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EVOKED POTENTIALS AND PSYCHOPHYSICS
OF
BINOCULAR VISION

by

Samuel Craig Rawlings

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EVOKED POTENTIALS AND PSYCHOPHYSICS OF BINOCULAR VISION

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PREFACE

I wish to express my sincere thanks to the individuals who have helped in many ways in the process of this work--from alpha to omega.

To the members of my dissertation committee--Thorne Shipley, Neil Schneiderman, Carroll Truss, Ray Winters, and Blase Gambino--I extend special thanks. Thorne Shipley is the primary person who has guided not only this work but has provided continuous orientation and perspective throughout my graduate years. To a large extent, my education has come from him.

To the observers, Irene (Manning) Holmes, Madeline Popp, and Thorne Shipley, who participated in this study, I am grateful. Also, I wish to acknowledge the artistic contributions of Madeline Popp, who helped in construction of the figures, and Diane Nuber, who typed the manuscript.

My family is a real part of this total happening. My parents, Roy and Virginia Rawlings, have always been encouraging. To my wife, Janet, I can only say thanks.

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CHAPTER I

INTRODUCTION AND ORIENTATION

The purpose of the present work was two-fold. First, theoretical formulations are presented which pertain to the nature and definition of disparity, the binocular cue to stereoscopic depth perception. Second, the experimental portion of the study was concerned with relating psychophysically determined depth conditions and electrophysiological brain activity in the human observer.

In order to set forth the nature of the problem with which I shall be concerned in this paper, I should like to refer to an old but little known essay by a well-known authority on optics, Ernst Mach (e.g., 1926), and follow, for a moment, his pellucid and titillating discussion.

> "Why has man two eyes?" Mach (1943) asked in a lecture which was first published in 1867. "That the pretty symmetry of his face may not be disturbed, the artist answers. That his second eye may furnish a substitute for his first if that be lost, says the farsighted economist. That we may weep with two eyes at the sins of the world, replies the religious enthusiast.... man fulfills no purpose in the possession of his (two) eyes; nature is not a person, and consequently not so vulgar as to pursue purposes of any kind...a modern scientist... would (sic) say, with stern expression...But ask a more tolerant person, ask me. I, I

> candidly confess, do not know exactly why man has two eyes, but the reason partly is, I think, that I may see you here before me...and talk with you upon this delightful subject [p. 66-67]."

Mach's tantalizing introduction--which gives way to a "more learned explanation" of binocular vision--is successful in creating a receptive climate that makes it possible to communicate the import of this trudy complicated problem to one totally naive. In replying to his questions, he begins with unsophisticated, but intriguing answers, and in a few sentences has ripened the reader to the point where he can pick--though not yet eat--his fruit. "But since you are not satisfied with my brief and obvious answer(s)...let me put the matter in a purely orthodox way: Man has two eyes, what <u>more</u> can he see with two than with one [p. 67]?" Now the ultimate puzzle is at hand but he has slipped in an inherent assumption: that man, indeed, <u>can</u> see more with two eyes than with one. But, we cannot chastise Mach for this bit of trickery, because he goes on to treat the reader in unaffected simplicity, to one of the most charming presentations on the subject of binocular perspective and stereopsis that I have seen.

In the present paper, I will discuss and investigate aspects of binocular vision which can be traced back to Mach's questions: "Why has man two eyes?" and "...what more can he see with two than with one?" My treatment, however, is less philosophical (if one accepts the contemporary adulterated definition of philosophy), and more specific. Although I deal experimentally with a very small portion of what might be included in the category of binocular vision, the plan is one of synthesization.

The factors involved in stereopsis can be divided into three main classifications: (1) the physical; (2) the physiological; and (3) the psychological (not necessarily in this, or any, fixed order). Each may be quantified according to its own descriptive parameters, but if one is to approach an adequate explanation and understanding of the whole of stereopsis, or any stimulus-neurochemical-mental event, the three must be integrated. (The term mental is used here in the experiential sense.)

Most current experimental workers in physiology and psychology adequately control and employ, and are comfortable with the physical dimensions. The discussion of physiological-psychological relationships is a different story. I do not propose to resurrect the old "mind-body" enigma--at least, not in these loaded and anomalous terms. However, one of the greatest abysses in behavioral science seems to continue because physiological and psychological dimensions are treated as if they are autonomous. There are, I believe, several distinct reasons. First, researchers typically do not seek to measure both and, of course, this procedure is not always desirable or necessary. Second, there is little active investigation and less open discussion of the relationships of these two types of dimensions. Third, even when the physiological and experiential parameters have been quantified (usually by different people), fear, suppression, or overt hostility seem to be attached to the consideration that they might possibly describe a part of the same event.

The matter is further complicated when the term, "consciousness" is mentioned. Perhaps here lies the primary obstacle. Confusion, regarding the definition of consciousness, is partially due to the lack of knowledge about the physiological mechanisms involved at the temporal and spatial "point" where stimuli, or their neurochemical representations, enter awareness, i.e., when they satisfy the criteria so we can conclude that a stimulus was, in fact, perceived or experienced.

The point is that both physiological and psychological dimensions are meaningful and each is unique, but they are not mutually exclusive. The quantification and integration of the two allow a fuller understanding of the total event. When the whole of physiology is known, along with its ramifications, it will be possible to describe and explain all psychological occurrences--in terms of physiology. But the measurement of psychological dimensions will be as meaningful and valid as it is today; we will simply have a better understanding of the total picture.

Ah, but some scoff at such self-evident discourse. Yet where--beyond a mere sprinkling of reports in the literature and in an occasional loose symposium--has this comprehensive approach existed? Some say that this treatment is unreal and meaningless, since there is only one dimensional category. They confuse the total event with the different means of measuring it, and thereby shut themselves off from available information, or ways of getting it. Others reply that the technology is not sufficiently developed, and we can only speculate--armchairing but not eyeballing. And, speculation is currently a dangerous pastime because it places one in a vulnerable position among his objective colleagues--so they wait.

However, if we attempt to keep our minds and discussions open and are even moderately successful, then valid interpretation, explanation, and understanding will come easier.

The purpose and orientation in this paper was to quantify one psychological dimension and one physiological dimension in physically defined terms and then synthesize and discuss the relationships. In addition, theoretical formulations were developed and are presented, pertinent to the topic of concern in the present work.

CHAPTER II

HISTORICAL SIGNIFICANCE AND THE BEGINNINGS OF VISUAL SCIENCE

The phenomenon of vision, including numerous interwoven topics, is one of the oldest subjects of scientific inquiry. The story cannot adequately be covered or appreciated by relating the work that has taken place during the nineteenth and twentieth centuries. In fact, this negligence would tarnish the beauty which one may derive from the history of visual science. Clarke & O'Malley (1968), in their recent historical compulation and commentation, state that:

> "Because of the rapid advances made in science during the last hundred years and because of its present-day complexity and sophistication, there is a tendency to neglect the most distant past. The ancient Greeks seem to be so far away in thought, as well as in time, that we tend to forget that their ideas, some of which now appear to be archaic and curious, were in many instances the origins of concepts that today are held to be of the greatest importance [p. 1]".

So it is with reference to the neural structure, function, and experience of vision. In contrast to the above quotation from two historians, is the following one by a leading neurophysiologist:

> "...a science demanding synthesis of observations, experimental physiology, with its reliance on analysis and laboratory work, has little significant history before 1600. Leaders in medicine developed and practiced its therapies for many centuries before they felt the need to understand the nature and functions of the body's parts..." (Brazier, 1959, p. 1).

This second author is obviously speaking of a more restricted and exacting area of science. However, in comparison to many of her contemporaries, even this statement is a rather mild condemnation. The point is that we do not give due credit to the early writers, in this case especially the Greeks, and rather tend to judge their work on the basis of our present high-level scientific knowledge--as if it were all formulated during recent years. We point to previous mistakes and misconceptions with unhindered ease, as no doubt will our predecessors in regarding our work, and in our attempts at condensation often lose significant insights. But, be that as it may, it seems necessary, for a fuller understanding of what we know, to trace the historical unfolding of the knowledge of vision, beginning with the Greeks.

Recognition of the need for referring to early works is evident in Stephen Polyak's two comprehensive volumes on vision (1941, 1957). "But more than anything else," wrote Heinrich Kluver in the Forward to what he called Polyak's magnum opus, "it was his deeply felt desire to give full acknowledgement to the works of others and do justice to the men on whose shoulders we stand that motivated his occupation with historical matters" (Polyak, 1957, p. vi-vii).

One of the major controversies that existed throughout the ancient Greek period, which is directly related to the gross anatomy and physiology of vision, and can serve as a central theme about which the development of the knowledge of vision can be presented, concerned the problem of identifying the central organ of the senses (cf. Clarke & O'Malley, 1968; Farrington, 1947, 1959). (For maps and graphic presentations of the Greco-Roman period, with photographs of the ancient sites, see Van Der Hayden and Scullard, 1959).

According to the above historians Alcmaeon of Croton (fl. c. 500 B.C.), thought to be a pupil of Pythagoras (c. 582-500 B.C.) and himself influential upon the establishment of the Hippocratic school during the 4th century B.C., appears to be the first to practice dissection. Polyak (1957) says he dissected human bodies, but most historians disagree. Alcmaeon is credited with the discovery of the optic nerves and with describing the pathways from the eyes to the brain. (The early writers did not differentiate the optic tract, by name, from the optic nerve.)

Alcmaeon performed ophthalmic surgery (Clagett, 1957) and more importantly was proported to be the first to recognize the brain as the central organ of the senses and of the intellect (Galen, 166, 169-175 A.D.). The Hippocratic writers (c. 430-350 B.C.) added motor control to the functions of the brain and believed the brain to be man's most powerful organ. Plato (C. 429-347) in his trilogy of the soul assigned sensory reception, reasoning and memory to the brain (Clarke & O'Malley, 1968). It was primarily through Aristotle (384-322 B.C.) that the cardiocentric theory of the senses developed and his influence was so strong that this view became commonly accepted. Aristotle supported the heart supremacy theory on the basis of dissections and experiments with some 50 different types of animal life, primarily lower forms, and logically formulated his conclusions (Farrington, 1947).

With the establishment of the Museum of Alexandria under the first Ptolomies (323-246 B.C.), human dissection, and even vivisection on condemned criminals, became common practice. This was the only period in antiquity when such methods were used on a grandiose scale

(Kevorkian, 1959). This liberal atmosphere did lead to a tremendous increase in information about the structure and function of the nervous system. Aristotle's cardiocentric view was rejected as a result of the detailed anatomical work of Herophilos (fl. c. 300 B.C.), although his heart supremacy theory remained engraved elsewhere. While none of Herophilos' manuscripts exist today, he is given credit for correctly describing anatomical structure and physiological relationships of the various sensory organs--especially the visual system--and the brain, based upon systematic personal dissection. The Museum of Alexandria attracted physicians from other schools and came to be the most vast and well equipped research and teaching institute in antiguity, with about 100 professors on the staff who were paid by the state, a library of about one-half million or more rolls (these were made from papyrus units approximately 10 inches long glued together to form rolls, some of which were over 100 feet in length!), botanical and zoological gardens, an astronomical observatory, and facilities for dissection and physiological experiments (see esp. Mason, 1953; Sarton, 1959). "The main misunderstandings concerning the history of science (in particular during the Greco-Roman period) are due to historians of medicine who have the notion that medicine is (was) the center of science" (Sarton, 1952, p. x). The Museum and the Library of Alexandria was destroyed by Roman, Christian, and Muslum invasions and by the mid-600's A.D. was essentially nonexistant.

Before the decline of Hellenistic science and medicine in Alexandria the most productive and influential authority of the entire period and, in fact, until the 16th Century, came to this center to study. This man, to whom the eminent historian of science George Sarton (Cohen, 1957) refers as a "master of experimental physiology" (Sarton, 1954), was Galen of Pergamon (c. 130-200 A.D.).

Galen traveled to a number of schools including Pergamon, Alexandria, and Rome where he studied, practiced medicine, conducted anatomical and physiological research, and wrote. He is said to have written several hundred books although only about 80 are in existance today. There is some question as to whether he performed human dissections, but there is general agreement on the fact that most of his work is based upon the Barbary ape (a species of the macaque). Galen no doubt did have occasion to observe human anatomy, however, since he served for a period of time as physician to the gladiators in Pergamon (c. 157 A.D.) and traveled with the Roman legion as military surgeon during the war with the Barbarians (c. 180 A.D.).

The first complete translation from the original Greek into English of Galen's most important treatise for our purposes, On the usefulness of the parts of the body, 165, 169-175 A.D.) by M.T. May has only recently been published. In it Galen treats the entire body in minute detail and attempts to prove that the total organism is one functioning unit. These 17 books are packed with anatomical and physiological information, experiments, techniques, arguments and speculations. (Most of our present anatomical names can be traced to Galen's writings; Sarton, 1959). For example, on topics related to vision (Book X, The eyes), Galen differentiates between sensory (soft) nerves and the motor (hard) nerves on the basis of their structure and function, discusses couching of clouded lens (cataracts), describes the similarity between retina and brain tissue stating that the retina is a portion of the encephalon, gives a detailed anatomy of the parts of the eye, describes the uniting of the optic nerves at the chiasma (which he says resembles the Greek letter chi), and traces the nerves back to their place of origin at the sides of the lateral ventricles (lateral geniculate bodies).

CHAPTER III

THE DEVELOPMENT OF BINOCULAR CONCEPTS

It is with Galen (1965, 169-175 A.D.) that the first synthesized formulations of binocular vision were developed. He integrated mathematical, anatomical, physiological, and psychological aspects in a treatment which comes close to being a correct, although not complete, theory of vision with the two eyes. The geometrical principles compiled and created by Euclid (c. 300 B.C.) provided the geometry of external space and his descriptive optics. After showing that monocular visual angles are constant over distance, his binocular argument goes as follows. When a circular object is viewed, a cone is projected from each pupil to the circumference of the object. The monocular visual axes are represented by a line from the pupil to the center of the circle. The two visual axes intersect and, therefore, define one plane in space. If the axes do not intersect, doubling will occur. Doubling can be easily demonstrated, Galen points out, by depressing one eye so that the pupil is displaced vertically from the other. The translator's redrawing of Galen's Fig. 2, Book 10, p. 494, is almost exactly the same figure of two eyes viewing a sphere with a plane beyond, drawn by and credited to Leonardo (Boring 1942, Fig. 41; Woodworth, 1938, Fig. 201). Leonardo's drawing is original and the idea may be, independently his, but Galen's figure and descriptive narrative did exist some 1400 years earlier.

Galen also describes how a single object will appear at a different position as one eye or the other is closed, but when viewed with both eyes together the position of the object is midway between (a description of egocentric direction, or the "cyclopean" eye of Helmholtz). For anyone who wishes to demonstrate to himself this difference between the eyes and the combined effect with both eyes together, Galen recommends gazing steadily at a distant pillar. (A vertical seam in a concrete wall will have to serve the purpose for us.) If a pillar is available and one stands closer to it, another phenomenon may be demonstrated. Viewing with one eye then the other, one can see parts with each eye that cannot be seen with the other. But with both eyes viewing simultaneously these parts do not appear double.

Galen clearly was describing binocular perspective but did not go on to fully develop the concept that we now refer to as disparity. Perhaps this was due, in part, to the rejection Galen felt by those who were not well-trained in mathematics, for in several places he attempted to justify this type of presentation. For example, in Book 10 (p. 501), he states that "I did not intend to discuss this, not wishing to be hated by the many who would choose to suffer any ill you please rather than to have anything to do with geometry." In fact, Galen considered omitting the entire section of this book and would not have employed the theorems of geometry, but, he says, he was commanded by a god to do so. However, a rebuttle is given for those who would reject his work on this basis; for such persons who do not understand are implored to go and study Euclid's works and then come back when they have learned it.

Galen's gross anatomy and physiology included significant errors but the underlying conceptualizations show that he saw the necessity for structural and functional interaction. The optic nerves are described as meeting at the chiasma, and uniting so that we may see single. Vision is accomplished as a result of "pneuma" originating in the encephalon, flowing through the optic nerves which Galen thought to be hollow, to the eyes, mixing at the chiasma, and returning to its source. Galen also thought that the lens was the peripheral photoreceptor and held to the belief in the emission theory of vision.

Despite the inaccuracies, Galen displayed keen insight regarding binocular vision. The physiological explanation, i.e. flowing to the pneuma, might still be held as a gross analog to chemical transmission. Even assuming the analogy, today we immediately reject the pneuma concept because of the minute spatial and slow temporal aspects of chemical as contrasted to electrical parts of neural transmission.

In addition to the area of vision, Galen's works became the authority in anatomy, physiology and medicine until the sixteenth century. Arab treatises were written during the Dark Ages, and some were concerned with binocular functioning, but Polyak (1941, 1957) argues that this work appears to be copied, borrowed, or modified from the original Greek manuscripts. At any rate, little new knowledge was added during this period of time.

Interest and investigations relative to vision were renewed during the Renaissance. Systematic dissection and the study of anatomy were reinstituded, primarily in the person of Andreas Vesalius (1543), who corrected many of Galen's errors (Polyak, 1941). More important for the area of binocular vision was the work of Leonardo da Vinci (1452-1519) on perspective (see Richter & Richter, 1939, for a compulation of

Leonardo's original notes and figures with accompanying translation; Woodworth, 1938). Leonardo discusses binocular parallax and points out that the artist can never reproduce relief as it naturally occurs because the two eyes see a different perspective of the same object while a painting can only represent one. Anatomy was also studied in detail by Leonardo. He performed dissections and was especially concerned with the visual system (Sarton, 1948). Polyak (1957) is quite critical of Leonardo's anatomical sketches of the visual system and says he did not truthfully depict what he saw but drew imaginary organs.

Information on the visual system came from many sources beginning late in the 16th century. This more recent history has been adequately covered (Boring, 1942; Clarke and O'Malley, 1968; Polyak, 1941, 1957). Platter formulated the dioptrics of the eye; Kepler applied a mathematical treatment to describe the retinal image; and Scheiner demonstrated the formation of the retinal image in animal and human eyes. Aguilonius (1613) was the first to use the term "horopter" to describe equidistant binocular space. He incorrectly thought the horopter surface is represented by a plane, located at the point of fixation, parallel to the eyes. Aguilonius did state, following Euclid's geometry that lines drawn between two pairs of points, forming equal angles, intersected at positions which was represented by a circle. Des Cartes described a projected point-to-point binocular representation of single objects in space.

Newton (1730) was the first to discuss a partial decussation at the chiasma, at the turn of the 18th century. Hartley (1749) spoke of corresponding points between the two retinea as did Camper (1746) and Reid (1763). Vieth (1818) and Muller (1826) used the intersection of visual directions from these corresponding points to develop a theoretical horopter circle passing through the two eyes and any given points in space on that circle (Boring, 1942).

The real breakthrough for the present theory of binocular vision (Ogle, 1950, 1959, 1962; Graham, 1965) came in the publication of Charles Wheatstone's paper (1838). It is here that geometrical and retinal disparity, as the basis for relief, are thoroughly discussed for the first time. Wheatstone's development begins with the theory of corresponding points and the projected horopter space of the Vieth-Muller circle, for these were known at the time. However corresponding retinal points and intersecting visual directions only referred to single vision or equidistant objects.

Wheatstone expanded upon these ideas to describe perceived depth differences which result when slightly noncorresponding points or objects are presented to the two eyes and coalese such that single vision still occurs but now relief within the image arises; thus stereopsis. His argument was made abundantly clear when he created a relatively simple device for presenting slightly different images to the two eyes: the mirror stereoscope (Wheatstone, 1838, Fig. 8 and 9). He drew pairs of outlined figures of objects as they would be seen in real space from slightly different perspectives. The pair, or stereogram, was placed in the stereoscope so that each one was viewed monocularly. The resultant single binocular image gave rise to depth as it occurs under natural conditions, due to the difference in perspective between the two eyes. Within certain limits, the greater the difference between the two monocular figures, the greater the depth.

There arose a great controversy between Wheatstone and David Brewster (1842; also see Boring, 1942) over the origin of the stereoscope and concerning the interpretation of binocular vision. Brewster does give Wheatstone qualified credit: "Mr. Wheatstone seems to be the first person who made experiments on the binocular vision of unequal figures" (Brewster, 1842,

p. 356). While Brewster (1853) was no doubt more knowledgeable in optics, the interpretations of relief by Wheatstone have proved to be the more accurate. The law of corresponding points, Wheatstone argued, was too restricted since, following the exact definition, any point which was located at a position in space where the monocular visual directions did not precisely intersect, would be double.

Panum (1852) went on to develop somewhat of a compromise when he proposed that corresponding sensory areas existed in the retinae. Points which fell within these areas would not be double but rather fused and at different depths from, for example, a point of fixation where visual directions do intersect. These areas as they are represented [illegible]ve been measured across the horizo[illegible]d increase in size with ecce[illegible] Gliddon, 1932; Ogle, 1952). The [illegible]ve, about which these fusio[illegible]en measured and interpreted [illegible]932, 1952; Shipley & Rawlings, 1[illegible]

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Panum (1852) went on to develop somewhat of a compromise when he proposed that corresponding sensory areas existed in the retinae. Points which fell within these areas would not be double but rather fused and at different depths from, for example, a point of fixation where visual directions do intersect. These areas as they are represented in space, have been measured across the horizontal visual field and increase in size with eccentricity (Ames, Ogle, & Gliddon, 1932; Ogle, 1952). The shape of the horopter curve, about which these fusional areas lie, has also been measured and interpreted (Linksz, 1952; Ogle, 1932, 1952; Shipley & Rawlings, 1970a, 1970b).

The origin of the stereoscope is still a source of confusion, however Wheatstone is given credit by most people who may be considered authorities (Boring, 1942; Helmholtz, 1866; Holmes, 1859; Woodworth, 1938).

Brewster's lenticular prism stereoscope and modifications of it, such as the hand held variety designed by Oliver Wendell Holmes (1859, 1861) came into popularity in Victorian England, France, and the United States. Numerous stereoscopes were manufactured as the photographic process was being developed and stereo-photography became the rage, and to some extent still is (Hamilton, 1949; Jenkins, 1957; Morgan and Lester, 1954). Holmes, who was fascinated with the stereoscope, called it "...the most remarkable material product of human skill..." (1861, p. 16) and proposed the "... creation of a comprehensive and systematic stereographic library..." (1859, p. 748) where people could go and experience the world.

Curiously enough, it was during just this exact period in time that the mathematical and optical formulations of stereoscopy and visual space were worked out by Helmholtz (1866). He also developed theoretical treatments, such as that of the generalized horopter which added the vertical dimension in space to the Vieth-Muller horizontal horopter. Helmholtz also described and depicted instruments to be employed in the research of binocular vision, for example the telestereoscope.

At the same time that Helmholtz was working on the problems of binocular space and stereopsis, Hering (1942) was attacking similar problems. Helmholtz has been characterized as a (or possibly the) great empiricist while Hering was an explicit nativist (Boring, 1942). Hering's point of view was entirely different from that of Helmholtz, but his contributions were important and have led to much of the present knowledge and theory of binocular vision. The relationship of visual direction to local sign in binocular vision was developed by Hering. He postulated that nasal and temporal elements of the retina give rise to subjective farness and nearness and that the position in depth-space can be determined by the intersection of the corresponding visual directions. Binocular visual directions result from the combined monocular ones. The cyclopean eye concept of Helmholtz is very nearly the same idea although the apex of binocular directions was positioned differently and floated for different points in space or with eye movements.

Hering's approach has been followed by Tschermak (1952) while Ogle (e.g., 1950) adhered more closely to Helmholtz, at least for quantification purposes.

Psychophysical investigations have flourished during the past century and numerous variables have been shown to have effects on stereopsis. Stereoacuity increases as exposure time increases (Langlands, 1929; Ogle and Weil, 1958; Shortess and Krauskopf, 1961), decreases as the spatial density of binocular rivalry increases (Julesz, 1963), decrease as velocity increases (Lit, 1966), decreases as peripheral angle increases (Ogle, 1950; Rawlings and Shipley, 1969) and decreases under low illumination (Berry, Riggs, and Duncan, 1950; Lit, 1959; Muller and Lloyd, 1948).

The anatomical pathways of the visual system were described beginning in the mid-19th century using ablation and degeneration techniques. Panizza (1855) demonstrated that the occipital lobe was essential for visual function. Munk (1877) also helped to clarify the cortical areas involved in vision and found that the occipital and occipitoparietal areas were the centers of visual perception. Gudden (1847) and Forel (1887) were instrumental in showing that decussation took place at the optic chiasma. The localization of visual projections centered in and about the calcarine fissure was determined by Henschen (1893). Ramon y Cajal (1909-1911) traced the visual pathways and indicated that a uniting of corresponding areas, or their neural representations took place in the striate cortex.

Neuronanatomical models have been proposed by Talbot and Marshall (1941) and Rønne (1956) in an attempt to explain the temporal and spatial relationship of corresponding and disparate points as they are converging in the occipital cortex. The simplicity of these models has not been supported on the basis of more recent electrophysiological studies.

CHAPTER IV

STEREOPSIS

In the real world a number of cues are simultaneously operating which allow a person to localize visual objects on the basis of their distance. These distance or depth cues are typically divided into a two-class system that is rather obvious when the peripheral organs of vision are considered. There are two eyes; we can see with either alone, or with both together. Thus, distance may be determined by monocular or binocular cues.

The monocular cues to depth are: size; interposition; linear and aerial perspective (including texture gradients); movement parallax; the interplay of light and shade; and accommodation (Graham, 1965). It is generally agreed that learning and experience play a major role in the perception of depth from information gained through these monocular cues. There is no known intrinsic structural basis, other than what may develop over time, for judging the spatial distance of objects viewed with one eye alone. A possible exception to the foregoing statement is the discrimination of depth associated with accommodation, although in this case precision is very inaccurate (e.g. Baird, 1903; Ogle, 1950).

The binocular cues to depth in Graham's (1965) classification system are convergence and stereopsis. Convergence has been shown to be a very limited cue to depth (Gogel, 1961; Ogle, 1956; Zajac, 1960). Well trained observers in Gogel's study were able to employ convergence differences to make depth judgments slightly more accurate than naive observers, but this cue was still of minor or secondary importance.

The most precise discrimination of depth is achieved through stereoscopic resolution, which requires binocular interaction, and can be quantified in terms of the disparity between the two monocular images. Angular thresholds of stereopsis have been found to equal about 2 sec. of arc under ideal conditions (Howard, 1919; James, 1908; Langlands, 1929). The minimum distance between the axes of two neighboring cones in the very center of the human fovea is about 2 microns which corresponds to about 24 sec. of arc in the field of view (Polyak, 1957). This means that for disparity values of 2 sec. of arc the corresponding difference in position between the two retinae is about 0.17 microns or 0.08 of the distance between the axes of two cones. Furthermore, to make depth difference judgments under typical conditions requires a minimum of two points and these must first be resolved, which in effect means that one image must fall off the very center of the foveae. Individual receptor cells outside the fovea are separated by some 5-6 microns with outer-segment thicknesses of about 1.5 microns. Center to center distances between receptors close to, but outside the fovea, are greater than 6 microns. Therefore, the corresponding visual angles equal about 1 min. or more. In the spatial dimension, stereopsis is indeed one of man's most refined sensory skills.

It is generally agreed that the disparity value for the threshold of stereoscopic acuity equals about 10 sec. of arc. It must be noted however that this angular difference between the two eyes represents a measure of deviation about the mean equidistant value. Therefore, what is referred to as a depth judgment is actually derived from an equidistant judgment.

The simplest configuration giving rise to stereopsis based upon binocular disparity is presented in Figure 1. An overhead cross-section view through the eyes and two point sources in space is displayed with the Vieth-Muller circle horopter as reference. Binocular fixation is at P_1 and the second point, P_2, is horizontally displaced in the right visual field. The visual directions are shown as lines from the retinae to the point sources.

Disparity is usually defined as the difference between the angles α and β. In geometrical terms the two angles are equal for any pair of points that lie on the Vieth-Muller circle. Assuming a constant eccentricity, the angle ϕ in Figure 1, disparity increases as the distance from P_2 to the reference circle increases. Outside the circle disparity is referred to as divergent or uncrossed, and inside disparity is termed convergent or crossed. The insert (stereogram) in Figure 1 shows the monocular positions of the two point sources from the observers point of view. Empirical studies have shown that the horizontal horopter plane falls outside the Vieth-Muller circle (Ames, Ogle, & Glidden, 1932; Ogle, 1950; Shipley & Rawlings, 1970b) and the functional zero disparity horopter therefore does not equal the theoretical circle.

It is necessary to clearly differentiate between equidistance, i.e., horopter points, and stereoacuity. Quantification of both may take place simultaneously. For example, under the conditions in Figure 1, an observer may make a number of equidistant settings. For each judgment the variable point P_2 is moved along ϕ until the observer indicates that the two points are equal in distance. The mean of these settings yields an estimate of the horopter for the given offset

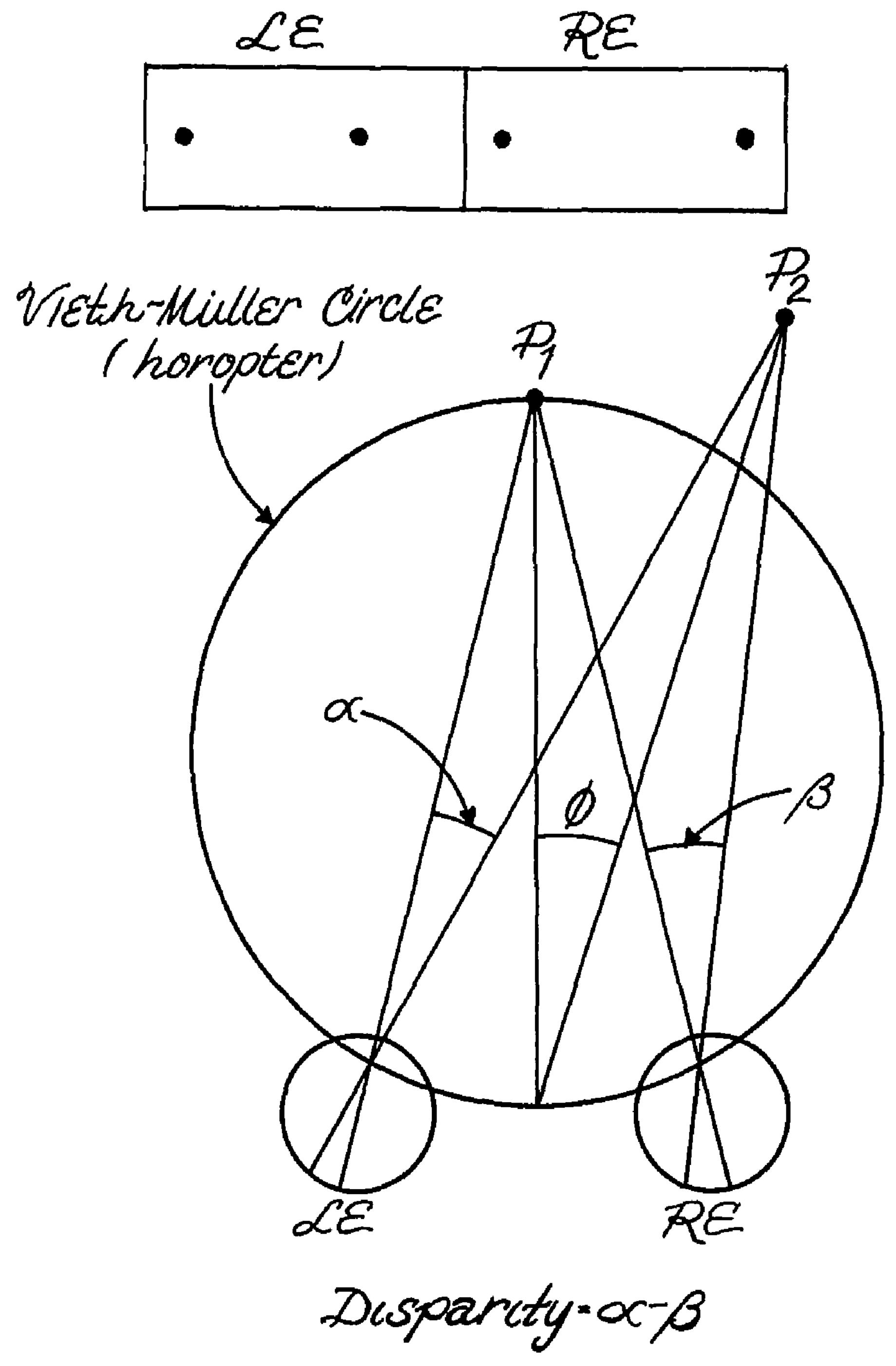


Fig. 1. Simplest Stimulus Configuration for Stereoscopic Depth Perception. Upper insert shows corresponding stereogram.

angle ϕ. Stereoacuity, on the other hand, is a variability measure about the horopter point. Typically the standard deviation or mean deviation is employed. The zero functional disparity value is given by the mean and the threshold of stereoacuity is given by the deviation, usually presented in min. or sec. of arc. The disparity range within which stereopsis exists increases rapidly with increased eccentricity. According to Ogle (1952), at the maculae patent stereopsis exists within a disparity range of about 30 min. of arc. while at 5 deg. eccentricity the value approaches 4 deg. of arc. These disparity ranges are far greater than the corresponding fusional areas of about 15 min. and 50 min. of arc, respectively.

CHAPTER V

THEORETICAL CONSIDERATIONS OF DISPARITY AND STEREOPSIS

As stated in the previous section, the basis for stereoscopic depth perception is disparity. It must be pointed out that the depth dimension involved is relative not absolute. The depth difference between the object in relief compared to an external reference is the basis for the judgment rather than the absolute distance from the observer (Ogle, 1962).

A more complicated problem arises when attempting to define disparity. Disparity has been loosely used in three different ways. Reference has already been made to two of these definitions. The three definitions of disparity are graphically displayed in Figure 2. The first, and easiest to quantify is geometrical disparity. For two points, P_1 and P_2, geometrical disparity is defined as the difference between the angles α and β subtended at the optical centers of the eyes.

The second definition of disparity refers to the difference in retinal subtense or arc length between the two eyes. In the left eye, for example, α' represents the angle between the two point sources

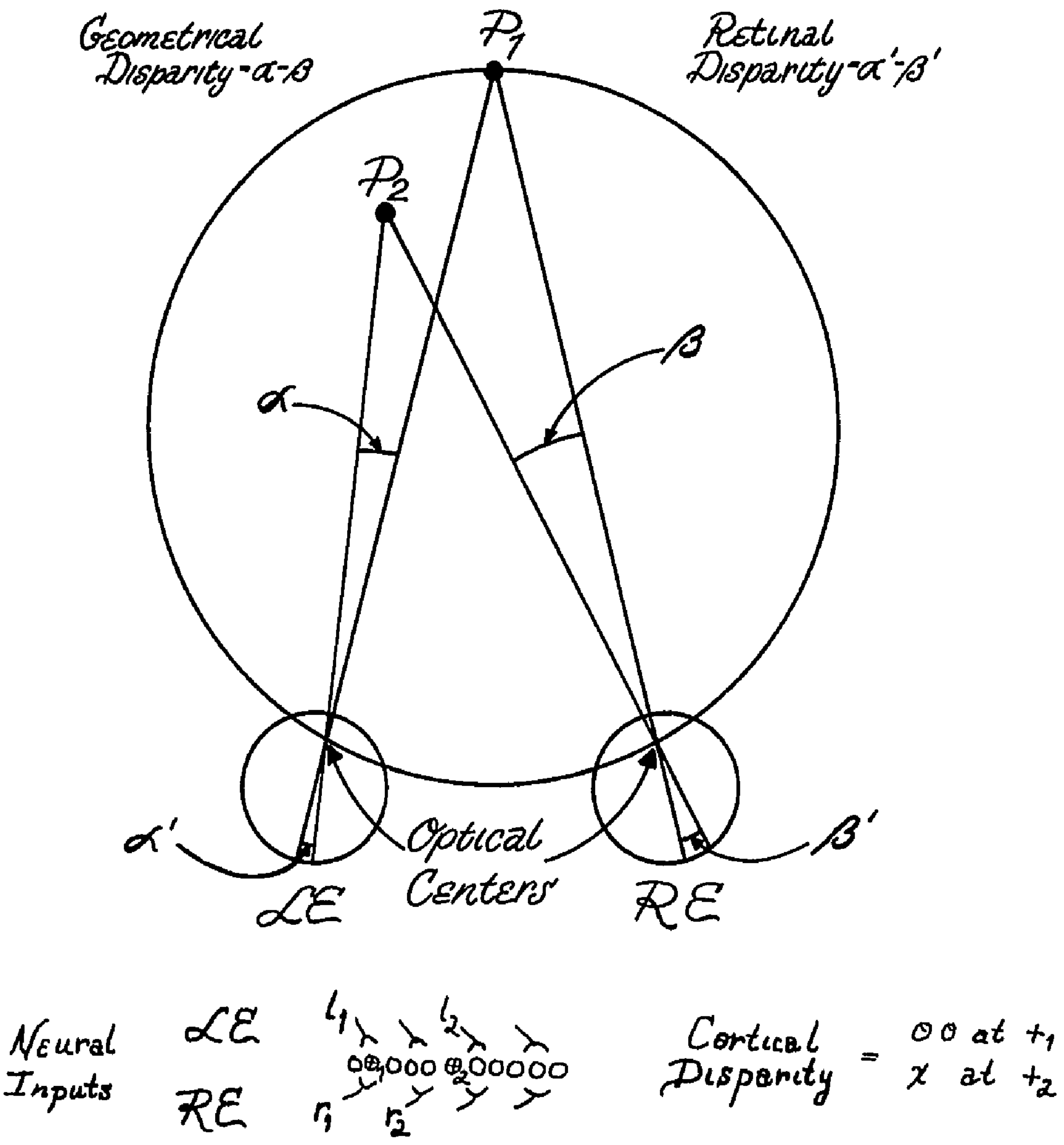


Fig. 2. Three Definitions of Disparity Graphically represented.

within the eye and behind the optical center. Retinal disparity is defined as the difference between α' and β'. Due to refraction and to the movement of the optical centers with convergence, geometrical and retinal disparity may not be equal.

Furthermore, what may be called functional or cortical disparity, may not be equal to either of the two previous disparity definitions. Figure 2 (bottom) is a schematic neuronal configuration showing cortical disparity. It is cortical disparity which is really the valid definition. When two points are judged equal in depth, no matter what the geometrical and retinal disparities may be, it is cortical disparity which is zero, as shown by the excitation ($+_2$) initiated by the combined neural activity from the left (l_1) and right (r_2) eyes. When two points are judged different in depth, no matter what the geometrical and retinal disparities may be, it is cortical disparity which exists and yields stereopsis. The neural input from l_2-r_2 in Figure 2 is a simplified representation of the binocular interaction and disparity ($+_2$). The cortical column arrangement found by Blakemore (1968) for disparity specific cells in the cat is a first step in the identity of anatomical and functional relationships at the central level.

By pointing out these three different disparities, and suggesting that the ultimate disparity must be cortical, it should not be inferred that the other two disparity types cannot be employed as a metric in depth discrimination studies. A geometrical or retinal disparity dimension can be used, but it is misleading to say that an empirically determined horopter point has a disparity of 5 min. of arc simply because that is where it falls with reference to the Vieth-Muller circle. Stereoacuity measures are less plagued by this inconsistancy because they are variability values.

Any comprehensive definition of disparity must be applicable to the total binocular field. A major problem in the past--and still a source of confusion--concerns the geometrical treatment of disparate objects. This is clearly seen in Kenneth Ogle's (1950, 1959, 1962) work (which does however provide the best contemporary source of information regarding binocular vision). He assumes the necessity of bifoveal fixation (1950, p. 136). For any point in space disparity is calculated with reference to that fixation point, i.e., the foveae. Disparity and stereopsis involve the simultaneous comparison of longitudinal retinal sections. Stated in another way, the difference in the two monocular retinal elements between the fixation point and the peripheral point becomes the basis for depth discrimination. In a restricted sense, this formulation holds for disparity calculations, but on two counts it is an inaccurate interpretation of what takes place. The two ways in which the most commonly accepted definition of disparity is wrong are:

(1) involvement of horizontal retinal sections between the depth target and the fovea; and

(2) requirement of bifoveal fixation of some physical point or target which identifies a plane in space. It is these two assumptions against which I shall argue over the next few pages.

First, to quantify disparity in the binocular visual field for positions above or below the horizontal meridian would necessitate a shaky assumption. The assumption required is that some mystical, or at least imaginary, vertical extent bisects the fixation point. This is displayed in the two monocular configurations shown in the form of a stereogram in Figure 3. The three peripheral points all have the same disparity values from the vertical line passing through the fixation point (F). The horizontally displaced point (P_1) is the typical case and does not require the assumption of a vertical reference.

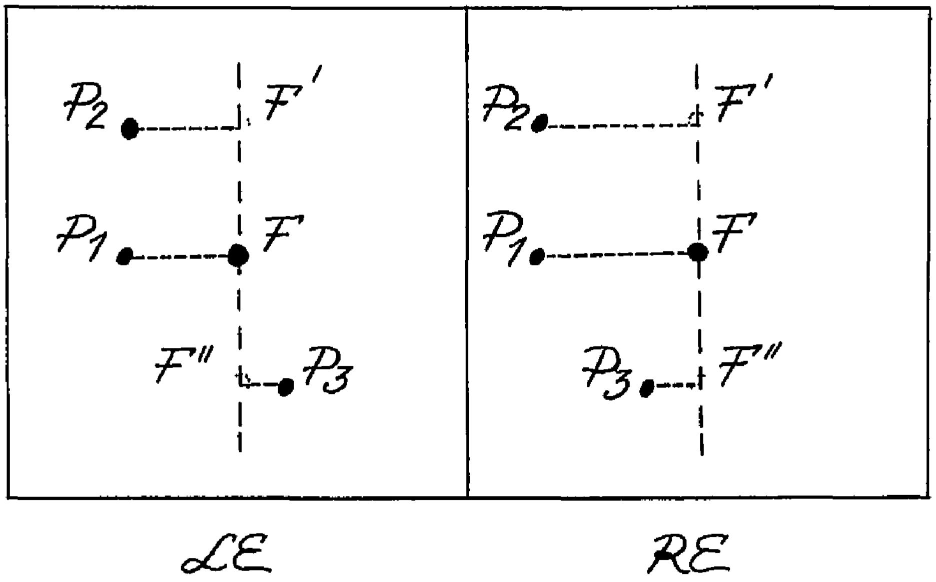


Fig. 3. Stereogram Displaying Disparate Points at Various Peripheral Locations

Disparity can be calculated directly from the angular difference between F and P_1 in the two monocular targets. Disparity for any combination of monocular points located along the horizontal meridian may be determined in the same fashion (sign changes are required if the point for one eye is on the opposite side of F than that for the other). The point, P_2, represents an example in which the aforementioned tenious assumption of a vertical extent from fixation must be made. If the longitudinal segments of the retinae must be compared for disparity calculations, then the fixation point cannot itself be used because it does not fall along the same horizontal meridian as P_2. Therefore the end point at the right side of the angular comparison necessary for the calculation of disparity for P_2 is located along the vertical extent of F at F'. The point P_3 is a second example which requires the assumption of a vertically extended reference from F. The disparity of P_3 is again equal to that of P_1, assuming a sign change if absolute differences are used between the two monocular pairs and calculations are made about F". The point, P_3, has two additional unique characteristics: there is no horizontal displacement from F in the fused image, i.e., the binocular visual direction is in the same vertical meridian as F; and, the two points would appear to be cortically represented in opposite hemispheres. Cortical fusion and disparity are possible, however, and recent evidence has been found for a double representation, i.e., bihemispherial, of vertical strips of retinal areas through the fovea (Blakemore, 1968). One might speculate that this strip could, in fact, serve as the vertical extent from the fovea which I have referred to as mystical or imaginary. The vertical strip found by Blakemore, however, represents a double projection and does not appear to be anatomically connected to the fovea.

A comprehensive theoretical definition of disparity which does not require a displaced fixation point, for calculation purposes, seems in order. In addition, this definition should not inherently require that horizontal retinal sections be compaired for calculating disparity because there is no anatomical basis for assuming that all retinal elements between point sources are involved in stereopsis. Such _is_ the case, however, for solid targets which are of different monocular horizontal extent. This type of stimulus, i.e., the aniseikonic target (Ogle, 1950), has continuous disparity across its horizontal dimension (Shipley & Rawlings, 1970c), and yields perceived stereoscopic tilt. All retinal elements subtended in binocular viewing are anatomically involved in tilt stereopsis. A comprehensive definition of disparity, therefore, must be applicable to a binocular stimulus having continuous disparity or for a binocular target having discrete disparity but not locked to the fixation point (Rawlings & Shipley, 1969). The following formulation does hold for these targets because disparity calculations do not require that the fixation point, or retinal elements between the fixation point and any peripheral target, be involved.

Disparity and stereopsis may take place solely in the periphery (or in the absence of the foveas). The point of fixation need not serve to identify a reference depth plane against which other targets are compared. To conceive of a stimulus configuration structured such that disparity and perceived depth may occur in localized areas of the binocular field, consider the following situation.

The two monocular conditions presented in Figure 4 show disparity which is localized in the periphery. For each of the three pairs of points, the stereoscopic judgment is made on the basis of depth differences between the two fused binocular points, i.e., within

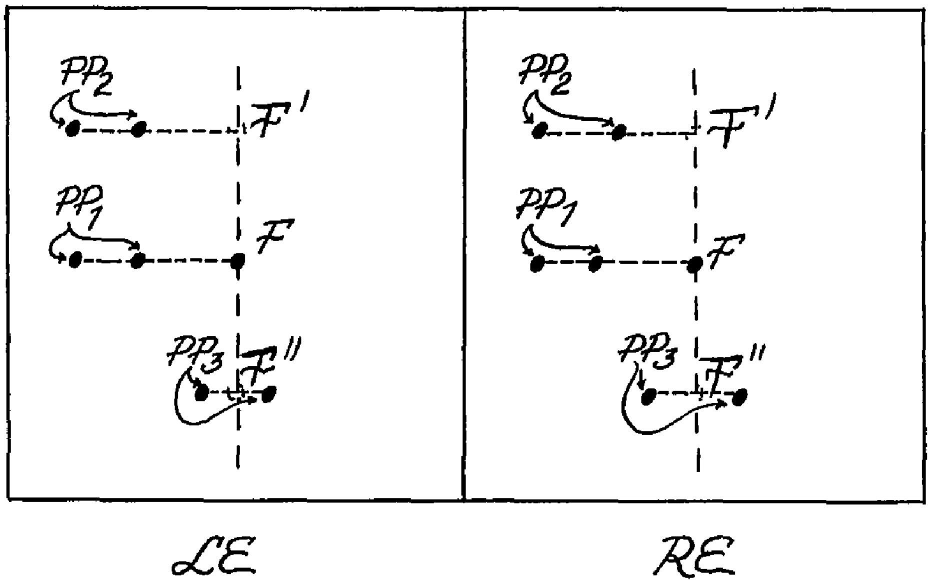


Fig. 4. Stereogram Displaying Disparate Pairs of Points at Various Peripheral Locations.

each set, the right and left points identify a different depth plane. (Of course the two points, within each pair, may also be set to be equidistant.)

The horizontally displaced pair of points (PP_1), again may represent disparity values in the usual sense, i.e., calculations can be made with reference to the fixation point. A previous study (Rawlings & Shipley, 1969) employing horizontally displaced pairs of equal separation, showed that localized stereoacuity fell off as the eccentricity of the pair was increased. Since the peripheral pair was always in the same horizontal meridian as the fixation point, disparity could have been calculated in the common manner, as is the case for PP_1 in Figure 4.

Disparity for the two other pairs of points PP_2 and PP_3 would require a vertical extension of the fixation point, if Ogle's disparity definition were to be used. However, if we calculate disparity with reference to fixation this would imply that the fixation point is involved in the depth discrimination. With a double point stimulus, where depth is judged on the basis of a comparison of the two, and the concept of localized stereopsis is employed, an even stronger case can be made against the inaccurate interpretation of the common definition.

In Figure 3 the fixation point did actually serve to define a depth plane and the peripheral points were compared to that plane. While the assumption that all elements within the retinal section between the two points are necessarily involved in stereoscopic judgments could not be accepted, disparity values could be calculated in the usual way if the vertical extension is assumed. It is also possible to calculate correct disparity values in the usual manner for the pairs of points in Figure 4. But, in this case, it becomes quite clear that the most common interpretation of the meaning of disparity is inaccurate.

Another situation which I offer as additional support that stereopsis is not necessarily locked to a foveal fixation point nor dependent upon horizontal retinal sections between the fixation point and a second peripheral point is graphically shown in Figure 5. The points, T_1, $T_2 \ldots T_6$, represent a time dimension for a single fused binocular point. The subscript for each T point refers to a discrete time wherein the right and left eye images are simultaneously flashed. For simplicity, I have constructed the right and left points so that a continuous directional change in depth would occur with each successive flash. The monocular points could as well be positioned so that

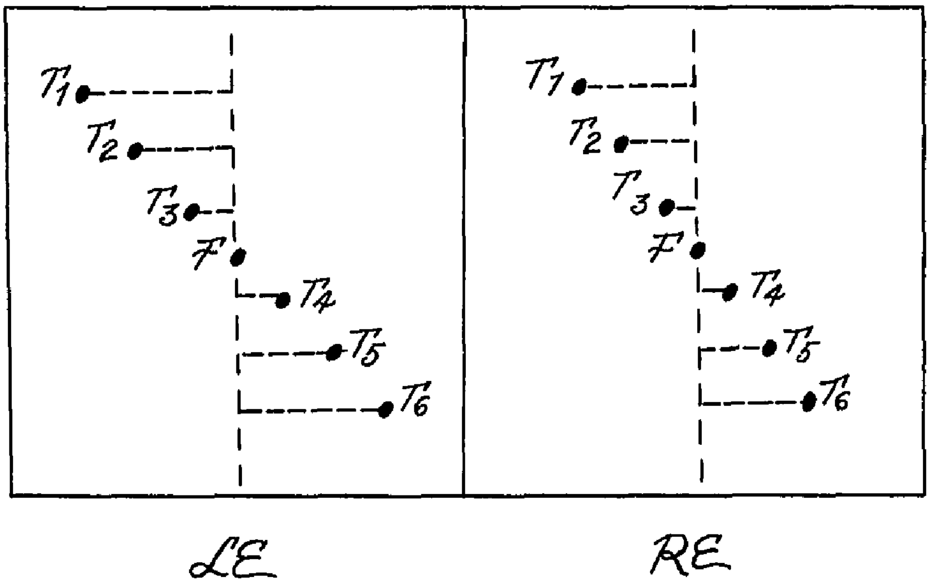


Fig. 5. Stereogram Displaying Disparate Points Varying over Time.

random directional depth changes take place. The observer's task in this type of presentation is to judge the directional change in depth of each stimulus flash as compared with the preceding one. The judgment does not require that a horopter be identified by the fixation point, although admittedly it would serve to enhance discrimination. (F could be left out of the figure.)

The final argument that depth need not be locked to foveal fixation and does not result from the interaction of retinal areas between the foveae and a peripheral stimulus I believe to be conclusive. The stimulus configurations shown in the three previous figures, as well as many others which could be ennumerated, might be used as examples.

A modification of the two-point target in Figure 4 is shown in Figure 6. It seems to most clearly and simply make the point. In this stereogram the points P_1 and P_2 cannot be locked to a fixation point, they cannot be judged in depth with reference to a plane established by the fixation point, there can be no horizontal retinal sections to the fixation point involved in stereopsis because there is no fixation point. The dotten circle (f) represent the foveal visual directions which may be locked or held constant by a binocular modification of the stopped retinal

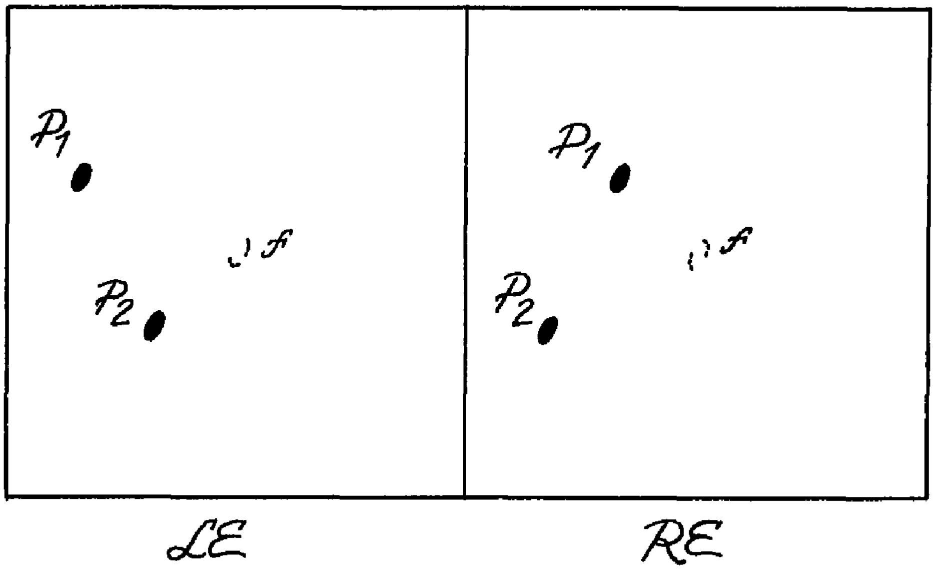


Fig. 6. Stereogram Displaying Disparate Points Without Binocular Fixation Point as Reference.

image technique (Ditchburn & Ginsborg, 1953; Riggs, Ratliff, Cornsweet, & Cornsweet, 1953). The foveal directions need not intersect in physical space. The stereogram in Figure 6 may imply that they do but either monocular half could as well be displaced vertically or horizontally, or tilted, depending upon the position of the eyes.

Another possibility is to fix the eyes by pharmacological and/or mechanical techniques (Barlow, Blakemore, Pettigrew, 1967) so that the retinal location of the images may be manipulated. The purpose is to fix the eyes (or images) so that monocular positioning is controlled without using a fixation point, or more specifically without stimuli that fall along primary foveal directions. Stereopsis still exists in the points P_1 and P_2 and they may be manipulated to produce depth between them, or set equidistant.

The temporal and spatial conditions of the monocular stimuli which yield stereopsis becomes an issue here. Stereopsis is a central function requiring simultaneous inputs from both eyes. Ogle (1963) found that for an exposure time of 18 msec., stereopsis was lost if temporal delay between the two monocular stimuli was 100 msec. or more. To achieve stereopsis in the binocular visual field a comparison must be made between the location or position of images in each eye. The spatial interaction of the monocular stimuli is also central and primarily cortical. Hubel and Wiesel (1962) found that the most units in area 17 of the cat were binocularly driven while at the lateral geniculate bodies binocular interaction seldom occurred.

These spatial conditions of stereopsis are not really new because they hark back to Wheatstone's (1838) ideas discussed earlier. Disparity is still horizontal, but horizontal between or within targets in the two monocular fields which are overlapped or locked in binocular fusion. To calculate disparity at any points in the binocular field requires only that the eyes be locked or fixed in position. If all monocular directions are known and plotted, two retinal maps result which may be subdivided by any coordinate system one may wish to use.

In conception, the simplest retinal maps are those shown in Figure 7. The equal interval divisions correspond to equal angular space. When the two retinal maps are locked in binocular fusion a cortical map results. For simplicity, the cortical map presented in Figure 7 has the same physical and angular divisions as the retinal maps. The cortical map represents the total horopter space. Any binocular stimulus configuration

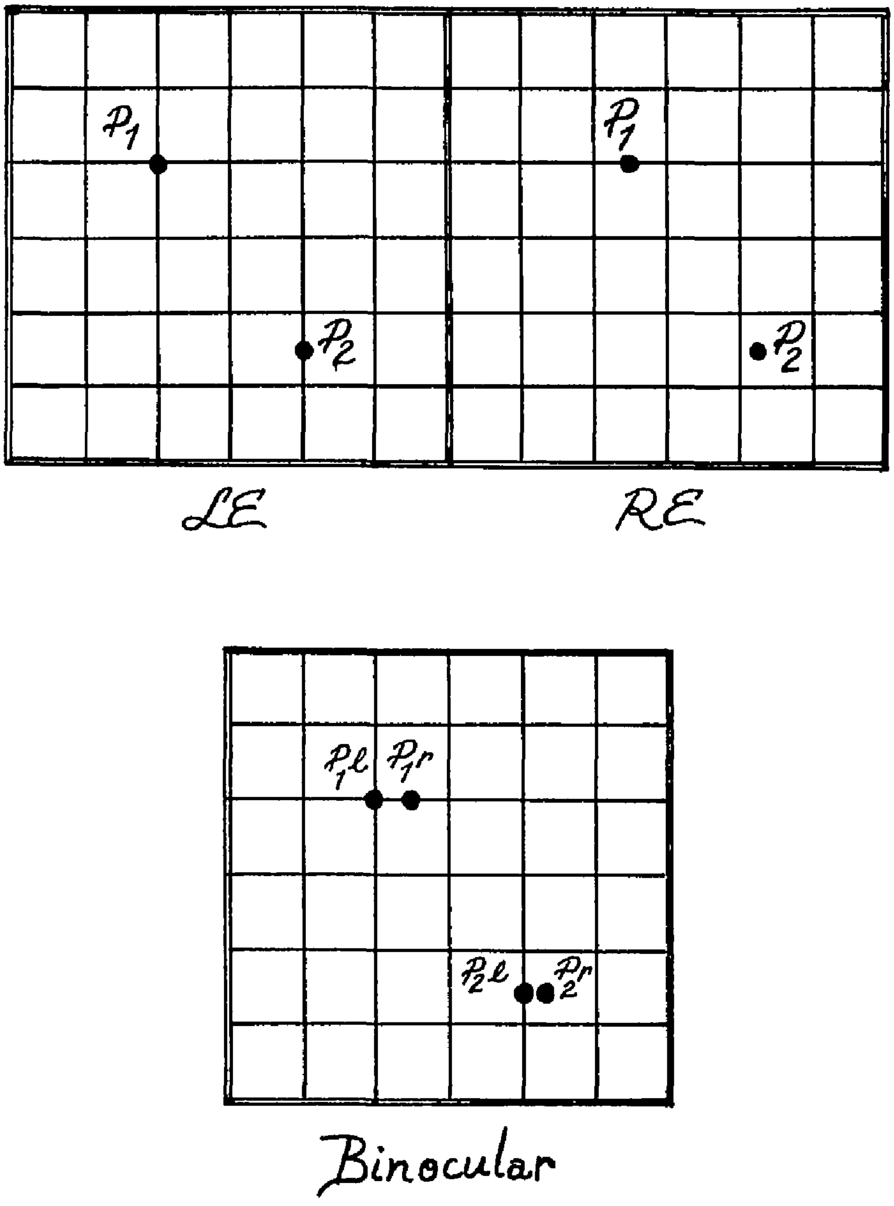


Fig. 7. Right Eye, Left Eye, and Binocular Disparity Maps

in which the two monocular inputs are projected to the same position, or give rise to matching neural activity for spatial location, would be perceptually equal in depth. Disparity is calculated as the horizontal difference between the two monocular targets, labelled with an additional subscript in the binocular map to indicate left (l) and right (r) eye inputs. For example, if each division in Figure 7 equals 2 min. of arc, then disparity for P_1 = 1 min. and disparity for P_2 = 30 sec. of arc.

The retinal and cortical maps, of course, are not so simple but the purpose of this presentation was not to describe the shape of visual space but rather to show that stereopsis may take place in any portion of the binocular field, a fixation point is not necessarily directly involved in stereopsis, and that horizontal retinal sections, between the fovea and other retinal areas, need not be included in defining disparity.

CHAPTER VI

NEUROPHYSIOLOGICAL EVIDENCE OF BINOCULAR INTERACTION AT CORTICAL LEVELS

Within the last decade several investigations have produced neurophysiological evidence which indicates that neural processing of binocular stimuli occurs in the occipital cortex. The experimental work began with single cell recordings in the cat.

Single cell recordings in the striate area of the cat by Hubel and Wiesel (Hubel, 1959; Hubel & Wiesel, 1959) led to the identification of individual binocular units and gave some information about their anatomical structure (Hubel & Wiesel, 1962). Cells were found to be situated in columns forming a functioning architecture. Binocular cells were rarely found in the lateral geniculate. More specifically, single cell electrophysiological studies have given information about the neural activity, at the cortical level, in stereopsis (Barlow, Blakemore, & Pettigrew, 1967; Blakemore, 1968). While Hubel & Wiesel initially found that most binocular cells (some 85% were binocularly driven) fired maximally for what they thought to be correspoinding nondisparate points in the retinae, the latter investigators have found cells which respond differentially as a function of binocular disparity. The maximal firing rate of each of these units was associated with a specific disparity value.

Out of a total of 137 units, 112 were binocularly driven and 87 of these were reliable. Barlow, Blakemore & Pettigrew (1967) argue that Hubel & Wiesel (1962) did not adequately control eye movements. Using pharmacological agents (Flaxidil and d-tubocurarine) eye movements were measured and found to approximate 6 min. of arc per hour. Mechanical methods were then employed in addition to the drugs. The conjunctivae were stretched, dried, and attached to a mental ring to further fix the eyes. Under these combined conditions no eye movements could be detected. Stimuli were then presented and their location more precisely controlled. Individual units were maximally facilitated by bar, slit, or edge stimuli having specific disparity values between the two monocular pairs. The range of disparity values was found to be 6.6 deg. in the horizontal and 2.2 deg. in the vertical. The investigators argue that their findings indicate a neural mechanism for depth discrimination in the cat cortex.

Similar electrophysiological investigations were being conducted at Bishop's laboratory in Sydney simultaneously with the work in Barlow's Berkeley laboratory.

The Sydney findings were published a few months after the California work (Nikara, Bishop, & Pettigrew, 1968; Pettigrew, Nikara, & Bishop, 1968). However, the neural mechanism for binocular depth discrimination in area 17 of the cat's cortex must be considered a mutual discovery. In fact, there was some collaboration between the two labs (in the person of Pettigrew, see Blakemore, 1968) and if it can be said that either was first, then at least as far as technique is concerned, one would have to give the edge to Bishop's group in Sydney.

Next is the question of an electrophysiological mechanism for stereopsis in man. Since, fortunately, the Museum at Alexandria has long since passed, we must consider techniques of recording and analysis from humans who are, and remain, intact.

The averaging of electroencephalographic (EEG) activity from the surface of the scalp is a recent development made possible by technological advance. The "averaging" computer takes amplified EEG potentials and sums over time, in effect adding the gross cortical responses which occur along a reference time base. The resultant curve is referred to as the evoked cortical potential (EP).

If the surface EEG activity contains some component of neural discharge which is related to stereopsis, then the evoked potential should reflect that activity in terms of amplitude and/or frequency of the waveform. If the gross neural discharge related to stereopsis is differential in degree, then the waveform of the EP should show that differential.

The purpose of the experimental portion of this study was to determine disparity values of stereopsis obtained through psychophysical methods. The stimuli were then presented back to the observer with disparity values based on his own judgments, and EPs were recorded to the different discrete values of disparity.

Two papers have just been published which report modifications in the EP as a function of disparity changes. The first (Regan & Spekreijse, 1970) used Julesz (1960) random dot stereograms. These targets have no monocular cues to depth and no monocular form pattern. Slight changes in the EP curve occurred as disparity values of 10 min., 20 min., and 40 min. of arc were introduced. The second study (Fiorentini & Maffei, 1970) used two oscilloscopes with vertical lines moving laterally across the screen. The spatial frequency of the lines of one scope was varied while the other was held constant. This produced a perceptual inclination in the fused binocular stimulus. Changes in the EP were found as the two monocular stimuli became increasingly mismatched.

As can be seen, both of these studies employed complex stimuli and neither controlled the psychophysical dimension. Disparity in the first study and percentage of change in the second were defined not according to judgments made by the observer but rather to a set physical scale. Both reports were basically descriptive. However, it can be concluded from these studies that changes in electrophysiological activity recorded from the human scalp seem to correspond with changes in disparate visual stimulation.

CHAPTER VII

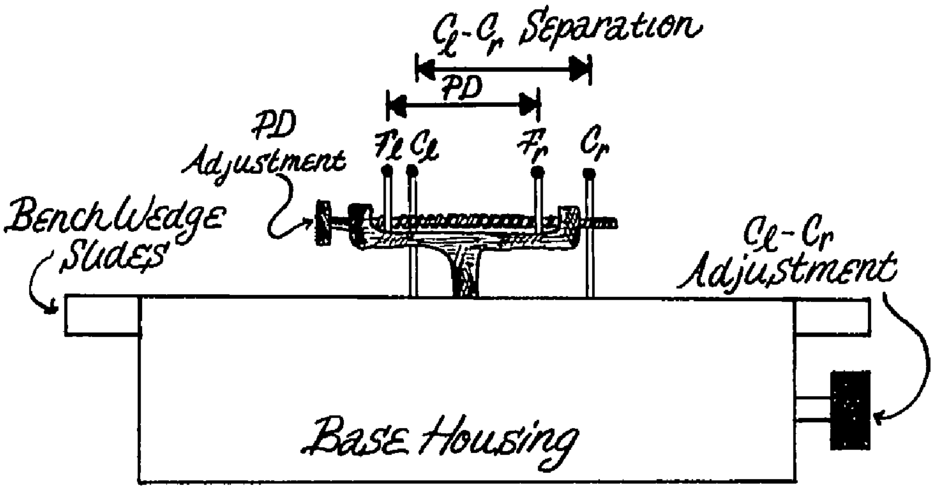
METHOD OF INVESTIGATION

Subjects. Four observers, experienced in making stereoscopic judgments, served as subjects. Three of the four had participated in previous experiments in which visual depth judgments were made. Evoked potentials had been recorded from all four observers to various sensory stimuli. Their visual acuities were corrected to 20/20. All were dark adapted about 20 minutes.

Apparatus. The apparatus consisted of two main parts as shown in Figures 8, 9, and 10.

A diagram of the apparatus for visual stimulus presentation is shown in schematic form in Figure 8. Ten μ sec. duration point light sources at a frequency of 2 pulses/sec. were provided by a Grass Photo-Stimulator Model PS-2. Flexible fiber optic light guides transmitted the photo-flash from the photostimulator to four points in physical space (F_l, F_r, C_l and C_r) located in the same horizontal plane. The active diameter of the light guides subtended approximately 2.73 min. of arc and the intensity was 1.4 millilamberts. Observation distance was one meter. The separation of the two monoocular fixation points (F_l and F_r) was adjustable and set to the interpupillary

Front View



Overhead View

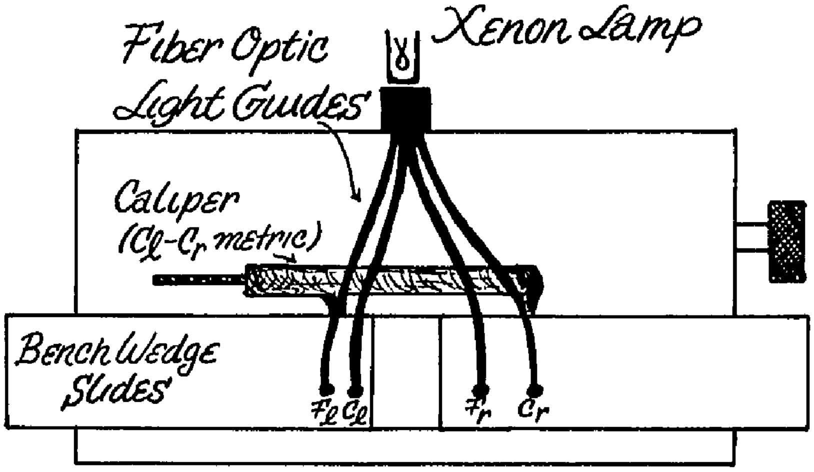


Fig. 8. Schematic Diagram of Stimulus Apparatus with Metric for Angular Disparity Calculations

distance (PD) of the observer so that foveal visual directions were parallel. The two monocular comparison points (C_l and C_r) were offset 1.5 deg. to the right of fixation. The comparison points were mounted on bench wedge slides which were adjustable in simultaneously opposing directions by a finely threaded bolt. Rotation in one direction moved C_l closer to F_l and C_r farther from F_r while rotation in the other direction resulted in opposite movements of the comparison points with reference to the fixation points. A vernier caliper was fixed to the bench slides and made possible a metric reading to an accuracy of 0.02 mm. (or about 4 sec. of arc) for any given position of the two comparison points. Physical disparity values were directly determined by reading the caliper and subsequently converted into angular disparity values.

Figure 9 shows the physical configuration as presented to the observer. Polaroid filters placed before the light sources and in front of the eyes were oriented so that F_l and C_l were visible only to the left eye and F_r and C_r only to the right eye. The four monocular points were easily fused and resulted in binocular vision. Stereoscopic perception of depth, based solely on binocular disparity, was readily achieved by all observers in the experiment.

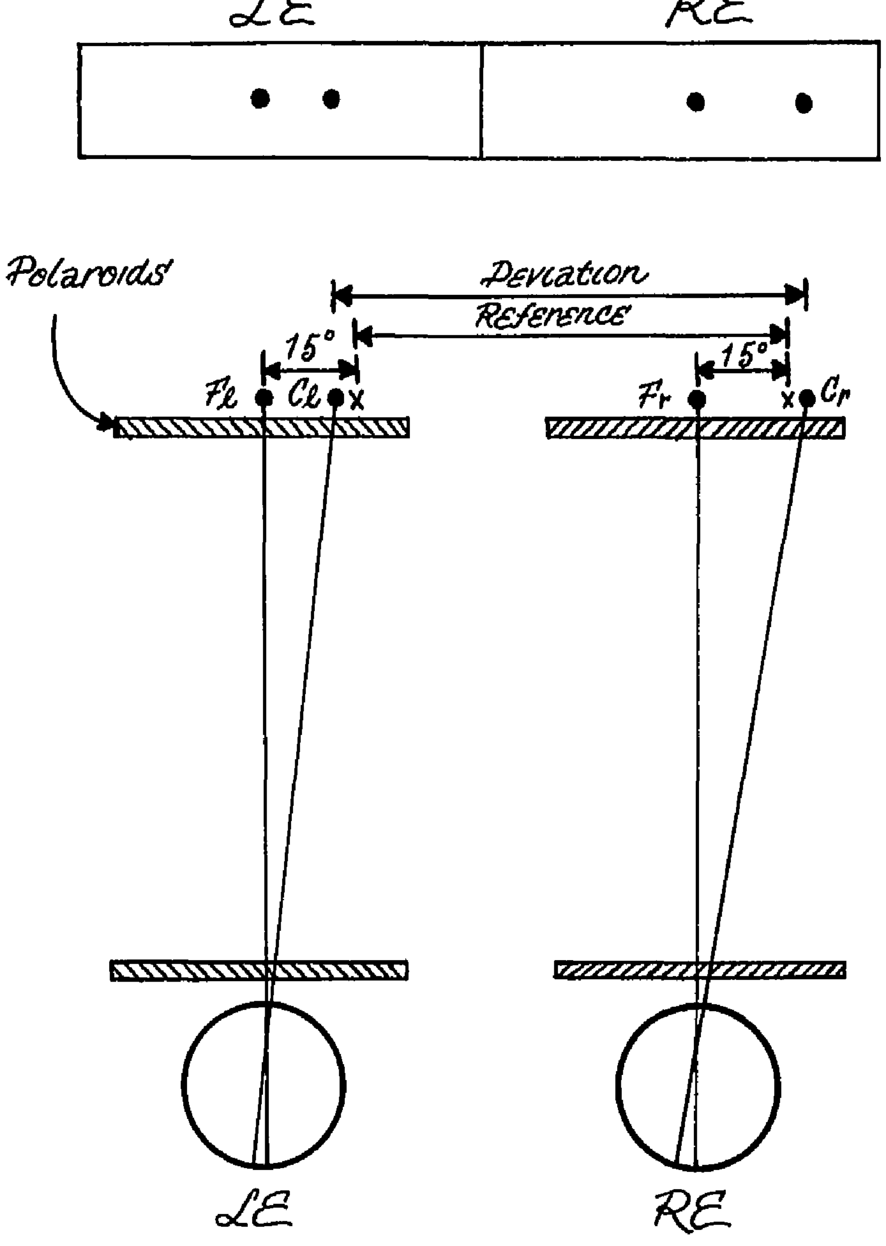


Fig. 9. Schematic Diagram of Stimulus Configuration for Stereoscopic Depth Perception. Upper insert shows corresponding stereogram.

(Several naive observers who were placed in the apparatus for test purposes also had little difficulty in perceiving the depth effect.)

The simultaneously opposing movement of C_l and C_r resulted in lateral displacement of these points from X (the 1.5 deg. angular offset from fixation). In Figure 9, an example of the displaced C_l and C_r is shown which would normally yield a perceptual depth difference between the two fused binocular stimulus points. The insert shows the stereogram form of the same four points. In this case the binocular comparison point would appear farther than the fixation point. Since the caliper was synchronized with C_l/C_r movement, the physical value necessary to calculate angular disparity, was directly determined. After establishing the reference separation between C_l and C_r, when the peripheral point was judged equidistant, the difference in the caliper reading for any other position of the comparison points gave a physical metric. In Figure 9 this metric is the difference between the reference and deviation values. Transforming into angular terms, disparity is defined as:

$$\text{tangent angle} = \frac{(C_l - x) + (C_r - x)}{\text{O.D.}}$$

where OD = observation distance.

For discussion purposes it is assumed that the equidistant horopter point in Figure 9 is positioned at 1.5 deg. of arc in each eye.

The experimental arrangement for recording EPs is presented in block diagram form in Figure 10. Pulses from the Grass Photo-Stimulator provided the visual point stimulation as previously described and also served as a synchronous negative 6 volt square wave to trigger the Neurac Averaging computer. The observer was fixed with his mouth positioned in a dental wax bite board. Bipolar electrodes were attached to the scalp along the midline just above the inion and 6 cm. above the inion. Leads from the recessed disc silver electrodes transmitted the ongoing electrical brain activity to the pre-amplifier (American Optical Differential Amplifier Model 596). Additional amplification took place in the computer. A Tektronix Type 532 Oscilloscope with Type H Plug-In Unit provided a continuous monitoring display of the amplified potential difference between the two electrode inputs. The computer was pre-set to sum the electrical activity of 64 stimuli in a 500 msec. epoch. Onset of the computer time sweep and onset of the stimuli were simultaneous. Frequency bandwidth was from 0.1--45Hz. The two memory banks of the computer, 60 points each, were

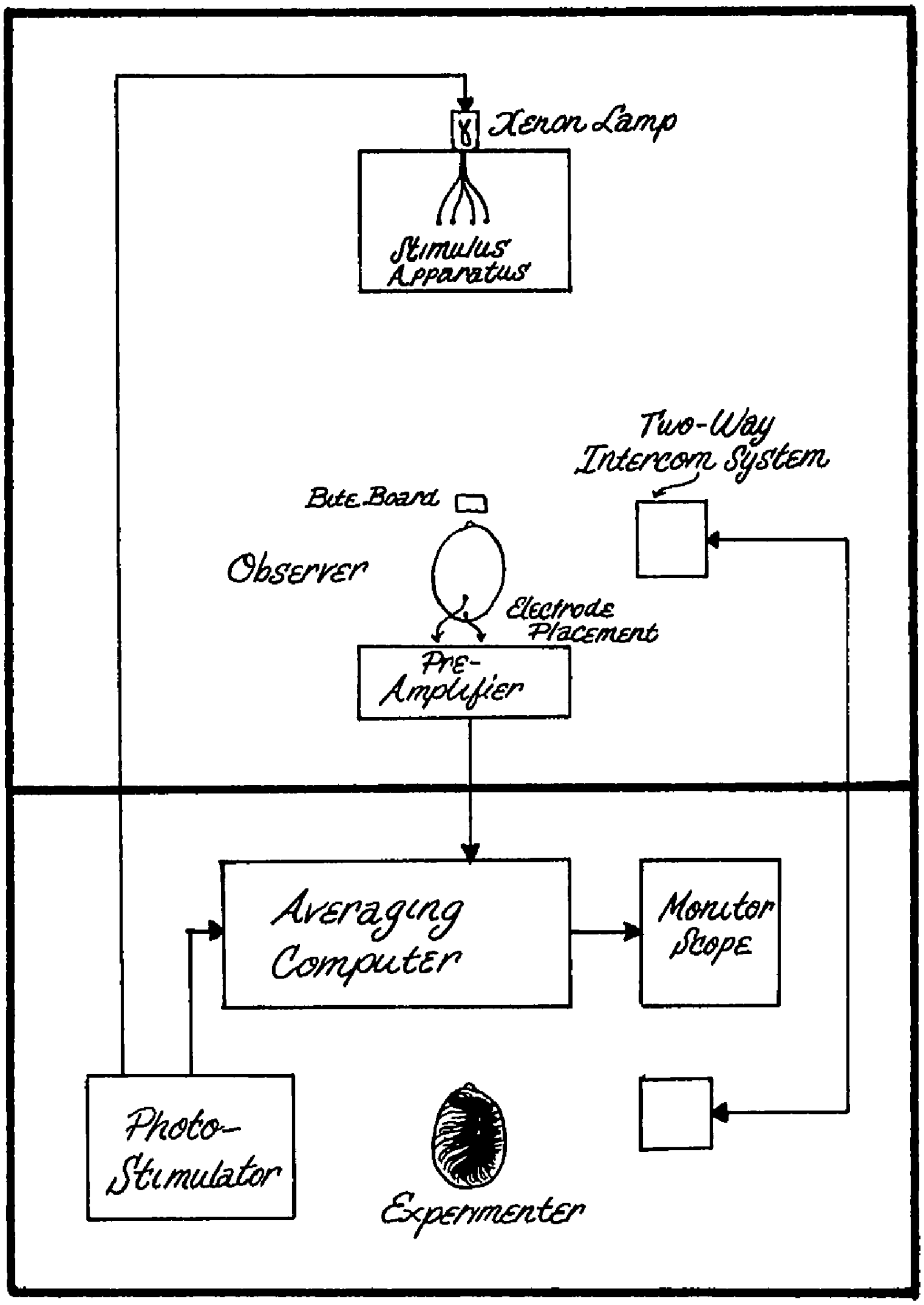


Fig. 10. Block Diagram of Apparatus Arrangement for Recording Evoked Potentials.

used to provide a 120 point resolution. Each point of the 500 msec. display therefore represented just over 4 msec. A two-way intercom allowed voice communication between the experimenter and observer who were in separate electrically shielded rooms.

Procedure. The separation of F_l and F_r was set at the interpupillary distance for each observer, who was then fixed into the bite board. The experimental room was essentially free of light except for the point sources but any stray light was occluded from view by a viewing hood and appropriate masking. The point sources were introduced and binocularly fused by the observer. Psychophysical settings were then recorded using a modified form of the method of adjustment (Guilford, 1954). The flash rate was constant at 2 pulses per sec. throughout all portions of the experiment. As the comparison points were varied, the perceived depth change was not always continuous and sometimes the point appeared to "jump" in depth if disparity was changed too rapidly. Typically, however, the perceived depth difference between the two fused binocular points was rather smooth. The experimenter adjusted the separation of the comparison points, in a counterbalanced order, until the observer was satisfied that the two binocular points were equidistant, different in depth, or outside the limits of stereovision--depending upon the criterion. Twelve judgments were recorded for each observer under each condition.

The primary experimental portion of this study was concerned with recording gross evoked potentials (EP) for different disparity values. For these electrophysiological records, the angular separation of the comparison points was based upon each observer's own settings. Disparity settings for the main set of EPs were determined in the following way. First, equidistant settings were made to determine the zero functional disparity value. Then values were recorded for the comparison point depth localizations of "clearly nearer" and "clearly farther." These depth difference judgments were clear, relatively easy to make, and reliable. After determining the means of each of these three settings, i.e., equal, clearly nearer, and clearly farther, two additional disparity values were calculated in each depth direction using the difference between the means as a unit. The total stimulus set employed for the EPs included seven disparity settings each taken twice and were presented in the following order.

1. + 3 N, difference between means of equality and clearly nearer X 3.

2. + 2 N, difference between means of equality and clearly nearer X 2.
3. + 1 N, psychophysically determined mean of clearly nearer.
4. E, psychophysically determined equidistant.
5. + 1 F, psychophysically determined mean of clearly farther.
6. + 2 F, difference between means of equality and clearer farther X 2.
7. + 3 F, difference between means of equality and clearly farther X 3.

This study was also concerned with obtaining EPs to disparity values great enough so that stereopsis was lost. Fusion of the monocular comparison points always broke down before the perception of depth differences, so the criterion for this case was not simply diplopia but loss of perceived depth between the fixation point and the comparison point. The observer's task was to hold the monocular fixation points fused while disparity was increased in the comparison points beyond the limits of stereovision. EPs were then recorded to this binocular configuration.

The gross electrophysiological activity under two other conditions was also recorded following the same basic procedures already described. The conditions were fixation in space three times the perceived separation of the two binocular points but above the fixation point, and the same, below the fixation point. The purpose of these additional conditions was to determine if reliable EPs could be recorded under different types of stimulus presentations and to compare the curves with the major set.

CHAPTER VIII

RESULTS

Average gross evoked potentials (EPs) recorded from the human scalp have great variability among subjects, under different recording techniques, and as a function of the type of stimulation (Cobb & Morocutti, 1967; Donchin & Lindsley, 1969; Perry & Childers, 1969). Therefore before presenting the curves evoked by the various disparate visual configurations in this study and in order to place them in better perspective, it seems necessary and appropriate to first show EPs resulting from the simplest similar stimulus target.

In Figure 11, two curves from each of three observers are displayed which were recorded under essentially the same conditions as those in the later figures. The difference is that these curves were evoked by one foveal binocular point source (the same fixation point used for the disparity conditions). An upward deflection indicates electrical activity at the upper electrode was positive with reference to the lower.

The components in the curves may be compared to Ciganek's (1961) classification method as noted by the Roman numerals in the traces of subject MP. However the recording techniques and resulting curves are

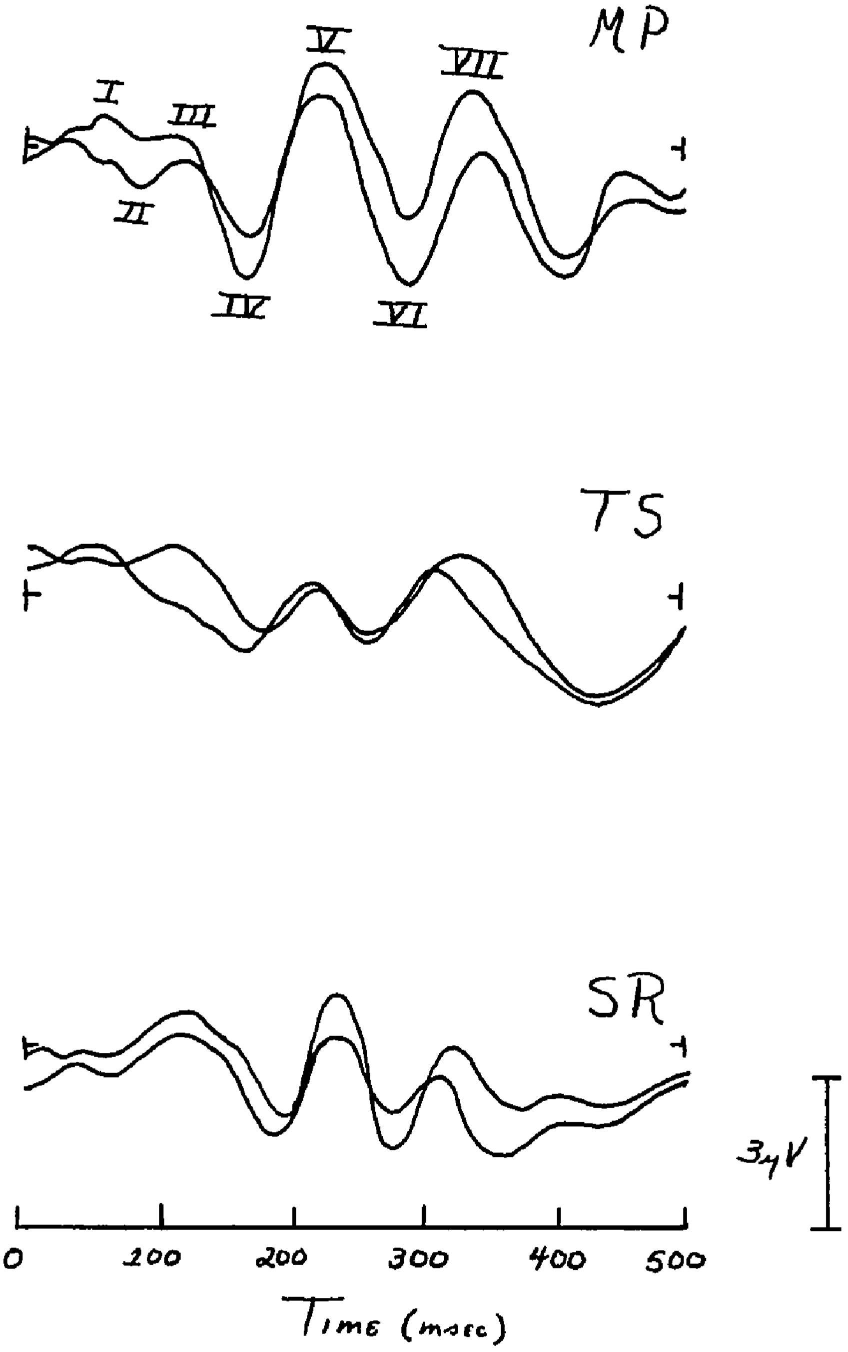


Fig. 11. Binocular Foveal Evoked Potentials for Three Observers Recorded from Bipolar Electrodes over the Occipital Cortex

generally more similar to those obtained by Harter & White (1968); Perry & Copenhaver (1965), Remond (1969) and Shipley, Jones, & Fry (1966). Small but reliable early components may be seen but the first large downward deflection peaks at 160-190 msec. followed by an upward deflection peaking at 225-240 msec. The temporal portion of the EPs up to 300 msec. is the area of concern and all of the following figures have a time base of 0-300 msec.

Figures 12, 13, and 14 show the EP waveforms for three observers from psychophysically determined disparity conditions as listed in the METHOD section. Equidistance (E) and near and far conditions (+ 1 N, + 2 N, + 3 N, + 1 F, + 2 F and + 3 F) appear above and to the right of each appropriate pair of EPs. The functional disparity value in decimal minutes of arc for each set of curves is given.under the condition notation. These values were calculated angular differences from the mean setting of equality. (The equidistant reference value is always 0.0 min. of arc.) It can be seen from the standard deviations listed in the figures under the functional disparity values for conditions E, + 1 N, and + 1 F that these distributions are quite narrow and the judgments reliable. This is the case even though the judged differences between

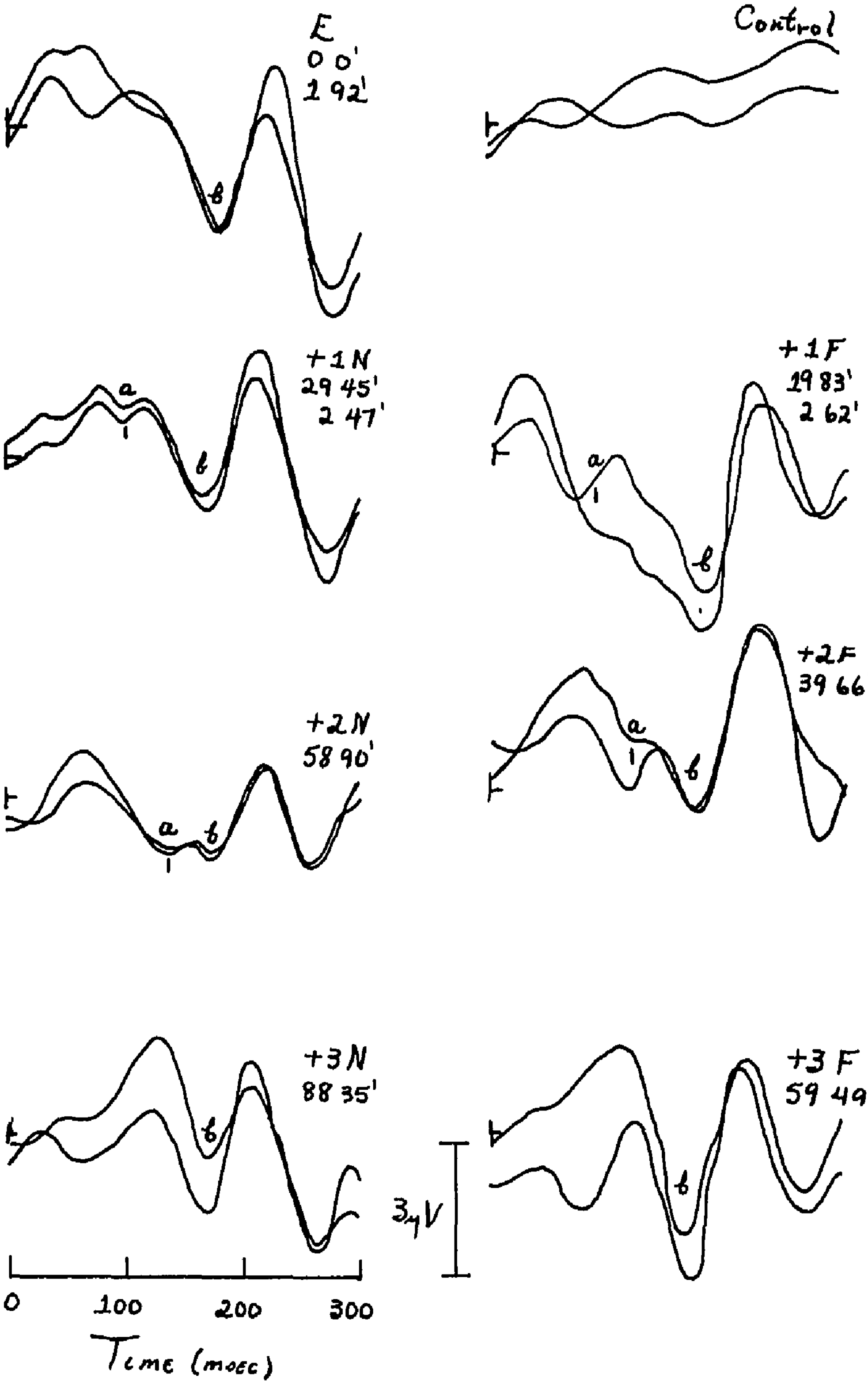


Fig. 12. Evoked Potentials for Psychophysically Determined Disparity Conditions; Observer MP. Small vertical line in each pair indicates the mean latency of component a.

equality and clearly nearer or clearly farther are large in comparison to stereoscopic disparity values most often reported.

This finding appears to be due, in part, to the criterion used for making stereoscopic judgments. Equality of depth has been the typical standard, but equidistant judgments set restrictive limits upon the type of stereoscopic measures that are possible. We do not go strolling along shifting from one horopter world to another but rather are able to simultaneously compare and judge on a continuous dynamic basis.

The EP records, representing electrophysiological activity, for the most part, are reliable and similar for each observer for each stimulus condition. There are differences between observers as shown in Figures 12, 13, and 14. Part of the difference may be due to the range of disparity over which the seven conditions were taken. For example, the psychophysically determined disparity units for MP (Figure 12) are much larger than those for SR (Figure 13).

First, in Figure 12, the EPs for the equidistant condition are quite similar to the EPs for binocular foveal stimulation (cf. MP in Figure 11). Systematic variations in the curves of MP appear as disparity values were changed. Specifically, the early doublets

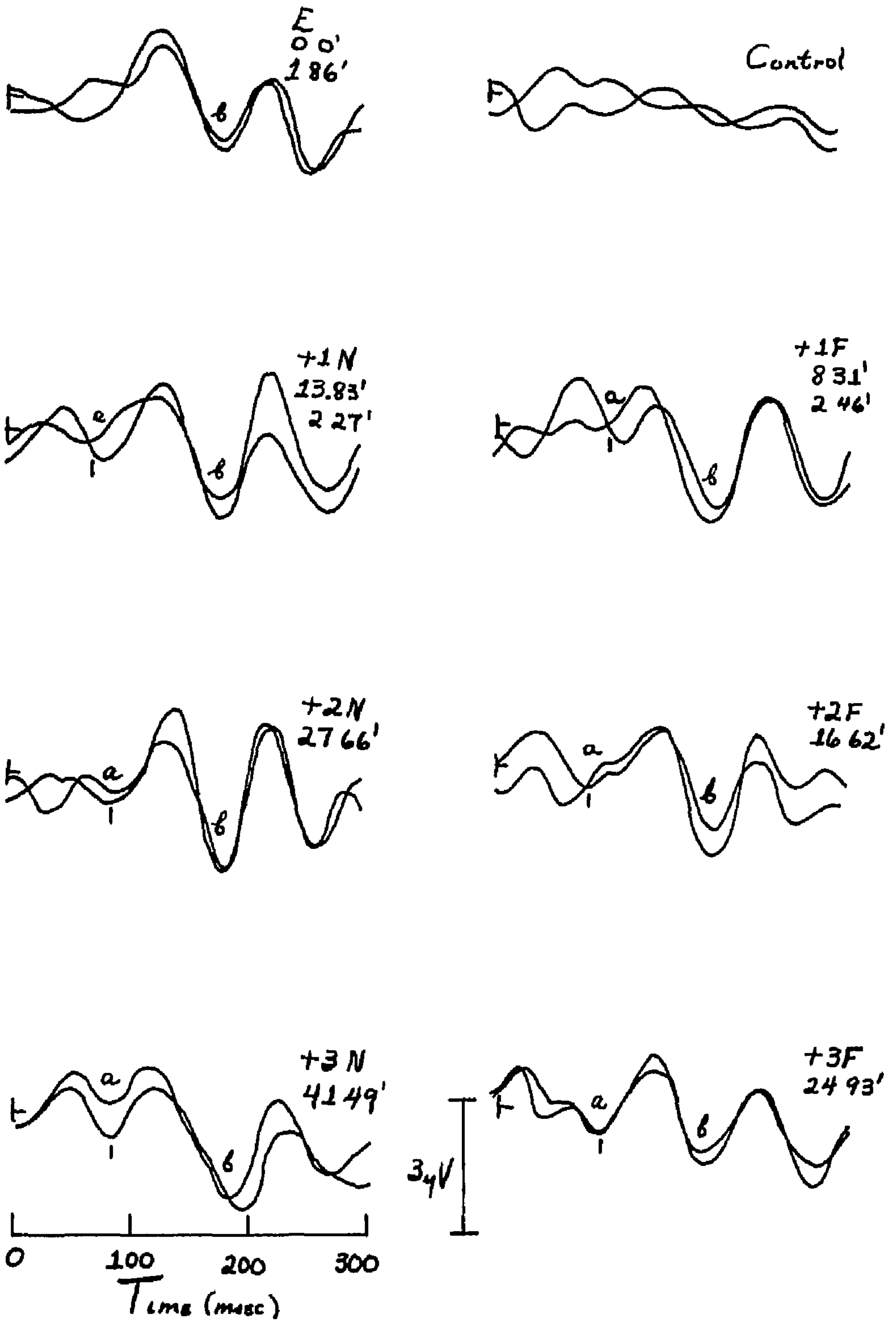


Fig. 13. Evoked Potentials for Psychophysically Determined Disparity Conditions; Observer SR. Small vertical line in each pair indicates the mean latency of component a.

in the + 1 and 2 N and F conditions are most noticeable. Beginning with the equality records and progressing + 1, + 2, and + 3 in either direction a systematic change in the early portion of the EP takes place. The downward component (labeled throughout as a) in + 1, which peaked at about 100 msec., is shifted to the right (125-150 msec.) in + 2. Component a also approaches the potential difference of component b located consistently at about 175 msec. in all of the EPs of MP. For the + 3 conditions the critical a wavelet does not appear clearly differentiated from the b component. It may be overlapped but the amplitudes of b are not consistently larger. If the a component is an electrophysiological correlate of disparity for this observer the question arises regarding what becomes of this critical portion of the curve in the + 3 conditions. There is a psychophysical argument that the electrical binocular disparity activity is gone in + 3 N and F because this observer did have difficulty maintaining perceptual depth differences for the extreme near and far conditions.

A similar early downward a component is identifiable in the EPs from observer SR (Figure 13). The latency shift for the different conditions is not as reliably located nor dramatic as in the data of MP

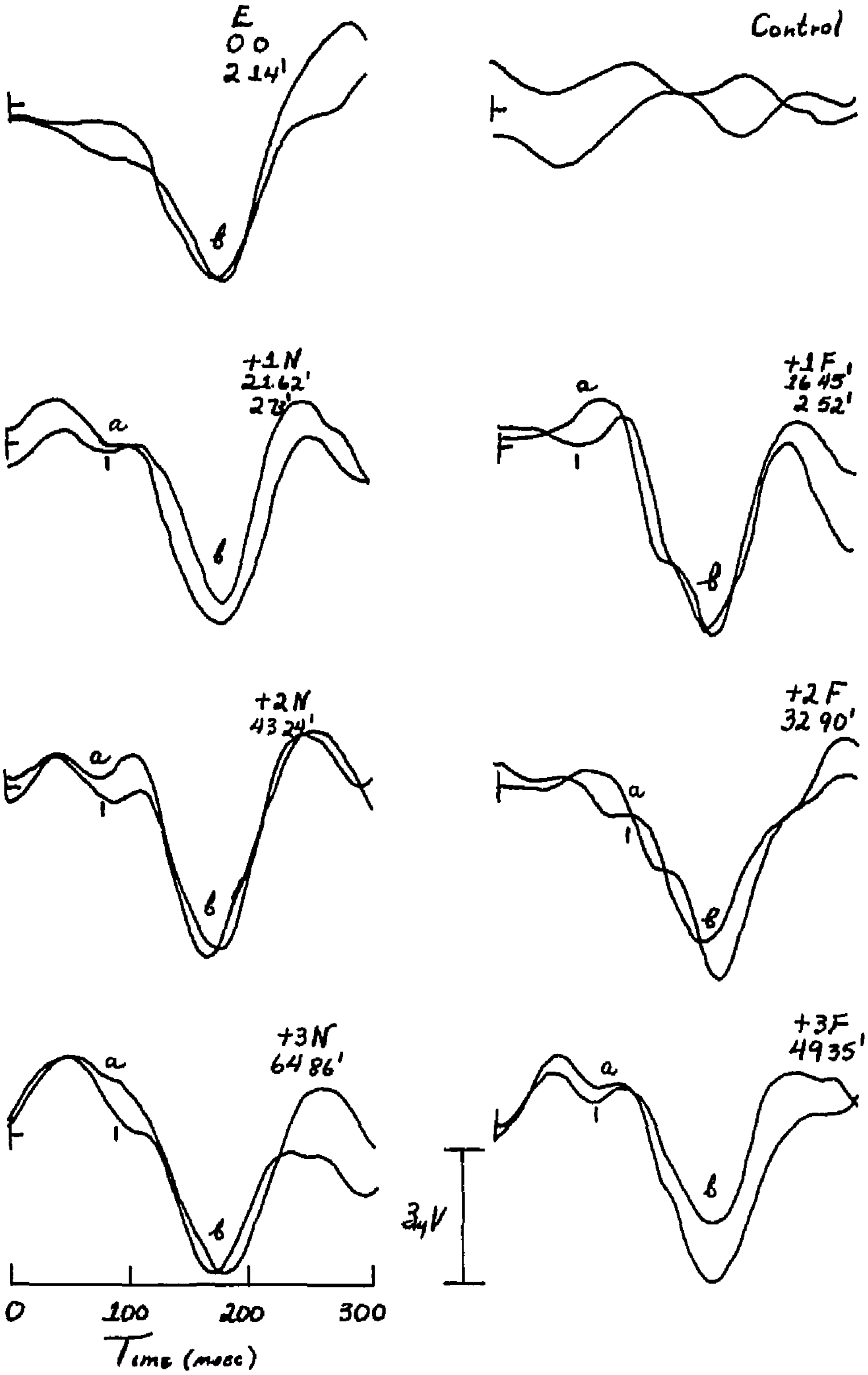


Fig. 14. Evoked Potentials for Psychophysically Determined Disparity Conditions; Observer IM. Small vertical line in each pair indicates the mean latency of component a.

but then the difference in the disparity values were smaller (actually about one-half the disparity for each corresponding condition). Solid stereodepth was easily held by SR in the extreme near and far conditions and the a component is easily seen in + 3 N and F.

A third set of data is presented in Figure 14 from the observer IM. For all conditions, a large b component is present and consistent in both latency and amplitude. Following the a component through the seven conditions one again finds a variation corresponding to increased disparity values. This observer was the least experienced of those who participated in this study and the a component is also less pronounced (throughout all of the EPs in Figure 14) than in the other observer's records.

Evoked potentials from another observer were taken with predetermined geometrical disparity values. In Figure 15 the a component is located at about 160 msec. for both near and far depth conditions and is clearly differentiated. The waveforms are unlike those of the other observers but the a component becomes more prominent as disparity was introduced.

Evoked potentials to disparity values large enough so that stereodepth was lost are shown in Figure 16.

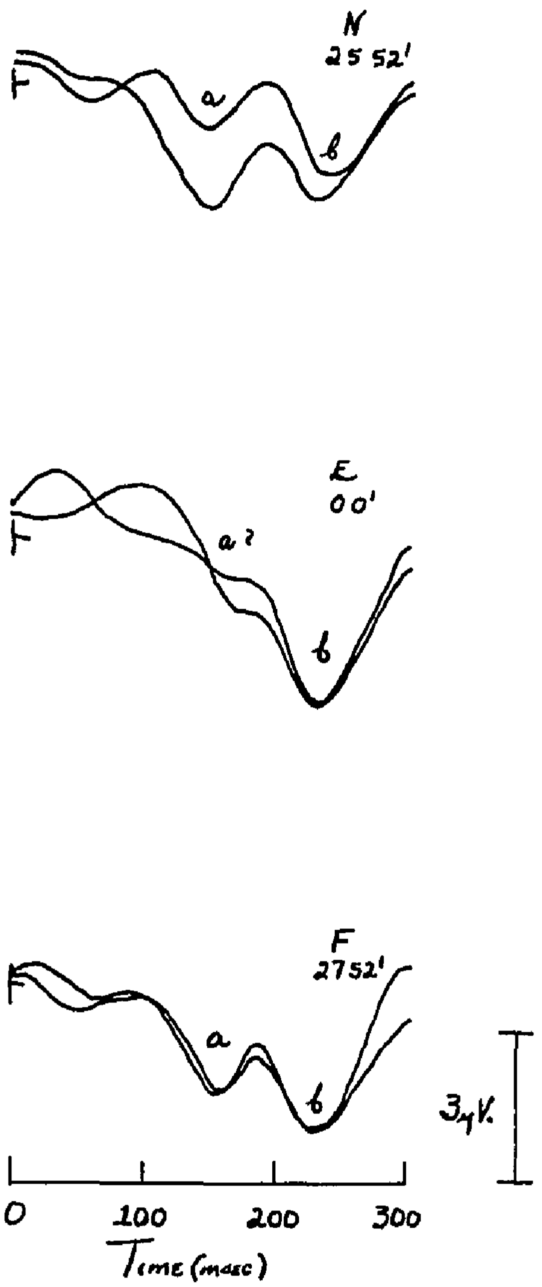


Fig. 15. Evoked Potentials for Fixed Disparity Conditions; Observer TS

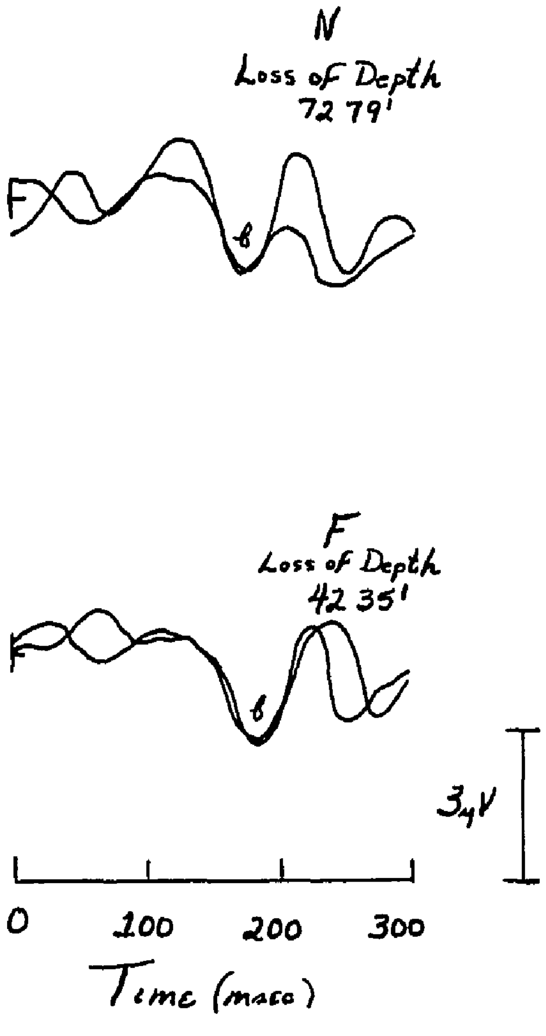


Fig. 16. Evoked Potentials for Disparity Values Outside the Range of Stereoscopic Vision; Observer SR.

The reliability was poor under these conditions especially before 100 msec. and beyond 200 msec. This variability does correspond to changes in the visual stimulus. It was difficult to hold the two fixation points in binocular fusion and during these runs different pairs were sometimes wrongly fused and at other times four points were perceived.

It was possible to "fixate" in space above, or below the fused fixation points. The four sets of curves in Figure 17 shows the results of these conditions. The reliability was consistently poorer even when stereoscopic depth was perceptually clear. Observer TS reported it was very difficult to get a depth effect when fixating in the above condition and the EPs which were recorded do not, in fact, resemble EPs for other depth conditions. Only one slow broad wave appears from about 100-250 msec. For the same observer in the fixation below condition, the EPs show an indication of the a and b components. The a and b components in the EPs for the fixation conditions above and below, for SR, may be identified especially in the above condition. The EPs in Figure 17 support the main findings (Figures 12, 13, and 14) but are inadequate for making a strong case for disparity coding in the absence of a binocular fixation point.

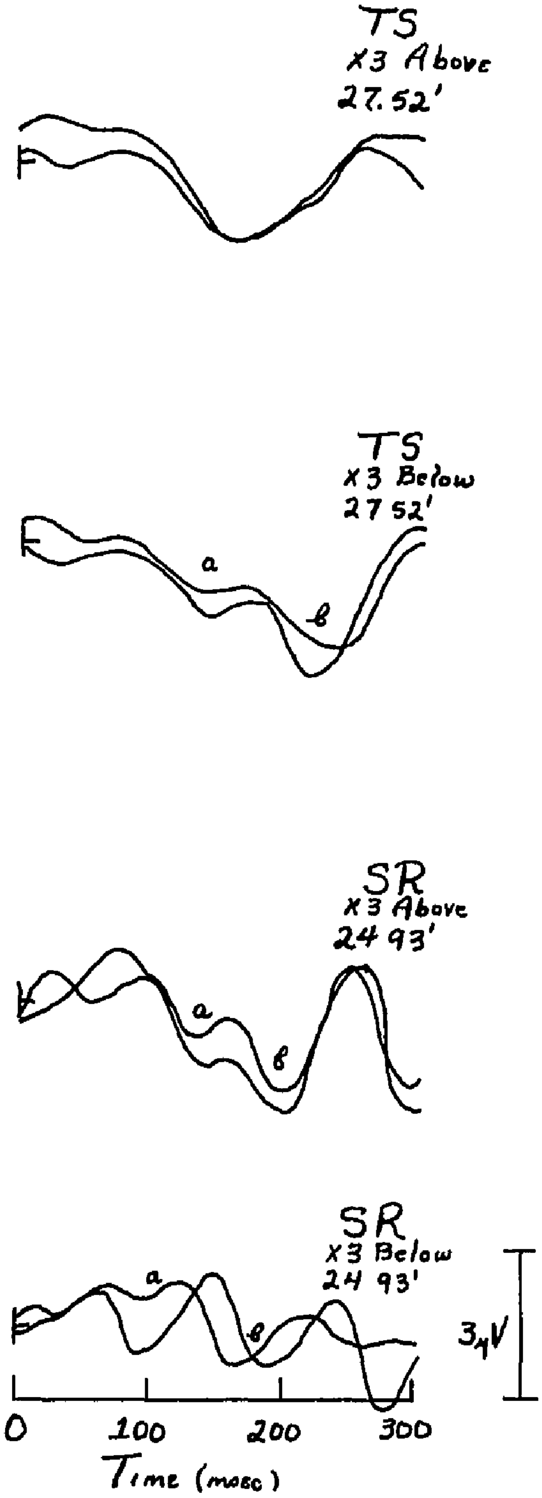


Fig. 17. Evoked Potentials for Fixation Conditions Above and Below the Physical Fixation Point.

Figure 18 is presented for the purpose of displaying the change in the critical component, a, of the EPs taken from the three main observers (Figures 12, 13, and 14). Each point represents the mean latency of component a for two EPs for each functional disparity condition for each observer. The latency of the a component, as marked in the three pertinent figures, was determined by measuring the position in time of the maximum deflection of each appropriate wavelet.

The general trend which may be seen in this summary figure suggests that the latency of a increased as functional disparity increased. The trend is in the same direction and of a similar degree for the near and far functional disparity conditions. As noted previously, the change is not systematic for every two-point comparison. However, within each observer's data points the trend is maintained. The argument for increased latency with increased functional disparity is stronger when all three sets of data are plotted and inspected simultaneously.

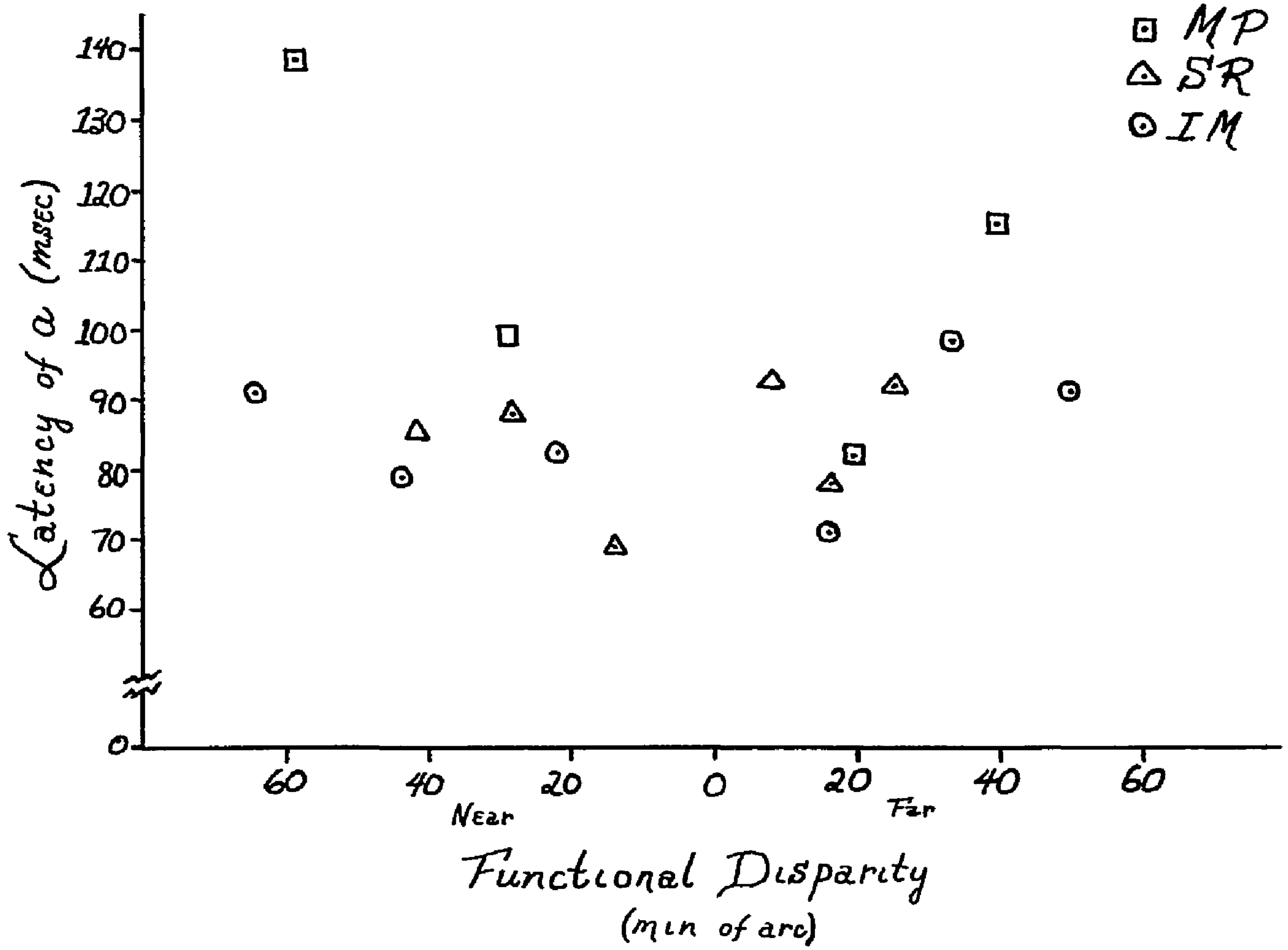


Fig. 18. Latency of Component a plotted Against Functional Disparity; Observers MP, SR, and IM. The latency of the component increases as functional disparity increases for both near and far stereoscopic depth.

CHAPTER IX

DISCUSSION

The major finding of this investigation was the identification of a relatively early component (a) in the scalp recorded evoked potential which varies with psychophysically determined disparity in a two-point binocular stimulus. The latencies of the maximum deflection of the a component range from about 70 to 140 msec. depending on the amount of functional disparity. The EP records show that the critical component may vary in time and that across observers, the change tends to be systematic. As stereoscopic depth increased in a binocular peripheral point, with a foveal fixation point as reference, in either the nearer or farther direction the latencies, of the neural activity of which this wave is comprised, tends to increase.

Taking the stereoscopic depth perception/EP component relationship at face value and describing how the two change adds little to the understanding of the neural processes and mechanisms involved in binocular function. Before an explanation can be more than speculative, it is necessary to determine what electrophysiological activity might be recorded in the

EP from scalp electrodes. Two lines of research are particularly pertinent to the analysis of the EPs presented in this study: the single cell work on disparity specific cortical units; and, the investigation of the relationships between single unit responses and gross EPs.

Electrophysiological investigations of disparity specific binocular units in area 17 of the cat were discussed in CHAPTER VI. Barlow, Blakemore & Pettigrew (1967) reported that over 80% of the units from which they recorded were binocularly driven. After determining the two monocular receptive fields (minimum response field), the optimal position for maximum facilitation was identified for simultaneous binocular stimulation. Disparity was then calculated as the difference in displacement from the initial monocular field centers to their location under binocular conditions. The disparity range for 87 units was 6.6 deg. of arc horizontally and 2.2 deg. of arc vertically. The horizontal disparity spread, they note, is extremely large compared with the 10 sec. of arc threshold of stereopsis found in human psychophysical studies. It is further implied that the reason is due primarily to poorer discrimination in the cat, than in man, which is likely one important factor. However, the comparison they make is not the proper one. Blakemore (1968) was correct when he later stated that "...this figure (the horizontal disparity value) should more reasonably be compared with the upper disparity limit for obtaining a reliable sense of depth [p. 94]." He also presented data from units sampled with a functional column in the cat's cortex which in one case yielded a horizontal range of 0.3 deg. of arc and in all instances yielded a smaller disparity range.

Two types of comparisons between the unit activity in the cat and psychophysical judgments in man are possible: those related to corresponding depth areas; and those related to the range of depth over large disparity values. First, the 10 sec. threshold in man is more appropriately compared with the standard deviation of the disparity range calculated from Blakemore's "depth column" recordings. This comparison is valid because both types of data are related to the identification of a single position, or small area, of localized depth. Nikara, Bishop, & Pettigrew (1968) investigated corresponding areas and reported a 0.6 deg. standard deviation of the disparity range from electrophysiological unit response in the cat's visual cortex.

The second type of valid comparison may be made between the stereoscopic depth limits, psychophysically determined (Ogle, 1952), and the horizontal disparity spread found in the single unit recordings reported by Barlow, Blakemore, & Pettigrew (1967). In comparing these two approaches it may be seen that under certain conditions the total disparity range was quite similar. For example, at 6 deg. eccentricity the horizontal disparity ranges were about 4 deg. of arc.

The disparity conditions employed as binocular stimulation for the EP recordings in this study cover a wide range of stereoscopic vision. The electrophysiological potentials, therefore, are more in line with the type of single cell data which represent a large spread of disparity specific cortical detectors.

Individual psychophysically determined depth locations, i.e., the E, + 1 N, and + 1 F conditions, on the other hand, yield data of the corresponding area type.

The investigation of electrophysiological activity recorded simultaneously from single units and from the cortical surface is appropriately discussed at this point. In the visual cortex of the unanesthetized paralyzed cat Cruetzfeldt, Rosina, Ito, & Probst (1969) found relationships between the type of neuron and components in the surface activity. An early component of the EP, at 15-50 msec., was related to discharge of on-center fibers and the beginning of excitatory postsynaptic potentials. The main component, peaking at about 50 msec., correlated with inhibition of inhibitory units. The following reverse electrical shift up to about 100 msec. was found to correspond to the activity of both excitatory and inhibitory cells. In figures showing net activity the differential responses were less distinct but, in general, the EPs over time reflected summed responses of the individual neuron types. The surface EP was smoother and larger in amplitude. This might indicate that a one-to-one correspondence between individual neuronal activity is not maintained in the EP. This finding points out a primary problem in evaluating the EP. Differential distances of neurons from the electrode placement contaminate the EP and the assumption cannot be made that all cortical cells involved in the total ER curve have equal weighting. It becomes even more of a problem in scalp recorded potentials because of folding of the brain and variability in placing the electrodes directly over the area of interest.

Fox & O'Brien (1965) found a close relationship between single cell firing and different components of the slow-wave potential. Spontaneous extracellular activity over time also was found to be closely correlated to neuronal firing (Fox & Norman, 1968). These data have been questioned by Freeman (1969) because of the possible contamination due to electrical activity of cells surrounding the single units.

Vaughan (1969) has developed a "volumn-conduction" theory in an attempt to specify cortical generators related to scalp activity. Creutzfeldt (1969) questioned the validity of such a model because it appears too simplified when one considers differential neuronal activity contained in the surface EP. Adey's (1967) "tricompartmental" model of cerebral tissue fits more closely with Creutzfeldt's position. It can be concluded that even when single units and surface EPs are recorded simultaneously, interpretation of the EP is no simple matter.

Hubel & Wiesel (1965) have added additional processing steps beyond the primary visual cortex (area 17) where binocular cells were initially found and (Hubel & Wiesel, 1970) area 18 in the macaque monkey was proported to serve two functions related to binocular vision. The two halves of the visual field are connected through this cortical area and disparity specific binocular cells were found in area 18 rather than 17. Blakemore (1968) proposed a "master cell" notion in a neural disparity model. This unit, one for each depth column in the cortex, would signal disparity messages to other cortical areas which would lead, presumably, to the stereoscopic experience.

There has not yet been single unit disparity detectors and EPs recorded simultaneously but this would appear to be one further step in determining the neural mechanisms of stereoscopic depth perception. Specific disparity units have been found in the visual cortex of both the cat and monkey. EPs reported in this study and others (Fiorentini & Maffei, 1970; Regan & Spekreijse, 1970), exhibit differential forms as a function of disparity. Both types of neural activity were recorded in the visual cortex. The primary visual cortex may only be a first cortical processing point for stereopsis and it may not be the only neural pathway that leads to the perception of depth.

Sensory experience and corresponding EPs have been found which fail to show systematic changes as a function of stimulus parameters. Regan (1968) reported discrepancies between perceived flicker and EP amplitude. EPs decreased in amplitude, as a general anesthetic is infused, while the sensory thresholds to electrical shock remained relatively constant (Clarke, Bulter, & Rosen, 1968).

A more general problem concerns information about the anatomical location and the physiological activity of "conscious perception" which is presented unavailable except in the arousal-sleep dimensions (Jouvet, 1967; Lindsley, 1960). Shevrin & Fritzler (1968) reported low amplitude, but reliable, EPs to visual stimulation below threshold. In effect, this indicates that phychophysical-physiological comparisons may sometimes be made on the basis of data which, strickly speaking, are not directly related. Gastaut, Regis, Lyagoubi, Mano, & Simon (Cobb & Morocutti, 1967) recorded EPs at the occipital cortex to somatosensory and auditory stimulation. With our present knowledge one may or may not conclude that these subjects "saw" the current and the clicks. Another example of drawing improper conclusions regarding electrophysiological response and perceptual experience makes a less ambiguous case. An electroretinogram may be recorded at the eye. Does the person see?

Sensory experience and EP relationships have been found but integrating them into comprehensive theories has proven to be a challenging and somewhat perplexing task as can be appreciated from the recent Neurosciences Research Program Work Session (MacKay, 1969). The participants--from single unit neurophysiology, to gross electrophysiology, to psychophysics--raised many questions which were left unanswered. For example: what physiological classifications are meaningful?; how does cortical folding effect the EP?; what are the relationships between EPs recorded by different (e.g., bipolar vs. monopolar) techniques? Discussions as to the status of methods, techniques, analysis, and especially attempts to integrate findings from diverse areas into some meaningful principles were somewhat less than successful and actually rather disappointing. It can be generally concluded that, at present, simple analysis has not been replaced by more sophisticated methods and often the latter leads one into complexities that are irrelevant and away from an understanding of the basic data. Communication of results also tends to be inhibited.

In the context of previous work, the present study suggests that EPs reflect, or at least may indicate, some net electrical activity about the recording site that may be traced to neuronal polarization and discharge initiated in part, by external stimulation. Electrophysiological activity associated with the highly refined perceptual function of stereopsis is shown in the early components of these evoked potential recordings. The question as to whether the critical component of the EPs corresponds to differential neural activity in groups of disparity specific cortical units remains open.

Jung (1961) discussed twelve different parallels between neuronal activity and visual experience. Eleven of the twelve are what might be termed gross discriminations, i.e., diffuse illumination was the stimulus. The twelfth parallel involved stimulation around light-dark borders. Stereoscopic functioning falls into this highly refined spatial category, and is even more complex than border contrast because of the necessary binocular input and interaction. If the delicate spatial arrangement shown in psychophysical studies is maintained at cortical levels (as has been shown in the visual cortex of the cat), the argument for specific disparity detectors--as contrasted to gross detectors, e.g., illumination--in the human brain is supported.

CHAPTER X

SUMMARY

The purpose of this study was two-fold. First, theoretical formulations regarding the nature and definition of binocular disparity were presented. Second, the experimental portion reports results on the relationship between stereoscopic depth perception and the corresponding cortical electrophysiological activity (evoked potentials recorded from the scalp) in the human observer.

A comprehensive definition of disparity was discussed which is applicable to the total binocular field. Employing stereograms as illustration, an argument was developed in an attempt to show that stereoscopic depth perception may take place any part of the binocular field and is possible in the absence of a binocular fixation point.

In the experimental part of the study a simple two-point binocular stimulus (the points separated by 1.5 deg. of arc) was presented at a distance of one meter. Disparity was varied and psychophysically determined depth judgments were recorded for equality, clearly nearer, and clearly farther conditions. The angular unit between equality and nearer or farther was employed to construct seven functional disparity conditions. Evoked potentials were then recorded for each binocular stimulus condition.

The major finding of the experimental portion of this study was the identification of a relatively early component in the evoked potential which increased in latency as binocular disparity increased. Since the disparity conditions were psychophysically determined for each observer, i.e., they represented stereoscopic depth judgments in terms of functional disparity, the evoked potential component found corresponded to perceived stereopsis.

The meaning of scalp recorded evoked potentials was discussed with reference to specific disparity detectors, reported in single cell studies, in the visual cortex of the cat. The change in latency of the critical component of the visual evoked potential was interpreted as evidence that neuronal activity corresponding to stereopsis occurs in differential cortical locations for different perceived depth conditions.

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