JOURNAL OF NEUROPHYSIOLOGY
Vol. 48, No. 2, August 1982. *Printed in U.S.A.*

Spatial and Temporal Sensitivity of Normal and Amblyopic Cats

STEPHEN LEHMKUHLE, KENNETH E. KRATZ, AND S. MURRAY SHERMAN

Department of Psychology, Brown University, Providence, Rhode Island 02912; Department of Anatomy, Louisiana State University Medical Center, New Orleans, Louisiana 70119; and Department of Neurobiology and Behavior, State University of New York, Stony Brook, New York 11790

SUMMARY AND CONCLUSIONS

1. We used the behavioral technique of conditioned suppression to measure spatial and temporal contrast sensitivity to counterphased, sine-wave gratings in eight cats. These included two normally reared cats before and after bilateral ablations of cortical area 17 and part of area 18, two cats raised in total darkness, two cats raised with binocular lid suture, and two cats raised with monocular lid suture. Visual deficits induced by cortical lesions or visual deprivation were evaluated with respect to the preoperative data of the normally reared cats.

2. The cortical lesions had virtually no qualitative effect on the cat's visual capacities. Contrast sensitivity was reduced at higher but not lower spatial frequencies, and this can be described succinctly as a loss of spatial acuity.

3. Dark-reared and binocularly sutured cats qualitatively exhibited poorer visual capacity than that of the cortically ablated animals. The contrast sensitivity resultant from these two forms of binocular deprivation was basically similar and consisted of significant sensitivity losses at all spatial and temporal frequencies. Much more than high spatial frequencies was affected, and this amblyopia cannot be characterized simply as a spatial acuity loss.

4. Monocularly sutured cats had normal vision and contrast sensitivity with the nondeprived eye, but with the deprived eye they displayed the most severe amblyopia and poorest contrast sensitivity of any of the cats. Again, sensitivity losses were evident for all spatial and temporal frequencies, and this amblyopia is more severe than a loss of spatial acuity.

5. These psychophysical data are related to the status of W-, X-, and Y-cell pathways in these cats. Sensitivity to low spatial frequencies and integrity of the Y-cell pathway is correlated with good visual capacity. Since Y-cells are uniquely sensitive to low spatial frequencies, then the Y-cell pathway seems sufficient and perhaps necessary for reasonable visual performance.

6. Finally, because the amblyopia of normally reared cats with lesions of striate cortex is far less severe than that of the lid-sutured and dark-reared cats, it follows that the constellation of deficits reported for striate cortex in these visually deprived cats cannot provide an adequate neural explanation for their amblyopia. Attempts to relate deprivation amblyopia to striate cortex abnormalities should thus be reconsidered.

INTRODUCTION

Measurements of spatial contrast sensitivity in amblyopia[1] have revealed two general

[1] We use the term amblyopia in the sense that it is defined in medical dictionaries and textbooks of ophthalmology. For instance, amblyopia is defined in *Stedman's Medical Dictionary* (23rd ed., Williams & Wilkins, Baltimore, 1976) as, "Dimness of vision; partial loss of sight." In: *Textbook of Ophthalmology* by H. G. Scheie and D. M. Albert (9th ed., Saunders, Philadelphia, 1977) the definition given on p. 333 is as follows: "Amblyopia is defined as a reduction in visual acuity (with the proper correction in place) in an eye that is ophthalmoscopically normal." Thus we shall refer to deficits in visual performance in cats that are caused either by cortical lesions or rearing with visual deprivation as amblyopia.

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forms of the visual deficit that differ in severity (22). The milder form of amblyopia involves a loss of sensitivity only to higher spatial frequencies, and this is often characterized as a loss of spatial resolution or acuity. The more severe form is characterized by a loss of sensitivity to higher and lower spatial frequencies, and thus more than spatial resolution is lost. At present, the underlying neural deficits for these two clinical conditions of amblyopia can only be suggested (23, 39, 52, 53, 71).

Some insights into these neural deficits might be gained by studying behavioral contrast sensitivity in experimental animals that can also be studied with neuroanatomical and neurophysiological techniques. The cat provides a good model system for such an approach, since a great deal is known of its three parallel neural pathways from retina through the lateral geniculate nucleus to the visual cortex. These are the W-, X-, and Y-cell pathways (for recent reviews, see Refs. 36, 46, 47, 52, 54, 56, 61).

All retinal ganglion X- and Y-cells and an as yet unspecified proportion of W-cells project to the lateral geniculate nucleus (7, 10, 28, 62, 70). Unlike X- and Y-cells, these W-cells exhibit very poor contrast sensitivity, poor temporal and spatial resolution, slowly conducting axons, and sluggish responses to visual stimuli (8–10, 62, 70). Compared to Y-cells, X-cells have more slowly conducting axons (although still faster than those of W-cells), smaller receptive fields, more linear spatial and temporal summation, better sensitivity to high spatial frequencies and, consequently, better spatial resolution, poorer temporal resolution, and poorer sensitivity to lower spatial frequencies (7–10, 34, 36, 46, 47, 59, 61, 62, 70). Geniculate X-cells project exclusively or nearly so to cortical area 17, whereas geniculate W- and Y-cells project to many areas of visual cortex, including areas 17, 18, 19, and the lateral suprasylvian cortex (17, 18, 26, 37, 42, 45, 60; for recent reviews, see Refs. 36, 46, 56, 61). Therefore, area 17 appears to be an indispensable link in the X-cell pathway but not in the W- and Y-cell pathways.

Despite our knowledge of these W-, X-, and Y-cell pathways in cats raised normally (36, 46, 47, 56, 61) or with visual deprivation (56) and despite the current interest and usefulness of psychophysically determined contrast-sensitivity functions, rather little attention has been directed to obtaining such functions from experimentally manipulated cats (however, see Refs. 4, 5). For example, many of the behavioral assessments of visually deprived cats have concentrated on their reduced spatial acuity (12, 15, 20, 57, 68). It is thus not clear if the visual deficits in the visually deprived cats also encompass losses in sensitivity to lower spatial frequencies.

Recently, Blake and DiGianfilippo (5) measured contrast sensitivity as a function of spatial frequency in cats reared in total darkness. These authors found that dark rearing not only reduces spatial acuity but also leads to abnormally poor sensitivity to lower spatial frequencies. These cats thus exhibit poor sensitivity for a wide range of spatial frequencies, and their amblyopia cannot be adequately described in terms of a loss of spatial acuity.

The purpose of the present study was to determine the nature of the amblyopia found in cats reared with various forms of visual deprivation and in cats with ablations of visual cortex. To do this, we measured the spatial and temporal contrast sensitivity exhibited psychophysically by these cats. Since a great deal is known about the neural status of the central visual pathways in these cats, such psychophysical data can provide insights into both the normal functional significance of these pathways as well as the neural basis of various forms of amblyopia.

MATERIALS AND METHODS

Subjects

Spatial and temporal contrast-sensitivity functions were measured in eight adult cats. Two were obtained as presumably normal adults. After contrast sensitivity was determined for the normal cats, they underwent surgery, under aseptic conditions and using sodium pentobarbital, to remove cortical area 17 and part of area 18 (see below), and they were retested following a 2- to 4-wk postoperative recovery period. The remaining six cats were born and reared in the laboratory until they were tested at 1 yr of age. Two had the lids of one eye sutured closed beginning at or before the time of normal eye opening (i.e., 5–8 days of age). For one of these (*MLS1*), the lids were closed for

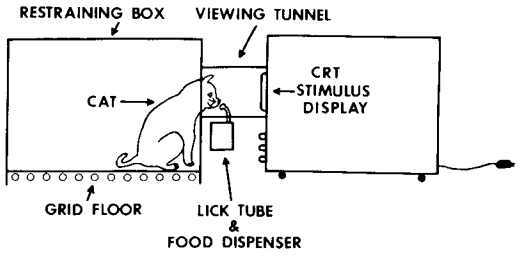

FIG. 1. Schematic illustration of the apparatus used in these experiments.

16 mo and were parted for an additional year before testing began; for the other (*MLS2*), the lids were closed for 8 mo and testing began several weeks after the lids were opened. Two other cats had both eyes sutured closed at 5–8 days of age. For one (*BLS1*), the lids were closed for 5 mo and testing began 2 mo after eye opening; for the other (*BLS2*), the lids were closed for 12 mo and testing began 6 mo after the eyes were opened. During the rearing of the four lid-sutured cats, the eyes were inspected daily to ensure that no openings developed in the lids. The final two cats (*DR1* and *DR2*) were reared in total darkness until 5 mo of age, at which time they were housed in the normally lighted animal colony. Their testing began at 9 mo of age.

Visual stimulus

Vertically oriented, temporally modulated, sine-wave gratings were generated on a cathode-ray tube at a frame rate of 200 Hz. The stimulus display was 17 x 18° at the cat's viewing distance of 27 cm. The gratings were generated by standard procedures. We could continuously vary the stimulus contrast (defined as $(L_{max} - L_{min})/(L_{max} + L_{min})$, where L_{max} and L_{min}, respectively, are the maximum and minimum luminance values across the grating) between 0 and 0.6, spatial frequency (cycles per degree of visual angle), and temporal frequency (cycles per second of temporal modulation by sinusoidal counterphasing). The average luminance of the display ($\frac{1}{2}(L_{max} + L_{min})$) was 15.2 cd/m. A homogeneous field of the same luminance could be presented on the cathode-ray tube instead of the grating pattern.

Psychophysical methods

We used the behavioral technique of conditioned suppression to obtain estimates of spatial and temporal contrast thresholds in these cats. The application of this method for cats has been described in detail elsewhere (4, 41) and is outlined briefly below.

Figure 1 shows a schematic drawing of the behavioral apparatus. The cat was placed in an operant chamber. It was trained to place its head in a viewing port and lick a metal tube through which small amounts of pureed beef were delivered according to a variable-ratio reinforcement schedule. This procedure served to position the cat's head and eyes with respect to the stimulus display described above. The number of licks made by the cat were continuously monitored electronically. Normally, after a few days of initial training, a cat establishes a constant lick rate, which is typically about 2/s. The cat's body weight was maintained at 85% of its weight attained previously through ad libitum feeding.

After this initial conditioning, the cat was trained to suppress licking during the presence of a 0.6 contrast, counterphased, sine-wave grating of about 0.5 cycle/deg. The grating replaced the homogeneous field for 10 s, after which time a mild electric shock was delivered to the grid floor. Following several weeks of training, the cat consistently reduced its lick rate during the presence of a detectable grating. Base-line lick rates were established by counting the number of licks in a 10-s period before the grating appeared. This initial phase of training was deemed complete when the suppression ratio (the number of licks during the 10 s that the grating was present divided by the base-line amount), averaged across 15 or more consecutive trials, was less than 0.4 for three consecutive daily sessions.

Once the cat was trained, contrast thresholds were estimated by the use of a modified staircase procedure (4). At the beginning of an experimental session, the grating contrast was set at its maximum value of 0.6. If the cat correctly detected the presence of the grating, the grating contrast was reduced for the next trial. A correct response was defined as a suppression ratio less than 0.5. The contrast was decreased from trial to trial until the cat failed to detect the grating (i.e., exhibited a suppression ratio greater than 0.5). Then, the contrast was increased on the next trials until a correct response was made, etc. At the beginning of the staircase, contrast changes were relatively large (0.20–0.10) and toward the end, relatively small (0.05–0.003). A contrast threshold was arbitrarily defined as the average of the bottom steps of the last three reversals of the staircase. Typical staircases for the deprived and nondeprived eyes of *MLS2* are illustrated in Fig. 2.

Contrast thresholds for a given spatial and temporal frequency were estimated during a single experimental session. If, for some reason, the staircase could not be completed during one session, the data were disregarded, and a new staircase was begun the next day. Contrast thresholds were measured in this way twice at each spatial and temporal frequency. When the difference be-

tween the two thresholds was greater than 0.1 log unit, a third threshold value was obtained. The variability among these determinations never differed more than 0.3 log unit. Contrast sensitivity, which is defined as the reciprocal of the contrast threshold, was first plotted as a function of spatial frequency for a low counterphase rate (1 or 1.5 Hz). Then analogous temporal contrast-sensitivity functions were plotted at either a spatial frequency of 0.25 cycle/deg or the spatial frequency to which the cat displayed the greatest sensitivity on the spatial-sensitivity function.

For the monocularly sutured cats and in some conditions for the binocularly sutured cats, viewing was monocular. Otherwise, viewing was binocular. Monocular viewing was achieved by placing a contact occluder on the cornea after the cornea was anesthetized by topical application of Ophthetic solution.

The cats were free to adjust their own accommodation and pupil sizes. Each cat exhibited roughly the same intermediate size of pupil. Also, the cats were refracted with a retinoscope and each was judged to be emmetropic. The visual display at 27 cm was placed well within the cat's accommodative range (cf. Refs. 1 and 5), and thus we feel that optical factors did not significantly affect visual performance of any of the subjects (see also DISCUSSION).

Surgical procedures

Bilateral cortical lesions were placed in the two normally reared cats. We used surgical methods that have been previously described (51) and that are briefly outlined below.

Surgery was performed under aseptic conditions. The cats were anesthetized with barbiturate. A large craniotomy bilaterally covering the posterior half of cerebral cortex was performed, and the flap of removed bone was stored in saline for replacement at the end of the surgery. The dura was then reflected to expose the posterior half of cortex. Based on the maps of Tusa et al. (64), area 17 and a portion of area 18 next to the border with area 17 was determined. All of this cortical region was bilaterally removed by aspiration that was directed with the aid of a Zeiss operation microscope. Gelfoam was packed into the ablated region, the dura was replaced, Gelfilm was placed over the dura, and the bone flap was placed over the Gelfilm. The wound was then closed with sutures and wound clips.

Histological procedures

After the two cats with visual cortical lesions were completely tested psychophysically, they were deeply anesthetized with barbiturate and perfused transcardially with physiological saline followed by 10% Formalin in saline. The brains were stereotaxically removed, embedded in egg yolk, sectioned coronally while frozen at 40 μm, and the sections were alternately stained either for myelin or Nissl substance (51). This histological material was used to ascertain the extent of the visual cortex lesions.

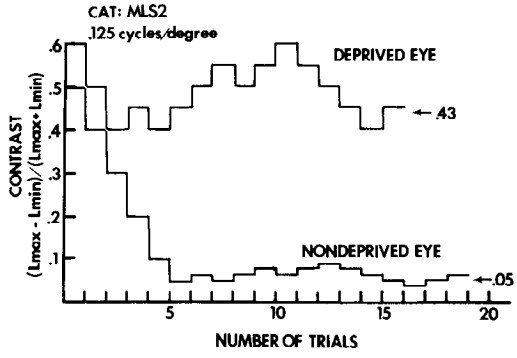

FIG. 2. Examples of staircases collected for *MLS2* at 0.125 cycle/deg for both its deprived and nondeprived eyes. Contrast is plotted as a function of the number of trials in each session. For the nondeprived eye, *MLS2* suppressed on trials 1–5 without error, covering a contrast range of 0.50–0.05. The step sizes were 0.10 on trials 1–4, and 0.05 on trial 5. The step size was 0.01 from trials 5–19. During these latter trials, *MLS2* both suppressed and failed to suppress during the presentation of the grating. If the cat failed to suppress, contrast was increased on the next trial; if the cat suppressed, the contrast was decreased on the next trial (see text). The threshold (0.05) was estimated by averaging the contrast values of the bottom steps of the last three contrast reversals. The staircase shown for the deprived eye of *MLS2* can be read in a similar way. On trials 1 and 2, *MLS2* correctly suppressed during grating presentation. The step size was 0.10 starting at 0.60 for these trials. After trial 2, step size was 0.05. The remaining trials yielded a staircase with a threshold of 0.43.

RESULTS

Casual behavioral observations of the visual performance of these cats indicated that each group had markedly different visual capacities. Cats with the cortical lesions appeared quite normal and exhibited no obvious visual deficits (1–3). Binocularly sutured and dark-reared cats were often hesitant in their visually elicited movements and responded sluggishly to rapidly moving stimuli (50, 67). Monocularly sutured cats, using their deprived eyes, were inactive and appeared to be essentially blind (50, 66). The subsequently derived spatial and temporal contrast sensitivity for each cat is remark-

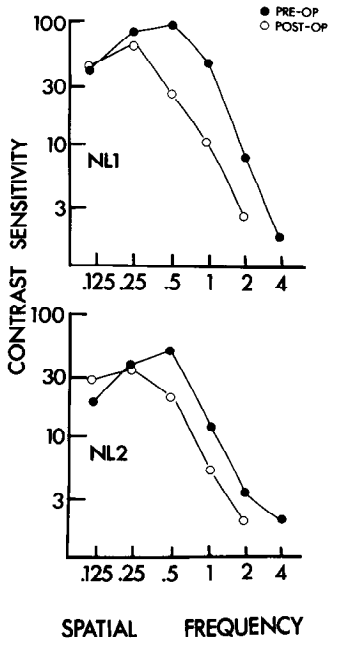

FIG. 3. Spatial contrast-sensitivity functions at a temporal rate of 1.5 Hz for two normal cats (*NL1* and *NL2*) before (filled circles) and after (open circles) an ablation of area 17 and part of 18. Functions for *NL1* are shown in the upper figure, and functions for *NL2* are shown in the lower figure. Contrast sensitivity (the reciprocal of the contrast threshold) is plotted on the ordinate and spatial frequency (cycles per degree of visual angle) on the abscissa.

ably consistent with these casual observations. These contrast-sensitivity measurements are presented separately for each group in order of the increasing severity of the visual impairment.

Normally reared cats

Contrast sensitivity was determined for the two normally reared cats (*NL1* and *NL2*) before and after bilateral removal of cortical area 17 and parts of area 18. Spatial contrast sensitivity at 1.5 Hz was first determined, and then temporal contrast sensitivity at a relatively low spatial frequency (0.25 cycle/deg) was measured.

PREOPERATIVE BEHAVIOR. Figure 3 shows the spatial contrast-sensitivity functions for these cats. These spatial functions show a peak sensitivity near 0.5 cycle/deg, with decreasing sensitivity at higher and lower spatial frequencies. Spatial resolution (i.e., the highest spatial frequency to which the cats respond) at 0.6 contrast is slightly more than 4 cycles/deg. These data are comparable to those previously reported by Blake and Camisa (4). Furthermore, Fig. 4 illustrates the contrast sensitivity of these cats at 0.25 cycle/deg for 1.5, 15, and 25 Hz. A monotonic decrease in sensitivity with increasing temporal frequency is seen. Following this behavioral testing, lesions of visual cortex were produced in these two cats.

Extent of cortical lesions

The lesions of cats *NL1* and *NL2* were assessed by inspection of both cortical tissue as well as the lateral geniculate nuclei. The pattern of retrograde degeneration among geniculate neurons in laminae A and A1 combined with the excellent retinotopic maps of visual cortex (64) and the lateral geniculate nucleus (48) provides an accurate estimate of the damage to cortical areas 17 and 18. Smaller geniculate neurons exhibit retrograde degeneration following lesions to appropriate regions of area 17, but not area 18, and the larger neurons do so following lesions that affect both areas 17 and 18 (17).

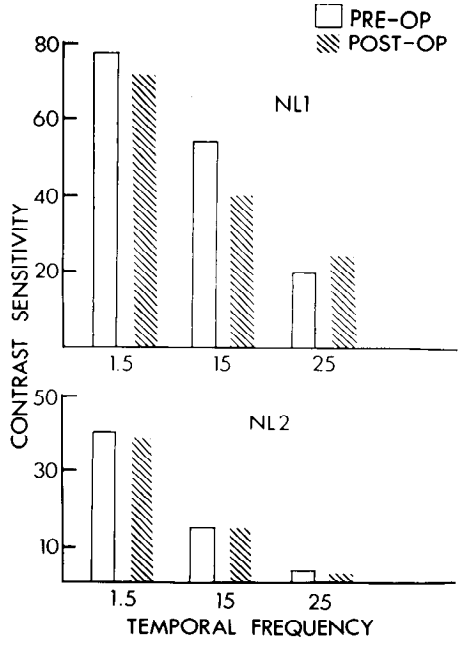

FIG. 4. Contrast sensitivity (reciprocal of the contrast threshold) for three temporal rates (1.5, 15, and 25 Hz) at a spatial frequency of 0.25 cycle/deg for two cats (*NL1* and *NL2*) both before (open bars) and after (cross-hatched bars) removal of area 17 and part of 18. Data for *NL1* are shown in the upper figure; data for *NL2* are shown in the lower figure.

Figures 5–8 illustrate tracings of representative histological sections through visual cortex and the lateral geniculate nucleus. They are interpreted as follows.

The ablation to cat *NL1*, based on inspection of cortical tissue (Fig. 5), appears to involve all of area 17 except for the representation of the extreme periphery of visual field in the splenial sulcus. The border between areas 17 and 18, which represents the vertical meridian of visual field (64), is missing, and thus the adjoining strip of area 18 was also removed. These conclusions are confirmed by the retrograde degeneration seen in the lateral geniculate nucleus (Fig. 6). No degeneration was seen in the lateral portion of the geniculate that represents the extreme periphery. Smaller cells (related to area 17) exhibited retrograde degeneration in the remainder of the nucleus. Furthermore, larger cells were also affected along the medial border of the nucleus, where the vertical meridian is represented, and this suggests that the corresponding portion of area 18 was also ablated.

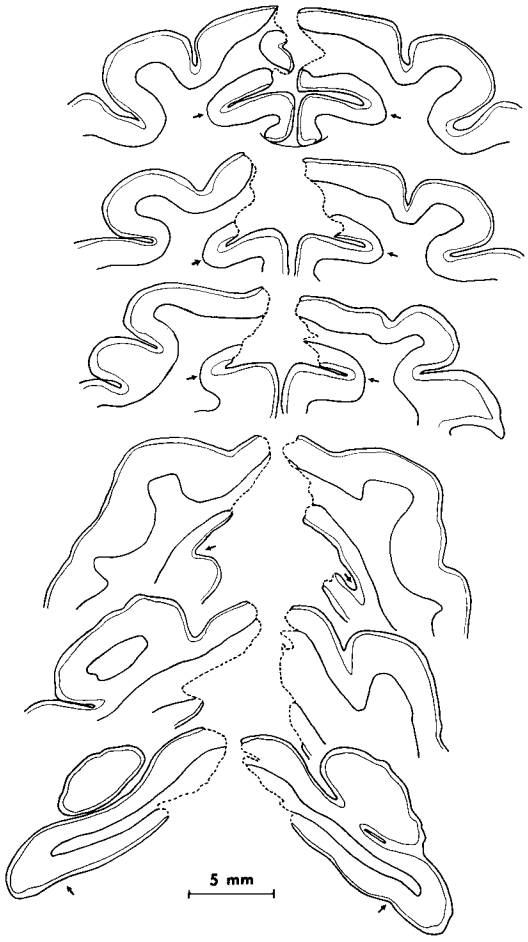

FIG. 5. Tracings of cortex through lesion site for cat *NL1*. Six regularly spaced sequential coronal sections are shown with rostral at top and caudal at bottom. Arrows indicate the border of area 17 on the medial surface of the hemisphere; the 17/18 border on the dorsal surface has been removed by the lesion. All of area 17, except the representation of peripheral visual field, and part of the central representation of area 18 were bilaterally ablated (see text for details).

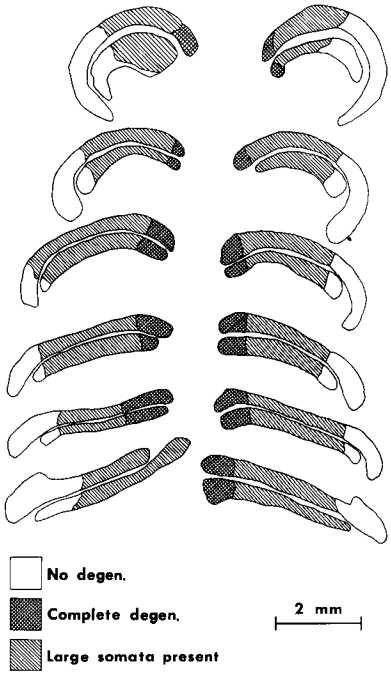

FIG. 6. Reconstruction of retrograde degeneration through the lateral geniculate nuclei of cat *NL1*. Six regularly spaced, sequential sections are shown with rostral at top and caudal at bottom. Zones of no degeneration, of degeneration involving small cells only (large somata present), and of complete degeneration are separately indicated. This pattern of retrograde degeneration correlates well with the pattern of cortical damage illustrated in Fig. 5.

The lesion for cat *NL2* appears similar but involves more of the peripheral representation of visual field than does that for cat *NL1*. This can be seen in Figs. 7 and 8. For both cats, the ablation involved most of area 17, including all but the peripheral representation, and some of area 18 representing the vertical meridian.

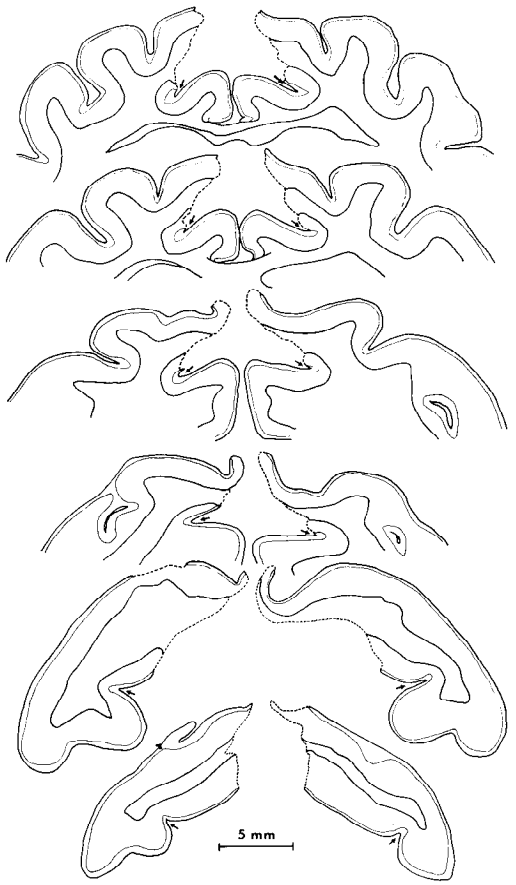

FIG. 7. Tracings of cortex through lesion site of cat *NL2*; conventions as in Fig. 5. This lesion is similar to that of cat *NL1*, except less of the peripheral representation of area 17 was spared.

POSTOPERATIVE BEHAVIOR. Cats *NL1* and *NL2* were retested following a 2- to 4-wk postoperative recovery period. Figure 3 compares the pre- and postoperative spatial contrast-sensitivity functions at 1.5 Hz. For each cat, the major effect of the cortical lesions was to reduce sensitivity selectively for the higher spatial frequencies with little or no effect at lower ones. That is, visual acuity was reduced by less than a factor of two by the ablation, whereas sensitivity to gratings of 0.125 and 0.25 cycle/deg was unchanged. The postoperative contrast sensitivity remained fairly constant over a 6-mo period of testing. Thus, the amblyopia induced by this lesion is best characterized as a reduction in sensitivity to higher spatial frequencies or simply reduced visual acuity.

To examine further the effect of this cortical lesion on sensitivity to lower spatial frequencies, contrast sensitivity was compared pre- and postoperatively at 0.25 cycle/deg for temporal frequencies of 1.5, 15, and 25 Hz. These data are shown in Fig. 4. Even at the higher temporal rates, there is no systematic loss in sensitivity to lower spatial frequencies as a result of these cortical lesions.

Binocularly sutured cats

Spatial contrast-sensitivity functions at 1.5 Hz are shown in Fig. 9 for the two binocularly sutured cats. These functions were measured during binocular viewing. However, contrast thresholds were measured at 0.5 cycle/deg for both binocular and monocular viewing, and no difference in contrast sensitivity was detected. The contrast-sensitivity functions of both binocularly sutured cats peaked at about 0.25 cycle/deg, and sensitivity declined for lower and higher spatial frequencies.

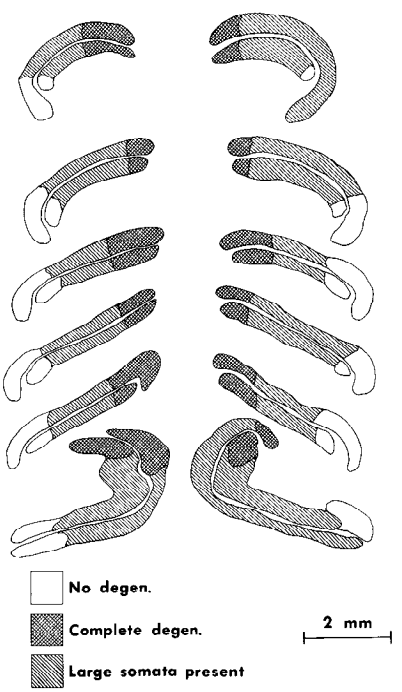

FIG. 8. Reconstruction of retrograde degeneration through the lateral geniculate nuclei of cat *NL2*; conventions as in Fig. 6. The pattern of geniculate degeneration correlates well with the cortical reconstructions in Fig. 7.

The binocularly sutured cats suffered a loss of sensitivity that was fairly constant for all spatial frequencies (cf. Figs. 3 and 9). The spatial resolution at 0.6 contrast was roughly 2.0 cycle/deg for cat *BLS1* and 1.5 cycle/deg for cat *BLS2*. These values are comparable to the spatial resolution achieved by the normally reared cats following the visual cortex lesions.

Figure 10 shows for these cats the temporal contrast-sensitivity functions at the most sensitive spatial frequency (0.25 cycle/deg). Sensitivity peaks near 3 Hz. Figures 9 and 10 show that the best contrast sensitivity exhibited by these cats is roughly 10 (for *BLS1*) and 30 (for *BLS2*) compared to values of 50–100 for the normal cats (e.g., Figs. 3 and 4). Also, the sensitivity losses exhibited by the binocularly lid-sutured cats occur across all temporal as well as spatial frequencies.

Dark-reared cats

Figure 11 shows spatial contrast sensitivity functions at 1.5 Hz for the two dark-reared cats, and Fig. 12 shows the analogous temporal functions at the most sensitive spatial frequency (i.e., 0.5 cycle/deg). Overall,

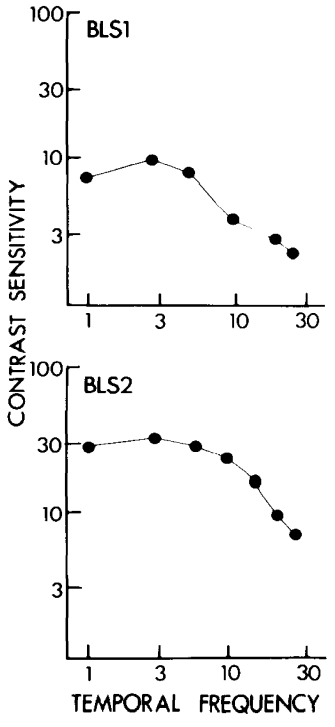

FIG. 10. Temporal contrast-sensitivity functions at a spatial frequency of 0.25 cycle/deg for two binocularly sutured cats (*BLS1* and *BLS2*); conventions as in Fig. 3.

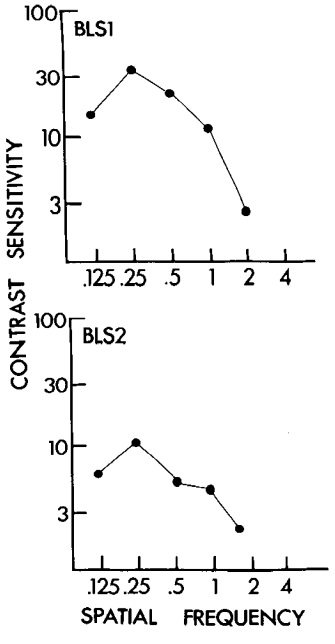

FIG. 9. Spatial contrast-sensitivity functions at a temporal rate of 1.5 Hz for two binocularly sutured cats (*BLS1* and *BLS2*); conventions as in Fig. 3.

the sensitivity deficits of the dark-reared cats are generally similar to those of the binocularly lid-sutured cats. Spatial resolution at 0.6 contrast was 2.0 cycles/deg for *DR1* and roughly 3.0 cycles/deg for *DR2*. Spatial sensitivity peaked at 0.5 cycle/deg for both dark-reared cats (12 for *DR1*, and 28 for *DR2*). Temporal contrast sensitivity was highest at around 1–3 Hz for both cats.

Monocularly sutured cats

The spatial contrast-sensitivity functions of the nondeprived and deprived eyes of two monocularly sutured cats are shown in Fig. 13. Again, the temporal frequency at which these functions were obtained was 1.5 Hz. The contrast-sensitivity functions for the nondeprived eyes of these cats are quite similar in shape and absolute values to those obtained from normal cats (see Fig. 3 and Ref. 4).

With the deprived eye, however, sensitivity was greatly reduced for both low and high spatial frequencies. For instance, each cat

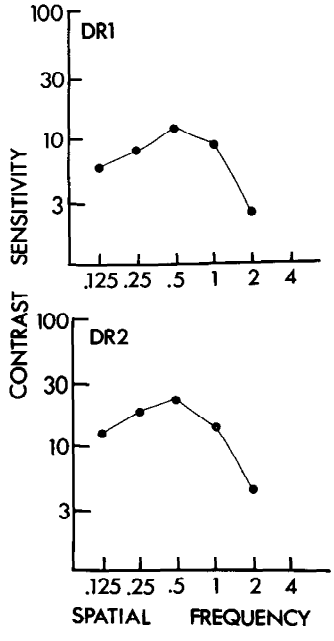

FIG. 11. Spatial contrast-sensitivity functions at a temporal rate of 1.5 Hz for two dark-reared cats (*DR1* and *DR2*); conventions as in Fig. 3.

with its nondeprived eye could detect a 2 cycles/deg grating of 0.6 contrast, but neither could detect with its deprived eye a grating of 0.6 contrast with a spatial frequency greater than 1 cycle/deg. The measured difference in spatial resolution between the eyes was roughly 2 octaves for each cat. However, such a measure of resolution reflects sensitivity only to the higher spatial frequencies, and we emphasize that the deficits for these cats involve all spatial frequencies. This amblyopia also exists across a wide range of temporal frequencies. The temporal contrast-sensitivity functions of the nondeprived and deprived eyes for the monocularly sutured cats are shown in Fig. 14. The functions for the nondeprived eye again resemble those of normal cats (4) with peak sensitivity of roughly 100 near 3 Hz. The functions for deprived eyes are dramatically reduced for all temporal frequencies with no obvious attenuation for lower temporal frequencies. At 3 Hz, the sensitivity difference between the eyes is roughly 1.5 log units. Early monocular suture thus leads to an amblyopia characterized by severe sensitivity losses over a wide range of spatial and temporal frequencies. This is a much greater sensitivity loss than observed for binocularly sutured or dark-reared cats.

DISCUSSION

The results reported in this study are summarized in Fig. 15. They indicate that the amblyopia in cats caused by lid suture or dark rearing is characterized by a sensitivity loss over a wide range of spatial and temporal frequencies. This is fundamentally different from and considerably more serious than a simple loss of spatial acuity. In contrast to these visually deprived cats, normally reared cats with lesions of cortical areas 17 and parts of 18 exhibit a sensitivity loss limited to higher spatial frequencies and thus can be simply characterized as a loss of acuity. Since early visual deprivation produces more serious visual impairment than does a cortical lesion in normally reared adults, it suggests that visual deprivation causes the development of abnormalities in

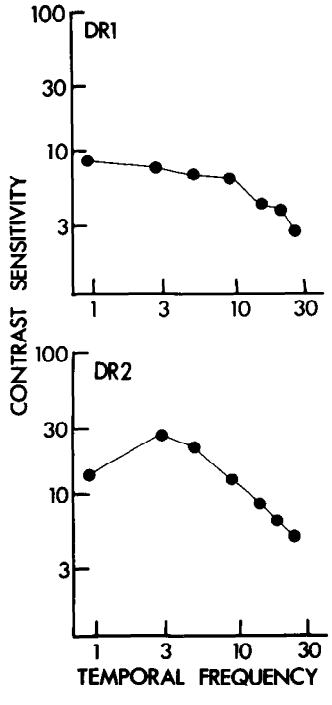

FIG. 12. Temporal contrast-sensitivity functions at a spatial frequency of 0.5 cycle/deg for two dark-reared cats (*DR1* and *DR2*); conventions as in Fig. 3.

addition to those in the geniculostriate pathways. Below, we will attempt to correlate these psychophysical data with our knowledge of the functioning of the W-, X-, and Y-cell pathways in these cats (see INTRODUCTION).

Optical or neural deficits

The deficits in visual performance among the cats of this study could conceivably be due to abnormal physiological optics rather than to neural abnormalities. Ophthalmoscopic and retinoscopic examination of the eyes revealed no evidence of any optical distortion that could have caused these visual deficits (see MATERIALS AND METHODS). We did not, however, measure the cats' accommodative states during the psychophysical measurements. The unlikely presence of emmetropia during the retinoscopic examination but not during psychophysical measurement still cannot adequately explain the data. Errors of focus affect higher spatial frequencies much more than lower ones and,

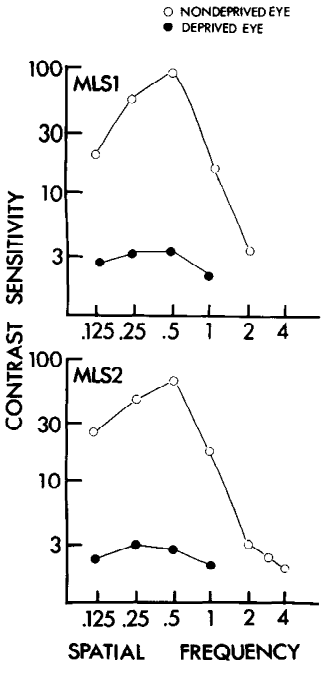

FIG. 13. Spatial contrast-sensitivity functions at a temporal rate of 1.5 Hz for nondeprived (open circles) and deprived eyes (filled circles) of two monocularly deprived cats (*MLS1* and *MLS2*); conventions as in Fig. 3.

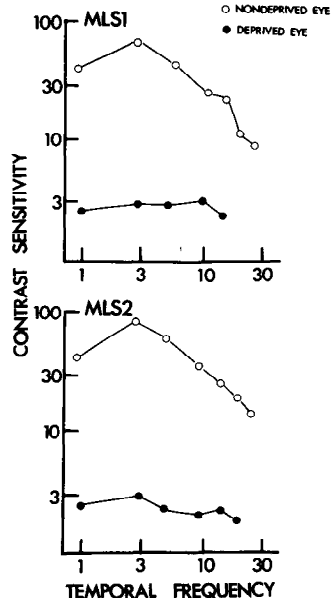

FIG. 14. Temporal contrast-sensitivity functions at a spatial frequency of 0.5 cycle/deg for the nondeprived (open circles) and deprived eyes (filled circles) of the two monocularly sutured cats (*MLS1* and *MLS2*); conventions as in Fig. 3.

unless implausibly large, such errors cannot explain the severe losses of sensitivity to all spatial frequencies seen in the visually-deprived cats. On the other hand, such errors are a possible explanation for the postoperative deficits seen in cats *NL1* and *NL2*. This would require that cortical lesions, as were made in these cats, cause errors in dynamic accommodation that are difficult to measure, but there is no evidence for such an effect (see also Refs. 1–3). Even if this were the case, which would imply no measureable postoperative deficits of a neural origin for cats *NL1* and *NL2*, this would serve only to exaggerate the lack of importance of the X-cell pathway and striate cortex for form vision (see below). In any case, optical explanations for the visual deficits seen in our cats seem most unlikely, and below we focus instead on plausible neural explanations for these deficits.

Neural basis of behavior in normally reared cats

PREOPERATIVE BEHAVIOR. Recent psychophysical evidence from humans has empha-

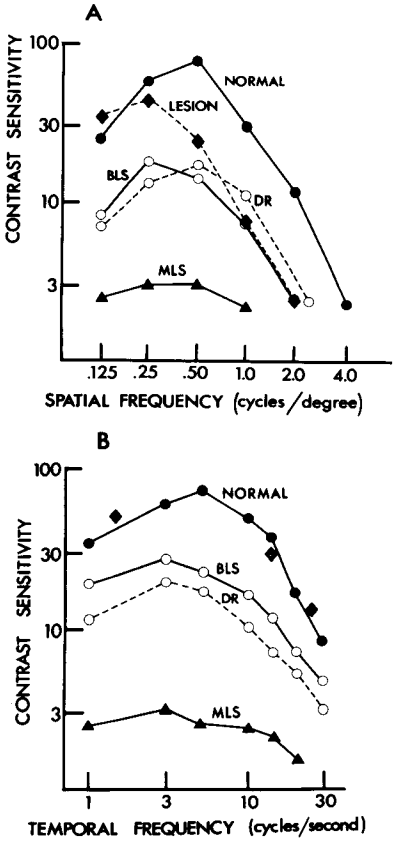

FIG. 15. Averaged spatial and temporal contrast-sensitivity functions for normal (filled circles), cortically lesioned (closed diamonds), dark-reared (open circles, dotted line), binocularly sutured (open circles, solid line), and monocularly sutured cats (triangles); conventions as in Fig. 3. There are two cats in each group. *A*: spatial functions at 1 or 1.5 Hz. *B*: temporal functions at 0.25 or 0.5 cycle/deg.

sized the importance of low spatial frequencies to form vision. In fact, it has been suggested that the lower spatial frequencies carry basic information concerning spatial patterns, whereas the higher frequencies add detail and raise spatial acuity (e.g., Refs. 21, 24). Y-cells seem to be the best candidate for the neuron type involved in basic form analysis (34, 52, 54). These cells are uniquely sensitive to the lower spatial frequencies, since W-cells are relatively insensitive to all spatial frequencies (62) and X-cells exhibit attenuated sensitivity to these lower spatial frequencies (34, 59). It has thus been suggested that Y-cells analyze the basic form information and X-cells add details and raise spatial acuity (34, 52, 54). The function of the insensitive and poorly responsive W-cells remains obscure. Contrast sensitivity in normal cats (Fig. 15) might then be determined by combined activity in the X- and Y-cell pathways (4).

POSTOPERATIVE BEHAVIOR. The geniculocortical X-cell input is limited exclusively or nearly so to area 17, whereas the W- and Y-cell inputs directly innervate many other areas of visual cortex as well (see INTRODUCTION). Thus, the bilateral lesions to cats *NL1* and *NL2* that involved most of area 17 and part of area 18 would have effectively eliminated the X-cell pathway from cortical circuitry and spared an as yet unspecified but significant amount of the W- and Y-cell pathways. Given the above hypothesis for the functional significance of the W-, X-, and Y-cell pathways, the postoperative behavior of cats *NL1* and *NL2* is precisely what we would predict for cats without an X-cell pathway. Analogous data have already been presented by Berkley and Sprague (1–3). That is, the remaining Y-cell (and perhaps W-cell) pathways are sufficient for excellent form vision, and the deficit is limited to a partial loss of spatial acuity and sensitivity to the higher spatial frequencies (see Fig. 15). Whether cats *NL1* and *NL2* postoperatively exhibit other deficits not tested by us (e.g., a loss of stereopsis, etc.) obviously cannot be determined from our data. We do not wish to imply that the X-cell pathway and striate cortex contribute only to high acuity vision, but that these parts of the visual system are not essential to reasonable form vision.

However, an important proviso to this interpretation must be made. Neither of the lesions completely eliminated area 17, and thus some cortical X-cell pathways probably survived. Consequently, the possibility exists that the excellent postoperative behavior seen in cats *NL1* and *NL2* is due to the remaining X-cell pathways or striate cortex. Both lesions removed all of the representation of the central 30–50° of visual field. Berkley and Sprague (1–3) reported analogous behavioral consequences of similarly incomplete lesions, and these authors offered

three reasons why the remaining striate cortex was an unlikely source for the excellent postoperative visual performance. First, the spatial acuity loss is much less than that predicted by the relationship between acuity and ganglion cell density, given the dramatic decline in ganglion cell density in the remaining representation of visual field. That is, the remaining peripheral representation of the X-cell pathway cannot subserve the high postoperative acuity seen. Second, neither their cats nor ours showed any evidence of averting their gaze during testing to direct the stimuli onto peripheral retina. Third, these animals show much less of a spatial acuity loss than that seen in normally reared cats with bilateral retinal lesions (made with a laser) involving the central 2–3° of visual field. In cats *NL1* and *NL2*, considerably more than this representation was destroyed in area 17 and thus in the X-cell pathway.

On balance, while we cannot completely rule out the possibility that the excellent postoperative behavior of these cats is due to uninterrupted portions of the X-cell pathway, the most compelling explanation seems to be that it is due to the remaining Y-cell (and perhaps W-cell) pathways and does not reflect X-cell activity. This interpretation is consistent with the fundamental role that has been suggested for Y-cells in basic form analysis (34, 52, 54).

Neural basis of behavior in lid-sutured and dark-reared cats

A great deal of attention has been focused on receptive-field properties of striate cortex neurons in cats raised with lid suture or in total darkness. There is general agreement that such deprivation causes these neurons to develop dramatically abnormal properties (see Refs. 6, 25, 43, 56 for recent reviews of this literature). These abnormalities range from nearly complete unresponsiveness of these neurons when the deprived eye is stimulated in monocularly sutured cats (67, 69) to reduced neural responsiveness and stimulus selectivity in binocularly sutured and dark-reared cats (38, 65, 67).

However, Fig. 15 illustrates fairly clearly that the deficits of visual performance found in lid-sutured and dark-reared cats must have a neural basis that includes abnormalities in addition to and independent of any found in striate cortex. This conclusion follows from the observation that lid suture and dark rearing produce a more profound visual impairment (evident from casual observations of behavior and reduced sensitivity to lower spatial frequencies) than does bilateral elimination of striate cortex. Therefore, the deficits described for striate cortex in these visually deprived cats cannot provide an adequate neural basis for the resultant amblyopia. The numerous attempts in the literature to explain such deprivation amblyopia on striate cortex abnormalities must therefore be reconsidered.

Also, since the geniculocortical limb of the X-cell pathway passes through striate cortex, the observation that the visually deprived cats are more amblyopic than are the cats with striate cortex lesions implicates deprivation-induced deficits in an extrastriate component of the W- and/or Y-cell pathways. Since Y-cells are particularly sensitive to lower spatial frequencies (34, 62) and the visually deprived cats exhibit sensitivity losses for such stimuli, it seems likely that the Y-cell pathway is rather seriously affected by lid suture and dark rearing. Effects of deprivation on the W- and X-cell pathways are more difficult to deduce from our psychophysical data.

In support of this notion, considerable physiological and morphological evidence points to a fairly selective effect of deprivation on geniculocortical Y-cells following lid suture and dark rearing (11, 13, 14, 16, 19, 31, 32, 37, 40, 44, 55, 72). Also, electrophysiological studies indicate that cortical inputs from deprived Y-cells are more affected than are those from deprived X-cells (29, 38, 42, 58, 63). The effects of deprivation on geniculate X-cells are more subtle and limited to reduced spatial acuity in lid-sutured cats (27, 33, 35, 44; however, see Refs. 11, 49) but not dark-reared (30) cats. Effects of visual deprivation on the W-cell pathway have not yet been reported. Several studies have questioned the conclusion that geniculate Y-cells are abnormal in deprived laminae (13, 49), but the evidence overall rather convincingly indicates a fairly selective and serious effect of lid suture and dark rearing on geniculate Y-cells (see Ref. 56

for a detailed discussion of this). Since our psychophysical data presented here also clearly indicate an effect of these deprivation conditions on the Y-cell pathway, these effects of lid suture and dark rearing on geniculocortical Y-cells may represent much of the neurological substrate for the amblyopia seen in these cats. By this reasoning, most or all of the known visual cortical areas would be seriously affected by lid suture and dark rearing, because geniculocortical Y-cells affected by such visual deprivation directly innervate these cortical areas (see INTRODUCTION).

Spatial acuity and contrast sensitivity

A final point that we wish to emphasize from our data has already been made by Hess and colleagues (22, 24). That is, spatial acuity reflects only sensitivity to higher spatial frequencies and ignores the apparently more important lower spatial frequencies. Figure 15 serves to illustrate this point. For instance, by any qualitative and most quantitative assessments of visual capacity, binocularly sutured and dark-reared cats are dramatically more impaired visually than are the normally reared cats with cortical lesions (see above). However, the spatial acuity of these visually deprived cats is actually equal to or better than that of cats *NL1* and *NL2* postoperatively.

This example also serves to underscore the importance of low spatial frequencies to visual capacity. Cats sensitive to these frequencies (cats *NL1* and *NL2* postoperatively) qualitatively see well, and cats less sensitive to these frequencies (cats *BLS1*, *BLS2*, *DR1*, *DR2*, *MLS1*, and *MLS2*) qualitatively see less well. On the other hand, the loss of sensitivity to higher spatial frequencies exhibited postoperatively by cats *NL1* and *NL2* does not seem qualitatively to impair their general visual performance, at least on the tests of spatial vision that we employed (see also Refs. 1–3).

Concluding remarks

We have provided a partial psychophysical description of various visual deficits in cats. The description involves the measurement of spatial and temporal contrast sensitivity. Early visual deprivation by lid suture or dark rearing causes severe sensitivity losses over a wide range of spatial and temporal frequencies. In this regard, these lid-sutured and dark-reared cats are like many humans who have a severe amblyopia and who are also insensitive to a wide range of spatial and temporal frequencies (22). Both visually deprived cats and humans with severe amblyopia exhibit generally poor vision. In the visually deprived cats, there are deficits in the Y-cell pathway and perhaps deficits in the X-cell and W-cell pathways as well. Humans with severe amblyopia may have similar central neural deficits. However, it is not clear to what extent the human visual system is organized in terms of W-, X-, and Y-cell pathways similar to those in the cat, and there is no evidence as yet that indicates how appropriate visually deprived cats might be as a model system to study any of the forms of human amblyopia.

In contrast to the visually deprived cats, normally reared cats with most of area 17 and part of area 18 bilaterally removed exhibit a loss of sensitivity only to higher spatial frequencies. This lesion fairly selectively interrupts the X-cell pathway. These cats postoperatively are like strabismic humans who have an amblyopia that involves only the higher spatial frequencies (22). Both the lesioned cats and these strabismic humans exhibit relatively good vision. Strabismic humans with a mild amblyopia thus may have deficits limited mostly to the X-cell pathway although, as noted above, similarities between the cat and human visual systems are still largely speculative.

From this, we have constructed the following working hypothesis. Lower spatial frequencies and the Y-cell pathway are sufficient and perhaps necessary for excellent form vision. Deficits in the Y-cell pathway lead to reduced sensitivity to lower spatial frequencies and thus poor form vision. Because of the importance of lower spatial frequencies to form vision, behavioral tests such as acuity measurements that do not assess these lower spatial frequencies provide an inadequate description of visual performance. Deficits in the X-cell pathway lead to reduced spatial acuity, but otherwise visual capacity is excellent. We emphasize the largely speculative nature of these conclu-

sions. They are offered in the spirit of a working hypothesis to be tested and not as a set of established conclusions.

ACKNOWLEDGMENTS

We thank Candace Hubbard, Margaret Rudolph, Mike Monsarrat, and Margaret Hoole for their time and effort in obtaining behavioral data from the cats. We also thank Sally Gibson for histological processing.

This research was supported by Public Health Service Grants EY 03038, NS 15473, and 5S07RR07085-16.

Received 14 September 1981; accepted in final form 17 March 1982.

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