VISUAL ACUITY AND EYE MOVEMENTS

Thesis by

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This thesis is dedicated to my parents, Perry and Claire Gilbert, and to my wife Gretchen, for their continuous inspiration and loving support.

ABSTRACT

Several longstanding theories and some recently published experimental evidence support the hypothesis that eye movements serve to improve acuity. By measuring eye movements during a simple acuity task, and during a control non-acuity task, we have shown that certain patterns of eye movement are characteristic of acuity tasks. Similarly, specific patterns of eye movement are generated during spatial localization tasks. These observations provide circumstantial evidence for the existence of mechanisms by which eye movements mediate acuity and spatial localization information.

Through a comparison of acuity for stabilized retinal images with acuity for normal retinal images we have found that eye movements improve acuity very slightly at most, and that even this small improvement may be adequately accounted for by the residual fade-out effects commonly observed during prolonged viewing of stabilized images. Measurement of distance and angle estimation ability in both normal and stabilized vision reveals much the same result. Stabilization diminishes the accuracy of these estimates only slightly, as might be expected from the persistent fade effects observed during the stabilized trials. Residual retinal image movement in the stabilized trials was less than approximately 3 min arc. If such acuity improving mechanisms exist, they either operate on very small retinal image movements (less than 3 min arc), or they

improve acuity only slightly (e. g. , by less than 0. 1 log unit in sine wave grating contrast sensitivity). Thus eye movements serve to sustain all sensory visual inflow by countering the slow process of fading of a stabilized image. They do not, however, play a vital role in the much more rapid processes which determine visual acuity as well as distance and angle estimation ability.

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CHAPTER I

"A rolling eye, a roving heart."
Thomas Adams, Sermon, 1629

"She that has good eyes
Has good thighs."
John Suckling, The Goblins, 1638

No era has bred much agreement on the functions or correlates of eye movements, and ours is no exception. This thesis concerns two alleged uses of eye movements, first, as an aid to acuity:

> The limiting retinal factor in acuity seems to be the relation of receptor width to the highest optical gradient in a moving pattern [with movement produced by ocular rotation], rather than the average static illumination on one cone compared with its neighbors.
> W. H. Marshall and S. A. Talbot, 1942 (1)

> Thus, there never has been any experimental basis for the "dynamic" theories of visual acuity, according to which micronystagmus provides the basis for a mechanism which sharpens contrast and aids in acuity...
> G. Westheimer, 1965 (2)

> The decrease in visual acuity with stabilized retinal images contributes [experimental] evidence to a certain extent in favor of the dynamic theory of visual acuity.
> M. Millodot, 1966 (3)

and, second, as an aid in estimating distance and direction:

> Every accurate comparison between two spatial dimensions, such as lines, angles or surfaces in the field of view, is made with the help of ocular movements.
> H. von Helmholtz, 1910 (4)

> The experiments reported above show that the perception of geometrical illusions does not depend on eye movements.
> R. M. Pritchard, 1958 (5)

Far from being simply semantic differences, which in proper context would seem much more harmonious, these statements embody distinctly contradictory ideas concerning the role of eye movements in human vision. The conflicting theories are discussed in detail in the following chapters. The experiments reported here attempt to resolve the disputes by establishing either the existence or the absence of physiological mechanisms which through the action of eye movements either improve acuity, or improve estimates of distance or direction.

The following chapter gives the description of two rather intricate pieces of apparatus which were employed in these experiments, i. e., the eye movement measuring system, and the retinal image stabilization apparatus. Chapter III deals with the behavior of eye movements during simple acuity and distance estimation tasks. Chapters IV and V treat the problem from the complementary angle, that is, by measuring performance in these tasks both with and without retinal image motion. Thus Chapter IV treats changes in acuity due to cancellation of retinal image movement, and Chapter V treats distance estimation with and without retinal image motion.

One of the advantages of research on visual systems is the wide range of available methods and theoretical frameworks. Although the particular problem frequently suggests the method to be used, the method has a much more inexorable impact on the

results, in particular, on the range of validity of the results. These factors necessitate fairly explicit definition of the type of experimental approach, as well as the theoretical framework within which the results are valid and, more importantly, useful.

The first step in this definition of method and theoretical framework is schematized in Fig. 1. This is done not so much to limit the application of my results, but rather to curb, or at least to circumscribe, the expectations of the reader. Fig. 1 should be interpreted to mean that the experiments discussed herein employ psychological or psychophysical methods in order to arrive, via an occasional mathematical argument, at physiological mechanisms in the visual system.

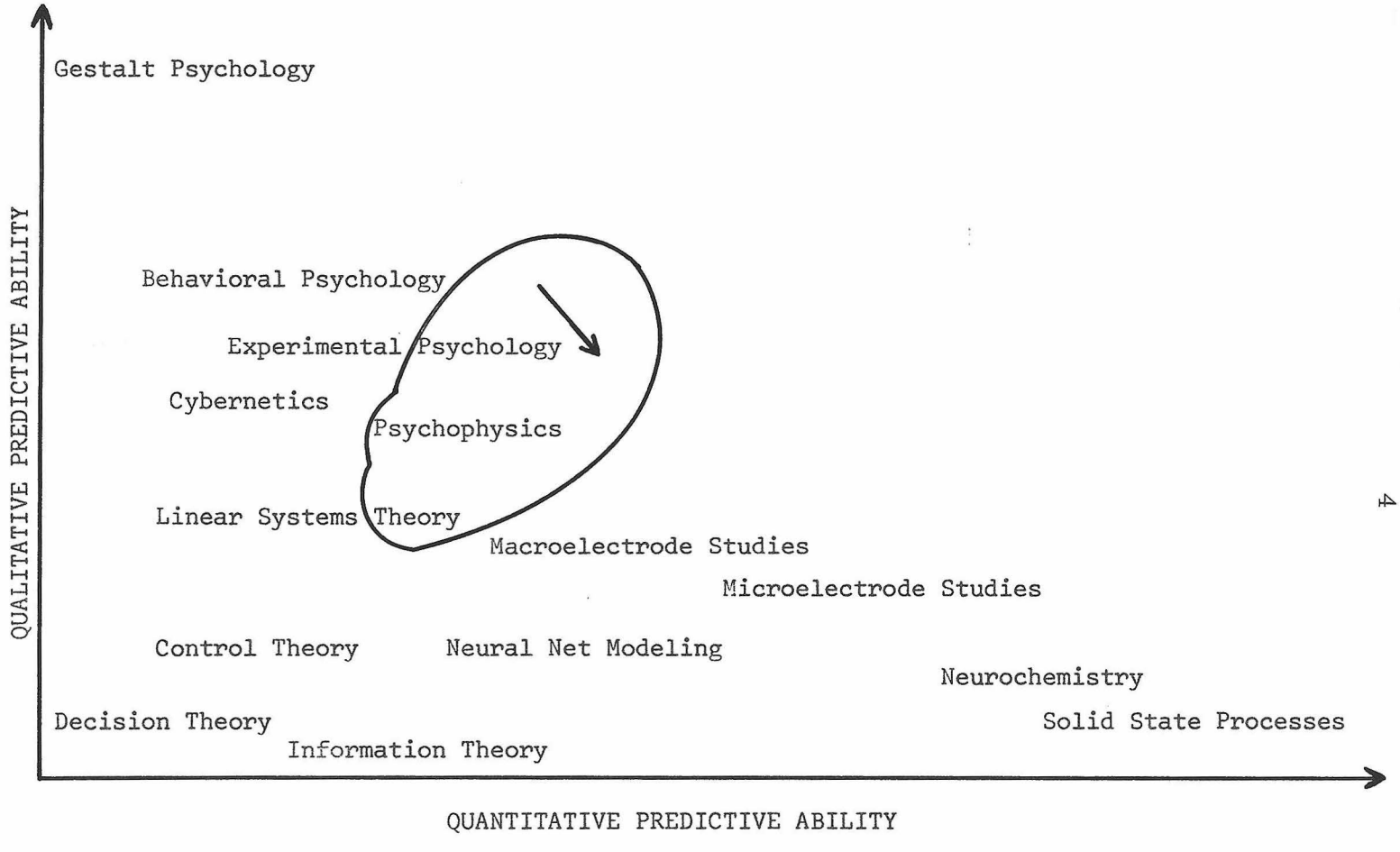

Fig. 1-1 A somewhat arbitrary expansion of vision research into its components, with the realm of the experiments reported in this thesis indicated by the contour. The arrow indicates the orientation of the investigation.

1 Marshall, W. H. & Talbot, S. A. "Recent Evidence for Neural Mechanisms in Vision Leading to a General Theory of Sensory Acuity" In H. Klűver (Ed.) Biological Symposia Vol. VII Visual Mechanisms, Lancaster: Cattell Press, p. 138 1942.

2 Westheimer, G. "Visual Acuity" Ann. Rev. Psychol. 16, p. 368, 1965.

3 Millodot, M. "Foveal and Extra-Foveal Acuity with and without Stabilized Retinal Images" Brit. J. Physiol. Optics 23, p. 103, 1966.

4 von Helmholtz, H. Physiological Optics Vol. III (trans. by J. P. Southall), Optical Society of America, Menasha, Wisconsin, p. 168, 1925.

5 Pritchard, R. M. "Studies of Visual Perception with a Stabilized Retinal Image" Ph. D. thesis, Univ. of Reading, p. 142, 1958.

CHAPTER II

EXPERIMENTAL APPARATUS

Introduction: The experiments to be described utilized two distinct systems: the first measures vertical and horizontal components of eye movements; the second stabilizes target images on the retina. Because the results described later in this thesis rely heavily on the accuracy of the devices, the construction and performance characteristics of these two systems are described in this chapter. Details concerning the design of these systems and their predecessors are treated elsewhere (1, 2, 3) and will not be discussed.

Both stabilization and movement measuring systems rely on a contact lens to follow the motions of the eyeball. For eye movement recording, a small lamp is attached to a rigid stalk protruding from the lens. As the eye moves, the lamp casts the shadow of a fixed edge back and forth over the face of a photomultiplier. The voltage output of the photomultiplier provides, in our apparatus, a linear measure of eye position over a 4^{o} range.

In order to stabilize target images on the retina, a small mirror is attached to the same contact lens stalk. A beam of light containing the target image is reflected off this mirror and subsequently projected on the retina. Movement of the eye (and therefore of the mirror) through an angle α causes deflection of the target beam through an angle 2α. To achieve stabilization the reflected beam is

passed through a telescope of magnification 1/2 and projected on the retina. Once this is done, eye movement through an angle α causes the target image to be translated through an angle α in the same direction, and the image is said to be "stabilized," since it does not move across the retina as the eye moves.

Contact Lenses

The crucial mediator of eye movements in both of the above systems is the contact lens. Several different types are currently in use in other vision research laboratories. The two chief variants, as used by Ditchburn's group (4) and by Yarbus (5), are shown in Fig. 1. The full scleral contact lens, illustrated on the left, differs only slightly from the type athletes wear (aside from the stalk) in that the lens makes contact with the limbus, the junction of cornea and sclera, and is more closely fitted to the sclera. In the athletes' type of full scleral lens, the plastic arches clear of the limbus since pressure on this area causes the subject pain. Those using the version illustrated put a local anaesthetic, for example, amethocaine, into the eye before wearing. Such discomfort is considerably greater with the Yarbus-type suction caps, as is the probability of corneal abrasions. For increased adhesion of the cap to the eye Yarbus serrates the edge of the cap. A detailed comparison of the two types of lenses is given by Barlow (6). He concludes that the full scleral lens may slip as much as $\pm$ 3.5 min arc while the subject is looking ahead, whereas the suction type slips only $\pm$ 40 sec arc under this condition. These slippage estimates vary considerably from subject to subject, making

Fig. 2-1 Methods of attachment to the eyeball.
Left: the "full scleral" contact lens used by Ditchburn, showing an attached metal rod bearing a small lamp for measurement of eye movements.
Right: the "suction cap" developed by Yarbus, showing the platform for support of stabilized targets.

necessary individual slippage measurements for each subject and each lens. In an effort to decrease the slip associated with scleral lenses, and at the same time to minimize the pain associated with suction devices, the arrangement shown in Fig. 2 was developed, and used in all studies reported here. These are triple curvature contact lenses, with light weight tubes attached, through which suction may be applied.

Fitting and Construction: All subjects had full scleral molds taken of their eyes by Mr. Robert Graham of Pasadena, a specialist in the fitting of contact lenses. Triple curvature plastic lenses were then made to his specifications, and checked by him for snugness of fit and optical correction. All subjects were corrected to 20/20. A light plastic stalk was cemented to the lens in a position where it would interfere least with the eyelids. Finally, a thin polyethylene tube (Intramedic I D. 015"xO D. 043") filled with 2 percent sodium bicarbonate connected the space between lens and limbus to a water manometer. By raising or lowering the manometer the lens was sucked onto the eye to any desired degree. With 23 cm of water negative pressure, subjects needed no anaesthetic and could remain with the lenses in their eyes for periods up to one hour without ensuing discomfort or visual defects. No subject has yet experienced a corneal abrasion as a result of wearing these lenses.

Bending of the Stalk: Two links in the system may give rise to error in eye movement following. The first, and simplest to check, is movement of the stalk and lamp (or mirror) relative to the rest of

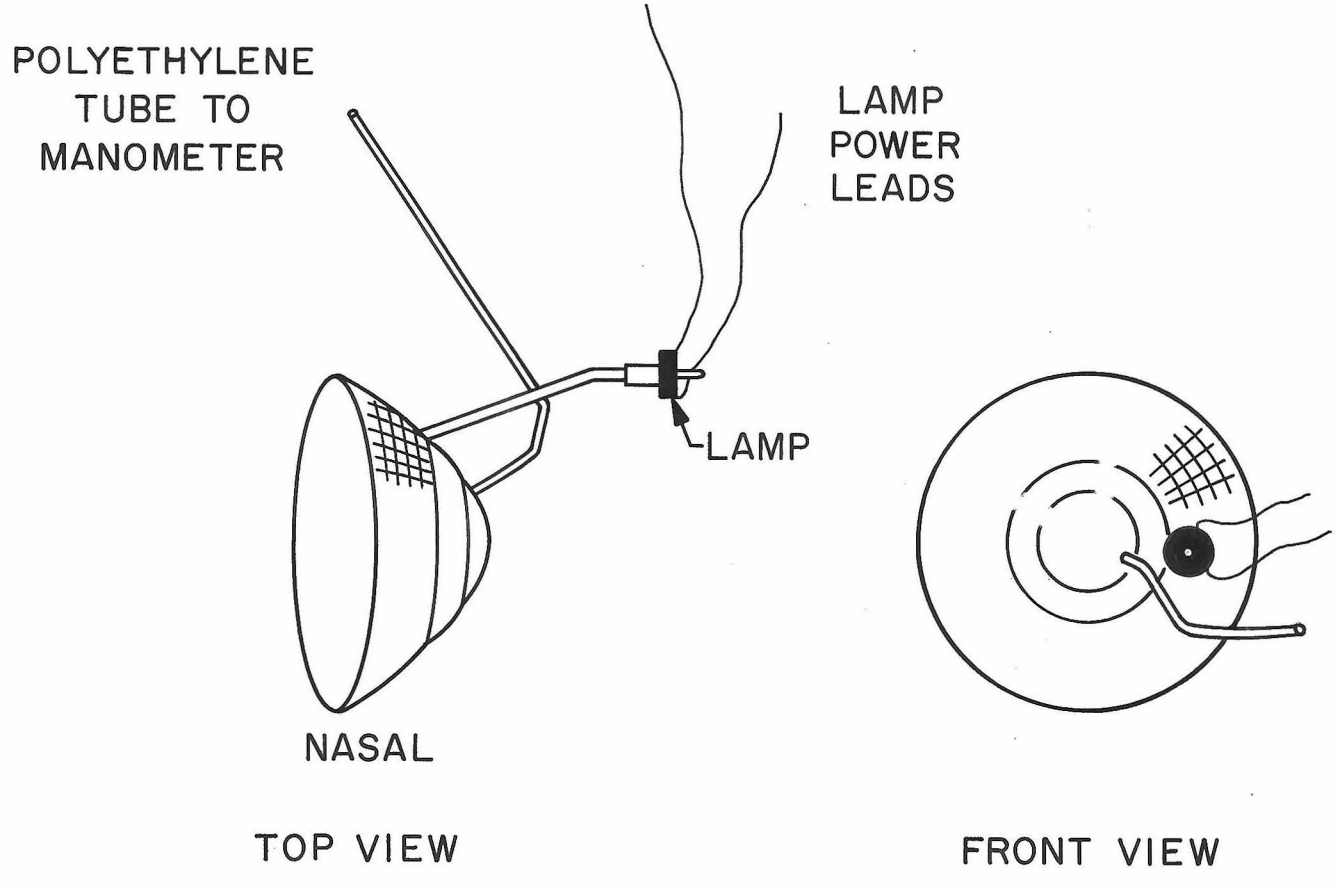

Fig. 2-2 Diagram of one of the modified full scleral contact lenses, showing engraved grid for slippage measurement, stalk with lamp attached (for measurement of eye movements), and polyethylene tube through which suction could be applied.

the lens. Second is slippage of the lens over the eyeball. To rule out the first possibility, the lens was embedded in a block of paraffin from which stalk and lamp protruded. This block was clamped under a microscope and weights of various sizes were suspended from the end of the lamp. Bending of the stalk was observed through the microscope, and amounted to .0128 mm per gram weight at the tip. Using Westheimer's (7) estimate of 27,000 deg/sec^2 as the maximum acceleration of the eye during a flick, and treating the stalk-lamp combination as a leaf spring with the above Hooke's constant and with all its mass (0.18 gm) concentrated at the tip, one finds that the stalk bends 4μ due to maximal flick acceleration, giving an eye position measurement error of 0.4 min arc. The tungsten lamp filament could not be observed to move even after the most intensive jarrings. The mirror could be attached to the stalk with equal tightness.

Lens Slippage Over the Eyeball: Of the several methods we used to quantify lens slippage, the most reliable and direct consisted of observing through a microscope the movement of scleral blood vessels relative to marks on the inside surface of the lens. For this purpose a grid of accurately spaced grooves was machined on the inner surface of the lens, with 0.0025" separating lines of the grid. The grid extended from the corneal portion to the temporal edge of the lens. Black wax was rubbed into the grooves to enhance their visibility. Under 24 power magnification (Wild M5 stereomicroscope) an observer could detect easily displacements as small as one-third of a grid unit (6 min arc) between blood vessel and lens.

During all slippage experiments the subject's head was held by a bite bar, and his eye brightly illuminated by a microscope lamp. His instructions were either to fixate a small (4 min arc diameter) black point on white paper 6 feet in front of him, or to flick from one to another of two such points. Slippages were nearly identical for the two subjects under all conditions studied.

Two factors, suction and direction of regard, greatly affected slippage. With no suction (i. e. 0 cm vertical displacement between water level in the manometer and center of the lens) the lens remained immobile while the eye went through saccades and drifts of up to 30 min arc. Increasing suction decreased slip until a negative pressure of approximately 15 cm was reached. Further increase in suction gave a slight additional decrease in slippage. However, nearly all blinks displaced the lens a degree or more relative to the sclera, and the greater the applied suction, the more slowly the lens would creep back to its initial position. As a compromise between these effects of pressure we elected to work with 23 cm pressure. This allowed the lens to return after a blink in roughly 5 seconds.

Since the "full scleral" contact lens rests not on the sclera proper but on the conjunctiva and extraocular muscle insertions, one might expect that when these elastic bodies stretch and contract as the visual axis moves, the lens may shift over the sclera with them. This indeed occurs; but fortunately the effect is minimal when the eye is near the straight ahead position, probably because tension across the conjuctiva is also at a minimum here. By watching blood vessels of the conjunctiva move over those of the sclera one sees that the

conjunctiva behaves like a hemispherical rubber sheet, clamped at the outer edges to the skull, and attached around the limbus to the sclera. The lens behaves as though it were attached to the conjunctiva, about two mm from the edge of the cornea. This is the neighborhood of the scleral end of the lens' arch over the limbus. At 13 cm pressure, when the subject fixates first the central position and then a point 4° nasal, the lens follows smoothly but only travels $3^{\circ}24'$; and the conjunctiva 2 mm from the corneal edge goes through the same motion as the lens, though elsewhere the conjunctiva slides both over the sclera and under the lens. If the eye continues in the same direction another 4°, the lens this time will only traverse 3°, and the slippages between lens, conjunctiva, and sclera will be more pronounced. Increased suction greatly flattens blood vessels of both conjunctiva and sclera, indicating that suction does not pull one from the other, but rather presses the lens upon the sclera.

With 23 cm of water suction and eye straight ahead, how much does the lens slip? When the subject fixated a point straight ahead and did not blink or flinch, we could see no slippage over 30 second intervals of time. That is, the error is less than 6 min arc in this interval. When the subject drifted slowly or made a saccade 4° in any direction away from the straight ahead position, the lens came to rest 9 min arc short of the final position of the scleral blood vessels used for reference. The same factor of 3.7% attenuation holds quite well for the two subjects tested (DSG and GSC) and for all their movements within 4° of the straight ahead position, regardless of direction, amplitude, or velocity. We could see no slip

perpendicular to the direction of movement.

The above discussion refers only to steady state errors, and tells nothing about the ability of the lens to track rapid eye movements. In fact, the observer can detect no transient slippage for either saccades or rapid drifts; however, the method is ill suited for the determination of rapid transients, since quite some time is required for the observer to note relative positions of lens and blood vessels.

To answer the question of how much a lens slips due to its own inertia during a flick, we applied a similar force across the lens-scleral junction, but with the eye stationary, and measured the resultant slip. Specifically, we found that a 1 gram weight when hung on the end of the stalk (at 23 cm pressure) caused an 8 min arc displacement of the lens over the eyeball. When the weight was removed the lens returned to its normal position. The torque with respect to the center of the eye caused by this weight is 3430 gm cm^2/sec^2 (1gm weight at 3.5 cm) and this torque when transmitted through the lens-sclera junction caused 8 min arc slip. During a flick the maximal torque transmitted through this same junction is equal to the product of the rotational inertia of the lens and the maximum flick acceleration. The maximum acceleration, as mentioned before, is 27000 degrees/sec^2, or 470 radians/sec^2. The moment of inertia of the lens about the rotational axis of the eye was estimated as follows: lamp, wire, and cone joint weigh 85 mg and are 3.5 cm from the center of the eye, giving a rotational inertia of 1.0 gm cm^2; the stalk weighs 0.1 gm and is 2.2 cm long, so a simple integration

gives 0.6 gm cm^2 for its rotational inertia; the lens plus tear solution has a weight of about 1.1 gm, and, when approximated as a segment of a thin spherical shell, has a rotational inertia of 1.2 gm cm^2; therefore the sum of the rotational inertias involved is 2.8 gm cm^2. The manometer tube was neglected because it is taped to the subject's temple shortly after leaving the lens, thereby behaving more like a spring than a mass, and this action is included in the measurement of static lens slip. The torque transmitted across the lens-sclera junction during a flick is therefore 1360 gm cm^2/sec^2. Since this is four-tenths of the torque which causes 8 min arc slip, and since slippage increased linearly with torque over the region we were able to measure, we expect transient slippage due to lens inertia during saccades not to exceed 3.2 min arc. The large acceleration during a flick is not sustained for more than a few milliseconds, and since the one gram weight was applied for more than a second in order to register 8 min arc slip, transient slippage due to lens inertia is probably less than 3.2 min arc during a flick.

Eye Movement Recording

Subject Restraints: The recording apparatus combines techniques presented by Fender (8) and Byford (9). Two channels are shown schematically in Fig. 3; the assembly is duplicated under the subject's left eye (not shown) to provide simultaneous recording of horizontal and vertical components of movements of both eyes. The subject's head is firmly held by both a dental cement bite bar containing an impression of his teeth (upper and lower jaws back to the

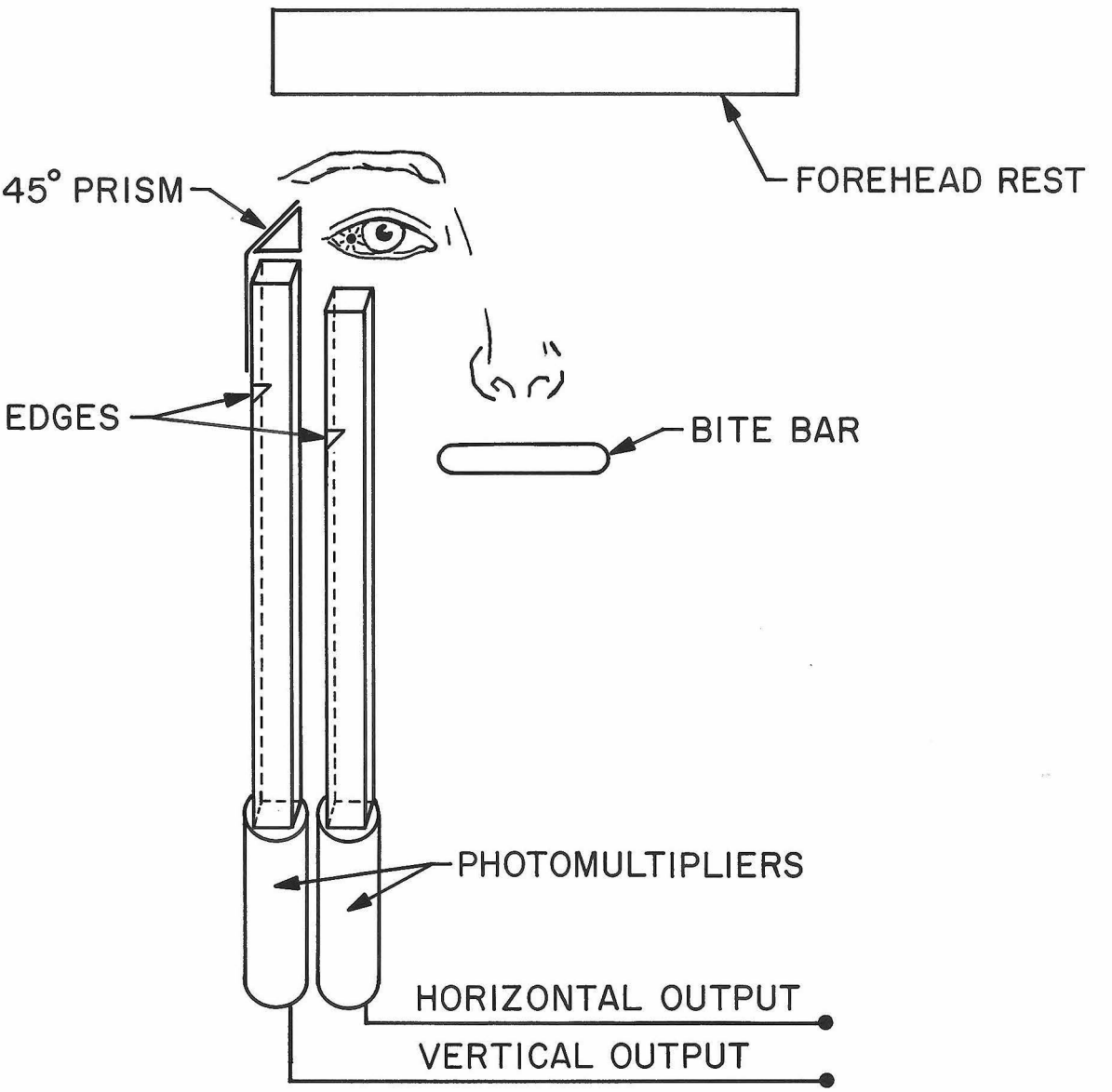

Fig. 2-3 System used for recording vertical and horizontal components of right eye movements. The lamp attached to the subject's lens casts shadows of the edges onto the photomultiplier faces. This causes the photomultiplier output voltages to vary with eye position.

molars) and a forehead rest also molded to his head with dental cement. Both impressions are molded to solid aluminum stock, which, in turn, is bolted to the photomultiplier assembly. During all experiments the subject was seated comfortably in a medical examination chair with his head held rigidly vertical by the above supports.

Lamps: A variety of small medical lamps were used. Rimmer Bros. #c11 (unmounted) and Sylvania Mite-T-Lite, drawing respectively 200 and 20 milliamps, proved to be the most satisfactory in terms of weight and lifetime. The lamps were epoxied to a cone joint (for attachment to the stalk of the lens) and to black paper light shields, which prevented the lamps from shining directly into the subject's eyes. Very fine wire (Belden 44 AWG) was soldered to the lamp leads and connected to a battery through a potentiometer. The wire leads were taped to the subject's temple after allowing ample slack for eye movements.

Phototube Construction and Positioning: At the beginning of each experiment the photomultiplier assembly was adjusted to the position shown in Fig. 3, so that, with the subject staring straight ahead, half the photocathode received light from the lamp while the other half lay in the shadow cast by the fixed edge. This position was determined by moving the photomultiplier assembly until a maximum voltage output was obtained, and then positioning the assembly to give half the maximum voltage. The level and gain of the final output signal could then be set either by altering the high voltage across the

photomultiplier, or by changing the level and gain of the DC amplifiers which processed the photomultiplier output.

The rectangular tubes leading to the photocathode are 7x12x120 mm and lined with a non-reflecting black paper. The fixed edge is 60 mm from the photocathode and 95 mm from the lamp. The position of the fixed edge in the tube may be varied to increase either the sensitivity or the range of the measuring system. RCA photomultipliers (model 7767) are used in all channels; their high voltage supply (usually 1200 v DC) is provided by two Kepko (model ABC 150M) power supplies which had 1.0 mv rms maximum ripple plus noise, 0.05% variation with changes in load, and less than 0.05% drift in eight hours. Each high voltage supply feeds two photomultipliers in parallel. Immediately above each photocathode is a rectangular mask fitted to eliminate non-linearities near the edge of the tube.

Linearity of the Eye Recording System: To test for linearity of the eye movement recording system a one inch diameter steel sphere was built to function as a dummy eyeball. Two micrometers could rotate the sphere about perpendicular axes. By means of a ten foot optical lever the micrometers were calibrated to give angular displacements accurate to 1 min arc over a 225 min arc range. One of the small medical lamps was attached to a steel shaft protruding from the sphere. The lamp was 3.5 cm from the axis of rotation of the sphere, just as it was on the lens stalk.

With the dummy eyeball clamped in position above the photomultipliers, and one micrometer drive accurately horizontal and

the other micrometer vertical, the DC amplifier output voltage was recorded for many different sphere positions. A plot of the results is shown in Fig. 4. From this it may be seen that the output voltage is close to linear over a 4^{o} range in both vertical and horizontal channels.

Frequency Response: By rotating a slotted disc between photomultiplier and lamp it was possible to measure the frequency response of the entire eye movement recording system. The effective input signal was a repetitive trapezoidal waveform whose duty cycle depends on the width of the slots in the disc. For a 50% duty cycle the response was of uniform amplitude as the disc rpm increased, until the repetition rate of the trapezoid reached 330 cycles per second. Response was 3 db down at 450 cps. Thereafter the falloff was roughly 10 db/decade. This low pass filter effect is entirely due to the photomultiplier, whose high frequency gain increases with load.

Calibration of the Eye Movement Recording System: In order to account for the brightness of the lights and the variable gains of the high voltage power supply, the DC amplifiers, and whatever apparatus was used ultimately to record eye movements, it was found most convenient to introduce a calibration step at the photomultipliers at the start of each experiment. This was done by wiring a solenoid to pull opaque vanes a short distance across the face of each photocathode. At the end of a two second interval the solenoid was de-energized and springs returned the vanes to their initial locations. During this calibration step the subject fixated centrally, so that on

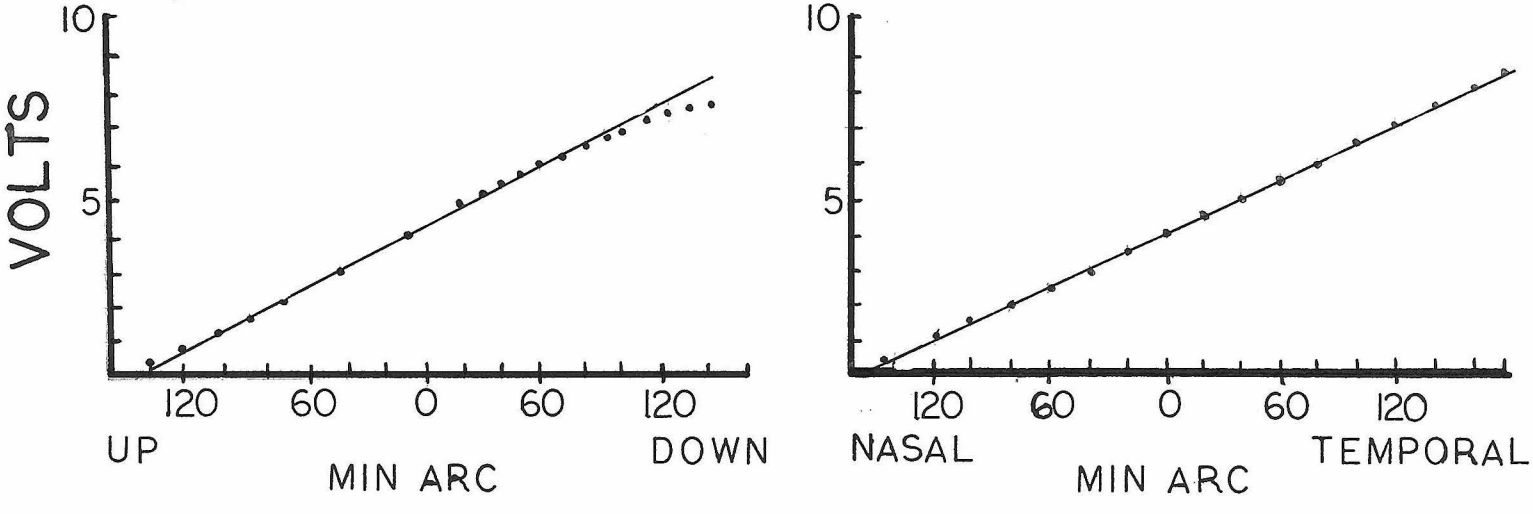

Fig. 2-4 Photomultiplier output as a function of dummy eyeball rotation along vertical and horizontal meridia, illustrating the linearity of the eye movement recording apparatus.

the recording medium a two second wide rectangular pulse appeared on each channel with small superimposed eye movements. The vanes moved between rigidly fixed stops so that the calibration steps were of uniform amplitude. Calibration of the calibration steps was done by matching the rectangular pulse amplitude (caused by the vane) to the amplitude caused by a known eye rotation. Here the dummy eyeball was again used.

Recording Media: The outputs of the DC amplifiers were recorded on one or more of several machines. Most commonly used was a Honeywell 1406 Visicorder, a 5 channel oscillograph with a frequency range from 0 to 330 cps (flat within $\pm 10\%$ to 200 cps) and linearity within 5% of full scale (8 inches). Where higher frequencies were of interest, a Tektronix 564 storage oscilloscope with 3A6, 3A3, and 3B4 plug-ins plus polaroid camera was used. The oscilloscope was either run directly from the DC amplifiers, or could be run from analog tape playback. A CEC 7 channel AM-FM tape recorder (model PR-3300), operating at a tape speed of 1 7/8 ips (flat to 300 cps), was commonly used to record experiments for later analysis.

Digital Analysis: For digital analysis, each analog record must be converted to digital form and transmitted to the computer. The facilities available for this purpose were designed and constructed at Caltech. Details of its workings have been described extensively (for example, see reference 10), so only the meager outlines will be given here. Either "live" or tape recorded voltages are fed to a

plugboard-programmed, no-memory computer ("The Kludge") which performs three functions: first, it can select data to be transmitted (threshold circuits act to transmit only that data lying above, below, or between certain levels - and/or the times at which the signal crosses a given level); second, it can convert the selected data to digital form at a rate of up to 10 kc; third, it can transmit the digitized (12 bits plus sign) data through the IBM 7288 multiplexer to a collection routine (BIO-40) time-shared on the IBM 7040. At the input to the Kludge is a 6 channel multiplexer. Sampling of each channel is also plugboard controlled, though the net rate can never exceed 10 kc. Thus data is "preprocessed" by the Kludge, sent to BIO-40, and, each time one of the BIO-40 buffers (in 7040 core) is filled, the contents of the buffer are written on digital tape. Although data selection and transmission rate are plugboard programmed into the Kludge, either the Kludge or BIO-40 may be programmed to determine the number of samples sent. BIO-40, furthermore, accepts and writes on digital tape identifying characters to be associated with the data. When the digital tape is written, "on line" processing ceases. All further analysis is carried out via batch processed jobs running under the IBJOB system; that is, Fortran IV or IBMAP programs. These programs read the aforementioned digital tape by interrogating a tape reading, unpacking (our 12 bit data "words" are packed in groups of three on tape) subroutine (KERFUS). Thereafter processing conforms to standard batch processing techniques.

Ancillary Devices: An electronic flick detector designed by

G. W. Beeler (11) was used in several experiments. This band-pass filters the eye position signal in the region (18 to 70 cps) of the spectrum most characteristic of flicks. The filtered signal then enters a threshold detector (variable) which emits a pulse for all flicks larger than a predetermined magnitude. At maximum sensitivity the unit can detect flicks as small as 3 min arc, provided that a velocity of roughly 3°/sec or more is achieved in about 7 msec or less.

Optical System

The optical system used for presentation and stabilization of visual stimuli is identical in all essentials to that described by Clowes and Ditchburn (12). The apparatus for stimulation of the left eye is shown schematically in Fig. 5. This is duplicated for the right eye. Section "P" of the apparatus is a projector which allows either or both of two targets to be projected into the system, depending on whether shutters, S and S', are open. The light source is a GE 18 amp T10 bulb with a horizontal ribbon filament. The luminances of either target can be controlled in two ways: first, by altering the positions of the optical wedges (W and W'); and second, by partially closing the 2 mm apertures, A and A', by means of solenoid-driven vanes (not shown). In either case the net luminance seen by the subject can be monitored on photomultiplier PM (disregarding the constant transmission losses in the remainder of the system).

Lenses L1 and L1' collimate the source beams, providing uniform illumination across each target plane. Lens L2 focuses the resulting beam on the contact lens mirror, M2, since any non-focused

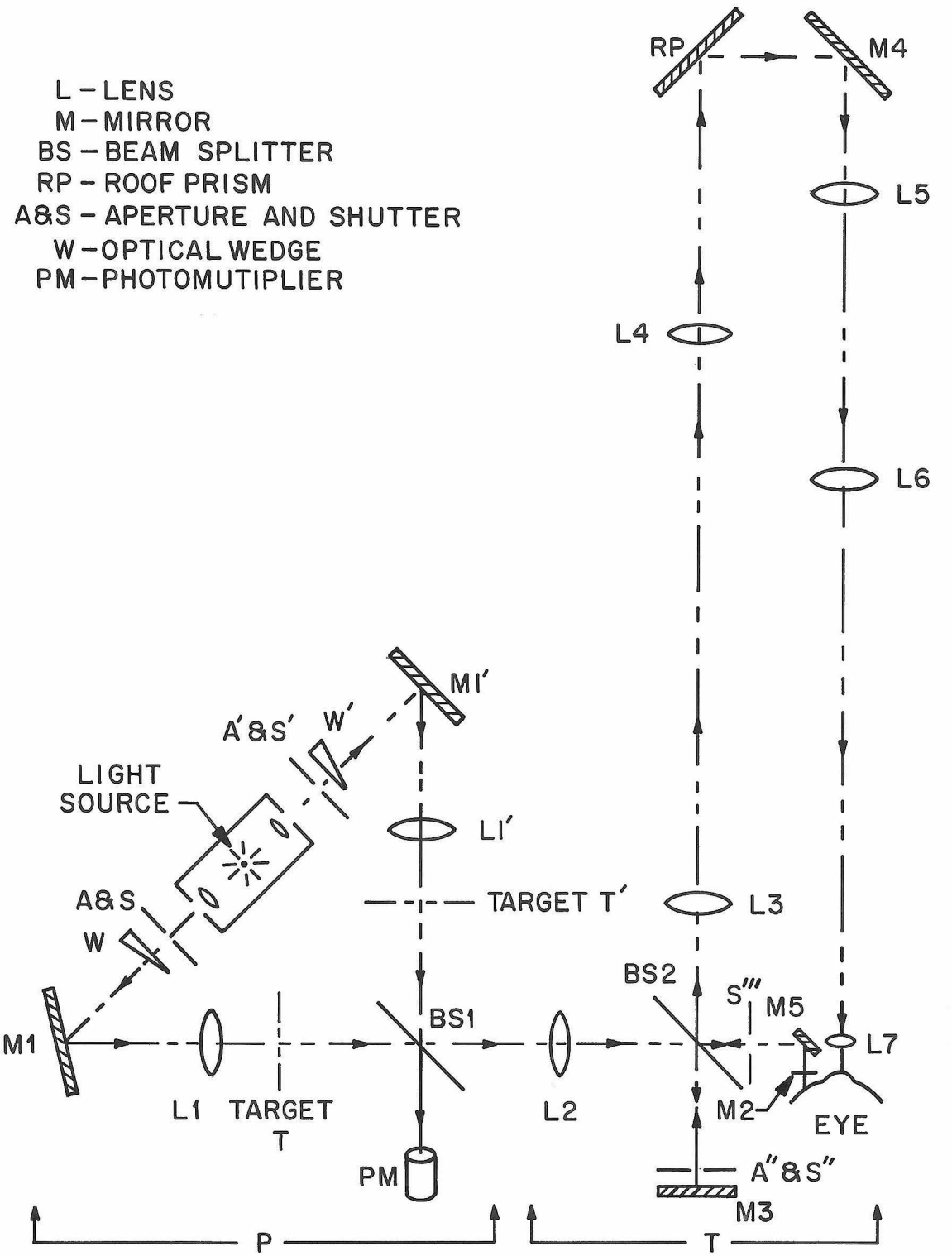

Fig. 2-5 Optical system for stabilization of retinal images. P is a projector which allows two targets of variable brightnesses to be optically superimposed, and T is the telescopic system used for stabilizing the projected targets.

beam would be too large for the mirror to deflect. The targets must be placed one focal length from L2 since this results in a beam of parallel light rays incident on the contact lens mirror from any point of the target. If the targets were not a focal length away, movements of the lens mirror would change the magnification of the image, with consequent loss of stabilization.

The remainder of the system, T, collects the beam reflected off the lens mirror, and routes it, after the appropriate number of reflections and after magnification by 1/2, into the eye. For non-stabilized viewing, shutters occlude M5 and expose a fixed mirror, M3, which, except for moving with the eye, performs the functions of the contact lens mirror. Lenses L3 and L4 act as a telescope of unit magnification to increase the field of the system. The roof prism, RP, and mirror M4 provide the requisite number of reflections for stabilization; L5 and L7 act as a telescope of magnification 1/2. L6 is the field lens of the telescope, which not only greatly increases the field of view, but also may be translated along the axis of the telescope to provide fine control over the angular magnification. All lenses are achromatic doublets; L1 through L5 are 6 cm in diameter, and the telescope eyepiece is 1.5 cm in diameter.

For experiments involving moving points of light as targets, M1, L1, and L2 were removed; a 50 cm focal length lens was substituted for L2; and a cathode ray tube face (Hewlett Packard 122A oscilloscope with P2 phosphor) placed in the position of M1. Needless to say, conditions for stabilization do not apply to this arrangement, so only normal vision was used. The advantage of this system over

direct viewing is that the targets presented to each eye may be independently controlled, but may appear fused into a single image.

Performance Data for Stabilization System: The telescopic system described above images the light source aperture, A or A', into the plane of the eye pupil, a condition known as Maxwellian view. If the source were instead imaged on the retina, only a small region of the retina would receive maximal light flux. Maxwellian view causes a much larger area of the retina to receive the same maximal light flux. Since the target is illuminated by parallel rays from the source, and the source is focused on the pupil, the target is optically at infinity. The exit pupil of the apparatus is stationary with respect to the apparatus, and is approximately 8 mm in diameter, thus the eye pupil is well within the exit pupil for all eye movements considered here.

One final important adjustment must be mentioned, that is, the contact lens mirror must be perpendicular to the visual axis in order for the retinal image to be stabilized. This may be easily accomplished by bending the lens' stalk. Perpendicularity was checked prior to each experiment by having the subject look at the source of a simple star collimator; the beam reflected from his mirror was made to coincide with the source point.

The degree of compensation provided by the optical system for eye movements may be measured directly by substituting a telescope with a graticule and a small eye mirror mounted on the front for the eyeball, as described by Clowes (12). Movement of the target image over the micrometer as the telescope rotates is a

direct measure of the lack of compensation. For 2^{o} telescope movements the relative displacement between target and graticule was 3 min arc or less in the central 2^{o} of the field and up to 4 min arc in the periphery, neglecting the extreme edge of the field where compensation was poor. Thus the retinal image in the central 2^{o} is at least 97.5% compensated for eye movements, while within a 3^{o} radius compensation is better than 96%.

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CHAPTER III

CHARACTERISTICS OF EYE MOVEMENTS

Introduction: Certain characteristics of eye movements have been dealt with extensively in the literature, particularly those regarding the action of the eye as a "position servo" and as a tracking mechanism. Less emphasis has been placed upon the relevance of eye movements to the visual input. This chapter attempts to forge just such a link, by relating the characteristics of eye movements to the type of visual information absorbed during execution of the eye movements.

Before presentation of the experimental data, the basic capabilities and limitations of the extraocular muscles are set forth in terms of their anatomy, physiology, and innervation. These are then related to the three categories of eye movement: flick, drift, and tremor. The manner in which these components of eye movements are arrayed in different visual tasks, and the degree of control exercised over them, constitute the subject matter of the experiments.

Anatomy and Innervation of the Extraocular Muscles

General Characteristics: Six extraocular muscles are found in all vertebrate classes, as well as in man. These are the four rectus muscles, usually termed superior, inferior, medial and lateral, and the two obliques, inferior and superior. In man all except the inferior oblique originate at the annulus of Zinn, a cartilaginous

structure surrounding the optic nerve. The inferior oblique originates in a depression on the superior maxilla, on the nasal wall of the orbit. Extraocular muscle development and anatomy are elegantly described by Gilbert (1). Ewald Hering (2) in 1879 illustrated the rather complex effect that contraction of any one muscle has on rotation of the eyeball. Only the horizontal recti directly oppose each other throughout their range of contraction; thus none of the other four muscles has a single antagonist, but two or more must work together to balance the contraction of any one of the four. The superior oblique is innervated by the trochlear nerve (IV); the lateral rectus by the abducens (VI); and the remaining four muscles by the oculomotor nerve (III).

Neural Pathways to the Eye Muscles: The nuclei of the three cranial nerves mentioned above all lie in the brainstem, i. e., relatively far from the primary visual pathways. Walls (3) attributes this to the propinquity of vestibular and oculomotor nuclei, saying that the original function of eye movements in the evolutionary scheme was to provide a stable platform for the retina, where "stable" was defined by the vestibular apparatus, not the visual input. The oculomotor nucleus lies ventral to the aqueduct of Sylvius, near the midline. The IVth nucleus lies close by, but somewhat laterally and ventrally. The VIth nucleus lies in the tegmental portion of the pons. It has been suggested that Perlia's nucleus, on the midline between the oculomotor nuclei, functions in convergence; although more recent experiments on macaque and man do not bear this out (c. f. Warwick 4).

Stereotaxic stimulation of parts of the oculomotor nucleus in

cats has not clarified the organization of this nucleus. All investigators believe the IIIrd nerve to be homolateral in function, as is the abducens, but the trochlear is not; and the majority (Danis (5) and Szentagothai (6)) think that the anterior section of the oculomotor nucleus controls the muscles with insertions on the upper part of the orb, while the posterior section controls those with insertions on the lower part of the orb - nerves to the medial rectus lying in between.

A few pathways to these nuclei have been worked out. The parabducens nucleus sends processes through the nearby abducens, and via the medial longitudinal fasciculus to the medial rectus section of the contralateral oculomotor nucleus. This pathway insures the coordinated function of the horizontal agonist-antagonist muscle pair, even though the cell bodies of their respective nerves lie in different nuclei on either side of the midline.

The lateral vestibular nuclei have been shown to connect to IIIrd, IVth, and VIth nuclei by Crosby (7). Electrical stimulation of almost any part of the brainstem produces deflections of the eye; and, according to Wagman et. al. (8), stimulation almost anywhere on the cortex or subcortex of the macaque produces either version or centering of the eyes. As CNS electrical stimulation is susceptible to many interpretations no review will be given here. The interested reader is referred to the work of Bender (9) for a review of this voluminous literature.

Cellular Aspects of the Extraocular Muscles: Cooper and Daniel (10) have found up to 50 muscle spindles per human extraocular muscle, and gamma efferent nerve fibers to the intrafusal muscle fibers as

well. In this and other cellular aspects the six muscles are apparently similar. It is still not known whether muscle fibers extend the entire length of the muscle. Multiterminal innervation of single fibers is well established but polyneuronal innervation has only been demonstrated in cat eye muscles (11).

The ratio of muscle fibers to motor nerve fibers is about 3:1 for human extrinsic eye muscles, making these the most richly innervated muscles of the body. The exact ratio is difficult to specify since some of the nerve fibers are sensory. Donaldson (12) has analyzed the axon diameters of the occulomotor nerve of the goat and found that 30% of the axons are about 5μ in diameter, while the others are in the neighborhood of 15μ across. He postulates that many of the smaller fibers serve a gamma efferent function, controlling stretch of muscle spindles. Bach y Rita (13) has evidence (vide infra) that the small nerve fibers in the cat are motor axons to small muscle fibers, but not gamma efferents.

There is a spectrum of muscle fiber sizes in human extraocular muscles, ranging in diameter from 9 to 40μ. The same fiber spectrum occurs in the cat, and here the morphological and physiological properties of the large and small fibers have been carefully investigated (13, 14). The fine, "slow" extrafusal fibers have multiple en grappe nerve endings, poorly defined fibrils (Felderstruktur), low (3 per second) spontaneous end plate potential (EPP) rates, a low (25 cps) fusion frequency, and finally a long latency (20 msec) and rise time (20 msec). There is some dispute about whether slow fibers conduct active muscle spikes:

Bach y Rita (13) claims they do, although he "often" encountered slow fibers which did not. Hess (14) on the other hand, claims that, in the normal state, only slow graded potentials are seen in these fibers, with graded contraction determined by the degree of depolarization.

The large "fast" fibers have quite different characteristics: single en plaque motor nerve endings, well defined fibrils (Fibrillenstruktur), high (19 per second) spontaneous EPP rates, an extremely high fusion frequency (500 cps), negligible latency, and a rise time of 5 to 7 msec with a half decay-of-contraction time of 8 msec. Figures relating to contraction refer to a muscle loaded by 2 to 6 g, and stimuli sufficient to produce 2 to 3 g twitch tension (13). Two-thirds of the muscle fibers in cat are of the fast type, and these are usually more numerous close to the center of the muscle. Selective contracture of the slow fibers with succinylcholine produces a tension of one-third the maximal tetanic tension. These characteristics have led to the hypothesis that slow fibers are responsible for the slow, "tonic" movements of the eye, while both types contribute to rapid vergence motions.

Sensory Innervation: As mentioned above, muscle spindles are common in human eye muscles although, surprisingly, they do not occur in cats. Wolter (15) described five different types of supposedly sensory nerve endings in human eye muscle, none of which ended on muscular tissue. Golgi tendon organs have also been found. Bach y Rita (16) recorded from stretch receptors in cat eye muscle and found a wide range of properties: both spontaneously

discharging and threshold receptors occur, in parallel and in series with the contractile elements, sensing both length and rate of stretch. Despite this panoply of sensory nerves, no stretch reflexes have been found in the extraocular muscles, indicating a unique relationship between the brainstem and this set of muscles since almost all other muscles with direct CNS innervation have stretch reflexes.

Even more surprising is the fact, known since the days of Helmholtz, that we have no independent "position sense" to tell us which way our visual axis is pointing. An occluded, lightly anaesthetized (cocaine in the conjunctival sac) eye may be rotated by the experimenter without the subject being aware of any movement, and without causing perceptible reflex movement in the other fixating, unoccluded eye (17). The same results hold if both eyes are occluded and rotated. Similarly if the subject is asked to rotate his occluded eyes, he cannot tell whether they have been held stationary or not, and if they are held but not occluded he interprets his visual world as if he had moved his eyes, i. e., his visual world seems to rotate. The local anaesthesia applied during these experiments does not impair the subject's normal eye movements. Thus any stretch or position information derived from the receptors in the muscles does not reach the conscious levels, and is not even used at the lower levels to correct visual information or to cause reflex movement. Just what it is used for remains one of the deeper mysteries of the field. The experimental data, then, point to the fact that all information about eye position is derived from commands, "efference copy," going out to the eye muscles and from visual feedback, rather than

from proprioceptive feedback from the muscles themselves.

Eye Movements - Background

Movements of the eye are conveniently broken down into three categories: flick, tremor, and drift. The fundamental reason for this categorization is the differing appearances of the three modes of movement in a plot of eye position versus time.

Tremor: Continuous small oscillations of the eye, with amplitude between 5 and 15 sec arc (18), and frequency in the range 30 to 80 cps, are called tremor. Since the inter-receptor spacing in the fovea is 2-2.6μ (Polyak, 19)), and the distance from the rear nodal point of the eye to the retina is 17 mm, the angular separation of the foveal cones is 24 to 30 sec arc. Ten degrees from the fovea the inter-receptor spacing is 2 min arc. Thus tremor moves the foveal image at most one inter-receptor space at 30 to 80 cps, but not nearly this amplitude in the periphery. The cause of eye tremor is thought to be unfused contractions of fast muscle fibers corresponding to the maintained nerve discharge to these muscles. Although the direct confirmation of this has not been carried out with humans, the data on cat eye muscle properties (20) is consistent with this assumption.

Flicks: These are the very rapid movements of the eye. Some are under voluntary control and called for this reason "saccades", but the smaller "fixational" flicks with amplitudes less than about 10 min arc are made without the knowledge, and even against the will of the subject, as will be shown later in this chapter. Fixational flicks

have a characteristic direction and amplitude for any particular subject but their time course is similar to that for saccades. The peak velocity of either form of flick is roughly proportional to the log of the amplitude (21), and the duration is proportional directly to the amplitude (20). Typical magnitudes are 40 msec duration and 350 degrees/sec peak velocity for a 10° saccade.

Evidence for the manner in which eye muscles operate during a flick comes from two chief sources: electromyography of the extraocular muscles in humans, and studies of isometric and isotonic flicks in man and in excised cat lateral recti. Needle electrodes in as many as four eye muscles, providing simultaneous records of the electrical activity in two agonist-antagonist pairs, give the following information (22): during a 20° saccade there is a high, maintained discharge in the agonist, inhibition of the antagonist, and co-contraction of the muscle pairs not involved in moving the eye. Tamler (22) concludes that the agonist pulls continuously and with a constant firing rate of the motor units throughout the saccade, whereas activity in the antagonist is totally inhibited, obviating the possibility of active checking by the antagonist at the end of a flick. Movement artifacts, however, make these claims somewhat difficult to fully substantiate.

Direct electrical stimulation of partially excised cat lateral recti by Robinson (20) indicates that there is very little variation in tension rise time with an increase of the stimulus rate above 100 cps or with an increase of muscle length. Since he stimulated both large and small fibers, the relation of these measures to the fiber

population is somewhat vague. With no stimulation Robinson found that the passive tension developed in the muscle is proportional to its change in length (2 g per degree). In humans he found that attempts at saccades with a restrained, occluded eye resulted in 50 msec of rapidly increasing tension followed by a slow, 350 msec, decay to a steady level which is 2/3 of the peak tension. This lingering high tension, if it is not caused by proprioceptive feedback, which is unlikely in light of the earlier discussion, contradicts the work of Tamler et. al. (22) who describe no large, continued muscle potentials following the saccade. More recent work by Bach y Rita and Jampolsky (private communication, 1967) indicates that there may be a small maintained discharge following the saccade, although there still appears to be a dichotomy between the large post-saccade tension measured by Robinson and the small post-saccade muscle potentials measured by Jampolsky.

Two classes of drugs have large effects on the extraocular muscles and their innervation. Succinylcholine causes contraction of slow fibers in the extraocular muscles, with no commensurate shortening of the fast fibers (13). Barbiturates in even moderate doses cause the rate of flicking to increase threefold or more (23). The action of succinylcholine is due to its ability to mimic the end plate transmitter, acetylcholine, and depolarize the muscle fiber. Sensitivity to these molecules is apparently localized under the end-plates in large, fast muscle fibers, but spread out along with the en grappe nerve endings over the surface of the slow muscle fibers. These facts are thought to account for the much greater susceptibility

of slow fibers to succinylcholine. The mechanism by which barbiturates increase the flick rate is not understood.

Drifts: As the name implies, drifts are slow movements of the eye, usually with a velocity less than 10 min arc per second. When made voluntarily, as during a tracking task, they are called smooth following movements to distinguish them from the saccadic jerks. Bach y Rita and Ito (13) think it likely that drifts are caused by the slow occulomotor system, i. e., by the smaller motor axons innervating small and slowly conducting muscle fibers. Drift during fixation has been extensively studied (24, 25). Because its amplitude and direction are little affected by visual factors the authors concur that drift is primarily a manifestation of some instability of the occulomotor system. Large drifts during slow tracking tasks, on the other hand, are not instabilities at all, but true tracking movements. Rashbass (23) has offered evidence that these smooth following movements reflect a velocity tracking system, whereas the saccadic movements reflect an independent position tracking system.

In closing this summary of the components of eye movement, we should note that movements of large amplitude and intermediate in velocity between flicks and drifts are occasionally seen, though no subjects appear to use such movements in any consistent manner.

Eye Movement Experiments

Introduction: The object of this series of experiments was to discover whether or not the components of eye movements, described in the

preceding section, are arranged in a pattern characteristic of the visual task being performed. Data from previous investigations, which are described fully in Chapters IV and V, have linked eye movements with two particular types of visual tasks: those involving acuity targets, and those calling for visual estimates of length or orientation. However, evidence for these links is rather indirect. In particular, no one has demonstrated a unique relationship between the pattern of eye movements and either of these visual tasks. The experiments reported below seek to elucidate the extent, and perhaps the mechanism, of the coupling between visual information inflow and eye movements by analysis of eye movement patterns generated during two such visual tasks.

Since eye movements are quite erratic and susceptible of many interpretations when an extended pattern is presented, we decided to use the simplest possible optical inputs, namely one or two point light sources, in the two visual tasks. In order to separate patterns of eye movement specific to the target from eye movement patterns specific to the task, two control experiments were carried out. The first involved no change of target geometry, but the task was changed from one of the acuity type to one involving no acuity discriminations. A comparison of the results of these two experiments gives the eye movement patterns associated exclusively with acuity discriminations.

In a similar fashion eye movements were measured during a task which involved estimates of distance and direction. As a control, eye movements were measured with a closely related target which

required no estimate of distance or direction. A comparison of these results shows patterns of eye movement unique to the distance and direction estimation task.

Eye Movements During A Simple Acuity Task: During an earlier investigation we found that the ostensibly simple command to fixate a point light source could be interpreted in two quite distinct ways by the subject, and that the resulting eye movements were noticeably dissimilar. Fixation according to one interpretation means that the eyes should be held as motionless as possible; according to the other interpretation, fixation means that the spot should be seen clearly and distinctly for the duration of the experiment. Subjects were instructed to perform each of these tasks, described to them in the above terms. To put the same distinction in a more physiological context, motionless fixation involves conscious minimization of motor outflow, whereas what we will call sentient fixation requires the conscious maximization of sensory visual inflow. The fact that the target remains the same, and only the subject's criteria change, provides a direct method for identifying those parameters of eye movements which are specific to a simple acuity task.

Fig. 3-1 and 3-2 show the eye position vs. time data under the two fixation conditions as recorded on the Visicorder. The records were obtained from a single subject (DSG) during one experimental session. Several factors are immediately obvious from these records: first, that left and right eyes behave virtually identically under either fixation criterion; second, that flick rate and flick

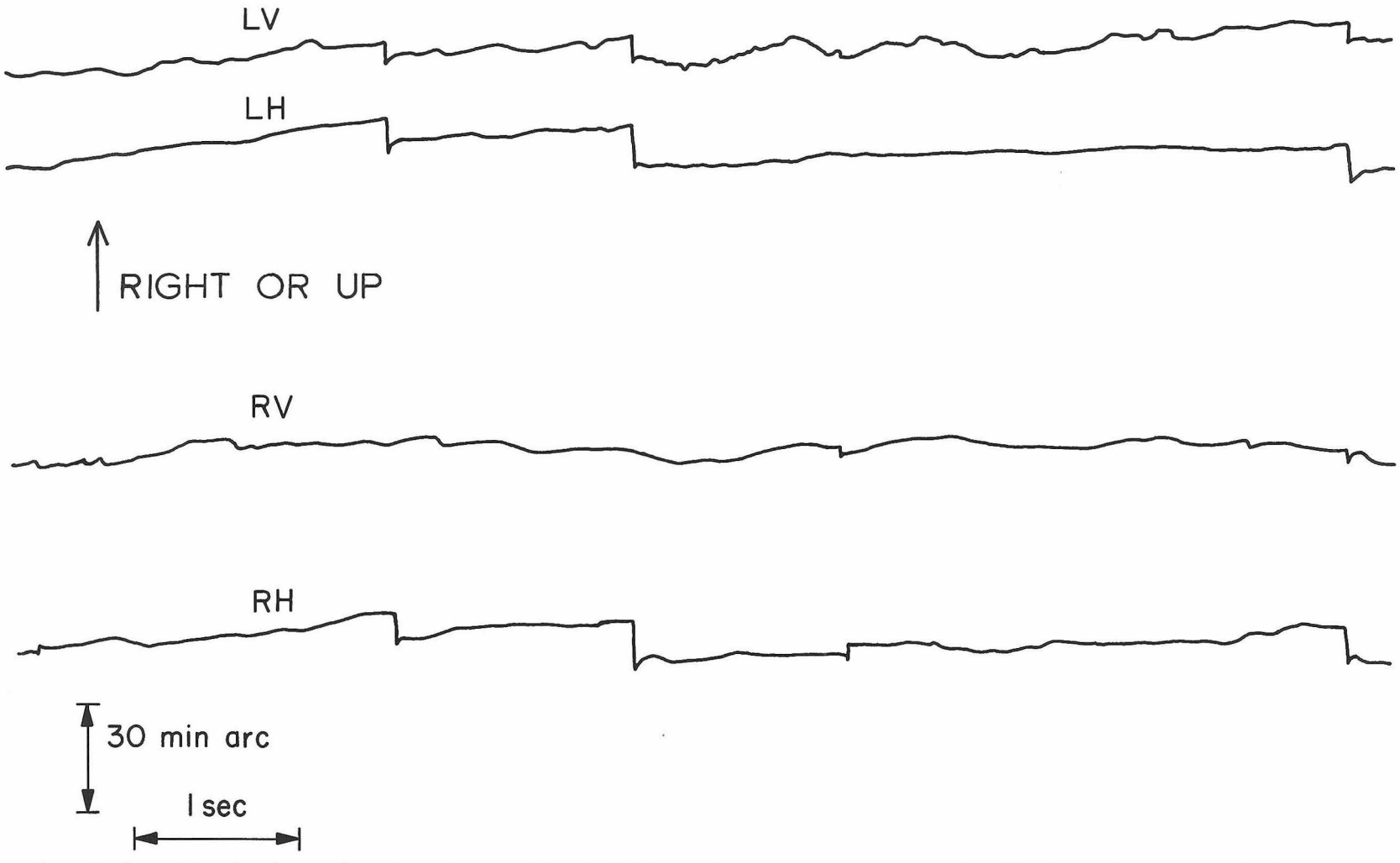


Fig. 3-1 Motionless fixation for subject DSG. These are traces of a Visicorder record showing movements both vert. & horiz. of left & right eyes. Gain of right vertical channel is 1/2 that of the others.

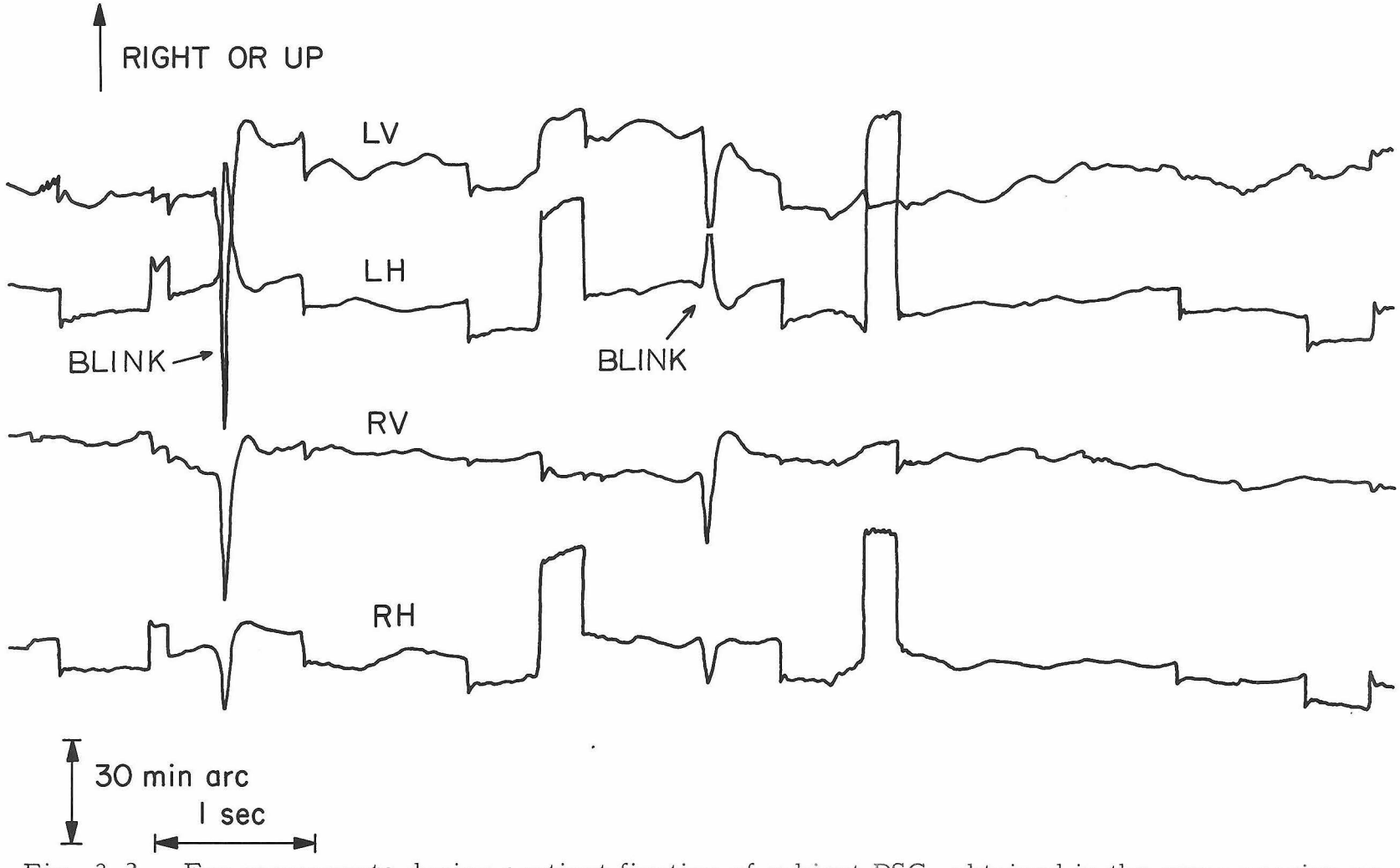


Fig. 3-2 Eye movements during sentient fixation of subject DSG, obtained in the same session as those of the previous figure. Gain of the right vertical channel is again lower than that of the others.

amplitude are increased during sentient fixation; third, flick direction is more random during sentient fixation.

The above observations are confirmed by the histograms of Fig. 3-3 and 3-4. For both subjects flick amplitudes become larger and interflick intervals become shorter during sentient fixation. Finally, both subjects when trying to hold their eyes motionless have a definite preferred flick direction, but during sentient fixation their flick direction becomes more random.

These histograms were acquired from records of the left eye, monocular fixation (right eye covered by a patch) in a dark room with the subject viewing a stationary bright point (diameter 4 min arc) on the oscilloscope through the telescopic system previously described. Records of binocular fixation revealed no notable differences between monocular and binocular conditions. Preferred flick direction is the same for both eyes and is identical to that in monocular viewing; occasional rapid drift vergence motions (about 8 min arc nasal movement simultaneously in each eye, corrected in about 1 second) were seen during sentient fixation, but the vast majority of flicks and drifts were conjugate, i. e., in the same direction, of nearly the same amplitude, and synchronous in the two eyes. Table 3-1 gives the characteristics of the records from which the histograms were made. The two subjects have substantially different mean flick rates; however, both increase significantly during sentient fixation.

By playing the tape recorded horizontal and vertical measures of eye position into the corresponding channels of an oscilloscope, and taking a time-lapse photograph of the spot moving on the screen, one

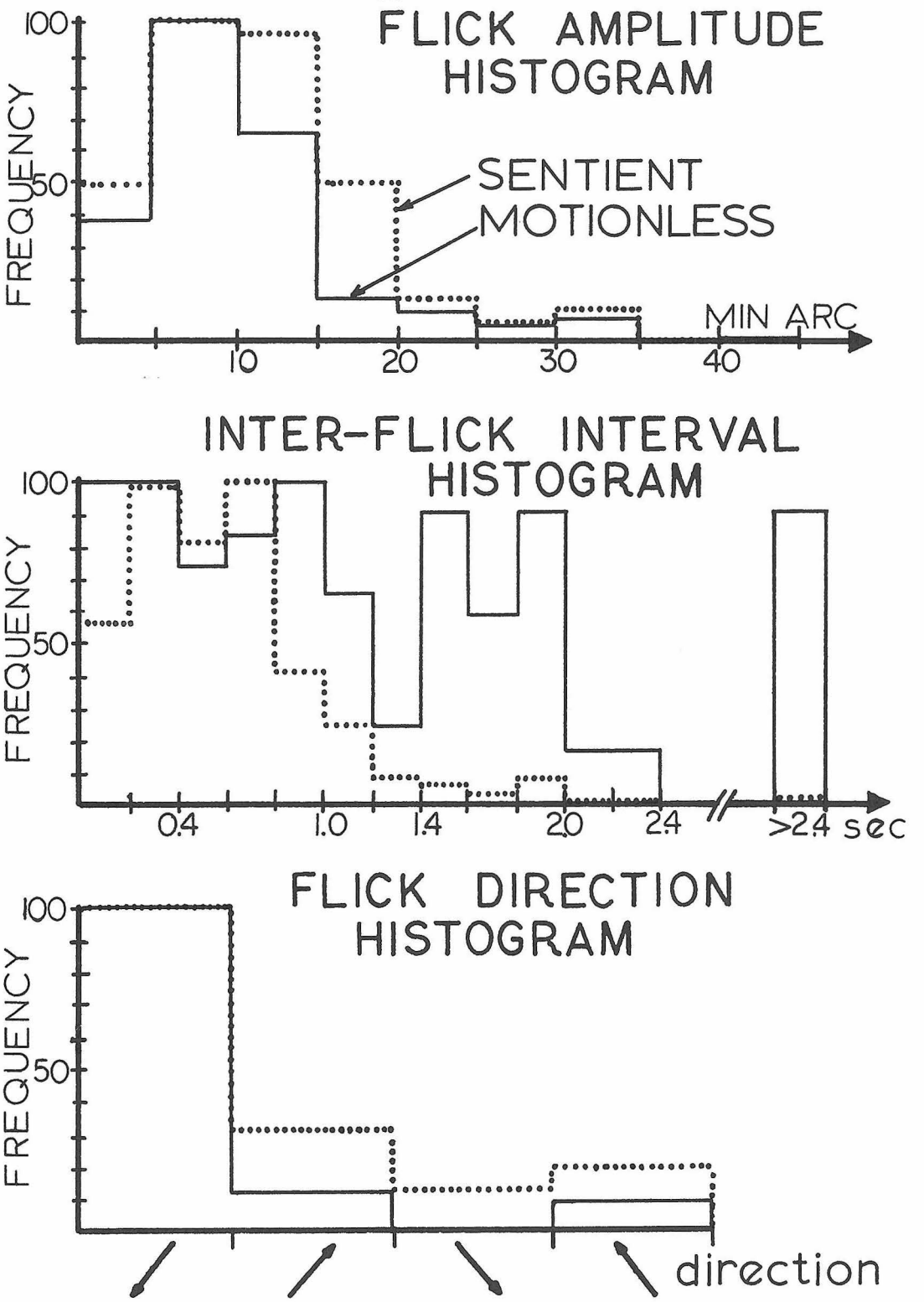
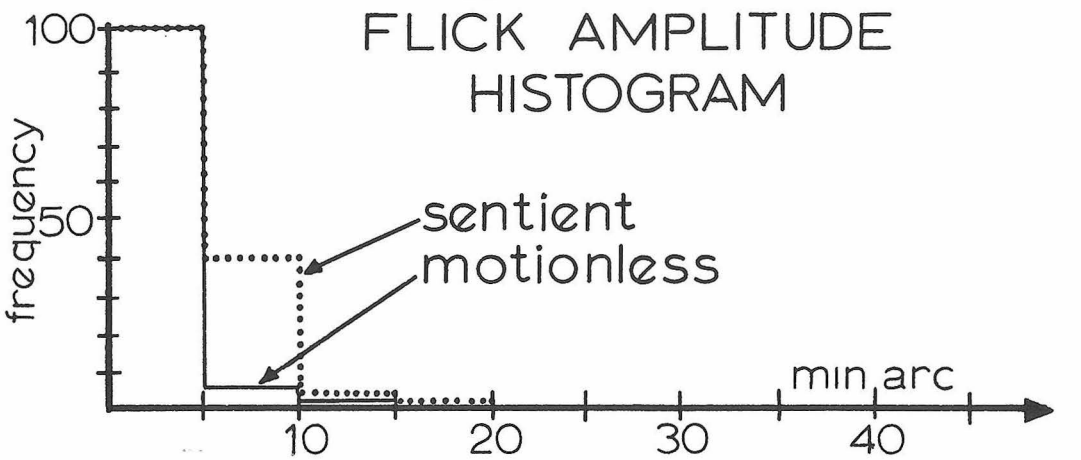
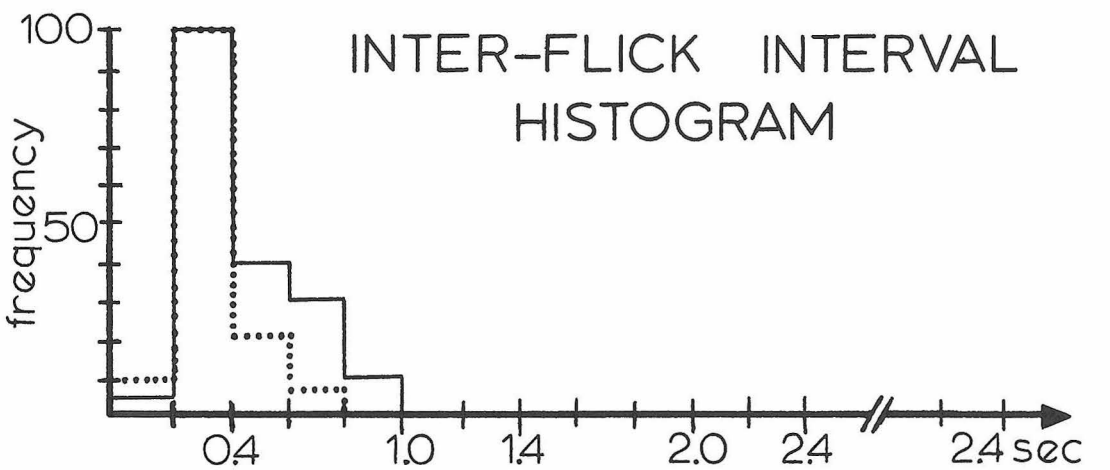


Fig. 3-3 Histograms illustrating the differences between motionless and sentient fixation for subject DSG. All histograms are normalized by setting the peak frequency to 100.





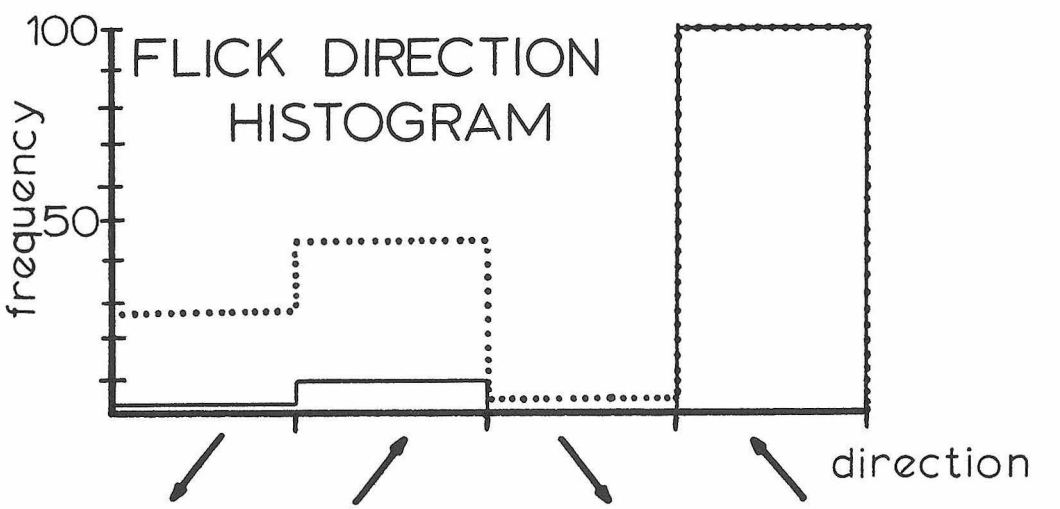


Fig. 3-4 Histograms illustrating the differences between motionless and sentient fixation for subject GSC. All histograms are normalized by setting the frequency to 100.

SUBJECT	CRITERION	RECORD LENGTH (sec)	NO. OF FLICKS	MEAN FLICK RATE (per sec)
DSG	MOTIONLESS	134	109	0·81
DSG	SENTIENT	106	151	1·43
GSC	MOTIONLESS	53	107	2·02
GSC	SENTIENT	54	140	2·59

Table 3-1 Characteristics of the records from which the histograms in Figs. 3-3 and 3-4 were made.

can generate a histogram of eye position as a function of horizontal and vertical spatial coordinates with the frequency-of-occurrence coordinate represented by the extent of exposure at any spatial location. Such histograms are shown in Fig. 3-5, for each of the fixation criteria. Both represent one minute time exposures, made on a single roll of high contrast film, and with oscilloscope spot brightness held constant. The subject is DSG, fixating with his left eye. It may be easily seen that the deviations of the visual axis from the point target are at least twice as large in the case of sentient fixation as in the case of motionless fixation, though the shapes of the distributions are very similar.

During motionless fixation the subject's percept is distorted in several ways: the spot seems to blur and lose its whitish blue color; the black background often brightens to a dull grey while the spot brightness seems to diminish; one or more halos may appear around the spot; and, finally, the autokinetic effect is pronounced, i. e., the spot appears to drift slowly around in space. These effects take two to twenty seconds to develop, and recur sporadically during motionless fixation. With sentient fixation these effects are rarely seen and are of short duration when seen.

One other response to these two fixation criteria is worthy of note; namely that the rate of blinking increases markedly under sentient fixation. Further, in sentient fixation blinks tend to occur in bursts of two or three in less than a second, rather than roughly equally spaced in time. That this is simply a cornea clearing or wetting operation is doubtful because contact lenses do not diminish

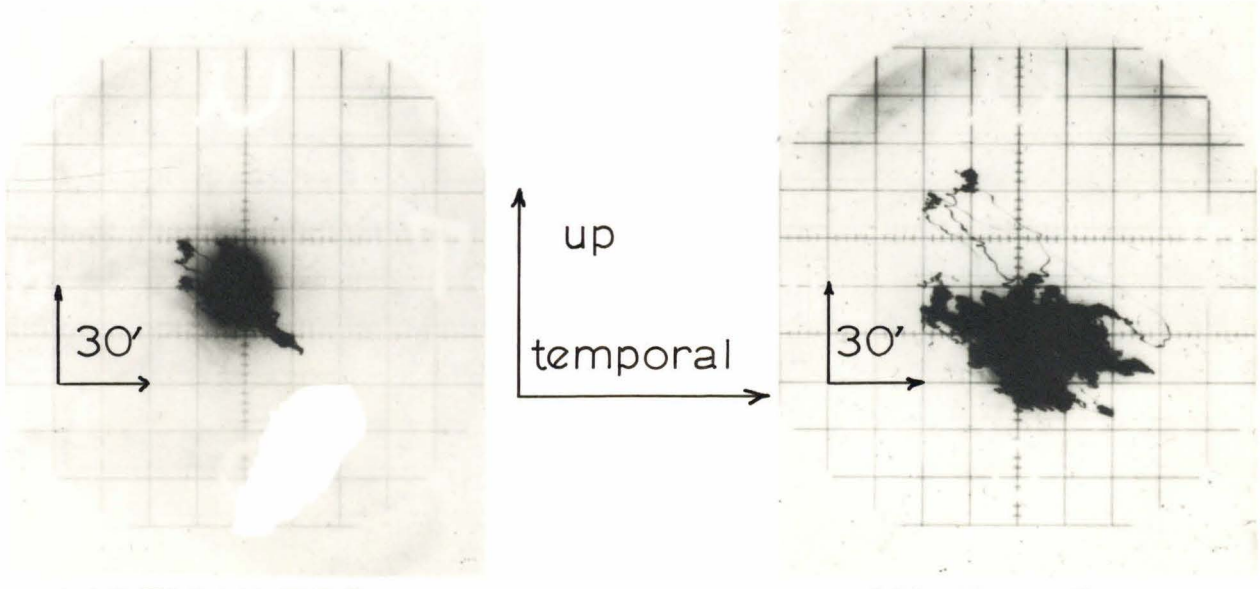


FIG. 3-5 ONE MINUTE FIXATION SPATIAL HISTOGRAMS.

the blink rate. It is possible that blinks are part of a mechanism for transiently stimulating the retinal receptors. The usefulness of this operation will become apparent in the discussion of stabilized image fade out in Chapter IV.

Discussion: The subject's inability to correctly perceive color, brightness, size, and location during motionless fixation leads one to inquire into the differences in patterns of eye movement which allow these properties to be correctly apprehended during sentient fixation. Two causes may be adduced for improved acuity and improved knowledge of spatial relationships during sentient fixation. The instructions may "set" the subject's cortex to the task of interpreting the visual input during sentient fixation, and this process may be relatively independent of all peripheral events (eye movements and receptor inputs). Because of the similarity between the subject's observations during motionless fixation and his observations while viewing a stabilized retinal image, it seems more likely that peripheral events are a major cause of the improved percepts obtained during sentient fixation. The records of eye movements during fixation were examined for two peripheral events which could cause improved percepts: repetitive scanning behavior, and random scanning behavior, either of which might serve to mediate acuity or localization information.

The effect of contiguous flicks and drifts, as may be seen in Fig. 3-1 and 3-2, is to scan the receptors over the image of the point target. In motionless fixation the nature of this scanning is

somewhat regular: drift is roughly constant in velocity and direction, while 80% to 90% of all flicks are in the opposite direction. It should be pointed out that this scanning behavior takes place independently of conscious will and even conscious knowledge. This was tested in a later experiment by having the subject press a button whenever he detected a movement of his eye. During motionless fixation he detected no movements (except blinks) and during sentient fixation only flicks larger than 10 min arc were detected. The regular scanning behavior undergoes several radical changes in the case of sentient fixation: the regular rhythm seen in motionless fixation still persists, but in addition there is scanning of larger amplitude, with numerous additional flicks; few of which compensate in direction or amplitude for the preceding drift, but some of which occur in pairs (sometime triplets) and compensate for each other, as is evident in Fig. 3-2.

Close inspection of the records reveals that compensating flick pairs occur in motionless fixation as well, although less frequently and with lower amplitude than those occurring during sentient fixation. Both subjects produced compensating flick pairs at a rate of 0.18 per sec during motionless fixation; this rate increased to 0.27 per sec for GSC, and to 0.46 per sec for DSG during sentient fixation. On the basis of their increases in mean flick rates between motionless and sentient fixation conditions, one would predict a pair production rate of only 0.23 per sec for GSC and 0.32 per sec for DSG in sentient fixation. Thus the proportion of flick pairs to all other flicks is larger in sentient fixation than in motionless fixation

for both subjects.

Flick, drift and tremor have been examined individually by Ditchburn, Fender and Mayne (26). By imposing controlled movements on an otherwise stabilized image, they determined that "fade out" of the image could be counteracted by motions of the image similar to those produced by flicks. Tremor-like movements counteracted fade to a lesser degree; whereas drift contributed nothing. The primary role played by flicks is consistent with the increased flick rate found during sentient fixation. Similarly the small differences in drift characteristics in the two forms of fixation would imply that they contribute little.

These observations lead to the conclusion that, apart from some large paired saccades, there is no distinctly periodic scanning of the eye during sentient fixation which does not occur during motionless fixation as well. The chief novel feature of sentient fixation, as compared with motionless, lies in the increased amplitude and frequency of occurrence of flicks.

Eye Movements During a Spatial Localization Task: There are two simple ways in which flicks could aid visual acuity; either by placing the target image rapidly and stably on a "fresh" set of receptors, or by transiently stimulating a swath of receptors as the target image glided over them. Similarly, information concerning spatial relationships could be derived from either stimulation at the end points or from stimulation along the trajectory of the target image. If the swath of stimulated receptors does contribute to either of these

mechanisms, one might expect the swath to have a simple geometry and to be controlled or repeated with some degree of regularity. These considerations led to an investigation of the control exercised over the path of the visual axis during a saccade, hereafter referred to as the saccadic trajectory.

In order to trigger saccades, two different experimental conditions were used. Both required the subject to locate, flick towards, and fixate a point in his visual field, but in one case the subject had much more information about the location of the point than he had in the other case. Specifically, one task required the subject to flick on command from one point to another, both of which were continuously visible. The second task involved following a point which jumped from one location to another a priori unknown location in the visual field.

Results: Fig. 3-6 and 3-7 illustrate the paths taken by the visual axis during saccadic movements. In Fig. 3-6 the subject was instructed to flick from one motionless, continuously visible point to another on command, and to fixate the point on arrival according to the motionless criterion. Commands to change fixation points were given verbally once per second.

A different stimulus arrangement was used in Fig. 3-7. Here the subject was instructed to follow a bright point which jumped in less than a millisecond from one position to another. Neither the time, nor the direction of jump were known to the subject. Profiles in time of these two sorts of movements are shown in Fig. 3-8.

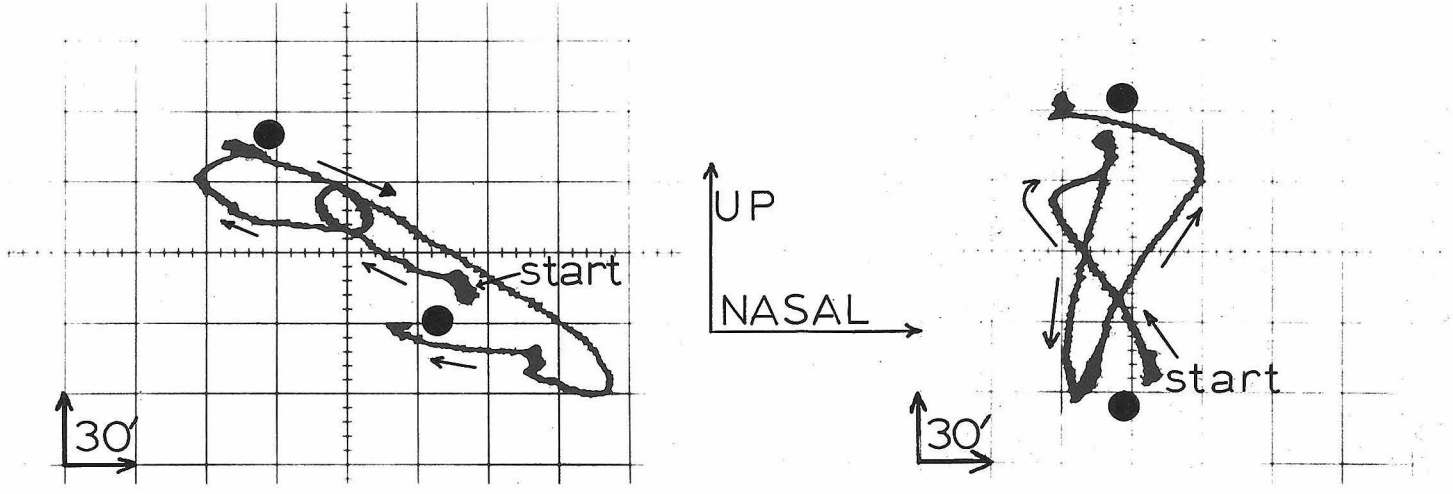


FIG. 3-6 SACCADIC TRAJECTORIES BETWEEN TWO BRIGHT POINTS (● MARKS APPROXIMATE POINT POSITION).

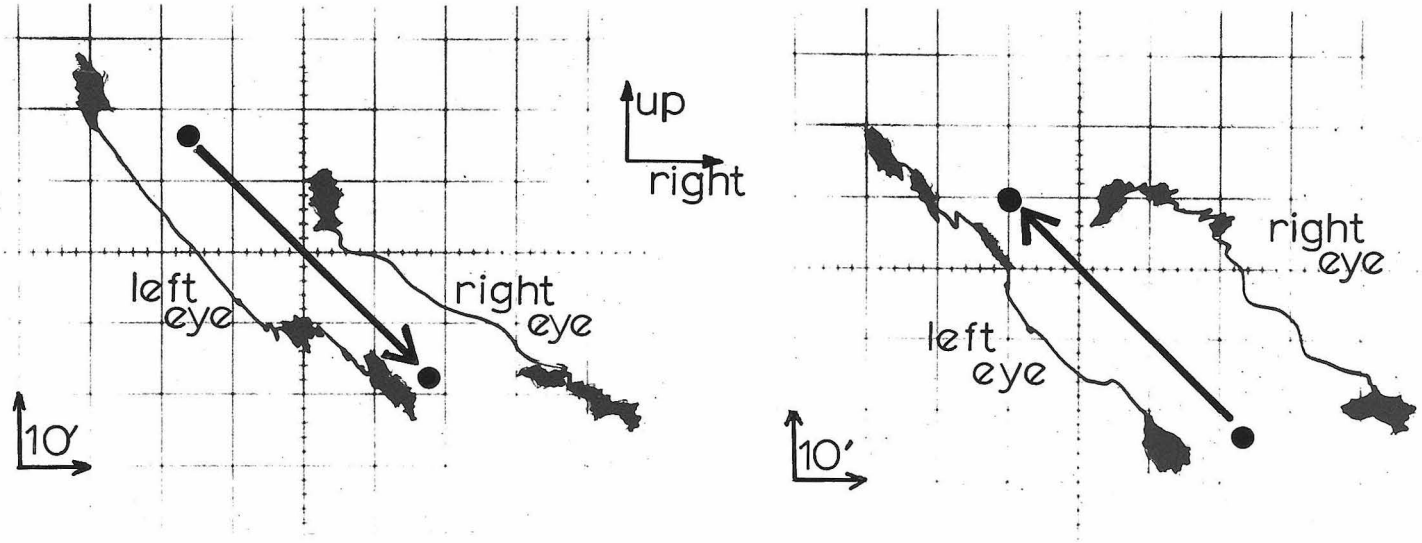


FIG. 3-7 BINOCULAR SACCADIC TRAJECTORIES FOLLOWING A BRIGHT POINT (ARROW MARKS POINT'S TRAJECTORY).

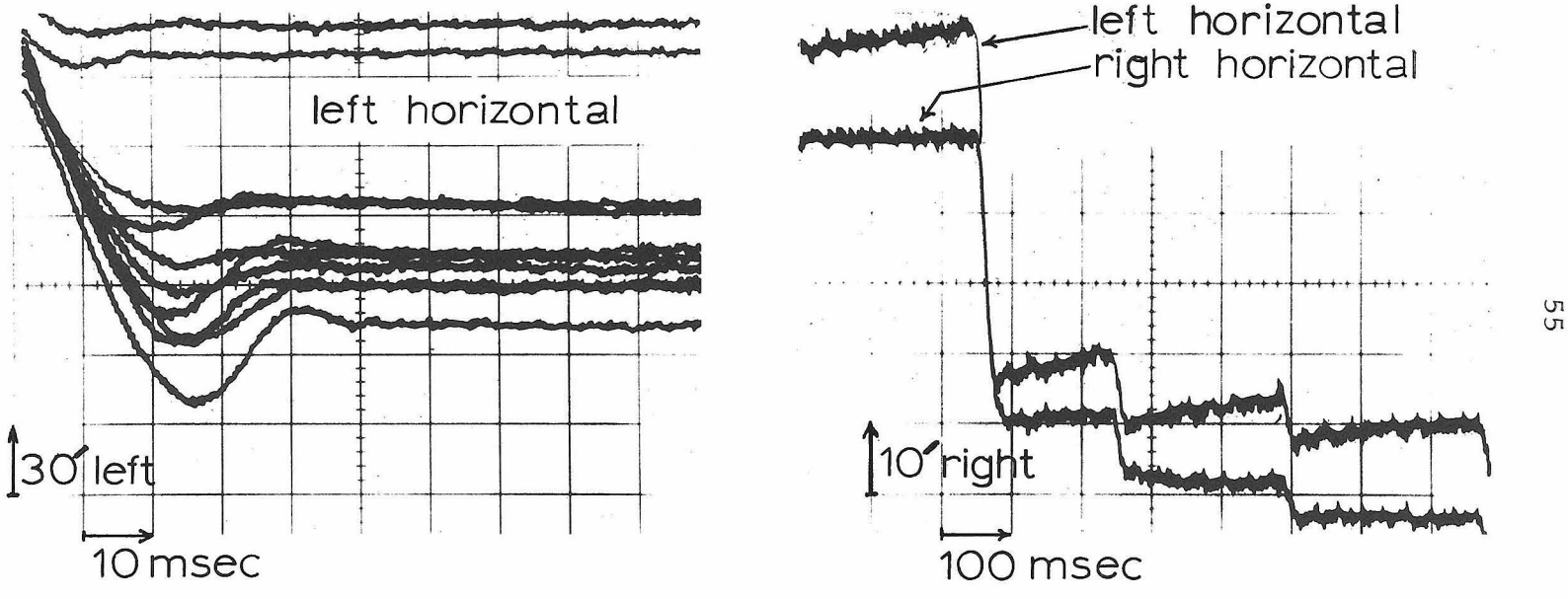


FIG. 3-8 TIME PROFILES OF HORIZONTAL SACCADES BETWEEN TWO POINTS (LEFT), AND FOLLOWING A POINT (RIGHT).

The traces on the left are the horizontal components of left eye rotation during ten successive saccades, with the oscilloscope triggered by horizontal eye velocity. The traces on the right are the binocular horizontal components of a single saccade, with the oscilloscope triggered by the target movement.

The two adjectives which seem to best fit these two types of saccadic movement are "sloppy" and "wary". When time of initiation, direction, and amplitude of the target jump are well known, the subject executes a sloppy saccade; that is, the trajectory of the saccade in space is rarely close to a straight line; overshoot and even ringing may occur in both vertical and horizontal directions; yet the whole movement is over within about 50 msec, and the endpoint is close to the correct location. Wary saccades, on the other hand, occur when the subject lacks knowledge of the direction and/or amplitude of target movement. He then executes a series of saccades, commonly two to four, all a reaction time or more apart, each of which has a straight trajectory, and each of which brings him closer to the final position of the target. The initial saccade of the series is usually the largest, and may even be larger than the target movement - in which case the second flick is in a direction opposite that of the first. The situation shown in Fig. 3-8 is the most common; the first saccade stops short of the target and succeeding saccades position the eye correctly in the course of the next half second or more.

The possibility that sloppy trajectories are due to lens slip over the eyeball was ruled out by several observations: varying the suction on the lens from 3" to 20" of water did not diminish the saccade overshoot, nor the saccade rise time, during 1.5^{o} saccades. Further, wary saccades during the same experiment showed no overshoot, even though the peak velocities reached by sloppy and wary types were often the same. Three subjects were tested, and all responded with distinct sloppy and wary saccades to the two types of

visual targets described above. The two sections of Fig. 3-6 each show two sloppy and one wary saccade, indicating that the subject is not always consistent in the type of saccade he produces. These observations, and the others we have made of flick trajectories, are consistent with the following interpretation: when the subject remembers or learns from non-visual cues the location of a target, his first saccade towards it will be large, fast, and sloppy. Thereafter wary saccades may correct any residual error. On the other hand, when target location is a priori unknown, and is being derived from purely visual cues, the subject initiates a sequence of short, direct, incremental, wary saccades.

We set out to examine whether saccadic trajectories might play a role in the improvement of acuity or spatial localization. The seemingly uncontrolled and certainly non-repetitive trajectories of sloppy saccades do not fit easily into any such role. The direct trajectories of wary saccades, on the other hand, may be interpreted as having such a function. For example, information concerning distance to the target point may be derived from the number of wary saccades needed to follow it, or from the number of cones stimulated by the target image during the wary saccades. These hypotheses are tested in Chapter V. The above evidence indicates only that a relatively unique pattern of eye movements, wary saccades, accompanies visual spatial localization.

Fixational Flick Trajectories: One intriguing observation is that the flick trajectory reflects the subjects' knowledge or lack of knowledge

about target position. When following a target, saccades tend to be direct and without overshoot, whereas non-tracking tasks result in sloppy saccades. During motionless fixation it was noted that the eye continued to flick. The question arises whether fixational flicks are the result of a visually driven eye re-centering system, in which case one would expect wary flicks, or are part of a scanning mechanism.

Determination of the trajectories of fixational flicks presents difficult problems. Not only are they close to the noise level of the eye position measuring system, but also they are too small to trigger an oscilloscope or flick detector. For these reasons records of eye movements were analyzed digitally. A flick was defined in the following way: any change greater than 3 min arc of either the vertical or horizontal component of eye position inside a time interval of 2 msec was counted as a flick provided that it did not have the large rebound characteristic of a blink. The trajectories of these small flicks in space were plotted by a specially developed computer routine which plots eye position as a sequence of letters on a graph; the positions of the letters indicate the relative eye positions, while the letter itself (ABC...Z*1234...90+-$) indicates the time order, mod 40, of the sequence of eye positions. Thus a flick going in a straight line at constant velocity and lasting 80 samples (16 msec) would be represented by a straight line of 80 equally spaced letters in the order ABC...Z*123...90+-$ABC...Z*123...90+-$. Any point at which the eye dwelt for more than one sample time is represented by an equal sign (=).

One such plot of a typical fixation flick is shown in Fig. 3-9. The sequence begins 20 msec before the flick is actually detected, and lasts a total of 40 msec. This particular flick has all the finer characteristics of a sloppy flick, i. e., it is indirect and overshot. This is further illustrated in Fig. 3-10 and 3-11 which show the horizontal and vertical time profiles of the same flick whose trajectory is plotted in Fig. 3-9.

Are all fixational flicks sloppy? To date only one subject has been tested in this regard, and one out of every three of his flicks during motionless fixation was sloppy; the remainder were of the wary type. This implies that 2/3 of this subject's motionless fixation flicks are visually driven tracking movements. To call them eye-centering movements is erroneous since there exists abundant evidence (27, 28, 29) that fewer than 2/3 of fixation flicks center the eye, in the sense of returning it to its mean position. In accord with this it was found that the endpoints of fixational flicks are widely distributed, and that their trajectories only rarely overlap even though most flicks move the eye in a single direction. These observations contraindicate the presence of a periodic scanning mechanism utilizing repetitive stimulation of a swath of receptors during flicks.

The possibility that fixational flicks are merely indications of motoneuron or muscular noise has not been ruled out. Several observations indicate that this is unlikely. First, during motionless fixation 80% to 90% of all fixation flicks are in one direction; in particular, they oppose the predominant drift direction. This was checked by a second experiment, which sought to rule out the

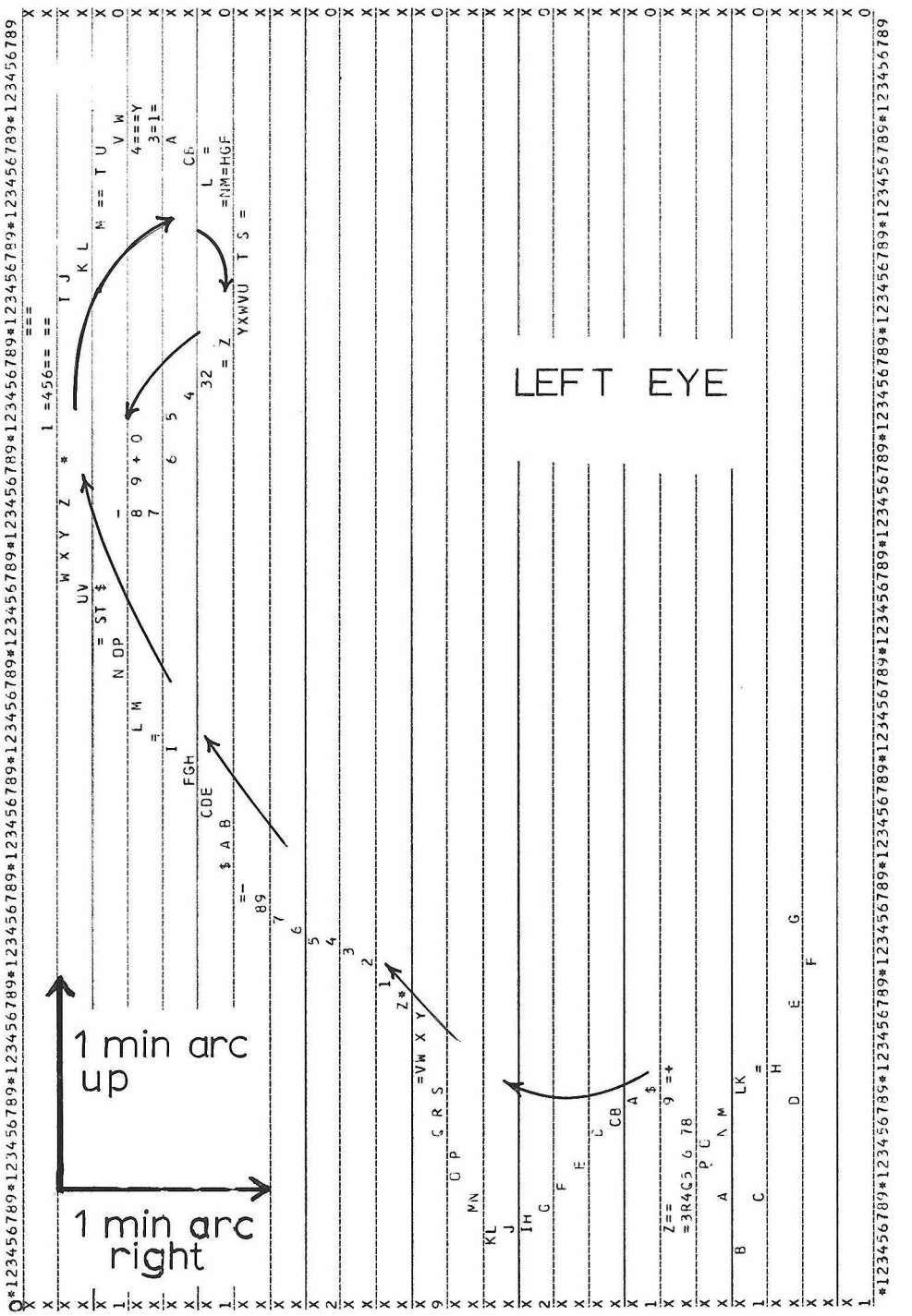


FIG. 3-9 TRAJECTORY OF SMALL FIXATION FLICK. LETTERS ARE 0.2 MSEC APART.

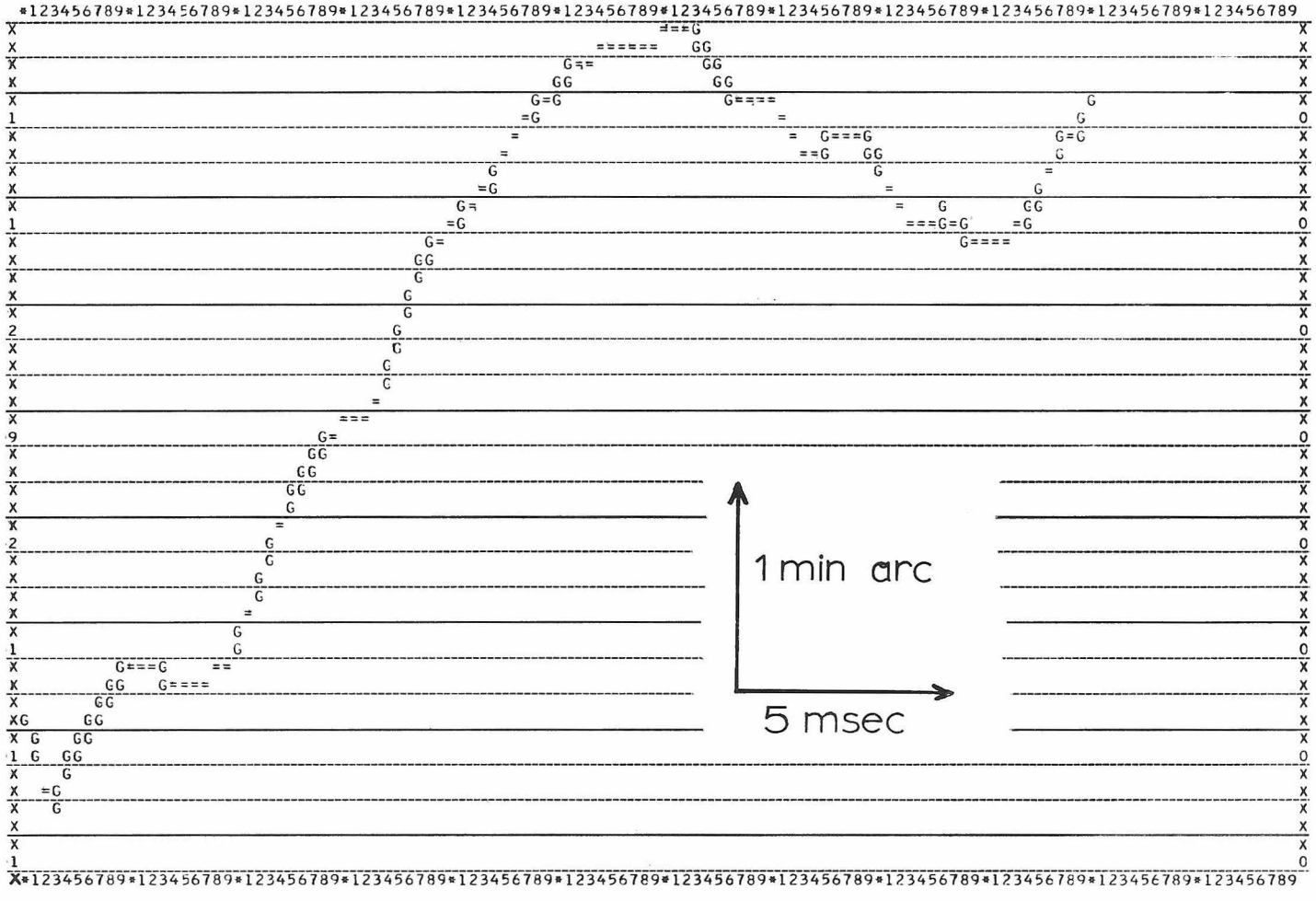


FIG. 3-10 TIME PROFILE OF HORIZONTAL COMPONENT OF PRECEDING FIXATION FLICK.

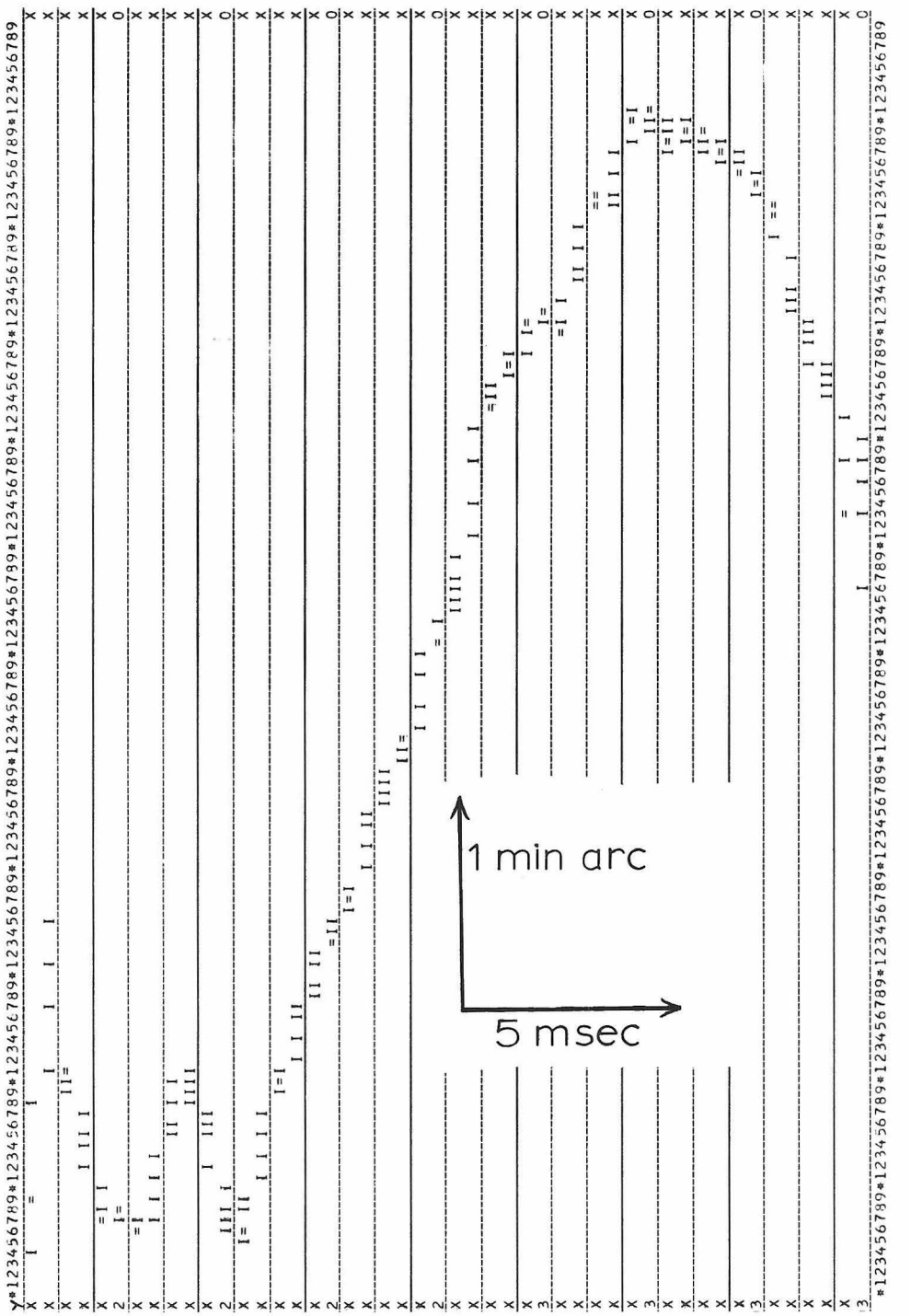


FIG. 3-11 TIME PROFILE OF VERTICAL COMPONENT OF PRECEDING FLICK.

possibility that such flicks are simply the results of noise which always pushes the eye in the same direction, regardless of drift direction. Gregory and Zangwill (30) report that the autokinetic effect may be induced by deviation of the eyes to an extreme position, and then fixating a small central spot. Because of the ancient, though disputed - c.f. the discussion in (31) - relationship between the autokinetic effect and drift in the eye, it was conjectured that the direction of eye drift might be influenced by the same procedure. This turned out to be the case, and it was noted that even with drift in non-normal directions, roughly 80% of all fixational flicks were in a direction opposite that of the preceding drift. Thus fixational flick direction is not determined by a random process independent of other eye movements, but is closely linked to drift direction.

Aside from the above experiment, the drift component of fixational eye movements was manipulated in one other manner; that is, by attaching a 1 g weight to the stalk of the contact lens 2.9 cm from the center of the eye. Surprisingly, even with this great downward torque on the eye, subject DSG continued to drift upward and flick downward during motionless fixation, just as he had in the unloaded condition. The mean rate of drift remained unchanged. This experiment indicates that the cause of wandering of the eye during motionless fixation is not a slight imbalance of extraocular muscles, but rather involves either a proprioceptive or a visual feedback loop; that is, some form of control which counteracts a greatly increased muscle load.

Eye Movements While Viewing Sine Wave Gratings: In collaboration with Derek Fender, the author recently published a study of eye movements during observation of sine wave gratings of different spatial frequencies (31). These patterns are described in the following chapter. The results of this investigation are presented here in abbreviated form, since they also show that eye movement characteristics are highly dependent upon the type of pattern viewed. Details concerning the experiment and analysis may be found in reference 31.

The horizontal component of left eye rotation was measured while one subject viewed five sine wave gratings of different spatial frequencies. Because of the simple structure of the patterns, eye movement as a function of time could be easily converted into light flux into a receptor as a function of time by computing the sine of successive eye positions and introducing an appropriate scale factor. The power spectrum of light flux into a single receptor was then calculated for each of the five patterns. The power spectrum provides a measure of the relative dominance of the rates at which the light flux into the receptor is flickering. The five power spectra were compared with the known sensitivity of the eye to flickered illumination, and from this an estimate of the relative sensitivity of the eye to the five different patterns was made. This estimate matches quite closely the measured sensitivity of the eye for these patterns.

This analysis shows that eye movement characteristics, together with flicker sensitivity characteristics, suffice to explain the results of a particular acuity test. Whether these

characteristics are not only sufficient, but also necessary, to explain the results of sine wave grating acuity trials is the question tested and answered in the next chapter.

Conclusions: The pattern of eye movements is highly dependent upon the amount and kind of visual information desired by the subject. This has been illustrated by the overall statistics of eye movements during fixation, under two different criteria, and by classification of the types of trajectories taken by large saccades.

When positional information is desired by the subject, saccadic trajectories tend to be straight, but poorly matched in amplitude and direction to the target movement. Thus a series of linear successive approximations is made to the target's new position by a sequence of saccadic trajectories. Whether or not these eye movements mediate the position information is the topic of Chapter V. Here only the close association of the pattern of eye movements and the type of information input is noted. When target position information is known to the subject, saccadic trajectories tend to be anything but linear, yet the endpoint is quite well matched in amplitude and direction to the target position.

When information relating to the color, brightness, and size of a stationary point are desired by the subject, flick rate and flick amplitude increase, and flick directions become more diverse. These observations are in accord with several experiments (26, 32) which relate these parameters to the prevention of fading. Whether or not these movements serve to improve acuity - as opposed to

merely preventing fade-out - is the subject of the next chapter. The eye movement patterns themselves show no trace of a simple repetitive scanning mechanism which could improve acuity, although the two thirds of fixational flicks which do have direct trajectories may partake in a more complicated mechanism serving the same purpose. Since direct saccadic trajectories are associated with visual tracking of unpredictable targets, their appearance in such large numbers during motionless fixation requires explanation.

This study of patterns of eye movement admits the possibility eye movements serve to improve acuity and the ability to localize objects in space. It has been shown that each of these tasks is accompanied by a characteristic regime of eye movements. The following chapters test whether the different regimes of eye movements are incidental to the influx of these sorts of visual information or are a necessary link in the process.

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CHAPTER IV

ACUITY, A LINEAR ANALYSIS

Introduction. Visual acuity depends on three physiological systems: The optics of the eyeball, which blur the retinal image; the mosaic of receptors, which samples only discrete areas of the retinal image; and, finally, the neural interconnections of the retina and brain, which process the information derived from the receptors. Properties of the first two of these systems are described in the initial section of this chapter, together with a novel, computer-derived, index of their performance.

The central portion of the chapter concerns the hypothesis that eye movements improve acuity. This is tested with a variety of targets as well as with a variety of experimental methods. Circumstantial evidence favoring the hypothesis was presented in the preceding chapter. The set of data obtained in this investigation of the information processing capabilities of the retinal and cortical nerve nets is then transformed and compared, in the closing section of this chapter, with the results of other psychophysical and physiological studies of visual information handling.

The procedure which allows these diverse physiological systems to be described in a common set of terms, and to be related to one another, is linear systems analysis. This is a somewhat mathematical artifice by which, given an improbable set of inputs and their respective outputs, as well as severe restrictions on the

(biological) system in question, one may predict with a surprising degree of accuracy the output of the system corresponding to almost any definable input. The cardinal virtue of this type of analysis is its predictive ability, especially for systems in cascade. Its cardinal sins are, from a biological point of view, two: A cavalier disregard for the particular mechanism by which the system operates, only inputs and outputs are considered; and an inability to deal with nonlinear systems, and with systems whose parameters vary with time. These restrictions are discussed fully in the following sections.

Linear systems analysis provides, then, a conceptually simple and experimentally direct, quantitative means of studying information transfer through the visual system, from blur of the retinal image to "blur" in the cortical projections of the visual world. Although this type of analysis could be extended to include color, binocular, and target movement effects, these factors are not included in this analysis.

Retinal Image Formation and Receptor Sampling

Optical Point Spread-Function: Over the course of the last hundred years many ophthalmologists attempted to describe all the sources of blur in the retinal image in terms of the geometry and refractive indices of the cornea, lens, vitreous and aqueous humors, etc. These measures are exceedingly difficult to make on a normal eye, and, once approximated, are even more difficult to combine so as to estimate the amount of blur when a particular target is imaged on the

retina (1).

A more workable and concise description of the aberrations of any optical system was introduced via linear systems analysis in the late 1950's. This is the spread-function, that is, the distribution of illuminance across the blurred image of a point source. This does not distinguish among the contributions to retinal blur caused by each of the tissues of the eye, but only describes the net, resultant blur in the image of a very simple target, a point source of light. The spread-function therefore avoids the still unanswered question of how much each tissue contributes to blur, but, balancing this fault, it serves the purpose of allowing computation of the blur in the retinal image of any well-defined target.

This prediction ability arises in the following fashion: Consider any monochromatic target to be a planar collection of point sources of light. Apart from a multiplying constant, the point spread-function for the eye specifies the luminance distribution on the retina caused by each point of the target. Each multiplying constant is simply proportional to the intensity of the corresponding target point source. Then the retinal image is just the sum of all the point spread-functions, one of which is associated with each point of the target. Mathematically, this amounts to a convolution of the point spread-function with the luminance distribution of the target.

Two important assumptions are implicit in the above statements. First, it is assumed that there is only one point spread-function. This is not true over the whole field of the eye, for the blur in the image of a point near the periphery of the retina is much

greater than that of a point imaged on the fovea. Instead of considering a variable point spread-function, which leads to insurmountable computational difficulties, the following discussion is limited to acuity in the region of the fovea, where one may assume the point spread-function to remain reasonably constant, and where, after all, the region of maximum acuity is located.

The second assumption is that light from several points of the scene may be summed arithmetically to give the retinal image luminance. Light waves will add in this manner only if the effect of phase may be neglected, and this is commonly the case. Incoherent illumination of the target will give rise to mutually incoherent light waves emanating from each point of the target. Such waves should produce no macroscopic interference effects in the retinal image.

The final restriction on the use of spread-function is this: Any variation of the optics of the eye will produce a change in the spread function, thus a spread function is defined only for a fixed pupil size and state of accommodation - as well as for only a single wavelength of light.

Spread-Function Measurement: It is very difficult to explore the luminance distribution around the image of a point on the retina without burning a hole in it. A more practical maneuver is to cast the image of a bright line onto the retina and to measure the blurred distribution of light energy around this image. Not only does this reduce the maximum light flux needed to measure blur, but also the point spread-function may be computed, assuming only rotational symmetry, directly from the experimentally determined line

spread-function. Flamant (2) first determined the line spread function in a human eye in 1955. Her findings were confirmed by Westheimer and Campbell (3), and Krauskopf (4); although, quite recently Campbell and Gubisch (5) presented evidence that the line spread function may be narrower than previously indicated. Data from the first three investigations are plotted in Fig. 1, along with the function which all three groups agreed best represented their data, that is,

$$L(x)=L_o \exp(-0.7\,|x|)$$

where x is distance on the retina from the center of the line image.

Although this function is probably reliable for intermediate values of x (between 1 and 4 min arc), it is probably not reliable near x=0 because of the high rate of change of intensity there, nor is it reliable beyond x=4 because of the extremely low luminance levels in this region. Fry (6) estimates that the peak luminance is 4 orders of magnitude greater than that 2 min arc from the peak, instead of 1 order of magnitude greater, as this formula implies. Nevertheless these are the best experimental data yet obtained.

The above formula, and the assumption that the point spread-function is circularly symmetric, were used by the author to derive the point spread-function. The basic relationship is that the point spread-function is equal to the Hankel Transform of the Fourier Transform of the line spread function. The 7094 was used to evaluate numerically the integral involved. Details of the mathematical argument may be found in Appendix I.

A least squares fit routine, developed by G. W. Beeler and

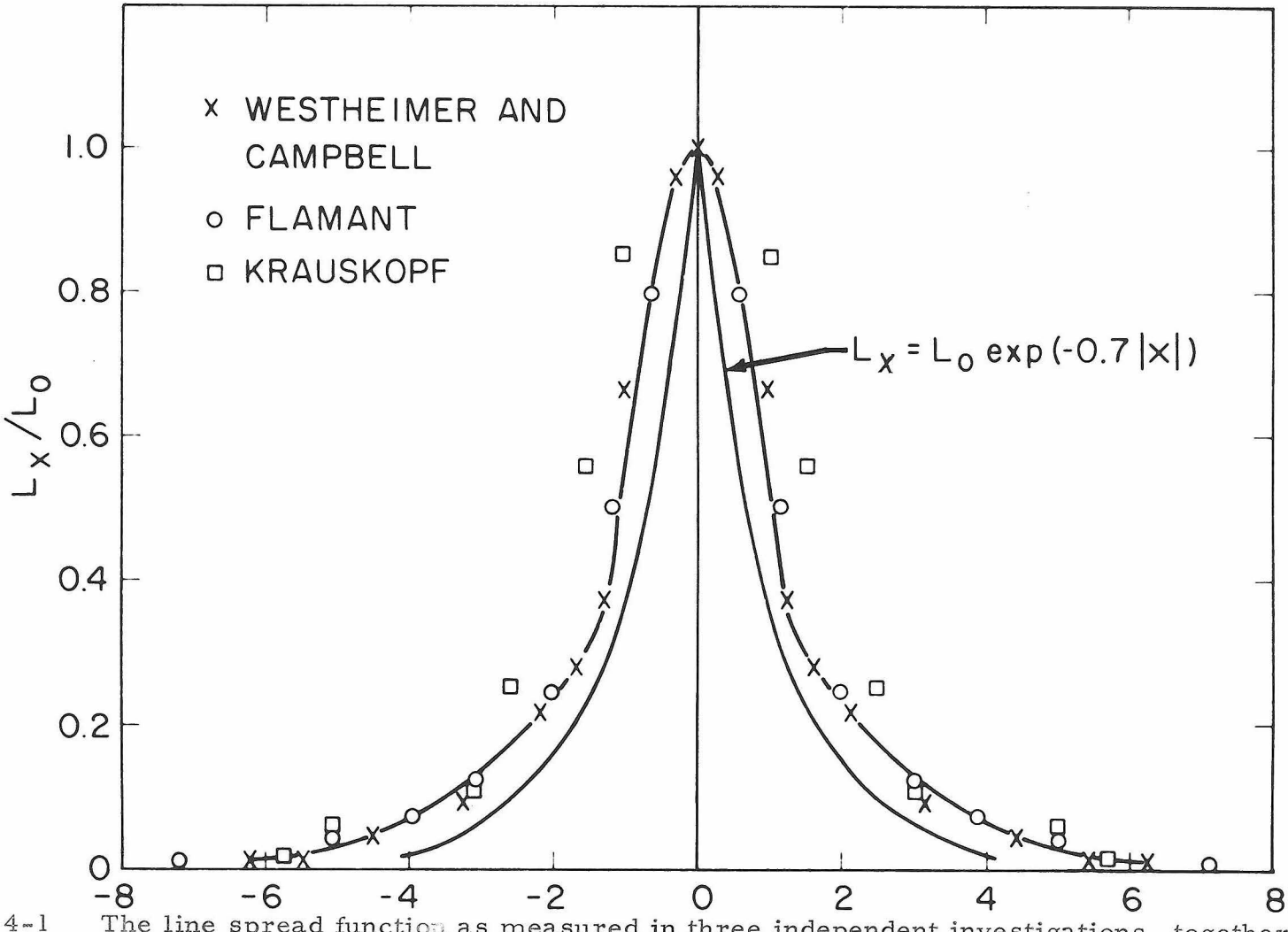

Fig. 4-1 The line spread function as measured in three independent investigations, together with the analytic function which best mimics the slope of the data.

the author, was programmed to find the best exponential fit to the point spread-function. The three exponentials best fitting the point-spread function, in order of increasing complexity, are:

$$P(r)=\exp[-.85r+.44]$$

$$P(r)=\exp[.015r^2-1.0r+.7]$$

$$P(r)=\exp[-.006r^3+.102r^2-1.35r+.96]$$

where r is distance along the retina in min arc.

Point Spread-Function and the Receptor Population: A more physiological view of the point spread-function may be obtained by assuming that each receptor integrates the flux falling on its outer segment. Polyak states that the outer segment of a foveal cone is 1.1 to 2.0μ in diameter, and that the inter-receptor spacing is 2 to 2.6μ in the central fovea. The rear nodal point of the eye is 17mm from the retina in the normal eye, therefore the angular spacing of the foveal cones is 24 to 30 sec arc. The intercone spacing 10° from the center is 10μ or 2 min arc. These figures permit the point spread-function to be plotted in terms of light flux into neighboring receptors as shown in Fig. 4-2. The bar above each receptor is proportional in length to the integrated light flux into the tip of that receptor; the bar below each receptor is proportional in length to the logarithm of this flux, and therefore proportional to the receptor potential if lateral inhibitory effects are neglected at this level. Thus Fig. 4-2 illustrates the inputs and outputs of adjacent foveal cones when the eye is looking at a single star.

Fig. 4-3 refers to the same conditions except that the point of

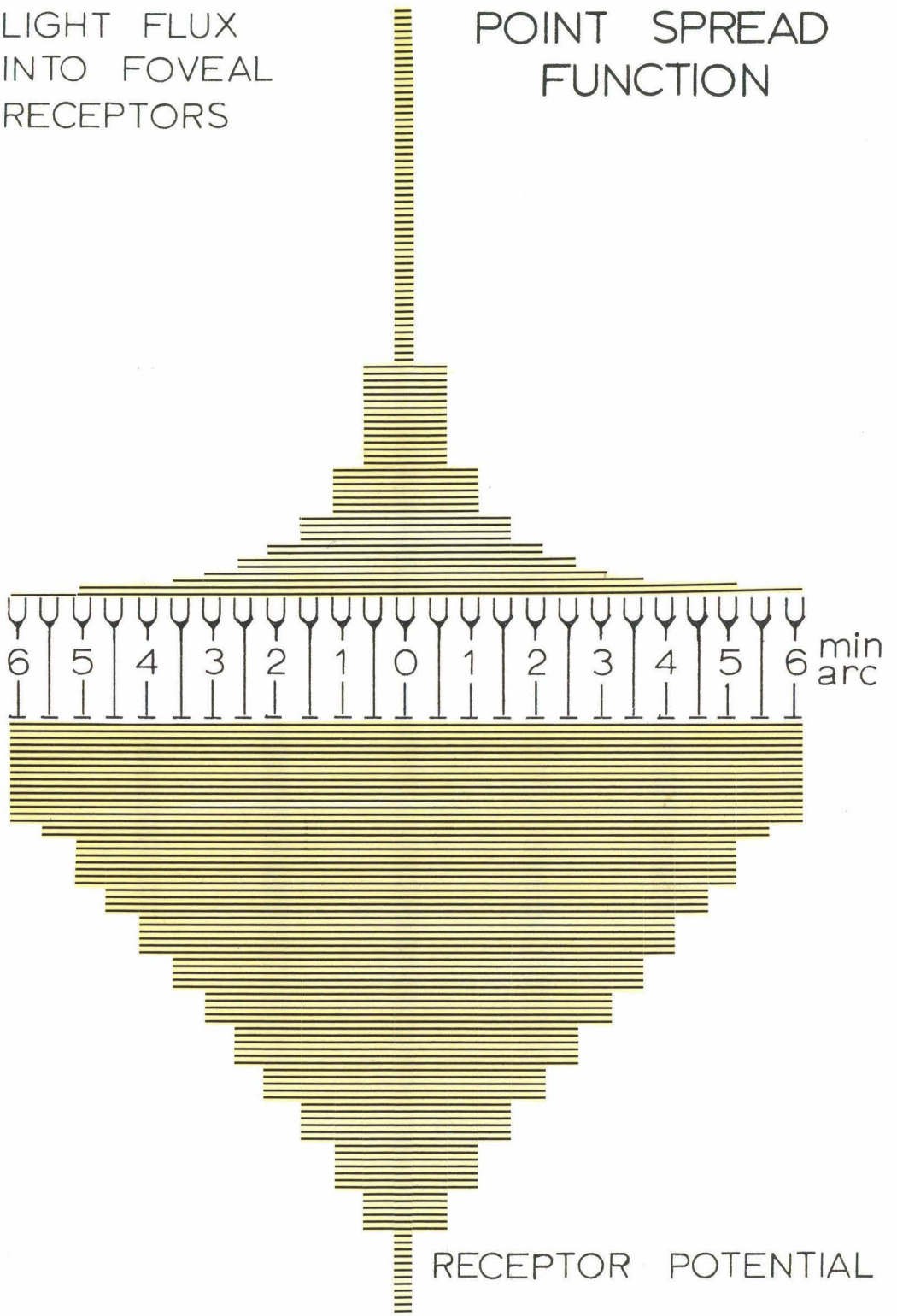

Fig. 4-2 Foveal receptor inputs and outputs when fixating a point source. The peak of each distribution is normalized to 9 cm. The point spread-function was calculated using the line spread-function shown in the previous figure.

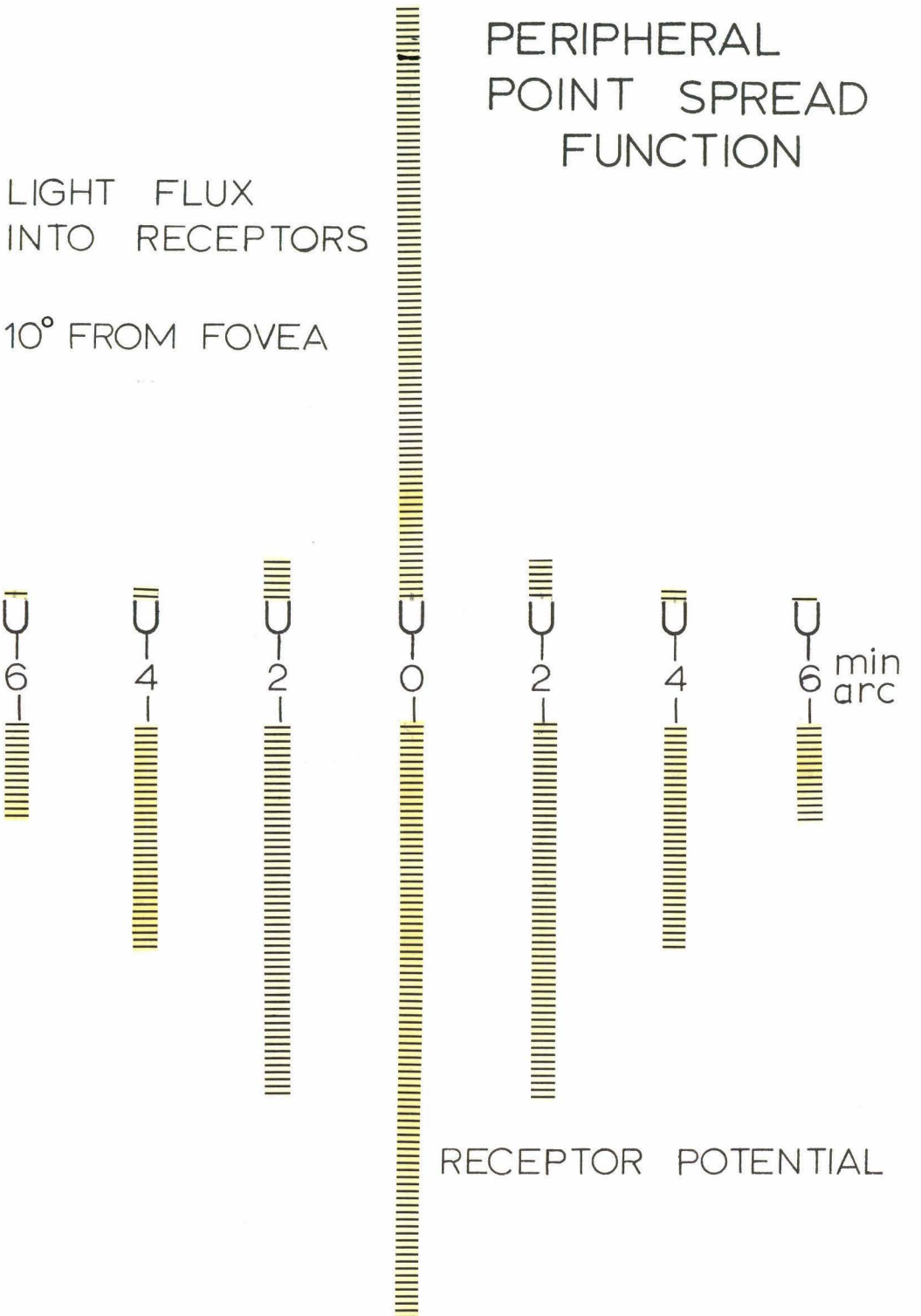

Fig. 4-3 The relative distributions of peripheral receptor inputs and outputs using the same point spread-function as shown in the previous figure. The peak of each distribution is normalized to 9 cm.

light is imaged 10° from the central fovea, in a less dense receptor population. In both cases it was assumed that the peak of the luminance distribution fell on the center of a receptor. For a description of the mean receptor fluxes, averaged over all possible positions of the peak of the luminance distribution, see Fender and Gilbert (7). Fig. 4-2 and Fig. 4-3 represent only cross-sections through the circularly symmetric point spread-function and distribution of receptor potentials. Receptors are assumed to be colinear, though this is rarely the case.

Two points are of interest in Fig. 4-2 and Fig. 4-3. The first is that blur introduced by the optics of the eye spreads the point image over only a few receptors - indicating that the optics of the eye are well matched to the size and spacing of the retinal receptors. The second point is that the effective "blur" is drastically increased by the logarithmic transformation of light flux to receptor potential. It is this neural "blurring" which requires elimination by a contrast enhancement mechanism such as lateral inhibition. Results dealing with lateral inhibition in the human retina will be presented later in this chapter. Meanwhile we shall investigate the existence of a contrast enhancement mechanism which relies upon eye movements to scan receptors back and forth under an image such as that in Fig. 4-2, and thereby eliminate some of the "neural blurring."

Eye Movements and Acuity

Background: There is a considerable amount of circumstantial evidence in favor of the hypothesis that eye movements play a role in

the visual mechanisms determining acuity. The previous chapter describes marked changes in the character of eye movements during acuity tasks. Eye movements and flicker sensitivity provide a basis for explaining sine wave grating acuity (7). Weymouth, Anderson, and Averill (8), Marshall and Talbot (9), and Jones and Higgins (10) have all postulated rather explicit mechanisms by which eye movements could aid acuity.

These theories are all based on the fact that every photoreceptor studied to date is more sensitive to the rate of change of illumination than to the actual level of illumination. Eye movements cause the spatial gradations of illumination over the retina to result in rapid fluctuations in time of the illumination falling on any particular receptor. The above authors hypothesized that the human visual system can extract more information from the fluctuations in time of receptor outputs than from the fluctuations in space of receptor outputs.

A recent extension of these ideas may be found in the work of Bryngdahl (11), who has correlated eye movements with the ability to discriminate flickered illumination from continuous illumination. He found that the rates of flicker produced by eye movements are well matched to the rates of flicker for which the eye is maximally sensitive, within certain constraints on the size of target detail.

Prompting these theories concerning eye movements and acuity is the fact that the eye can perform feats of acuity which are very difficult to explain using only the measures described in the last section. The primary case in point is vernier acuity (_____)

in which a displacement of one line with respect to a second line may be as small as 2 sec arc and still be reliably detected. This minimum detectable vernier offset is far less than the diameter of the narrowest foveal cone (13 sec arc). When blur of the vernier image on the retina is taken into account, the task becomes even more remarkable. Two sec arc from the center of a line image on the retina, the luminance has decreased, according to the line spread function, by a factor of 2.3 per cent from the peak luminance value, yet this very slight modulation in luminance over a tenth of a cone diameter is detected and used to determine the relative positions of the two lines. Clearly some sort of spatial and/or temporal averaging must be carried out to extract this tiny signal from the inherent noise.

Just as there is an obvious need to establish an acuity-improving mechanism, and circumstantial evidence relating this mechanism to eye movements; there is also a sizeable body of experimental evidence indicating that eye movements do not play a significant role in the improvement of visual acuity. Ratliff (12) found that during brief exposures, the orientation of a high contrast, narrow bar pattern was detected more reliably as eye movement during the exposure decreased in amplitude. The advent of image stabilization systems during the last decade led to more direct experiments. Riggs et al (13) determined that acuity was unimpaired for single line targets, 6 to 30 sec arc wide, when these were stabilized on the retina. Similarly, Krauskopf (14) reported that acuity for bars up to 8 min arc wide was marginally poorer in

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stabilized vision than in normal vision. The last two investigations were devoted primarily to characterizing fade out of these patterns in stabilized vision, and, as a result, their observations on the subject's acuity for these patterns are somewhat anecdotal. Before presenting the direct evidence concerning the hypothesis that eye movements improve acuity, it would be valuable to make more concrete the distinction between fading of a stabilized target, and acuity for a stabilized target, since the two are often confused.

Acuity vs. Fade Out: Fading of a stabilized target, also known as "fade out," is a gradual process which occurs over a period of several seconds after the target is stabilized on the retina. The subject during this period observes that colors desaturate; sharp contours become less distinct and may fragment; bright areas of the target appear less bright and dark areas appear to brighten. These effects become gradually more pronounced until the subject sees only an empty grey field which may turn very dark (15), or from which the target may suddenly reappear (16). Evidence collected from observations of fading images (17) and from EEG (18) and ERG (19) data during fade out indicates that the fading process is not simply accommodation of retinal neurons, but rather is connected with cortical processing of visual information.

In the initial moments of viewing a stabilized target, the above effects occur to no perceptible degree and the target appears with seemingly normal clarity. Acuity for a stabilized target refers to acuity measured in this time interval preceding fade out. In testing

whether eye movements serve to improve acuity, the concern is with maximum acuity possible under the conditions of no retinal image movement. There is no argument over the fact that eye movements serve to sustain visual acuity by preventing fade out. The issue is whether or not eye movements mediate an improvement of acuity.

Acuity and Eye Movements - Previous Experiments: Three studies have been directly concerned with the problem of whether or not eye movements improve acuity. All of these used the same technique of measuring acuity in normal vision and comparing the results with acuity measured in stabilized vision. This technique does not test mechanisms by which eye movements alone improve acuity, without reliance on coincident retinal image movement; but there is no evidence for the existence of such mechanisms.

In the initial study, Keesey (20) tested two subjects in normal and stabilized vision with vernier, fine line, and narrow bar grating targets. Acuity, as defined by the threshold value of the angle subtended by the critical dimension of the target, was found to be the same for both normal and stabilized viewing, with target exposure durations ranging up to 1.3 seconds.

Fender and Nye (21) had four subjects realign an offset pair of vertical vernier lines during extended observation. The vertical distance between the ends of the lines was varied from 0 to 30 min arc. All subjects performed slightly better in normal vision than in stabilized vision. As a typical example, the probable error of the vernier setting for subject HBC was 9.6 sec arc in stabilized vision and 6.5 sec arc in normal vision with no vertical gap between the ends

of the vernier lines. The authors attribute this apparent improvement in normal visual acuity to the random scanning of the retinal image over the receptors by means of eye movements. Fade effects were presumably eliminated by flickering only the stabilized targets at a rate of 22 cps.

Data agreeing with both of the above contradictory results have recently been presented by Millodot (22). He asked two subjects to report the orientation of Landolt C gaps which were viewed normally as well as stabilized on the fovea. One subject's acuity, 20/16 in Snellen notation, remained the same in the two conditions. The second subject, MM, had an average acuity of 20/25 in normal vision, but this deteriorated significantly in stabilized vision to an average acuity of 20/36. MM had a much more tightly fitting lens than the first subject, and the author ascribes the acuity difference between subjects, and the difference between his and Keesey's results, to the degree of stabilization obtained.

Millodot also found a large difference in the fading effects noticed by the two subjects. For MM, targets disappeared completely within a few seconds and remained invisible as long as large eye movements were avoided. The other subject reported that targets took much longer than this to disappear, and intermittently reappeared. These different fade effects the author also ascribed to the different degrees of stabilization.

Target exposure duration was varied but was always less than one second in Millodot's experiments. The experimenter evidently uncovered and covered the target with his hand, and this led to

somewhat confusing fade effects: "In fact, if the experimenter, placing a Landolt ring on the ledge in the middle of the screen, left his hand there for several seconds, it would fade into the empty grey field, but as soon as he removed it the ring reappeared and the hand and arm left an after-image. However, there was enough time to resolve the ring before it disappeared." (p. 95 ref. 22) Despite these marked after-image and fade out effects, Millodot did not attempt to relate them to a loss of acuity, but rather lumped all effects of stabilization into a single acuity measure.

In summary, of the three investigations testing the hypothesis that eye movements improve acuity, one yields results in favor, one against, and one undecided. Or, in terms of subjects, Fender and Nye report 4 subjects all having different normal and stabilized acuities; Keesey reports 2 subjects having identical normal and stabilized acuities; and Millodot reports one of each variety. The only published hypothesis attempting to settle this conflict is that offered by Millodot. On the basis of one subject's results, he tentatively concludes that both his and Keesey's results showing equal normal and stabilized acuity are due to imperfect stabilization, caused, at least in his case, by lens slippage, and that an eye movement mechanism does indeed improve acuity.

Eye Movements and Acuity - Experiments

Introduction: The goals of the series of experiments which I have carried out are twofold: first, to resolve the issue of whether or not eye movements improve acuity; and, secondly, to discover whether

eye movements improve performance in a more general contrast discrimination task. This last goal requires further clarification: It will be noted that all the experiments described above used exclusively targets having high contrast and small critical detail. Targets with these characteristics are also used in this series of experiments, but, in addition, targets with low contrast and large detail, i. e., sine wave gratings, are used as well.

The reasons for this extension of earlier experimental techniques are three: First, large detail, low contrast targets are a significant class, especially for nocturnal animals, for example, and their detectability may quite conceivably be improved by some eye movement mechanism. Second, acuity for sine wave gratings may be used to predict, via linear analysis, acuity for many other targets. Third, and as a practical matter, it is extremely difficult to stabilize on the retina small critical detail in the target's image. Millodot, for example, worked with Landolt C gaps on the order of one min arc in width, yet his lens slippage - neglecting destabilization due to optics - was up to one min arc for his best subject, and five min arc for the other subject. Thus the gap in the C can hardly be called stabilized, since it was free to move through at least its own diameter, causing large on-off signals due to the high luminance gradient in this region. With sine wave gratings, on the other hand, low and spatially more uniform luminance gradients minimize these ever-present destabilization effects.

In the following experiments acuity was tested in normal and stabilized vision, using four distinct acuity target types, but with

primary emphasis on sine wave gratings. Four subjects were used, and three different experimental techniques. Only monocular acuity, left eye, was tested.

Targets: Sine wave gratings were used as targets in the majority of experiments. These are fuzzy bar patterns of various bar widths whose contrast may be altered during the course of the experiment. A typical sine wave grating is shown in Fig. 4-4, together with a plot of the luminance in the image of this pattern vs distance across the image. λ is the wavelength of the pattern; $1/\lambda$ is the spatial frequency of the pattern (cycles/min arc). The mean luminance of the pattern, averaged over space, is labelled I, and the maximum deviations from this level are of amplitude Δ I. The depth of modulation of the pattern is defined to be $\Delta I/I$, that is, the ratio of the maximum deviation from mean luminance to the mean luminance.

The usual acuity task associated with these patterns is to change the modulation in the pattern, at constant mean luminance, until the pattern is just noticeable. The modulation of the pattern at this point is referred to as the threshold modulation for the grating of spatial frequency $1/\lambda$. Commonly sensitivity is used instead of threshold modulation. Sensitivity is defined as the reciprocal of threshold modulation, and therefore may be thought of as a measure of acuity.

To call the above procedure an acuity task is to depart from the usual meaning of the word acuity. Snellen charts and Landolt C's, two of the well established means of measuring acuity, involve recognition of smaller and smaller target elements all at high contrast;

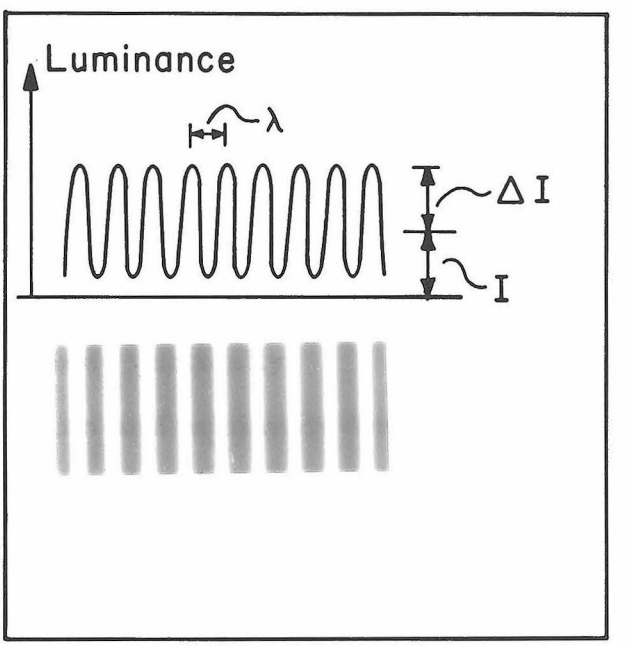

Fig. 4-4 A section of a sine wave grating, together with a plot of the luminance across it. Also shown are the wavelength, λ, of the pattern, the mean luminance, I, and half the peak to peak amplitude, Δ I. The modulation of the pattern is defined as the ratio $\Delta I/I$. The reciprocal of the modulation of the pattern at threshold is called the sensitivity, $I/\Delta I_{threshold}$. The spatial frequency of the pattern is $1/\lambda$.

whereas the sine wave grating task involves recognition of a wide range of sizes of target elements at lower and lower contrast. However this sine wave grating task does provide the information usually obtained from the standard acuity tasks. Short wavelength patterns are detected only at high contrast; so that the detectability of small, high contrast target elements is measured by the sine wave grating task as well as by the conventional acuity tests.

All sinusoidal targets were photographic transparencies bounded by a black circular aperture 7.5° diameter. The range of spatial frequencies was 0.005 to 0.58 cycles per min arc, with gratings in between of 0.007, 0.009, 0.01, 0.015, 0.02, 0.025, 0.03, 0.04, 0.05, 0.06, 0.07, 0.08, 0.10, 0.15, 0.20, 0.25, 0.30, 0.35, 0.40, and 0.45 cycles per min arc. The bars in all patterns were oriented vertically.

The maximum and minimum density of each slide was determined by projecting each slide at a magnification of about 30x onto a screen in the plane of which was situated a photomultiplier cathode. The cathode was masked except for a 1x10 mm slit oriented parallel to the projected bars. The voltages corresponding to maximum and minimum target density were measured at the photomultiplier output for all slides. These voltages were matched by substituting calibrated Kodak neutral density filters for the target in the projector. Target density could be estimated to the nearest 0.03 log unit by interchanging neutral density filters which differed by 0.1 log unit.

Retinal luminance was calibrated by aiming an S.E.I. photometer into the telescope of the optical apparatus and reading the

luminance with no target in the system. Together with the slide density measurements this provides enough information to calculate the mean luminance and modulation of the output pattern - provided that the optical system itself does not degrade the image. Although this last point was not checked in detail, several of the high spatial frequency gratings were imaged through the system, and the output image was examined at about sixfold magnification through a telescope. No loss in the modulation of the image could be observed when this pattern was compared with that of the same target imaged through a high quality dissecting microscope at sixfold magnification. With large diameter achromatic lenses and coated optics throughout the system it is doubtful that the optical system diminished the modulation of the targets significantly.

The density profiles across the sine wave gratings were measured on a microspectrophotometer. These were all smooth sine-like curves with a maximum deviation from sinusoidal of approximately 25 per cent of the peak to peak amplitude. All deviations from a true sinusoidal trace were of a logarithmic nature, due to the logarithmic response of the film used in making the targets.

An important property of these targets from a theoretical point of view is their spectral purity, i.e., the degree to which the Fourier Transform of the density profile approximates a delta function. This is a function of the width of the target; the wider the target, the more pure the spectrum. An analysis of the spectrum of the gratings, and the effect of the 7.5^{o} aperture, is given in Appendix II.

The other target types used in this experiment are of a more traditional nature. A 15x15 array of Landolt C's, shown enlarged in Fig. 4-5, was used. The entire array was reduced photographically and the negative projected in the stabilizing apparatus. The degree of reduction was varied to give gaps between the ends of the C of 1, 2, 2. 5, 3, and 4 min arc. The subject saw high contrast black C 's on a white, featureless background, and was asked to tell the orientation of a particular C, identified by its coordinates in the array. Each slide could be projected in eight different orientations, so no subject was able to memorize the array.

Two less versatile target types were used. A standard Snellen chart was reduced and each line made into a separate transparency. The reduction factor was such that the angular size of any letter when viewed through the apparatus was identical to the angular size of the letter when viewing the actual chart from 20 feet away.

Lastly, two square notches 4 min arc wide and 4 min arc deep were machined in a 29 min arc diameter lead sphere (#8 shotgun shot) and the sphere mounted on an insect pin. The insect pin could be rotated by the experimenter so that one of the notches appeared in the black disc seen by the subject in one of three positions, top, bottom or side of disc. The subject's task was to identify the position of the notch.

Degree of Stabilization: To test whether scanning improves acuity it would be desirable to reduce retinal image movement to less than one receptor diameter. This is impossible with any system which monitors eyeball movement and moves the target a corresponding

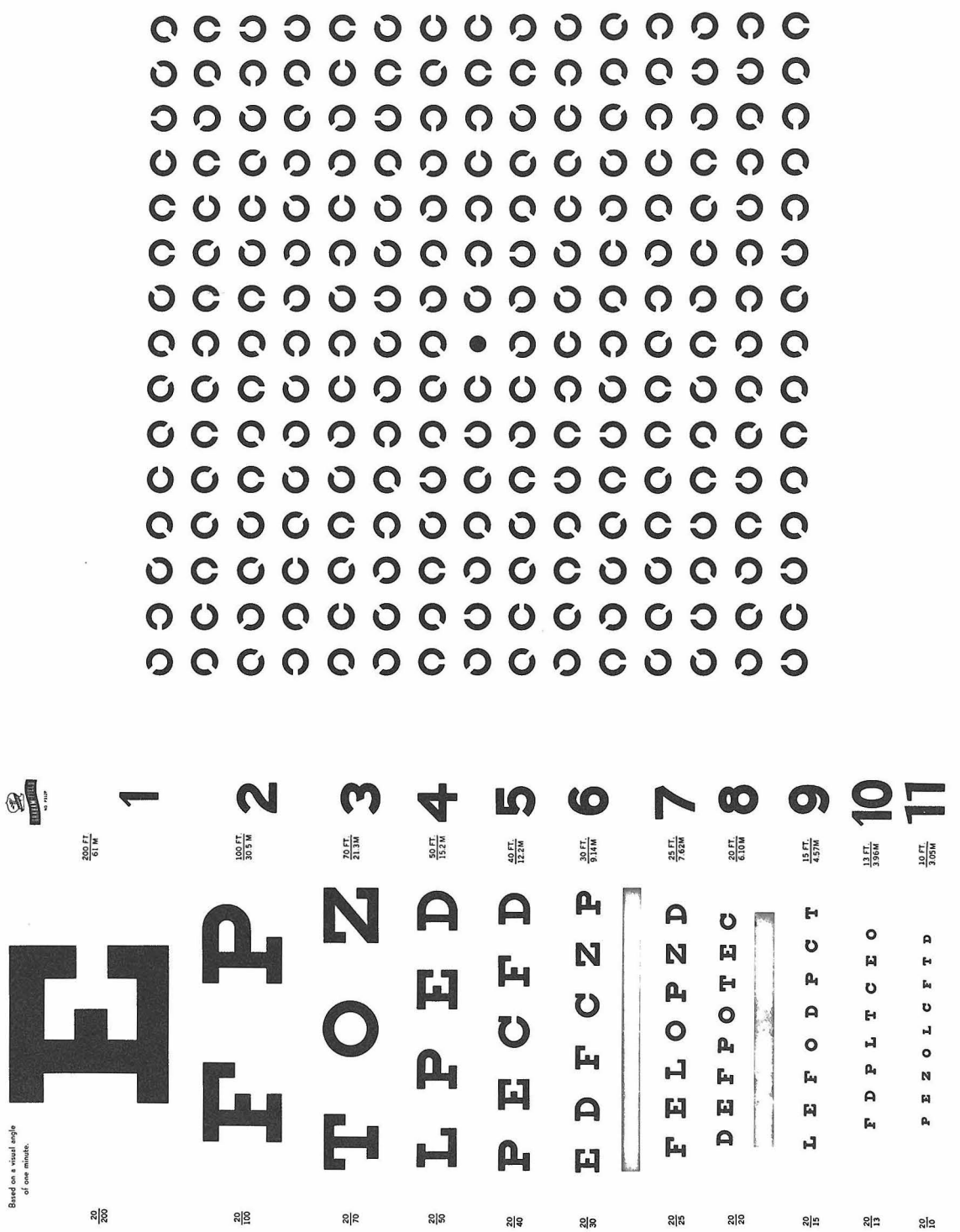

Fig. 4-5 Landolt C and Snellen chart targets.

distance, because the eyeball and its components do not have this degree of rigidity. One could make the acuity measures on afterimages, which presumably are stabilized perfectly on the retina or cortex, but this course is both technically and conceptually hazardous. Subjective decisions during acuity tasks require time, and in the normal case there is a constant flux of light into the receptors during this time. Any acuity mechanism which relies on a time average of light flux into the receptors - with or without scanning over space - would be stymied by an afterimage type of acuity test, which entails an abnormally bright and brief surge of energy into the receptors. In support of this hypothesis, Keesey (20) has shown that humans require an exposure of at least 200 msec in order to attain maximum acuity. The other difficulty is that afterimages appear only intermittently unless an extremely bright flash is used, bringing up the question of which afterimage should be used to measure acuity, and from this, the unsettled question of the nature of afterimages and their relevance to normal visual input. For these reasons, we chose to have the target image continuously present on the retina, and stabilized within the bounds described next.

Two factors cause most of the errors in stabilization in the optical system described in Chapter 2. The first is slip of the contact lens over the eyeball, and the second is error in alignment of the optical system or aberrations of its components. Movement of the subject's head, within the limits of the head restraining apparatus, lead to only minimal amounts of destabilization. Slippage of the lens, as described in Chapter 2, consists of the lens moving 96.3 per cent

of the distance the eye moves, plus an additional lag during flicks of roughly 3 min arc.

The optical system, as also described in Chapter 2, has 97.5 per cent compensation in the central 4^{o} field, and 96 per cent compensation over the central 6^{o}. The total field of the apparatus is slightly in excess of 7^{o}, however the peripheral degree of the field is useless for acuity judgements due to the excessive aberrations in this region. Unfortunately, both lens slip and residual errors in the optical system move the target in the same direction over the retina. The resultant movement of the image over the retina, as calculated from these objective measurements, is less than 7 per cent of the net eye movement, with a transient 3 min arc error introduced by flicks. It should be emphasized that final adjustment of the optical system was made by each subject, using subjective criteria for the degree of stabilization, e.g., rapidity of fading, appearance of high contrast edges of the target during eye movements, etc. The above estimates of optical system error are the average errors measured by replacing the eye with a telescope after two subjects had performed such adjustments. Thus the stabilization error referred to above is subjectively the minimum error, and objectively less than 7 per cent of the excursion of the eye from the center of the field.

In addition to the above precautions, subjects were asked not to base their decisions on the appearance of the target following blinks or large saccades. The final stringent requirement on the subject's eye movements was that he should restrain them so as to keep the stabilized target as nearly centered in the field as possible.

The net effect of these restrictions was to force the subject's decisions to be made while his visual axis traversed an area approximately 30 min arc in diameter. This permits a 2 min arc maximum steady error and a 3 min arc transient error following flicks. The steady error is thus 4 foveal inter-receptor spaces, and consequently well within the tails of the point spread-function, thus insuring that the maximum change in receptor potential due to lens slip is less than 2/3 of the maximum difference between any two receptor potentials.

Control of Mean Luminance: During all of the following experiments mean target luminance was held constant at 80 cd/m^2 by means of an electronic feedback system. The target luminance was integrated over space by focusing the target beam to a point on the photomultiplier as shown in Fig. 2-5. The output voltage of the photomultiplier was amplified, level shifted, and finally used to power a speaker coil which moved an opaque vane across source aperture A'. By appropriate manipulation of the coil position and the variable level shift, the null point of the servo could be varied so that a mean target luminance of 80 cd/m^2 could be obtained. Before each experiment these settings were twiddled to make the mean target luminance, as photometered through the eyepiece of the optical system, match an S.E.I. photometer reference level of 1.37 log ft. lamberts, which is equal to 80 cd/m^2.

With this feedback system operating, the maximum excursion of the mean target luminance from its initial setting was within 10% of its initial level in all experiments. This was determined by

monitoring the photomultiplier output on an oscilloscope during all experiments; noting the maximum excursion of the trace from the initial level; and, upon completion of the experiment, photometering the target luminance which matched this maximum excursion. Therefore mean retinal luminance was 80 $\pm$ 8 cd/m^2 during all experiments.

During one of the experiments the target beam was chopped in square wave fashion at 1 cps by a vane riding on a speaker coil. This implicates the frequency response of the feedback system. No brief flashes were observed with this chopping system, because both chopper and feedback system had similar risetimes of about 15-20 msec. The limiting factor in the time response of both was the speaker coil movement, and both chopper and feedback system employed identical speaker coils, driven by identical power amplifiers.

Experiment I: Rapid Comparison of Stabilized and Normal Targets

The initial experiment was direct and non-quantitative. The subject was asked to report verbally whether or not he could detect any change in his resolving ability or in apparent contrast as he switched between normal and stabilized vision. The subject controlled a switch which caused alternate blockage of normal and stabilized optical paths, and he was free to push it as often or whenever he wished. He was further asked to ignore fading effects in stabilized image presentations, and to base his decision on his

resolving ability prior to the onset of fade out.

Four subjects, all with three or more hours experience in viewing stabilized targets, were tested in this manner. Two subjects (DSG & GSC) were tested with all four types of targets; the remaining two were tested with gratings only. With ball and Snellen targets, only the center of the subject's visual field was tested. Targets in the periphery produced anomalous responses which are discussed in Chapter 5, and are not relevant to the question at hand. In testing with grating targets, the experimenter slowly lowered optical wedge W, which lowered the modulation of the target. Simultaneously the feedback system would raise W' in order to keep mean retinal luminance constant. As the contrast was lowered, and particularly near threshold contrast, the experimenter would stop changing the contrast and ask the subject whether he could detect any loss of acuity in stabilized vision. A similar procedure applied to ball and Snellen targets.

All subjects' replies were negative. None could discern any loss of acuity in stabilized vision, regardless of target used or state of contrast. All reported similar fade out effects, but in the few seconds prior to these effects, acuity - as reported subjectively - was unimpaired.

Although this experiment was notable for the unaniminity of the opinions expressed; two factors make it subject to question. First, although optometrists rely on this sort of subjective comparison of acuities in the fitting of eyeglasses, it gives no objective proof, thus it would be desirable to measure normal and stabilized

acuities independently, and to compare them objectively - instead of subjectively as in this experiment. Second, there is the possibility that the subject relies on some form of memory of the target as seen in normal vision and bases his decision on this in the few seconds between onset of stabilized vision and beginning of fade out. These uncertainties are remedied in the following experiment.

Experiment II: Independent Measures of Stabilized and Normal Grating Acuity

In this experiment, threshold amounts of modulation were measured for two subjects (PWN & GMM) in both normal and stabilized vision, over the full range of grating wavelengths. Stabilized and normal observations were presented in random order, and the different targets were presented randomly as well. Four determinations were made of each threshold - a process which required four separate 40 minute experimental sessions per subject, at most one per day, over the course of a week.

To measure the modulation at threshold, the experimenter slowly lowered the modulation by lowering wedge W until the subject pressed a key which turned on a light near the experimenter. At this point the experimenter recorded wedge position, and then raised the modulation slowly until the light was turned off, when he again recorded wedge position.

The subject was instructed to press the key when he could no longer see the pattern, and to release it when it reappeared. To assist the subject to establish stable criteria of disappearance and

reappearance, a trial run was made with each pattern, under both normal and stabilized conditions. No data were taken on trial runs. When combined with source intensity and target modulation data, wedge position gave the % modulation of the target pattern. The arithmetic average of the two modulations selected by the subject was defined as the threshold modulation.

Targets were at least one log unit above threshold modulation at the beginning of each trial, and one trial required between 20 and 40 sec to complete. Subjects had ten minutes to adapt to the mean target luminance at the start of each session. The experimental room was kept darkened during the entire session.

Results - Experiment II: Normal and stabilized results for subject PWN are shown in Fig. 4-6; those for subject GMM are plotted in Fig. 4-7. The reciprocal of threshold modulation, sensitivity, is plotted against the spatial frequency of the target. Each point represents the mean of four measurements. The standard deviations associated with these measurements are also shown.

The hump shape of all curves is significant, and agrees well with other investigations of acuity for sine wave gratings in normal vision (23, 24, 25), as well as estimates of this acuity derived from results of other acuity tests (26, 27). Simply put, the hump shape means that acuity is greatest for bars approximately 17 min arc apart and falls off for bars either farther apart, or closer together. Later in this chapter we shall relate this to neural interactions in the visual system.

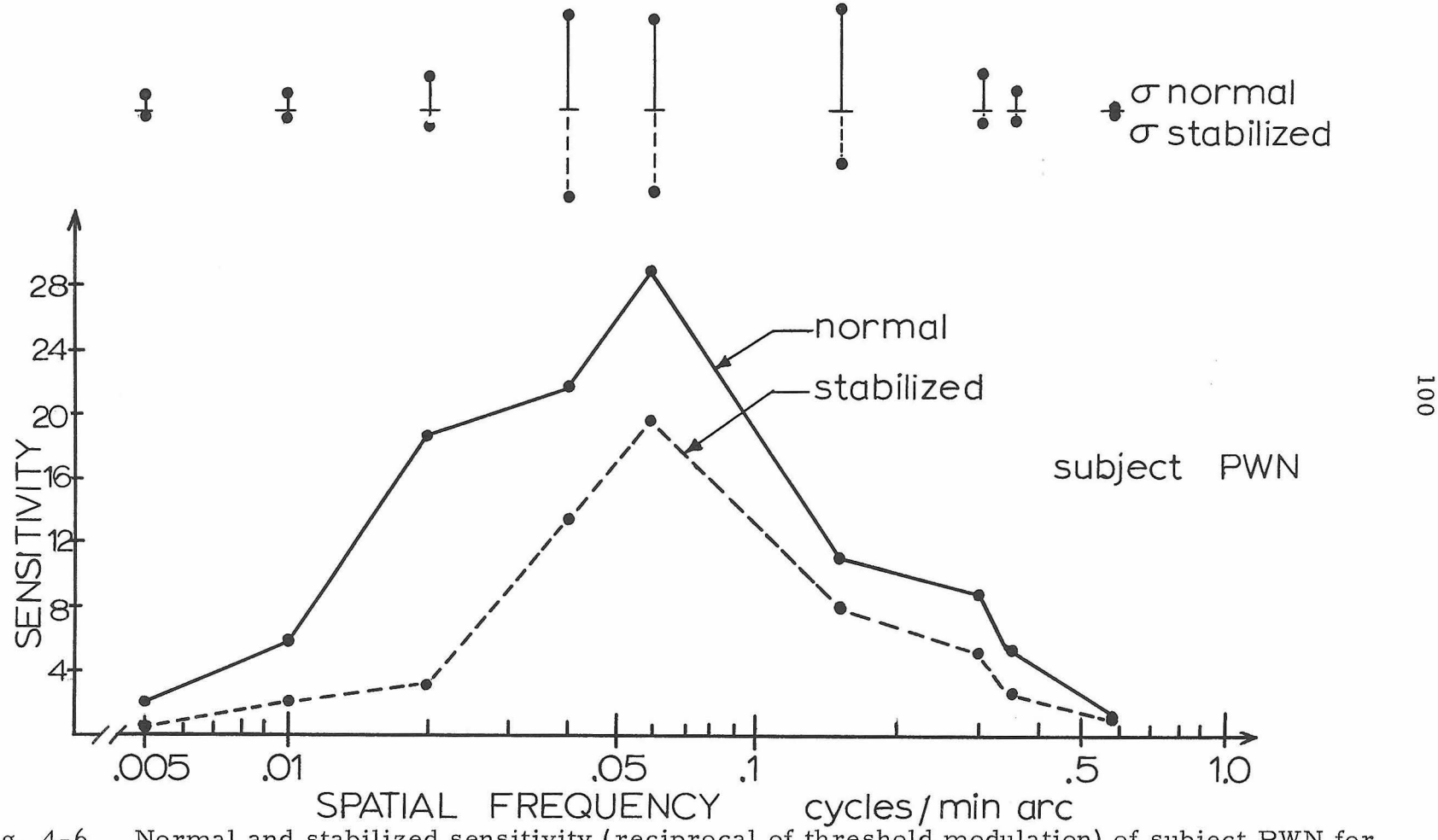

Fig. 4-6 Normal and stabilized sensitivity (reciprocal of threshold modulation) of subject PWN for sine wave gratings of various spatial frequencies. The mean of four determinations is plotted, and the standard deviation associated with each point is represented by the length of the bar above that point.

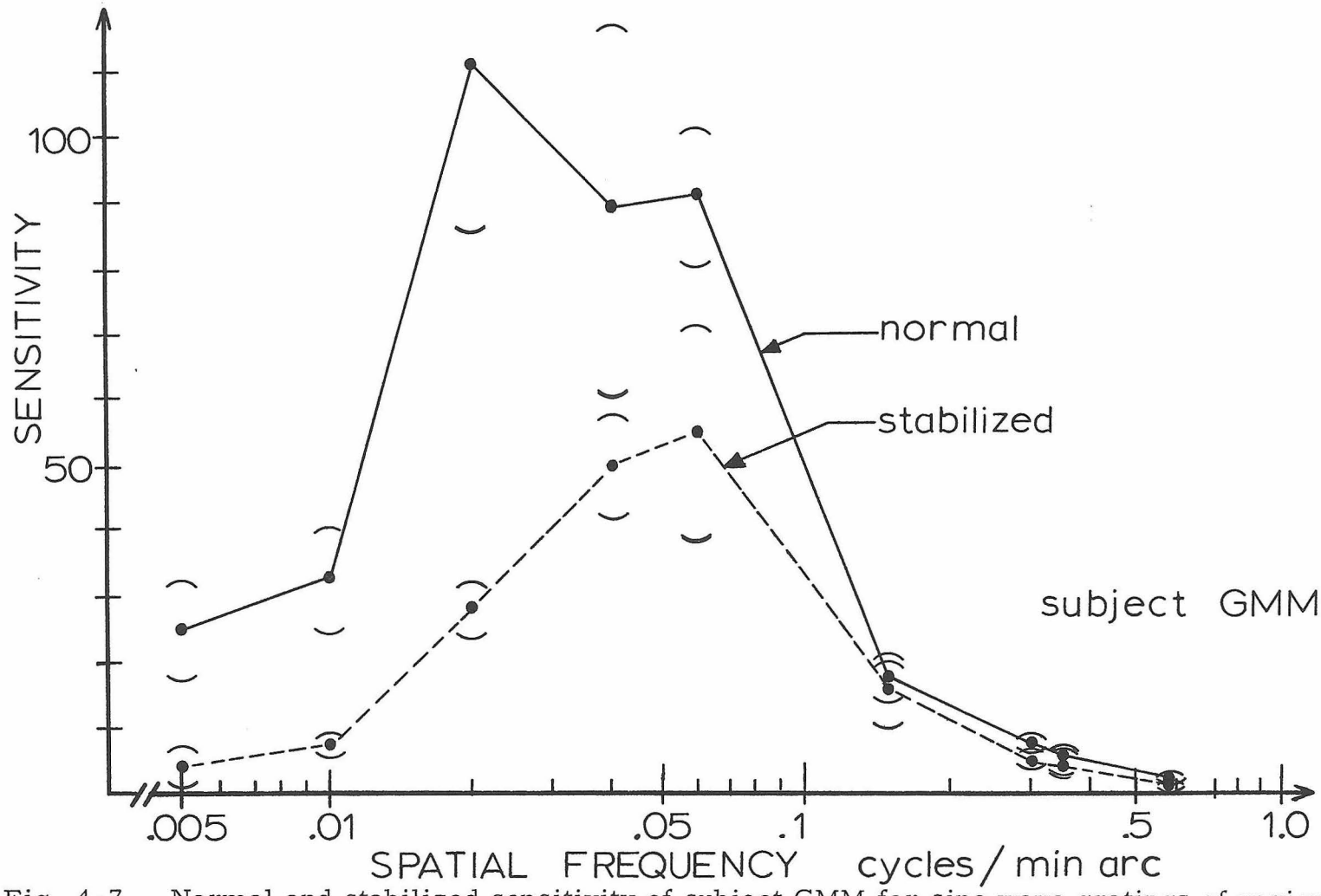

Fig. 4-7 Normal and stabilized sensitivity of subject GMM for sine wave gratings of various spatial frequencies. The mean of four determinations is plotted as a point, and magnitude of the standard deviation associated with each point is represented by the distance from the point to the parenthesis above or below it.

Inter-subject variation in the absolute height of the curves means they chose different criteria for appearance and disappearance of the target. No attempt was made to control or manipulate these criteria, since all that is required to answer the point in question is a set of criteria which does not change between normal and stabilized observations.

Both plots show that stabilization significantly and consistently diminishes sensitivity, especially for targets below .05 cycles/min arc. The average over all targets of the difference between the log of normal mean sensitivity and the log of stabilized mean sensitivity is 0.28 for PWN and 0.36 for GMM, that is, there is a 2.8 db gain in sensitivity for PWN provided by eye movements, and a 3.6 db gain for GMM. For the four lowest spatial frequency gratings the apparent gain provided by eye movements is much greater: 4.5 db for PWN, and 5.5 db for GMM.

Some explanation of the diametrically opposite results of this and the previous experiment is in order. The first possibility considered was that 5 db changes in modulation of sine wave gratings, in the threshold region, could not be detected by the subject in the rapid comparison scheme of experiment 1. This was tested with GMM, and he could easily detect a 5 db modulation change in a slightly supra-threshold .01 cycle/min arc grating. Modulation of the grating was changed during a three second interval between normal and stabilized observations. No controlled observations were made with smaller modulation changes; although the subject did indicate that he could distinguish 2 db modulation changes, but nothing smaller.

The alternate explanation of the conflicting results of these two experiments is that fade out effects caused spurious responses in the second experiment. Since each trial required some tens of seconds to complete, and since stabilized fade out both increases with time and lowers stabilized sensitivity in this experimental design, fade effects alone could cause the discrepancy. Further, both subjects agreed that fade effects were pronounced when viewing low contrast gratings, and that the apparent target behavior, e. g. , its rapid reappearance or disappearance, indicated to them that fade effects played a considerable role in their responses.

In summary, this experiment shows that stabilization causes a slight but significant loss of visual acuity, especially for the wider bar patterns. Fading effects were, however, not eliminated. The next experiment deals again with measurement of grating acuity, but, this time with several precautions against fading effects.

Experiment III: Independent Measures of Flickered Normal and Stabilized Grating Acuity: To eliminate these interfering fade effects two changes were made in the above procedure. The subject was given control of wedge position so that he could raise or lower target modulation at the rate best suited to eliminate the effects of fading from his decisions, and so that he could return to any modulation level to check himself. The knob controlling wedge position turned through about 15 revolutions in the course of any one trial, and the starting position of the knob was varied randomly by the experimenter from trial to trial, thus there was negligible knowledge or memory on the part of the subject of absolute wedge position.

The other major change in experimental procedure was to flicker the target beam, since this results in the temporary abatement of fading effects. A vane was moved in and out of aperture A in Fig. 2-5 near the source of the target beam, in square wave fashion, at 1 cycle per second by a speaker coil similar to that in the feedback circuit. The target beam was thus totally occluded every other second; although the mean luminance seen by the subject remained constant due to the compensatory oscillation of the feedback circuit. Although this did not eliminate fading completely, the first few hundred milliseconds of the target-on part of the cycle were relatively free of fading effects. The target was flickered in the same manner during determinations of acuity in normal vision.

Acuity Sans Temporal Modulation: In flickering the target to obtain objective measures of acuity, uncontaminated by fading effects, we have sacrificed the answer to one question, that is, whether or not the mechanisms determining acuity can do without any temporal modulation of the light flux into the receptors. This important possibility merits a slight digression.

The major piece of evidence that acuity mechanisms are able to operate with no temporal modulation of the light flux into the receptors is that faded stabilized images spontaneously regenerate from time to time (14, 16, 28). In direct conflict with this result are other investigations (29, 30, 31), carried out for the most part with suction type lenses, which conclude that any regeneration of a "stabilized" image is due to destabilization caused by lens slippage.

Pritchard (31) reports that flick amplitude is highly correlated with both time to fade and time to regenerate, i.e., the larger the flick the longer the time needed for subsequent fadeout or the shorter the time needed for subsequent regneration. He also states that the subject's impression, while viewing a stabilized image, is that regeneration is commonly accompanied by a discernible eye movement. Since lens slippage also increases with flick amplitude, the implication is clear.

The apparatus described in Chapter II yields for two subjects (DSG & GSC) intermittent regeneration of stabilized images. The same subjects had been previously tested for lens slippage; their results are reported in Chapter II. The subjects were tested to determine the cause of this regeneration. Both observed the foveally fixed ball target in stabilized vision during three successive two minute long runs, while their eye movements were simultaneously recorded. They were instructed to motionlessly fixate the target and press a button for the duration of each fade out. Four inches of water suction was applied to their lenses. Ball contrast was lowered slightly to assist fade out. The mean target luminance was 80 cd/m^2.

Results of 19 regenerations for subject GSC, and of 43 regenerations for DSG are shown in Fig. 4-8. It will be seen that the probability of a flick occurring .5 to .75 sec before regeneration is abnormally large for subject GSC, and that the same holds for subject DSG in the interval .75 to 1.0 sec before regeneration. Both subjects estimated their reaction times to lie between .5 and 1.5 sec in this subjectively rather difficult task. When combined with the

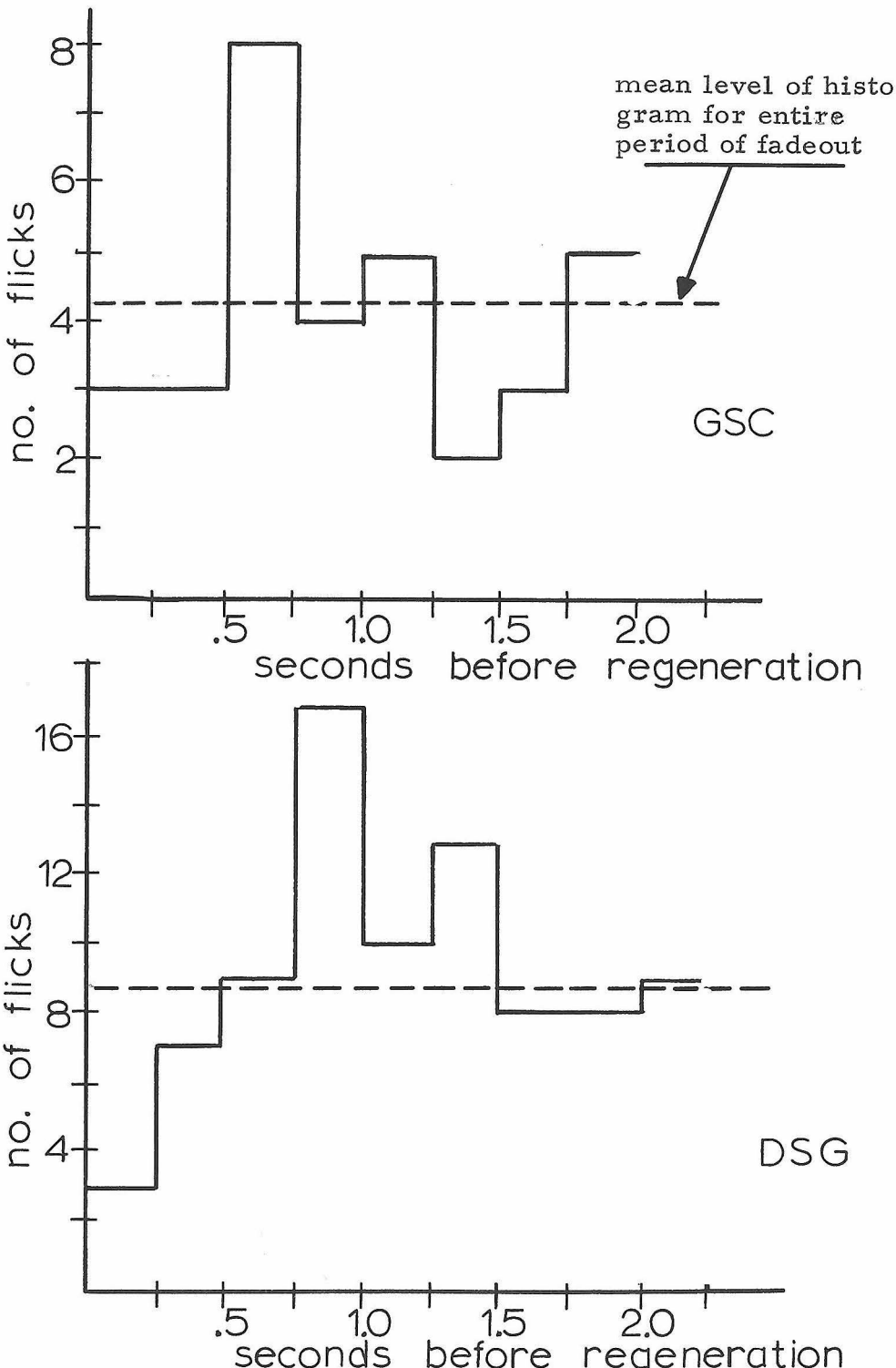

Fig. 4-8 Histograms of the number of flicks, greater than 5 min arc in their vertical components, occurring just prior to the subject's report of regeneration of a faded, stabilized image. All blinks caused report of regeneration within 0.75 sec. Neither fadeouts ended by blinks, nor fadeouts less than 4 sec duration are included above.

observations that GSC had a mean interflick interval during fade out of 1.1 sec while DSG had a mean interflick interval during fade out of 1.2 sec, and that lens slippage during a flick is on the order of 3 min arc, the results of Fig. 4-8 indicate that a single flick occurring a reaction time before report of regeneration causes sufficient lens slippage to bring the target back into view. Both subjects in a separate sentient fixation trial also confirmed Pritchard's assertion that regeneration is commonly accompanied by discernible eye movement.

The above observations, together with those in the references cited, shift the burden of proof onto those who would argue that acuity mechanisms can operate without considerable temporal modulation of the light flux into the receptors.

The normal scanning motions of the eye put a temporal modulation into the receptors which is dependent upon the retinal image geometry, that is, the target shape, as well as the velocity and direction of eye movements. In this experiment, assuming for the above reasons that temporal modulation is necessary, we replaced this sort of information-packed temporal modulation with a simple 1 cps on-off square wave, which contains no information about either target shape or velocity of eye movements. One cycle per second temporal modulation was chosen since Keesey (20) has shown that grating acuity determinations could be accurately carried out in less than a second, and since this frequency is conducive to elimination of fading.

The object of this experiment, then, is to test whether or not the normal, information-packed, temporal modulation of the

receptors is necessary in making judgements regarding visual acuity.

Conditions of Experiment III: In summary, the experimental conditions for experiment III were these: 15 sine wave gratings, with spatial frequencies from .005 to .58 cycles per min arc, all fitted in a 7.5^{o} diameter opaque circular mask, were projected into the subject's left eye (natural pupil) with a mean target luminance of 80 ± 8 cd/m^2. In each trial modulation was set initially one or more log units above threshold. The subject then lowered the modulation at whatever rate he desired, usually in less than a minute, until he signalled the experimenter to record below-threshold modulation. The subject then raised the modulation and, in a similar manner, signalled the experimenter to record above-threshold modulation. The instructions to the subject were to reduce contrast until the grating disappeared, then to raise contrast until it reappeared, keeping constant criteria for each of these decisions. He was further instructed to refrain from large eye movements and blinks, and to base no decision on the appearance of the target following such an eye movement. Target spatial frequency and condition (normal or stabilized) were randomized, although all targets appeared in both conditions during a single session. The subject wore the contact lens with 9" H_2O suction during both normal and stabilized determinations; the only change between the two conditions was that the stabilized image beam was occluded by S''' in Fig. 2-5 and the normal image beam was opened by S''. The two beams were equivalent in position on the exit pupil, in mean luminance, and in target modulation. The

stabilized beam was centered by the subject on his retina. In both conditions the target appeared every other second, remained on for a second, and was replaced by a featureless grey field of the same mean luminance. Stabilized patterns were adjusted by the subject until he considered himself to be fixating the center of the pattern. The phase of the sinusoidal luminance with respect to the center of the pattern varied from target to target.

Experiment III Results: The results of ten trials in each condition for each spatial frequency are shown in Fig. 4-9 for subject DSG. A similar plot for subject GSC is shown in Fig. 4-10. The average sensitivity is plotted against spatial frequency of the target, for both normal and stabilized conditions. The bars above each point of the normal and stabilized curves show the standard deviation associated with each average. That is, the average of ten sensitivity measurements is plotted as a point, and the standard deviation of these measurements is equivalent to the length of the bar above that point. Finally the number next to each bar is a measure of the probability that the true normal and stabilized mean sensitivities are equal for that particular spatial frequency. More simply, the number is the probability that normal acuity is equal to stabilized acuity for one particular pattern. These probabilities were derived using the paired variates t test (ref. 32, p. 91). Both subjects observed that residual fading effects were still present, even with the flickered target.

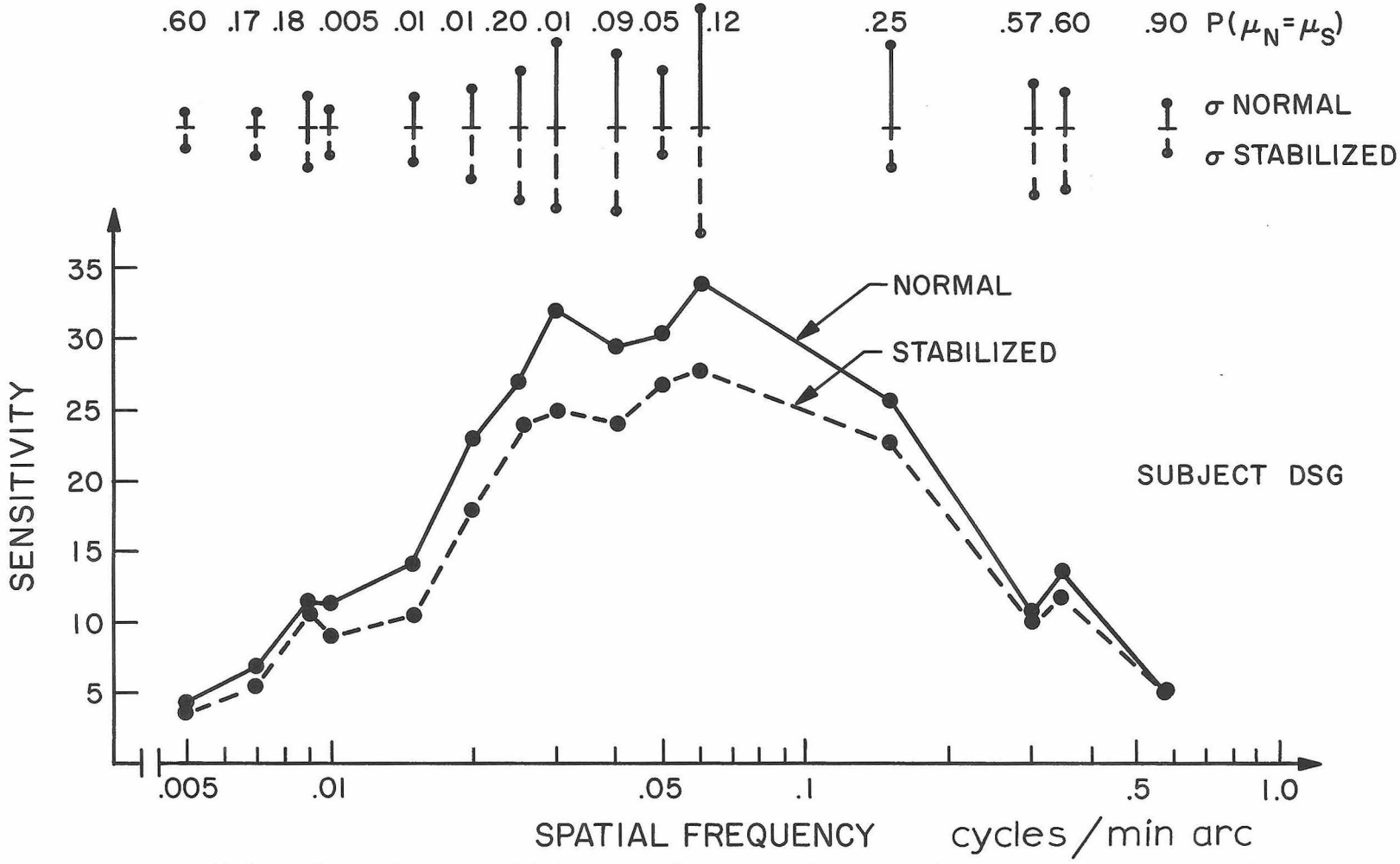

Fig. 4-9 Flickered grating sensitivity as a function of spatial frequency for subject DSG. Each point represents the mean of ten determinations. The standard deviation of the determinations is represented by the length of the length of the bar above each point. Probabilities that the means of normal and stabilized distributions are identical are given above the standard deviations.

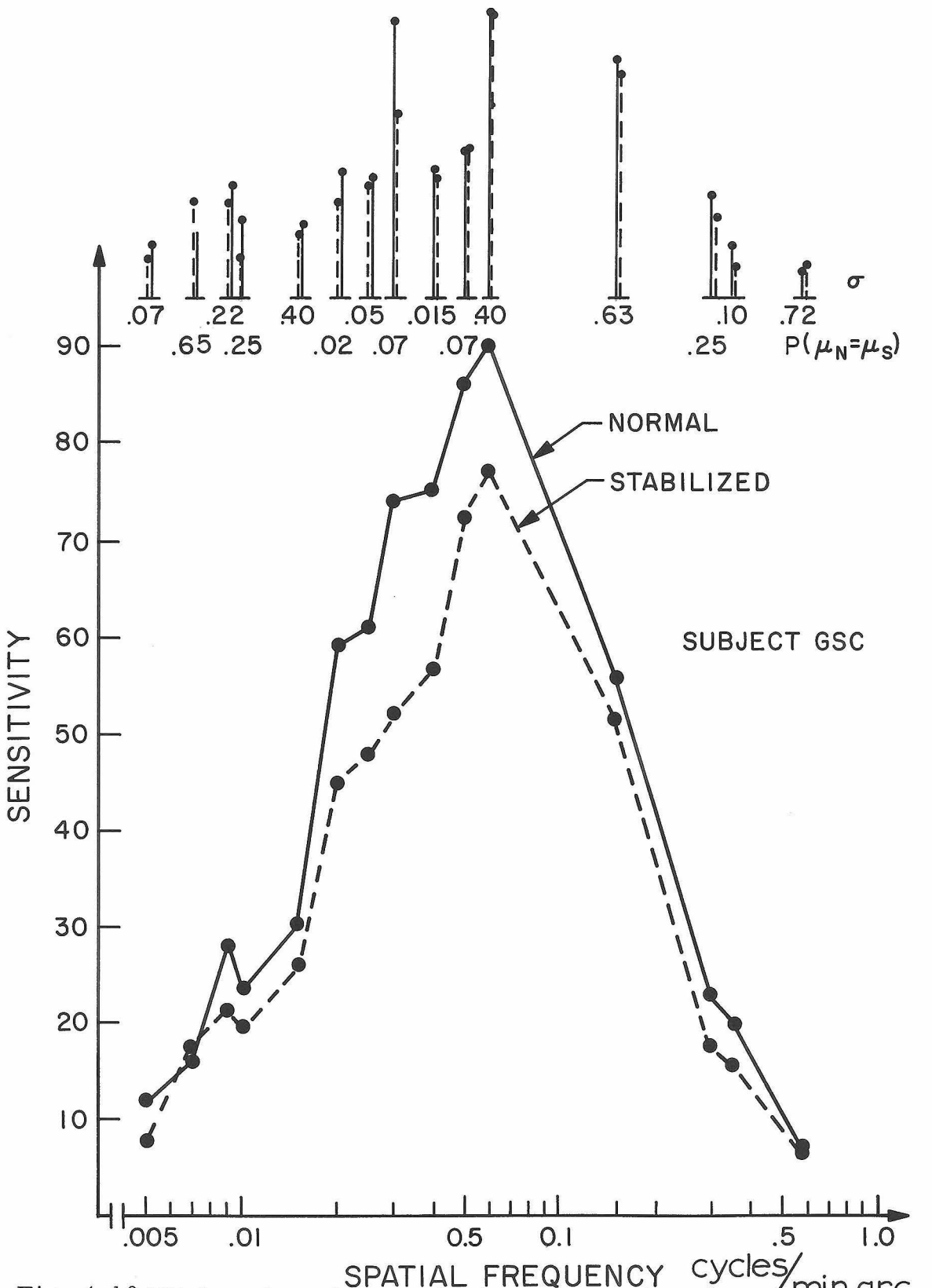

Fig. 4-10 Flickered grating sensitivity as a function of target spatial frequency for subject GSC.

Discussion: Except in one case (GSC, .007 grating) mean stabilized sensitivity was always less than mean sensitivity in normal vision. No particular significance is attached to the slight ripples in any curve, since these are within the error limits of the target density measurements.

Likewise the difference between subjects in absolute level of the sensitivity curves is attributable to the different criteria adopted by the two subjects. DSG reported disappearance when the pattern lost its sinusoidal characteristics, whereas GSC reported disappearance when no systematic fluctuations in luminance were visible. Further criterion definition is a lengthy process and will be omitted; the salient fact is that two essentially different criteria yield data which, aside from a level shift, are nearly identical, and produce similar ratios of normal to stabilized acuities.

Does stabilization reduce acuity? As drawn, the curves imply that it does. When the standard deviation of each point is considered, however, it is evident that stabilization reduces acuity only slightly at most. For subject GSC, only three of fifteen targets give rise to a discrepancy of more than one standard deviation between normal and stabilized sensitivities. If the t test results are averaged over the two subjects, then only three targets (.02, .03, .04 cycles/min arc) have sensitivity means significantly different at the 5% level, and none are significantly different at or below the 1% level.

For both large and small wavelength patterns stabilization impairs acuity least, leaving only the middle region - bars 5 to 12 min arc wide - whose percept is affected by stabilization. Two

additional facts suggest a reason for this strange phenomenon. In an independent experiment, the time required for a stabilized image to fade out was measured. Subject DSG was presented with each of the sine wave gratings, each at its mean, normal vision, threshold modulation, with no flickering of the target. The average of four trials per target, plotted in Fig. 4-11, show that time to fade increases from 8 to 20 sec as the target spatial frequency increases from .005 to .15 cycles per min arc. Spatial frequencies higher than this did not fade out in 1 minute.

The other fact is that the low spatial frequency patterns were extremely difficult to judge subjectively. With five bars or less in the pattern, it was difficult to set a stable criterion for disappearance or reappearance of the pattern. This was reflected in the large standard deviations of the measured threshold modulations of low frequency patterns. The point is obscured in Fig. 4-9 and Fig. 4-10 because the reciprocal of threshold modulation, sensitivity, is plotted.

These facts lead to the following interpretation of the results plotted in Figs. 4-9 and 4-10. At the lowest spatial frequencies the primary difficulty is establishing a stable set of criteria. This leads to a greater variance in the results than even the rapid fading which takes place with these targets. The result is no significant difference between normal and stabilized curves in this region. With spatial frequencies above .015 cycles/min arc there are 5 or more bars in the target, and the decision regarding appearance of the target is carried out much more reliably by the subject. However, fading

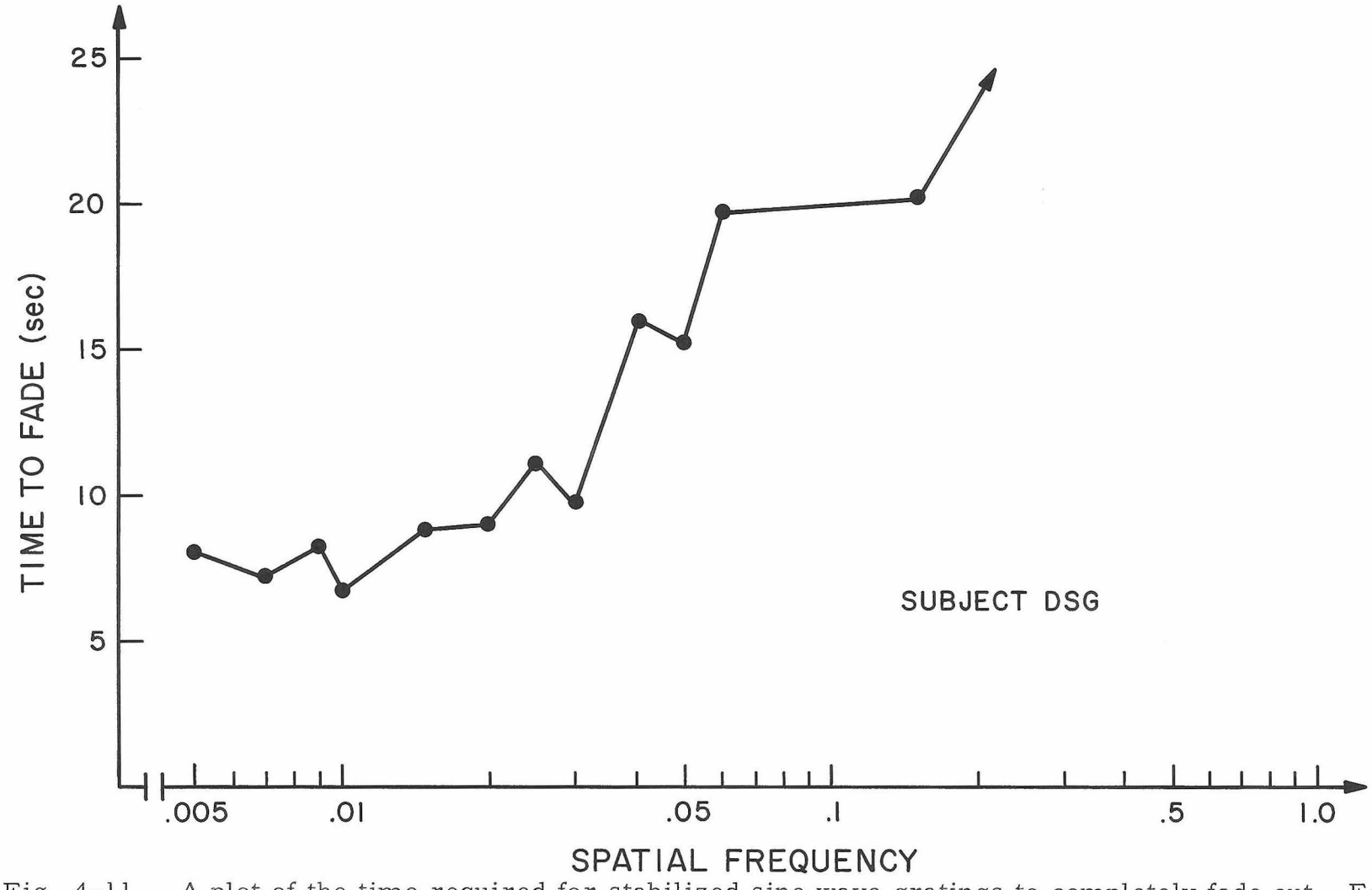

Fig. 4-11 A plot of the time required for stabilized sine wave gratings to completely fade out. Each point represents the mean of four determinations. Each grating was set to normal vision threshold modulation, and 80 cd/m^2 mean luminance.

still occurs rapidly, leading to maximal influence of fading effects on acuity judgements for spatial frequencies between .01 and .06 cycles/min arc, the very interval in which both subjects have significantly different normal and stabilized sensitivities. Targets with spatial frequencies above .06 cycles/min arc fade out slowly, leading to less and less contamination of the results by fading as the spatial frequency increases. Correspondingly the difference between normal and stabilized curves becomes less and less significant as spatial frequency increases. Thus it appears that the residual fade effects noticed by both subjects are a major cause of the difference between normal and stabilized sensitivities, particularly for the intermediate spatial frequency patterns.

Further evidence for this point comes from a comparison of flickered and unflickered sensitivity curves. If the effect of flicker on grating acuity is solely to reduce stabilized fade out, as seems likely, then reduction of fade out brings normal and stabilized sensitivity curves much closer together. The average difference between normal and stabilized mean sensitivities with the unflickered gratings of experiment II was 3.6 db for one subject, and 2.8 db for the other. With flickered gratings these factors are reduced threefold to 0.9 db and 0.7 db. Complete elimination of fade effects, these figures clearly imply, would result in equal normal and stabilized sensitivities, in accordance with the results of the first experiment.

Conclusions: Stabilization reduces sensitivity by, at most, 0.1 log units. There is reason to believe that even this small reduction is

attributable to fading effects, as explained above. When the results of experiment I and III are taken in conjunction, it is evident that the neural mechanisms determining both absolute resolving power, with high spatial frequency gratings, Snellen targets, and Landolt C's, as well as discernment of larger patterns, e. g., low spatial frequency gratings, rely minimally or not at all on the scanning effects of eye movements. Conversely, eliminating the scanning effects of eye movements does not increase the effectiveness of these mechanisms.

Aside from testing with a more general class of patterns the hypothesis that eye movements improve acuity, the other aim of this endeavor was to relate neural and optical forms of blur in the human visual system, and, in particular, to derive a measure of lateral inhibitory effects among the neurons of the retina and brain. These topics are treated in the following section. They are of interest not only in their own right but also because they provide further confirmation of the conclusions in this section, as well as serving as a basis of comparison for the results reported above with those of independent physiological and psychophysical investigations.

Transformations of the Sine Wave Grating Thresholds

Assumptions Underlying Sine Wave Grating Predictive Ability: In order to derive a measure of lateral inhibition from the sine wave grating results, one must make the assumption that the entire human visual system behaves in a linear, time invariant manner. Campbell (33) has tested this assumption in several elementary ways and found

it to be reasonably good. A linear optical system is one which images all sine wave grating targets into sine wave gratings, but with a characteristic loss in contrast dependent only upon the wavelength of the grating. The usefulness of this property lies in the fact that any one-dimensional target can be resolved into the sum of sinusoidally modulated components - that is to say, any target whose density varies along only in one coordinate, e.g. square wave gratings, single narrow bars, triangular wave gratings, etc., may be perfectly mimicked by a stack of sine wave gratings of carefully chosen wavelength and contrast. Thus knowledge of how all sine wave gratings are imaged by the optical system permits one to predict the manner in which any one-dimensional target is imaged by the optical system.

A strong similarity to the explanation of the usefulness of the point spread-function earlier in this chapter will be noted. There, two dimensional images were synthesized from the image of a point source; here, one dimensional images are synthesized from sine wave grating images. If the optical system is rotationally symmetric, i.e., a grating in any orientation produces, except for rotation, the same image, then these two explanations are, in fact, equivalent descriptions of the optical system. If the system is not rotationally symmetric, then a complete description of it requires responses to gratings in all orientations. The two assumptions basic to sine wave grating analysis of an optical system are analogous to those described for analysis via point spread-functions. The first assumption is that sine wave gratings are imaged by the optical system into sine wave

gratings with only, perhaps, a change in contrast and/or multiplication by a constant magnification factor. The second assumption is that of superposition, i.e., the response of the system to two gratings is equivalent to the sum of the responses to each grating alone.

For true optical systems, the "response" to an input target may be simply described by the luminance distribution across the image produced by the optical system of that target. For the human visual system there is, of course, no optical image produced at the output of the system. The response cannot be measured in the usual fashion, but nevertheless there are many responses of the system which yield information about the transfer of any target image through the entire visual system. One such response is the threshold modulation. A plot of threshold modulation vs target spatial frequency is called the modulation transfer function, or MTF. This is the response measured in the last experiment and it is the response tested for linearity by Campbell. This response he found gave an accurate prediction of the human thresholds for square wave gratings and various bar patterns. In the following we use the responses measured in the last experiment to predict the extent of lateral inhibition.

We begin by deriving the response of the total monocular visual system to a very narrow bar of light in the visual field. A narrow bar of light may be synthesized from the sum of all sine wave gratings, each with a different spatial frequency and each with the same modulation. Thus the response to a narrow bar of light may be synthesized from the sum of the responses to each of the sine wave

gratings. This summation is neatly carried out by taking the inverse Fourier Transform of the modulation transfer function. For those familiar with linear systems analysis, this is equivalent to inverse Laplace (or Fourier) transforming the system transfer function to obtain the impulse response.

Computation of the Total Visual System Line Spread-Function: Several different techniques were employed to perform this calculation. Polynomials up to and including third degree were least squares fitted to the MTF as well as to the log of this function and the antilog of the result was inverse Fourier transformed. Quadratic fits to the log of the MTF seemed to mimic best the shape of the curve. Fourier Transforms are shown in Fig. 4-12 for subject DSG. The point at x=0 is not defined by this procedure. The log of the averages of his normal and stabilized MTF's were fitted with quadratic polynomials and the delogged fitted curves were inverse Fourier transformed and scaled so that peak of the normal curve equals one. The transform is symmetric about the vertical axis, but only one half of it is depicted in Fig. 4-12. Both the normal and stabilized curves lead to similar spread-functions representing the net response of the visual system to a narrow bar of light input. Lateral inhibitory areas, i.e., areas of negative response, are in evidence beside the excitatory center. As one might expect from the similarity of the MTF curves, both normal and stabilized MTF's have approximately the same transform, indicating, within the bounds of the above assumptions, that neural processing is carried out in similar - if not identical - fashions in the two conditions.

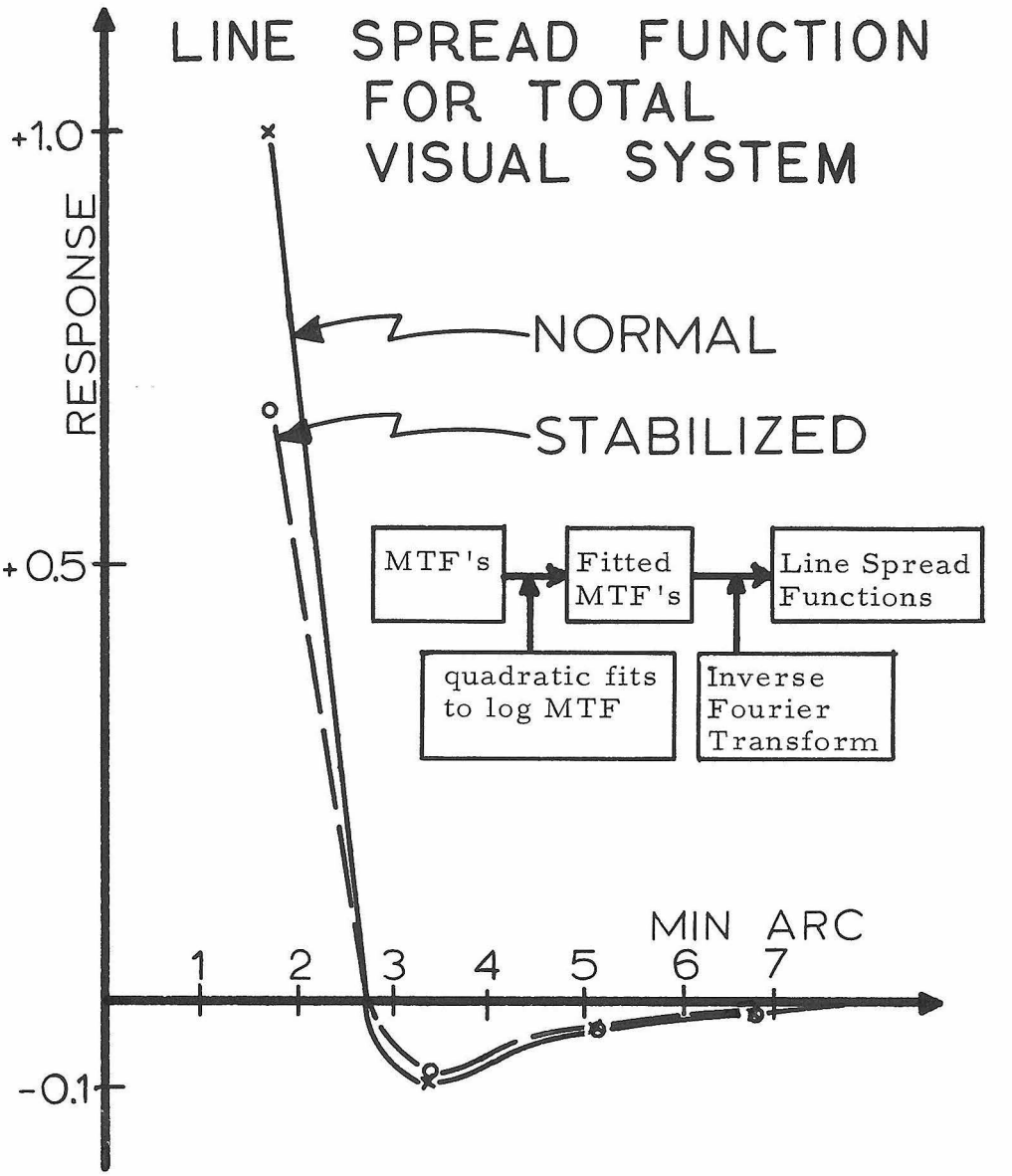

Fig. 4-12 Cross section of the response of DSG's visual system to a narrow bright line, as derived from his normal and stabilized grating acuity data. Both curves are symmetric around 0 min arc, and presumably continuous, although the acuity data do not predict response data in the neighborhood of 0 min arc. The flow chart shows the sequence of operations which produced these curves.

Definition and Computation of the Neural Line Spread-Function: The curves of Fig. 4-12 represent a transform of the response of the total visual system for truncated sine wave gratings. Thus edge effects of the pattern, and degradation of the retinal image by the optics of the eye both contribute to the final picture.

Pattern edge effects will be neglected since the pattern edges were several degrees outside the fovea. The spectral components added to the target by the presence of edges are described in Appendix II. In support of this approximation are the observations of Schober and Hilz (27),who found that target diameters greater than 1^{o} did not alter threshold modulation for a 0.05 cycles/min arc square wave grating.

Degradation by the optics of the eye may be eliminated by treating the whole visual system as a series of linear systems in cascade. Consider the entire system to consist of the target grating imaged through the optics of the eye onto the retina,and then processed by the nerves of the retina and brain. The transfer function of the entire system was measured and the transfer function of the optics of the eye was measured independently. Therefore dividing the transfer function of the entire system by the transfer function of the optics of the eye yields simply the transfer function for the part of the system of primary interest, the response of the retina and brain, called here the neural transfer function. The inverse Fourier Transform of this gives the neural line spread function, i.e., the neural response to a narrow line of light directly on the retina, and this result, at long last, has some physiological substance.

The neural line spread-function, it must be emphasized, does not necessarily reflect the spatial array of nerve activity in the retina or in the brain when a line is imaged on the retina; rather it represents only the processing of what was once the spatial array of light on the retina. But in fact a large part of this processing does occur in the retina, and is so spatially localized that the array of nerve activity does indeed reflect the shape of the neural line spread-function. Therein lies the physiological substance of the end product of this grueling series of transformations.

The mathematical manipulations necessary to calculate the neural line spread-function were carried out by a series of digital computer subroutines written by the author. The transfer function of the optics is estimated by the analytic function derived in Appendix I. This must be divided point by point into the MTF and the result inverse Fourier transformed. The results of this calculation are shown in Fig. 4-13, again for subject DSG, and again using a quadratic fit to the log of the MTF. The peak value is undefined by this calculation as well, so the normal and stabilized neural spread-functions are normalized by scaling their values at 1.7 min arc to unity, as was done in Fig. 4-12.

The lateral inhibitory area is noticeably less extensive, but its magnitude is increased, when blurring by the optics of the eye is eliminated by the above procedure. Slight changes in the shape of the MTF lead to oscillation of the neural spread function with diminishing amplitude out to 5 min arc, thereafter the response is negligible for both conditions. Normal and stabilized MTF curves of three subjects

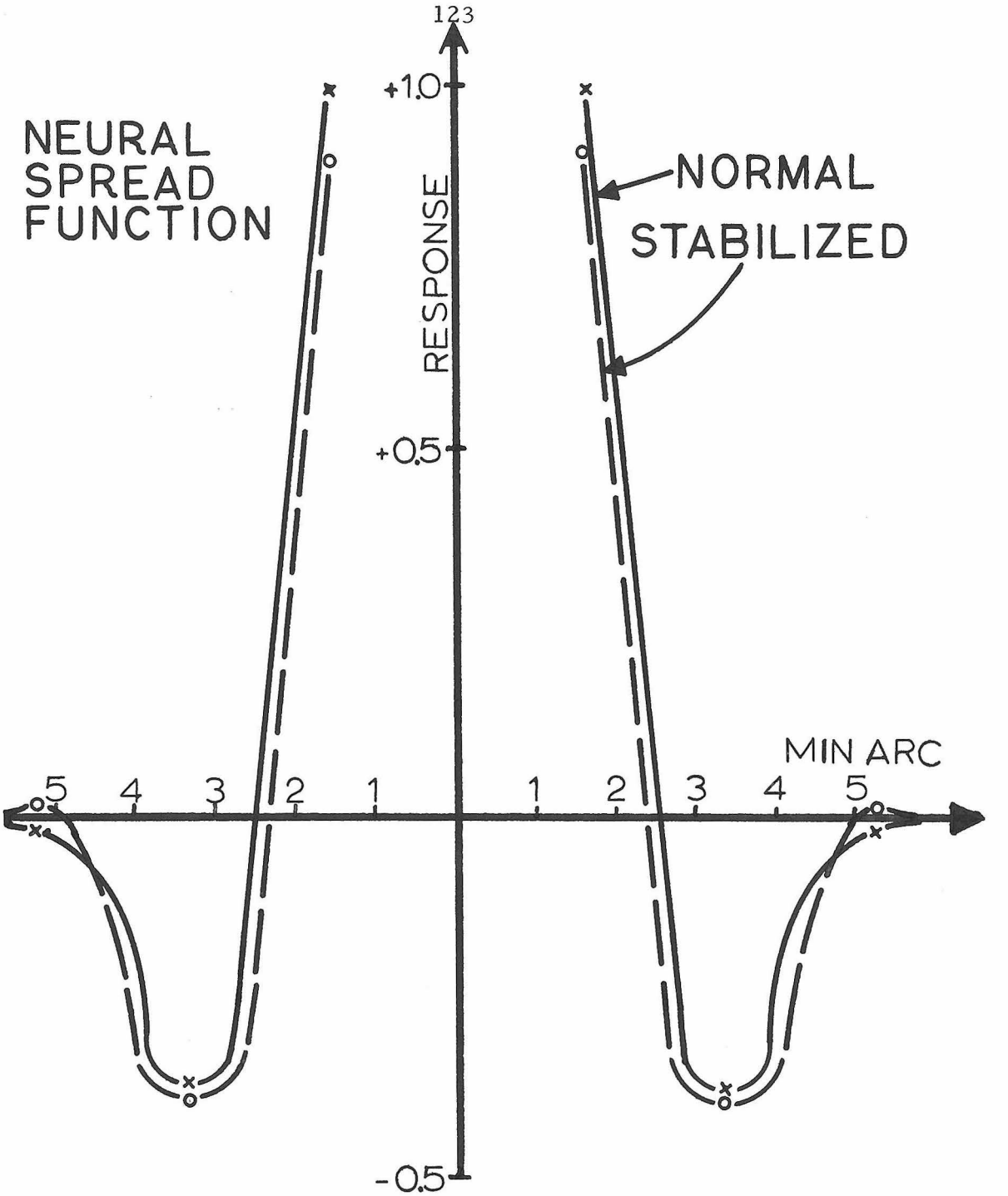

Fig. 4-13 DSG's neural spread-functions, derived from his normal and stabilized modulation transfer functions and the transfer function of the optics of the eye. The sequence of operations which produced these curves is identical to that shown in the previous figure, except that the fitted MTF's are each divided by the transfer function for the optics of the eye.

were subjected to the above processing; one, PWN, gave results identical with those in Fig. 4-13, the other, GMM, had no overshoot at 5 min arc in the stabilized vision condition - otherwise his curves are identical to those plotted. The MTF's used in this analysis were those obtained in experiment II. Their shapes were virtually identical to those obtained in the flickered grating experiment.

It is of considerable interest to compare Figs. 4-1, 4-12, and 4-13. Fig. 4-1 represents the blur in the retinal image of a bright line, and shows that the halo of light surrounding the line image is relatively bright 4 min arc from the center of the line image. Fig. 4-12 implies that the subject sees a dark halo instead of a bright halo 4 min arc from the line. Finally Fig. 4-13 shows the extent of lateral inhibition necessary to change the bright halo on the retina into a perceived dark halo.

There are several intriguing questions these figures raise about lateral inhibition. Why is the inhibitory effect so strong that it more than compensates for retinal blur? Some say its purpose is to enhance edges, yet edges closer together than roughly 5 min arc will not be enhanced by lateral inhibition, as may be seen from Fig. 4-13. Thus it seemingly is of no assistance in, for example, vernier acuity, in which vernier offsets much less than 5 min arc are easily detected. Indeed lateral inhibition is of no assistance in any of the classical acuity tests, since these commonly involve edges roughly 1 min arc apart. Further, eye movements do not interact with the slow spread of lateral inhibition to increase acuity since normal and stabilized acuities are, for all practical purposes, identical.

Comparison with Other Data on Lateral Inhibition

Physiological Data: Following the initial elucidation of the mechanism of lateral inhibition in the eye of the arthropod Limulus by Hartline and coworkers (34), similar responses were found in the vertebrate retinal ganglion cells of goldfish, cat, rabbit and monkey. The essential feature of these responses is that a small spot of light in the center of the "receptive field" of the cell will cause the cell to discharge repetitively, whereas placing the spot a short distance from the center of the field on the retina will inhibit the firing of the cell to a level which is less than its normal "spontaneous" firing rate. The complementary response, i. e., inhibition with the spot on the center of the field and excitation for the spot in the surround, is also prevalent in vertebrates. Although rabbit ganglion cells possess a similar sensitivity to stimulus geometry, their cells are especially responsive to various "trigger features" of the stimulus, such as direction of motion (35). For this reason their lateral inhibitory properties are not considered further.

Most of the ganglion cells of the cat retina show a simple lateral inhibitory type of response, with about 50% of the cells having an excitatory center ("on center" types), the remainder show inhibition for a spot of light in the center ("off center" types). The diameter of the center is approximately 0.7°; the diameter of the surround, i. e., the area of the field which causes the opposite response, is approximately 2.5° (36).

Cat and spider monkey have quite similar ganglion cell

receptive fields. Hubel and Wiesel (37) have measured the distribution of diameters of centers of receptive fields in spider monkeys and find that these increase from 4 min arc to 2° in width as the distance of the receptive field from the fovea increases from 4° to 50°. They were unable to measure foveal receptive fields, presumably because axons from ganglion cells serving the fovea have very small (about 1μ) diameters (38). Hubel and Wiesel did not measure the diameter of the surround. Their results from a spider monkey ganglion cell, 4° from the fovea, are compared with the human foveal neural spread-function derived from sine wave grating acuity in Fig. 4-14.

Psychophysical Data: A number of different tests have been performed on humans to determine the width of the total visual spread-function. In 1960, von Békésy derived from a series of measurements of the apparent width of Mach bands, and apparent luminances of narrow bars of light, a line spread-function for the entire visual system which he called the "neural unit" (39). To show that this was a general property of sensory experience, and that it may be used to describe the handling of spatially arrayed stimuli by nerve nets, as well as to predict the discriminations of which the system is capable, he also measured the spread-function governing spatial discrimination on the skin of the lower arm. Both spread-functions have similar shapes but different extents. The total visual system spread-function he derived is shown in Fig. 4-15.

Wolfe (40) in 1962 measured the visual spread-function by asking subjects to choose the one of a pair of photographs which had better picture definition. All photographs were of the same scene,

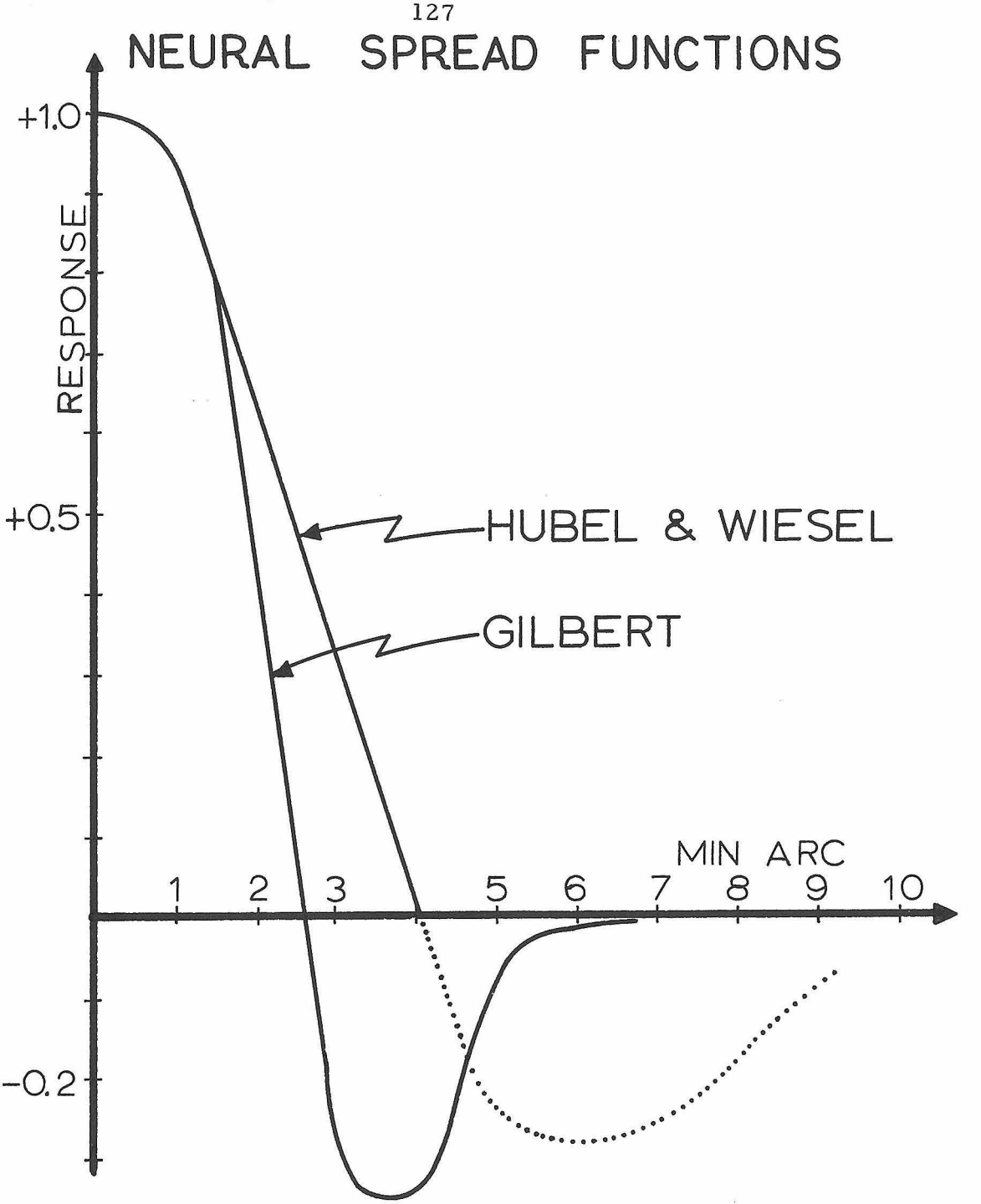

Fig. 4-14 A comparison of the neural spread function, derived from sine wave grating acuity data, with the retinal ganglion cell response of a spider monkey. The ganglion cell was 4^{o} from the fovea.

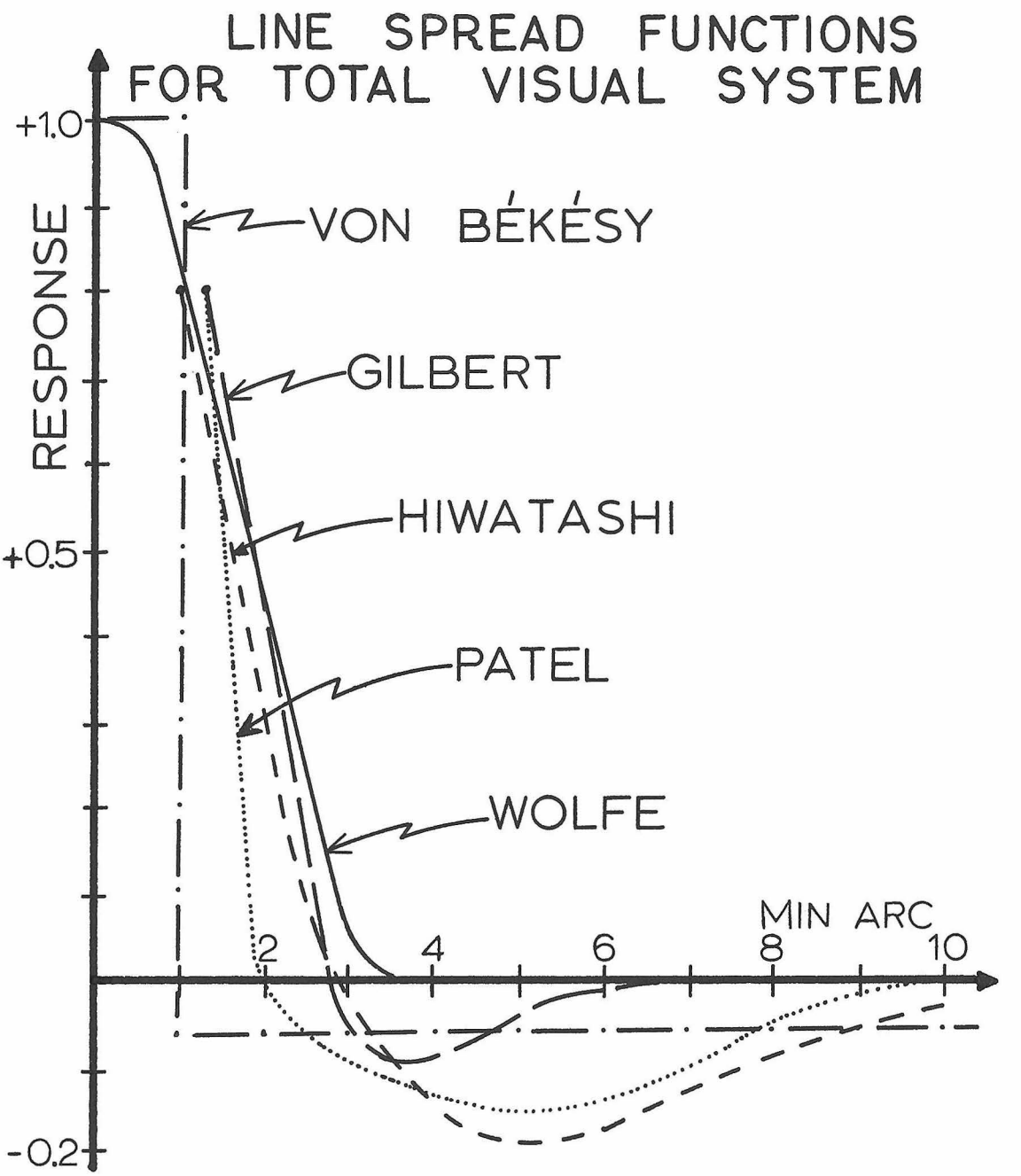

Fig. 4-15 Psychophysically determined spread functions for the human visual system. See text for details.

but taken with cameras having different spread-functions. The idea is that a subject can distinguish between photographs taken by a camera having a spread-function wider than the subject's, but not between photographs taken by a camera which has a spread-function more narrow than the subject's. He found that the human visual system has a spread-function equivalent to that of a camera with a 1 to 3 min arc diameter spread-function. Camera, and most optical, spread-functions have no inhibitory surround, so this single peaked spread-function is presumably the equivalent of the central peak plus inhibitory surround spread-function generated neurally. This single peak spread-function is shown for comparison in Fig. 4-13.

Seven months after I first derived the neural spread-function, there appeared in Journal of the Optical Society (May 1966) a paper by Patel (41), who had carried out the same series of transformations on MTF data acquired in non-stabilized vision for several different mean luminances. Two important differences should be noted between his experimental conditions and mine: his test field was only 2^{o} in diameter, vs my 7.5^{o} field, and his target (an oscilloscope face, P31 phosphor) was colored, whereas mine was black and white. His total visual system line spread-function at a mean retinal luminance of 100 trolands is shown in Fig. 4-15 .

The neural line spread-function he derived has an excitatory area slightly less than 2 min arc in diameter. Values of the spread-function this close to the center of the distribution cannot be derived from either his or my MTF data without extrapolation of the MTF curve beyond the region in which it has been measured. For this

reason my spread-function curves stop 1.7 min arc from the origin. Any extrapolation involves assumptions about the behavior of the MTF at zero spatial frequency. The assumption which Patel makes agrees well with line spread-function measurements of the optics of the eye, but these measurements disagree with the calculated spread-function of the optics of the eye by 4 orders of magnitude (see Fry (6)). In any case, the inhibitory area which Patel computed is not based on these assumptions, and has the same width as that in Fig. 4-13, but is shifted closer to the origin by 1 min arc.

Later in 1966 I found that Hiwatashi and co-workers (42) had published a similar analysis in a Japanese journal in 1964. They, however, neglected to divide their MTF by the line spread-function of the optics, so only the line spread-function of the entire visual system was derived. This is shown as well in Fig. 4-14. Their results apply to a 6^{o} field, mean luminance 30 ft. lamberts, and a P4 phosphor (non-stabilized vision).

Recently Davidson and Cornsweet (43) have refined von Békésy's technique and measured a spread-function for the whole visual system. The result of their analysis of Mach bands is identical to von Békésy's over the region shown in Fig. 4-15, except that Davidson's inhibitory area decreases indefinitely with distance from the center, whereas von Békésy considers inhibition insignificant beyond 12 min arc. Both obtain ratios of strength of excitation to strength of inhibition equal to 1.6. These are the ratios of areas under the positive and negative parts of the spread-function respectively.

Conclusions: The close agreement on one hand among the psychophysical measures of the visual spread-function, and on the other between sensitivity of the retinal ganglion cells of primates and the derived neural spread-function, provides supporting evidence for, but no means entirely confirms, two significant sets of conclusions. First, that the human visual system may be profitably treated as a linear optical system, and that threshold measurements are indicative of suprathreshold responses. Second, that the response of the entire visual system to a point of light has the same characteristics as that of a single retinal ganglion cell response to the same target, implying that the major factors limiting acuity occur in the retina, at or before the ganglion cell layer, that these factors are static, i.e., unrelated to eye movements, and finally that the brain does not compensate for the distorted intensity information, i.e., negative light intensity around a point image, contained in the ganglion cell outputs.

Insofar as the grating line spread-function for the visual sytem is similar to those derived from entirely different targets one may conclude that the same mechanisms are operative in grating acuity, Mach band perception, and general picture definition. Further, the close similarity between normal and stabilized spread-functions indicates that the interaction of eye movements with the slow spread of lateral inhibition is not used in any contrast-enhancing manner by the visual system, nor are the scanning effects of eye movements utilized to improve acuity. Thus the mechanisms governing acuity for diverse targets, as defined by their net spread-function, remain unchanged when retinal image motions due to eye movements are cancelled.

Neural processes limiting contrast detection, therefore, involve either "snapshots" of the retinal output or, less likely, a more intricate scheme for compensating the effects of eye movements.

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CHAPTER V

THE ROLE OF EYE MOVEMENTS IN MONOCULAR ESTIMATES OF DISTANCE AND DIRECTION

The previous chapters have described eye movements characteristic of acuity and spatial localization tasks, and investigated the role of eye movements in acuity tests. This last set of experiments concerns the function of eye movements in spatial localization tasks, in particular visual estimates of distance and direction.

Since at least the days of Helmholtz the possible role of eye movements in our perception of separation, direction, congruence and other spatial attributes has been recognized, although as yet there has been no clear differentiation between the knowledge of spatial attributes derived from knowledge of eye or retinal image movements, and that derived from the steady distribution of light over the retina.

To make these sources of spatial information more explicit, consider the problem of estimating the distance between two points, say two stars in an otherwise starless sky. One strategy is to fixate a point in the vicinity of the two stars and obtain the desired distance information from the spatial displacement of the images of the two stars on the retina. A very different strategy is to fixate first one star and then the other, and derive distance information from the extent of ocular rotation needed to accomplish this task. A third strategy utilizes the same eye movements as the last, but

instead of deriving distance information from the extent of eye rotation, the same information is obtained from an estimate of the number of receptors stimulated during the change of fixation. Rather than review the very tenuous evidence supporting these specific mechanisms, I shall summarize experimental evidence for and against the general hypothesis that eye movements aid discriminations of distance and direction.

But first, some hedging: depth and movement perception are omitted, as are spatial discriminations involving targets subtending large angles in the visual field. Obviously there are situations wherein eye movements - not to mention head and neck movements - are necessary for spatial discriminations, for example, in judging the dimensions of a room in which you are standing. Discriminations involving such large amplitude movements, though important, are not included.

Evidence in Favor of the Hypothesis that Eye Movements Improve Spatial Discriminations

The most direct evidence linking distance estimates and eye movements comes from the Russian school. Both Yarbus (1) and Leushina (2) have found that the measured amplitude of eye movement during estimation of the length of a bar is correlated with the subject's estimate of the length of the bar - even for incorrect estimates. They left unresolved, however, the problem of whether an erroneous eye movement causes an incorrect estimate, or whether an incorrect estimate causes an erroneous eye movement - and this is the crux of the present problem.

Similarly, the observation that disorders of spatial perception are frequently concomitant with disorders of eye movements (3) leaves the causal relationship unsettled, but again links the two processes.

The sequences of wary saccades described in Chapter III would fit nicely into either of the specific eye movement mechanisms described above. Short, direct, and incremental saccadic trajectories are, under this interpretation, the only external sign of the brain inching its yardstick (pardon the unlikely metaphor) across the visual world - where the yardstick may be either the extent of ocular rotation during one wary saccade, or the length of the swath of receptors stimulated during one wary saccade. The fact that these types of eye movements characteristically accompany visual tasks lends weight to the interpretation. However, the spatial discrimination tasks discussed in this chapter, although based on visual localization, are more complex than the simple localization tasks described in Chapter III; thus the inference that wary saccades occur in all spatial discrimination tasks is not well founded.

The remainder of the "evidence" consists of frequently repeated hypotheses, and pseudo-quantitative observations. Gippenreitor noted that eye movements during recognition of a target were often similar, and referred to them as "measuring movements" of the eye (4). Certain of the visual illusions are often attributed to differences in the size or activity or accuracy of the extraocular muscles (5). Pritchard (6) found, however, that

several of the standard illusions appeared to a greater or lesser degree even in stabilized vision. Other, less prominent, errors of spatial estimation have also been attributed to eye movements. For example, the overestimation of vertical distances relative to horizontal ones has been laid to less frequent eye movements in the vertical direction than in the horizontal direction (5). Similar explanations are adduced for the fact that vertically oriented angles appear smaller than horizontally oriented ones, as well as for the fact that bisection of a straight horizontal line involves persistent biases (7).

Evidence Against the Hypothesis that Eye Movements Improve Spatial Discriminations

Leushina (2) asked subjects to signal the completion of a position estimation task, and during the task he recorded the subject's eye movements using an EOG technique. He found that in approximately 25% of the trials subjects reported the estimate complete before movement of the eyes had terminated. All stimulus positions were within 20° of the fixation point, and estimates were made by release of one of two buttons, each of which was associated with one of two possible positions of the peripheral light stimulus. Leushina found also that the more accurate the estimate of position, the more accurate - on average - was the jump of the eyes to the stimulus. Since saccades are known to be programmed in advance, and not redirected due to visual input in mid-flight, the above finding argues that the distance estimate was completed before

the eye movement occurred.

Two major objections may be raised to Leushina's experiment. First, he relies on two extremely variable measures, namely eye and hand reaction times and EOG-measured saccadic end points, which, aside from making his argument a statistical one, introduce many extraneous factors which greatly influence these measures, ranging from the subject's interpretation of just when he could cease fixating (and Leushina does not report what the subject's instructions were) to control of eyelid movement. Second, Leushina's experiment only tests a restricted class of eye movement mechanisms, specifically those which provide distance (fixation point to peripheral point) information from movement of the eye through the entire angular distance. Mechanisms assisting estimates of direction are not considered, nor are mechanisms providing distance information by movement of the eye either randomly about the fixation point or through small excursions toward the peripheral stimulus but not through the entire distance.

Pritchard's work, showing that the geometrical illusions do not depend on eye movements (6), has already been mentioned. He found also that reversals of a reversible figure are unaffected by stabilization of the image. Along the same lines, Pheiffer, Eure, and Hamilton (8) obtained evidence that such reversals occurred prior to eye movements in normal vision.

The finding that saccadic trajectories are uninfluenced by visual input within roughly 100 msec of the saccade (9) implies that distance and direction information (within the limits of saccadic

positioning error) cannot rely on eye rotation through the entire distance. However, Fig 3 - 7 shows that saccadic positioning error can be as much as $1/3^{o}$ in a 1^{o} saccade, if only the large initial saccade is considered, and this error is much larger than that shown by other indicators of our distance sense, as will be shown presently. Thus, although saccadic trajectories probably have a preprogrammed distance and direction, this information may come from previous eye movements, and, of all the indicators of the subject's estimate of distance, this is one of the most faulty.

There is a considerable amount of evidence that proprioceptive sensing of eye position is not used as a basis for spatial discriminations in humans (see Whitteridge (10), and Brindley and Merton (11) for reviews). Not only may an occluded eye be moved without the subject's knowledge, but also ability to discriminate eye position in the dark is severely limited. Such evidence does not rule out the possibility that efference to the extraocular muscles is sent also to the cortex and there assists in spatial discriminations.

Evidence gathered in tachistoscopic experiments verify what by now should be quite evident, i. e. that spatial discriminations are possible without the aid of eye movements. However, the question of whether movements improve these discriminations is difficult to answer on the basis of tachistoscopic experiments, since spatial discriminations, like acuity, improve as exposure duration increases. The quandary is this: since tachistoscopic spatial discriminations are poorer than ones involving extended exposures, the cause may be effective elimination of some mechanism involving

eye movements but the cause may also be elimination of any other time dependent process which refines spatial discriminations. Alternatively, one could compare responses to tachistoscopic stimuli obtained when the eyes were nearly stationary to those obtained when the eyes were moving, and claim that this tests the hypothesis that eye movements improve spatial discriminations. This tack, unfortunately, tests only one of many possible eye movement strategies.

Spatial discriminations possible in tachistoscopic stimuli are worthy of note: Harcum (12) has treated subjects' localization ability for peripheral light flashes in polar coordinates. Sperling (13) has quantified subjects' ability to perceive and reproduce relative positions of target elements. Kraemer and Easley (14) have treated localization ability in both polar and Cartesian coordinates. None of these studies offers comparisons of flash presentation performance with longer presentation time performance.

Description of Experiments

The hypothesis we would like to test is this: Movements of the eye during monocular estimations of distance and/or direction improve these estimates. Since paralysis of the eye is difficult to achieve in a living animal, whereas near perfect compensation of the retinal image movement is easy to achieve, the hypothesis actually tested is this: movements greater than about 3 min arc of the retinal image over the retina during monocular estimations of distance and/or direction improve these estimates. The experiments consist of measuring the accuracy of such determina-

tions in normal and in stabilized vision. An improvement in the normal vision scores would indicate the presence of some eye movement strategy which aids these estimates. On the other hand, similar scores in normal and stabilized vision would prove that no such eye movement strategy is operative.

The hypothesis of interest and the hypothesis tested are different, and leave two possibilities untested. First, the possibility that retinal image motion on the order of 3 min arc contributes significantly to the estimates. This we have sought to minimize by making the distances to be estimated more than an order of magnitude larger, namely 118 min arc. The second possibility is that eye movement independently of retinal image movement, contributes additional information. Though conceivable, no such mechanism has ever been postulated.

Targets: Due to the Troxler effect (fading of peripherally viewed stimuli) plus the usual fading of stabilized images, very bright points of light were used as targets. Three or more such points were used in each target to define a reference distance or angle, and a variable distance or angle. The subject's task was to indicate when the variable dimension was equal to the reference dimension. To obtain sufficiently bright points, light pipes (AO fiber optic light guides) with one end in the source aperture (Fig. 2 - 5, S or S') and the other in the target plane were used, with all other light from the source occluded. The target plane ends of the light pipes were each firmly affixed to one of the target array supports. The light pipes

were circular in cross section with a diameter of 0.5 mm (4 min arc). The brightness of all the points could be varied simultaneously by the subject to assist in prevention of fading, by moving wedge W or W' in Fig. 2 - 5. Both subjects tended to use the brightest possible points (approximately the same brightness as a field of 4.0 log ft - lamberts), and neither one chose to flicker the points.

Each point gave rise to a secondary, much dimmer, image of itself displaced about 30 min arc to the left of the primary image. These were due to secondary reflections in beamsplitter 1; both subjects were warned not to base any estimates on these rather than on the primary images. Aside from these images the field seen through the telescope appeared uniformly black. Room lights were left on during the experiment, since this too seemed to prevent fading. For the same reason, the subject was instructed to look at the room rather than at the target field between trials.

All target dimensions were measured first with micrometers in the target plane, and then by viewing the target through the exit pupil by means of a telescope. Rotation of the telescope until its crosshairs were aligned with one target point and then another gave the primary calibration of the angles subtended by the target in terms of mm of distance in the target plane per angular rotation of the telescope (0.115mm/min arc). Micrometer drive micromanipulators (which could be read accurately to 0.1mm) were used to set up the geometry of the target, as well as to give readouts of the variable distance settings. No optical distortions of the 4^{o}

diameter field used in these experiments could be detected during the primary calibration.

The subjects used in this series of experiments were the same as those used in the experiments reported in Chapters III and IV (DSG and GSC). All targets were presented monocularly (left eye), with the subject wearing the lens even while making normal vision estimates, and with 23cm H_2O suction applied to the lens throughout all sessions.

Experiment I

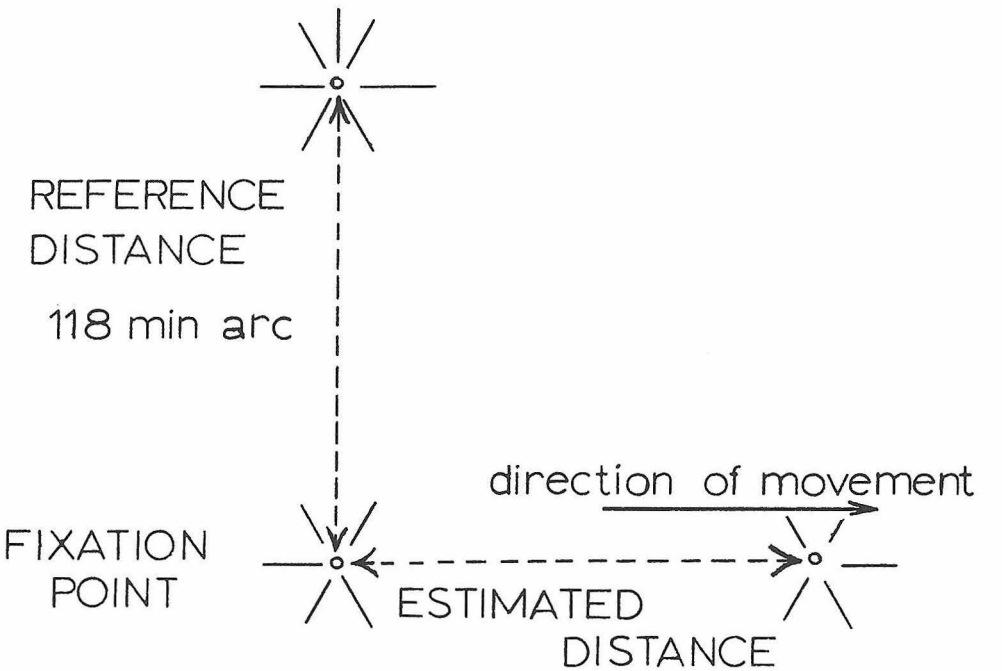
The initial test of the foregoing hypothesis consisted of two parts: a distance estimation task, and an angle estimation task. In both, one of the light pipes was used as a central fixation point. By appropriate tilting of mirror M5 in Fig 2 -5, the subject adjusted the position of the stabilized fixation point - while watching both normal and stabilized images - until the normal and stabilized images of the fixation point were superimposed. This procedure was repeated at the beginning of each session, and during each session whenever the subject felt that the fixation point in stabilized vision was not falling on the center of his fovea.

Distance Estimation: Target geometry and results for the distance estimation portion of this experiment are shown in Fig 5 - 1. Three points were used to determine a vertical reference distance, and a horizontal variable distance. In each trial the variable point was moved slowly nasally away from the fixation point (starting about 20 min arc from the fixation point) until the subject indicated equality of

the two distances. Neither subject nor experimenter knew the correct position of the variable point until the experiment was complete. The experimenter did not look at the micrometer dial until the subject indicated equality; in addition the experimenter attempted to move the variable point at random rates during any particular trial. No training trials or sessions were given.

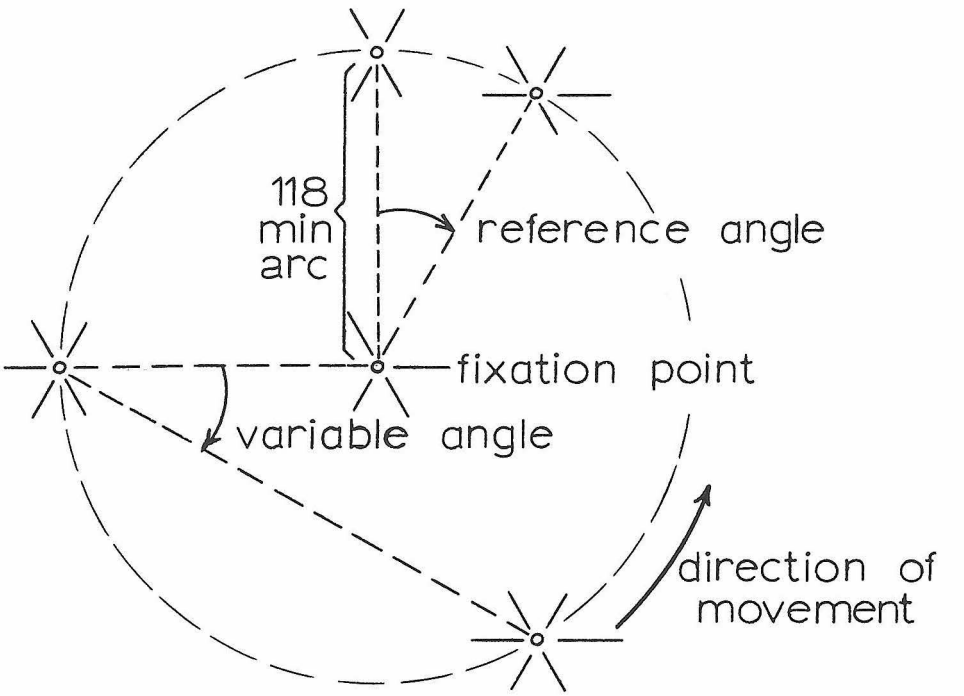
Five trials were given in stabilized vision, followed by five in normal vision, and this procedure was repeated four times over the course of approximately 50 minutes. The experiment was repeated on subject DSG using a reference distance of 109 min arc. The same bias and approximately the same standard deviations were obtained. The mean distance of the variable point from the fixation point - as reported equal to the vertical distance by the subject - is given in Fig 5 - 1, together with the standard deviation of this estimated distance. The distribution of estimated distances in all conditions was unimodal and slightly skewed toward shorter distances.

Angle Estimation: The target geometry used to measure angle estimation ability is shown in Fig 5 - 2, together with the results of this test. All points except the fixation point were made to lie on a circle of radius 118 min arc in order that variations of localization ability, which are known to fall off with distance from the fovea, might be held constant for all peripheral points. The variable point was made to traverse the lower half of this circle, from temporal to nasal, until the subject indicated that variable and reference angles were equal. The angles presented from trial to trial were rando-



CONDITION	SUBJECT	MEAN min arc	STANDARD DEVIATION min arc	NUMBER OF TRIALS
normal	DSG	114	6.9	20
stabilized	DSG	117	6.0	20
normal	GSC	91	2.9	20
stabilized	GSC	95	6.5	20

Fig. 5-1 Configuration of target lights as they appeared to the subject (monocular, left eye) in the distance estimation task of experiment 1. The subject's task was to stop movement of the right point when reference and estimated distances appeared equal. Means and standard deviations of the estimated distances are given.



reference angle →		10°	25°	30°	40°	45°	50°	60°	70°
DSG	μ	11	26	28		40	44		77
normal	σ	3.6	1.4	3.3		2.2	2.0		4.3
DSG	μ	14	25	22		41	33		69
stabilized	σ	3.6	1.9	2.1		5.1	1.8		7.3
GSC	μ	9	23	24	31	40	44	54	
normal	σ	1.3	2.7	0.2	3.7	2.3	4.3	3.3	
GSC	μ	16	24	25	37	38	50	60	
stabilized	σ	5.4	2.9	3.3	2.4	7.8	6.7	5.5	

Fig. 5-2 Target configuration for the angle estimation portion of experiment 1. The subject's task was to stop movement of the lowest point, as it traversed the lower half of the circle, when reference and variable angles appeared equal. Means and standard deviations of the angles estimated in five trials are given.

mized, but normal and stabilized conditions were alternated every five trials. Both reference and estimated angles could be calculated from readings, accurate to 1^{o}, on a protractor above the target, over which rode pointers mechanically linked to the northeast and the variable points. The same precautions taken in the case of the distance estimates were taken here (e. g. alignment of fixation point, randomized moving of the variable point, no training trials, duplication of the results on subject DSG in a later session, etc.). Five estimates in normal vision, and five in stabilized vision were made by each subject of each angle.

The arms of the variable angle were of differing lengths in order that the task be as independent as possible of simple distance estimations of the gap between the end points of the angle, and rely more on estimates of direction relative to the two verticles of the angles to be matched.

Conclusions, Experiment I : The results of the distance estimation task show that the mean of the normal vision estimates is slightly worse than the mean of the stabilized vision estimates for both subjects, whereas the relationship of the standard deviations of these estimates varies between subjects. The persistence in stabilized vision of the illusion that the vertical distance is equivalent to a shorter horizontal distance has not been previously reported (cf. ref. 5, p. 37) and indicated that the source of this illusion does not rely on preferential movement of the retinal image in any fashion.

The results of the angle estimation task show that the mean

stabilized estimate is often closer to the correct value than the normal vision estimate, and in one case (GSC 40°) not only is the mean stabilized estimate closer, but also the stabilized standard deviation is smaller than the normal one. A more comprehensive comparison of normal and stabilized capabilities may be obtained by looking at the averages over all angles of the standard deviations of the estimates and the errors of each mean estimate from the reference angle, as shown below:

	DSG Normal	DSG Stabilized	GSC Normal	GSC Stabilized
Average error of mean estimate	3.7°	6.8°	5.0°	3.1°
Average standard deviation	2.8°	3.8°	2.5°	4.8°

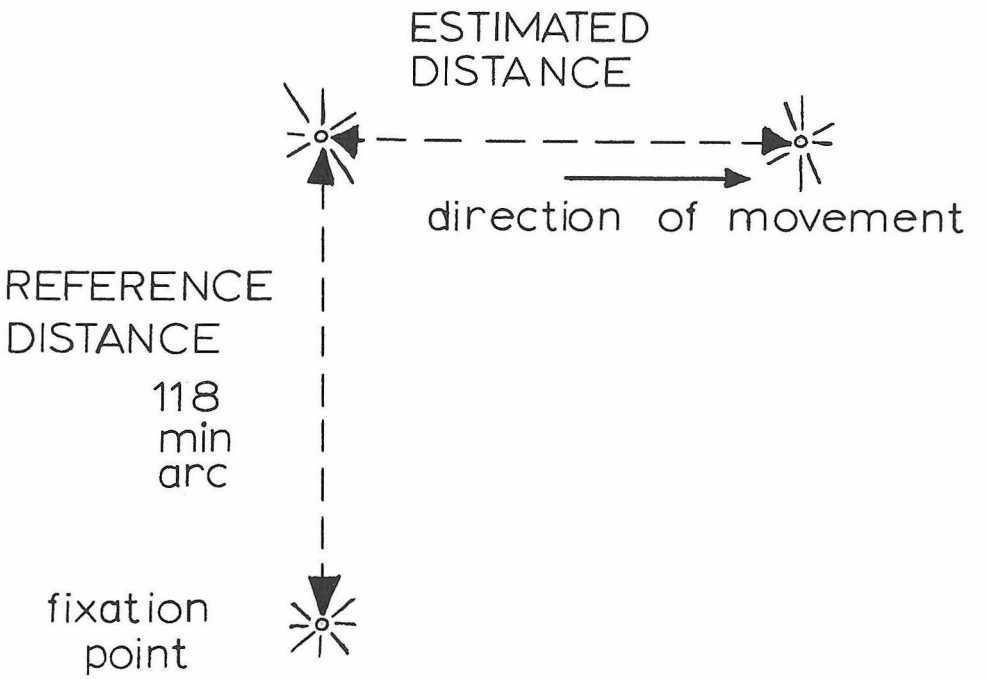
Since retinal image movement results in no order of magnitude improvements in distance or angle discriminations of this type, it becomes necessary to determine how much the slight improvement in normal vision, particularly in the standard deviations of these estimates, is due to retinal image motion, and how much is due to errors introduced by fading of the stabilized image. Although many precautions were taken against fading, as noted above, their effectiveness was limited. Either the entire pattern, or a few points in it would disappear quite often. Subject DSG estimated that during stabilized trials the entire target was visible about 7% of the time, whereas for subject GSC this figure lay around 5%. In partial compensation for this disparity in viewing times between normal and stabilized trials, the variable point was moved at approximately half

speed in stabilized trials, and stopped whenever the subject signalled a particularly persistent fade out. Despite these efforts both subjects estimated the ratio of total viewing time in normal vision trials to total viewing time in stabilized trials at about 8 to 1. In a typical trial, this ratio was approximately 15 sec to 1 or 2 sec. When this disparity is taken into account, the stabilized estimates are seen to be remarkably close to the normal estimates and the contribution of a measuring system reliant on retinal image movement appears unlikely.

Experiment II

The preceeding experiment shows that distance from the fovea in stabilized vision is estimated nearly as well as the same distance when the eye is free to roam over the target. There is a possibility that, although radial distance from the fovea is estimated accurately without retinal image movement (and this sort of estimate is necessary for saccadic programming), distances between two points both outside the fovea cannot be estimated accurately without retinal image movement. This possibility was tested in a later session with the target geometry shown in Fig. 5 - 3. There were no changes in experimental procedure between this and the distance estimation portion of experiment I.

The results indicate that both subjects are able to perform this task with the same degree of repeatability, as indicated by the similarity in the standard deviations, as that shown in experiment I. This, together with the fact that subject GSC showed more accuracy in this task than in that of experiment I, indicates that distance estimation



CONDITION	SUBJECT	MEAN min arc	STANDARD DEVIATION min arc	NUMBER OF TRIALS
normal	DSG	114	3.0	10
stabilized	DSG	97	5.6	10
normal	GSC	106	3.3	20
stabilized	GSC	108	6.1	20

Fig. 5-3 Target configuration and results of experiment II, which tests the accuracy of distance estimates not radially arranged about the fovea.

ability is neither confined to estimates of radial distances from the fovea, nor is it significantly better for estimates of this sort. Thus, the sorts of distance estimates which are vitally necessary for precise control of saccadic eye movements seem to be neither better nor worse than other sorts of distance estimates, demonstrating again the independence of eye movement and distance estimation mechanisms.

If eye movements are of assistance in the estimation of angles, one might guess that the strategy involves placing the fovea at the vertex of the angle to be estimated, and then moving along one or the other arm of the angle. This, together with the saccadic programming mechanism, which definitely needs information regarding direction relative to the fovea, suggests that subjects may be especially precise in estimating angles which have their vertices in the fovea. This hypothesis, however, was contraindicated in the second part of experiment I, when an angle which could be constrained to have a vertex 118 min arc from the fovea, was estimated equally well both with and without the constraint.

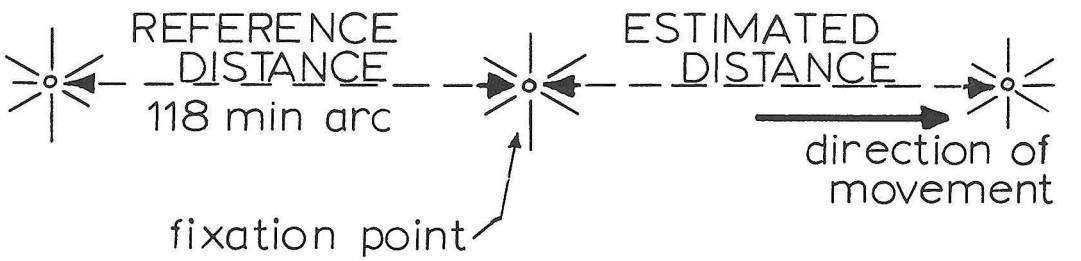
In conclusion, the results of this experiment together with those of the preceeding one imply that the distance and direction estimates most necessary for the control of eye movements are not significantly more accurate than other sorts of distance and direction estimates. In other words, our ability to estimate elementary spatial arrays is not strongly tied to a fovea-centered coordinate system, even though this type of coordinate system is highly characteristic of our voluntary eye movements.

Experiment III

The possibility remains that eye movements may subserve a mechanism involving superposition of image and afterimage to sharpen spatial discriminations. In the previous experiments no such superposition was possible without 90^{o} torsional movements of the eyeball - an infrequent occurence. To test the superposition hypothesis the target geometries shown in Fig. 5 - 4 and Fig. 5 - 5 were employed in two separate sessions for each subject. The experimental procedure was as described in the first part of experiment 1.

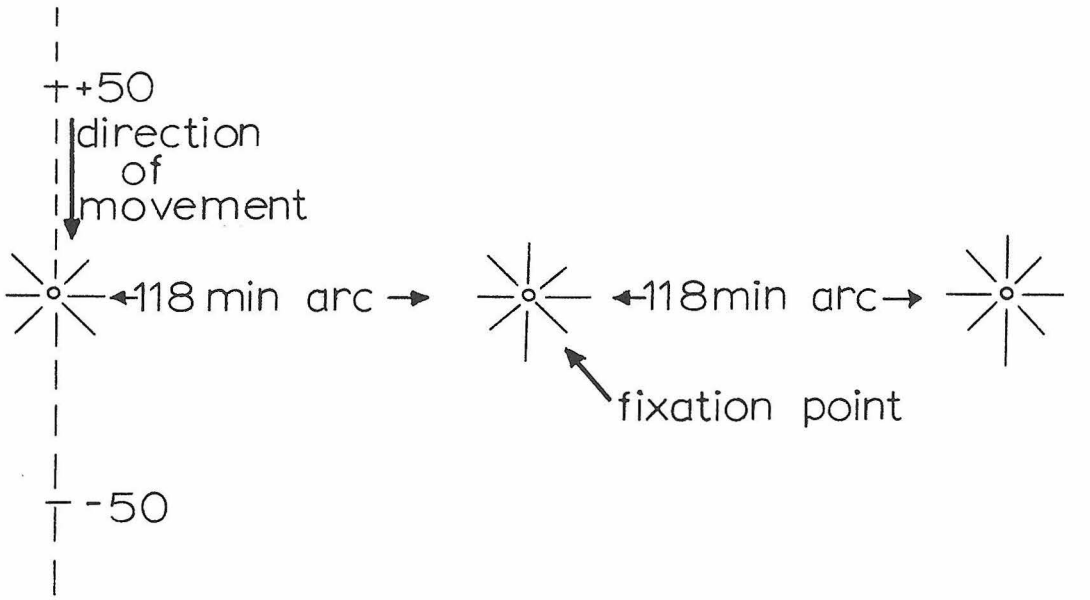
Neither subject shows an increase in aptitude for the distance estimation task shown in Fig. 5 - 4, even though this task allows superposition of image and afterimage, whereas the previous distance estimation tasks did not. Moreover, the fact that the means of the normal vision estimates are farther from the true value than are the means obtained in stabilized vision may be interpreted as disproving the existence of a superposition mechanism, which, one would expect, would give a mean close to the true mean. The large standard deviation shown by subject GSC for the task of Fig. 5 - 4 reflects two processes which occurred in that session, but in no other. The first was unusually persistent fading which the subject reported throughout the last half of the session. The second, perhaps related, process was a steady increase in the length of the estimated distance. No other results in this series of experiments showed such a trend.

For the task depicted in Fig. 5 - 5, the variable point moved about 2^{o} downward until judged colinear with the other two points.



CONDITION	SUBJECT	MEAN min arc	STANDARD DEVIATION min arc	NUMBER OF TRIALS
normal	DSG	115	3.4	20
stabilized	DSG	119	6.8	20
normal	GSC	109	4.3	20
stabilized	GSC	121	14.0	20

Fig. 5-4 Target configuration for experiment III, part 1, which tests for the existence of an afterimage superposition mechanism.



CONDITION	SUBJECT	MEAN min arc	STANDARD DEVIATION min arc	NUMBER OF TRIALS
normal	DSG	-5.2	2.3	20
stabilized	DSG	-2.6	2.7	20
normal	GSC	-1.0	1.8	20
stabilized	GSC	+4.3	2.8	20

Fig. 5-5 Target geometry for experiment III, part 2. The subject's task is to stop downward movement of the variable point when it appears colinear with the other two points. The scale refers to the angle subtended by the setting error at the eye.

The procedure was the same as that followed in the preceeding distance estimation experiments. Even though this target seems eminently suitable for either a superposition mechanism (fixation of the right point, and then the center point, results in the after-image of the center point being superimposed on the image of the left point when colinearity is reached) or a simple eye muscle mechanism (colinearity is reached when contractions of the horizontal recti result in the narrowest possible swath of receptors being stimulated), the increased aptitude of both subjects for this task shows up in both normal and stabilized standard deveiations. Again, retinal image movement introduces no significant improvements in spatial estimations of this simple sort, nor does it lead to any large deterioration in the accuracy of these estimates.

Summary and Conclusions

Several simple spatial discrimination tasks were presented to two subjects under both normal and stabilized monocular viewing conditions, in order to determine whether or not retinal image movement, as generated by eye movements, would improve these spatial discriminations. For any given task (except angle discrimination) five stabilized then five normal trials were made, and this sequence was repeated until the end of the session. Normal and stabilized conditions were changed randomly in the angle estimation task, as were the reference angles. Subjects were untrained, and neither subject nor experimenter knew the setting which would equalize the reference and variable distances or angles, since these were

calculated following completion of the experiment. Only results of the subject's first session with the target are given.

We may make the following conclusions with considerable certainty: retinal image movement leads to no extensive loss or gain of ability to resolve distances or angles within 2° of the fovea; this ability is not fovea-centered, that is, distances from the fovea are not estimated a great deal better than others, nor are angles most sensitively estimated when the vertex of the angle is on the fovea; and finally, a distance estimation task which permitted superposition of image and afterimage as an aid to distance estimation was carried out with comparable precision in normal vision and in stabilized vision. These results render unnecessary the assumption, lately ressurected by Platt (15) but apparently first put forward by Helmholtz (16), that eye movements play an essential role in visual estimates of distance and colinearity.

The original question was whether eye movements lead to any improvement in monocular spatial discriminations, whereas the answer given above indicates that there is no large or consistent improvement. Certain of the data admit the possibility that eye movements cause a twofold reduction of the error in spatial discriminations. Some fraction of this improvement, however, must be attributed to the longer viewing time in normal vision, approximately eightfold longer in all experiments reported above. The fraction remaining, that improvement due to retinal image movement alone, is so small that it is below the resolution limit of this set of experiments. The resolution limit might be improved by

increasing the number of trials or sessions, in order to obtain a more stable baseline for each subject. This was, in fact, tried with subject DSG, and it was found that more trials per session led to more prevalent and persistent fading, whereas multiple sessions with the same subject gave rise to variations in the data commensurate with inter-subject variations. Moreover, multiple sessions tended to attune the observer to extraneous cues, for example, positions of secondary reflections of the target points, possible algorithms for solution of the angle estimation task, and mean time taken by the experimenter to move the variable point to the correct position. Thus the abundance of possible extraneous clues as well as the vagaries of fading of peripheral stabilized images provide major impediments to the establishment of more reliable performance baselines.

In summary, we have established that retinal image movements neither increase nor decrease the error in simple spatial discriminations of the type presented here by more than a factor of two, which is the resolution limit of these experiments.

Considerations for further work: Both subjects reported having very little confidence in their estimates of distance and direction in stabilized vision, and both were greatly surprised to find how close their normal and stabilized estimates were. This, I feel, may be interpreted as evidence that eye movements usually do occur in making estimates of spatial relations, but, instead of improving these estimates, the movements are made primarily for confirmation of the estimate. Just what retinal image movement is necessary for

this confirmation, or for giving the subject confidence in his estimate, deserves more attention.

All target geometries used in this series of experiments were purposely constructed so that neither reference nor estimated distances or angles could be moved in their entirety onto the fovea. For smaller targets, this constitutes a function of eye movements, and a study of the areas of the fovea chosen for very small targets compared to those chosen for targets which do not quite fit into the fovea may reveal anisotropies of the fovea with respect to distance or direction estimation ability. Similarly, a study of eyeball trajectories during execution of such tasks should reveal the "confidence giving mechanism."

Finally, the extraordinary nature and complete lack of survival value of the tasks performed in this series of experiments should be realized. The closest task carried out in nature is done rapidly, once, and without the stringent geometrical concept of equality. Moreover, the information loads on fovea and periphery are much higher under normal circumstances. How then does a fine ability to estimate peripheral distances and angles, and an extremely poor ability to judge the correctness of the estimates fit into this more complex melieu?

Walls (cf. ref. 17) would claim that, since foveas are relatively recent evolutionary developments, spatial discriminations would not await their arrival but, rather, develop equally well over the whole of the retina. Thus our ability to make these fine discriminations in the peripheral retina is a primeval characteristic

independent of eye movements, which, he argued (17), have served throughout evolutionary history primarily to stabilize retinal images on the receptor arrays. The data presented here are consistent with this view. The subject's lack of confidence in his stabilized vision estimates may thus be interpreted as the price one pays for a fovea - the periphery has lost credibility.

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CHAPTER VI

Summary and Conclusions

Eye Movement: The search for regimes of eye movements which are characteristic of particular visual tasks led to three discoveries: the differences between sentient and motionless fixation, the differences between wary and sloppy saccades, and the dependence of eye movements on the spatial frequency of a sine wave grating target.

Sentient fixation requires the conscious maximization of sensory visual inflow, whereas motionless fixation requires the conscious minimization of motor outflow to the eye muscles. During motionless fixation subjects have a lower flick rate, a more uniform flick direction, and lower flick amplitudes than during sentient fixation. Slow in-and-out vergence motions occur occasionally in sentient fixation, but are rarely evident during motionless fixation. Compensating flick pairs may be found in both motionless and sentient fixation, but the proportion of flick pairs to all other flicks is markedly higher in sentient fixation. Fiorentini and Ercoles (1), and Steinman et al (2) published studies soon after my investigation was completed which used the motionless fixation criterion. Neither of theses studies defined a sentient fixation criterion. All conclusions regarding motionless fixation are in accord with those presented here, although Fiorentini views compensating flick pairs as due to muscular noise. However, the unexpectedly large number of such flick pairs

in sentient fixation indicates a visual rather than a purely motor cause. It appears reasonable to suppose that compensating flick pairs are triggered by the visual cortex in order to counter the fade effects associated with stabilized images.

Fade effects observed during motionless fixation are similar to those which occur during viewing of a stabilized retinal image. Fade effects rarely occur during sentient fixation. Thus the sentient fixation eye movements described above, together with a high rate of blinking, serve to eliminate these fade effects and thereby maintain the inflow of accurate visual information. Whether or not eye movements mediate this information influx, rather than simply sustain it, is the question answered in the later experiments.

The degree of control exerted over the path of the visual axis during a saccade differs radically under two experimental conditions. Rapid repetitive changes of fixation between two continuously visible points result in large, roundabout saccadic trajectories, labelled here as "sloppy". The following of an unpredictable target point, on the other hand, is done by means of several direct saccadic trajectories, each bringing the visual axis closer to the target position. This behavior is called a sequence of "wary" saccades. Sloppy saccades have not been recognized by modelers of the eye movement control system; these types of saccades seem to indicate that accurate positioning of the visual axis may be carried out from memory, and, more importantly, that the end points of such saccades are far more determinate than the saccadic trajectory. In other words it is not the temporal array of muscle contractions

which is remembered, but only the final muscle lengths.

Sequences of wary saccades, made while following a point, may be easily interpreted as measuring movements of the eye, which assist in accurate localization of the moving point. Similarly, wary types of fixation flicks may be interpreted as visually controlled scanning or centering mechanisms. Evidence was presented to show that fixation flicks are not simply muscular noise. Both Fiorentini and Steinman agree that fixation flicks appear to compensate for the eye's previous motion - even in the dark. A more quantitative study of this compensation is presently being conducted in our laboratory by G. J. St. Cyr.

Finally, records of eye movements obtained during a sine wave grating acuity task show that eye movement patterns alter when either the depth of modulation or the spatial frequency of the target grating is changed. Transformation of the eye movement data and the target luminance distribution into time series representing light flux into a receptor, and comparison of these time series with the known sensitivities of the eye to various rates of flicker, provides an adequate basis for prediction of the relative sensitivities of the visual system to gratings of different spatial frequencies.

In sum, these results show that different regimes of eye movements are highly correlated with several kinds of visual tasks. Although the evidence is circumstantial, a kind of guilt by association, the conclusion that eye movements play a vital role in spatial vision appears inescapable. However, the conclusion is false, as the following experiments show.

Eye Movements and Acuity: Stabilization of the retinal image provides one of the simplest and most comprehensive means of testing the hypothesis that eye movements improve acuity. Such tests have, in the past, led to conflicting results. The three experiments related in this thesis all indicate that the discrepancies can be accounted for by variations in the amount of stabilized fading experienced by the subjects.

Four subjects were tested with classical acuity targets as well as with sine wave gratings of various spatial frequencies. The degree of stabilized fade-out was different in each of the three experimental conditions. Rapid subjective comparison of normal and stabilized acuity made all four subjects report that their normal and stabilized acuities were identical. When two subjects' grating contrast thresholds were measured by the time consuming method of limits, both showed significantly poorer stabilized acuity. When the same method was altered to reduce fading, stabilized sensitivity increased greatly but still remained slightly (0.1 log unit) below normal sensitivity. However, fade effects were by no means completely eliminated in the last experiment, so these remain the most likely cause of the residual difference in sensitivities. Further, fade out effects were found to be largest at just those spatial frequencies where normal and stabilized sensitivities were most disparate. These results set exceedingly narrow bounds on the extent to which eye movements improve acuity, and thereby cast considerable doubt on the existence of any such mechanism.

Linear Analysis of Acuity: Blur of the retinal image may be conveniently expressed in terms of the point spread-function. Although this changes with eccentricity from the fovea, the accommodative state of the eye, and the wavelength of light used, it is a valuable first step towards quantitative prediction of retinal luminance distributions. I have illustrated tne way in which the point spread-function changes when it is sampled by the receptor mosaic and subsequently is reflected in the receptor potentials of adjacent receptors. The fate of the point spread-function, following these transformations, is the subject of many tenuous inferences.

One such inference, based on the assumption that the visual system behaves as a linear optical system, was made in the following way: Inverse Fourier transforming the sine wave grating modulation transfer function is equivalent to reconstructing the response of the entire visual system to bright line. This response is seen to be flanked on either side by zones of lateral inhibition, which is in comforting agreement with data on retinal ganglion cell responses as well as with data on Mach bands. Division of the MTF by the Fourier transform of the line spread-function of the optics of the eye yields, after inverse Fourier transforming, the response of the retina and brain to a narrow bright line on the retina - the neural spread-function. Although there is remarkably close agreement among the neural spread-function, the results of Mach band measurements, and ganglion cell responses, the neural spread-function is presently on a shaky theoretical footing, since, as Westheimer (3) pointed out, there are several nonlinear stages in the visual system; for

example, the transformation from light flux to receptor potential is logarithmic, and the asymmetry of Mach bands implies the existence of a nonlinearity, as does the very concept of a threshold.

Distance and Direction Estimation: Several experiments were undertaken to test the hypothesis that eye movements improved monocular visual estimates of distance and direction. An effort was made to design targets which would test the hypothesis in a general manner, yet with a simple target geometry, and in such a way that variations in acuity across the retina would least confuse the measurements. Since image stabilization was also employed to test this hypothesis, precautions had to be taken against fade out, which occurs especially rapidly in the peripheral retina. These considerations led to the use of arrays of bright points consisting of a central fixation point and two or more points approximately 2^{o} from the fixation point, each of which defined either a reference or a variable distance or angle. The subject's task consisted of stopping movement of the variable point when variable and reference distances or angles were judged equal.

The subject's ability to accurately carry out these tasks was little affected by stabilization of the image. The error in the average estimate increased at most twofold due to stabilization. However, fade out due to stabilization decreased the viewing time in all stabilized vision trials to roughly 1/8 their normal vision duration. In view of this large discrepancy in viewing times, the slight increase in the error of stabilized estimates is not considered significant.

With distance estimation and acuity reasonably accounted for

without recourse to a visual mechanism which requires eye movements, what function do eye movements serve? Prevention of fading is certainly one major function; another, as tacitly assumed by those who model the eye movement control system, is to direct the fovea to interesting locations, or, as Aristotle said of the chameleon (4):

> "It keeps twisting its eyes round and shifting its line of vision in every direction, and thus it contrives to get a sight of any object that it wants to see."

The primary import of this study is to remove from neurophysiological consideration several possible visual mechanisms. The receptor array, this report indicates, is capable of extracting a wide range of acuity and spatial localization information from a spatially stable distribution of light intensity impinging on the array. This may be viewed as a vindication of the many microelectrode studies which involve immobilization of the receptor array. This procedure apparently does not impede the visual information gathering of humans, and presumably of other forms as well. However, in man, powerful accommodation effects curtail this information gathering and render stabilized images invisible in a matter of seconds.

Flickering the image becomes progressively less effective as a means of restoring its visibility, as does the interposition of other images. Thus visual acuity depends on time, and this factor provides a sufficiently difficult obstacle to the investigation of the

neural mechanisms underlying acuity. Complication of the task with possible retinal image movement mechanisms, is, as shown here, unnecessary.

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Appendix I

Derivation of the Point Spread Function From the Line Spread Function

Let $g(x,y)$ be the general point-spread function.

Then the one-dimensional line spread function, $g_1(x)$, is defined by

(1) $$g_1(x) = \int_{-\infty}^{\infty} g(x,y)\, dy$$

where the image of the line is assumed to lie along the y axis.

Assume $g(x,y)=g(r)$, i.e., that the point spread function is circularly symmetric. $r=\sqrt{x^2+y^2}$

The next step is to develop an expression for the Fourier transform of $g(r)$:

Let $F[g]$ denote the Fourier Transform of g.

By definition:

$$F[g(x,y)]=\frac{1}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} g(x,y)e^{-i(\xi_1 x+\xi_2 y)}dxdy$$

substituting $x=r\cos\theta$ $\quad y=r\sin\theta$ $\quad \xi_1=\rho\cos\phi$ $\quad \xi_2=\rho\sin\phi$ $\quad dxdy=r\,drd\theta$

$$\xi_1 x+\xi_2 y=r\rho\cos(\theta-\phi)$$

$$F[g(r)]=\frac{1}{2\pi}\int_o^{\infty} r\, g(r)dr \int_o^{2\pi} e^{-i\rho r\cos(\theta-\phi)}d\theta$$

Note: $$\int_o^{2\pi} e^{-ir\rho\cos(\theta-\phi)}d\theta=\int_o^{2\pi} -ir\rho\cos\theta\, d\theta$$

$$=2\pi J_o(\rho r)$$ (Sneddon Fourier Transforms, p.515)

So $$F[g(r)]=\int_o^{\infty} r\, g(r)J_o(\rho r)dr$$

which is the zero order Hankel Transform of $g(r)$, denoted by $H(g(r))$.

Next it will be shown that the one dimensional Fourier Transform of the line spread function, when rotated about its vertical axis, is identical to the above Fourier Transform of the point spread function.

$$F[g_1(x)]=\frac{1}{2\pi}\int_{-\infty}^{\infty}g_1(x)e^{-i\rho x}dx$$

$$=\frac{1}{2\pi}\int_{-\infty}^{\infty}\int_{-\infty}^{\infty} g(\sqrt{x^2+y^2})dy\ e^{i\rho x}dx$$

Substituting:

$x=r\cos\theta$
$y=r\sin\theta$
$dydx=r\ drd\theta$

$$F[g_1(x)]=\frac{1}{2\pi}\int_{o}^{\infty}r\ g(r)dr\int_{o}^{2\pi}\exp(-ir\rho\cos\theta)d\theta$$

Note again: $\int_{o}^{2\pi}\exp(-ir\rho\cos\theta)d\theta=2\pi J_o(\rho r)$

So $F[g_1(x)]=\int_{o}^{\infty}r\ g(r)J_o(\rho r)dr$

Q.E.D.

Observe that $F[g_1(x)]$ is intrinsically a one dimensional function, since $g_1(x)$ is; whereas $F[g(r)]$ is two dimensional. The fact that $F[g_1(x)]$ and $F[g(r)]$ reduce to the same form, that is, $H(g(r))$, means that $F[g_1(x)]$, when rotated about its vertical axis, generates a surface which is identical to $F[g(r)]$. Henceforth $F[g_1(x)]$ will refer to this surface. One could inverse Fourier Transform this surface to obtain directly the point spread function, but the procedure is tedious. Instead, a helpful property of Hankel Transforms will be used to simplify the integrations required.

The reason for reducing both Fourier Transforms to Hankel Transforms is that these transforms are self-inverting, i.e., if H(g) represents the Hankel Transform of g then:

$$H\ (H(g)) = g \qquad *$$

*Sneddon op cit., p. 53

From these relationships:

$$F[g] = H(g) = F[g_1]$$

we ascertain:

$$g(r) = H(F[g_1(x)])$$

or, finally:

$$g(r)=\int_o^\infty \rho F[g_1(x)]J_o(\rho r)d\rho$$

Where $$F[g_1(x)]=\frac{1}{2\pi}\int_{-\infty}^{\infty} g_1(x)e^{-ipx}dx$$

This last integral is easily evaluated analytically for

$$g_1(x)=L_o e^{-0.7|x|}$$

$$F[g_1(x)]=\frac{Lo}{2\pi}\int_{-\infty}^{\infty} e^{-0.7|x|}e^{-ipx}dx$$

$$=\frac{Lo}{2\pi}\,\frac{1.4}{.49+\rho^2}$$

The problem then reduces to evaluating this integral:

$$g(r)=\frac{1.4Lo}{2\pi}\int_o^\infty \frac{\rho Jo(\rho r)}{0.49+\rho^2}d\rho$$

This was carried out numerically on an IBM 7094 digital computer, using a Simpson integration routine (SIMSON) with an automatic error control scheme which provides four significant figures. Results are plotted in Fig. 4-2.

Appendix II

Target Spectra and Effect of The 7.5° Aperture

The spectral purity, otherwise known as the harmonic content, of the sine wave grating targets used in the experiments reported in Chapter 4 is described in this appendix. We associated a single spatial frequency with each target; this spatial frequency was simply the reciprocal of the wavelength of the grating. Since the targets are of finite extent, they contain other spatial frequencies, that is, spectral impurities, associated with the circular aperture through which they were viewed.

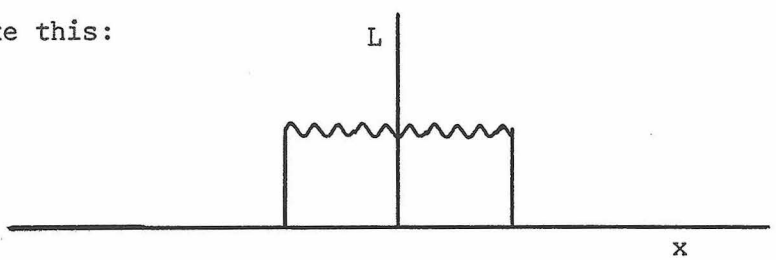
If the MTF of a linear optical system with a field diameter greater than 7.5° were measured with these gratings, distortions of the measured MTF would result. The degree of distortion would depend upon the amount of spectral impurities present in the targets. Although the fovea subtends less than one-third of the target diameter, the field subtended by the whole retina is much greater than 7.5°. Thus, despite fact that edge effects can be neglected as far as foveal acuity is concerned, they are important to the peripheral retina. Moreover, they can be quite simply derived analytically. Thus the following discussion of target spectra not only provides a measure of the reliability of the MTF's described in Chapter 4, but also it provides convenient measures, so to speak, of the amount of grating pattern relative to the amount of aperture pattern.[1]

1. For a less analytic and more pragmatic discussion of the significance of edge effects in vision, see E. T. Burtt and W. T. Catton, Science 151:224, 1966.

The first section deals with a sine wave grating truncated by a long vertical slit, since this one dimensional simplification is much easier to handle conceptually and analytically than the two dimensional circular aperture, yet it illustrates well the spectral changes caused by the presence of edges. The spectrum of a sine wave grating in a circular aperture is presented in the second section.

One Dimensional Approximation:

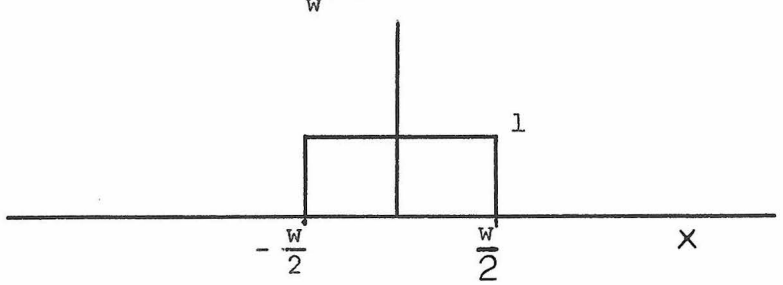
The one-dimensional luminance profiles of our targets look roughly like this:



which, neglecting variations of luminance along the y axis, may be resolved into these components:

$$L(x)=[a \sin(2\pi f_o x)+c]\,\mathrm{rect}_w(x)$$

where $\mathrm{rect}_w(x)$ is:



We are interested in the shape of the Fourier Transform of L(x), i.e.:

$$F[L(x)]=F[(a \sin 2\pi f_o x+c)\,\mathrm{rect}_w(x)]$$

$$=F[a \sin 2\pi f_o x]*F[\mathrm{rect}_w(x)]$$

$$+F[c\,\mathrm{rect}_w(x)]$$

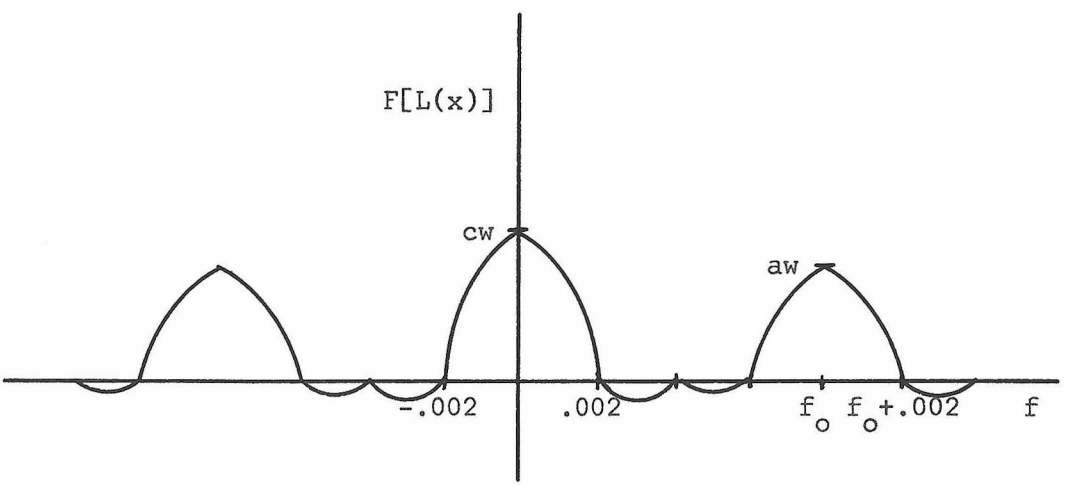
where * denotes convolution

Now $F[a \sin 2\pi f_o x]=a\delta(\pm f_o)/2i$

and $F[\mathrm{rect}_w(x)]=w\frac{\sin\pi wf}{\pi wf}$

so $F[L(x)]=aw\frac{\sin\pi w(f\pm f_o)}{\pi w(f\pm f_o)} + cw\,\frac{\sin\pi wf}{\pi wf}$

W is fixed at 450 min arc for all gratings, thus the spectrum of L(x), for a grating of spatial frequency f_o is:



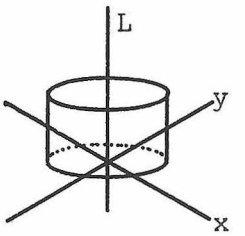
The ratio of c to a varies from grating to grating but is usually in the neighborhood of 5 to 10. Several aspects of this spectrum are noteworthy: First, the DC component must always be larger than the component due to sinusoidal modulation, since for luminance - which can never be negative - c must be larger than a. This holds true for any input pattern regardless of width or harmonic content. Second, the spectrum approaches two delta functions as the width of the pattern increases, and the rate of approach to this sort of spectrum is independent of the spatial frequency of the pattern. In other words, for a fixed pattern size all sine wave targets have an equal amount of spectral "smear." It is, however, common to plot f along a logarithmic axis, in which case the spectral smear appears to narrow with increasing spatial frequency, and conversely, to broaden at low spatial frequency.

The Circular Aperture

Truncation of the sine wave grating by a circular aperture, instead of by a long slit aperture as described above, introduces nothing conceptually novel, but does complicate the analysis of the spectral components of the target by requiring consideration of one additional space dimension, and consequently, one additional spatial frequency dimension.

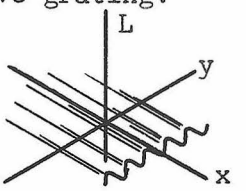
Proceeding as before, we decompose the luminance distribution of the target into three components:

a pillbox:



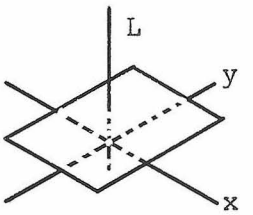
$$P(x,y)=\begin{cases}1 & \text{for} \sqrt{x^2+y^2} < r \\ 0 & \text{elsewhere}\end{cases}$$

an infinite sine wave grating:



$$S(x,y)=a \sin(2\pi f_o x)$$

and a constant term:



$$C(x,y)=c$$

The target luminance distribution, T(x,y), may be expressed as

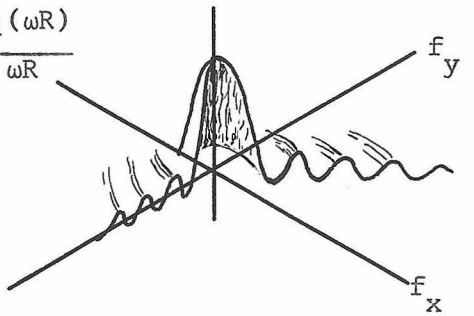
$$T(x,y)=[S(x,y)+C(x,y)]P(x,y)$$

We then reconstruct the spatial frequency distribution of T(x,y) from the well known[1] frequency distributions of P, S and C. The relationship of their spectra is:

$$F[T]=F[S]*F[P]+F[C]*F[P]$$

1. see, for derivations, E. L. O'Neill Introduction to Statistical Optics, Addison Wesley, Reading, Mass., p.84, 1963.

$F[P]=\frac{J_1(\omega R)}{\omega R}$



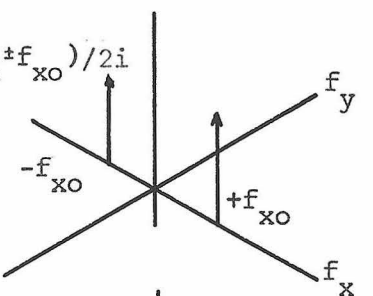
$\omega=2\pi r \quad r=\sqrt{f_x^2+f_y^2}$

where R=225 min arc$=\frac{7.5^\circ}{2}$

J_1= a first order Bessel function.

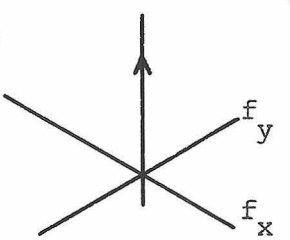
the rotational analog of the $\frac{\sin x}{x}$ curve described previously.

$F[S]=a\delta(f_x \pm f_{xo})/2i$



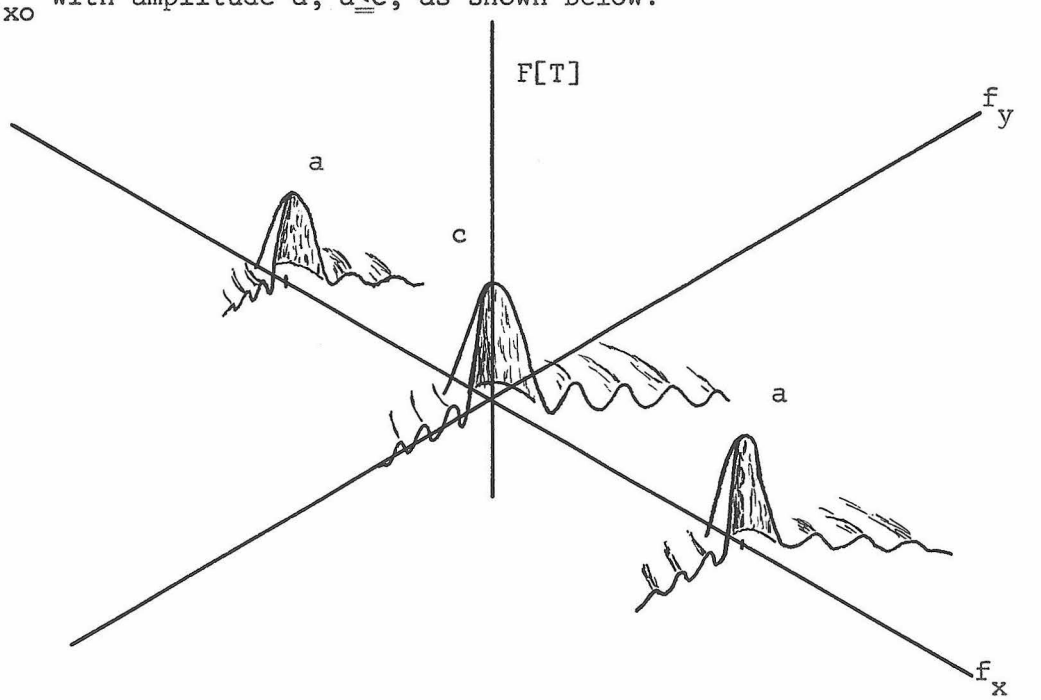
two delta functions

$F[C]=c\delta(f_x)$



a delta function at the origin

The target spectrum is therefore the Bessel pattern reproduced about the origin, with peak amplitude C, and reproduced about $+f_{xo}$ and $-f_{xo}$ with amplitude a, $a \leq c$, as shown below:



The first zero of J_1 is at 3.83, i.e.,

$$J_1(3.83)=0$$

and this first cutoff may be used as a convenient measure of the spread of spatial frequencies around $\pm f_{xo}$.

$$3.83=\omega R=2\pi f_c(225) \text{ cycles/min arc}$$

$$f_c = 0.0027 \text{ cycles/min arc}$$

Thus the main lobe of each of the three J_1 patterns in the above sketch is 0.0054 cycles/min arc wide at the base, regardless of the spatial frequency of the grating f_{xo}. As one might expect, this is slightly wider (by 0.001) than the spectral smear calculated for the one-dimensional case.

In the frequency domain the acuity task may be viewed in the following way. The subject is initally presented with a target which has a large amplitude (c) low frequency lobe extending from 0 spatial frequency out to 0.0027 cycles/min arc, and a slightly smaller amplitude (a) lobe centered at the spatial frequency of the grating. The two main lobes overlap slightly for the grating of .005 spatial frequency, but do not overlap for the rest of the gratings. Then as (a) decreases, and (c) remains constant, the subject must determine the lowest amplitude (a) may have and still be recognizably different from the distribution about the lobe of amplitude (c).

This view of the task points out the subject's difficulty with low spatial frequency gratings, for here the main lobes of the grating and aperture distributions very nearly overlap. This frequency analysis also shows the extent to which one spatial frequency may be associated with a particular target, as was done in determining the modulation transfer functions. Instead of relating mean sensitivity to one particular spatial frequency, each mean sensitivity should be associated with a band of spatial frequencies of width approximately 0.005 cycles/min arc. A sketch of these distributions of spatial frequencies at threshold is shown below. Data are from the stabilized curve in Fig. 4-9.