

OBLIQUE EFFECTS IN NORMALLY REARED MONKEYS (*MACACA NEMESTRINA*): MERIDIONAL VARIATIONS IN CONTRAST SENSITIVITY MEASURED WITH OPERANT TECHNIQUES

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Abstract—The present paper describes a newly completed operant methodology for the assessment of spatial vision in pigtail macaque (*Macaca nemestrina*) monkeys. Automated techniques for the generation, calibration, and presentation of sinusoidal grating stimuli, and for control of the operant experiment, are described in detail.

Contrast sensitivity functions have been obtained in four animals for gratings in vertical, oblique, and horizontal orientations. The data demonstrate that the monkey visual system, like that of humans, shows variations of contrast sensitivity with grating orientation at high spatial frequencies. One monkey showed a classical oblique effect, i.e. similar sensitivity for vertical and horizontal and a lower sensitivity for oblique gratings. The other three monkeys showed contrast sensitivity differences between horizontal and vertical gratings. The similarity of monkey and human contrast sensitivity variations and the implications of these results for use of the macaque monkey as an animal model for human vision are discussed.

INTRODUCTION

Spatial contrast sensitivity functions (CSF's) are widely recognized as a fundamental description of spatial vision (Campbell and Robson, 1968; Campbell and Green, 1965; Kelly, 1972). The characteristic form of the CSF varies with the orientation of the sinusoidal gratings used as stimuli. For most subjects, contrast sensitivity is reduced for obliquely oriented gratings (45 deg right oblique or 135 deg left oblique) relative to vertical (90 deg) or horizontal (0 deg). This oblique effect typically shows up for central viewing of high spatial frequency gratings at low rates of temporal modulation (Berkeley *et al.*, 1975; Campbell *et al.*, 1966; Camisa *et al.*, 1977; Mitchell *et al.*, 1967). This effect can be shown to persist in the absence of optical astigmatism, and is also present when most of the effects of the eye's dioptics are by-passed by forming interference fringes directly on the retina (Campbell *et al.*, 1966; Mitchell *et al.*, 1967).

The form and magnitude of these meridional variations in contrast sensitivity appear to vary somewhat among human populations (Annis and Frost, 1973; Timney and Muir, 1976), and among individuals (Ogilvie and Taylor, 1959; Mitchell *et al.*, 1967; Zemon *et al.*, 1980). Ogilvie and Taylor (1959) report one subject whose per cent visibility for a fine wire was greatest at oblique orientations. The data of Mitchell *et al.* (1967) also indicate slight sensitivity differ-

ences at high frequencies between horizontal and vertical for several subjects.

Some of these differences in sensitivity between vertical and horizontal in individual subjects may be due to meridional amblyopia. Individuals with astigmatism often exhibit a meridional amblyopia; i.e. meridional variations of acuity and contrast sensitivity even when cylinder corrections are worn, or when the grating stimuli are generated directly on the retina by interference fringes (Freeman *et al.*, 1972; Mitchell *et al.*, 1973; Freeman and Thibos, 1975; Boothe and Teller, 1981).

The neural bases of the oblique effect are not fully understood (*cf.* Appelle, 1972, for a review). Since optical considerations have been ruled out, the neural structure and function of the visual system must be responsible. Mitchell *et al.* (1967) discuss the inadequacies of several theories based on retinal receptor packing. Explanations based on the orientation tuning of single units in the visual cortex received some attention by the same authors.

Mansfield (1974) and Mansfield and Ronner (1978) suggest that it is the relative numbers of cells maximally sensitive to horizontal, vertical and oblique orientations within the neuronal population which is the basis for behaviorally observed orientation anisotropies. Colonnier (1964) has sought an explanation in terms of the patterns of dendritic arborization in cortical cells. The effect of asymmetrical patterns of eye movements in different orientations has been considered, but orientation effects persist when target

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presentations last only 1 msec (Higgins and Stultz, 1950), too brief a period for an eye movement response. Environmental influences on the development of the oblique effect have been suggested (Annis and Frost, 1973; but *cf.* Mayer, 1977, and Switkes *et al.*, 1978).

It is not likely that the answer to the question of the neural bases of the oblique effect will come from human studies. The neurophysiological and anatomical analyses which are required must be carried out on an animal model. Before such studies are undertaken, however, it is necessary to establish the presence and pattern of meridional variations in contrast sensitivity in the species to be tested.

The macaque monkey is emerging as the animal model of choice for human vision. Many basic visual functions, including spatial contrast sensitivity (De Valois *et al.*, 1974), color vision (De Valois *et al.*, 1974), and stereoacuity (Sarmiento, 1975; Harwerth and Boltz, 1979) have been shown to be virtually identical in the two species when tested under identical conditions. Furthermore, specific forms of visual deprivation imposed on macaque monkeys during infancy produce deficits in adult macaque visual capacities which mimic the amblyopias seen in the human population (von Noorden, 1973; *cf.* Boothe, 1981, for a review), and there are strong similarities in the development of visual acuity and contrast sensitivity in the two species (Teller *et al.*, 1974; Teller *et al.*, 1978; Teller and Boothe, 1979; Boothe, 1981).

There are two published reports of analogies to the oblique effect in macaque monkeys (Boltz *et al.*, 1979; Bauer *et al.*, 1979). Boltz *et al.*, tested two rhesus monkeys using an operant reaction time paradigm and sinusoidal gratings. More contrast was required to reach a criterion reaction time for oblique gratings than for horizontal and vertical gratings for spatial frequencies between 4 and 20 c/deg. The authors state that the magnitude of the effect found in their two monkeys was larger than that observed in human subjects tested in the same apparatus, although the human data are not shown. Bauer *et al.*, taught two animals to align a cursor with the orientation of a square wave grating. They showed that both monkeys generally took more time to align the cursor with oblique gratings than with horizontal or vertical gratings at spatial frequencies just below the maximum frequency at which the animal could complete the alignment task. At higher and lower spatial frequencies, no significant differences were found between scores for obliques and horizontal or vertical gratings. The results of these two reports concur in demonstrating some type of sensitivity or response reduction for obliquely oriented gratings in macaque monkeys, but are inconsistent about the spatial frequency range over which an oblique effect was observed. Further, oblique effects in human subjects have classically been defined in the psychophysical literature as variations in acuity and/or contrast sensitivity, not in terms of

reaction or response times, so neither study yields a close parallel to human studies.

During the past 8 years, we have undertaken a series of studies intended to explore further the behavioral parallels between spatial vision in macaque and human, and to extend the parallels into the realm of visual development. The present paper is the first of a series in which we report detailed studies of spatial vision and its development in macaque monkeys, using new equipment and operant techniques. The purpose of this paper is threefold: to describe in detail our operant training techniques, equipment, calibrations, and data analyses; to replicate the work of De Valois *et al.* (1974b) on contrast sensitivity functions in macaque monkeys; and to present illustrative data on a classical psychophysical phenomenon—meridional variation in contrast sensitivity—taken on both normal laboratory-reared monkeys and normal humans under closely parallel conditions. Preliminary reports of some of these results have appeared earlier (Williams, 1978; Boothe *et al.*, 1980; Teller and Boothe, 1979).

METHODS

Overview

A diagrammatic view of the operant testing apparatus is shown in Fig. 1. Each monkey subject is tested while looking out of its home cage through a molded face mask. The monkey views a visual display consisting of two cathode ray tubes (CRT's), displaced horizontally by 20 deg, center to center. On each trial, a spatial sinusoidal grating is displayed on one of the two CRT's and a homogeneous field of matched space-average luminance is displayed on the other. The monkey receives a liquid reward for pulling a grab bar on the side corresponding to the location of the grating. Thus, the monkeys are faced with a standard spatial two-alternative forced-choice psychophysical task (Green and Swets, 1966). The equipment is automated via interfacing with a computer (DEC PDP11/10).

Data for the two human subjects were obtained, using the same apparatus as for the monkeys, with a conventional forced-choice method, except that a chin rest was used rather than a face mask, and feedback was given with a tone rather than with food rewards.

Subjects

The monkey subjects used in these experiments were pigtail macaques (*Macaca nemestrina*) ranging in age from 5–18 months. All animals were separated from their mothers within 1 or 2 days after birth, and cared for according to normal laboratory protocol at the Infant Primate Facility at the University of Washington (Ruppenthal, 1979). Two of the monkeys (animals N3 and N4) were part of a study of the development of contrast sensitivity in infant monkeys (Boothe *et al.*, 1980), and had been participating in operant pattern discrimination experiments from the age of 2

weeks. The other two (monkeys N1 and N2) were trained at 3 and 6 months of age, respectively. The two human subjects were one of the authors, and an experienced psychophysical observer (ages 29 and 35 yr).

Refractions

All subjects, human and monkey, were refracted by one of three ophthalmologists. Cycloplegic was administered in dim light by giving one drop of 10%

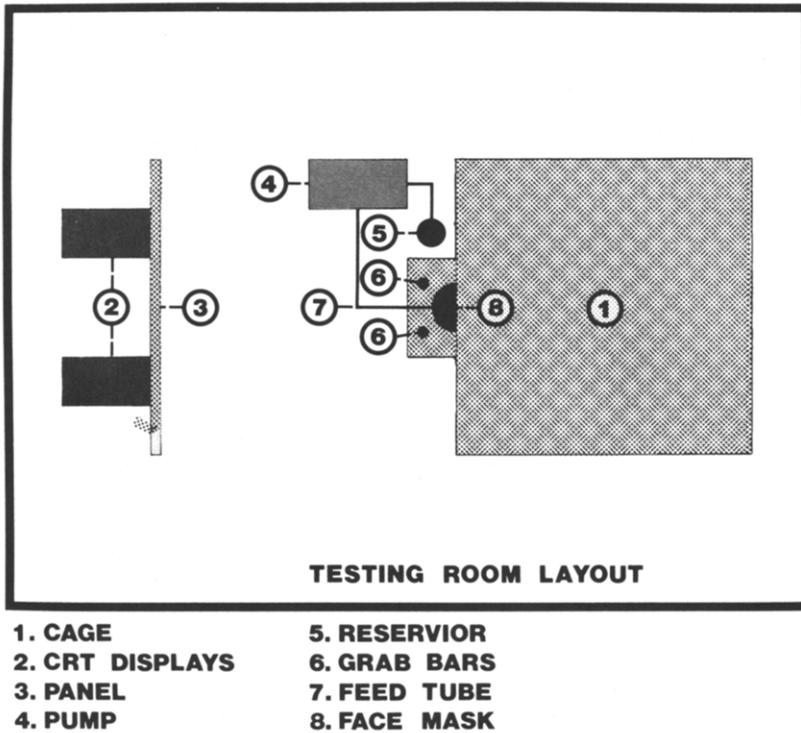


Fig. 1(a)

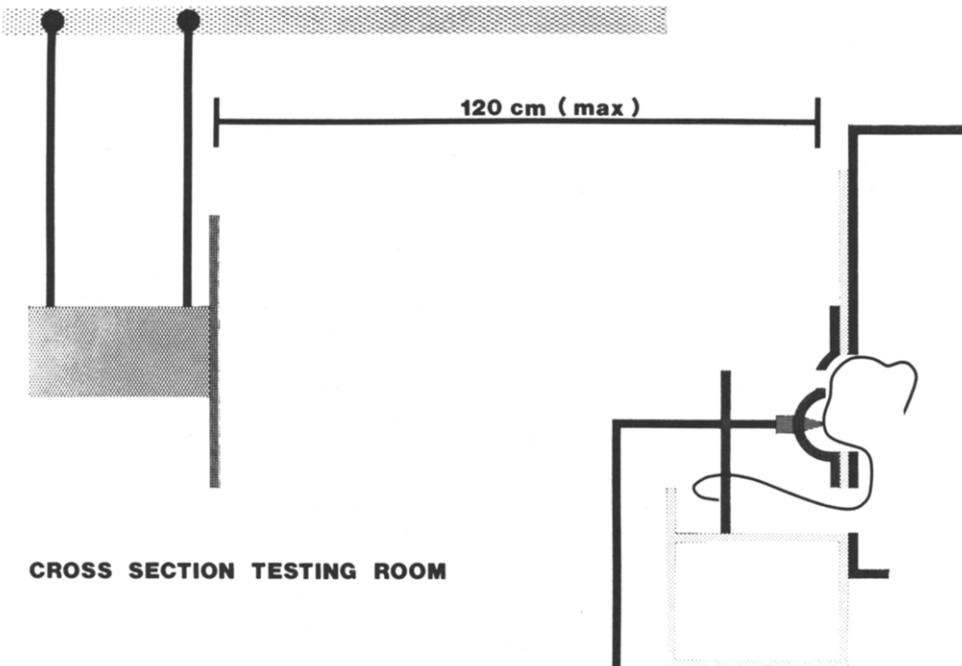
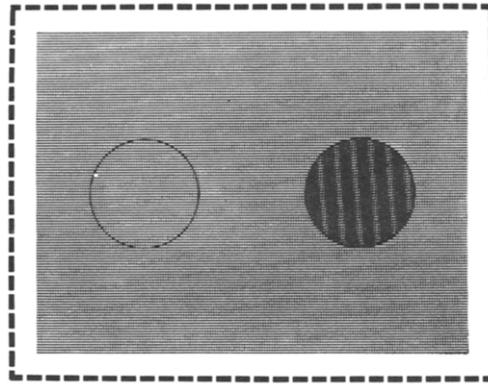


Fig. 1(b)



MONKEY'S VIEW OF DISPLAY

Fig. 1(c)

Fig. 1. Schematic view of the operant testing room and components of the operant apparatus; (a) Top view of testing room. The monkey's cage (1) is positioned in front of the CRT displays (2) with surrounding luminescent panel (3). The pump (4) is connected to a milk or juice reservoir (5). When the monkey responds correctly by pulling the appropriate grab bar (6), approx. 1/2 cc of liquid reinforcement is delivered through the feed tube (7) to the monkey with his face positioned in the face mask (8); (b) Cross section of the testing room. Each CRT (at the left of the figure) is hung from a track, such that the viewing distance (120 cm max) can be changed easily by rolling the CRT's closer to the face mask cage, shown at the right. The sectioned view of the cage illustrates the face mask mounted on the front wall of the cage, with a feed tube inserted through the mouth hole. The line figure serves to illustrate the position of the monkey's face in the mask as he views the stimulus display through the eye holes and reaches out through the arm hole to pull a grab bar. The grab bars and switches are secured to a response box mounted on the front wall of the cage, just below the face mask; (c) Monkey's eye view of the stimulus display which illustrates the nature of the two-alternative forced-choice pattern discrimination task. On the trial illustrated, the animal must distinguish between a sinusoidal pattern on the right, and the homogeneous field of matched space-averaged luminance on the left, each surrounded by a background field of approximately the same mean luminance and color as the P31 phosphor.

neosynephrine and one drop of 1% cyclogyl, three times separated by 5 min intervals. The monkey was then given an intra-muscular injection of ketamine. Retinoscopy was conducted on the anesthetized animal in dim light 1/2 hr after administration of the last drop. The retinoscopic readings were often inconsistent, even within one animal on two readings by the same ophthalmologist separated by only a few min. We did not systematically track down the source of this variability. The refractions shown in Table 1 were the readings obtained nearest to the date of operant testing. Astigmatism in all monkeys was less than 0.75 D (Table 1), and both human subjects had negligible spherical error and less than 0.25 D of astigmatism.

Shaping procedure

The monkeys are trained and tested in specially designed face mask cages (Sackett *et al.*, 1971; Boothe and Sackett, 1975). The face mask (Fig. 1) consists of a piece of opaque white plastic molded into the shape of a monkey's face, and mounted on the cage wall. When the monkey places his face in the mask he can view the stimulus display through eye holes cut out of the mask, and obtains liquid reward through a tube inserted into a mouth hole (Fig. 1b). An arm hole is

cut in the cage wall just under the face mask. Two grab bars are mounted outside the cage, one to the left and one to the right of the mask, within easy reach through the arm hole.

Each animal is shaped, under computer control, to perform the operant discrimination as follows. The monkey is first taught to pull on either grab bar in order to receive approximately 1/2 cc of milk or juice. Next, with the grab bars within the monkey's field of view through the eye holes, a salient visual stimulus (spatial square wave) is positioned directly behind one of the bars. The monkey is now rewarded only for pulling the bar in front of the stimulus. The other bar has no effect. The side on which the stimulus appears is changed every 8–10 trials. The number of reinforced trials/position is gradually reduced until the stimulus is made to appear randomly on the left or on the right. Also, a time out period, signalled by an auditory tone, is introduced following an incorrect response. The homogeneous field is then gradually faded in behind the non-rewarded grab bar, contingent upon trial outcome, until the luminance matches the space-averaged luminance of the patterned field.

Once this pattern discrimination task is learned, the correct stimulus is changed to a high contrast spatial sinusoidal pattern, and gratings of a number of differ-

Table 1

Animal	Mnemonic	Age	Refraction
T77158	N1	50 WKS	OD + 0.75 + 0.50 × 90 OS + 1.00 + 0.50 × 120
M78180	N2	36 WKS	OD + 0.75 + 0.25 × 90 OS - 0.25 + 0.75 × 90
T79040	N3	33 WKS	OD + 1.75 OS + 1.75
T79397	N4	20 WKS	OD + 1.25 OS + 0.75

Monkey subject data. Animals numbers that were assigned by U of W Regional Primate Research Center are listed in the first column. Mnemonic assigned to each animal for identification in this paper is listed in the second column. The monkey's age in weeks at the midpoint of the testing period during which CSF data were collected, and refractions obtained as explained in text, are listed in the last two columns.

ent spatial frequencies are introduced. Finally by varying the contrast level of the grating and measuring the monkey's discrimination performance at each contrast, psychometric functions, which plot per cent correct as a function of contrast, can be produced for each spatial frequency.

The entire shaping procedure is completely automated under computer control. The experimenter has control over all parameters of each shaping program (e.g. inter-trial interval, number of reinforced trials per grating position, length of the time out period following incorrect responses) at the time the run is set up. During shaping the animals are trained for approximately 2 hr time slots, two or more times per day. The monkeys obtain all of their liquid diet in this manner during the shaping period.

Once training is complete, the CSF measurements are also completely automated. The experimenter specifies the conditions of each experimental run (e.g. time-out period following incorrect responses, grating orientation, number of spatial frequencies, number of contrasts per frequency and contrast values for each frequency, and the number of trials per condition). A typical CSF (seven spatial frequencies, four contrasts per frequency, 20 trials per condition replicated and averaged to 40 trials/point) requires over 1000 trials. Most monkeys will complete each replication within a two hour session. If not, the experimental run is continued into the next session.

The face mask technique has several advantages for controlling the parameters of a visual psychophysical experiment in monkeys. The viewing distance can always be specified as the distance between the face mask eye hole and the visual stimulus, since the monkey must put his face tightly into the mask to see the stimuli and receive his reward. Both binocular and monocular testings are possible; either eye hole can be blocked off to restrict viewing to one eye. An artificial pupil can be mounted in front of the eye hole along with spectacle lenses in order to control pupil size and refractive error in an atropinized eye. Infrared emitting diodes and photocells, mounted

inside the mask, detect the presence of the monkey's face in the mask. The output of the photocells can be used to turn on the visual display, or open a shutter which normally occludes one or both eye hole(s), in order to control strictly the position of the face in the mask with respect to the stimulus.

Stimulus display system

Two CRT's (Tektronix 602 Display Unit) are surrounded by an electroluminescent panel (Grimes Manufacturers) which provides a background field of approximately the same color and brightness as the P31 phosphor of the CRT's. Each CRT field is masked down to an 8 cm circular aperture using a translucent piece of plexiglas. The inner edge of the plexiglas is bevelled so that it vignettes the edges of the grating display. The background field serves to control adaptation level and pupil size during the course of an experiment. Photographs taken through the face mask eye holes of three animals while they were working in a CSF experiment demonstrate that, in the lighting conditions of our stimulus display, pupil size remains relatively constant about 5.5 mm.

A raster is generated on the CRT screen in the standard manner by synchronizing the X- and Y-axis inputs (Campbell and Green, 1965). The X-axis ramp input is set to give a refresh rate of approximately 70 Hz. The Y-axis input is a sawtooth triggered from the onset of the ramp and set to a frequency such that each frame of the raster consists of 384 lines. The gratings can be rotated electronically using a modified version of the method described by Fullmer and Freeman (1973). Orientations between 0 deg (horizontal) and 90 deg (vertical) in 10 deg steps can be produced.

Variations in the Z-axis input are used to produce the desired luminance waveform. Input to the Z-axis is derived from a digital-to-analog converter which reads a sequence of 384 values stored in computer memory representing the desired spatial pattern. For example, within the linear range of the display, a sinusoidal luminance grating can be produced by storing a sine sequence in memory. Outside the linear range,

the relationship between input voltage and output raster luminance can be calibrated, and the sine sequence in memory can be transformed to compensate for any observed nonlinearity to produce a sinusoidal luminance pattern.

Figure 2a illustrates this calibration and nonlinear transformation procedure. The relative luminance of the homogeneous CRT screen (all 384 lines set to equal brightness) is plotted on the ordinate. The abscissa labelled "requested Z-axis voltage" and the square symbols show the voltage which must be applied to produce 32 equal luminance steps. These square symbols illustrate the nonlinear relationship between input voltage and output screen luminance. A table of the voltage values required to produce the 32 equal luminance steps plotted by the squares is

stored in memory. Now, when a specific luminance is desired, the Z-axis voltage needed to generate that luminance can be interpolated from the table values. The result of this nonlinear scaling is shown by the nonlinear abscissa labelled "applied Z-axis voltage". This nonlinear scaling between requested voltage and applied voltage makes the relationship between voltage requested and luminance linear as shown by the circles. Data as shown in Fig. 2a were obtained for each CRT unit via calibrations, and the nonlinear scaling software was used to generate all Z-axis inputs used in the display.

During the initial CRT calibration phase, the intensities of the two CRT's are carefully matched at maximum luminance of the homogeneous field using a photometer. For an operant trial, the sinusoidal

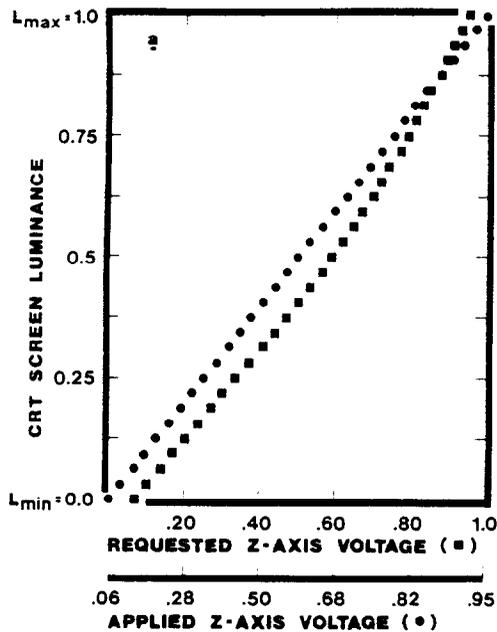


Fig. 2(a)

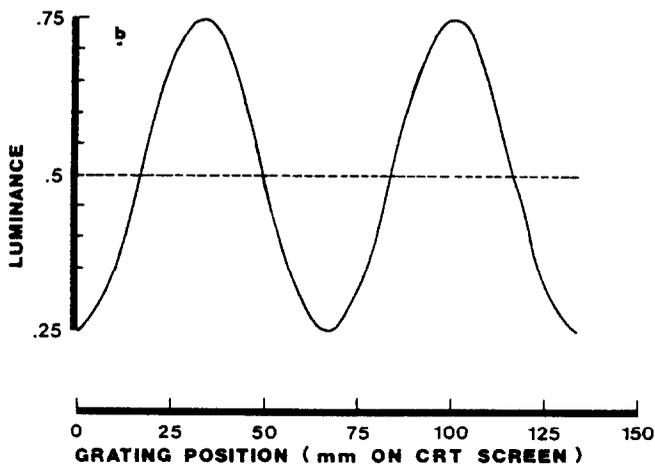


Fig. 2(b)

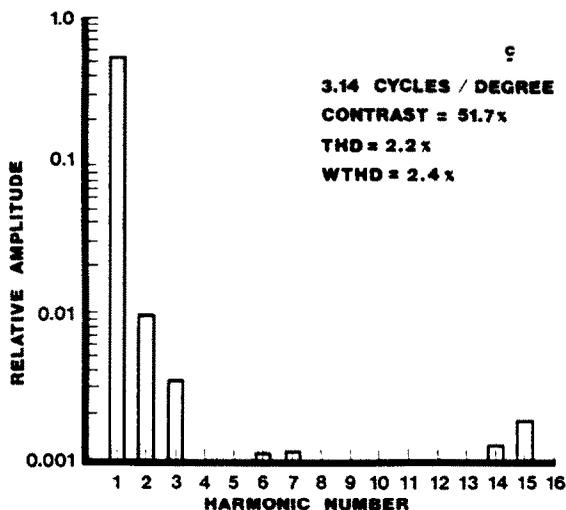


Fig. 2(c)

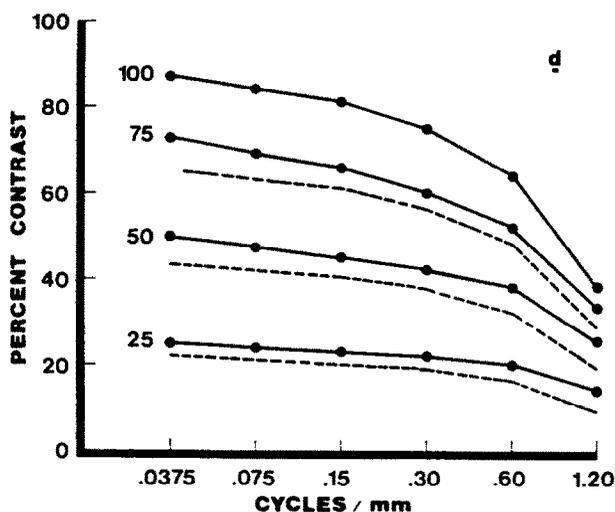


Fig. 2(d)

Fig. 2. Calibration of the CRT display system. (a) Plot of the input/output relationship between requested Z-axis voltage (0.0 to 1.0 V) and CRT screen luminance for a homogeneous raster (filled square symbols). The filled circles plot the same 32 equal luminance steps on a nonlinear "applied" Z-axis voltage scale. (b) Luminance profile of a 0.15 c./mm grating measured using the calibrating optical system described in the text. The photomultiplier output was sampled 256 times for each cycle of the grating. (c) Power spectrum determined by subjecting 1 cycle of the luminance profile in (b) to an FFT analysis. Amplitude relative to the mean level is plotted on a log scale for the first 16 harmonics, the 1st harmonic being the fundamental spatial frequency. Total harmonic distortion (THD) and weighted total harmonic distortion (WTHD) are calculated as explained in the text. (d) Calibrations of contrasts for gratings spanning a six octave range of spatial frequencies. Measured percent contrast for 100, 75, 50 and 25% Z-axis modulation are plotted (filled circles) on a linear scale as a function of spatial frequency in c./mm at the CRT screen. Dashed curves, from top to bottom, represent contrasts expected from taking 75, 50 and 25% of the measured contrast produced by 100% Z-axis modulation.

grating, produced by modulating screen luminance about the half-luminance level, is compared to a homogeneous field of the same mean luminance on the other CRT. To insure that the trial outcome is based solely on a pattern rather than a brightness discrimination, the space-averaged luminance of the two CRTs (one with a grating, the other with a homo-

geneous field) must be exactly matched. Using the nonlinear scaling table, the voltage needed for a half-bright level is known for both the homogeneous field and the grating. After scaling, the two fields should be closely matched in mean luminance. Given that the visual system is extremely sensitive to brightness differences, an additional safeguard against brightness

artifacts is included. From trial to trial the mean luminance of each CRT is "jittered", i.e. randomly incremented or decremented by a small amount, or not changed. The maximum "jitter" factor used corresponds to a change in mean luminance (27 cd/m² as measured with an SEI exposure meter) of 4%, or about 1 cd/m², an increment larger than the normal human brightness increment threshold. The fact that discrimination performance always goes to chance at sufficiently low contrasts in our experiments, is used as an additional safeguard that brightness cues are not being used to make the discriminations.

The nonlinear scaling operation does not fully compensate for nonlinearities associated with spatially modulated patterns. Measurements of a single raster line reveal that the line spread functions for individual lines are changing shape over much of the apparent linear range. For spatially modulated patterns, the appropriate linear range would be that over which the line spread function for individual raster lines remains constant. However, we have found that this restricted appropriate linear range is too small to be practical for generating the contrasts needed for our experiments. Therefore, we have carried out extensive calibrations to demonstrate that the distortions introduced by this nonlinearity into our grating displays are acceptable.

Stimulus calibrations

Two kinds of calibration procedures are routinely conducted on our sinusoidal gratings: measurements of contrast and harmonic distortion. The CRT raster occupies and 8 cm × 8 cm square area of the screen. With a 384 line raster, spatial frequencies ranging from 0.0375 c/mm to 1.2 c/mm can be produced. At our normal viewing distance of 120 cm, these values correspond to frequencies from 0.78 c/deg to 25.1 c/deg. The lowest frequency grating is not normally used in our CSF studies because only three cycles would appear in the display, with consequent low frequency fall-off artifacts in the CSF (Hoekstra *et al.*, 1974; Kelly, 1975; van den Brink and Bilsen, 1975; Savoy and McCann, 1975; Estevez and Cavanaugh, 1976). Each of nine gratings spaced at equal octave steps within this spatial frequency range is calibrated to determine (1) the contrast, $C = (L_{max} - L_{min}) / (L_{max} + L_{min})$, where L_{max} and L_{min} are luminance at the peak and trough of one cycle of the sinusoidal grating, and (2) total harmonic distortion (THD).

For calibration of the sinusoidal gratings, an optical system is mounted in a Tektronix camera attachment case which can be attached easily to the front of each CRT. The optical system produces a real image

in space of the display magnified 2.5 times. A 0.2 mm aperture in the image plane samples light output from a small region of the display*. A photomultiplier positioned directly behind this aperture provides an electrical signal proportional to the luminance of the sampled region, which is amplified and sent to the computer via an analog-to-digital converter. In order to counteract long-term drift in the photodetector, it is desirable to take frequent null readings. To facilitate this, a shutter controlled by the computer is mounted directly in front of the aperture.

The luminance profile of the grating is measured by sweeping the image of the pattern past the aperture and sampling the output signal 256 times per cycle (Fig. 2b). A number of sweeps are averaged to improve the signal-to-noise ratio in the luminance profile. The contrast of the grating pattern can then be determined by measuring the peak and trough luminances. Both the contrast of the fundamental and the THD of one cycle of the displayed pattern can be obtained by subjecting the luminance profile to a Fast Fourier Transform (FFT) analysis. An example of the amplitude spectrum resulting from the FFT is shown in Fig. 2c for one cycle of the luminance profile in Fig. 2b. The amplitude of the fundamental component relative to the mean luminance level is a measure of the contrast of the grating at its fundamental spatial frequency. Contrast determined from the FFT analysis closely approximates the contrast calculated from peak and trough measurements for all gratings. An estimate of the THD, defined as

$$THD = \sqrt{\left(\sum_{i=2}^n A_i^2\right)}$$

where

$$A_i = Re^2 + Im^2,$$

Re and Im = real and imaginary parts of the Fourier transform at the *i*th harmonic,

and

n = harmonic number of Nyquist frequency
(in this case *n* = 128),

is calculated for each grating. Typical THD values for our CRTs range from 4% for low frequency gratings to 12% for high frequency gratings.

Since we are interested only in the effect of distortion on the visual system, distortion at harmonics corresponding to spatial frequencies beyond the range of response of the visual system can be ignored. Consequently, we have also calculated the weighted total harmonic distortion (WTHD) for each grating. The contribution of each harmonic is weighted according to the sensitivity of the visual system at the corresponding spatial frequency. To calculate the weighting factors, an exponential function was fit to a typical adult monkey CSF (see Results for description of function and curve-fit method). Weights were then calculated as the ratio of sensitivity at the appropriate

* This aperture of course has its own transfer function. At the highest spatial frequency (1.2 c/mm) the modulus of the transfer function of this sized aperture has fallen off by less than 5%, a factor which would not substantially affect our calibrations of grating characteristics.

spatial frequency to sensitivity at the peak spatial frequency (approx. 6 c/deg). Thus, a harmonic at 6 c/deg would contribute 100% of its amplitude to the WTHD, while lower and higher harmonics would contribute something less than 100% of their amplitudes. Harmonics beyond the high frequency cut-off of the CSF contribute nothing to the WTHD. Typical WTHD values for gratings viewed at 120 cm range from 5% for the lowest frequency (1.5 c/deg) to 3% for the higher spatial frequencies (12 to 25 c/deg). Even at low spatial frequencies, where the lower harmonics are within the response range of the visual system, these distortion values are not large enough to suggest detectable artifacts at threshold contrast levels.

Estimates of contrast for six of the nine spatial frequencies for Z-axis input modulations of 25, 50, 75 and 100% are shown in Fig. 2d. The measurements show that (as expected) the contrast of the grating display decreases with increasing spatial frequency. Furthermore, the contrasts produced by 75, 50, and 25% modulation do not correspond to 75, 50, and 25% of the contrast produced by 100% modulation (dashed curves in Fig. 2d). In general, we find that contrast is linearly proportional to input modulation below 50% for all spatial frequencies. Therefore, the contrast produced by 50% input modulation is determined for each spatial frequency and stored in a table in computer memory. When a specific contrast 50% or lower is requested, the Z-axis modulation which will produce that contrast can be calculated from the tabulated values.

The contrasts of the 0 deg, 40 deg (counterclockwise) and 90 degree gratings used in this study are measured separately for 50% Z-axis modulation. Any differences in contrast found between horizontal, oblique and vertical gratings are corrected in the display software.

Psychophysical procedure and data analysis

Contrast sensitivity is determined for spatial frequencies between 1.5 and 25 c/deg, with each grating consisting of six or more cycles of the sinusoid. For each spatial frequency, 4–5 contrasts are chosen, typically in 0.2 log unit steps, such that the animal's performance will range from near chance (50% correct) for the lowest contrast, to near 100% correct for the highest contrast. Trials are run in a randomized order until 20 trials have been obtained for each contrast at

each spatial frequency for a single orientation. Three orientations of the grating, vertical (90 deg), right oblique (40 deg), and horizontal (0 deg), are run in counterbalanced order (i.e. ABCCBA) over a period of not more than six days, until a total of 40 trials are accumulated for each condition.

An estimate of the median (75% correct), SD, and SEM for each psychometric function are obtained by a probit analysis (Finney, 1971) computer program. In probit analysis, per cent correct values are transformed to probit values, such that the cumulative normal curve which we have found usually provides an adequate fit to our psychometric functions is transformed to a straight line. Linear regression analysis is then used to derive maximum likelihood estimates of the slope and intercept of the best-fitting probit line.* The median effective contrast (75% correct point) and the standard deviation of the best-fitting cumulative normal, as well as standard errors of these estimates, can be calculated from the probit line using equations described by Finney (1971). Symbols in Figs 3 and 4 represent estimates of the median contrast sensitivity while error bars represent ± 1 SEM. 95% confidence intervals may be roughly estimated by doubling the lengths of these lines.

The smooth curves drawn through the data points in Fig. 3 are exponential functions of the form $S = 100 \cdot W^A / (C \cdot \text{EXP}[B(W-W')])$ where S = contrast sensitivity, and A , B , C , and W' are parameters corresponding, respectively, to steepness of the low and high frequency fall-off, the absolute sensitivity level, and the peak spatial frequency. This curve is similar to the one suggested by Wilson (1978) on the basis of measurements of line spread functions of the human visual system. Most of these curves fall within the confidence intervals of all data points. The curves were fit on log-log coordinates using a computer routine for least squares estimation of non-linear parameters. High spatial frequency cut-offs were estimated by extrapolating these curves to a contrast sensitivity equal to 1 which is equivalent to a threshold contrast of 100%.

RESULTS

In Fig. 3, three CSF's are plotted for each of four monkeys and two human subjects. Data for monkey N2, plotted in Fig. 3a, indicate that contrast sensitivity is reduced for oblique gratings relative to horizontal and vertical gratings, ranging in spatial frequency from 6–25 c/deg. The maximum effect at high spatial frequencies is about 0.4 log unit in sensitivity and 0.3 octave in cut-off frequency. The effect for this monkey is similar to that found in one of our human subjects (Fig. 3e).

CSF's for three other monkeys, N1, N3, and N4, and for human subject D.R., plotted in Figs. 3b, c, d and f, exhibit interesting variations of an orientation anisotropy. For monkey N1, sensitivity is reduced for both oblique and horizontal gratings, relative to verti-

* Probit analysis is a particularly powerful tool for the analysis of forced-choice data, since provision can be made for the lower and upper asymptotes of the cumulative normal curve. For example, in a two-alternative forced-choice experiment, the natural response rate or lower asymptote ("natural mortality", Finney, 1971) is 50%, i.e. chance performance. If the stimulus is made salient enough, all responses should be correct, and the upper asymptote will be 100% ("natural immunity" is zero, Finney, 1971). The concepts of natural mortality and natural immunity are not equivalent to a simple stretching of the cumulative normal curve (see chap. 7 of Finney).

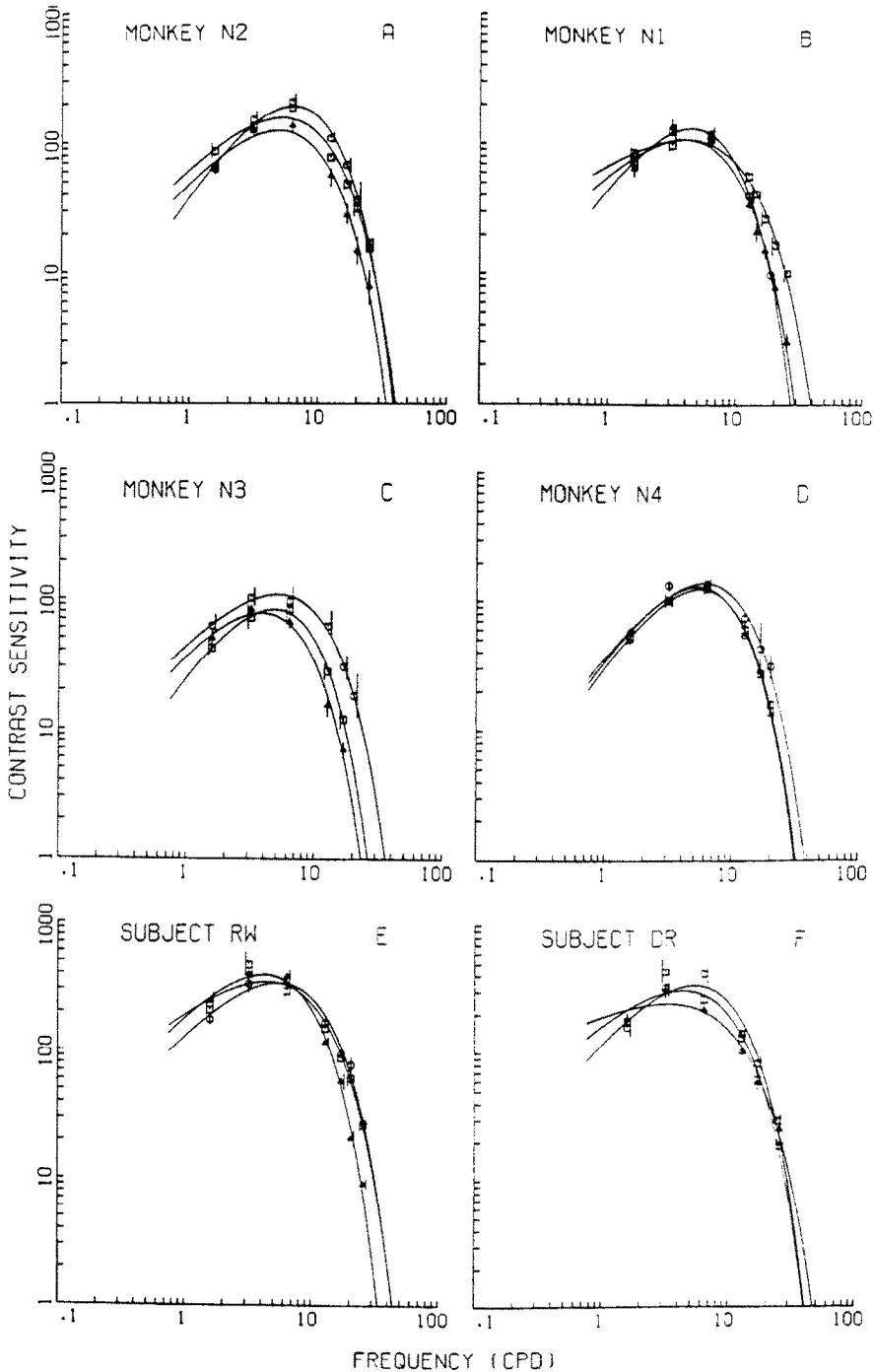


Fig. 3. Contrast sensitivity functions for four *Macaca nemestrina* (a-d) and two human subjects (e and f). Each subject was tested at three orientations: Vertical (\square), horizontal (\circ) and right oblique (\triangle). One monkey (a) and one human subject (e) show classical oblique effects, with sensitivity for vertical and horizontal gratings exceeding sensitivity for obliques for high spatial frequencies. The other three monkeys and subject DR show variations on this pattern, with highest sensitivity for vertical (b) or horizontal (c, d, and f), and lower sensitivity for the other two orientations.

cal gratings for spatial frequencies above 10 c/deg. Monkeys N3 and N4, on the other hand, show greatest sensitivity to horizontal gratings, with oblique and vertical orientations suffering a reduction in contrast sensitivity at high spatial frequencies. For monkey N3

the maximum sensitivity difference between the best and worst orientations is larger than for the other three monkeys represented in Fig. 3, reaching nearly 0.8 log unit at 20 c/deg and 0.4 octave in cut-off frequency. Observer D.R. shows yet another meridional

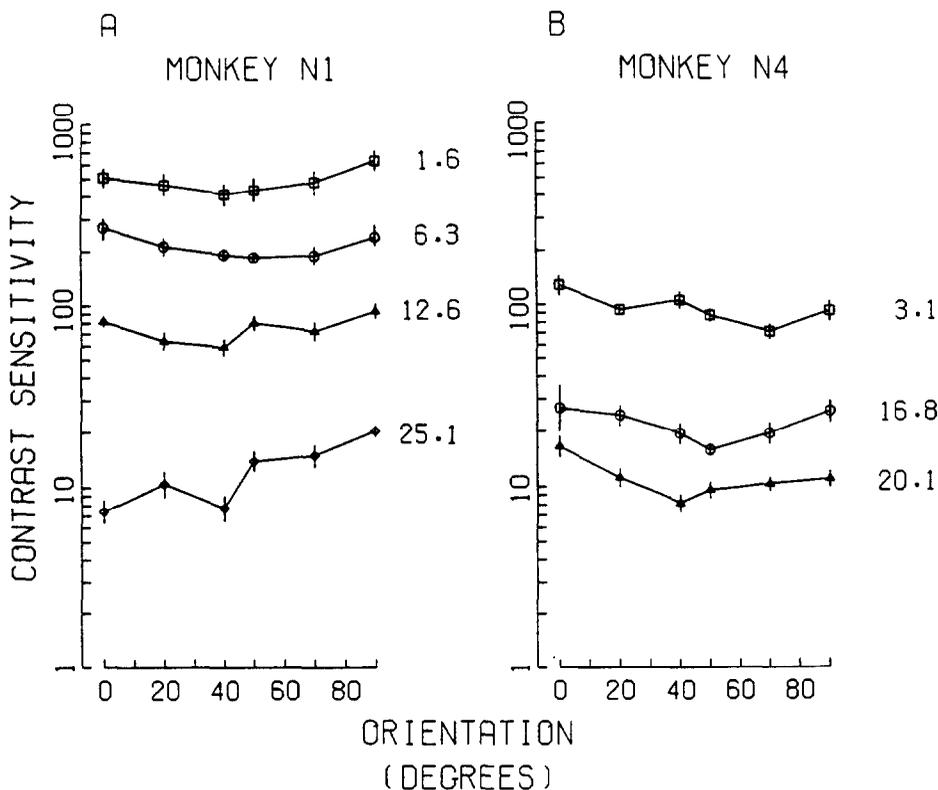


Fig. 4. Contrast sensitivity as a function of the orientation of the grating for several spatial frequencies. (a) Results obtained from monkey N1 for spatial frequencies of 1.6 (\square), 6.3 (\circ), 12.6 (\triangle), and 25.1 (\diamond) c/deg. The curve for 1.6 c/deg has been shifted up by 0.5 log unit for clarity. (b) Results obtained from monkey N4 for spatial frequencies of 3.1 (\square), 16.8 (\circ), and 20.1 (\triangle) c/deg.

variation—both oblique and horizontal gratings yield slightly superior contrast sensitivity than vertical gratings. The sensitivity differences between orientations are smaller for observer D.R. than for the other human subject and the monkey subjects. The 95% confidence limits for the different orientations would overlap at spatial frequencies above 10 c/deg. Also, the relatively shallow high frequency fall-off of the oblique data gives a higher cut-off frequency and poor fit of the curve at low frequencies for subject D.R.'s oblique CSF.

For two monkeys contrast sensitivity measures were obtained for several additional grating orientations between horizontal and vertical. The data are shown in Figs 4a and 4b for monkeys N1 and N4, at grating orientations of 0, 20, 40, 50, 70 and 90 deg counterclockwise from horizontal. For monkey N1 (Fig. 4a) the effect of grating orientation on contrast sensitivity is small for spatial frequencies of 1.6, 6.3, and 12.6 c/deg. However, at 25.1 c/deg, contrast sensitivity is reduced for orientations near 0 and there is a trend toward gradually improving sensitivity as the orientation changes towards 90 deg. The horizontal vs vertical difference is consistent with that seen in the CSF's for this monkey (Fig. 3b).

For monkey N4 (Fig. 4b) there is a trend toward sensitivity to a 3.1 c/deg grating being gradually

reduced as the orientation is changed from 0 to 90 deg. At 16.8 c/deg the function relating contrast sensitivity to orientation shows a definite dip at 50 deg. The error bars at horizontal are too large to pick up small horizontal vs vertical differences. At the highest spatial frequency (20.1 c/deg), sensitivity at 90 deg is reduced relative to 0 deg, consistent with the horizontal vs vertical sensitivity difference observed in this monkey's CSF's (Fig. 3d), and there is an additional dip in sensitivity near 40 deg.

DISCUSSION

This report is the first of a series describing studies of spatial vision and its development in *Macaca nemestrina* monkeys, using new equipment and operant techniques. The novel features of the system include complete automation of data collection and computer control of Z-axis modulation which is based on detailed calibration of the CRT stimulus display system. The combination of efficiency and stimulus control allows us to generate data of high precision and low variability in short time periods, so that small as well as large psychophysical effects may be studied. In this discussion we will emphasize the utility of the detailed spatial calibrations, compare the present data to the previous data of De Valois *et al.*

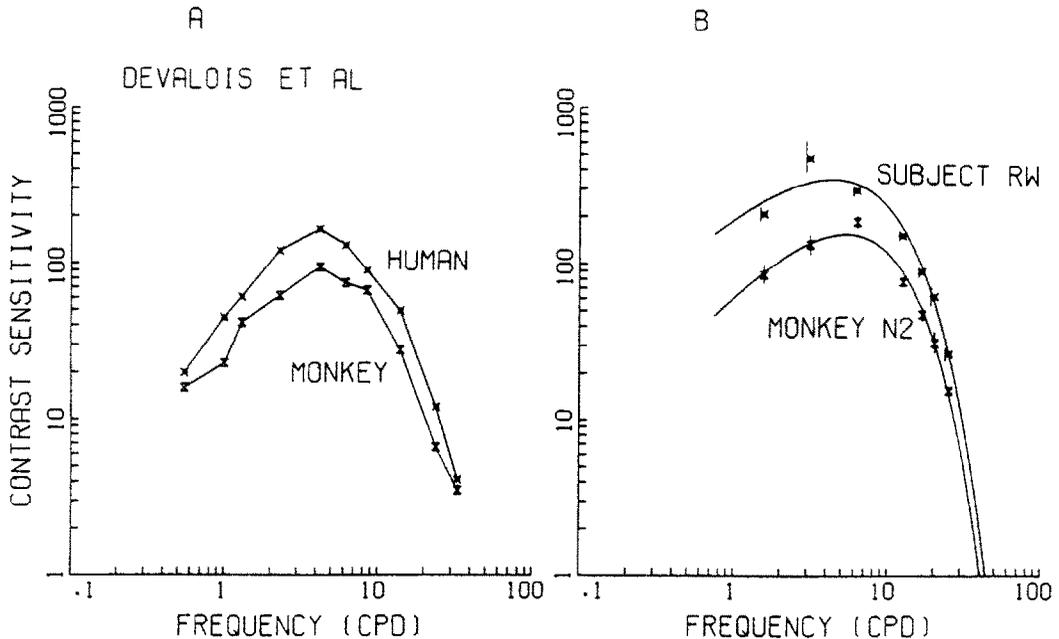


Fig. 5. Direct comparison of human and monkey CSF's from two different studies. (a) CSF's replotted from De Valois *et al.* (1974b) for a human and a monkey observer. (b) CSF's (vertical gratings) for human observer RW and monkey N2 replotted from Fig. 3.

(1974b), and discuss the implications and limitations of the present data concerning oblique effects in monkeys.

To illustrate the value of detailed calibration of the CRT display system, the high spatial frequency fall-off of the CSF's in Fig. 3 may be compared to the fall-off of contrast at high spatial frequencies measured for sinusoidal gratings generated on the CRT (Fig. 2d). At a viewing distance of 120 cm, the 0.6 and 1.2 c/mm stimuli correspond to 12.6 and 25.1 c/deg gratings, respectively. The fall-off in grating contrast occurs in exactly the same spatial frequency range as the high frequency fall-off of contrast sensitivity of the visual system. An error in the direction of overestimating high frequency grating contrast would give an estimate of the high frequency fall-off which is too steep and the resulting extrapolated cut-off frequency of the CSF would be too low. For example, if we had plotted our CSF data in terms of nominal contrast, cut-off frequencies would decrease by about 0.3 octave, (e.g. from 50–40 c/deg). Thus, accurate determination of psychophysical cut-off frequencies with CRT displays can only be made after detailed luminance and contrast measurements of the display have been done. We suspect that some of the variation in extrapolated cut-off frequencies in the literature is caused by this factor.

In Fig. 5a we have replotted two CSF's from the De Valois *et al.* (1974) study. One human and one macaque (rhesus) function are shown, both of which were obtained at the highest luminance level used in the study (17 cd/m²). CSF's at the most sensitive grating orientation for observer RW and monkey N2 from

the present study are replotted in Fig. 5b. Monkey N2 showed the highest contrast sensitivity of any animal tested to date in our laboratory. The results of the two studies are consistent in several details. In both studies the human CSF's exhibit overall slightly higher sensitivity than the macaque CSF's over the entire spatial frequency range tested. The peak sensitivities in both studies fall in the range from 3 to 6 c/deg. Near the peak of the CSF's, the sensitivity difference between monkey and human observers is about 0.25 log unit in Fig. 5a and 0.4 log unit in Fig. 5b. At 30 c/deg the sensitivity difference has diminished to about 0.1 log unit in Fig. 5a and to 0.2 log unit in Fig. 5b. Finally, the cut-off frequencies, for both humans and monkeys, are virtually identical across the two studies. Best-fit curves are not shown in Fig. 5a, since the function used to fit our data does not give an appropriate fit to the low frequency end of the De Valois *et al.*, data, possibly because fewer cycles were present in their display at the lowest frequencies.

In absolute terms, our subjects, both human and monkey, exhibit slightly higher sensitivity near the peak of the function, than did the subjects of De Valois *et al.* The causes of this difference may be related to the mean luminance level (ours is nearly double theirs), experimental techniques, or intersubject variability. We used our most sensitive subjects at their most sensitive orientation for this comparison. Comparisons with other subjects or orientations yield results more similar to those of De Valois *et al.*

The results shown in Fig. 5 indicate that our data indeed replicate the data reported by De Valois *et al.*

(1974b). The sensitivity difference between human and macaque CSF's in fact shows the same pattern in the two studies. The human CSF's show the greatest sensitivity advantage over the monkey CSF's at low- and mid-range spatial frequencies. At the high frequency cut-off, the CSF's from human and macaque subjects converge near 40–50 c/deg.

To illustrate the nature and precision of the results that can be obtained with our methodology, we have looked for classical oblique effects in four monkeys and two human subjects. All subjects show consistent variations of contrast sensitivity with grating orientation at high spatial frequencies, with individual differences in the orientation(s) of maximum sensitivity. The oblique effect in pigtail macaque monkeys is highly similar to the effect observed in the human population. Similar variations of the classical orientation anisotropy for human observers have been noted in the literature (Mitchell *et al.*, 1967; Ogilvie and Taylor, 1959; Zemon *et al.*, 1980). Since results are shown for human and monkey subjects, tested on the same apparatus and with closely similar psychophysical techniques, the results as a whole provide the best evidence to date of classical meridional variations in contrast sensitivity in normal, laboratory-reared macaque monkeys.

Finally, some limitations on the generality of the present results must be noted. Only four monkey subjects have been tested. All four were from the same breeding colony and laboratory-reared under the standardized conditions of our infant primate nursery. The variations in the CSF with orientation differed markedly, even in this small and relatively homogeneous sample. Both the choice of gene pool and the visual environment appear to have effects on meridional differences in sensitivity (Annis and Frost, 1973; Timney and Muir, 1976; Freeman *et al.*, 1972; Mitchell *et al.*, 1973; Boothe and Teller, 1981). Animals obtained from various populations and species in the wild, or reared in laboratories under other conditions, may or may not show similar variations in CSF's with grating orientation.

Neurophysiologists and neuroanatomists searching for the neural substrates of psychophysically observed oblique effects, should be aware of the existence of marked individual differences in the pattern of variation of sensitivity with grating orientation. Neither all monkeys nor all humans show the classical oblique effect, that is, sensitivity to horizontal and vertical gratings being equal while sensitivity to obliques is depressed. In fact, individual differences in the pattern of meridional variation occur with such regularity that it will probably be necessary to test individual monkey subjects behaviorally before they can be usefully employed in studies of the substrates of the oblique effect.

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