INFORMATION TO USERS

This was produced from a copy of a document sent to us for microfilming. While the most advanced technological means to photograph and reproduce this document have been used, the quality is heavily dependent upon the quality of the material submitted.

The following explanation of techniques is provided to help you understand markings or notations which may appear on this reproduction.

1. The sign or "target" for pages apparently lacking from the document photographed is "Missing Page(s)". If it was possible to obtain the missing page(s) or section, they are spliced into the film along with adjacent pages. This may have necessitated cutting through an image and duplicating adjacent pages to assure you of complete continuity.

2. When an image on the film is obliterated with a round black mark it is an indication that the film inspector noticed either blurred copy because of movement during exposure, or duplicate copy. Unless we meant to delete copyrighted materials that should not have been filmed, you will find a good image of the page in the adjacent frame.

3. When a map, drawing or chart, etc., is part of the material being photographed the photographer has followed a definite method in "sectioning" the material. It is customary to begin filming at the upper left hand corner of a large sheet and to continue from left to right in equal sections with small overlaps. If necessary, sectioning is continued again—beginning below the first row and continuing on until complete.

4. For any illustrations that cannot be reproduced satisfactorily by xerography, photographic prints can be purchased at additional cost and tipped into your xerographic copy. Requests can be made to our Dissertations Customer Services Department.

5. Some pages in any document may have indistinct print. In all cases we have filmed the best available copy.

University
Microfilms
International

300 N. ZEEB ROAD, ANN ARBOR, MI 48106
18 BEDFORD ROW, LONDON WC1R 4EJ, ENGLAND

MILLER, MICHAEL

CONTRAST SENSITIVITY FUNCTIONS IN NORMAL AND DESTRIATED MONKEYS

City University of New York PH.D. 1979

University
Microfilms
International 300 N. Zeeb Road, Ann Arbor, MI 48106 18 Bedford Row, London WC1R 4EJ, England

CONTRAST SENSITIVITY FUNCTIONS
IN NORMAL AND DESTRIATED MONKEYS

by

MICHAEL MILLER

A dissertation submitted to the Graduate Faculty
in Biomedical Science in partial fulfillment of
the requirements for the degree of Doctor of Philosophy
at the Mount Sinai School of Medicine
of The City University of New York.

1979

This manuscript has been read and accepted by the Graduate Faculty in Biomedical Science in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

July 17, 1979
date

Chairman of Examining Committee

July 17, 1979
date

Executive Officer

Morris B. Bender

Ivan Bodis-Wollner

Tauba Pasik

Supervisory Committee

The City University Of New York

ABSTRACT

CONTRAST SENSITIVITY FUNCTIONS IN NORMAL AND DESTRIATED MONKEYS

by

Michael Miller

Advisers: Professors Pedro and Tauba Pasik

The functional properties of extrageniculostriate vision for spatial frequency detection was examined in Rhesus monkeys. Monkeys were presented with a forced-choice between two stationary stimuli, a homogeneous target and a vertically oriented sinusoidal grating. Stimuli were transilluminated figures at seven spatial frequencies, 0.5, 1.0, 2.0, 4.0, 8.0, 16 and 32 c/deg in 0.1 log unit steps of contrast from 0.79 to 0.006. Contrast thresholds were determined before and after histologically verified total bilateral ablation of the striate cortex by two procedures, an adaptive up-down method and the method of constant stimuli.

Contrast sensitivity (threshold^{-1}) functions for normal and destriated monkeys have the characteristic shape of an inverted "J." The high and low frequency limbs are related exponentially with spatial frequency and the peak of the curves are about 2.0 c/deg. The dimensions of the functions, however, change significantly following the ablation. Sensitivity is depressed at all spatial frequencies by a factor of about 22, i.e. a mean 27 decibel flat loss. The high frequency cut-off point which gives a measure of visual acuity, averaged for the group, is 43 c/deg preoperatively and 12 c/deg postoperatively, a

3.6-fold loss of resolution. The variability of the response at each frequency in the up-down method and the slope of the psychometric function derived from the method of constant stimuli provide a measure of instability and precision, respectively. These indices are inversely related. Preoperatively, precision was significantly greater at high than at low spatial frequencies. Postoperatively, precision is similar at all frequencies and is lower than preoperatively determined values.

The results show that destriated monkeys can detect gratings although to a lesser degree than normal animals. Along with previous findings of a persistent though deficient capacity for bar orientation discrimination, these data may explain the residual pattern perception already demonstrated in such animals. Since variability of performance during contrast threshold determinations is dependent upon spatial frequency preoperatively but not postoperatively, it appears that, whereas two mechanisms operate in normal monkeys, only one functions in destriated animals. Based upon available evidence, it may be conceivable that these mechanisms are related to the electrophysiologically identified X- and Y-cell systems. A model for suprathreshold performance is proposed using values of contrast thresholds and of the slope of the psychometric function.

ACKNOWLEDGEMENTS

I wish to thank Drs. Pedro and Tauba Pasik, Professors of Neurology at the Mount Sinai School of Medicine of C.U.N.Y. Their aid and counsel was instrumental in every phase of this study.

Dr. Ivan Bodis-Wollner, Associate Professor of Neurology at the Mount Sinai School of Medicine of C.U.N.Y. provided invaluable instruction and guidance through the world of contrast sensitivity. Both he and Lee Mylin made it possible for me to produce the stimuli for this study.

I would like to thank Dr. Morris Bender, Professor Emeritus of Neurology at the Mount Sinai School of Medicine of C.U.N.Y., Dr. William Battersby, Professor of Psychology at Queens College of C.U.N.Y., and Dr. Anthony Movshon, Associate Professor of Psychology at New York University for their criticisms and editorial assistance.

Heartfelt thanks to Victor Rodriguez for his technical assistance in all phases of the project.

I appreciate the help of Dr. Aran Safir, Professor of Ophthalmology at the Mount Sinai School of Medicine of C.U.N.Y. for the use and interpretation of results from the Ophthalmetron. I would like to thank Alba Flores for her aid in refracting the monkeys.

I would like to express my gratitude to Norman Katz and Marilyn Ilvento for their help in the photography and Julio Aviles for his aid on the histology.

I wish to thank Minerva Travieso for typing the voluminous drafts and the final version of this dissertation.

For her support through joy and grief, I thank Christine Waters.

This project was funded by a grant, #MH02261, from the National Institute of Mental Health to Drs. P. and T. Pasik.

TABLE OF CONTENTS

TABLE OF CONTENTS (CONTINUATION)

TABLE OF CONTENTS (CONTINUATION)

LIST OF TABLES

LIST OF FIGURES

LIST OF FIGURES (CONTINUATION)

INTRODUCTION

The optical system of the eye globe forms an image of a visual stimulus over the mosaic of photoreceptors. The function of these structures coupled with subsequent processing of the central nervous system defines the resolving power of the visual system. The resolution of stimuli occurs within the realms of time and space. The discrimination of stimuli with respect to time determines quantities such as flicker fusion frequency. The capacity to resolve differences in space defines visual acuity.

Two major determinants of visual acuity are luminance and retinal location (Mandelbaum and Sloan, 1947). At photopic levels, visual acuity is maximal in the fovea, from which there is a precipitous decline. On the other hand, the fovea is relatively blind at scotopic luminance and under those conditions maximal acuity is attained four degrees from the center of the visual field. Classically, this phenomenon is explained by the differential arrangement of rods and cones (Østerberg, 1947). Moreover, this distribution coincides with the distribution of retinal ganglion cells as well as the topographic representation in the lateral geniculate body and the cortex.

Neurons along the retinogeniculostriate pathway in the monkey respond to a restricted band of spatial frequencies (DeMonasterio, Gouras and Tolhurst, 1976; Marroccq 1976; Schiller, Finlay and Volman, 1976). Psychophysical findings in humans verify these results (Blakemore and Campbell, 1969). In addition, investigations have shown orientation selective mechanisms within the visual system (Campbell and Kulikowski, 1966; Gilinsky, 1968), the results of which are corroborated by unit studies of the monkey visual cortex (Hubel and Wiesel, 1968). Thus, the occipital cortex acts as a structure in which the processing of spatial frequency and orientation are superimposed (Maffei and Fiorentini, 1977). As these properties are instrumental for pattern recognition, such arrangements supports the concept that the striate cortex is essential for this function (Blakemore and Campbell, 1969).

Monkeys deprived of striate cortex, however, exhibit visual behavior which includes some residual capacity for pattern discrimination (Schilder, Pasik and Pasik, 1971). Moreover, such animals can discriminate an oblique from a vertical bar although with less precision than normal animals (Pasik, Pasik, Nolan and Solomon, 1976). The purpose of this study is to explore the capability of Rhesus monkeys with and without striate cortex to make discriminations based upon spatial frequency information.

LITERATURE SEARCH

Visual acuity can be defined by the angle, in degrees, subtended by the finest detectable detail for a given set of conditions (Bartley, 1951). Clinical tests of acuity such as the Snellen alphabet, the Landolt ring, and the just perceptible interspace require subjects to detect gaps in high contrast stimuli. These tests,however, do not examine detection thresholds for coarser stimuli at reduced levels of contrast.

Recently, acuity testing has involved the use of gratings composed of a repeating sinusoidal waveform. Along one dimension luminance varies sinusoidally, whereas luminance is constant in the perpendicular dimension. Thus, a grating appears as a continuous series of alternating light and dark bars. With such stimuli, contrast and spatial frequency (number of cycles of a waveform included in one degree of visual angle) can be varied. Over the past fifteen years, sinusoidal gratings have become the stimulus of choice in vision research, since the data can be analyzed by Fourier methods. According to Fourier analysis, sinusoids represent the simplest waveform. Complex stimuli including those containing sharp edges such as square wave and triangular waves can be reduced for analysis into their sine wave components. Possibly more important, sinusoids of various amplitudes and periods can be superimposed to construct any more complex waveform.

A. Contrast Sensitivity Functions

One of the most useful psychophysical values in describing responsiveness in a task is threshold performance which signifies the point in a continuum at which an effect begins to be produced. A contrast threshold can be determined for each spatial frequency which describes the grating with the minimal contrast required to perceive a waveform. Although various definitions of contrast have been adopted in the classic literature, the present study uses the current concept which has been applied to contrast sensitivity functions wherein contrast is considered as the difference in peak and trough luminance divided by their sum. This definition is useful in that contrast ranges from zero to one and it is founded on peak to mean luminance as opposed to a peak to peak luminance difference. A graph of the contrast threshold at each spatial frequency is shaped like a "J". It identifies the limits of suprathreshold and infrathreshold performance, the areas above and below the curve, respectively.

Contrast sensitivity, the reciprocal of the threshold, plotted against spatial frequency results in an inverted "J"-shaped function (Shade, 1956). The point at which the curve intersects the abscissa, the line $y = 1.00$ (contrast = 1.00), represents a grating discriminable only at maximum contrast. This point which is about 50 cycles per degree (c/deg) in humans adapted to photopic conditions has been correlated with clinical acuity measures such as the Snellen alphabet and the Landolt ring (Green, 1970). In the monkey, the cut-off point is about 46 c/deg (DeValois, Morgan and Snodderly, 1976) a value which correlates well with acuity measures previously determined in normal monkeys (Weinstein and Grether, 1940; Weiskrantz and Cowey, 1963; Cowey and Ellis, 1967). As spatial frequency decreases, less contrast is necessary for a subject to perceive the grating, hence the threshold decreases and contrast sensitivity increases proportionately. This trend continues until a peak sensitivity is attained at about 4.0 c/deg. As the frequency falls below this peak, contrast sensitivity is attenuated. Whereas the high frequency limb can be expressed as an exponential function of spatial frequency, the low frequency limb is inconsistent (Blakemore and Campbell, 1969). The nature of the decay of sensitivity at low spatial frequencies is not clear. Some investigators have speculated on the possible role of eye movements or some type of inhibitory effect (Nachmias, 1967; Kelly, 1977).

Spatial characteristics of stimuli, such as target size and number of cycles, exert a profound influence upon the contrast sensitivity function. Variations of the size of the target predominantly affect the low frequency response. Not only does sensitivity increase but the contrast sensitivity function shifts to the left with larger targets (Campbell and Robson, 1965; Barakat and Lerman, 1967). A crucial variable in low spatial frequency detection is the absolute number of cycles contained in the grating. Apparently with less than four cycles the response depends more upon the number of cycles than on the spatial frequency (Savoy and McCann, 1975). Other studies espouse that seven cycles is the critical number (Barakat and Lerman, 1967).

The overall contrast sensitivity function also is determined in part by the mean luminance of stimuli (Shober and Hilz, 1965). A decrease in mean luminance is associated with a reduction of contrast sensitivity at all spatial frequencies and a shift to the left of the peak sensitivity and the high frequency cut-off point. In addition, at luminance levels below 5×10^{-4} ftL the low frequency decline is lost.

The manner of temporal presentation further shapes the contrast sensitivity function. Presenting the stimuli either abruptly or gradually does not influence the response except at spatial frequencies below 0.5 c/deg. In that range, sensitivity is increased markedly by abrupt presentation (Furchner, Thomas and Campbell, 1977). The stimulus duration also determines some dimensions of the contrast sensitivity function. With short exposures, the peak sensitivity shifts to the left (Nachmias, 1967), and no low frequency decline is evident (Arend, 1976). Temporal modulation increases sensitivity at low frequencies, whereas the high frequencies are relatively unaffected (Robson, 1966; Kelly, 1978).

How does the optical apparatus affect contrast sensitivity? Taking into account the properties of the dioptric media, a subject's response to sinusoidal gratings on an oscilloscope can be predicted from that determined by projecting diffraction patterns directly upon the retina. Thus, the optics of the eye does not appear to affect grating detection. If that were the case, the critical structures limiting resolution of visual stimuli of a non-astigmatic emmetrope would be the neural elements (Campbell, 1974). Contrast sensitivity may be impaired by the size of the pupil (Campbell and Green, 1965). As the pupillary diameter increases above 2.0 mm, contrast detection is decreased markedly due to spherical aberration. Conversely, maximum constriction of the pupil may create diffraction effects. Uncorrected myopes demonstrate a general depression of contrast sensitivity at all frequencies (Maffei and Fiorentini, 1976), whereas deficits of sensitivity are most marked at high frequencies for astigmatic humans (Campbell and Green, 1965).

Contrast sensitivity functions also have been described in nonhuman primates, the squirrel monkey (Merigan, 1976), owl monkey (Jacobs, 1977), and Rhesus (Harding and Yates, 1976) and other macaques (DeValois, Morgan and Snodderly, 1974). The response of the latter animals to grating stimuli is similar to that of humans as noted by the shape and dimensions of the contrast sensitivty function and of the effect of mean luminance upon it (see above) (DeValois, Morgan and Snodderly, 1974).

B. Bases for Pattern Perception

In the past ten years, a great emphasis has been placed upon the possible role of integrating spatial orientation and spatial frequency information as an important determinant of pattern perception (Blakemore and Campbell, 1969). Psychophysical experiments have explored the role of orientation selectivity in humans (Campbell and Kulikowski, 1966; Gilinsky, 1968). In a masking experiment, a maximal effect is observed if the test grating is oriented similarly to the masking grating. No such influence is apparent with perpendicularly oriented stimuli. The masking effect is reduced to 50% when the angle between conditioning and test gratings is 12 to 15 degrees. Apparently, this phenomenon does notdepend upon the optics of the eye, and, therefore, appears to be a direct result of neural processing (Campbell, Kulikowski and Levinson, 1966).

Furthermore, there is psychophysical evidence that the human visual system also uses a number of spatial frequency channels (Campbell and Robson, 1965; Blakemore and Campbell, 1969). An elevation of contrast threshold is observed in subjects who are initially adapted to a sinusoidal grating of the same frequency. A lesser degree of this masking effect is seen when the frequency of the test grating is different than that of the adapting (conditioning) stimulus. The rise in threshold is limited to a narrow range of frequencies spanning a bandwidth of about one octave (a doubling of the frequency) (Blakemore and Campbell, 1969). The bandwidths of channels are about 3.5 and 1.5 octaves at low and high spatial frequencies, respectively (Legge, 1978).

The concept of a multiple channel spatial frequency system is supported by the measurements of Graham and Nachmias (1971) who observed that detection of complex gratings composed of two overlapping sinusoidal waveforms could be explained by the summed response to the individual components. The integrity of this multiple channel system is maintained even at low luminances and high drift rates (Graham, 1972). Contrariwise, other information demonstrates an interaction among channels, possibly based on lateral inhibitory processes (McCarter and Roehrs, 1976).

The function of two distinct visual mechanisms in normal humans has been explored using temporally modulated gratings (Kulikowski and Tolhurst, 1973). The modulation is accomplished either by presenting the grating in alternation with a blank screen equated for mean luminance, or by shifting the phase of the sinusoidal grating 180 degrees. The temporal frequency is constant during both types of presentations.

The phase shifting procedure produces changes in local luminance which are twice as large as those generated by the alternation method. Human subjects are twice as sensitive to the shifting gratings at frequencies below 2.5 c/deg and equally sensitive to both types of presentations at frequencies above 6.0 c/deg. Furthermore, temporally modulated gratings of frequencies above 4.0 c/deg appear to be stationary at low contrast (Kulikowski, 1971). According to the authors, this evidence implicates the operation of two systems, one sensitive to temporal modulation and low frequencies, and another insensitive to time-varied stimuli and responsive to high spatial frequencies. Additional support for these conclusions are given by masking experiments (Tolhurst, 1973; Legge, 1978).

The identity of the two systems is highlighted by the separation of the flicker threshold from the grating detection threshold, that is to say, the temporal and spatial components of the stimulus (Keesey, 1972). With low spatial frequency gratings, flicker is detected at lower contrast than that required for detection of the spatial aspects of the grating, and at high spatial frequencies the effect is reversed, i.e. spatial discrimination occurs at lower contrasts than flicker detection (Kulikowski and Tolhurst, 1973). The two systems appear to interact to some degree (Bodis-Wollner and Hendley, 1979), and both seem to be affected equivalently by optical aberrations such as myopia and amblyopia (Wood and Kulikowski, 1978).

C. Cortical Processing

The striate cortex is considered to be essential for pattern perception. In fact, it is the first structure in which spatial orientation and frequency information are superimposed. Neurons in the visual cortex of cats and monkeys are classified as simple, complex and hypercomplex cells by their differential response to bar stimuli (Hubel and Wiesel, 1962, 1968; Pettigrew, Nikara and Bishop, 1968). Simple cells are excited maximally by line stimuli with a specific orientation. Complex cells also respond to line stimuli, but unlike simple cells, they fire maximally to an appropriately oriented stimulus independent of its location within a relatively larger receptive field. Moreover, they respond optimally to the displacement of such stimulus in a specific direction. Hypercomplex cells are sensitive to stimuli covering restricted portions of the receptive field and, therefore, comprise a great variety (Hubel and Wiesel, 1965, 1968).

The response of simple and complex cells to grating stimuli also has been examined. Simple cells appear to respond in a sustained fashion, whereas stimulation of complex cells yields transient responses (Ikeda and Wright, 1974). This is reminiscent of X- and Y-cell types, respectively, which have been described at retinal (Enroth-Cugell and Robson, 1966; DeMonasterio, Gouras and Tolhurst, 1976) and geniculate levels (Cleland, Dubin and Levick, 1971; Marrocco, 1976). It has been suggested that the slow conducting geniculate X-cell axons drive the simple and some hypercomplex cells, and that complex cells are driven by fast conducting Y-cell axons (Hoffman and Stone, 1971; Stone and Dreher, 1973). This is contrary to the implications of serial elaboration put forth by the studies of Hubel and Wiesel (geniculate neuron to simple cell to complex cell to hypercomplex cell) as it extorts the presence of multiple parallel systems of inputs and not one pathway.

The parallel network hypothesis is substantiated by the contrast sensitivity functions of simple and complex cells. Neurons in the striate cortex of the cat (Campbell, Cooper and Enroth-Cugell, 1969; Ikeda and Wright, 1975) and of the monkey (Campbell, Cooper, Robson and Sachs, 1969; Schiller, Finlay and Volman, 1976) respond to limited bands of spatial frequencies. These bandwidths are the narrowest in the visual system, measuring about one and three octaves for the simple and complex cells, respectively (Maffei and Fiorentini, 1973a).

Do the cortical neurons which respond selectively to spatial frequencies also exhibit orientation specificity? By moving sinusoidal gratings with a particular angularity across the receptive field, it is possible to combine the effects of spatial frequency and orientation. The interaction of these factors play a role in determining the amplitude of the response of cortical cells (Campbell, Cooper and Enroth-Cugell, 1969). Not only do these units exhibit frequency selectivity, but the response amplitude decreases linearly with orientations above or below the preferred angle. The interaction of spatial frequency and orientation information is, in fact, highly organized in the striate cortex. Units responsive to the same orientations are stacked in columns, whereas isospatial frequency responses are obtained in rows parallel to the pial surface. Thus, a lattice network of cells is present in which each unit responds to a unique orientation and spatial frequency combination (Maffei and Fiorentini, 1977).

The striate cortex primarily receives input from the retinogeniculostriate pathway. Efferents from the retina, however, do not go solely to the lateral geniculate nucleus. Some project to the superior colliculus and various other midbrain structures. Presentation of a sinusoidal grating distinguishes three classes of retinal ganglion cells, X-, Y- (Enroth-Cugell and Robson, 1966: Cleland, Dubin and Levick, 1971; DeMonasterio, Gouras and Tolhurst, 1976), and W-cells (Stone and Hoffman, 1972; Schiller and Malpeli, 1977). X-cells which respond lineraly to contrast project predominantly to the parvocellular laminae of the dorsal lateral geniculate nucleus. In monkeys, geniculate efferents project only to the striate cortex (Polyak, 1957). Y-cells, on the other hand, respond nonlinearly to contrast and their axons terminate in the magnocellular laminae of the geniculate nucleus and the midbrain, primarily the superior colliculus (Schiller and Malpeli, 1978). The response characteristics of W-cells are less well defined and they project mostly to midbrain structures (Fukuda and Stone, 1974). Visual information from the colliculus reaches the circumstriate cortex through the inferior pulvinar (Mathers, 1971: Ogren and Hendrickson, 1977) presumably via Y- and/or W-cells. It should be noted that circumstriate cortex of the monkeys is rich in complex cells (Hubel and Wiesel, 1970).

D. Lesion Studies

Lesions along the retinogeniculostriate pathway produce well known visual field defects. A total bilateral cortical ablation in the monkey, however, does not eliminate visually guided behavior (Klüver, 1941; Pasik and Pasik, 1971). Such subjects retain the ability to detect differences in luminous flux, acting like a simple photocell. The difference threshold for flux ($\Delta F/\bar{F}$) in monkeys without visual cortex is 0.23 (Klüver, 1942). When the ablation is restricted so that the striate cortex (area 17) still is removed totally but the circumstriate cortices (areas 18 and 19) are only partially damaged, quite different behavior results. After extensive training such monkeys are capable of discriminating stimuli differing in total luminous flux, but also between flux-equated figures varying in luminance and area (Pasik, Pasik and Schilder, 1969; Schilder, Pasik and Pasik, 1971). Moreover, such animals apparently can master discriminations based upon wavelength cues (Pasik and Pasik, 1971; Schilder, Pasik and Pasik, 1972), and can reach accurately to visual stimuli (Weiskrantz, Cowey, and Passingham, 1977; Feinberg, Pasik and Pasik, 1977, 1978).

Extensive lesions of the visual cortex abolish form vision (Klüver, 1941). This conclusion, however, should be taken with caution because such monkeys were able to discriminate between a 38 cm^2 square from a stimulus containing 76 circles, 0.5 cm^2 each of the same luminance, thus demonstrating some capacity to make judgements based upon topological cues. Following a more restricted lesion, however, monkeys can be retrained to differentiate between a circle and a triangle of equal luminance, area and flux (Schilder, Pasik and Pasik, 1972). This remaining form vision may be attributed to residual capacity to discriminate various orientations and spatial frequencies. In fact, normal and destriated monkeys can differentiate between vertical and horizontal bars. Moreover, the bar need only be over 5 degrees from vertical in order for the normal animal to detect the difference. Destriated animals require a difference in excess of 17 degrees (Pasik, Pasik, Nolan and Solomon, 1976). Spatial frequency detection has not been determined in totally destriated Rhesus monkeys. Visual acuity has been examined in monkeys with partial striatectomies (Weiskrantz and Cowey, 1963). Whereas normals can discriminate between lines spaced as closely as 0.57 to 1.09 min of arc, operated animals require from 0.64 to 1.66 min of arc. It appears that the reduction of acuity is related directly to the amount of macular cortex excised.

Some clinical studies of contrast sensitivity have been conducted in humans with cerebral lesions (Bodis-Wollner, 1972; Bodis-Wollner and Diamond, 1976). Three types of deficits have been described, a high frequency loss, a mid-frequency or notch loss, and a flat loss of contrast sensitivity at all spatial frequencies (Bodis-Wollner, 1972) lending further support to the multi-channel hypothesis. There appears to be no relationship between the type of loss and the pathology of the lesion, but high frequency losses may result from the elevated susceptibility of the associated channels to hypoxia, hypotension or both (Bodis-Wollner, 1976).

MATERIALS AND METHODS

A. Subjects

The subjects were six experimentally naive Rhesus monkeys (*Macaca mulatta*) that weighed between 1.7 and 2.4 kg at the beginning of the study. Table 1 gives their sex and their weights at various phases of the study. Four animals (878, 880, 887 and 890) completed the study. One other monkey (879) contracted a cutaneous *Staphylococcus aureus* infection after surgery and was not tested postoperatively. The last subject (881) died from an enteritis, after about half way in the preoperative testing.

B. Neurological and Ophthalmological Examination

B. 1. General. Subjects were examined for convergence, and for pupillary and blink reflexes in response to light stimuli. General behavior in the home cage and experimental apparatus was also noted.

B. 2. Electrooculography. Animals were tested for the presence of two visually induced eye movements, optokinetic (O.K.N.) and flicker-induced nystagmus (F.I.N.) (Pasik & Pasik, 1975).

A monkey was placed before a stimulus in a dark room and restrained in a primate chair specially equipped with a form-fitting helmet. Three platinum needle electrodes were inserted subcutaneously at the bridge of the nose and the outer canthi, thereby allowing horizontal eye movements to be recorded for each eye individually. The potential difference between electrode pairs was amplified and recorded on paper by a Grass

Table 1. Subjects

Monkey	Sex	Start (kg)	Surgery (kg)	End (kg)	PTP (wks)
878	M	2.3	2.5	2.7	21
879	F	2.3	2.7	--	--
880	M	2.4	2.6	2.8	20
881	F	2.1	--	--	--
887	M	1.7	2.2	2.6	16
890	M	1.8	2.3	2.6	16

M and F signify male and female, respectively. Start, Surgery, and End denote the weight of the subjects at these points of the study. The postoperative training period (PTP) extends from the day of surgery to the day of refraction and/or perfusion. Dashes indicate phases through which an animal did not pass (see text).

Model 7 Polygraph. Amphetamine sulfate (0.75 mg/kg) was administered intramuscularly to assure alertness throughout the session. Immediately after, O.K.N. to the right and to the left was elicited by the motion of vertical bars moving across a rear projection screen at 1.8 Hz. Stimulation lasted two minutes. About one hour after the amphetamine injection, F.I.N. testing began. A stationary, stroboscopic light at 10 Hz lasting three minutes served as the stimulus for F.I.N., which was induced either directly or through a translucent diffuser (Ganzfeld) (Miller, Pasik,and Pasik, in press).

B. 3. Refraction. Objective refraction of the subject's eyes was obtained by means of an automated apparatus called the Ophthalmetron (Safir, Knoll, and Mohrmann, 1970). The Ophthalmetron automatically measures refractive errors according to the principles of retinoscopy, i.e. the far point determined by the optics of the eye (Safir, 1972).

Monkeys were refracted after all of the preoperative and postoperative data had been accumulated on the day of surgery and at the completion of the study, respectively. About an hour before taking measurements the subject was anesthetized by an intraperitoneal injection of sodium pentobarbital solution (40 mg/kg). Each eye was treated with two drops of a cycloplegic (1.0% tropicamide ophthalmic solution). To produce reliable results the subject was held stationary in a stereotaxic frame and the eyelid was retracted with a speculum. The speculum was particularly important because manually pulling of the eyelid may impose an artificial astigmatism.

In order to make a reading, the eye was aligned with the light source in the Ophthalmetron. During a measurement which took only three seconds, a beam of infrared light scanned the subject's fovea and the photodetector analyzed the reflected beam. A written record expressed the power of the optics in diopters at each meridian of the eye. A number of trials were run to insure against misleading results due to incorrect alignment, artificial astigmatism, and possible effects of variation in the curvature of the lens over time.

C. Apparatus

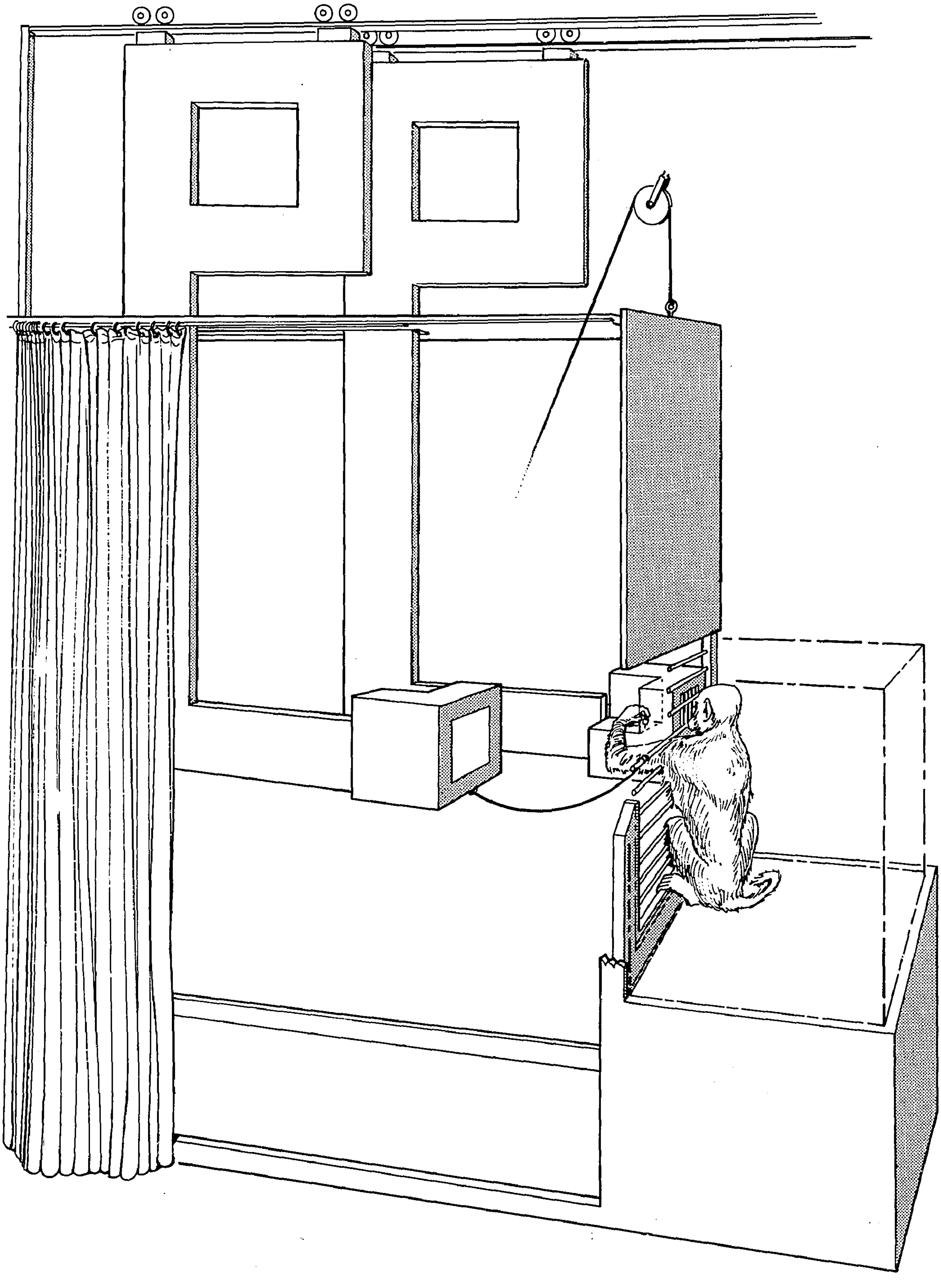
C. 1. Pulling-in device. A forced two-choice situation was presented to the subjects by equipment modelled after Klüver's (1941) pulling-in apparatus (Schilder, Pasik, and Pasik, 1971; Fig. 1). The construct is composed of two compartments, a housing for the subject and the stimuli.

A monkey is placed in a cubicle measuring 60 cm in height, 60 cm in width, and 50 cm in depth. An adapting light situated on the ceiling of the subject compartment appears to the monkey below as a panel 50 cm by 45 cm of relatively homogeneous light with the mean luminance of 1.6 cd/m^2 (see Appendix A.1.). The product of the area and of the adapting light matches the sum of the same products of the two stimuli. The evenness is produced by diffusing the light from two General Electric F8T5-CW fluorescent bulbs with pieces of 3/8 inch thick milk and frosted plexiglass spaced 13 cm and 2 cm from the light source, respectively. The front wall of the cubicle contains a series of eight horizontal 7 mm stainless steel bars. The bars, spaced 5 cm from each other, span the width of the cubicle. Separating the subject cubicle from the stimulus

Fig. 1. Pulling-in device

A forced two-choice situation was presented by the illustrated apparatus. A subject is placed in the compartment on the right from which the subject can view the two stimuli (on the left) when the guillotine door is retracted. To indicate a choice, a monkey pulled on a string attached to a stimulus box bringing the stimulus and the reward within reach.

Each stimulus box, measuring 20 cm on each side, consisted of two parts. The anterior portion was in direct line of sight from the subject cubicle and house the stimulus, whereas the posterior portion which contained the reward was obscured from the animal's sight. The rear section of the stimulus portion had a homogeneous luminous source produced by a serpentine-shaped argon bulb (Model W45 Aristo Grid lamp) and a diffusing material of 1/4 inch thick milk plexiglass. The source transilluminated a target which was slide into a slot before it. The posterior portion of the stimulus box was L-shaped with its open segment (10 cm high, 13 cm wide, and 11 cm deep) pointing medially. The open segment enabled the subject to reach around the anterior portion of the box for the reward (1 cm cube of apple) which was placed on a centrally located pin. The spine of the "L" prevented the monkey from reaching for the apple from the lateral side, forcing a medial approach.



compartment is an opaque guillotine door. It is placed immediately behind the bars, but within the subject compartment and enables the experimenter to separate the monkey from the stimuli. The circuit regulating the adapting light is controlled by a microswitch attached to the upper edge of the guillotine door and the top of the subject compartment. Therefore, the adapting light is turned on only when the door is closed.

The stimulus compartment is 180 cm high, 60 cm wide, and 180 cm deep. The principal component of this section is the two boxes separated by a distance of 25 cm center to center (a minimum of 21 degrees of visual angle when the monkey is at the front of the cage) which house the stimuli. Each box provides a homogeneous light source, the mean luminance of which is 154 cd/m^2 ± 2% (Appendix A.2.). To produce a stimulus, a target is placed in front of the diffuse light source. A target constitutes the transilluminated portion of a photographic negative. A negative is placed in a holder made of clear plexiglass which is masked with opaque black photographic tape Scotch No. 235 except for a 9 cm square opening. Therefore, each stimulus subtends 8 degrees of visual angle in the starting position. The mean luminance of the stimuli thus obtained is 20 cd/m^2. In the back of the stimulus box is a pin on which a cube of apple, 1 cm on a side, is placed at the appropriate times. It serves as an anchor for the reward and assures reliable and repeatable placement on a point directly behind the center of the target.

Each stimulus box is suspended from a separate track in the ceiling of the testing room by a C-shaped strut. A box is attached to the leading edge of the lower arm. Lining the length of the upper arm of the supporting strut is a set of runners which allow each stimulus box to roll independently toward the monkey along its track. Stops are placed along the track to limit the excursion of the stimulus to a distance between 1 and 65 cm from the stainless steel bars. At any place along the excursion, the centers of the stimuli are level with a point midway between the forth and fifth bars. A stimulus box rolls towards the subject at the slightest pull on a string tied to the bottom of the stimulus box and the third bar from the floor.

A false ceiling and the floor are 90 cm from the center of the targets. The lateral walls, of which the left one is a black opaque curtain, are 30 cm from the center line of the stimulus compartment. A small hole in the curtain allowed the experimenter (sitting outside) to view the responses of the monkeys. All exposed surfaces of the stimulus compartment are painted black. Therefore, the stimuli appear to the subject as two figures floating at eye level in a black space.

C. 2. Targets. A set of targets was produced for each of seven spatial frequencies, 0.5, 1.0, 2.0, 4.0, 8.0, 16 and 32 c/deg, with contrast varying from 0.79 in approximately 0.1 log unit steps. The targets for 0.5-8.0 c/deg were provided by achromatic negatives taken of a cathode ray oscilloscope screen. The oscilloscope produced vertically oriented sinusoidal waveforms according to the technique outlined by Campbell and Green (1965). Using an oscilloscope facilitates varying the contrast, which is defined as the difference of the maximum and minimum luminance divided by their sum, and spatial frequency, which is the number of periods of a sine wave component in one degree of visual angle. The fine tuning of the oscilloscope is instrumental in producing a functional series of targets varying in contrast and spatial frequency.

A Graflex camera mounted on a tripod and with the front lens parallel to the oscilloscope screen was used to obtain negatives of 4 inch by 5 inch format Kodak Technical Pan Film SO 115 (Appendix B.1.). This film was chosen over other films such as Kodak Ektrachrome and Polaroid 55 Positive/Negative because it alone satisfied three essential requirements. 1. The resolving power is extremely high (125 lines/mm at a contrast of 0.23) which is important in duplicating the high spatial frequencies. 2. The full scale of grays can be obtained. This is necessary to produce the gradient inherent in sinusoidal functions and the subtlety of the maximum and minimum luminances at low contrasts. 3. The Technical Pan is unique in that not only does it develop the gray scale, but reproduces the high contrasts essential to this study.

An alternative approach was devised to obtain the 16 and 32 c/deg stimuli since the oscilloscope was unable to reproduce the fine gratings which were necessary to make these targets. At each frequency, a 35 mm slide of a square wave grating was projected directly onto the film by a photographic enlarger and defocused in different amounts to produce the set of contrasts. By defocusing, the grating lost its sharp edges and approached a sinusoid. According to Fourier analysis, the most prominent component of a square wave other than the fundamental or first harmonic is the third harmonic. In a square wave of 16 c/deg at a contrast of 1.00, the third harmonic is 48 c/deg at a contrast of

0.33. Monkeys are unable to detect the latter gratings (DeValois, Morgan, and Snodderly, 1974). In the series used in this study, the contrast of the fundamental is reduced to 0.79 or less, and therefore, the contrast of the third harmonic is insignificant in the detection of gratings at 16 c/deg. This reasoning applies even more to the 32 c/deg for which the third harmonic is at 96 c/deg, far above the limit of spatial resolution.

Two targets without any perceptible grating were produced for use as homogeneous stimuli by creating on the oscilloscope a grating of 60 c/deg at a contrast of zero. All negatives were developed according to a strict regimen (Appendix B.2.). After being calibrated, the density of each negative was reduced (Appendix B.2.) so that the mean density of each film was matched with the homogeneous target. Targets were calibrated for contrast, density, and waveform (Appendix A.3.).

D. Procedure

The following method was applied before and after bilateral removal of visual cortex (see below).

D. 1. Pretraining. During pretraining, two identical homogeneous targets were fitted into the stimulus boxes. Animals were taught to relate the stimulus box in the forward position (1 cm from the bars) with a reward. While the room and stimulus box lights were on, subjects were trained to take a piece of apple from the tip of a metal rod. The rod was progressively moved farther from the subject and closer to a stimulus box. Eventually, the apple was placed on the medial edge of the stimulus box and within the monkey's direct sight. The reward was granted only when the monkey used the arm opposite to the box for which it was reaching, i.e. the right arm for the left box and the left arm for the right box. Subsequently, the apple was moved closer to the pin and hence, away from the monkey's sight until the subject reached for the apple sitting on the pin. This procedure was repeated for the other stimulus box. After learning that the stimulus box meant a reward, the boxes were placed in their test positions 65 cm from the bars. To get a box into the forward position and bring the reward within reachable distance, the monkey had to pull on the attached string. Once this task was mastered, the guillotine door was interposed between trials, and soon thereafter the room lights were turned off completing the pretraining period.

D. 2. Formal testing.

D. 2. a. Discrimination test. Following pretraining, each monkey was taught to discriminate a grating of a certain spatial frequency at the maximum contrast of 0.79 from a homogeneous stimulus matched for mean luminance, area, and hence, luminous flux. The position of the grating which was always the reward stimulus, was changed right to left according to pseudorandom sequence created by combining a series of Gellerman schedules in this and all formal testing in the study (Gellerman, 1938). One hundred trials were given each day until criterion proficiency of 90% correct responses was attained and maintained for 200 consecutive trials.

D. 2. b. Frequency thresholds. After mastering the basic discrimination, a frequency threshold determination was attempted (see Table 2). In this test, the highest contrast grating for all seven spatial frequencies was presented in a random order and then the reverse of that sequence. This procedure was repeated five times, i.e. a total of 70 presentations. Thus, each target was given a total of ten times per session. Ten sessions were given with different random series amounting to 100 trials at each frequency. As it is generally accepted in the forced two-choice paradigm, the 75% point was designated as the contrast threshold (Engen, 1971). Contrast thresholds were determined only at spatial frequencies resulting in at least 85% correct responses. An additional determination was given after contrast threshold was obtained at 8.0 c/deg preoperatively and 2.0 c/deg postoperatively.

D. 2. c. Contrast thresholds. Contrast thresholds were determined with gratings of various contrasts, but at the same spatial frequency. These procedures were applied to the seven spatial frequencies in the order of 1.0, 4.0, 2.0, 0.5, 8.0, 16 and 32 c/deg. That is, first each monkey was trained to criterion on the discrimination of the maximum contrast target followed by the threshold determination for that frequency (Table 2).

Two approaches were used to determine the threshold, an up-down procedure (Bekesy, 1947) and method of constant stimuli. The methods differ in that the former is an adaptive procedure, i.e. the stimulus on any trial is determined by the response in the preceding trial, whereas in the latter technique the response of the subject has no bearing upon subsequent trials. The up-down procedure was used to

Table 2. Schedule of Formal Testing

Preoperative stage	Postoperative stage
1. Discrimination-1.0 c/deg	1. Discrimination-1.0 c/deg
2. Freq. thresh. *	2. Control for flux cues-1.0 c/deg
3. Discrimination-1.0 c/deg*	3. Freq. thesh.
4. Contr. thresh.(u.-d.)-1.0 c/deg	4. Discrimination-1.0 c/deg
5. Contr. thresh.(c.s.)-1.0 c/deg	5. Control for flux cues-1.0 c/deg
6. Discrimination-4.0 c/deg	6. Contr. thresh. (u.-d.)-1.0 c/deg
7. Contr. thresh.(u.-d.)-4.0 c/deg	7. Contr. thresh. (c.s.)-1.0 c/deg
8. Contr. thresh.(c.s.)-4.0 c/deg	8. Discrimination-2.0 c/deg
9. Discrimination-2.0 c/deg	9. Control for flux cues-2.0 c/deg
10. Contr. thresh.(u.-d.)-2.0 c/deg	10. Contr. thresh.(u.-d.)-2.0 c/deg
11. Contr. thresh.(c.s.)-2.0 c/deg	11. Contr. thresh.(c.s.)-2.0 c/deg
12. Discrimination-0.5 c/deg	12. Discrimination-1.0 c/deg
13. Contr. thresh.(u.-d.)-0.5 c/deg	13. Control for flux cues-1.0 c/deg
14. Contr. thresh.(c.s.)-0.5 c/deg	14. Freq. thresh.
15. Discrimination-8.0 c/deg	15. Discrimination-4.0 c/deg
16. Contr. thresh.(u.-d.)-8.0 c/deg	16. Control for flux cues-4.0 c/deg
17. Contr. thresh.(c.s.)-8.0 c/deg	17. Contr. thesh.(u.-d.)-4.0 c/deg
18. Discrimination-1.0 c/deg	18. Contr. thresh.(c.s.)-4.0 c/deg
19. Freq. thresh.	19. Discrimination-0.5 c/deg
20. Discrimination-16 c/deg	20. Control for flux cues-0.5 c/deg
21. Contr. thresh. (u.-d.)-16 c/deg	21. Contr. thresh.(u.-d)-0.5 c/deg
22. Contr. thresh.(c.s.)-16 c/deg	22. Contr. thresh.(c.s.)-0.5 c/deg
23. Discrimination-32 c/deg	
24. Contr. thresh.(u.-d.)-32 c/deg	
25. Contr. thresh.(c.s.)-32 c/deg	

The order of presentation for the various phases of the study, discrimination test (Discrimination), frequency threshold (Freq. thresh.), and contrast thresholds (Contr. thresh.) determined by the up-down method (u.-d.) and the method of constant stimuli (c.s.), are listed. Sessions given only to monkeys 887 and 890 are noted by an asterisk (*).

hone in on threshold and the method of constant stimuli produced a more rigorous test of liminal performance.

Each up-down session began with the presentation of a high contrast grating. If the subject made a correct response, the contrast of the next presentation was dropped one 0.1 log unit step. When the monkey responded incorrectly the contrast was raised one increment. A series of steps in one direction either ascending or descending was called a run. Five sessions were given. The first session consisted of 75 trials always starting at 0.79 contrast. The remaining four sessions began at a level five or six steps (0.5 to 0.6 log units) above the contrast threshold calculated from the data of the first up-down session and were 60 trials long. The means of the midpoints of all runs in the last 25 trials of each session was considered the threshold for that session. The mean of the thresholds for the last three sessions was assigned as the contrast threshold for the up-down method.

Once the up-down procedures were completed, the method of constant stimuli was begun. Seven stimuli were chosen pivoting about the threshold obtained by the previous method, three steps above and below the contrast threshold or the nearest higher level. On some occasions, however, it was necessary to shift the set of steps so that no more than ten errors were made during the first 35 trials presented (about 75% performance). These targets were presented according to the same procedure used in the frequency threshold determination (see above).

D. 2. d. Controls. To experimentally control for cues other than those presented, two types of tests were given postoperatively. In the first, the possibility of utilizing minimal differential flux cues were checked. For this purpose, an additional session was administered after the discrimination was mastered. In those sessions, a 0.5 log neutral density filter was placed before the right-side stimulus. Thus, a gross luminous flux difference was imposed so that the rewarded target emitted more flux in half of the trials (when on the left) and less flux in the other half (when on the right). If the animal were following a flux cue, it would choose the same box consistently, resulting in a drop to chance performance. If on the other hand, performance was maintained at the level of the preceding session despite the flux discrepancy, it could be assumed that minimal flux cues were not operant in the original discrimination.

The second control, checked for the possibility of the subject following extraneous non-visual cues of which the experimenter may have been unaware. In this case, two homogenous targets were presented simultaneously for twenty trials. A drop to 50% performance would indicate that no such spurious cues were apparent. This control was also given to all subjects preoperatively.

D. 3. Surgery and histology. Bilateral one-stage ablation of the occipital lobes was performed under general anesthesia, obtained by intraperitoneal injection of 40 mg/kg pentobarbital (Pasik, Pasik, and Schilder, 1969). Under sterile conditions, the monkey was placed in a stereotaxic frame and a bone flap was removed from the occipital region about 2 cm in front and 1 cm behind the lambda point. Following turning of a dural flap hinged on the midline, the occipital lobe of each hemisphere to the lunate sulcus was removed using aspiration and bipolar cautery. The remaining striate cortex was aspirated from the calcarine fissure until the pia within the sulcus was isolated from the surrounding nervous tissue. The latter phase required a Zeiss operating microscope at a magnification of 10x. Before closure, dural substitute (silicone rubber impregnated Dacron cloth) was placed over the brain. The dura was sutured, the bone replaced, and the muscle and skin sewn in layers. Seven days later, the stitches of the skin were removed and the monkey commenced with the testing procedures. Survival times are given in Table 1.

At the completion of the experiment two animals (#878, 880) were perfused under deep anesthesia. After tying off the brachial arteries and descending aorta, 3 ml of heparin was injected through the ascending aorta visualized by retracting the left kidney, followed by 500 ml of isotonic saline and 500 ml of 5% formalin. Drainage occurred through the severed inferior vena cava. The brain was removed and placed in 10% formalin for one week. After being photographed, it was dehydrated, embedded in celloidin, and cut into sections at 40 µm. The lesion was reconstructed from serial sections taken at 1 mm intervals and stained with cresyl violet. Special note was made of retrograde degeneration in the thalamic nuclei, namely the lateral geniculate nuclues, pars dorsalis and the pulvinar for which sections at 0.5 mm were utilized.

RESULTS

A. Preoperative Stage

A. 1. Neurological and ophthalmological status.

A. 1. a. General. All monkeys demonstrated signs of normal nervous system function. Blinks occurred quickly to sudden light or tactile stimulation and pupils constricted to increased illumination. Subjects were alert in the testing situation, responding quickly (within 5 sec) after the guillotine door was opened. In the home cage, they were inquisitive, and intently observed the experimenter's every move.

A. 1. b. Spontaneous saccades and pursuit eye movements were normal in all directions of gaze and all monkeys were able to converge on a stimulus moved towards them. There was no spontaneous nystagmus in a light or dark room.

Nystagmus was induced by moving (O.K.N.) and stationary (F.I.N.) stimuli in three of the monkeys (878, 887, 890). Although only a single trial was made with each type of stimulation, the responses from these animals did not differ substantially from normal animals previously tested (Valciukas, Pasik, and Pasik, 1973; Pasik, Pasik and Valciukas, 1970; Miller, Pasik, and Pasik,in press). Optokinetic stimulation in one direction induced a nystagmus to the opposite side using the convention in which nystagmus is named by the direction of the quick phase. The peak frequency of the response ranged from 1.5 to 1.8 nystagmic beats/sec. Monocular flicker stimulation induced a nystagmus in the direction of the stimulated eye, for example, right eye stimulation elicited a nystagmus towards the right. The peak frequency of F.I.N. was 0.6 to 1.1 beats/sec and 0.7 to 1.4 beats/sec under standard and Ganzfeld stimulation, respectively.

A. 1. c. Refraction. Four animals were refracted preoperatively and the results are given in Table 3. These monkeys were found to be emmetropic or within 1.33 diopters (D) of emmetropia. In addition, all animals tested exhibited some degree of astigmatism, the magnitude of which varied from 1.63 to 2.38 D. The variability of the cylinder was greater than that for the sphere. This is comparable to values obtained with human subjects (Safir, Hyams, Philpot, and Jagerman, 1970).

A. 2. Pretraining. Monkeys were trained to pull on the string and subsequently reach for the reward. It took from five to 11 days for animals to exhibit this behavior consistently to both stimulus boxes.

A. 3. Formal testing. The properative order of presentation of the various discrimination tests and threshold determinations can be found in Table 2.

A. 3. a. Discrimination tests. In all discrimination trials a homogeneous target was paired with a rewarded grating of maximal contrast. The subjects passed through three characteristic phases while learning the initial discrimination. Because these periods were not easily delineated, no attempt was made to quantify their durations. An <u>acclimation phase</u> began when the subject first persevered through fifty consecutive trials. The hallmark of this period was the tendency for the monkey to acquire labile position habits. A monkey became familiar with the apparatus, and often pulled on a string without looking at

Table 3. Refraction of Normal Monkeys

Monkey	Eye	Sphere (Diopters)	Astigmatism Cylinder (Diopters)	Astigmatism Axis (Degrees)
878	O.D.	0.88 (0.18)	1.75 (0.71)	153 (40)
	O.S.	0.13 (0.18)	1.63 (0.18)	10 (7)
879	O.D.	0.19 (1.01)	2.13 (0.78)	111 (10)
	O.S.	0.17 (0.29)	1.75 (0.25)	133 (10)
887	O.D.	0.50 (0.35)	1.63 (1.59)	33 (18)
	O.S.	-0.73 (1.02)	2.11 (0.86)	121 (6)
890	O.D.	0.38 (0.53)	2.38 (0.53)	3 (4)
	O.S.	-1.33 (0.29)	1.67 (0.72)	138 (24)

Right eye and left eye are indicated by O.D. and O.S., respectively. Values for sphere and astigmatism are means and parenthetical values are standard deviations. The number of trials for each value varied from two to four. Note that the differences between above values for axis of astigmatism should be calculated such that they are expressed as acute angles which may necessitate subtracting from 180 degrees.

the stimuli. During the discrimination phase the subject learned the task. This period started when the animal began to orient toward the stimuli albeit only a glance. With time the monkey gazed longer and longer at the stimuli. By the latter part of this phase, coinciding with an improvement of performance, only occasionally a string was inadvertently pulled before the targets were examined. The monkey did not reach for the apple during the latter trials, unless the rewarded stimulus happened to be chosen. The criterion phase started at the session in which 90% correct responses were made. During this phase the monkey looked directly at the stimuli while making a choice. The discrimination was mastered and criterion proficiency was attained.

Similar periods of training were spent in all phases. The results of the discrimination tests at each spatial frequency are given in Table 4 for each animal. All monkeys mastered the test at all frequencies. The initial discrimination was always at 1.0 c/deg (see Table 2 for schedule of tests) and was learned in a mean of 651 trials with 213 mean errors. The variability among animals was considerable, ranging from 75 to 354 errors. Subsequently, spatial frequencies were learned much more rapidly and except for three animals at 4.0 c/deg, only the minimum number of trials was required to attain criterion levels. This indicated the ability of the subject to transfer what was learned during discrimination and threshold determination at one spatial frequency to another. A more sensitive index of transfer is the performance in the first ten trials presented at each spatial frequency. Such scores also are found in Table 4. It is clear that a score close to 50%

Table 4. Discrimination Test with Normal Monkeys

Monkey	Spatial Frequency (c/deg)													
	1.0		4.0		2.0		0.5		8.0		16		32	
	TT (TE)	E	TT (TE)	E	TT (TE)	E	TT (TE)	E	TT (TE)	E	TT (TE)	E	TT (TE)	E
878	350 (75)	5	250 (23)	10	200 (0)	0	200 (1)	1	200 (0)	0	200 (0)	0	200 (1)	0
879	604(164)	4	250 (33)	10	200 (1)	0	200 (1)	1	200 (0)	0	200 (0)	0	200 (1)	0
880	450(127)	5	250 (21)	10	200 (0)	0	200 (4)	4	200 (5)	1	200 (0)	0	200 (2)	0
881	950(354)	3	200 (1)	0	200 (1)	0	200 (0)	0	200 (0)	0	N.T.		N.T.	
887	650(224)	5	200 (2)	0	200 (4)	0	200 (1)	1	200 (0)	0	200 (0)	0	200 (0)	0
890	900(335)	6	200 (4)	0	200 (0)	0	200 (0)	0	200 (0)	0	200 (0)	0	200 (0)	0
$\bar{x}$	651(213)	5	225 (14)	5	200 (1)	0	200 (1)	1	200 (1)	0	200 (0)	0	200 (1)	0
s.d.	239(113)	1	27 (13)	6	0 (2)	0	0 (2)	2	0 (2)	0	0 (0)	0	0 (1)	0

Spatial frequencies are listed in the order of presentation. Values represent the total number of trials (TT) and the total errors (TE) made through attaining criterion performance. The errors in the first ten trials are listed in the column designated E for each spatial frequency. $\bar{x}$ and s.d. denote the mean and standard deviation, respectively, for the group. N.T. indicates a spatial frequency at which a monkey was not tested.

(mean of 4.7 errors) was made on the first spatial frequency. At the other spatial frequencies, animals made only one or no errors in all but a few instances. Three notable exceptions were monkeys 878, 879 and 880 which made ten incorrect responses at 4.0 c/deg. That is to say, they consistently chose the homogeneous target. This reversal in behavior cannot be due to deficient matching of the stimuli for luminous flux since $\Delta F/\bar{F} \leq 0.05$ and the differential threshold for this dimension is 0.23 (Klüver, 1942).

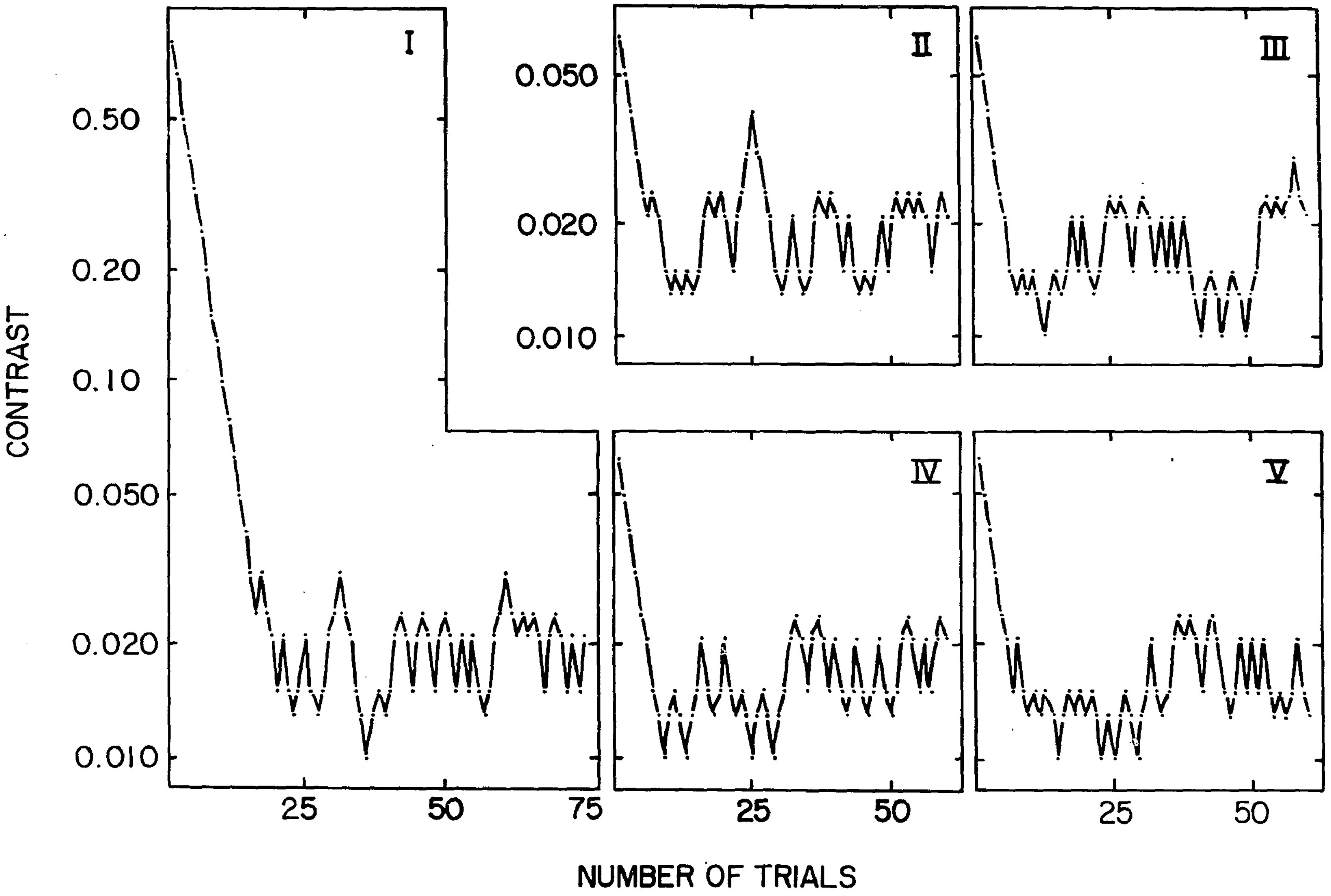
A. 3. b. Frequency thresholds. The frequency threshold determination was attempted only in monkeys 887 and 890 following the first discrimination at 1.0 c/deg (see Table 2 for order of presentation). Both animals performed below 75% proficiency at 32 c/deg and above threshold at 16 c/deg. In similar tests following the contrast threshold determinations at 8.0 c/deg, however, these two monkeys and all others discriminated the maximum contrast targets of all spatial frequencies at better than 90% proficiency.

A. 3. c. Contrast thresholds.

A. 3. c. 1. Up-down method. A typical performance in the five sessions presented according to the up-down procedure is depicted in Fig. 2 for one animal at 1.0 c/deg. The beginning of most sessions was marked by a long descending run (a train of correct responses) which was followed by a series of alternating ascending and descending runs. Since performance usually stabilized during the latter part of a session, the means of the midpoints of all runs in the last 25 trials was designated as the threshold for that session. To minimize possible

Fig. 2. Sample sessions of the up-down method
for monkey 887 at 8.0 c/deg

Each point signifies the contrast step presented on a particular trial and adjecent points are joined to illustrate the continuity of the session. A session began at a high contrast and depending upon whether the response was correct or incorrect, contrast was decreased or increased, respectively, in the following trial. The mean midpoint of all ascending and descending runs over the last 25 trials in each of the third, fourth, and fifth sessions is designated as threshold, and the overall standard deviation is the "instability index". It should be noted that both calculation were made with regard to log contrast and only for the former was the antilog determined. For this example, threshold is 0.018 and the index is 0.099.


I
II
III
IV
V
CONTRAST
0.50
0.20
0.10
0.050
0.020
0.010
0.050
0.020
0.010
25
50
75
25
50
25
50
NUMBER OF TRIALS

learning factors manifested by improvement over time, the mean of the thresholds for the last three sessions was assigned as the contrast threshold for the up-down procedure.

The contrast thresholds and their reciprocals, contrast sensitivities, are listed for all spatial frequencies tested in Appendix C. 1. for each monkey. The mean values of contrast threshold are plotted against spatial frequency in Fig. 3. Thresholds are lowest in the middle range of frequency (2.0 to 4.0 c/deg) and increase in the high and low frequencies. This type of data has been expressed and analysed in terms of contrast sensitivity versus spatial frequency. Such plots can be found in Fig. 4 (triangles) per individual animal and for the group in Fig. 5.

The oscillations which occurred during the sessions of the up-down method were used as an estimate of instability of the visual system at threshold. The standard deviation of the mean midpoint of all runs used in the threshold determination can be considered as an "instability index" and its values for each spatial frequency are given in Table 5. It is apparent that this index is higher for low frequencies than for high frequencies. In fact, the mean index for 8.0, 16 and 32 c/deg (0.066; s.d. = 0.015) is significantly lower ($p < 0.01$; using a $\underline{t}$ test for independent samples) than that determined at 0.5, 1.0 and 2.0 c/deg (0.12; s.d. = 0.05). The index at 4.0 c/deg represents an intermediate value.

A. 3. c. 2. Method of constant stimuli. The results from testing according to the method of constant stimuli are presented in Appendix C.2. for each monkey and Fig. 6 (top) illustrates the

Fig. 3. Mean contrast threshold function for normal monkeys determined by the up-down method

This function is a plot of log contrast threshold against log spatial frequency. Each solid symbol signifies the mean threshold for the group, and the bars denote one standard deviation from that mean. The open symbol describes an extrapolated high frequency cut-off point. The line denotes the best fitting curve.

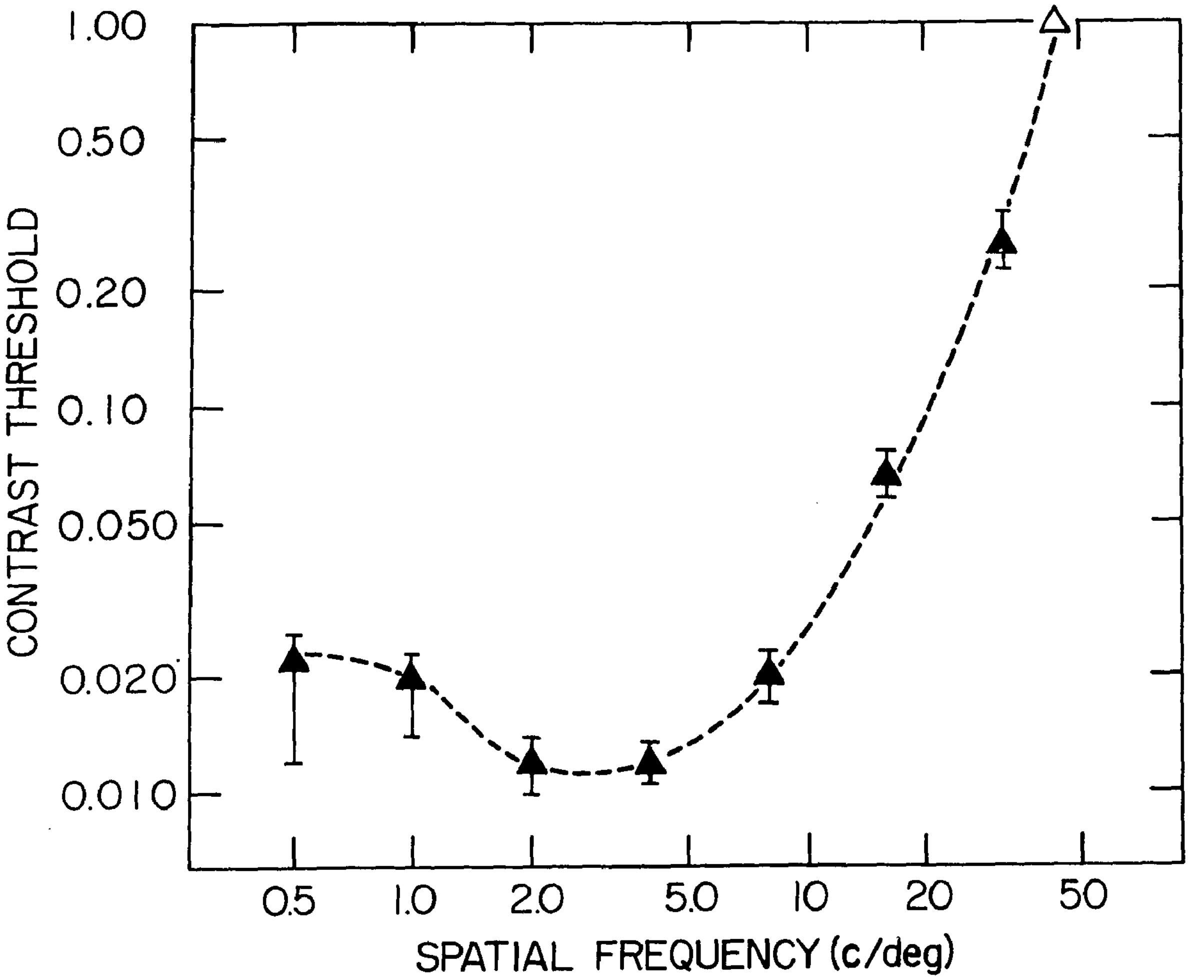

1.00
0.50
0.20
0.10
0.050
0.020
0.010
CONTRAST THRESHOLD
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

Fig. 4. Individual contrast sensitivity functions for normal monkeys determined by the up-down method and the method of constant stimuli

Log contrast sensitivity, the reciprocal of threshold, is plotted against log spatial frequency for all six animals. Data was accumulated by the up-down method (▲---▲) and the method of constant stimuli (●—●). Open symbols represent extrapolated values. The curves of best fit show that the high and low frequency limbs are related exponentially to spatial frequency.

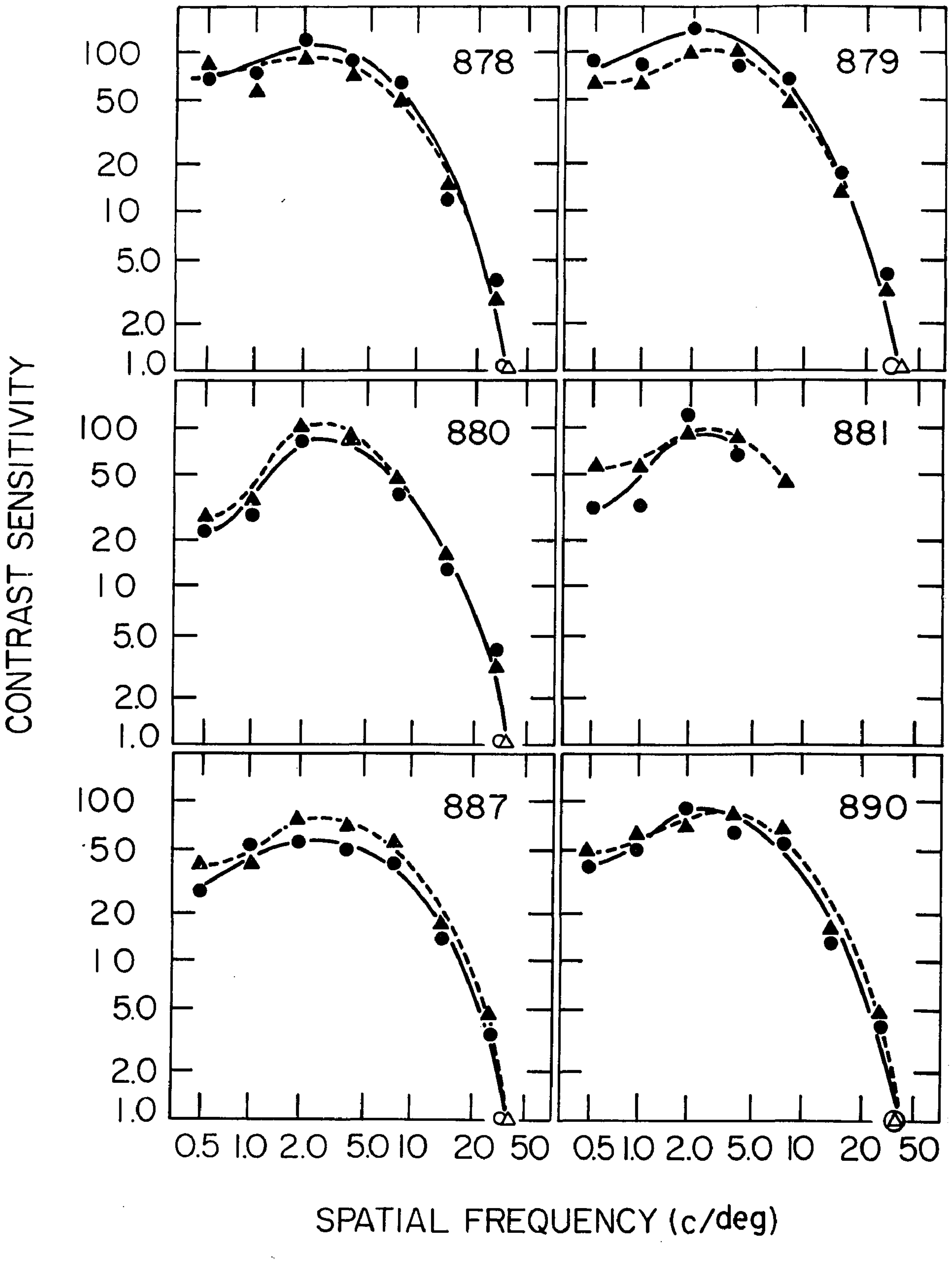

878
879
880
881
887
890
100
50
20
10
5.0
2.0
1.0
CONTRAST SENSITIVITY
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

Fig. 5. Mean contrast sensitivity function for normal monkeys determined by the up-down method

The mean contrast sensitivity at each spatial frequency tested for the group is noted by the solid symbols. Bars denote one standard deviation from the mean. The high frequency cut-off point is indicated by an open symbol. The high and low frequency limbs are an exponential function of spatial frequency.

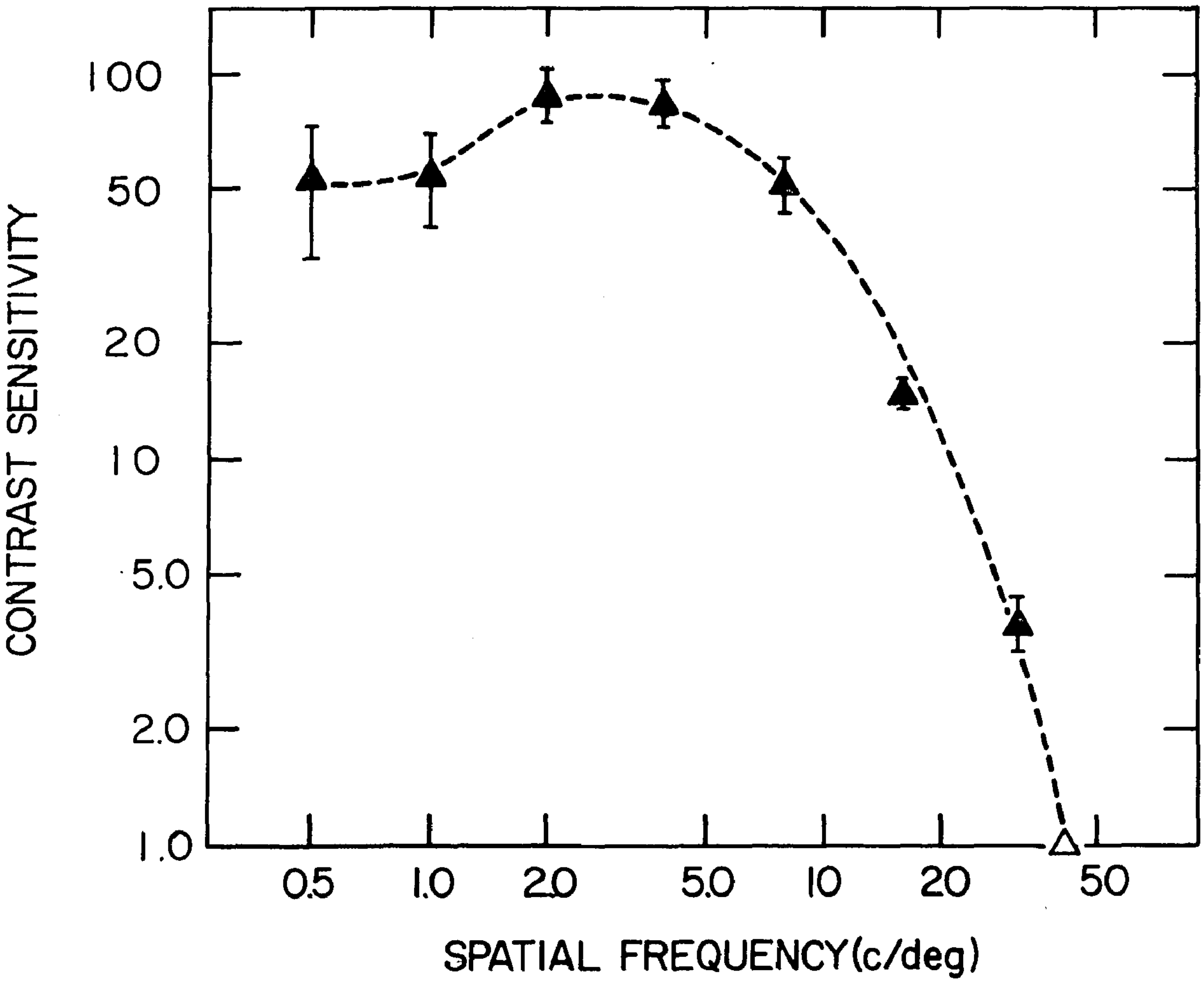

CONTRAST SENSITIVITY
100
50
20
10
5.0
2.0
1.0
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

Table 5. Instability Index in Normal Monkeys

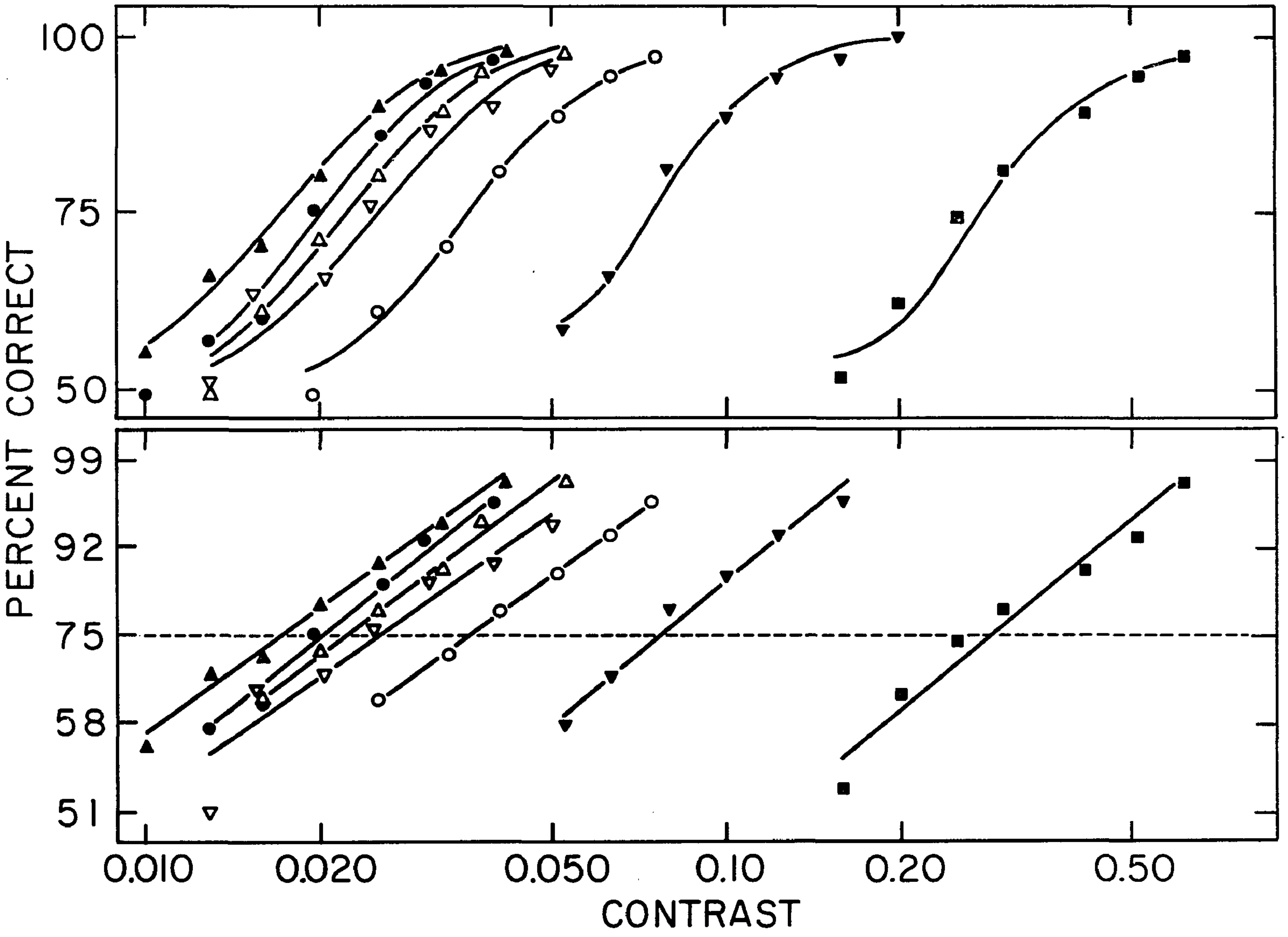
Monkey	Spatial Frequency (c/deg)						
	0.5	1.0	2.0	4.0	8.0	16	32
878	0.11	0.068	0.10	0.084	0.084	0.062	0.090
879	0.23	0.085	0.075	0.082	0.078	0.054	0.060
880	0.15	0.22	0.095	0.092	0.054	0.035	0.048
881	0.074	0.16	0.19	0.10	0.053	N.T.	N.T.
887	0.10	0.14	0.076	0.099	0.080	0.080	0.080
890	0.067	0.089	0.11	0.071	0.074	0.060	0.070
$\bar{x}$	0.12	0.13	0.11	0.088	0.071	0.058	0.070
s.d.	0.06	0.06	0.04	0.011	0.014	0.016	0.016

$\bar{x}$ and s.d. denote mean and standard deviation, respectively, for the group. N.T. indicates a spatial frequency at which a monkey was not tested.

Fig. 6. Psychometric functions for a normal monkey (887)

Top. The family of psychometric functions, correct responses against log contrast, describe perithreshold performance at 0.5 (O), 1.0 (△), 2.0 (▲), 4.0 (●), 8.0 (▽), 16 (▼), and 32 c/deg (■). Each curve is based on the response at seven contrast levels and asymptotes at 50% and 100% performance.

Bottom. Each psychometric function has been transformed into a linear function of performance on a probability scale against log contrast. In the transformation, correct responses at the 50% level or lower, and at 100% level are not plotted. Therefore, lines describing performance at a particular spatial frequency may be based on less than seven points. The regression coefficient for all lines is greater than 0.95. The 75% point is designated as threshold.


100
75
50
99
92
75
58
51
PERCENT CORRECT
0.010
0.020
0.050
0.10
0.20
0.50
CONTRAST

performance for one representative animal. The percent correct responses plotted along the ordinate is equivalent to the absolute number of correct responses since 100 trials were presented at each contrast step. Performance at all spatial frequencies describes a family of sigmoid curves otherwise known as psychometric functions. These curves asymptote at the 50% and 100% correct levels and the inflection points representing the thresholds are at 75%. The threshold was generally found somewhere between the second and fifth steps.

In order to reliably determine threshold performance a table of $\underline{z}$ scores was rescaled so that $\underline{z}$ equalled zero at the 75% level instead of the conventional 50% level. This table (Appendix C.3.) was used to transform percent correct responses into $\underline{z}$ scores. Using the method of least squares, straight lines were fitted to the data, $\underline{z}$ scores versus log contrast (Fig. 6, bottom). The general equation for functions describing performance in the method of constant stimuli is

$$\underline{z}(c) = m\ (\log c) + b$$

where $\underline{z}(c)$ is the $\underline{z}$ score of performance at contrast c, m is the slope of the psychometric function, and b is a constant represented by the y-intercept. This value m expressed in terms of $\underline{z}$ score per unit contrast has been used as an index of "precision" (Guilford, 1954). This index for each spatial frequency is given in Table 6 for individual animals. It is apparent that normal monkeys operate at two levels of precision. There is a greater degree of precision at 4.0 to 32 c/deg ($\bar{m} = 5.7$; s.d. = 0.5) than at 0.5 to 2.0 c/deg ($\bar{m} = 5.2$; s.d. = 0.5). According to the $\underline{t}$ test for independent samples, this difference is

Table 6. Psychometric Precision in Normal Monkeys

Monkey	Spatial Frequency (c/deg)						
	0.5	1.0	2.0	4.0	8.0	16	32
878	5.1	5.0	5.8	5.0	6.4	5.6	5.8
879	5.0	4.7	5.0	5.9	6.3	5.5	5.2
880	6.5	5.7	5.3	6.4	5.5	6.3	5.3
881	5.0	4.7	5.0	6.7	N.T.	N.T.	N.T.
887	4.9	4.9	4.9	5.7	5.1	5.4	5.4
890	4.6	4.9	5.7	6.2	5.4	5.1	5.9
$\bar{x}$	5.2	5.0	5.3	6.0	5.7	5.6	5.5
s.d.	0.7	0.4	0.4	0.6	0.6	0.4	0.3

Notation as in Table 5.

significant at the 0.01 level.

Thresholds were interpolated from the transformed psychometric functions. Thresholds and sensitivities are listed in Appendix C. 4. for all animals. The shape and dimensions of the contrast sensitivity function determined from the data of the method of constant stimuli is described by an inverted "J"-shaped curve, the dimensions of which are similar for all animals (Fig. 4, circles). The empirical peak is 2.0 c/deg for all monkeys, and the calculated peak sensitivity ranges from 60 to 114 at 1.8 to 2.1 c/deg. The extrapolated high frequency cut-off points are from 41 to 44 c/deg.

Fig. 7 depicts the mean contrast sensitivity function derived from the above data. The peak of this function at 2.0 c/deg and a contrast sensitivity of 96 divides the curve into a high and a low frequency limb. The former declines exponentially from the peak and the best fitting function obtained by the method of least squares based on five data points is described by the equation.

$$S(\nu) = 10^{-0.048\nu + 2.0} \qquad (r = 0.99)$$

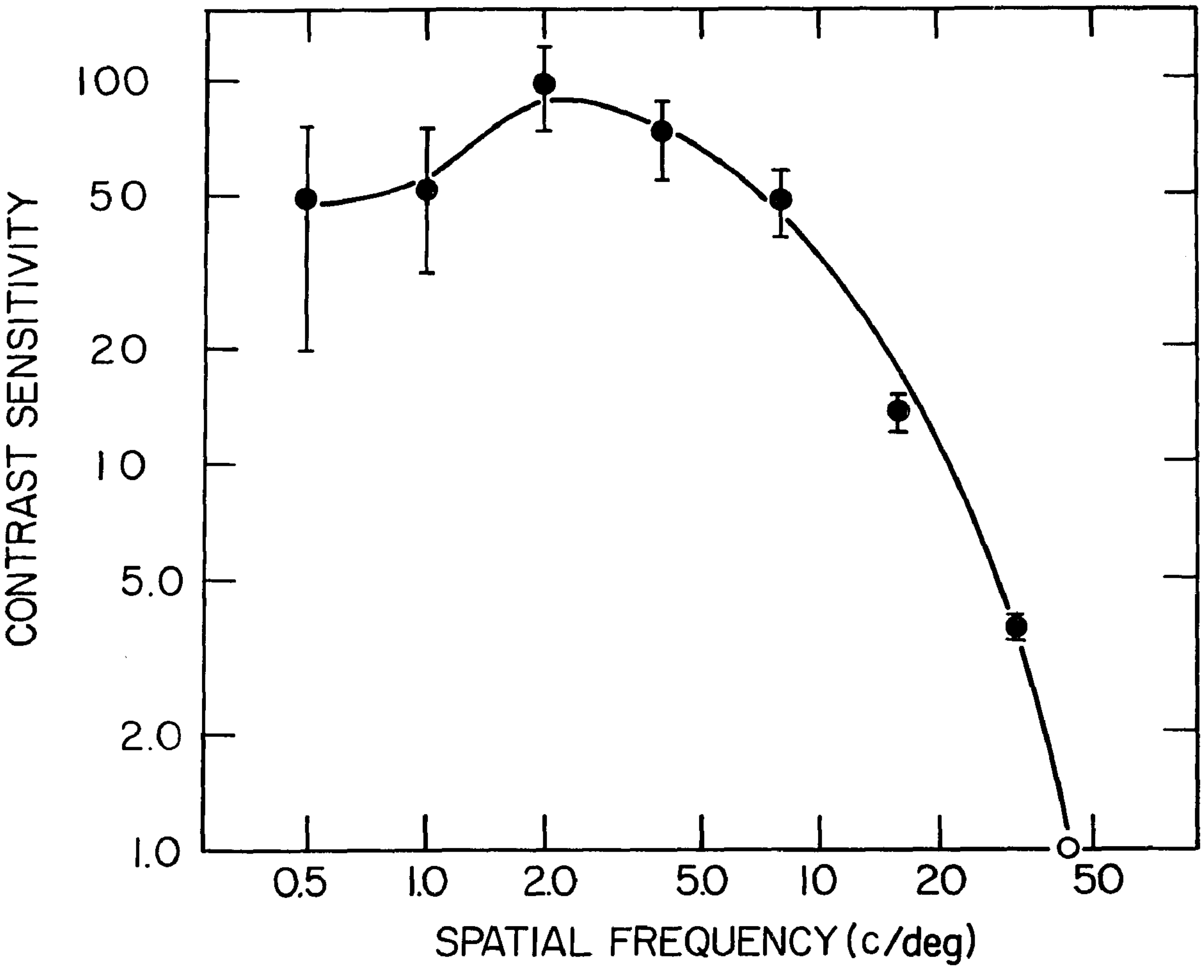
where $S(\nu)$ is the contrast sensitivity at the spatial frequency ν. The cut-off frequency at which contrast is 1.00 ($S(\nu) = 1.00$) is 43 c/deg. Similarly, the low frequency limb based on three points is an exponential function of spatial frequency and follows the line expressed by

$$S(\nu) = 10^{\,0.21\nu + 1.6} \qquad (r = 0.98).$$

By computing the intersection of the above equations, the peak can be determined more precisely. In the case at hand, the calculated peak is at 1.9 c/deg and a sensitivity of 88.

Fig. 7. Mean contrast sensitivity function for normal monkeys determined by the method of constant stimuli

Notation as in Fig. 5.


CONTRAST SENSITIVITY
100
50
20
10
5.0
2.0
1.0
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

It is noteworthy that the values of sensitivity at middle and high frequencies are consistent over the group, whereas at low frequencies a greater than four-fold difference is observed.

A. 3. d. Controls. Occasionally in the course of the testing, two homogeneous targets were presented simultaneously for a series of 20 trials. The subjects responded nonpreferentially. The average response to one target varied from 46 to 55%, indicating that no extraneous cues were operating in the original discriminations.

B. Postoperative Stage

B. 1. Neurological and ophthalmological status.

B. 1. a. General. Gross behavioral changes from the normal preoperative status were evident in the period immediately following the ablation. Monkeys assumed a position in the rear of the cage and generally did not leave their perch even when the cage door was left wide open. Exploration of the front of the cage was minimal and usually occurred only if food pellets were placed audibly in the hopper. The movement towards the front was accompanied by nondirected groping. In an unfamiliar environment monkeys maneuvered clumsily, bumping into large objects and navigating with the aid of their hands. Eventually, however, visually guided behavior returned, such as the ability to reach for objects with a certain degree of accuracy. Other behaviors also improved in time, but not to the level observed in the properative animal. At no time in the four months following the operation did any animal respond to a threatening gesture. Constriction of the pupils and a blink reflex to light were present immediately after the ablation.

B. 1. b. Eye movements. In the immediate postoperative period there was a relative paucity of spontaneous saccades and monkeys were unable to follow targets in motion with their gaze. In time, however, saccades occurred as often as in the normal and smooth pursuit eye movement were elicited by large high contrast objects passing through their visual fields. At this time, convergence could be evoked by approaching stimuli. Spontaneous nystagmus was not observed in a light or dark room.

Monkeys had a regular nystagmus in response to moving (O.K.N.) and stationary stimuli (F.I.N.). Representative electrooculograms of both types of nystagmus are shown in Fig. 8. It is apparent that the peak frequency of O.K.N. decreased after surgery (range 0.6 - 1.2 beats sec). F. I. N., however, increased but only when elicited in a Ganzfeld situation (1.6 - 2.3 beats/sec).

B. 1. c. Refraction. The refractive errors of the four destriated monkeys are shown in Table 7. All animals were within 1.17 D of emmetropia and exhibited some astigmatism. The cylinder of the astigmatism ranged from 0.50 to 3.08 D. No significant difference in the sphere or the cylinder occurred as a result of the ablation. The axis of the cylinder did change significantly following the striatectomy in two instances, the left eyes of monkeys 878 and 887. The variability of the measurements was comparable to the preoperative values.

B. 2. Pretraining. Pretraining started one week after surgery. All subjects required between four and seven days to master the pulling

Fig. 8. Recordings of nystagmus in normal and destriated monkeys

Electrooculograms of optokinetic (O.K.N.) and flicker-induced nystagmus (F.I.N.)are from monkeys 887 and 890, respectively. F.I.N. was evoked in a Ganzfeld situation. Each set of three traces records the stimulus (STIM.), right eye (O.D.) and left eye (O.S.) over a period of 20 seconds. Note the postoperative changes in frequency of O.K.N. (decrease) and F.I.N. (increase).

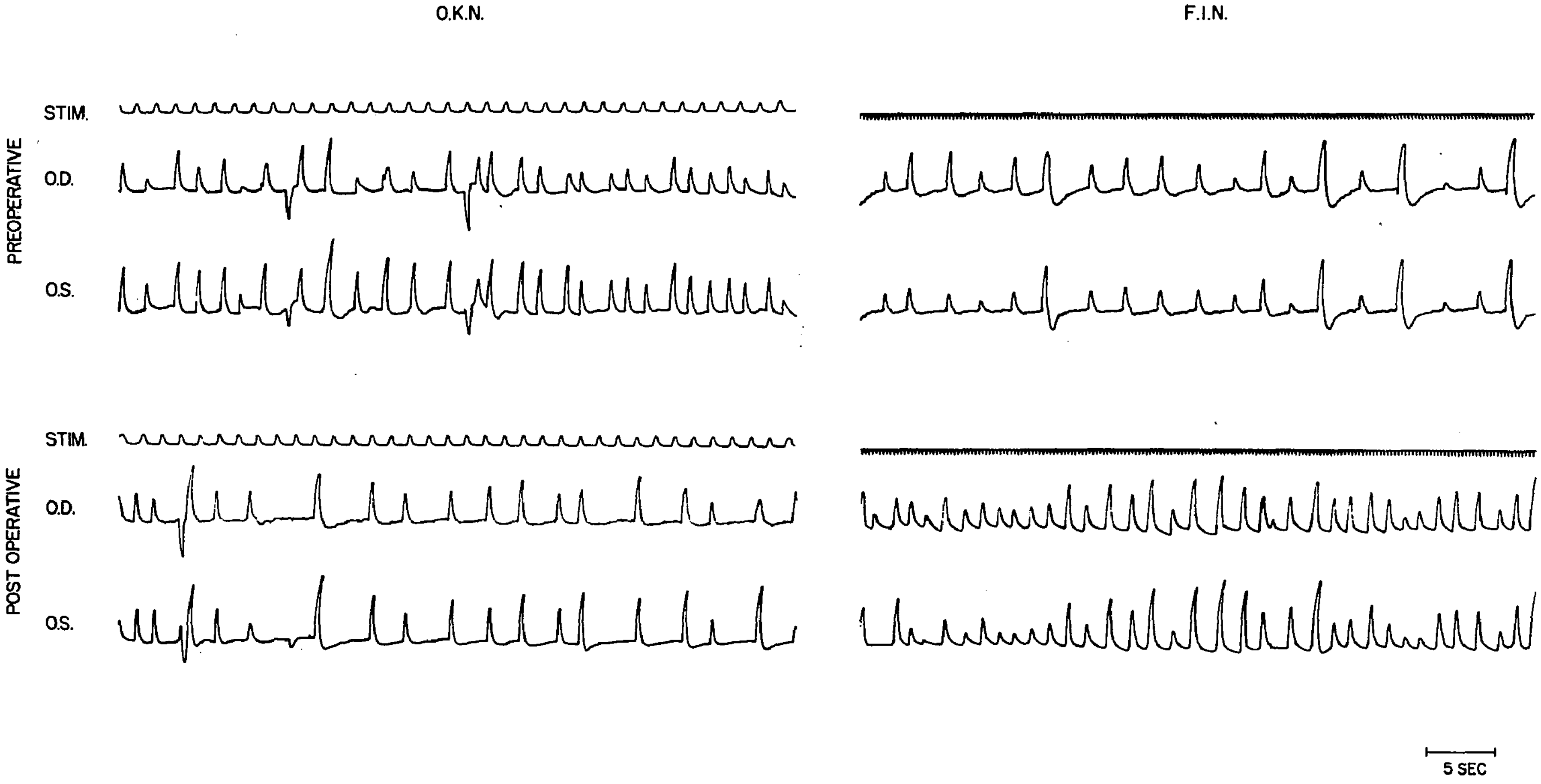

O.K.N.
F.I.N.
PREOPERATIVE
STIM.
O.D.
O.S.
POST OPERATIVE
STIM.
O.D.
O.S.
5 SEC

Table 7. Refraction of Destriated Monkeys

Monkey	Eye	Sphere (Diopters)	Astigmatism Cylinder (Diopters)	Astigmatism Axis (Degrees)
878	O.D.	0.0 (0.50)	1.25 (1.52)	168 (20)
	O.S.	-0.50 (0.35)	1.75 (0.0)	158 (11)
880	O.D.	0.0	0.75	165
	O.S.	-1.00	0.50	115
887	O.D.	0.50 (0.46)	1.31 (0.80)	19 (33)
	O.S.	0.58 (0.52)	1.42 (0.14)	5 (15)
890	O.D.	0.75	2.25	20
	O.S.	-1.17 (0.72)	3.08 (0.76)	135 (13)

Notation as in Table 3. Only a single trial was made with each eye of monkey 880 and the right eye of monkey 890, and, therefore, no standard deviations are given.

and reaching task, that is in a briefer period than needed in the original pretraining at the start of the study.

B. 3. Formal testing. The postoperative schedule of the various discrimination and threshold determination tests can be found in Table 2.

B. 3. a. Discrimination tests. The postoperative training of each animal is summarized in Table 8. Following a prolonged period of testing, all animals mastered the initial discrimination between the high contrast grating at 1.0 c/deg and the homogeneous target. Every monkey passed through the acclimation, discrimination and criterion phases. The first two phases were protracted, each lasting about 1,300 trials. During the acclimation phase each animal operated at about the 50% correct level. During the discrimination phase, it was noted that monkeys frequently deviated their gaze to one side while facing the stimuli before making a choice, as if to be looking at them through the corner of their eyes. By the time criterion was attained, subjects had been presented from 2,600 to 3,536 trials and made from 920 to 1,377 errors. After the contrast threshold was determined at 1.0 c/deg (see Table 2 for order of testing), the discrimination at 2.0 c/deg was mastered by all animals in the minimum number of presentations. Only one monkey (880, however, showed a perfect transfer effect as noted by the lack of errors in the first 10 trials (Table 8). Learning the discrimination at 4.0 c/deg took slightly longer than at 1.0 or 2.0 c/deg as three animals needed 250 to 300 trials and made a mean of 25 errors in attaining criterion. There was good transfer in the fourth monkey (880). The discrimination at 0.5 c/deg was mastered in the

Table 8. Discrimination Tests with Destriated Monkeys

Monkey	Spatial Frequency (c/deg)											
	1.0			2.0			4.0			0.5		
	TT	(TE)	E	TT	(TE)	E	TT	(TE)	E	TT	(TE)	E
878	2860	(1191)	5	200	(19)	5	250	(28)	2	200	(19)	1
880	3526	(1377)	5	200	(4)	0	300	(31)	1	200	(14)	0
887	2600	(994)	5	200	(11)	3	200	(16)	3	200	(10)	0
890	2800	(920)	5	200	(10)	3	250	(23)	3	200	(15)	1
$\bar{x}$	2949	(1121)	5	200	(11)	3	250	(25)	2	200	(15)	1
s.d.	407	(206)	0	0	(6)	2	41	(7)	1	0	(4)	1

Notation as in Table 4.

minimum period with a mean of 15 errors and perfect transfer in all animals.

B. 3. b. Frequency thresholds. Two frequency threshold determinations were made (see Table 2 for order of presentation) and the mean results for the group are illustrated in Fig. 9. On the first set, only performances with the maximum contrast targets at 1.0 and 2.0 c/deg were greater than 85% and, therefore, only contrast thresholds at each of these frequencies were obtained (see above). At this stage subjects demonstrated not only a high, but also a low frequency cut-off point. Subsequently, a second frequency threshold was determined. This time not only the targets at 1.0 and 2.0 c/deg, but also those at 0.5 and 4.0 c/deg were discriminated at better than 85% proficiency. The performance with the grating of 8.0 c/deg was below this level but above the criterion for threshold.

B. 3. c. Contrast thresholds.

B. 3. c. 1. Up-down method. The up-down method was useful in estimating threshold for use in the constant stimuli method. Contrast thresholds were determined for the four spatial frequencies, 1.0, 2.0, 4.0 and 0.5 c/deg as prescribed by the frequency threshold determinations (see below) and in that order (Table 2). The results per individual animal are given in Appendix D. 1. These data are plotted for each monkey in Fig. 10 (triangles) and for the group in Fig. 11.

The "instability index" (see p. 39) for each spatial frequency tested postoperatively is given in Table 9. An analysis of variance shows no significant difference among the values at each spatial frequency ($F = 1.5$; $p > 0.25$).

Fig. 9. Frequency threshold functions for destriated monkeys

The performance on the first (●----●) and second (0——0) frequency threshold determinations are plotted as percent correct responses on a probability scale against log spatial frequency. Each point signifies the mean of four animals.

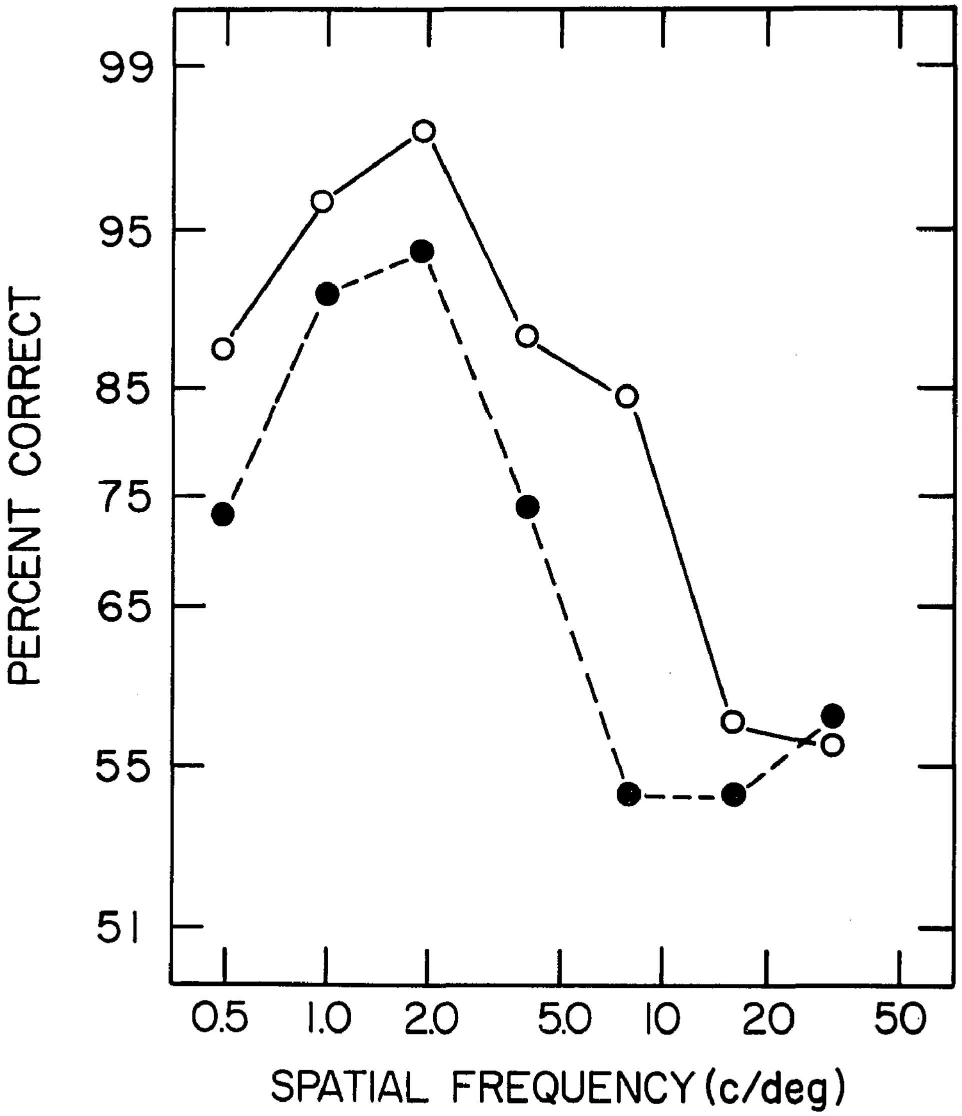

99
95
85
75
65
55
51
PERCENT CORRECT
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

Fig. 10. Individual contrast sensitivity functions for destriated monkeys determined by the up-down method and the method of constant stimuli

Notation as in Fig. 4. The contrast threshold for 8.0 c/deg was calculated from the frequency threshold information (see text).

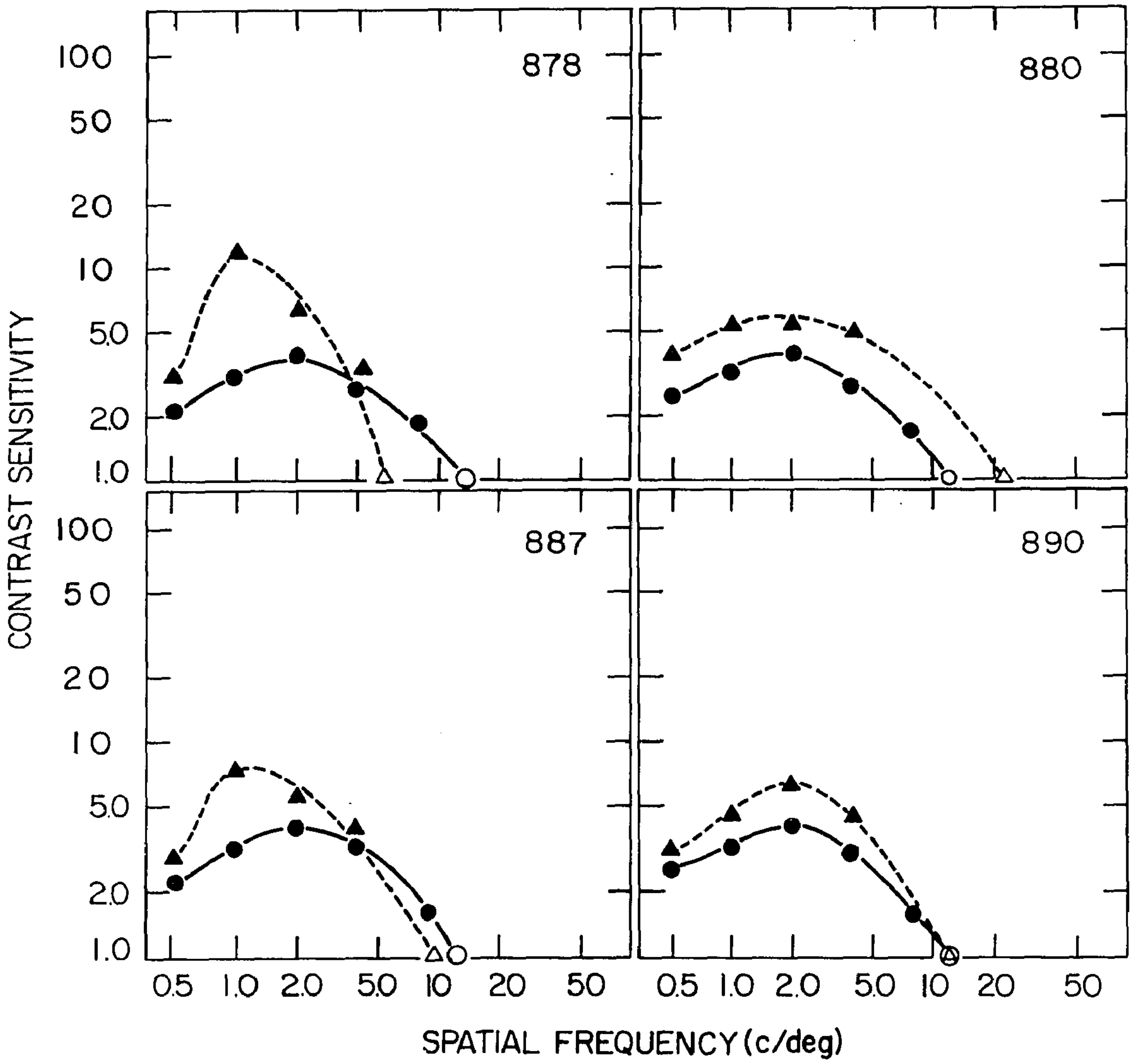

878
880
887
890
100
50
20
10
5.0
2.0
1.0
CONTRAST SENSITIVITY
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

Fig. 11. Mean contrast sensitivity function for destriated monkeys determined by the up-down method

Notation as in Fig. 5.

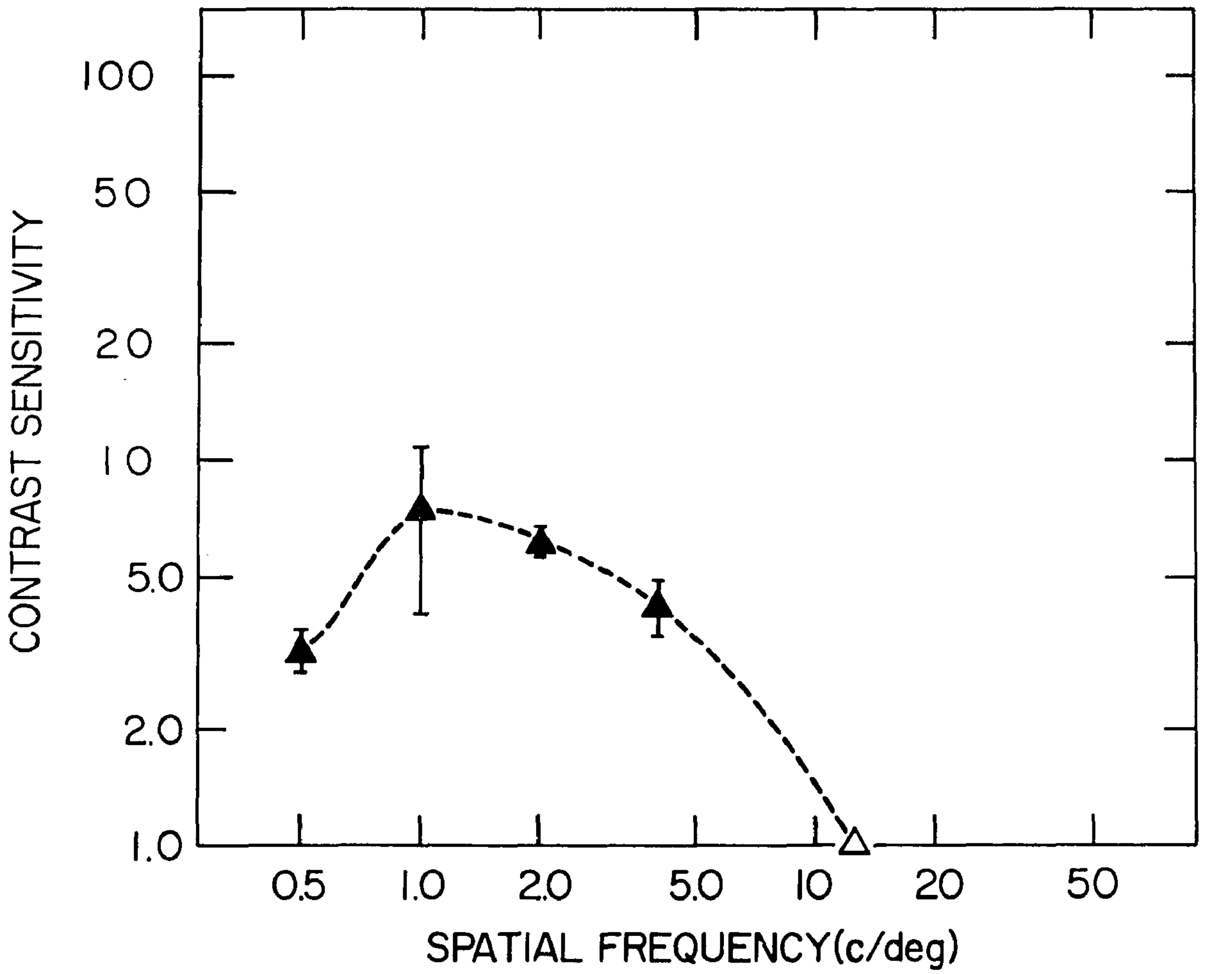

CONTRAST SENSITIVITY
100
50
20
10
5.0
2.0
1.0
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY(c/deg)

Table 9. Instability Index of Destriated Monkeys

Monkey	Spatial Frequency (c/deg)			
	0.5	1.0	2.0	4.0
878	0.15	0.24	0.26	0.20
880	0.13	0.14	0.17	0.17
887	0.14	0.19	0.17	0.16
890	0.15	0.16	0.16	0.15
$\bar{\bar{x}}$	0.14	0.18	0.19	0.17
s.d.	0.01	0.04	0.05	0.02

Notation as in Table 5.

B. 3. c. 2. Method of constant stimuli. The results obtained with the method of constant stimuli at each frequency are given in Appendix D. 2. for individual animals, and are plotted for one illustrative animal in Fig. 12. The psychometric functions generated by performance at each frequency are fitted to linear functions of z scores versus log contrast ($r > 0.95$) (see p. 49). The slope of these lines, mean of 3.6 (s.d. = 0.2) are similar at each spatial frequency (Table 10). Thus, "psychometric precision" is relatively constant over the group independent of spatial frequency.

The contrast thresholds were calculated from the psychometric functions by interpolating the 75% point, and subsequently sensitivities were determined. Fig. 10 contains the individual contrast sensitivity functions obtained with the constant stimuli method. The empirical peak sensitivities at 2.0 c/deg ranged from 3.8 to 4.2.

The high and low frequency limbs of the mean contrast sensitivity curve (Fig. 13) are described by exponential functions of spatial frequency. The high frequency limb,

$$S(\nu) = 10^{-0.062\nu + 0.73} \qquad (r > 0.99)$$

intercepts the line $S(\nu) = 1.00$ at 12 c/deg. The low frequency limb is described by

$$S(\nu) = 10^{0.14\nu + 0.33} \qquad (r = 0.97)$$

Each of the above equations are based on three points. It should be noted that to determine the equation of the high frequency limb, the sensitivity at 8.0 c/deg was not derived from a contrast threshold determination, but it was calculated from the frequency threshold

Fig. 12. Psychometric functions of a destriated monkey (890)

Notation as in Fig. 6.

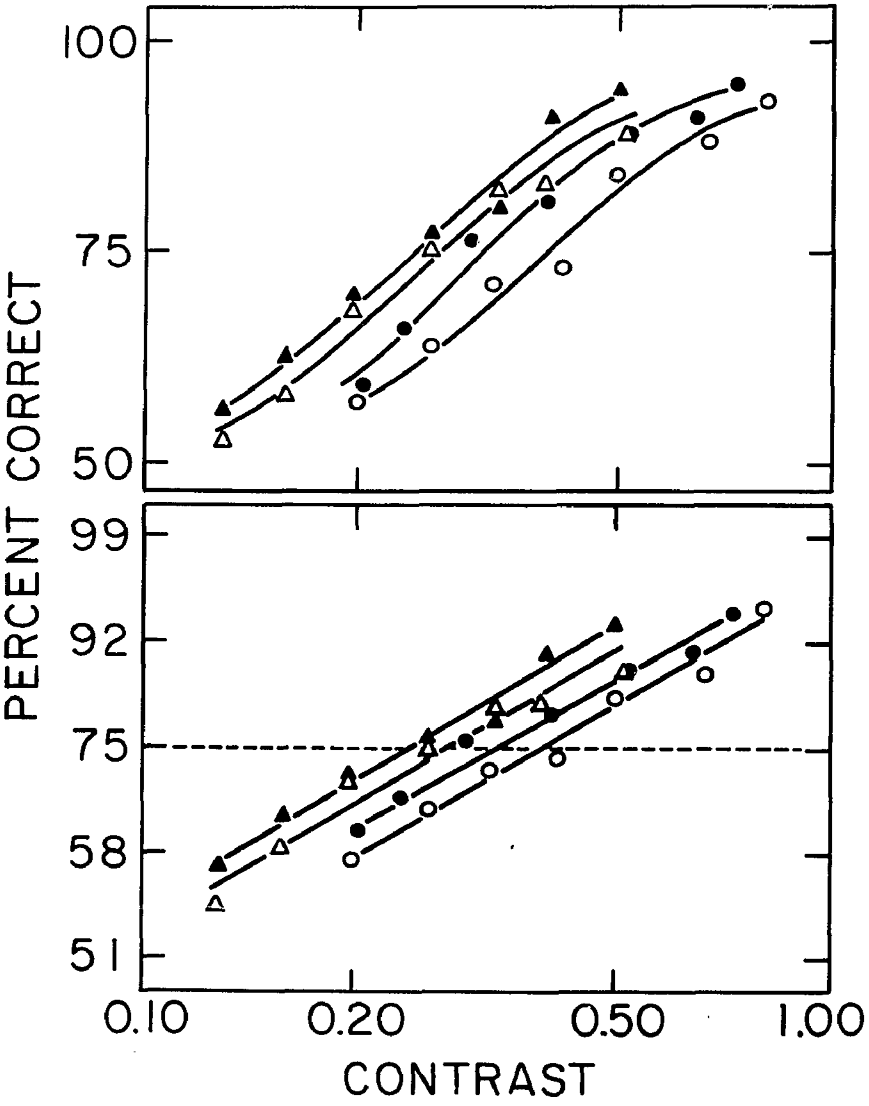

100
75
50
99
92
75
58
51
PERCENT CORRECT
0.10
0.20
0.50
1.00
CONTRAST

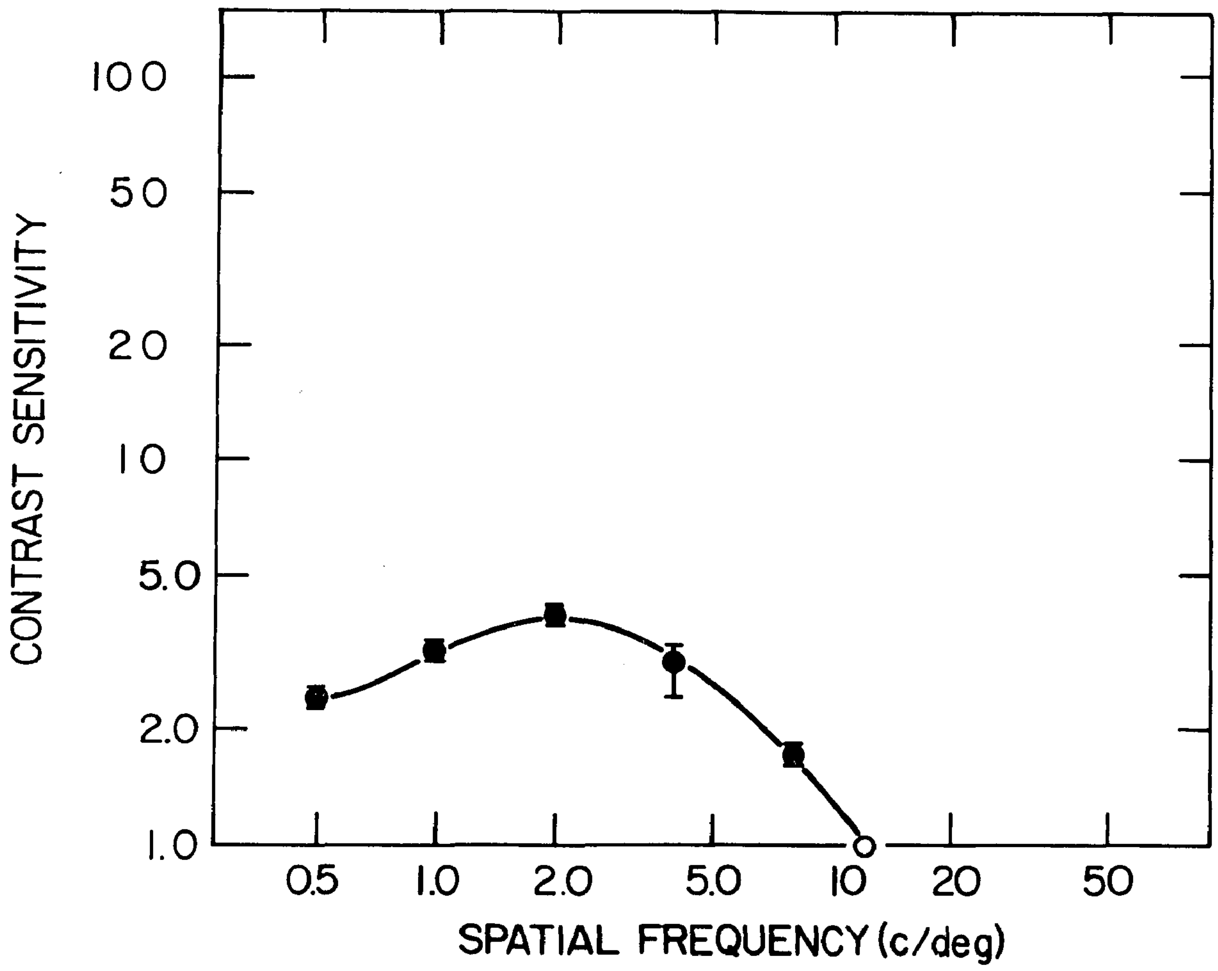
Table 10. Psychometric Precision of Destriated Monkeys

Monkey	Spatial Frequency (c/deg)			
	0.5	1.0	2.0	4.0
878	3.9	3.3	3.5	3.4
880	3.6	3.2	3.8	3.6
887	3.8	3.9	3.6	3.5
890	3.5	3.6	4.0	3.7
$\bar{x}$	3.7	3.5	3.7	3.6
s.d.	0.2	0.3	0.2	0.1

Notation as in Table 5

Fig. 13. Mean contrast sensitivity function for destriated monkeys determined by the method of constant stimuli

Notation as in Fig. 5.


CONTRAST SENSITIVITY
100
50
20
10
5.0
2.0
1.0
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

information. Such an estimation of sensitivity requires two values, the mean slope of individual psychometric functions from each animal and the point described by the performance at 8.0 c/deg during the frequency threshold sessions. From these data a theoretical psychometric function was specified and the 75% point was determined. Such a manipulation assumes that the "psychometric precision" is similar at all frequencies which is borne out by the empirical data (see p. 69).

B. 3. d. Controls. The comparison of performance in the last standard session of discrimination test to a control session given immediately after, in which 0.5 log neutral density filter was fixed to the right-side stimulus box are listed for each spatial frequency in Table 11. The monkeys continued to perform at criterion proficiency or better. Therefore, they could not possibly be using minimal flux cues in the original discrimination.

As in the preoperative period, when two homogeneous targets were presented simultaneously, no monkey demonstrated a preference for a particular stimulus, responses being between 40 and 60% for either target.

C. Effects of Striatectomy Upon Psychophysical Tests

Following the lesion, a significantly longer period was required to master the initial discrimination as five times more errors were accumulated in five times as many trials following the ablation ($p < 0.01$) (Fig. 14). Generally, the subsequent discriminations at the other frequencies were learned in the minimal amount of trials. Thus, the ability to transfer the knowledge gained in one situation to another similar situation was not lost.

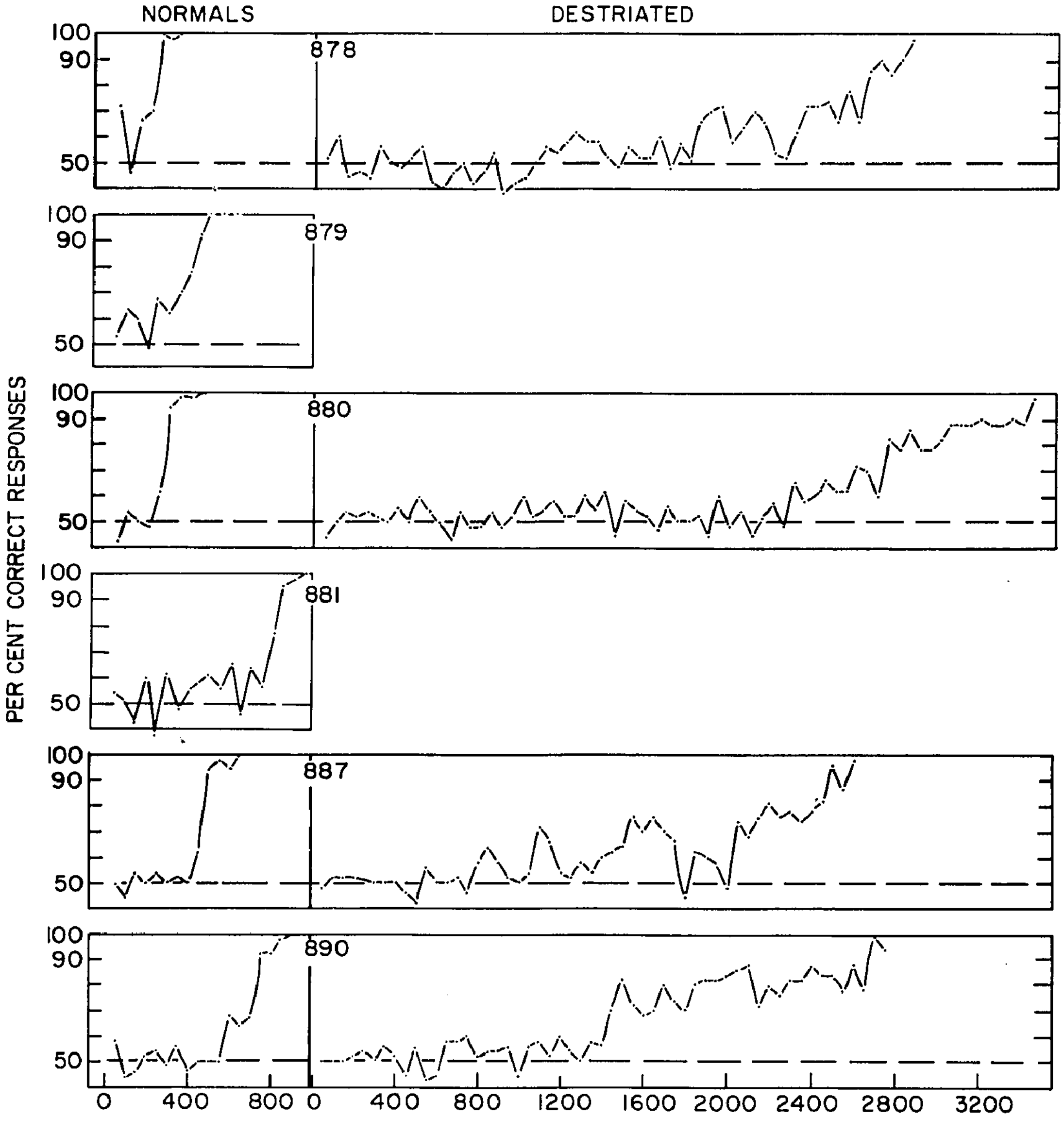
Table 11. Control for Flux Cues in Destriated Monkeys.

Monkey	Spatial Frequency (c/deg)							
	0.5		1.0		2.0		4.0	
	Std	Cnt	Std	Cnt	Std	Cnt	Std	Cnt
878	92	92	96	94	100	98	94	90
880	90	90	98	96	96	98	94	90
887	94	94	98	92	94	94	92	96
890	96	94	94	90	96	92	96	92

Scores are percent correct responses in 50 trials of the last standard discrimination test (Std) and of the control session (Cnt) for each spatial frequency. The 0.5 log neutral density filter transmits 32% of the light, and therefore imposes a 3.1-fold flux difference between the targets.

Fig. 14. Discrimination tests

The segments on the left represent the learning curves for the six animals in the discrimination between the homogeneous and the 0.79 contrast target at 1.0 c/deg. The segments on the right describe the relearning of the same task. Each point represents the percent correct in a session of 50 trials. Note the prolonged training necessary postoperatively to reach criterion in the task.


NORMALS
DESTRIATED
878
879
880
881
887
890
100
90
50
PER CENT CORRECT RESPONSES
0
400
800
0
400
800
1200
1600
2000
2400
2800
3200
NUMBER OF TRIALS

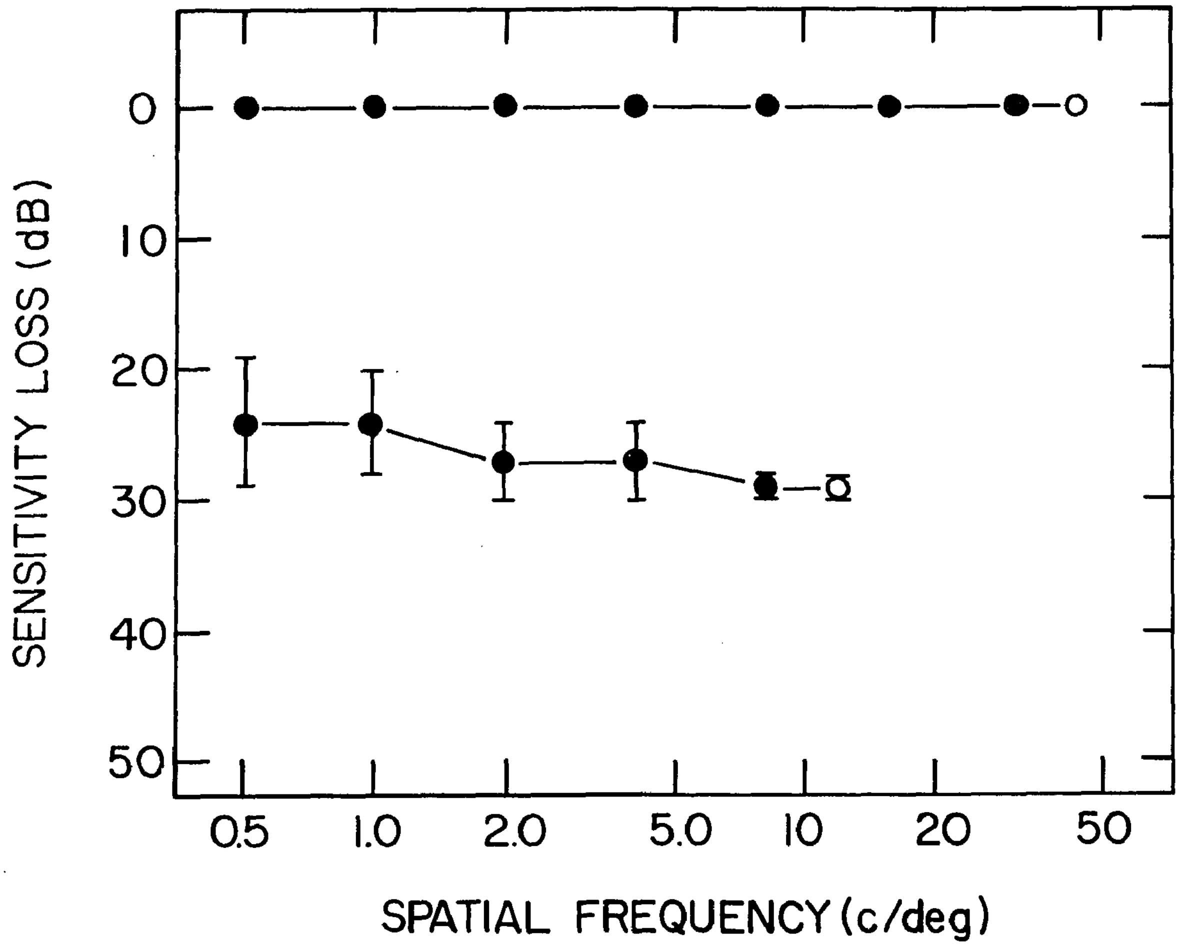
The frequency threshold determination indicates a significant difference in the preoperative and postoperative responses. The normal animal can discriminate gratings over a much wider range than the destriated monkey from greater than 32 c/deg to less than 16 c/deg, respectively. The contrast sensitivity functions indicate that at those frequencies which monkeys are able to discriminate before and after the ablation, a significantly higher contrast is required for the destriated animal to detect a grating. The magnitude of the loss as quantified by the method of constant stimuli can readily be judged on a "visuogram" (Fig. 15). Values represent twenty times the logarithm of the sensitivity ratio. The deficit can be described as a mean flat loss of 27 decibels (dB; s.d. = 2 dB), extending from frequencies below 12 c/deg, the extrapolated limit of postoperative performance. The peak sensitivity, although diminished 27 dB, was calculated as being 1.9 c/deg preoperatively and postoperatively. The mean value of the high frequency cut-off point fell from 43 c/deg in normal subjects to 12 c/deg in destriated monkeys. "Psychometric precision" declined significantly ($p < 0.01$; $\underline{t}$ test for dependent samples) as a result of the striate lesion over the entire range of spatial frequencies. Moreover, the "instability index" increased significantly ($p < 0.05$), according to a $\underline{t}$ test for dependent samples, following the ablation over the range of frequencies above 1.0 c/deg.

D. Anatomical Observations

Two animals (monkeys 878 and 880) were sacrificed on completion of

Fig. 15. "Visuogram" for the effects of the striatectomy

The effect of the lesion on the four animals tested preoperatively and postoperatively is illustrated by the "visuogram" for data obtained by the method of constant stimuli. The upper line signifies the standardized normal contrast sensitivity function from which the postoperative performance is measured. Solid symbols represent the means of empirically determined points, open symbols designate mean extrapolated values, and bars denote respective standard deviations.



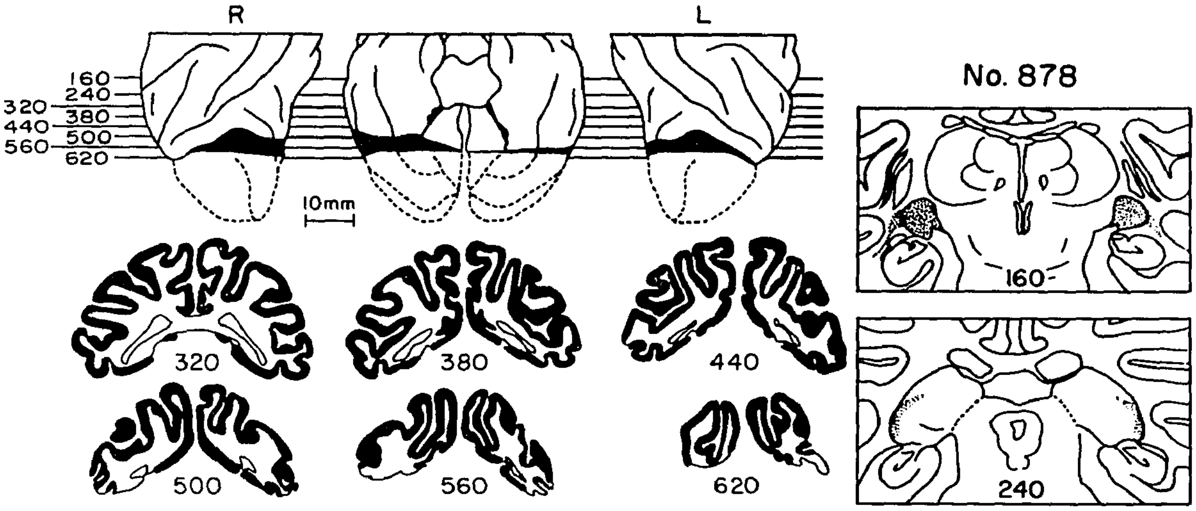
SENSITIVITY LOSS (dB)
0
10
20
30
40
50
0.5
1.0
2.0
5.0
10
20
50
SPATIAL FREQUENCY (c/deg)

the postoperative phase. The extent and totality of the striatectomy was determined by reconstructions from serial sections illustrated in Fig. 16 and 17. In each animal, the striate cortex (Area 17, OC) was completely absent on both sides. In addition, circumstriate cortices were partially damaged; an estimated 75% of Area OB and 25% of Area OA (Bonin and Bailey, 1947) was not included in the lesion. The optic radiations in both hemispheres underwent marked gliosis.

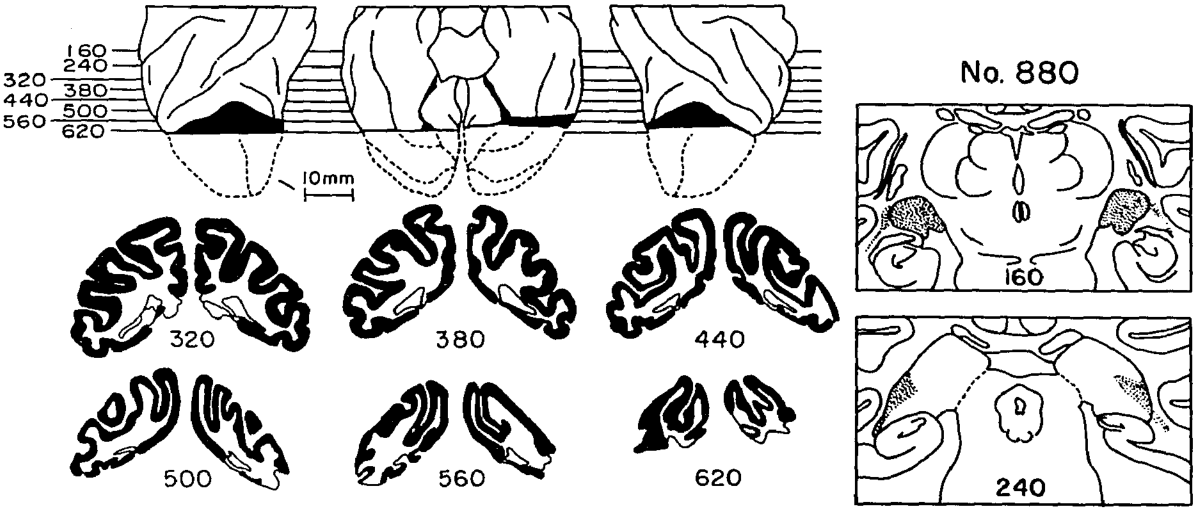
Retrograde degeneration was observed in the thalamic nuclei, the LGNd and the pulvinars. The characteristic layering of the LGNd was mostly absent, however, faint lamination was present in monkey 878. Under high magnification, few scattered pale staining neurons were observed. Alterations in the pulvinars following the cortical ablation was restricted to loci in the inferior and lateral nuclei.

Fig. 16. Reconstruction of the ablation

The absence of the occipital lobes is indicated by dashed lines and the absence of cortex is represented by black in the surface views and a fine line in the coronal sections. Degeneration and gliosis is shown in the sections of the thalamus by stippling. Numbers identify sections cut at intervals of 40 µm. R and L indicate the right and left, respectively, for all drawings. Note the completeness of the lesion as marked by the total absence of calcarine cortex and the occipital lobes of both hemispheres.


R
L
160
240
320
380
440
500
560
620
10mm
320
380
440
500
560
620
160
240

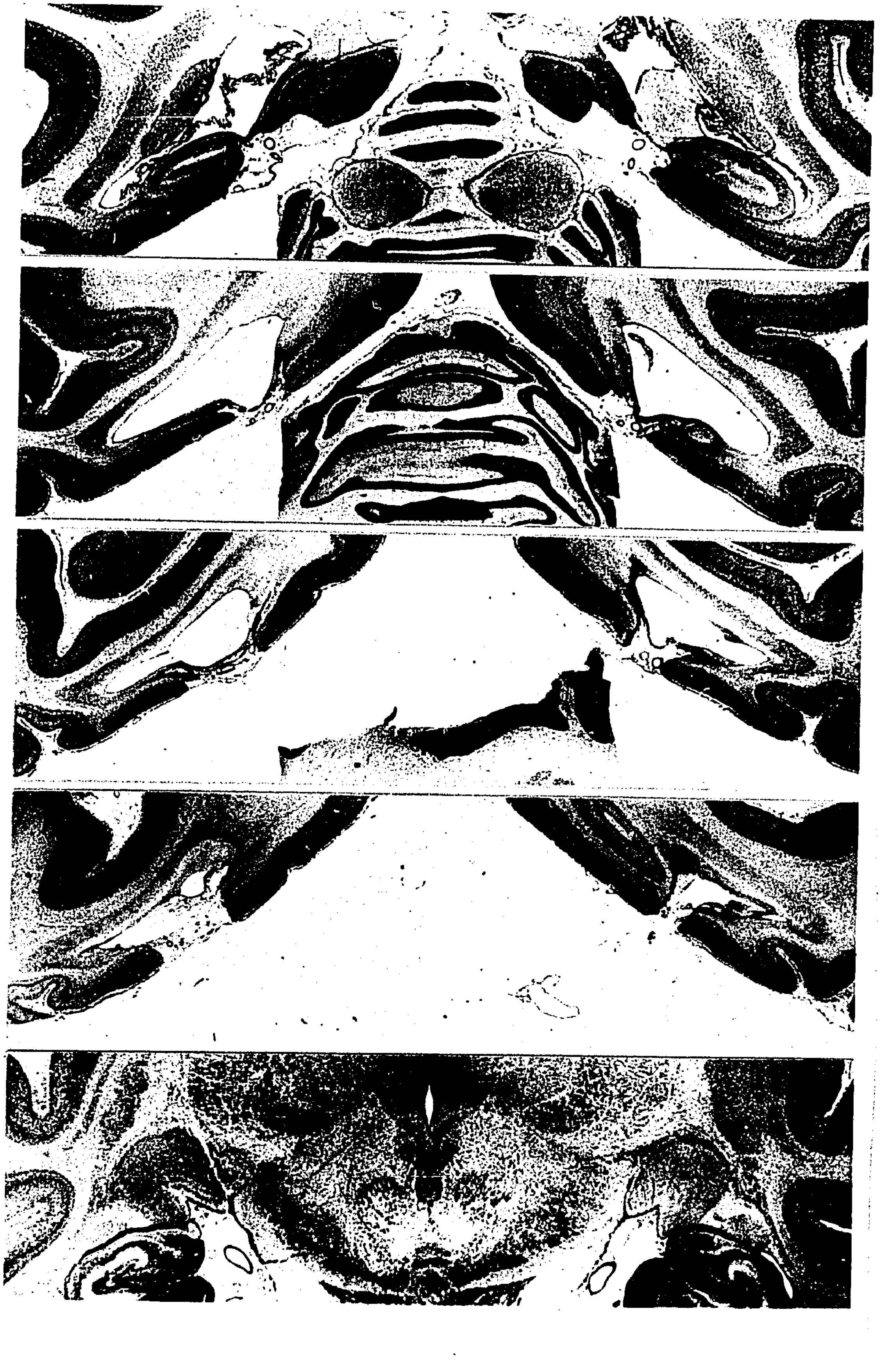
No. 878


160
240
320
380
440
500
560
620
10mm
320
380
440
500
560
620
160
240

No. 880

Fig. 17. Photography of the lesion

These photographs illustrate the striate lesion in monkey 880 with four coronal sections spaced at 2.5 mm intervals. Note the absence of the calcarine cortex at each level of both hemispheres. The lower panel is a section of the thalamus which demonstrates total gliosis of the dorsal lateral geniculate nucleus.



DISCUSSION

Contrast sensitivity functions describe the relationship between spatial frequency and sensitivity, the inverse of threshold, for constrast detection. It is clear from the findings of this study and previous investigations (DeValois, Morgan and Snodderly, 1974; Harding and Yates, 1976) that such function for normal macaque monkeys has the characteristic shape of an inverted "J". That is to say, in the midrange of spatial frequencies, about 2.0 c/deg, only a minimal amount of contrast is required to perceive a stationary waveform (lowest threshold and inversely highest sensitivity). With finer and coarser gratings, however, additional contrast is necessary for detection. The crucial results of this investigation are the functions describing the behavior of monkeys with total bilateral removal of the striate cortex. There is a similarity of the curves from normal and operated animals as noted by the peak sensitivity and the slope of the high and low frequency limbs.

Although the shape of the preoperatively and postoperatively determined functions is similar, the dimensions are markedly altered. Across the entire range of spatial frequencies, there is a uniform 27 dB loss in sensitivity. Flat losses of various degrees have been observed in humans with cerebral lesions (Bodis-Wollner and Diamond, 1976), but rarely as severe as that seen in totally destriated monkeys. The only documented correlation between a type of sensitivity loss and a localized interference with the visual system is a flat deficit induced by an artificial central scotoma (Kelly, 1978).

The high frequency cut-off point of the contrast sensitivity function is the finest grating which can be detected at 100% contrast and has been correlated with visual acuity in humans (Green, 1970). In the normal monkey, the present results of 43 c/deg is equivalent to a difference of 0.7 minutes of arc, using half a cycle as the minimal discriminable difference. This value can be correlated with previous measurements in the same species in which the range of acuity was found to be 0.6 to 1.1 min of arc (Weinstein and Grether, 1940; Weiskrantz and Cowey, 1963; Cowey and Ellis, 1967). The high frequency cut-off point of destriated monkeys was found to be 12 c/deg, which is equivalent to an acuity of 2.5 min of arc, i.e. their capabilities are no worse than 20/80 on the Snellen chart. This loss of acuity is greater than the two-fold loss reported by Weiskrantz and Cowey (1963) who essentially removed only macular cortex. It is important to note that the very large loss of sensitivity could not have been predicted by the relatively minor loss of acuity. Moreover, the shift in the high frequency cut-off point cannot be correlated with a specific type of sensitivity loss, e.g. high frequency, notch or flat (Bodis-Wollner and Diamond, 1976).

The present investigation shows that as long as spatial frequency is a variable affecting the response, the high and low frequency limbs are best described by individual exponential equations in both normal and destriated monkeys. Such relationship has been reported previously for the high frequency limb of normals (DeValois, Morgan and Snodderly, 1974).

Not all earlier studies agree upon a mathematical relationship between contrast sensitivity and low spatial frequencies. Generally, a best curve is fitted to the data points by eye (DeValois, Morgan and Snodderly, 1974). In another report, the low frequency limb is described by an exponential term (Harding and Yates, 1976). It should be noted that their equation is based on data accumulated at frequencies from 1.2 to 15 c/deg and presupposes both high and low frequency cut-off points. The meaning of the latter, however, is not clear.

Interestingly, the low frequency response of normal, but not of destriated monkeys, exhibit large variability among animals. To some extent comparable results in normals have been observed previously (DeValois, Morgan and Snodderly, 1974). This may result from the differential response of individual animals to stimulus parameters other than spatial frequency inherent to the detection of low frequency gratings. One such variable has been found in humans to be the number of cycles contained in the stimulus. Apparently, this critical figure has been considered as four (Savoy and McCann, 1971) or seven cycles (Barakat and Lerman, 1967). If such an explanation were valid, it would suggest that such influence may not be operant in the destriated monkey. Another interpretation of the variability in performance at low spatial frequencies might stem from a change in the number of spontaneous eye movements made during a discrimination since the latter have been considered as influencing the magnitude of the sensitivity at low frequencies (Kelly, 1977). It is possible that operated animals are more consistent in their spontaneous eye movements than normals. It should be noted that the response to a moving striped pattern (O.K.N.) declined after the ablation.

The amount of light reaching the retina is crucial to spatial resolution (Mandelbaum and Sloan, 1947). The findings of this study which describe performance at photopic levels, closely resemble data previously obtained under similar conditions in the normal (DeValois, Morgan and Snodderly, 1974; Harding and Yates, 1976). In studies in which thresholds at scotopic levels were explored, the contrast sensitivity function of these animals is significantly depressed, the peak shifts to the left by about two octaves, and no low frequency decline is evident (DeValois, Morgan and Snodderly, 1974). Although peak sensitivity did not shift following the removal of striate cortex in the present study, it is possible that destriated monkeys may be performing similar to normal animals under scotopic conditions. Such a hypothesis must be tested experimentally. One other approach to this problem would be to compare the present findings with a similar study using chromatic gratings at photopic and scotopic luminance levels.

Other factors influencing contrast sensitivty are pupillary size and refractive errors (Campbell and Green, 1965). The present experimental situation did not permit rigorous control of the diameter of the pupils. It is a fair assumption, however, that their size did not vary much during the course of a session since a relatively constant level of illumination was provided within the subject compartment through either the adapting light in the intertrial period, or the stimuli proper during the trial. Previous contrast sensitivity investigations in the monkey do not offer data on refraction. The present findings verified at least one emmetropic eye in all subjects. The values obtained might be slightly shifted on the basis of the smaller dimension of the monkey eye globe since the apparatus used for automatic retinoscopy was set up to test humans. In any event, the emmetropic condition did not change significantly after the ablation of the striate cortex. Thus, it appears that the alterations in the contrast sensitivity function are attributable solely to neural factors.

The performance during contrast threshold determinations suggests the operation of two systems for the analysis of spatial information as evidenced by the values of the "psychometric precision" (p. 49) and the "instability index" (p. 39). The meaning of these two measures is similar although their magnitudes are inversely related. Two significantly different levels of precision are observed in normal monkeys, a lower one for low frequencies and a higher one for high frequencies. Destriated monkeys, which are capable of detecting only low and middle frequencies, render the lowest precision values. Conceivably, these results may be related to the electrophysiologically defined X- and Y-cell systems. The former responds primarily to stationary gratings composed of middle and high spatial frequencies, whereas the latter is predominantly responsive to middle and low spatial frequencies as well as to the temporal characteristics of the stimuli (Stone and Fukuda, 1974).

The above speculation is substantiated by the pathways followed by the X- and Y-cell systems. The former projects mostly through the lateral geniculate nucleus to the striate cortex and probably accounts for the highest precision values obtained at higher spatial frequencies. Y-cells project both along the geniculostriate pathway and to the midbrain, primarily the superior colliculus (Fukuda and Stone, 1974). They may be responsible for the intermediate precision level observed in normal monkeys at low spatial frequencies. Ablation of the striate cortex effectively eliminates the geniculostriate pathways through retrograde degeneration of all principal X- and Y-geniculate neurons. The lowest precision exhibited by destriated monkeys at low frequencies may result from the remaining Y-cell pathways. This supposition would be bolstered by psychophysically determining the bandwidths of the functional channels before and after the ablation, or by assessing the response to temporally modulated gratings to which Y-cells are particularly receptive. It should be noted that this analysis should hold in spite of possible interaction effects between the X- and Y-cell systems. This discussion has not taken into account the role of a third system, the W-cells, which has been described in cat (Stone and Fukuda, 1974) and possibly in monkey (Schiller and Malpelli, 1977). Some of these neurons also should remain following striatectomy, but their heterogeneity makes it difficult to understand their function at present.

The change of the frequency threshold function from the first (1.5 to 2 months postoperative) to the second determination (one month later) was observed in all monkeys. An improvement was observed also preoperatively in the two monkeys which were tested twice. This may suggest the operation of a learning effect although the possibility of recovery of function over time can not be ruled out in the destriated monkeys. To test this empirically, however, two monkeys were kept alive for future psychophysical tests.

In general, contrast thresholds determined by the method of constant stimuli are more consistent over the group than those obtained by the up-down technique. Standard deviations for the mean data collected at each of the spatial frequencies tested are lower in the former procedure, particularly postoperatively. Moreover, thresholds determined by the up-down method are generally lower than analogous values provided by the method of constant stimuli. This may be an artifact of the stepping rule used. A more rigorous one, such as requiring a subject to make two or more correct responses before contrast were decreased, may produce more compatible results in future investigations (Levitt, 1970). Minor differences between procedures also may be due to the experimentally imposed additional accuracy of the method of constant stimuli which results from the larger number of presentations at a given contrast step and by the additional period of training at each spatial frequency preceding its sessions. This supposition is substantiated by the steadying of the performance of individuals and the group as the study progressed.

From perithreshold information it may be possible to extrapolate suprathreshold performance. A model can be developed by relating the slope of the psychometric function ("psychometric precision") to the size of a just noticeable difference (JND; Engen, 1971). When performance asymptotes at 100% and 0%, one JND is equivalent to the stimulus increment which is necessary to increase the level of performance from 50% (threshold) to 75%. The number of JND in the dynamic range of sensation can be extrapolated from a function graphed with number of JND on the ordinate and log contrast on the abscissa (Hodos, 1976). The line is determined by performance at threshold (0 JND) and at 75% (1 JND). In a two-choice situation, however, performance levels off at 100% and 50%, and therefore, the above reasoning cannot be strictly applied. Nevertheless, it is still possible to determine the ratio of the number of JND in which the normal and destriated monkeys divide the contrast range. This can be done by selecting a multiple of the JND (kJND) of any size provided it is kept constant, for example, the stimulus increment necessary to change the performance level by one transformed standard score from 75% (threshold) to 92% (Appendix C.3.). Using these values it is found that, at 2.0 c/deg, the monkeys of the present study can divide the range of detectable contrasts into 12 kJND and 3 kJND before and after removal of the striate cortex, respectively. Similar values are found at other spatial frequencies and the mean ratio of the normal to the destriated condition is 3.6:1. The loss is due to the decrease in both the "psychometric precision" and the reduction of the dynamic range. Such an analysis presupposes that the size of a JND varies with the logarithm of contrast (Fechner's law).

The present findings substantiate this assumption at liminal performance and similar results have been recorded at various suprathreshold levels in humans (Kulikowski, 1976). Moreover, differences in apparent contrast are logarithmic functions of contrast (Maffei and Fiorentini, 1973b).

Destriated monkeys are capable of discriminating differences in total luminous flux (Klüver, 1941; Pasik, Schilder and Pasik, 1971) when they exceed the threshold of $\Delta F/\bar{F} = 0.23$ (Klüver, 1942). It was imperative, therefore, that all targets of the present study were equated for mean luminance, and being of the same area, for luminous flux. In fact, the above ratio was always less than or equal to 0.05. In any event, the performance in control sessions ruled out the possibility that these animals could be using minimal flux cues to master the tests. In two previous studies, discrimination of flux-equated figures were given as a first test after total removal of striate cortex in monkeys. In one, targets differed in luminance and area (Schilder, Pasik, and Pasik, 1971). The other consisted of a vertical versus a horizontal bar of equal luminance and size (Pasik, Pasik, Nolan, and Solomon, 1976). Animals succeeded in solving both problems with less training than that required for the initial discrimination in the present investigation (maximum contrast target at 1.0 c/deg versus homogeneous target). This difference, however, may be more apparent than real since the savings fraction, preoperative minus postoperative error scores divided by their sum, is similar for all three tasks (-0.71 to -0.74).

Pattern recognition may result from the integration of orientation and spatial frequency information and the striate cortex apparently is essential for such function (Blakemore and Campbell, 1969). Following removal of Area 17, monkeys are capable of discriminations based upon orientation (Pasik, Pasik, Nolan, and Solomon, 1976) and spatial frequency cues as the present study has shown, although their capacities are considerable lower than normals. This may explain the ability of destriated monkeys to relearn to differentiate a circle from a triangle of high contrast after prolonged training (Schilder, Pasik, and Pasik, 1972). The deficits in pattern perception could be explained further by examining the capacity of normal and destriated monkeys to discriminate a given pattern from a computer digitized version of the same. Digitizing a black and white photograph into discrete homogeneous squares such that the shade of gray in each square is the average of the corresponding area in the original, creates an image which is difficult to recognize (Harmon and Julesz, 1973). The squares contain edges which according to Fourier analysis result from high frequency components. To a normal human and probably a normal monkey, these high frequencies effectively act as noise, which if large enough can block recognition of the image. By removing the frequencies above 12 c/deg (blurring the edges), the image becomes identifiable. Thus, a paradox is evident wherein destriated monkeys which can perceive only the low frequencies may be able to recognize the nonfiltered image whereas normal animals may not.

APPENDIX

A. Calibration of Light Sources

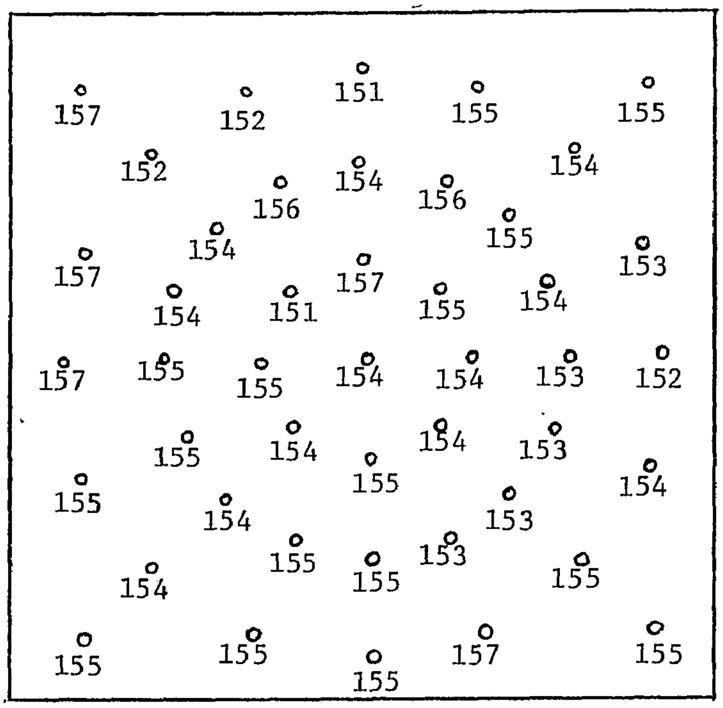
All luminance and density values were measured by a Gamma Scientific Photometer fitted with a photopic filter and a fiber optic probe. Relative measurements required only that the photometer record zero when there was no incoming light. For use in absolute luminance measurements a supplemental point was determined by a standard light souce, American Atomic Krypton 85, calibrated by an independent laboratory with sources traceable to the National Bureau of Standards.

A. 1. Adapting light. The fiber optic probe was placed at twenty five evenly spaced points and absolute luminance measurements were recorded in terms of cd/m^2. The values are given in the table below for luminance (L) at the position (P).

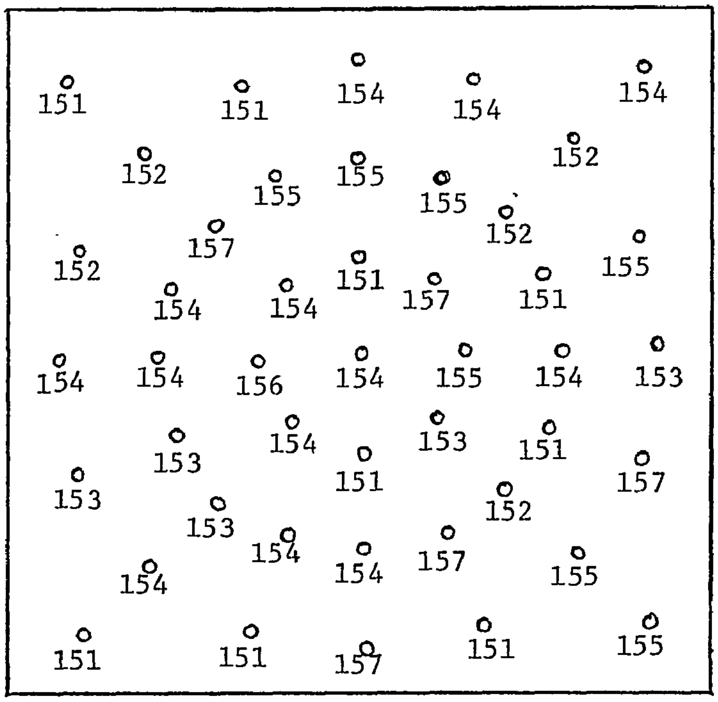
P	L	P	L	P	L	P	L	P	L
1,1	0.69	1,2	0.83	1,3	0.83	1,4	0.83	1,5	0.83
2,1	1.2	2,2	2.1	2,3	1.9	2,4	1.8	2,5	1.2
3,1	1.8	3,2	3.3	3,3	3.2	3,4	3.2	3,5	1.9
4,1	1.2	4,2	2.1	4,3	2.1	4,4	1.9	4,5	1.4
5,1	0.83	5,2	0.97	5,3	1.1	5,4	1.1	5,5	0.69

The average of the luminance values (1.6 cd/m^2) was designated as the mean luminance for the entire source.

A. 2. Stimuli light sources. The eveness of each diffuse light source was calibrated by measuring the luminance at 45 regularly spaced positions with the fiber optic probe (see diagrams below). "Hot" spots on the bulb were covered with an opaque material until a maximum



Right-side
Stimulus Box



Left-side
Stimulus Box

variation of 2% was achieved. The diagram above illustrates the template placed over a stimulus box and the absolute luminance at the 45 points.

A. 3. Targets.

A. 3. a. Contrast. The contrast (Cont.) for every grating used in the study is listed in the table in Appendix A.3.b. (p. 101). To determine the contrast of a grating, a special button with a 0.4 mm diameter aperture was fitted to the fiber optic probe. The button was slid across a transilluminated target to measure the luminance at the crests and troughs by recording maximal and minimal deflections on the photometer, respectively. For the 16 and 32 c/deg targets, the period of the waveform was too high to reliably determine these points. Therefore, the button was passed along a magnified image of the target produced by a Bausch and Lomb Tri-Simplex Microprojector fitted with a 25 mm Zeiss Luminar lens to ascertain relative luminance values. An image was projected and focused on the lower surface of a piece of lucite. For each target, measurements were taken at five positions by placing the probe at the level of focus. A contrast was calculated for each pair and the mean value was designated as the contrast for that target. For acceptance in the study the contrast had to be within 5% of the 0.1 log unit step it was designed to fit.

A. 3. b. Density. The mean density of the target, and hence the mean luminance (L_{mean}) of the stimulus was determined by two methods. First, an estimate was made from the contrast calibration as the mean luminance is the average of the maximal and minimal luminance.

Level	Spatial Frequency (c/deg)								
	0.5			1.0			2.0		
	Cont.	L_{mean}		Cont.	L_{mean}		Cont.	L_{mean}	
		A	B		A	B		A	B
0.79	0.79	19	19.8	0.82	20	20.5	0.77	22	20.2
0.63	0.66	21	20.5	0.64	20	19.7	0.62	21	20.0
0.50	0.49	22	20.0	0.51	20	20.3	0.49	22	20.6
0.40	0.40	20	20.0	0.38	19	20.2	0.39	21	19.2
0.32	0.32	21	20.1	0.33	19	19.4	0.33	21	20.6
0.25	0.26	21	20.8	0.26	21	20.4	0.26	21	20.0
0.20	0.20	21	20.2	0.20	20	19.4	0.20	21	20.1
0.16	0.17	22	20.4	0.16	20	20.2	0.16	19	19.8
0.13	0.13	20	20.3	0.13	22	20.2	0.13	20	19.9
0.10	0.10	20	20.1	0.10	20	19.8	0.10	19	20.1
0.079	0.076	21	20.5	0.083	19	19.6	0.081	21	20.8
0.063	0.063	21	20.4	0.063	20	19.8	0.065	19	20.9
0.050	0.051	20	21.0	0.052	22	20.2	0.050	20	20.3
0.040	0.041	21	20.4	0.038	21	20.3	0.042	19	19.5
0.032	0.033	21	20.3	0.032	21	20.1	0.032	19	19.9
0.025	0.025	21	20.0	0.025	20	20.1	0.025	21	19.8
0.020	0.019	22	19.8	0.020	20	19.7	0.020	21	20.4
0.016	0.015	22	20.1	0.016	20	19.8	0.016	21	20.3
0.013	0.012	21	20.0	0.013	19	20.4	0.013	21	19.9
0.010	0.010	22	19.9	0.010	19	19.8	0.010	20	20.5
0.008	0.008	22	19.7				0.008	21	19.9
0.006	0.006	21	19.8				0.006	21	19.6

Level	Spatial Frequency (c/deg)					
	4.0			8.0		
	Cont.	L_{mean}		Cont.	L_{mean}	
		A	B		A	B
0.79	0.73	20	20.3	0.80	20	19.1
0.63	0.63	19	20.2	0.66	21	19.4
0.50	0.51	20	20.5	0.50	21	20.0
0.40	0.39	19	20.0	0.40	21	20.0
0.32	0.30	19	19.5	0.33	21	19.8
0.25	0.24	19	19.2	0.25	22	19.7
0.20	0.21	20	20.3	0.20	20	20.3
0.16	0.17	19	20.6	0.15	21	19.6
0.13	0.13	19	20.2	0.13	22	20.4
0.10	0.0095	21	20.6	0.10	22	19.3
0.079	0.080	21	20.0	0.079	20	19.9
0.063	0.063	20	19.7	0.063	21	20.2
0.050	0.048	19	19.6	0.050	20	20.2
0.040	0.040	20	20.1	0.040	20	20.5
0.032	0.030	19	20.3	0.031	19	20.2
0.025	0.026	19	19.5	0.024	21	20.4
0.020	0.019	19	20.0	0.021	21	19.5
0.016	0.016	20	20.2	0.015	21	19.5
0.013	0.013	19	19.6	0.013	21	20.0
0.010	0.010	20	19.5	0.010	20	19.5
0.008	0.008	21	19.1			

Level	Spatial Frequency (c/deg)					
	16			32		
	Cont.	L_{mean}		Cont.	L_{mean}	
		A	B		A	B
0.79	0.83	20	20.0	0.77	21	20.3
0.63	0.62	21	20.3	0.61	20	20.1
0.50	0.49	20	20.0	0.51	21	20.6
0.40	0.41	21	19.9	0.42	19	20.2
0.32	0.33	20	19.0	0.30	20	19.8
0.25	0.26	21	20.6	0.25	21	20.2
0.20	0.20	20	20.1	0.20	20	19.3
0.16	0.16	19	20.1	0.16	20	19.6
0.13	0.12	20	19.0	0.12	19	19.9
0.10	0.10	21	20.1			
0.079	0.080	21	19.7			
0.063	0.063	20	19.8			
0.050	0.052	21	19.0			
0					20	20.0
0					20	20.1

These values are noted in column A in the chart above. A more rigorous procedure was based upon the mean luminance of 25 points. These points were chosen to measure the density of the center and three points in each of eight octants of the target. This method required defocusing and reducing the image of the target with the enlarger and systematically recording the density at the 25 points through a fixed template. Values are given for each target in Column B of the chart above. The mean luminance of all gratings was equated to within 5% of 20 cd/m^2, the value determined for both homogeneous targets. Thus, the maximal luminous flux difference between the grating and the homogeneous target was such that $\Delta F/\bar{F} < 0.05$.

A. 3. c. Waveform. The waveform of the grating was assessed by its appearance to the experiment's eye. The period of the waveform was determined by counting the number of cycles in the target. In addition, the quality of the waveform was determined at maximal contrast, that is to say whether the wave was square, triangular, or sinusoidal. Once it was obvious that the grid had no edges as in a square or triangular wave, the importance of the high frequency harmonic interference was reduced immediately.

B. Photographic Process

B. 1. Photographing the stimuli. The Graflex camera was positioned 23 to 25 cm from the oscilloscope screen and focused appropriate in order to make a one to one reproduction.

The range of stops used was 15 to 22 and the exposure times varied from 50 to 60 seconds for an oscilloscope screen with a mean luminance of 10 cd/m^2. To protect the film from spurious light the room was maintained in darkness while negatives were being taken and furthermore, a black photographic cloth was placed over the camera and oscilloscope. In the pulling-in apparatus, the stimuli are 65 cm from the subject. A 9 cm or 8 degree target must include four cycles in order to be 0.5 c/deg. The 12.7 cm wide negative, therefore, must contain 5.6 cycles.

To produce the other spatial frequencies, 1.0, 2.0, 4.0 and 8.0 c/deg, grating patterns were created on the oscilloscope composed of 11.3, 22.6, 45.2 and 90.3 cycles, respectively.

B. 2. Development and reduction. The negatives were developed in a completely dark room. Six negatives at a time were immersed in a small tank containing Kodak HC110 Developer, Dilution D (1:9) for eight minutes with agitation every minute. This developer was chosen because it produced the gray scale without compromising maximal contrast. The negatives were then placed in Kodak Stop Bath SB-1a for 25 to 30 sec. Subsequently, the films were placed in Kodak Rapid Fixer for two minutes with agitation every 30 sec. The fixer was washed off by immersing the negatives in running water for 15 minutes. To prevent water spots from appearing, negatives were bathed in Kodak Photo Flo for one minute and air dried. All solutions were maintained at 20°C.

To equate the negatives for mean luminance often a reduction procedure was necessary. Negatives were reduced individually by immersion in 30 ml of Kodak Farmer's Reducer. The time in solution varied depending upon the original density and was measured by the experimenter on an individual basis. Following the reducing step the negatives were washed, fixed, rewashed, and dried according to the same procedure used for developing. If after calibration the negative was still too dense, it was sent through the reduction procedure again.

C. Preoperative Stage

C. 1. Contrast thresholds and sensitivities for normal monkeys determined by the up-down method

Monkey	Spatial Frequency (c/deg)														P		H
	0.5		1.0		2.0		4.0		8.0		16		32		S	ν	
	T	S	T	S	T	S	T	S	T	S	T	S	T	S			
878	0.012	83	0.015	67	0.011	91	0.012	83	0.019	53	0.068	15	0.30	3.3	90	2.5	42
879	0.015	67	0.014	71	0.010	100	0.010	100	0.020	50	0.067	15	0.26	3.8	101	2.1	42
880	0.040	25	0.030	33	0.010	100	0.012	83	0.022	45	0.061	16	0.32	3.1	96	2.0	41
881	0.019	53	0.018	56	0.011	91	0.012	83	0.024	42	N.T.		N.T.		--	--	--
887	0.025	40	0.024	42	0.013	77	0.014	71	0.018	56	0.073	14	0.22	4.5	81	2.2	46
890	0.021	48	0.017	59	0.014	71	0.012	83	0.016	63	0.066	15	0.23	4.3	83	3.6	44
$\bar{x}$	0.022	53	0.020	55	0.012	88	0.012	84	0.020	52	0.067	15	0.27	3.8	90	2.2	43
s.d.	0.010	20	0.006	15	0.002	12	0.001	9	0.003	8	0.004	1	0.04	0.6			

Contrast thresholds and sensitivites are indicated by T and S, respectively. H signifies the high frequency cut-off point in c/deg. P designates the peak in sensitivity (S) and spatial frequency (ν) in c/deg. Means and standard deviations are noted by $\bar{x}$ and s.d., rspectively. N.T. indicates a spatial frequency at which a monkey was not tested.

C. 2. Performance of normal monkeys in the method of constant stimuli

Monkey	Spatial Frequency (c/deg)													
	0.5		1.0		2.0		4.0		8.0		16		32	
	C	%	C	%	C	%	C	%	C	%	C	%	C	%
878	0.033	99	0.038	99	0.025	100	0.030	98	0.040	99	0.20	100	0.61	99
	0.025	94	0.032	99	0.020	99	0.026	97	0.031	95	0.16	99	0.51	98
	0.019	90	0.025	95	0.016	96	0.019	96	0.024	91	0.12	91	0.42	87
	0.015	83	0.020	93	0.013	93	0.016	92	0.021	77	0.10	88	0.30	78
	0.012	72	0.016	88	0.010	79	0.013	82	0.015	70	0.080	77	0.25	76
	0.010	60	0.013	66	0.008	73	0.010	69	0.013	60	0.063	70	0.20	61
	0.008	50	0.010	49	0.006	58	0.008	56	0.010	51	0.052	58	0.16	54
879	0.025	97	0.038	100	0.025	100	0.030	100	0.040	100	0.20	100	0.61	100
	0.019	95	0.032	99	0.020	99	0.026	99	0.031	96	0.16	99	0.51	97
	0.015	90	0.025	97	0.016	97	0.019	97	0.024	89	0.12	95	0.42	91
	0.012	79	0.020	95	0.013	92	0.016	93	0.021	80	0.10	95	0.30	87
	0.010	69	0.016	85	0.010	84	0.013	83	0.015	71	0.080	90	0.25	73
	0.008	60	0.013	67	0.008	70	0.010	70	0.013	66	0.063	75	0.20	69
	0.006	49	0.010	60	0.006	56	0.008	60	0.010	51	0.052	61	0.16	55

Monkey	Spatial Frequency (c/deg)													
	0.5		1.0		2.0		4.0		8.0		16		32	
	C	%	C	%	C	%	C	%	C	%	C	%	C	%
880	0.10	100	0.083	100	0.025	98	0.030	100	0.063	99	0.20	100	0.61	99
	0.076	95	0.063	97	0.020	95	0.026	99	0.050	95	0.16	98	0.51	96
	0.063	91	0.052	95	0.016	92	0.019	96	0.040	91	0.12	96	0.42	89
	0.051	81	0.038	81	0.013	86	0.016	90	0.031	86	0.10	88	0.30	77
	0.041	72	0.032	76	0.010	80	0.013	79	0.024	75	0.080	79	0.25	73
	0.033	64	0.025	61	0.008	65	0.010	66	0.021	63	0.063	67	0.20	60
	0.025	51	0.020	56	0.006	52	0.008	53	0.015	53	0.052	55	0.16	49
881	0.063	96	0.063	97	0.025	99	0.040	99						
	0.051	91	0.052	94	0.020	96	0.030	97						
	0.041	83	0.038	82	0.016	91	0.026	90						
	0.033	79	0.032	74	0.013	84	0.019	82	N.T.		N.T.		N.T.	
	0.025	71	0.025	65	0.010	76	0.016	70						
	0.019	59	0.020	59	0.008	68	0.013	58						
	0.015	51	0.016	56	0.006	56	0.010	51						

Monkey	Spatial Frequency (c/deg)													
	0.5		1.0		2.0		4.0		8.0		16		32	
	C	%	C	%	C	%	C	%	C	%	C	%	C	%
887	0.076	97	0.052	98	0.042	98	0.040	97	0.050	95	0.20	100	0.61	98
	0.063	94	0.038	95	0.032	95	0.030	93	0.040	90	0.16	97	0.51	94
	0.051	88	0.032	89	0.025	90	0.026	86	0.031	87	0.12	94	0.42	89
	0.041	81	0.025	80	0.020	80	0.019	75	0.024	76	0.10	88	0.30	81
	0.033	70	0.020	71	0.016	70	0.016	60	0.021	66	0.080	81	0.25	74
	0.025	61	0.016	61	0.013	66	0.013	57	0.015	63	0.063	66	0.20	62
	0.019	49	0.013	49	0.010	55	0.010	49	0.013	51	0.052	58	0.16	52
890	0.051	96	0.038	97	0.025	99	0.030	98	0.040	99	0.20	98	0.61	99
	0.041	88	0.032	92	0.020	94	0.026	93	0.031	90	0.16	95	0.51	99
	0.033	84	0.025	82	0.016	91	0.019	86	0.024	84	0.12	91	0.42	92
	0.025	76	0.020	79	0.013	79	0.016	77	0.021	74	0.10	85	0.30	86
	0.019	64	0.016	70	0.010	74	0.013	61	0.015	72	0.080	76	0.25	75
	0.015	63	0.013	56	0.008	61	0.010	55	0.013	60	0.063	69	0.20	65
	0.012	52	0.010	48	0.006	52	0.008	47	0.010	53	0.052	53	0.16	54

Percent correct responses (%) at each contrast step (C) given during the sessions of the method of constant stimuli are listed. N.T. denotes a spatial frequency at which a monkey was not tested.

C. 3. Transformed standard scores

%	z	%	z	%	z
51	-2.055	68	-0.358	84	0.468
52	-1.750	69	-0.305	85	0.524
53	-1.555	70	-0.253	86	0.583
54	-1.405	71	-0.202	87	0.643
55	-1.281	72	-0.151	88	0.707
56	-1.175	73	-0.100	89	0.772
57	-1.080	74	-0.050	90	0.842
58	-0.995	75	0.0	91	0.915
59	-0.915	76	0.050	92	0.995
60	-0.842	77	0.100	93	1.080
61	-0.772	78	0.151	94	1.175
62	-0.707	79	0.202	95	1.281
63	-0.643	80	0.253	96	1.405
64	-0.583	81	0.305	97	1.555
65	-0.524	82	0.358	98	1.750
66	-0.468	83	0.413	99	2.055
67	-0.413				

Percent correct responses are given in the columns headed % and z signifies the standard score for these percentages. Note that z = 0.0 at 75%.

C. 4. Contrast thresholds and sensitivites for normal monkeys determined by the method of constant stimuli

Monkey	Spatial Frequency (c/deg)														P		H
	0.5		1.0		2.0		4.0		8.0		16		32		S	ν	
	T	S	T	S	T	S	T	S	T	S	T	S	T	S			
878	0.013	77	0.013	77	0.0088	114	0.012	86	0.019	53	0.078	13	0.28	3.6	104	1.8	41
879	0 .011	91	0.012	84	0.0079	127	0.011	91	0.018	56	0.064	16	0.25	4.0	114	1.8	43
880	0 .046	22	0.033	30	0.011	91	0.012	83	0.027	37	0.077	13	0.27	3.7	85	1.9	42
881	0.032	31	0.031	32	0.010	100	0.018	56	N.T.				N.T.		--	--	--
887	0.036	28	0.022	45	0.018	56	0.020	50	0.025	40	0.076	13	0.29	3.4	60	2.0	44
890	0.025	40	0.020	50	0.011	91	0.016	63	0.019	53	0.084	12	0.25	4.0	82	1.9	44
$\bar{x}$	0.027	48	0.022	52	0.011	97	0.015	72	0.022	48	0.076	13	0.27	3.7	88	1.9	43
s.d.	0.014	29	0.009	21	0.004	24	0.004	17	0.004	9	0.007	2	0.02	0.3			

Notation as in Appendix C. 1.

D. Postoperative Stage

D. 1. Contrast thresholds and sensitivities for destriated monkeys determined by the up-down method

Monkey	Spatial Frequency (c/deg)								P		H
	0.5		1.0		2.0		4.0		S	ν	
	T	S	T	S	T	S	T	S			
878	0.32	3.1	0.084	12	0.16	6.3	0.29	3.4	11	0.96	6.9
880	0.26	3.8	0.19	5.3	0.17	5.9	0.20	5.0	6.0	1.9	23
887	0.34	2.9	0.13	7.7	0.17	5.9	0.25	4.0	7.6	0.99	10
890	0.32	3.1	0.22	4.5	0.16	6.3	0.22	4.5	6.4	2.0	13
$\bar{x}$	0.31	3.2	0.16	7.4	0.17	6.1	0.24	4.2	7.4	1.0	12
s.d.	0.03	0.4	0.06	3.4	0.01	0.2	0.04	0.7			

Notation as in Appendix C. 1.

D. 2. Performance of destriated monkeys
in the method of constant stimuli

Monkey	Spatial Frequency (c/deg)							
	0.5		1.0		2.0		4.0	
	C	%	C	%	C	%	C	%
878	0.79	90	0.64	90	0.49	90	0.73	92
	0.66	85	0.51	87	0.39	86	0.63	88
	0.49	79	0.38	75	0.33	82	0.51	84
	0.40	77	0.33	75	0.26	78	0.39	77
	0.32	67	0.26	73	0.20	70	0.30	73
	0.26	57	0.20	62	0.16	58	0.24	63
	0.20	53	0.16	56	0.13	50	0.21	58
880	0.79	93	0.64	92	0.49	93	0.73	94
	0.66	88	0.51	86	0.39	91	0.63	88
	0.49	80	0.38	83	0.33	84	0.51	86
	0.40	78	0.33	72	0.26	77	0.39	81
	0.32	71	0.26	70	0.20	74	0.30	73
	0.26	63	0.20	60	0.16	61	0.24	64
	0.20	55	0.16	60	0.13	57	0.21	58
887	0.79	93	0.64	92	0.49	93	0.63	92
	0.66	89	0.51	90	0.39	87	0.51	89
	0.49	81	0.38	86	0.33	83	0.39	85
	0.40	73	0.33	82	0.26	79	0.30	79
	0.32	69	0.26	72	0.20	70	0.24	73
	0.26	61	0.20	63	0.16	62	0.21	66
	0.20	55	0.16	54	0.13	57	0.17	56
890	0.79	93	0.51	89	0.49	94	0.73	95
	0.66	88	0.38	83	0.39	91	0.63	91
	0.49	84	0.33	82	0.33	80	0.51	89
	0.40	73	0.26	75	0.26	77	0.39	81
	0.32	71	0.20	68	0.20	70	0.30	76
	0.26	64	0.16	58	0.16	63	0.24	66
	0.20	57	0.13	53	0.13	56	0.21	59

Notation as in Appendix C. 2.

D. 3. Contrast thresholds and sensitivities for destriated monkeys determined by the method of constant stimuli

Monkey	Spatial Frequency (c/deg)										P		H
	0.5		1.0		2.0		4.0		8.0*		S	ν	
	T	S	T	S	T	S	T	S	T	S			
878	0.45	2.2	0.32	3.1	0.26	3.8	0.37	2.7	0.56	1.8	3.7	1.8	13
880	0.40	2.5	0.31	3.2	0.25	4.0	0.35	2.9	0.60	1.7	4.0	1.9	12
887	0.47	2.4	0.31	3.2	0.25	4.0	0.30	3.3	0.62	1.6	4.1	2.1	11
890	0.39	2.6	0.26	3.4	0.24	4.2	0.33	3.0	0.62	1.6	4.2	1.9	11
$\bar{x}$	0.43	2.4	0.30	3.2	0.25	4.0	0.34	3.0	0.60	1.7	4.0	1.9	12
s.d.	0.04	0.2	0.03	0.1	0.01	0.2	0.03	0.3	0.03	0.1			

Notation as in Appendix C. 1. * Denotes that values at 8.0 c/deg are based upon performance in the frequency threshold determinations (see text).

REFERENCES

Arend, L.E., Jr. (1976) Response of the human eye to spatially sinusoidal gratings at various exposure durations, Vision Res., 16: 1311-1315.

Barakat, R. and S. Lerman (1967) Diffraction images of truncated, one dimensional, periodic targets, Appl. Optics, 6: 545-550.

Bartley, S.H. (1957) The psychophysiology of vision. In: S.S. Stevens (ed.), Handbook of Experimental Psychology, John Wiley and Sons, New York, pp. 921-984.

Bekesy, G. von. (1947) A new audiometer, Acta Otolaryng. (Stockh.), 35: 411-422.

Bisti, S. and R.C. Sireteanu (1976) Sensitivity to spatial frequency and contrast of visual cells in the cat superior colliculus, Vision Res., 16: 247-251.

Blakemore, C. and F.W. Campbell (1969) On the existence of neurones in the human visual system selectively sensitive to the orientation and size of retinal images, J. Physiol. (London), 203: 237-260.

Bodis-Wollner, I. (1972) Visual acuity and contrast sensitivity in patients with cerebral lesions, Science, 178: 769-771.

Bodis-Wollner, I. (1976) Vulnerability of spatial frequency channels in cerebral lesions, Nature, 261: 309-311.

Bodis-Wollner, I. and C. Hendley (1979) On the separability of two mechanisms involved in the detection of grating patterns in humans, J. Physiol. (London), in press.

Bodis-Wollner, I. and S.P. Diamond (1976) The measurement of spatial contrast sensitivity in cases of blurred vision associated with cerebral lesions, Brain, 99: 695-710.

Bonin, G. von and P. Bailey (1947) The Neocortex of Macaca Mulatta, The University of Illinois Press, Urbana, Ill.

Campbell, F.W. (1974) The transmission of spatial information through the visual system. In: F.O. Schmitt and F.G. Worden (eds.), The Neurosciences Third Study Program, M.I.T.Press, Cambridge, Mass., pp. 95-103.

Campbell, F.W., G.F. Cooper, and C. Enroth-Cugell (1969) The spatial selectivity of the visual cells of the cat, J. Physiol. (London), 203: 223-235.

Campbell, F.W., G.F. Cooper, J.G.Robson, and M.B. Sachs (1969) The spatial selectivity of visual cells of the cat and the squirrel monkey, J. Physiol. (London), 204: 120P-121P.

Campbell, F.W. and Green, D.G. (1965) Optical and retinal factors affecting visual resolution, J. Physiol. (London), 181: 576-593.

Campbell, F.W. and J.J. Kulikowski (1966) Orientation selectivity of the human visual system, J. Physiol. (London), 187: 437-445.

Campbell, F.W., J.J. Kulikowski, and J. Levinson (1966) The effect of orientation on the visual resolution of gratings, J. Physiol. (London), 187: 427-436.

Campbell, F.W. and J.G. Robson (1968) Application of Fourier analysis of the visibility of gratings, J. Physiol. (London), 197: 551-566.

Cleland, B.G., M.W. Dubin, and W.R. Levick (1971) Sustained and transient neurons in the cat's retina and lateral geniculate nucleus, J. Physiol. (London), 217: 473-496.

Cowey, A. and C. M. Ellis (1967) Visual acuity of Rhesus and squirrel monkeys. J. Comp. Phys. Psychol., 64: 80-84.

DeMonasterio, F.M., P. Gouras, and D.J. Tolhurst (1976) Spatial summation, response pattern and conduction velocity of ganglion cells of the Rhesus monkey retina, Vision Res., 16: 674-678.

DeValois, R.L., H. Morgan, and D.M. Snodderly (1974) Psychophysical studies of monkey vision. III. Spatial luminance contrast sensitivity tests of macaque and human observers, Vision Res., 14: 75-81.

Engen, T. (1971) Psychophysics I. Discrimination and detection. In: J. W. Kling and L.A. Riggs (ed.), Experimental Psychology, Holt, Rinehart and Winston, New York, pp. 11-46.

Enroth-Cugell, C. and J.G. Robson (1966) The contrast sensitivity of retinal ganglion cells in the cat, J. Physiol. (London), 187: 517-552.

Feinberg, T., P. Pasik, and T. Pasik (1977) Visually mediated space localization in monkeys without striate cortex, Fed. Proc., 36: 597.

Feinberg, T.E., T. Pasik, and P. Pasik (1978) Extrageniculostriate vision in the monkey. VI. Visually guided accurate reaching behavior. Brain Res., 152: 422-428.

Fukuda, Y. and S. Stone (1974) Retinal distribution and central projections of Y-, X-, and W-cells of the cat's retina. J. Neurophys., 37:749-772.

Furchner, C.S., J.P. Thomas, and F.W. Campbell (1977) Detection and discrimination of simple and complex patterns at low spatial frequencies, Vision Res., 17: 827-836.

Gellerman, L.W. (1938) Chance orders of alternating stimuli in visual discrimination experiments. Pedagogical Seminar and Journal of Genetic Psychology, 42: 206-208.

Gilinsky, A.S. (1968) Orientation-specific effects of patterns of adapting light on visual acuity, J. Opt. Soc. Am., 58: 13-18.

Graham, N. (1972) Spatial frequency channels in the human visual system: Effects of luminance and pattern drift rate, Vision Res., 12: 53-68.

Graham, N. and J. Nachmias (1971) Detection of grating patterns containing two spatial frequencies: A comparison of single-channel and multiple-channels models, Vision Res., 11: 251-259.

Green, D.G. (1970) Testing the vision of cataract patients by means of laser generated interference fringes, Science, 168: 1240-1242.

Guilford, J.P. (1954) Psychometric Methods, McGraw-Hill, New York, p. 127.

Harding, T.H. and J.T. Yates (1976) Monkey contrast threshold for aperiodic patterns, J. Opt. Soc. Am., 66: 131-138.

Harmon, L.D. and B. Julesz (1973) Masking in visual recognition: Effects of two-dimensional filtered noise, Science, 180: 1194-1197.

Hodos, W. (1976) Vision and the visual system: a bird's eye view, Progr. Psychobiol., 6: 29-62.

Hoffman, K.-P. and J. Stone (1971) Conduction velocity of afferents to cat visual cortex: a correlation with cortical receptive field properties, Brain Res., 32: 460-466.

Hubel, D.H. and T.N. Wiesel (1962) Receptive fields, binocular interaction, and functional architecture in the cat's visual cortex, J. Physiol. (London), 160: 106-154.

Hubel, D.H. and T.N. Wiesel (1965) Receptive fields and functional architecture in two nonstriate visual areas (18 and 19) of the cat, J. Neurophys., 28: 229-289.

Hubel, D.H. and T.N. Wiesel (1968) Receptive fields and functional architecture of monkey striate cortex, J. Physiol. (London), 195: 215-243.

Hubel, D.H. and T.N. Wiesel (1970) Cells sensitive to binocular depth in area 18 of the macaque monkey cortex, Nature, 225: 41-42.

Ikeda, H. and M.J. Wright (1974) Evidence for "sustained" and "transient" neurones in the cat's visual cortex, Vision Res., 14: 133-136.

Ikeda, H. and M.J. Wright (1975) Spatial and temporal properties of sustained and transient neurones in area 17 of the cat's visual cortex, Exp. Brain Res., 22: 363-383.

Jacobs, G.H. (1977) Visual capacities of the owl monkey (Aotus trivirgatus). II. Spatial contrast sensitivity, Vision Res., 17: 821-825.

Keesey, V. (1972) Flicker and pattern detection: a comparison of thresholds, J. Opt. Soc. Am., 62: 446-448.

Kelly, D.H. (1977) Visual contrast sensitivity, Optica Acta.,24: 107-129.

Kelly, D.H. (1978) Photopic contrast sensitivity without foveal vision, Optic Letters, 2: 79-81.

Klüver, H. (1941) Visual functions after removal of the occipital lobes, J. Psychol., 11: 23-45.

Klüver, H. (1942) Functional significance of the geniculostriate system, Biol. Symp., 7: 253-299.

Kulikowski, J.J. (1971) Some stimulus parameters affecting spatial and temporal resolution of human vision, Vision Res., 11: 83-93.

Kulikowski, J.J. (1976) Effective contrast constancy and linearity of contrast sensation, Vision Res., 16: 1419-1431.

Kulikowski, J.J. and D.J. Tolhurst (1973) Psychophysical evidence for sustained and transient detectors in human vision, J. Physiol., (London), 232: 149-162.

Legge, G. (1978) Sustained and transient mechanisms in human vision: Temporal and spatial properties, Vision Res., 18: 69-81.

Levitt, H. (1970) Transformed up-down methods in psychoacoustics. J. Acoust. Soc. Am., 49: 467-477.

Maffei, L. and A. Fiorentini (1973a) The visual cortex as a spatial frequency analyser, Vision Res., 13: 1255-1267.

Maffei, L. and A. Fiorentini (1973b) Neural correlate of perceptual adaptation to gratings, Science, 182: 1036-1038.

Maffei, L. and A. Fiorentini (1976) Spatial contrast sensitivity of myopic subjects, Vision Res., 16: 437-438.

Maffei, L. and A. Fiorentini (1977) Spatial frequency rows in striate visual cortex, Vision Res., 17: 257-264.

Mandelbaum, J. and L.L. Sloan (1947) Peripheral visual acuity, Am. J. Ophthalmol., 30: 581.

Marrocco, R.T. (1976) Sustained and transient cells in monkey lateral geniculate nucleus: conduction velocities and response properties, J. Neurophys., 39: 340-353.

Mathers, L.H. (1971) Tectal projection to the posterior thalamus of the squirrel monkey, Brain Res., 35: 295-298.

McCarter, A. and T. Roehrs (1976) A spatial frequency analogue to mach bands, Vision Res., 16: 1317-1321.

Merigan, W.H. (1976) The contrast sensitivity of the squirrel monkey, Vision Res., 16: 375-379.

Miller, M., T. Pasik, and P. Pasik (in press) Flicker-induced nystagmus in a Ganzfeld situation in monkeys, Exp. Neur.

Nachmias, J. (1967) Effect of exposure duration on visual contact sensitivity with square-wave gratings, J. Opt. Soc. Am., 57: 421-427.

Ogren, M.P. and A.E. Hendrickson (1977) The distribution of pulvinar terminals in visual areas 17 and 18 of the monkey, Brain Res., 137: 343-350.

Østerberg, G.A. (1935) Topography of the rods and cones in the human retina, Acta. Ophthal. (Suppl.), 6: 1-102.

Pasik, P. and T. Pasik (1975) A comparison between two types of visually-evoked nystagmus in the monkey. Acta. Otolaryngol. Suppl., 330: 30-37.

Pasik, P., T. Pasik, J.T. Nolan, and S.J. Solomon (1976) Bar orientation discrimination in normal and destriated monkeys, Neurosci. Abstr., 2: 1130.

Pasik, P., T. Pasik, and P. Schilder (1969) Extrageniculostriate vision in the monkey: Discrimination of luminous flux-equated figures, Exp. Neur., 24: 421-427.

Pasik, T. and P. Pasik (1971) The visual world of monkeys deprived of striate cortex: efffective stimulus parameters and the importance of the accessory optic system, Vision Res. (Suppl.), 3: 419-435.

Pasik, T., P. Pasik, and J. Valciukas (1970) Nystagmus induced by stationary repetitive light flashes in monkeys, Brain Res., 19: 313-317.

Pettigrew, J.D., T. Nikara, and P.O. Bishop (1968) Responses to moving slits by single units in cat striate cortex, Exp. Brain Res., 6: 373-390.

Polyak, S. (1947) The Vertebrate Visual System, University of Chicago Press, Chicago, p. 404.

Robson, J.G. (1966) Spatial and temporal contrast-sensitivity functions of the visual system, J. Opt. Soc. Am., 56: 1141-1142.

Safir, A. (1972) Automatic measurement of the refractive properties of the eye. Med. Res. Engin., 11: 12-20.

Safir, A., L. Hyams, J. Philpot, and L.S. Jagerman (1970) Studies in refraction. I. The precision of retinoscopy, Arch. Ophthal., 84: 49-61.

Safir, A., H. Knoll, and R. Mohrmann (1970) Automatic objective refraction, Trans. Am. Acad. Ophthal. Otolar., 75: 1266-1275.

Savoy, R.L. and J.J. McCann (1975) Visibility of low-spatial-frequency sine-wave targets. Dependence on number of cycles. J. Opt. Soc. Am., 65: 343-350.

Schilder, P., P. Pasik, and T. Pasik (1972) Extrageniculostriate vision in the monkey. III. Circle vs triangle and "red vs green" discrimination, Exp. Brain Res., 14: 436-448.

Schilder, P., T. Pasik, and P. Pasik (1971) Extrageniculostriate vision in the monkey. II. Demonstration of brightness discrimination, Brain Res., 32: 383-398.

Schiller, P.H., B.L. Finlay, and S.F. Volman (1976) Quantitative studies of single cell properties in monkey striate cortex. III. Spatial frequency. J. Neurophys., 39: 1334-1351.

Schiller, P.H. and J.G. Malpeli (1977) Properties and tectal projections of monkey retinal ganglion cells. J. Neurophys., 40: 428-445.

Schiller, P.H. and J.G. Malpeli (1978) Functional specificity of lateral geniculate nucleus laminae of the Rhesus monkey. J. Neurophys., 41: 788-797.

Shade, O.H. (1956) Optical and photoelectric analog of the eye, J. Opt. Soc. Am., 46: 721-739.

Sherman, S.M., J.R. Wilson, J.H. Kaas, and S.V. Webb (1976) X- and Y-cells in the dorsal lateral geniculate nucleus of the owl monkey, Science, 192: 475-477.

Shober, H.A.W., and R. Hilz (1965) Contrast sensitivity of the human eye for square-wave gratings, J. Opt. Soc. Am., 55: 1086-1091.

Stone, J., and B. Dreher (1974) Projection of X-and Y-cells of the cat's lateral geniculate nucleus to areas 17 and 18 of the visual cortex, J. Neurophys., 36: 551-567.

Stone, J. and Y. Fukuda (1974) Properties of cat retinal ganglion cells: A comparison of W-cells with X- and Y-cells, J. Neurophys., 37: 722-748.

Stone, J. and K.-P. Hoffman (1972) Very slow-conducting ganglion cells in the cat's retina: a major new functional type? Brain Res., 43: 610-616.

Tolhurst, D.J. (1973) Separate channels for the analysis of the shape and the movement of a moving visual stimulus, J. Physiol. (London), 231: 385-402.

Valciukas, J., P. Pasik, and T. Pasik (1973) Frequency spectrum of optokinetic nystagmus in the normal monkey, Vision Res., 13: 2361-2368.

Weinstein, B. and W.F. Grether (1940) A comparison of visual acuity in the Rhesus monkey and man, J. Comp. Psych., 30: 187-195.

Weiskrantz, L. and A. Cowey (1963) Striate cortex lesions and visual acuity of the Rhesus monkey, J. Comp. Phys. Psychol., 56: 225-231.

Weiskrantz, L., A. Cowey and C. Passingham (1977) Spatial responses to brief stimuli by monkeys with striate cortex ablations. Brain, 100: 655-670.

Wood, I.C.J. and J.J. Kulikowski (1978) Pattern and movement detection in patients with reduced visual acuity, Vision Res., 18: 331-334.

Zeki, S.M. (1969) Representation of central visual fields in prestriate cortex of monkey, Brain Res., 14: 271-291.