatial thresholds for optimal apparent motion. A comparison is given in the table below.

Opponent Cell Type	Wavelength Producing Maximum Activity	Wavelength Giving Greatest Spatial Thresholds for Optimal Motion
+ B – Y	440 n.m.	440 n.m.
+ G – R	520 n.m.	520 n.m.
+ Y – B	610 n.m.	600 n.m.
+ R – G	660 n.m.	680 n.m.

Similarly, DeValois (1965) added together the responses obtained from a sample of macaque lateral geniculate opponent cells to monochromatic light flashes (Fig. 8 a). It can be seen that the entire response at 520 n.m., for example, is given by + G – R cells.

Similar results to those of DeValois (1965) and DeValois et al.

(1966) were obtained by Boynton and Gordon (1965) using a "colour naming" technique referred to earlier (Fig. 8). The technique is questionable because the instructions given to a subject are restrictive since four specific colour names, blue, green, yellow and red, are given beforehand. This must pre-determine the experimental outcome. Graham (1965) has cited Rivers (1901) who found a group of Australian tribesmen to have only three colour names. One assumes that their colour vision was found to be normal. Myers (1908) stated that "Language affords no safe clue to sensibility. A colour name occurs when it is needful. When it is needless it will not be formed, be the sensibility to that colour ever so great". This is typified by the fact that Eskimos have many more verbal responses to snow than Europeans (Klineberg, 1954). Boynton and Gordon (1965) consider the colour-naming technique to be an adequate method for demonstration of the Bezold Brucke phenomenon, and Jacobs and Gaylord (1967) have used the technique to demonstrate chromatic adaptation. Very close similarities exist between the results obtained for colour naming and apparent movement response to monochromatic wavelengths.

Earliest investigations demonstrated that the sensitivity distribution of the receptive field determines its size when measured using stimuli of different intensities (Hartline, 1940). Both spectrally opponent and non-opponent receptive fields appear to possess overlapping excitatory and inhibitory sensitivity distributions (Wagner et al., 1963). The response characteristics of spectrally opponent cells to monochromatic wavelengths agree very closely with those of movement sensitive cells determined by spatial thresholds for beta motion. Results suggest that movement sensitive neurones receive stimuli which have previously undergone colour processing by spectrally opponent cells. The wavelength sensitivity distribution of a movement sensitive neurone would, therefore, be determined by that for a spectrally opponent cell, and receptive

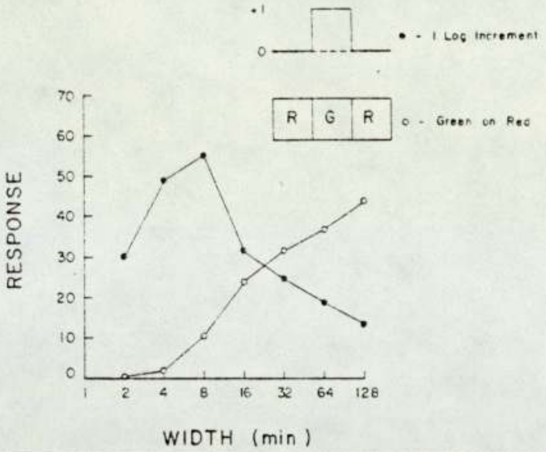


Fig. 19 Responses of an LGN +G -R cell to stimuli of different widths, each centered on the RF. This experiment was carried out with two types of stimuli: a 1-log-unit increment in white light (solid dots); and a shift from a red field to a green line on a red field, the red and green being equated for luminance to produce a pure colour change (open dots). Spatial tuning is seen for the luminance but not the colour stimulus.

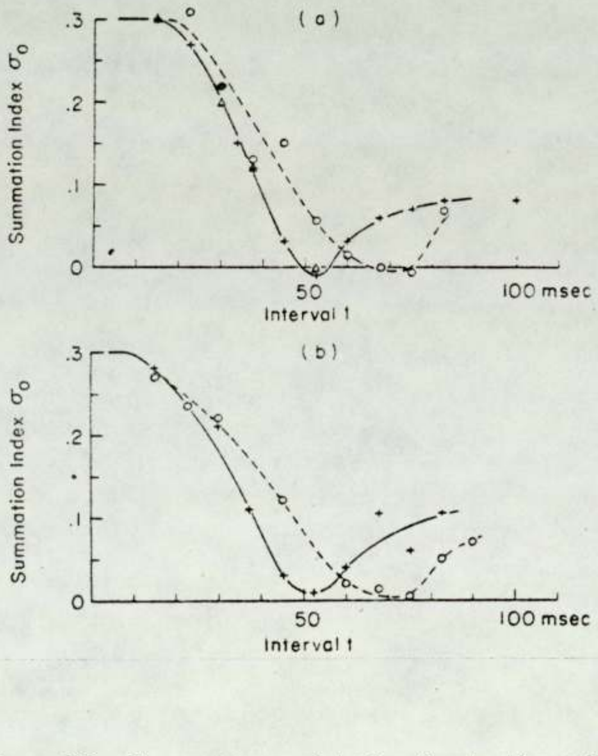


Fig. 20 Summation obtained at threshold between two pulses of light as a function of their temporal separation. Results for one subject are shown. Crosses represent a 328-td adapting level and open circles a 61·2-td adapting level. Part (a) is for positive pulses and (b) for negative pulses. (From Ikeda (1965).)

field size would vary accordingly.

A major underlying assumption of the experiment is that narrow bandwidth stimuli (mean bandwidth 4.7 n.m.), subtending about 2.0 mins. of arc, stimulate spectrally opponent cells by means of their cone inputs. Extensive overlapping of receptive fields occurs in the central retina and stimuli of such narrow bandwidth may be considered to be practically monochromatic. It has been pointed out, however, that spectrally opponent cells can only discriminate between wavelengths in the case of fairly large stimuli (DeValois and DeValois, 1975). With high spatial frequency stimuli, spectrally opponent and non-opponent cells become alike in their responses, opponent cells losing their ability to discriminate colours responding only to luminance. In these circumstances colour vision is lost (Van der Horst and Bouman, 1969). The response of a + G - R cell in the lateral geniculate to stimuli of different widths (DeValois and DeValois, 1975) is shown in Fig. 19. This would seem to indicate that a + G - R cell responds to a white spot subtending about 2 mins. or arc whilst failing to respond to a similar green spot. The green spot is presented on a red background of equal intensity so that only a colour change is present. Later, however, DeValois and DeValois (1975) state:-

> "The + G - R cell fires optimally to a green object on a green surround, i.e., with no contrast. A maximum colour contrast stimulus of green on red would be a quite ineffective stimulus, the green producing excitation from the receptive field centre, but the red evoking inhibition from the surround."

Small coloured stimuli on a black background therefore provide a very effective stimulus for spectrally opponent cells, and subjects viewing the stimuli can distinguish their colour. By the same token small white stimuli would provide an optimal stimulus for + Wh - Bl cells.

It has generally been assumed from early work that simple receptive fields are approximately circular or oval in shape (Hartline, 1940; Hubel and Wiesel, 1960). Results from Chapter VI, however, indicate that significantly larger maximum spatial thresholds are found for vertical apparent motion. Since identical stimuli are used, the the most likely reason for the 30 per cent difference between vertical and horizontal spatial thresholds is an elliptically-arranged receptive field of a movement sensitive neurone. The spatial arrangement of a receptive field will also influence the maximum spatial threshold for optimal apparent motion.

Results outlined in Chapter VII have demonstrated the effect of temporal overlap of stimuli on the maximum spatial threshold for optimal apparent motion. Apparent motion is not seen with synchronous stimuli even when both impinge upon the excitatory receptive field of a movement sensitive neurone. Results show, however, that optimal apparent movement is seen with quite extensive temporal overlap of stimuli. The interstimulus interval has been regarded as important by a number of workers (Neuhaus, 1930; Kolers, 1964; Kolers and Pomerantz, 1971) and the response of movement sensitive neurones are known to be dependent upon the angular velocity of the stimulus (Finkelstein and Grüsser, 1965; Grüsser et al., 1966). Thus it appears that stimulus velocity has different effects upon excitatory and inhibitory mechanisms, presumably because of their different temporal characteristics. Gantz (1975) has described the effect of presenting double pulses and varying stimulus onset-to-onset asynchrony. In its response to a brief light flash, the visual system undergoes a bivalent sequence of excitation followed by inhibition. If the asynchrony is about 40 - 70 m.sec the effect of the second stimulus is attenuated. Baumgardt and Segal (1946) obtained temporal summation when the asynchrony of the two stimuli was short, less than 40 m.sec. When the asynchrony was in the range of 50 - 80 m.sec, the second stimulus appeared relatively dim. With asynchrony in excess of 100 m.sec, however, the inhibitory interaction diminished considerably. Ikeda (1965) obtained similar findings (Fig. 20), inhibition occurring with asynchrony of 50 - 70 m.sec, the stronger pulse inhibiting the weaker. If one pulse was positive and the other negative, with this degree of asynchrony, summation occurred. Optimal apparent movement is seen when both stimuli impinge upon the excitatory receptive field, provided a difference exists in their onset-to-onset time of greater than 75 m.secs. This may be assumed only for the stimulus characteristics already outlined. It does indicate that the second stimulus of an asynchronous pair plays an inhibitory role, and that inhibitory influences acting upon a movement sensitive neurone reach it ahead of excitatory effects. Braddick (1973) has described a similar effect produced by the action of a flash during the interstimulus interval of apparent motion using random dot patterns (Julesz, 1960, 1971). The masking flash is considered to destroy the information necessarily stored by motion detectors. Braddick found that the action of the masking flash was greater if used in the early part of the interstimulus interval. The masking effect did not occur if the flash and pattern were delivered to different eyes suggesting that its effect occurred pre-cortically.

Further results employing temporal separation of the stimuli (Chapter VII) demonstrate that a small interstimulus interval, similar to that used by many early workers, increases the maximum spatial threshold. Results indicated that an interval of about 75 m.sec is optimal. It is self evident that stimuli having a very great temporal separation fail to produce beta motion. Graph IVa clearly shows that as the temporal separation is increased beyond 75 m.sec the maximum spatial threshold for beta motion falls. When the onset of the second stimulus coincides with the offset of the first, it appears to partially inhibit the response of the movement-sensitive neurone. If the second stimulus is delayed slightly, after cessation of the first, the movement-sensitive neurone responds fully. It would appear that excitation of the neurone continues for a short period after the

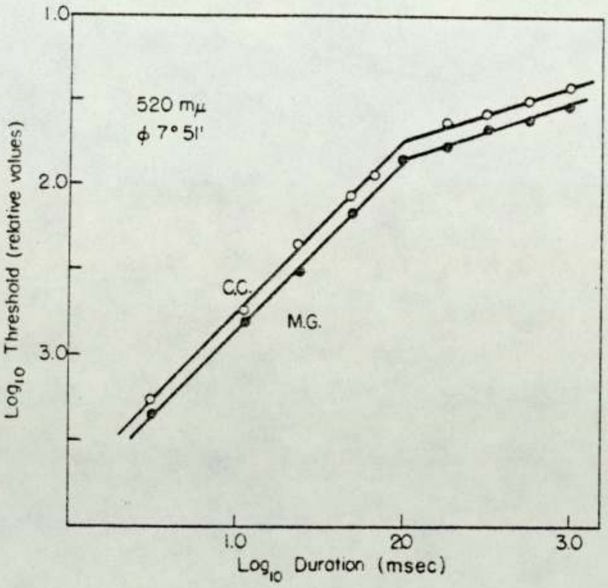


Fig. 21 An illustration of Bloch's law. The logarithm of the intensity of a flash threshold (units are arbitrary) plotted against the logarithm of its duration. For durations under 100 m.sec the slope = -1. This slope indicates 1 x t = k at threshold. Data for two observers. Flash wavelength = 520 n.m. Target size = 7° 51'. (From Baumgardt & Hillmann (1961).)

stimulus ceases. The maximum spatial extent of the receptive field occurs when the movement-sensitive neurone responds fully. At this point the maximum spatial threshold for beta motion reaches its greatest extent.

When the temporal duration of the alternating stimuli is increased, a similar change is observed in the maximum spatial threshold for optimal apparent motion (Chapter VIII). It has earlier been suggested that variations in the spatial threshold with stimulus wavelength arises from the spectral sensitivity of spectrally opponent mechanisms. The effects of stimulus duration, along with those of intensity, are photochemically related in terms of the Bunsen-Roscoe Law, which holds that

$$I \times t = k$$

where I is the stimulus intensity, t is its duration, and k is a constant. An identical relationship underlies most temporal perceptual phenomena, provided that t is less than the critical duration, and is termed Bloch's Law. An example of Bloch's Law is given in Fig. 21 from an experiment by Baumgardt and Hillmann (1961), in which detection thresholds were established for a large stimulus (48.6 sq. degrees of arc). Perfect temporal integration (Bloch's Law) applies for a stimulus duration of up to 100 m.sec, beyond which temporal integration is still found although no longer perfect. The estimate of critical duration is therefore 100 m.sec, agreeing well with the estimate for foveal vision of 99 m.sec mode by Herrick (1956). Barlow (1958) found perfect temporal summation for pulse durations up to 100 m.sec. Blackwell (1963) suggested the critical stimulus duration to be 87 m.sec, whilst work on the human electroretinogram also indicated the critical duration to be 100 m.sec (Johnson and Bartlett, 1956). The critical duration is known to be affected by a number of variables. Light flashes against black backgrounds produce shorter critical durations than found using dark backgrounds (Graham and Kemp, 1938; Barlow, 1958; Sperling and Jollife, 1965; Roufs, 1972a). This may be ascribed to receptor interactions.

Although the critical duration rarely exceeds 100 m.sec a marked increase is found with moving test targets (Van den Brink, 1957) producing values as high as 400 m.sec. Similar increases are found for shape recognition tasks involving Landolt-C test targets (Kahneman and Norman, 1964). Baumgardt and Hillman (1961) have shown that, even when the critical duration is exceeded, a linear relationship may still be found between intensity and stimulus duration. This was established for stimulus durations from 100 to 1000 m.sec. This linear relationship for slightly supra-threshold stimuli established by Blondel and Rey is inapplicable for higher luminances, where initial fluctuation occurs. With constant low intensity stimuli however, the visual response is dependent solely upon stimulus duration.

The effect of stimulus duration on optimal apparent motion, averaged for all wavelengths, is shown in Graph VI. Doubling the stimulus duration doubles the maximum spatial threshold over which optimal apparent motion is seen. The maximum spatial threshold for optimal apparent motion is dependent upon the size of the excitatory receptive field of a movement-sensitive neurone. It has been suggested earlier that this field size was dependent upon the wavelength sensitivity distribution of spectrally opponent cells. Evidence suggests the existence of a linear relationship between stimulus duration and excitatory receptive field size of movement-sensitive neurones, displaying the typical characteristics of temporal integration.

Graph V shows the response to increased stimulus duration, which appears very consistent for wavelengths shorter than 540 n.m. although less so for longer wavelengths. It has been suggested that a gradual change in the loxation of the third peak occurs, from 640 n.m. to 580 n.m., as the stimulus duration is increased. Similarly the fourth peak, initially noted with a cycle time of 350 m.sec, gradually appears to change location from 680 n.m. (the longest wavelength stimulus available) to 640 n.m. No change in position was noted for the first

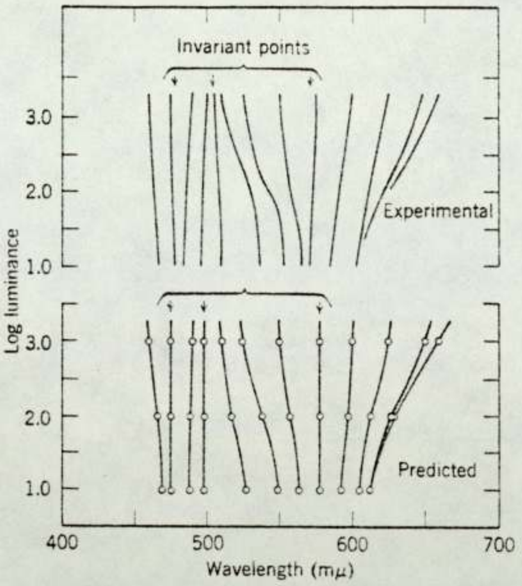


Fig. 22 The upper set of curves represents constant hue contours obtained by Purdy (1929). The lower set of curves represents computed contours as described in the text. (From Hurvich and Jameson, 1955.)

or second peaks at 440 and 500-520 n.m. respectively. It is well known that when a monochromatic light undergoes a substantial luminance change a subjective change in hue is produced, enabling it to be matched with a different monochromatic light of lower intensity. This is termed the Bezold Brucke Hue Shift. The constant hue contours (Fig. 22) experimentally predicted by Purdy (1929) were confirmed by a number of workers (Judd, 1951; Hurvich andJameson, 1955). Purdy had presented juxtaposed fields to the same eye for an indefinite period, during which the subject changed the wavelength of the dimmer field until a match for hue was obtained. Boynton and Gordon (1965) drew attention to two possible artefacts in Purdy's method. Since it has been well established that hue varies as a function of stimulus duration (Cornsweet, 1960), failure to control viewing time can produce extensive error. The most striking example occurs with a bright spectral red (630 n.m.) whose appearance changes to yellow or even green on prolonged viewing. Secondly, simultaneous contrast can occur between the halves of juxtaposed coloured fields. These artefacts were overcome by use of their colour naming technique referred to earlier. Significant effects were found with increased stimulus intensity (from 100 to 1000 trolands) in the yellow and red peaks (Fig. 23). It was found that long wavelength stimuli became yellower with extended viewing, compared to 300 m.sec flashes. Similarly DeValois et al. (1966) found the firing rate of lateral geniculate cells to be influenced by wavelength. Long wavelengths of low intensity produce more activity from + R - G than + Y - B cells, but the balance shifts toward + Y - B cells with increased luminance. This is consistent with the change in hue undergone by long wavelength stimuli with increasing luminance or flash duration.

Evidence suggests that changes in the maximum spatial threshold, for optimal apparent motion, with increased stimulus duration occur as a result of the Bezold Brucke Hue Shift. Increasing the stimulus

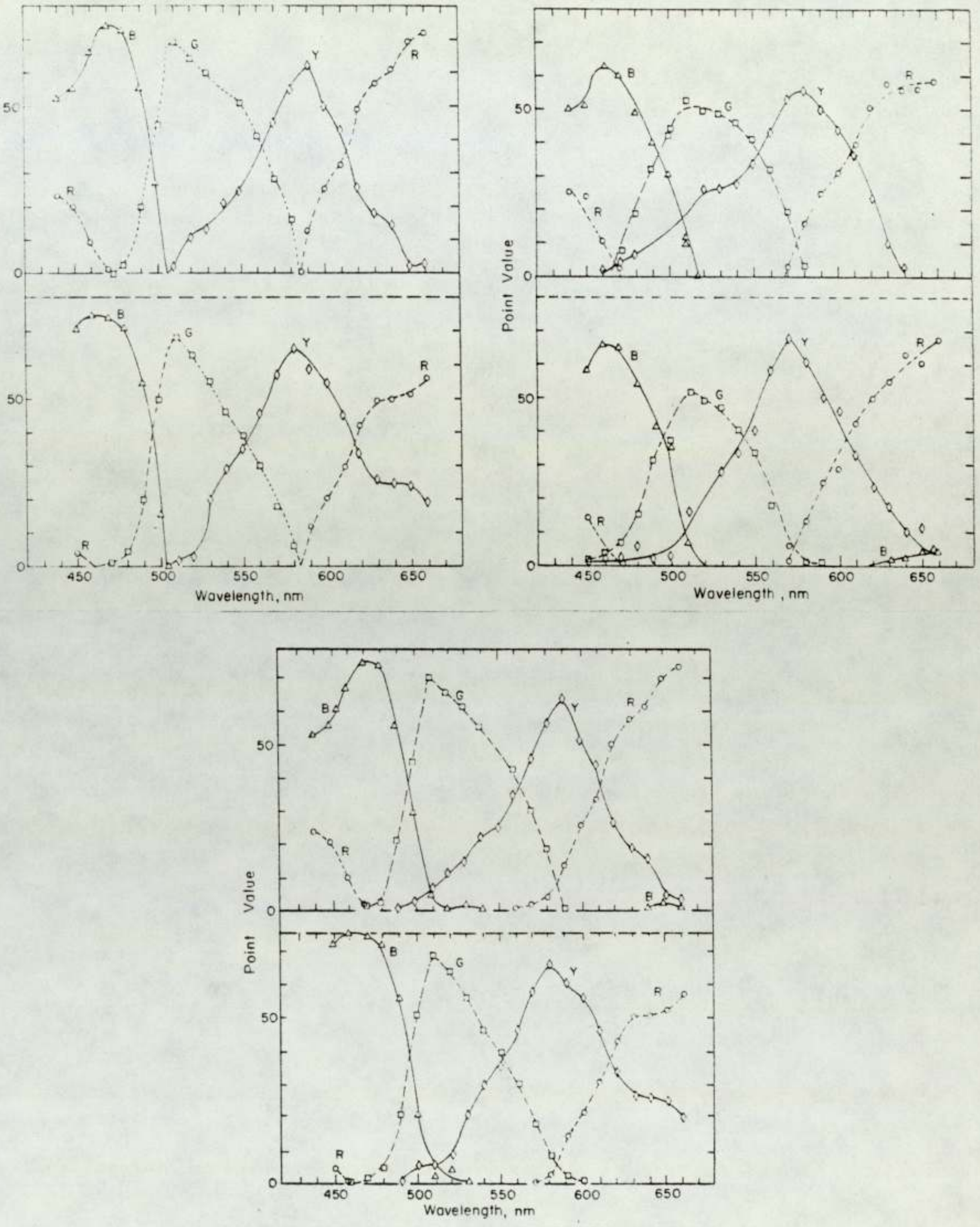


Fig. 23 Boynton and Gordon's (1965) colour naming data for three observers. Top for 100 trolands; bottom 1000 trolands.

duration causes the threshold peaks to occur at relatively shorter wavelengths, closer to the yellow region. This does not appear to occur at all for wavelengths shorter than 540 n.m. Threshold peak changes of 60 n.m. may occur for the third peak when stimulus duration is increased from 75 to 300 m.sec. The fourth peak may undergo a greater change. Changes observed by Boynton and Gordon (1965) for an increase in luminance of 1 log unit reached 15 n.m. for the yellow peak and 30-40 n.m. for the red maxima (Fig. 23). In respect of the Bezold Brucke Hue Shift temporal characteristics of the stimulus appear to play an important role. If spectrally opponent cells provide inputs to a movement-sensitive neurone, its response to a stimulus is dependent not only upon its duration and wavelength but also upon the interaction of these two factors.

The results outlined in Chapter IX clearly demonstrate that the maximum spatial threshold for optimal apparent motion varies with retinal location. The average increase in spatial threshold with retinal eccentricity is shown in Graph VIII. The trend up to 10° appears approximately linear. Richards (1971) inferred that the receptor field size of motion detectors increases in size rapidly with eccentricity, approximating to the logarithmic function of eccentricity over the range 0 to 16°. The technique utilised a small stationary test target, together with adaptation targets of various diameters. Richards ascertained the minimum adapting contrast for which a motion after effect was obtained, and generally targets having a diameter of 3 - 4° required less contrast for this to be produced. Since he suggested that motion detectors at the fovea subtend 3·5°, far greater than that found by most workers, it is not clear what type of motion detectors were stimulated. Peripheral vision is subject to substantial refractive errors which when corrected reduce - but not eliminate - differences which occur between peripheral and foveal motion thresholds (Leibowitz et al., 1972). It has been suggested by Leibowitz et al. (1972) that

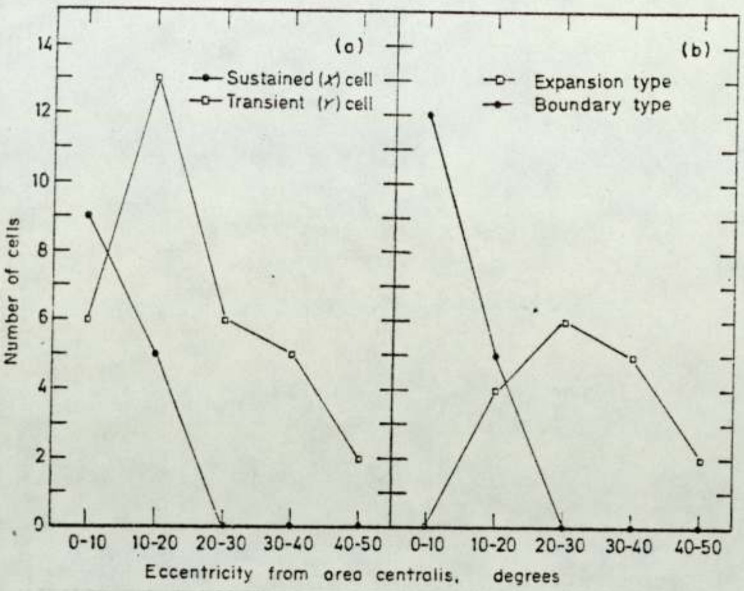


Fig. 24 Number of (a) "sustained" and "transient" cells, and (b) "expansion" and "boundary" cells encountered in different parts of the retina.

in the periphery all visual functions are degraded, but motion suffers least. Ikeda and Wright (1972) found that the receptive field size in cat increased linearly with eccentricity, confirming the results of earlier workers (Wiesel, 1960; Enroth - Cugell and Robson, 1966; Leicester and Stone, 1967; Fischer and May, 1970). Therefore, it is generally held that the peripheral retina has a higher motion sensitivity than does the fovea. Brown (1972) found that foveal acuity for a moving object declined linearly with angular velocity, whilst parafoveal acuity for a similar slowly moving target was better than that for a stationary object. This substantiates the argument that the peripheral retina is specialised for motion detection. Lichtenstein (1963), however, has presented evidence suggesting that the fovea is more sensitive to very slow motion than the periphery. Sekuler (1975) has argued that it is not possible to draw inferences concerning high velocity stimuli from Lichtenstein's data since the relationship may change completely. It is known that X and Y channels of both retinogeniculate and geniculostriate pathways differ in their receptive field size and conduction velocity (Enroth - Cugell and Robson, 1966; Hoffman, 1973). The optimum response of the two channels differ depending upon stimulus speed (Hoffman, 1973), Y cells exhibiting faster conduction and a more pronounced transient response to spatio-temporal modulation. Evidence suggests that the relative distribution of X and Y cells across the retina alters and that segregation between cells is maintained from the retina to the cortex, (Stone, 1972; Stone and Dreher, 1973). The distributions of "sustained" and "transient" cells, as well as "boundary" and "expansion" cells, with retinal eccentricity in the cat obtained by Ikeda and Wright (1972) is shown in Fig. 24. It is therefore suggested that X cells carry foveal information, whilst Y cells analyse peripheral stimulation. It has been noted that Y cells respond less to high spatial frequency stimuli than to low frequencies (Tolhurst, 1973). Tolhurst (1973) has suggested that the movement-dependent and movement-independent channels were human analogues of the transient and sustained (Y and X) neurones of the cat and monkey visual system (Enroth - Cugell and Robson, 1966; Gouras, 1968; Cleland et al., 1971). Sekuler (1975) has observed that the periphery displays a preference for low spatial frequency stimuli and high rates of temporal modulation or velocity. Results referred to earlier suggest that beta movement is not seen at the fovea if the velocity of the apparently moving object exceeds about 1.26 degrees per minute. The present results suggest that the excitatory receptive field of a movement-sensitive neurone increases with eccentricity. This allows beta motion to be seen with the apparent object having a higher velocity, reaching a maximum of about 5.5 degrees per second. This observation tends to confirm the suggestion that the periphery is more sensitive to higher rates of stimulus velocity - even when the velocity is quite low.

The general trend in the wavelength sensitivity pattern, exhibited foveally with a stimulus duration of 450 m.sec, is maintained with increasing eccentricity. Little change is noted in the percentage increase of the peak thresholds for optimal motion over the base line value. One possible exception is found in the blue end of the range at about 440 n.m. This peak becomes more prominent with increasing eccentricity particularly in the parafoveal region at 4°. The sensitivity of eccentric + B - Y spectrally opponent mechanisms therefore appears greater than that found centrally. Davson (1972) noted enhanced blue sensitivity in para- and peri-foveal regions between about 4 and 9 degrees of eccentricity. It is possible that rods play a role in colour perception and are particularly sensitive in blue region. A theoretical survey of existing evidence is provided by Stabell and Stabell (1973b). Foveal tritanopia, within a radius of 50 mins. of arc from the fovea, has been ascribed to the paucity of blue receptors. This was clearly demonstrated since the 420 n.m.

stimulus which was seen with eccentric fixation disappeared when fixated centrally. Ruddock and Burton (1971) have suggested three classes of receptor contribute to dichromatic colour matches established for centrally fixated bipartite fields of diameter 15 - 20 mins. of arc. Such matches are changed by light adaptation of the retina surrounding the matching field. They suggest that the loss of mechanism associated with the fovea is possibly due to very rapid adaptation of the blue discriminatory mechanism. It is possible that the peak threshold, found in the region of 440 n.m. with direct fixation of the stimuli, may be produced by the blue sensitive mechanism of a spectrally opponent cell.

Work on movement-sensitive neurones has provided a framework to which recent experimental findings on apparent movement may be related. Bierderman - Thorson et al. (1971) described a "fine-grain" movement illusion in which two spatially separated dots in the peripheral field produced an illusion of movement. The two dots were alternately flashed for 1 m.sec with a 50 m.sec interval. The dots subtended 3.5 mins. of arc, and were separated by only 6-10 mins. of arc so that they were not resolved as being separate. The spatial extent of the movement illusion described by the subjects was many times the spatial separation of the dots. This may be ascribed to the triggering of a peripheral movement-sensitive mechanism, producing the illusion of movement. Biederman - Thorson et al. noted that velocity thresholds for the perception of real movement are quantitatively compatible with the dynamics of the motion illusion, produced by closely spaced brief sequential flashes. Dichoptic presentation made viewing difficult but did not always abolish the illusion.

Frisby (1969, 1972) looked at the effect of stimulus orientation of a line on the phi phenomenon, and attempted to relate his results to the receptive field characteristics of complex cells. Since it is not possible to guarantee that the stimuli used by Frisby stimulate only complex cells, and not movement-sensitive neurones possessing simple receptive fields, the issue is difficult to resolve conclusively.

Braddick (1974) using random dot patterns (Julesz, 1960, 1971) obtained optimal apparent motion up to 15 mins. of arc. Tyler (1973) had suggested an upper limit of 10 mins. of arc. Banks and Kane (1972), looking at after-effects of apparent movement, suggested that inputs to motion detectors spanned a range of 12.5 mins. of arc. Braddick has suggested that apparent movement may arise from short range processes, but can also occur over much larger distances e.g. Kolers (1972) obtained apparent movement over 7.5 degrees. Values obtained for the so-called short range processes involved in apparent movement are close to those obtained in the experiments outlined. Similarly a number of determinations of receptive field size have been made using Herman grids. Baumgartner (1960) estimated the excitatory receptive field diameter, at the fovea, to subtend 5 mins. of arc. Spillmann (1971), however, has estimated the diameter of the receptive field to subtend 18 mins. of arc. In the peripheral retina the mean diameter of the receptive field is found to increase linearly between 20 and 60 degrees of eccentricity. Over this range the field centre doubled in size from 1.5 to 3 degrees (Jung and Spillmann, 1970). It should be recalled, however, that the spatial extent of optimal apparent motion depends both upon stimulus characteristics such as wavelength, stimulus duration, and inter-stimulus interval, as well as upon retinal location.

It is clear that apparent motion is a complex response, dependent upon the stimulus characteristics and their spatial arrangement. A number of conclusions, however, may be drawn from the experiments. These are as follows:-

Conclusions

Recent work has suggested that movement-sensitive neurones (specifically

M- or DS- neurones) provide a mechanism which apparent motion is perceived. The present work, investigating the effects of wavelength on beta motion, suggests that such mechanisms must receive inputs from spectrally opponent cells. The excitatory receptive field size of a movement-sensitive neurone, determined using asynchronous stimuli, varies by up to 30% depending upon stimulus wavelength.

Differences between horizontal and vertical spatial thresholds for beta motion suggests that excitatory receptive fields, found centrally, are distributed as vertical ovals. A 30% difference is found between their horizontal and vertical spatial extent.

Asynchronous stimuli having an onset-to-onset interval of less than 75 m.sec fail to produce apparent motion. This probably arises as a result of phase differences between the action of inhibition and excitation producing a masking effect. The effects of this masking inhibition fall with increasing onset-to-onset interval. The optimal spatial threshold for beta motion is obtained with a short inter-stimulus interval of about 75 m.sec. Since the response of a movement-sensitive neurone appears to determine the spatial extent of its excitatory receptive field, results suggest that the neurone continues to respond for a short period after the stimulus ceases. Delaying the onset of the second stimulus prevents inhibition of this continued response. With an interstimulus interval in excess of 75 m.sec the beta motion response and that of the movement-sensitive neurone begins to decay.

The maximum spatial extent of beta motion increases linearly with increasing stimulus duration, over the temporal limits from 75 to 300 m.sec (corresponding to cycle times of 150 to 600 m.sec). Beta motion was not seen outside these temporal limits. The maximum spatial threshold for beta motion increases from about 6 to 22.5 mins. of arc over this range. The upper velocity limit of the apparently moving spot did not exceed about 1.26 degrees per second. Since doubling the pulse duration effectively doubled the excitatory receptive field size, the effects of summation are exhibited.

Significant interaction occurs between pulse duration and wavelength. Changes in the pulse duration, with stimuli having wavelengths greater than 540 n.m., produces a change in the maximum spatial threshold for beta motion analogous to the Bezold - Brucke Hue Shift.

The excitatory-receptive field for movement-sensitive neurones appears to increase linearly with eccentricity up to 10°. Stimuli which indicate a perceptive field for beta motion of 20 mins. of arc at the fovea, produce a maximum spatial threshold of about 75 mins. of arc at 10 degrees eccentricity. An increased sensitivity to short wavelengths is seen for eccentricities of 4° and above. The increased blue sensitivity of the retinal periphery may be ascribed to the contribution made by blue-sensitive rods to peripheral colour mechanisms. The overall increase in the excitatory receptive field size of movement-sensitive neurones, has been linked with increased frequency of Y cells in the peripheral retina.

Recommendations

The following suggestions are offered for possible further research:-

1. With a suitably powerful light source the effects of stimulus intensity may be investigated.
2. In view of Braddicks (1974) observations, suggesting that apparent movement is mediated by more than one process, a comparison between the present results and those obtained using binocular stimuli may prove useful.

Acknowledgements

I would like to thank my supervisor, Mr. H. Yorke, for his kind and patient supervision throughout this project and all the experimental subjects who have given up their valuable time to take part. I am grateful to Mr. C. Peaston for his assistance in constructing the apparatus and to my typist, Miss S. Turner, for her valiant effort. In conclusion, I would like to thank my wife for her help and encouragement over the past three years.

T. J. Buckingham

Appendix 1. Characteristics of the Grubb-Parsons Interference Filters.

Peak wavelength (n.m.)	Peak transmission (%)	Bandwidth (n.m.)
422.6	40	6.2
440.1	44	4.4
461.9	48	6.3
481.1	44	3.2
501.8	50	4.2
522.5	45	2.9
543.9	40	3.3
561.2	56	4.8
580.9	42	6.6
600.4	51	4.0
621.7	56	4.7
644.6	59	5.1
661.6	67	4.7
681.9	56	6.3

Results

Chapter VI : 1. The Effect of Wavelength upon Horizontal Apparent Motion.

wavelength subject	440	460	480	500	520	540	560	580	600	620	640	660	680
S_1	14.51	14.85	11.96	14.30	20.76	15.40	11.83	14.51	14.99	13.96	13.75	11.83	13.61
S_2	11.41	12.58	14.58	18.15	14.64	10.45	10.79	17.94	17.74	13.89	14.37	13.13	15.68
S_3	16.23	13.82	13.06	15.68	15.33	13.20	12.10	14.92	12.86	10.79	12.65	14.85	18.77
S_4	12.17	11.55	12.72	19.80	17.05	12.10	12.44	14.30	16.64	12.72	11.83	12.79	16.36
S_5	15.68	14.58	14.64	16.84	15.61	13.34	13.48	12.99	15.19	16.02	12.86	12.17	13.41
S_6	14.71	14.78	15.47	16.78	15.06	14.58	11.89	13.96	16.09	12.03	12.03	14.64	13.41
S_7	15.13	12.51	11.28	16.91	17.19	12.72	13.68	16.09	13.06	12.44	13.27	12.31	19.46
S_8	15.54	11.00	11.89	16.43	17.67	15.61	11.96	14.30	13.54	15.19	14.09	13.61	14.99

Results

Chapter VI : 2. The Effect of Wavelength upon Vertical Apparent Motion.

wavelength subject	440	460	480	500	520	540	560	580	600	620	640	660	680
S_1	19.94	18.43	16.50	22.69	21.80	15.81	16.71	17.74	17.88	19.53	17.33	20.01	19.66
S_2	19.53	17.53	18.08	19.80	24.75	14.23	16.09	19.94	19.11	20.14	17.67	20.14	19.53
S_3	19.94	17.33	15.33	22.96	18.98	16.09	16.91	16.02	17.94	21.38	14.37	19.66	19.66
S_4	22.48	15.81	16.71	22.69	22.55	15.95	16.29	16.71	18.41	17.53	16.02	18.56	21.80
S_5	19.94	19.94	12.58	24.75	20.49	16.78	18.77	18.01	18.36	18.22	18.70	20.90	16.98
S_6	18.91	20.08	18.29	21.80	22.55	17.74	16.36	16.98	19.39	19.39	21.38	22.14	18.98

Results

Chapter VI : 2. Results for Horizontal Thresholds used in Comparison to those Obtained for Vertical Apparent Motion.

wavelength / subject	440	460	480	500	520	540	560	580	600	620	640	660	680
S_1	14.51	12.58	12.58	18.49	15.88	14.23	14.16	15.47	12.79	16.36	14.09	12.17	17.05
S_2	17.46	13.96	15.26	18.01	17.53	14.51	13.68	14.78	16.23	15.19	14.92	15.81	15.81
S_3	15.40	14.37	13.61	16.23	16.71	13.13	13.96	13.06	14.37	16.43	12.93	16.71	15.40
S_4	12.17	11.55	12.72	19.80	17.05	12.10	12.44	14.30	16.64	12.72	11.83	12.79	16.36
S_5	15.13	11.00	11.28	16.91	17.19	12.72	13.68	16.09	13.06	12.44	13.27	12.31	19.46
S_6	15.54	12.58	11.89	16.43	17.67	15.61	11.96	14.30	13.54	15.19	14.09	13.61	14.99

Results

Chapter VII : 1. The Effect of Temporal Overlap of Stimuli upon Apparent Motion.

	STIMULUS OVERLAP				STIMULUS SEPARATION		
	45°	30°	15°	0°	15°	30°	45°
S_1	11.76	14.64	15.68	18.56	16.64	2.31	10.45
S_2	12.99	16.84	18.08	19.25	12.58	8.18	6.74
S_3	11.14	16.57	17.46	18.49	13.27	12.10	10.59
S_4	11.00	13.06	14.64	18.08	16.84	13.75	12.72
S_5	11.00	13.96	15.06	16.78	15.33	13.96	11.69
S_6	9.97	15.06	15.47	17.74	15.19	15.26	10.31

Results

Chapter VII : 2. The Effect of Temporal Separation of Stimuli upon Apparent Movement.

	15°	30°	45°	60°	70°
S_1	20.08	20.69	17.94	15.06	11.62
S_2	20.56	17.67	17.39	17.26	12.17
S_3	17.46	19.80	16.50	15.68	10.73
S_4	18.22	19.18	18.01	15.06	11.76

Results

Chapter VIII : The Interaction of Stimulus Duration and wavelength on Apparent Motion.

wavelength cycle time	440		460		480	
150	6.74	7.56	7.43	5.98	5.98	3.03
	6.60	8.25	6.12	5.36	4.81	3.37
	5.98	4.81	5.98	5.23	5.98	5.50
	6.46	6.19	7.63	5.09	3.37	6.33
200	7.43	10.04	8.73	6.67	5.91	9.21
	7.63	7.43	6.81	7.56	7.63	5.50
	8.73	9.21	7.63	7.08	7.15	7.49
	8.04	7.84	8.25	6.26	6.88	7.49
250	10.86	8.11	7.49	7.29	7.77	8.73
	10.73	9.08	9.63	6.39	7.01	6.19
	8.73	11.21	6.88	6.33	7.15	7.08
	9.14	8.46	10.31	9.14	9.35	7.22
300	9.63	11.69	10.04	11.21	8.11	10.31
	14.92	9.69	10.04	13.20	11.07	11.83
	11.21	14.78	9.56	12.58	9.97	8.11
	10.18	15.74	12.38	9.63	7.84	11.89
350	15.26	14.03	13.96	12.38	9.42	12.72
	14.23	11.89	14.37	11.07	10.38	9.49
	12.58	11.69	11.69	10.59	13.54	13.75
	12.03	11.14	14.37	11.34	13.68	13.41
400	12.86	17.46	13.13	15.06	15.61	14.51
	15.61	14.03	15.26	13.34	14.85	12.99
	16.36	16.64	11.48	15.61	14.78	12.10
	15.81	14.64	13.75	12.44	13.54	12.44
450	15.26	15.06	19.66	15.06	19.18	17.33
	17.05	16.84	18.77	14.92	16.50	16.29
	16.09	17.53	15.33	18.63	18.56	17.33
	17.88	17.33	16.84	14.92	15.88	17.05
500	21.86	20.56	17.19	16.71	21.86	21.31
	22.76	18.63	21.93	21.73	19.39	16.64
	20.35	22.83	18.43	17.33	17.67	17.81
	19.80	17.67	20.42	16.98	18.63	19.18
550	21.18	20.76	17.46	18.22	23.65	20.63
	25.37	20.28	21.93	23.03	23.38	18.08
	25.37	22.35	23.17	21.45	18.36	23.38
	19.46	22.55	22.21	18.15	18.01	18.36
600	27.23	26.54	21.04	24.13	18.29	23.17
	23.06	23.51	23.45	20.49	23.03	20.28
	26.20	23.86	20.14	20.42	22.55	22.28
	23.93	24.68	24.68	20.63	20.49	21.45

Results

Chapter VIII : The Interaction of Stimulus Duration and wavelength on Apparent Motion.

wavelength cycle time	500		520		540	
150	7.77	9.69	7.91	7.70	4.40	4.81
	7.43	6.94	6.33	5.98	5.57	3.51
	5.98	7.36	6.74	6.88	5.98	7.56
	7.77	6.46	3.85	5.16	6.26	6.53
200	11.89	9.90	8.39	6.94	6.53	7.84
	7.63	9.56	8.25	8.04	6.26	6.74
	8.46	7.63	9.08	6.05	7.84	5.02
	8.25	9.49	7.36	7.08	8.80	6.19
250	9.56	12.58	8.18	9.01	8.73	10.86
	9.21	12.93	10.59	10.66	8.39	11.76
	9.35	10.59	9.08	8.46	10.52	12.10
	11.55	11.96	10.73	8.25	11.07	10.66
300	13.13	12.17	14.23	9.97	9.35	12.24
	11.34	13.61	12.99	11.55	14.54	13.82
	12.10	12.79	10.93	11.48	8.89	9.63
	15.74	12.24	10.66	10.18	8.04	9.63
350	12.93	15.61	15.40	11.48	14.92	12.93
	13.54	11.41	14.44	14.99	13.82	12.31
	15.47	10.93	11.41	12.93	11.28	15.54
	12.65	13.82	11.34	11.89	12.65	10.86
400	16.09	17.53	15.54	13.48	16.78	12.38
	16.09	19.53	14.03	12.58	15.95	13.82
	17.26	17.94	14.64	14.37	15.33	15.19
	16.29	16.16	13.68	15.26	13.41	14.23
450	21.59	18.22	14.51	15.74	13.82	16.64
	20.21	19.59	14.58	17.74	15.74	16.36
	17.53	21.86	16.50	16.50	17.46	16.16
	16.91	20.63	16.84	15.19	16.50	14.09
500	21.31	22.83	22.69	15.95	15.06	15.68
	19.59	24.20	19.39	16.57	19.39	18.98
	18.91	21.59	16.29	20.21	14.99	18.63
	19.32	19.87	22.69	20.01	18.63	18.36
550	19.39	24.48	20.56	19.59	21.45	17.67
	22.69	21.18	19.73	19.73	17.46	18.77
	18.08	18.77	19.39	17.39	18.70	20.28
	19.73	23.31	17.67	14.85	22.69	21.93
600	20.97	23.65	20.49	18.01	24.34	21.25
	23.31	20.42	21.93	21.11	20.35	20.08
	23.24	24.89	18.70	17.53	20.49	22.69
	20.14	26.81	18.63	16.64	20.21	23.51

Results

Chapter VIII : The Interaction of Stimulus Duration and wavelength on Apparent Motion.

wavelength cycle time	560		580		600	
150	4.40	4.81	3.09	6.05	4.61	4.74
	5.57	3.51	5.50	5.02	5.09	6.74
	5.98	7.56	6.19	5.98	5.98	2.82
	6.26	6.53	5.91	6.12	4.06	6.53
200	6.53	7.84	8.73	7.29	6.74	6.94
	6.26	6.74	7.22	8.25	8.59	5.91
	7.84	5.02	7.22	6.81	6.88	5.84
	8.80	6.19	5.50	7.01	8.18	8.18
250	8.73	10.86	8.18	10.04	10.18	11.89
	8.39	11.76	6.88	10.04	10.93	9.90
	10.52	12.10	8.94	6.05	10.86	12.65
	11.07	10.66	6.74	8.04	7.98	10.18
300	9.35	12.24	14.51	9.01	9.01	12.24
	13.54	13.82	12.03	9.49	8.94	11.14
	8.89	9.63	12.10	9.14	12.79	9.28
	8.04	9.63	14.78	12.38	10.93	10.31
350	14.92	12.93	11.34	10.31	9.01	9.42
	13.82	12.31	9.63	11.96	9.83	11.62
	11.28	15.54	10.52	12.65	11.00	11.00
	12.65	10.86	9.90	12.79	10.93	11.00
400	16.78	12.38	13.27	15.88	16.71	15.81
	15.95	13.82	13.48	14.78	16.02	13.68
	15.33	15.19	15.33	13.61	14.09	13.54
	13.41	14.23	13.34	15.68	16.84	14.09
450	13.82	16.64	15.81	18.29	19.94	18.15
	15.74	16.36	17.39	14.78	19.66	21.31
	17.46	16.16	18.70	16.36	16.50	16.91
	16.50	14.09	16.71	16.43	16.80	18.63
500	15.06	15.68	19.94	19.59	19.87	20.69
	19.39	18.98	18.70	18.08	21.31	18.36
	14.99	18.63	17.88	19.46	22.90	17.19
	18.63	18.36	17.12	16.64	17.46	20.21
550	21.45	17.67	20.63	22.14	23.24	22.07
	17.46	18.77	18.36	18.56	19.73	19.73
	18.70	20.28	24.41	18.49	19.39	23.24
	22.69	21.93	18.36	23.45	22.90	19.46
600	24.34	21.25	24.75	19.66	25.44	25.92
	20.35	20.08	21.11	27.02	22.90	20.42
	20.49	22.69	24.96	25.99	21.18	22.48
	20.21	23.51	21.86	24.89	21.45	21.11

Results

Chapter VIII : The Interaction of Stimulus Duration and Wavelength on Apparent Motion.

wavelength cycle time	620		640		660	
150	4.74	4.95	8.18	8.39	6.74	2.96
	5.43	6.94	6.60	5.23	5.36	4.88
	6.39	5.98	6.60	7.22	4.47	6.94
	3.99	4.88	4.95	5.57	5.71	5.78
200	6.67	6.46	6.88	7.49	7.84	5.64
	8.18	8.53	7.56	9.56	6.94	6.39
	7.49	5.50	9.08	10.18	5.09	8.25
	5.57	8.46	8.94	8.32	6.67	7.49
250	6.39	7.56	11.28	9.28	10.73	8.66
	6.81	9.28	9.83	11.48	9.69	8.18
	6.88	5.91	7.77	8.59	10.73	13.13
	8.11	9.49	7.91	7.84	7.98	8.46
300	11.28	11.55	14.51	11.07	10.38	10.79
	10.18	9.28	12.86	11.76	11.21	11.69
	12.10	9.42	11.07	12.72	11.62	8.25
	11.07	10.31	11.96	10.52	13.54	10.59
350	12.51	12.03	11.41	11.83	10.31	10.86
	13.89	14.58	11.62	15.88	9.83	9.49
	12.72	15.33	14.44	11.07	13.48	11.28
	15.26	12.17	11.89	12.10	10.59	13.41
400	12.51	14.44	12.93	14.09	13.13	15.26
	12.86	16.43	14.23	14.44	16.84	15.74
	12.99	16.29	13.20	14.16	14.78	17.26
	13.89	16.02	16.09	14.16	13.75	13.41
450	16.02	18.22	16.50	18.63	19.46	19.59
	17.60	18.70	17.05	18.98	17.33	17.26
	18.36	17.19	20.42	17.19	20.42	1898
	18.77	18.56	19.25	17.53	17.19	19.66
500	17.19	21.18	22.28	22.90	19.73	21.45
	18.84	21.18	19.66	18.98	20.21	19.46
	20.14	19.94	23.24	20.90	20.63	19.94
	19.73	17.39	22.90	24.13	19.73	22.76
550	22.28	23.65	25.03	20.14	15.26	14.37
	20.14	22.48	19.80	20.01	14.37	18.36
	20.63	18.08	20.21	23.93	19.66	19.46
	21.59	21.93	23.51	24.13	19.11	17.19
600	27.16	22.35	21.04	20.97	17.81	16.84
	25.03	22.55	22.35	25.99	22.00	19.11
	23.72	20.69	24.00	25.37	22.62	22.21
	22.00	21.31	21.93	24.61	20.14	22.41

Results

Chapter VIII : The Interaction of Stimulus Duration and Wavelength on Apparent Motion.

wavelength cycle time	680	
150	4.61	6.67
	5.78	6.46
	5.98	3.37
	6.39	7.01
200	5.57	7.22
	7.63	8.46
	6.53	8.87
	7.91	7.63
250	10.93	9.21
	9.35	9.90
	11.07	12.03
	11.96	8.73
300	13.13	11.00
	12.24	10.86
	11.55	13.41
	10.66	11.21
350	14.71	16.23
	14.71	17.39
	15.26	14.44
	16.29	12.17
400	16.36	15.26
	14.71	16.64
	15.47	15.26
	15.40	17.46
450	19.80	15.06
	17.05	17.39
	15.95	16.91
	17.88	18.56
500	21.31	20.63
	18.43	21.52
	23.51	22.62
	18.84	19.73
550	24.89	23.93
	22.48	22.55
	25.23	20.90
	22.28	20.56
600	24.34	23.65
	24.96	26.47
	21.04	26.13
	22.96	22.28

Results

Chapter IX : The Effect of Stimulus Location upon Apparent Movement

Wavelength Retinal Eccentricity	420	440	460	480	500	520	540
0^o	20.14 20.14 20.14 20.14 20.14 20.14	19.04 19.39 18.43 19.39 19.94 18.43	20.49 17.39 19.46 17.67 17.94 18.08	20.01 21.11 19.87 19.80 20.42 17.88	24.41 21.80 24.06 22.76 21.80 22.83	21.93 24.41 20.83 23.38 22.62 24.68	16.78 18.15 14.51 15.88 15.88 18.70
2^o	36.64 38.64 34.38 42.97 36.58 33.69	46.06 39.05 34.72 41.87 36.58 37.40	33.14 37.88 33.14 38.43 38.29 33.76	37.61 33.69 33.48 35.27 37.54 32.18	41.25 42.28 43.59 42.08 43.04 43.79	45.79 42.42 43.04 41.32 46.41 40.91	31.08 27.91 33.14 28.74 34.51 31.15
4^o	46.61 49.78 45.93 50.19 51.22 50.81	50.67 47.03 48.88 50.67 53.14 49.64	40.56 38.09 47.51 47.23 48.13 45.51	41.39 34.03 36.64 40.01 37.33 39.33	48.74 43.86 44.28 46.89 47.16 44.28	46.48 43.31 45.79 39.39 43.38 38.78	40.77 37.19 36.44 37.88 33.55 33.96
6^o	57.68 54.86 59.67 66.07 59.81 62.49	53.14 66.07 65.03 64.90 61.87 57.47	58.02 53.56 59.47 60.09 57.75 55.34	57.34 49.78 58.02 60.43 57.13 58.50	67.10 68.95 61.94 69.50 65.45 59.26	64.90 66.13 67.37 64.69 65.52 63.52	49.29 52.52 47.71 48.54 49.43 51.56
8^o	62.01 65.38 66.89 74.38 71.29 63.25	66.75 62.35 74.72 72.59 71.84 65.58	63.04 57.34 54.24 63.93 60.70 67.10	63.73 62.29 67.65 62.70 61.53 67.71	65.93 66.82 63.73 65.65 65.72 59.33	66.75 69.16 67.23 65.10 69.78 61.39	57.68 58.64 63.11 62.35 56.72 56.37
10^o	86.82 84.48 87.64 81.39 82.90 77.40	86.61 86.20 83.11 87.92 80.57 78.57	82.01 84.28 89.50 90.19 82.56 83.73	83.45 73.49 85.17 75.89 75.55 76.65	92.04 88.06 93.76 89.98 88.74 85.93	83.38 85.17 95.68 90.53 82.08 81.80	57.06 53.56 52.87 61.87 50.39 63.66

Results

Chapter IX : The Effect of Stimulus Location upon Apparent Movement

Wavelength / Retinal Eccentricity	560	580	600	620	640	660	680
0°	17.88 18.10 19.39 17.53 20.08 17.19	18.29 19.11 21.04 19.18 21.18 19.87	18.77 19.46 18.70 21.38 20.97 22.35	19.32 19.73 20.76 21.31 20.21 20.49	20.90 20.63 19.11 20.28 18.22 19.94	19.87 21.52 21.04 22.41 19.73 20.42	21.66 20.83 20.35 21.31 23.24 21.31
2°	30.53 31.28 35.13 29.15 28.95 32.86	36.37 33.62 34.38 35.13 43.11 36.92	37.88 38.98 39.19 37.33 42.42 37.68	40.49 40.29 39.81 36.16 41.39 35.82	37.68 34.17 41.87 33.07 41.18 40.91	31.42 31.42 37.06 31.35 37.61 37.61	36.92 38.16 38.64 41.11 41.59 37.88
4°	37.74 36.71 40.56 37.26 39.53 38.29	38.16 39.74 36.85 39.88 35.41 37.81	37.47 43.86 36.99 37.95 37.61 41.87	36.85 42.28 40.49 37.81 38.36 41.04	40.49 39.05 41.53 36.44 34.93 38.98	44.76 38.91 42.63 36.30 40.70 35.89	40.15 40.98 43.04 38.98 44.21 41.94
6°	55.07 62.70 52.11 51.63 57.20 62.84	53.28 57.27 43.31 47.03 50.19 55.96	55.96 58.92 50.46 51.97 55.00 58.44	53.62 54.79 54.45 49.43 54.31 55.89	55.27 59.19 51.70 55.62 55.00 52.25	52.39 55.27 62.29 55.41 56.37 55.48	67.37 62.35 67.37 60.09 64.62 66.13
8°	64.00 62.84 55.82 50.81 62.70 62.49	55.00 57.68 49.57 53.83 56.86 68.71	68.33 62.84 61.25 58.78 55.14 66.68	64.14 61.25 63.80 58.44 61.74 61.80	62.01 55.55 53.42 60.15 53.49 60.84	60.36 61.60 61.60 58.92 64.07 54.86	64.62 72.73 65.58 72.66 67.23 67.65
10°	71.22 71.43 53.90 75.21 57.61 67.65	63.18 71.56 60.64 63.45 73.83 75.27	73.42 78.78 69.43 71.01 73.35 71.70	72.39 62.97 73.69 65.45 74.24 69.23	70.33 73.28 65.38 63.38 69.78 71.43	73.76 69.71 73.76 63.52 69.50 69.98	77.75 75.96 73.14 72.66 64.14 75.00

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