

Effects of Visual Cortex Lesions upon the Visual Fields of Monocularly Deprived Cats

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ABSTRACT The visual fields of 16 cats raised with monocular eyelid suture were measured by means of a visual orienting test. We separately measured the fields of nondeprived and deprived eyes. Each cat was tested preoperatively, and 13 of the cats were tested following lesions of the visual cortex, superior colliculus, and/or optic chiasm.

Preoperatively with the nondeprived eye, every cat had a normal monocular field extending roughly from 90° ipsilateral to 45° contralateral to the eye being tested. Fields for the deprived eye seemed to depend upon the nature of the deprivation. Fourteen of the cats had complete lid fusions, and 13 of these had virtually identical deprived eye fields which essentially included only the monocular segment (i.e., roughly 45° to 90° ipsilateral). Only these 13 cats were tested postoperatively. The fourteenth cat with complete lid closure may have had a visual field for the deprived eye that included the entire ipsilateral hemifield, but its responses were extremely unreliable. Two of the cats had incomplete lid fusions which exposed the cornea and thus permitted some pattern vision during development. Their visual fields for the deprived eye included the entire hemifield. We conclude that rearing a cat with complete monocular lid occlusion produces for the deprived eye a field which is effectively limited to the monocular segment.

Following postoperative testing, histological verification of neural lesions was obtained for every cat except one. An optic chiasm transection in one cat rendered its deprived eye totally blind on these tests, presumably because crossing nasal fibers which represent the monocular segment were cut. The chiasm transection also reduced the nondeprived eye's field to 0° to 45° contralateral. Cortical ablations in the other 12 cats were contralateral to the deprived eye or bilateral, and they ranged in size from lesions of areas 17 and 18 to total occipitotemporal ablations. (Cats with the latter ablations also had tectal lesions to counteract hemianopia due to large cortical lesions.) Each of these 12 cats showed a dramatic postoperative increase of the deprived eye's visual field to include most or all of the ipsilateral hemifield. The smallest lesion (involving areas 17 and 18 contralateral to the deprived eye) produced such an expansion of the deprived eye's field. Collicular ablations in another cat suggest that these expanded fields following cortical lesions depend upon retinotectal pathways. Postoperative fields for the nondeprived eyes were more variable. Generally, smaller lesions caused little change in these fields from preoperative measurements; larger lesions tended to reduce the fields to include only the ipsilateral hemifield. Two cats with bilateral occipitotemporal cortical ablations and transections of the commissure of the superior colliculus exhibited no obvious behavioral differences between use of the nondeprived and deprived eyes, and the monocular fields included the ipsilateral hemifield for each eye.

One interpretation of these results is based upon prior suggestions that retinotectal pathways develop fairly normally in monocularly deprived cats, while geniculocortical pathways do not. The animals' preoperatively tested visual behavior and collicular response properties tend to reflect the status of cortical pathways, but following cortical lesions, the orienting functions of retinotectal pathways are more fully expressed. Since these retinotectal pathways are dominated by nasal retina, the entire nasal retina of the deprived eye after appropriate cortical lesions is functional for visual orienting.

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A cat raised with monocular lid suture develops serious abnormalities in the central visual pathways related to its deprived eye, and it also exhibits marked deficits in visually guided behavior when forced to use that eye. The purpose of the present study was to explore further the relationship between these neural and behavioral deficits.

In the lateral geniculate nucleus, cells in deprived laminae (i.e., those receiving direct retinal afferents from the deprived eye) are abnormally small (Wiesel and Hubel, '63a; Guillery and Stelzner, '70). Also, instead of the normal proportion of X- and Y-cells,² deprived laminae appear to have few recordable Y-cells, while the X-cells are relatively unaffected (Sherman et al., '72; LeVay and Ferster, '77; Garey and Blakemore, '77; Lin and Sherman, '78; Lehmkuhle et al., '78). In the striate cortex of deprived cats, the cells are influenced almost exclusively by the nondeprived eye, in contrast to the normal pattern in which most cells are binocularly activated (Wiesel and Hubel, '63b; Wilson and Sherman, '77). However, all of these deficits related to the deprived eye are relatively more serious in the binocular segment of the geniculostriate pathways than in the deprived monocular segment.³ That is, lateral geniculate cell sizes and the proportion of recordable Y-cells are fairly normal in the deprived monocular segment (Guillery and Stelzner, '70; Guillery, '72; Sherman et al., '72, '75; Hickey et al., '77). In turn, the deprived eye activates in a normal fashion many cells located in the deprived monocular segment of striate cortex but very few located in the binocular segment (Sherman et al., '74; Wilson and Sherman, '77). These differential effects of monocular deprivation on the binocular and monocular segments of the geniculocortical pathways are taken as evidence for competitive interactions between central pathways from each eye during development (i.e., "binocular competition," see Sherman et al., '74). Since cells in the deprived monocular segment cannot be at a competitive disadvantage with respect to those related to the nondeprived eye, these deprived neurons can develop relatively normally.

The visual orienting behavior of the cats also supports this hypothesis of binocular competition and correlates well with the pattern of deficits in the geniculostriate pathways. Thus, when using the deprived eye, a monocularly deprived cat clearly orients to

stimuli in the visual field of the deprived monocular segment (i.e., 35-45° to 90° from the vertical meridian and ipsilateral to the deprived eye), but orients poorly or not at all to stimuli in the binocular segment of visual field (i.e., within 45° of the vertical meridian, Sherman, '73, '74a; also see Sherman et al., '74).

Since this type of orienting behavior in normal cats is dependent upon cortical and/or tectal pathways (Sprague and Meikle, '65; Sprague, '66a,b; Sherman, '74b, '77a), it is of interest to consider the status of the superior colliculus after monocular suture. As in cortex, most collicular neurons are also influenced much more strongly by the nondeprived eye instead of the normal pattern of binocular activation (Wickelgren and Sterling, '69b; Hoffmann and Sherman, '74). Since the deprived retinotectal pathways seem fairly normal in response to electrical stimulation of the optic chiasm (Hoffmann and Sherman, '74), the dominance of tectal neurons by the nondeprived eye could reflect the activity of the corticotectal pathways (Wickelgren and Sterling, '69a; Rosenquist and Palmer, '71), which in turn presumably show the cortical pattern of nondeprived eye dominance. In support of this hypothesis of corticotectal influence is the finding that removal of much of the visual cortex in monocularly deprived cats allows the deprived eye to influence large numbers of collicular cells, presumably through the normal retinotectal pathways (Wickelgren and Sterling, '69b).

Normally reared cats made dependent upon their retinotectal pathways by large, bilateral lesions which remove all known areas of visual cortex show orienting responses with each eye throughout that eye's ipsilateral hemifield (Sprague, '66b; Sherman, '74b, '77a), presumably because nasal retina dominates the retinotectal pathways (Wickelgren and Sterling, '69a; Rosenquist and Palmer, '71; Sterling, '73; Kanaseki and Sprague, '74; however, see Graybiel, '75; Harting and Guil-

² Recently, a third cell type (W) has been described among retinal ganglion cells. Although the majority of W-cells seem to project to the midbrain, some of these cells project through geniculate neurons in the C laminae to cortex (Wilson and Stone, '75; Wilson et al., '76). W-cells differ in many ways from X- and Y-cells, but relatively little is known of them in normal cats, and virtually nothing is known of their properties following early visual deprivation.

³ The binocular segment of the central visual pathways is the portion whose neurons have receptive fields within the binocularly viewed portion of the cat's visual field. The monocular segments contain neurons whose receptive fields are in the peripheral, monocularly viewed crescents of the visual field (also Guillery and Stelzner, '70; Sherman et al., '72; Sherman, '73, '74a; Wilson and Sherman, '77).

TABLE 1

Cat	Surgery
RMD1V ¹	1. At 7 months postnatal, remove right occipitotemporal cortex. 2. After 4 additional months, remove left superior colliculus. Sacrifice after 4 further months.
LMD1V	1. At 7 months postnatal, section optic chiasm midsagittally. Sacrifice after 7 further months.
LMD2V	1. At 32 months postnatal, remove occipitotemporal cortex bilaterally and section commissure of the superior colliculus midsagittally. Sacrifice after 3 further months.
LMD7V	1. At 16 months postnatal, remove occipitotemporal cortex bilaterally and section commissure of the superior colliculus midsagittally. Sacrifice after 4 further months.
RMD8V	1. At 18 months postnatal, remove cortical areas 17, 18, and 19 bilaterally. Sacrifice after 4 further months.
RMD11V	1. At 11 months postnatal, remove cortical areas 17, 18, and 19 bilaterally. 2. After 3 additional months, remove left superior colliculus. Sacrifice after 5 further months.
RMD12V	1. At 15 months postnatal, remove left cortical areas 17 and 18. Sacrifice after 6 further months.
RMD16V	1. At 14 months postnatal, remove left cortical areas 17, 18 and 19. Sacrifice after 4 further months.
RMD1P	1. At 14 months postnatal, remove left cortical areas 17 and 18. 2. After 2 additional months, section commissure of the superior colliculus midsagittally. 3. After 2 additional months, remove right cortical areas 17 and 18. Sacrifice after 2 further months.
LMD2P	1. At 14 months postnatal, section commissure of the superior colliculus midsagittally. 2. After 3 additional months, remove right cortical areas 17 and 18. 3. After 5 additional months, remove left cortical areas 17 and 18. Sacrifice after 13 further months.
RMD3P	1. At 16 months postnatal, remove cortical areas 17, 18, and 19 bilaterally. Sacrifice after 7 further months.
RMD5P	1. At 18 months postnatal, remove cortical areas 17, 18, and 19 bilaterally. Sacrifice after 3 further months.
RMD8P	1. At 44 months postnatal, remove cortical areas 17 and 18 bilaterally. Sacrifice after 5 further months.

¹ Histology unavailable for this cat.

lery, '76). Thus, it seemed possible that cortical lesions in monocularly deprived cats would similarly unmask the retinotectal pathways and enlarge the deprived eye's field from the monocular segment to include the entire hemifield. Preliminary studies have shown this to be the case (Sherman, '74c). The goal of the present experiment was to confirm and extend this finding.

METHODS

This paper reports two separate and independent studies, one done by each author. Because the general questions, methods, and answers were essentially identical, we decided to combine them into a single report. Slight differences in technique are noted below, and cats tested by SMS at Virginia (the Vir-

ginia cats) are indicated with a "V" postscript, while those tested by JMS at Pennsylvania (the Pennsylvania cats) have a "P" postscript.

Subjects

Sixteen cats, born and reared in the laboratory, were studied. At the time of normal eye opening (6-10 days of age) each cat had the lids of the left (LMD) or right (RMD) eye sutured closed, and the cats were maintained in this fashion until they were studied as adults at least 7 months later (table 1). The lids of the deprived eye were then parted for behavioral testing, and the nondeprived eye was left open. During maturation, the animals were handled and examined at frequent intervals to habituate them to the investigators and to

check for the presence or absence of lid openings which would allow pattern vision (Loop and Sherman, '77). No lid openings (except at the medial canthus, which did not expose the cornea) were found in cats LMD1V, LMD2V, LMD7V, RMD1V, RMD8V, RMD11V, RMD12V, RMD16V, LMD2P, RMD1P, RMD3P, RMD5P, RMD7P, and RMD8P. Cats RMD4P and LMD6P had tiny openings in the lids other than at the medial canthus, and this presumably allowed some degree of pattern vision during development. In fact, such an aperture would be expected to serve as an artificial pupil and provide good pattern vision (Loop and Sherman, '77). These latter two cats were tested and, as will be shown, tended to exhibit different visual orienting behavior than the 14 cats with complete lid closure. However, from a separate study of visual discrimination abilities, LMD6P (raised with a lid opening) displayed deficits equal to those of LMD2P, RMD3P, and RMD8P (raised with no functional lid opening).

Surgical procedures

All of the 16 cats underwent one or a series of neural lesions consisting of visual cortex ablation, superior collicular ablation, mid-sagittal transection of the commissure of the superior colliculus, and/or mid-sagittal transection of the optic chiasm. For reasons given in RESULTS, three of the cats (RMD7P, RMD4P, and LMD6P) were not methodically tested postoperatively. Table 1 summarizes the surgical procedures for each of the other 13 cats, and further methodological details have been published previously (Sprague, '66a,b; Sprague et al., '77; Sherman, '74b,c, '77a,b). Every cat was tested before and after each surgical procedure, and a 2- to 4-week postoperative recovery period preceded further testing.

Behavioral testing

Visual orienting. These cats were tested for visual orienting behavior with techniques which have been described in detail previously (Sprague and Meikle, '65; Sherman, '73, '74a; Simoni and Sprague, '76). Each of the 16 cats was tested preoperatively and 13 were tested postoperatively. Below is given a description of these methods.

Each of the Virginia cats was food-deprived and tested on a table in a brightly illuminated room with overhead fluorescent lights plus

indirect light reflected off the white walls. This minimized shadows. The table was marked off into sixteen 15° sectors by intersecting guidelines designated 120°L, 115°L, etc., . . . 0°, 15°R . . . , etc., . . . 120°R, and the lateral canthi of the eyes were aligned with the 90° guidelines. The animal was pretrained to fixate the visual and/or auditory cues of the *fixation object*, which was a piece of dry cat food held in forceps and tapped on the table 50 cm from the cat's nose along the 0° guideline. While the cat was fixating in this manner, the *novel stimulus* (food held in a long forceps or any equivalent visual target at the end of a long, stiff wire) was suddenly presented vertically along one of the guidelines and 20-40 cm from the cat's nose. The cat was then released from restraint and its behavior noted. A brisk and rapid orienting response of head, eyes, and body to the novel stimulus was scored as a positive trial, and all other behavior as negative. Negative trials practically always (approximately 95%) consisted of ignoring the novel stimulus and approaching instead the fixation object. After each trial, the cat was fed a small piece of food, regardless of the response. Trials in which novel stimuli were introduced near the 0° guideline (fixation point) were scored differently because such stimuli could not elicit clear orienting responses. For these trials, positive responses consisted of the cat stopping short of the novel stimulus in its path to explore it; negative responses consisted of the cat apparently ignoring the novel stimulus until tactile contact was made which caused a distinct startle response; the rare (< 10%) trials which could not be clearly assessed were scored separately and are not further considered.

The cats were tested with both eyes open or with one covered by means of an opaque corneal occluder. Every 15° guideline was tested 50 to 100 times, in random sequence, separately for binocular, left monocular, and right monocular viewing. The person holding the fixation object ascertained that the cat looked at that object without detectable eye movements (i.e., $\geq 15^\circ$; Sherman, '73) except during orientations to the novel stimulus.

To control for inconsistent fixation, the proportion of orientations for each 15° guideline was compared to the baseline of spontaneous scanning movements that occurred without novel stimuli. These spontaneous scanning movements could easily be mistaken for visually elicited orienting. To obtain this

baseline performance, we instituted "blank" trials for which no novel stimulus or a stimulus placed well outside the visual field (i.e., $> 120^\circ$ peripheral) was presented when the animal was released from restraint. At least 100 of these blank trials (Sherman, '74a) were run at random throughout each viewing condition (binocular and monocular). The final response levels for each guideline have been normalized against these spontaneous response levels in the following way. If for a particular (binocular or monocular) viewing condition, the blank (spontaneous) response level is B% and the raw positive score for a given guideline is G%, then the normalized score for that guideline becomes $(G-B)/(100\%-B)$ if $G > B$, and is zero if $B \leq G$. The spontaneous response levels for these cats ranged from 4% to 13%.

The Pennsylvania cats were tested in a similar manner as described above, but with a few differences. Fewer guidelines were used, and thus fewer sectors of visual field were tested in a regular manner. These guidelines were at 0° plus 15° , 45° , 75° , and 90° to either side of the fixation object. Cat RMD5P postoperatively was also tested at 60° to the right of the fixation point. When orientation toward the 0° guideline was tested, the tapping which otherwise was used to strengthen fixation was stopped, but movement of the fixation object was still present.

It should be noted that in testing of both Virginia and Pennsylvania cats, the fixation object was characterized by both visual and acoustic cues, whereas the novel stimulus was only visual. Hence, if the novel stimulus were weak (i.e., fell into an amblyopic field), the cat might ignore it or respond erratically, because of the prepotency of the fixation object.

Histology

Histological controls were obtained for each cat except RMD1V at the completion of behavioral testing. The cats were anesthetized and perfused through the heart with saline followed by 10% formalin in saline. The brains were blocked stereotaxically, allowed to harden in fixative, removed from the skull, photographed or drawn, embedded in parlodion or egg yolk, and cut coronally into $40\text{-}\mu\text{m}$ sections. The sections were stained alternately with cresylecht violet for cell bodies and the Haidenhain-Woelke or Mahon methods for myelinated fibers. The extent of the lesions was reconstructed both from projection drawings of the sections through cortex, as well as

from the pattern of retrograde degeneration in the thalamus. For the former, we used the anatomical criteria of Otsuka and Hassler ('61) and Sanides and Hoffmann ('69), as well as physiological maps (Tusa et al., '78, '79; Palmer et al., '78). For the latter, we used the observations of Laties and Sprague ('66), Guillery ('70), and Niimi and Kuwahara ('73). For details, see Sherman ('77a,b) and Sprague et al. ('77).

RESULTS

Preoperative behavior

Visual orienting

Complete eyelid closure during development. Most of the cats with complete eyelid closure during development (METHODS) showed consistent and essentially identical visual orienting behavior following opening of the deprived eye in adulthood. Since this behavior has been described previously (Sherman, '73, '74a), it will be only briefly outlined here. Figure 1 illustrates for two typical cats (RMD16V and RMD5P) the monocular fields elucidated by the visual orienting test. Since in all cases the extent of field seen with both eyes open is the sum of the monocular fields (Sherman, '73, '74a), only monocular fields are shown in this and succeeding figures. Each cat with the nondeprived (left) eye responded to targets approximately 90° ipsilateral to $35\text{-}45^\circ$ into the contralateral hemifield. This is precisely what is expected for normal cats (Sprague and Meikle, '65; Sherman, '73, '74a,b, '77a; Hughes, '76). On the other hand, each cat with the deprived eye responded fairly exclusively to targets in the monocular segments ($35\text{-}45^\circ$ to 90° ipsilateral to that eye) and usually ignored targets presented in the binocular segment (approximately 45° ipsilateral to that eye to 45° into the contralateral hemifield). Relative blindness with the deprived eye in the binocular segment was further indicated by a typical startle response whenever the cat made tactile contact with a target placed in its path. With both eyes open, these cats responded throughout the visual field seen by each eye alone, and this implies that the deprived eye is not suppressed while the nondeprived eye is being used (cf. Sherman, '73).

The cats tended to improve their visually guided behavior using the deprived eye during the first several weeks or several months of testing (cf. Sherman, '73). However, as noted previously (Sherman, '73), responses with the

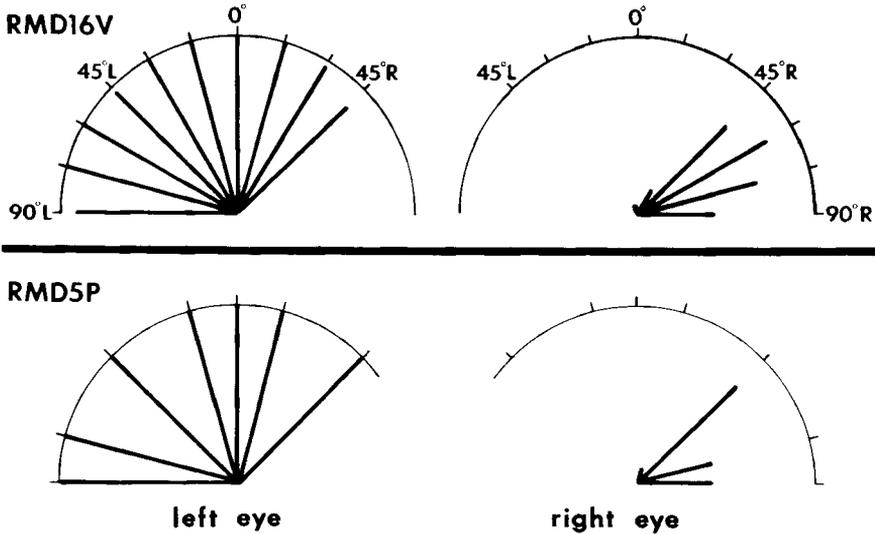


Fig. 1 Typical preoperative monocular visual fields for monocularly deprived cats. In both examples, the right eye was deprived. The plots in polar coordinates represent the normalized response levels for various sectors of visual field, and the circle segments indicate the 100% level. For the Virginia cats (upper example), each 15° sector of visual field was tested; for the Pennsylvania cats (lower example), some of these sectors were not routinely tested (METHODS). The field of the nondeprived eye typically extended from 90° ipsilateral to 45° contralateral. The field of the deprived eye was generally confined to the monocular segment (roughly 45° to 90° ipsilateral).

deprived eye were much inferior (i.e., less brisk and accurate) than were those for the nondeprived eye. On the other hand, clear and fairly brisk responses with the deprived eye were seen in the monocular segment (see also below).

The following general observations of behavior of the cats using the deprived eye were also made (cf. Sherman, '73): (a) visual placing to the edge of a brightly lit table was present but irregular and often misdirected; (b) following of a stimulus was possible only if it was kept moving in the monocular segment away from the midline; but it was easily lost, and in other regions, the stimulus did not elicit a following response; (c) orienting responses to targets (typically in the monocular segment) were usually slow, and target localization was poor compared to normal responses; (d) no localization of stationary stimuli placed in the monocular segment (i.e., food placed on the table) was seen, even for a stimulus of high contrast; (e) spontaneous jumping from the table never occurred; and (f) frequent scanning of the ipsilateral but not contralateral visual field occurred.

Some cats while using the deprived eye would occasionally appear to orient to stimuli

in the binocular segment, but these irregular responses were considerably poorer and less frequent than those elicited by stimuli in the monocular segment. It was difficult to determine if these infrequent "responses" to targets in the binocular segment were stimulus-evoked or due to spontaneous scanning that occasionally occurred in these cats, since the rate of these responses for most cats was lower than the spontaneous orienting rate (METHODS). The only potential exception to this general pattern of clear responses with the deprived eye in the monocular segment and few or none in the binocular segment may have been cat RMD7P. This animal showed some evidence of responses with the deprived eye throughout the hemifield ipsilateral to that eye. However, this cat was also unique, because it was the worst subject of the series. The animal was fractious and difficult to test, and responses tended to be erratic and inconsistent. For this reason, we are not completely certain that its behavior represents a true departure from the deprived eye fields described above for each of the other monocularly sutured cats.

Incomplete eyelid closures during development. Small, lateral lid holes (~1/mm diam.),

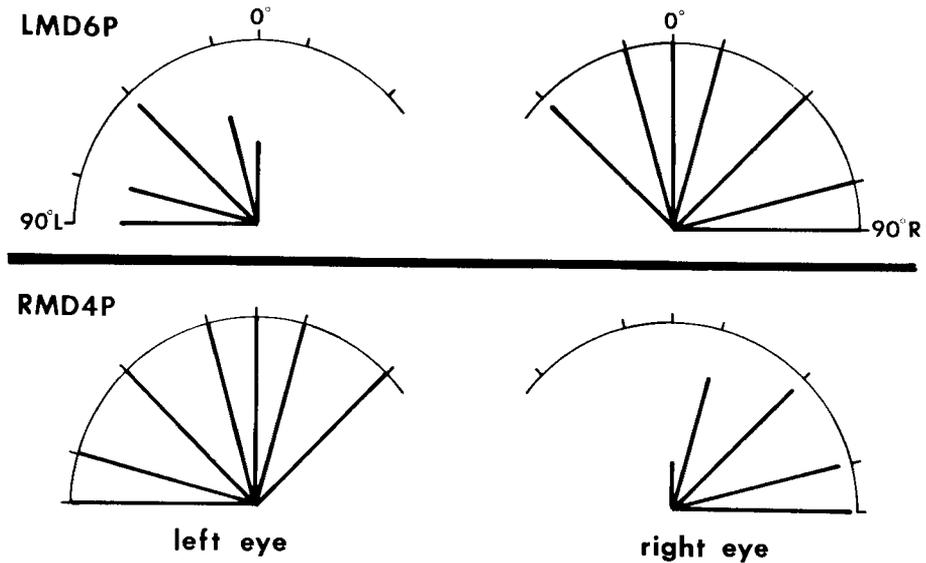


Fig. 2 Monocular fields for cats reared with incomplete lid closures for the deprived eye; conventions as in figure 1. The left eye was sutured for LMD6P; the right, for RMD4P.

which exposed the cornea, were present in cats RMD4P and LMD6P. These animals behaved quite differently on the visual orienting task than did the cats raised with complete eyelid closures. After these incomplete closures, the cats seemed to respond to targets equally well throughout most or all of the visual field ipsilateral to the deprived eye, while the typical pattern after complete closure consisted of orientation with the deprived eye exclusively or nearly so to stimuli in the monocular segment of visual field. (A possible exception was RMD7P, a cat with an effectively occluded cornea but with fields perhaps equivalent to cats RMD4P and RMD6P [see also above]). The accuracy and briskness of responses using the deprived eye were not qualitatively better in cats RMD4P and LMD6P than in those of cats with complete closures. We cannot as yet suggest an explanation for this puzzling development of a hemifield in an eye completely occluded except for a small lid aperture. Behavior for all of these cats with the nondeprived eye was normal. These results are illustrated in figure 2 for cats RMD4P and LMD6P.

Histological controls

As can be seen in table 1, many different neural lesions were made in these cats, often sequentially in several stages. Table 1 summa-

rizes the lesions only for those cats from which postoperative visual orienting behavior was systematically studied. Histological reconstructions have verified the extent to which the operations successfully ablated the intended tissue; usually small islands of cortical and collicular tissue inadvertently either survived extirpation or were damaged. These are described more completely below for a series of typical examples. Unfortunately, the histological material for cat RMD1V was lost in transportation, but since histology on each of the other cats essentially confirmed that lesions were as intended, we are reasonably confident that the lesions for RMD1V were as described in table 1.

Cortical ablations

The large bilateral occipitotemporal cortex lesions in cats LMD2V and LMD7V successfully removed all of the lateral, suprasylvian, and various amounts of the ectosylvian gyri in the posterior two-thirds of the hemispheres. Medially, the superior bank of the splenial sulcus was removed, and some damage was seen in parts of the cingulate gyrus. All of the known 13 cortical visual areas (Tusa et al., '78, '79; Palmer et al., '78) were removed, with severe atrophy in all geniculate laminae plus the medial interlaminar nucleus. Atrophy was also evident in the inferior, medial, and lateral

divisions of the pulvinar (Baden et al., '65; Sprague, '66a,b; Kawamura, '74; Niimi et al., '74). Lesions indistinguishable from these have been previously illustrated (Sprague, '66a,b; Sherman, '74b,c, '77a,b).

Lesions aimed at areas 17, 18, and 19 (RMD8V, RMD11V, RMD16V, RMD3P, and RMD5P) in all cases removed most of the intended tissue and resulted in cell atrophy in all laminae plus the medial interlaminar nucleus of the lateral geniculate nucleus. However, small islands of surviving cortex in areas 17 (splenial sulcus) or 18 (postlateral sulcus) were seen in some brains and were correlated with survival of patches of neurons in the laminar parts of the lateral geniculate nucleus; parts of the upper visual field representation of area 19 were spared in the posterior suprasylvian gyri, with surviving neuronal patches in the medial interlaminar nucleus; and small pockets of damage into areas lateral to area 19 in the suprasylvian gyrus were also evident in some cases. Reconstructions of lesions similar to these can be found in prior reports (Sprague, '66a; Sprague et al., '77; Sherman, '74a,b, '77a).

Histology of the smallest intended cortical lesions of area 17 and 18 (RMD12V, RMD1P, LMD2P, and RMD8P) revealed that the intended area was removed with minimal damage to neighboring area 19. However, except for cat LMD2P, which had an apparently complete lesion of area 17 (figs. 3, 4) some pockets of surviving cells were seen directly at the cortical level and indirectly in the pattern of retrograde degeneration of lateral geniculate cells. Note the considerable sparing of cells in the medial interlaminar nucleus plus laminae C1 and C2 in figure 4. This pattern has also been described in cats with similar lesions (Sprague et al., '77).

Collicular lesions

Unilateral ablations of the superior colliculus were made in cats RMD1V and RMD11V. Most of the colliculus was ablated in RMD11V with minimal damage to the underlying tegmentum. Given the relative success of this lesion and consistency of others similarly performed (Sherman, '74b, '77a,b), we assume that the collicular lesion of cat RMD1V was of similar extent. However, due to loss of the histological material for this cat, this point must remain in doubt.

Midsagittal transections of the commissure of the superior colliculus were performed in

cats LMD2V, LMD7V, RMD1P, and LMD2P. Such a split in decorticate cats can amplify collicular involvement in visual orienting behavior, presumably by blocking intercollicular suppression (Sprague, '66b; Sherman, '74b, '77a). The transection in the present study successfully split all but a few fibers (<5%) at the anterior and/or posterior limits of the commissure, with minimal damage to the superior colliculi, the commissure of the inferior colliculus, the posterior commissure, or the periaqueductal gray. Collicular lesions equivalent to these have been previously illustrated (Sprague and Meikle, '65; Sprague, '66a,b; Sherman, '74b,c, '77a,b).

Optic chiasm section

Cat LMD1V had its optic chiasm transected midsagittally. Subsequent histology clearly showed total transection of the chiasm along the midline.

Postoperative behavior

While using the deprived eye preoperatively, the cats with complete eyelid closures responded fairly well (but not normally) to stimuli in the monocular segment and poorly, if at all, to stimuli in the binocular segment. There was remarkably little interanimal variability in this pattern of behavior. (However, see the above reservation in the case of cat LMD7P.) Postoperative behavior is not considered for cats with incomplete eyelid closures, and due to the unclear preoperative behavior of LMD7P, postoperative behavior in this animal was not evaluated.

Cortical and collicular lesions

Cats LMD2V, LMD7V, and RMD1V. These cats, after large, bilateral occipitotemporal cortical lesions, presented a consistent pattern in the context of similar lesions previously described for normally reared cats (Sprague, '66a,b; Sherman, '74b, '77a). In a normally reared cat, a unilateral lesion renders the animal blind throughout the contralateral hemifield. If, however, either a split of the collicular commissure or an ablation of the colliculus contralateral to the cortical lesion is performed, visual orienting responses returns to the previously blind hemifield. Also, in normally reared cats, such a bilateral cortical lesion essentially causes blindness in both hemifields, but visual orienting can be sustained in both hemifields if the collicular commissure is transected. Figure 5 illustrates

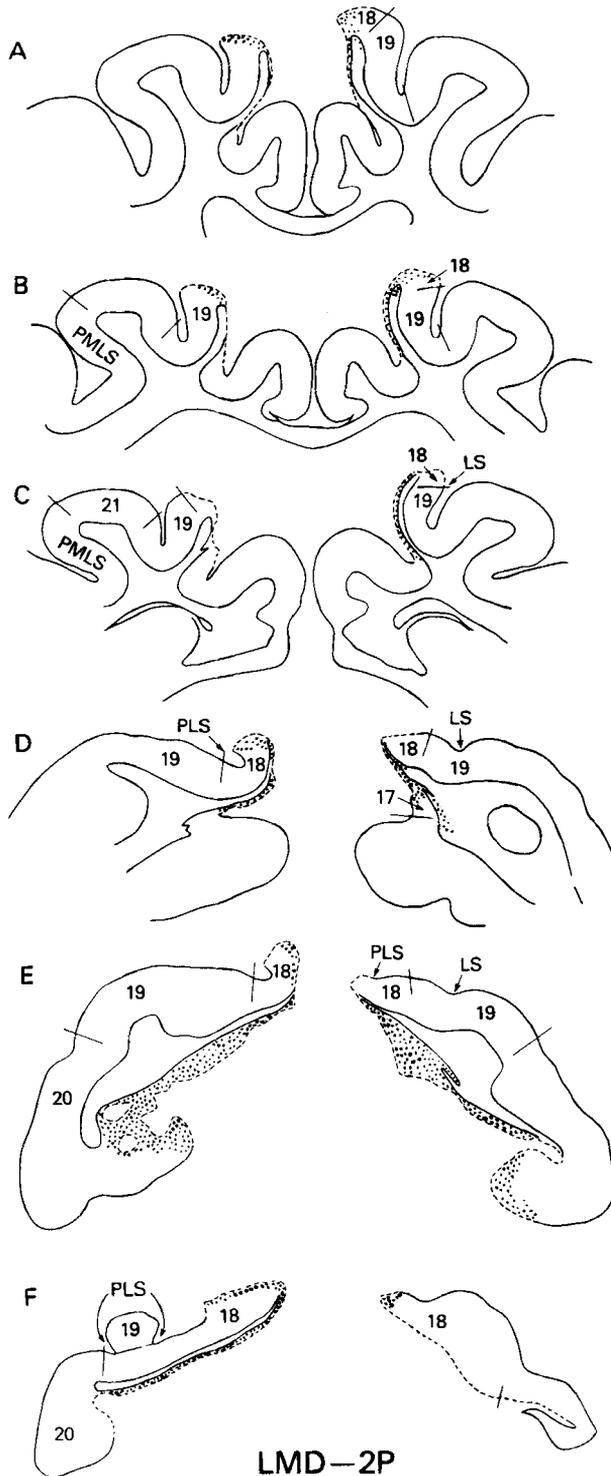


Fig. 3 Projection drawings of coronal sections through the cortex of cat LMD2P, showing the extent of the lesion. Dashed lines indicate the edge of the lesion; the stippling indicates areas of atrophy and denervation; the numerals denote the cortical areas. LS, lateral (marginal) sulcus; PLS, postlateral sulcus; PMLS, posteromedial lateral suprasylvian area (Palmer et al., '78).

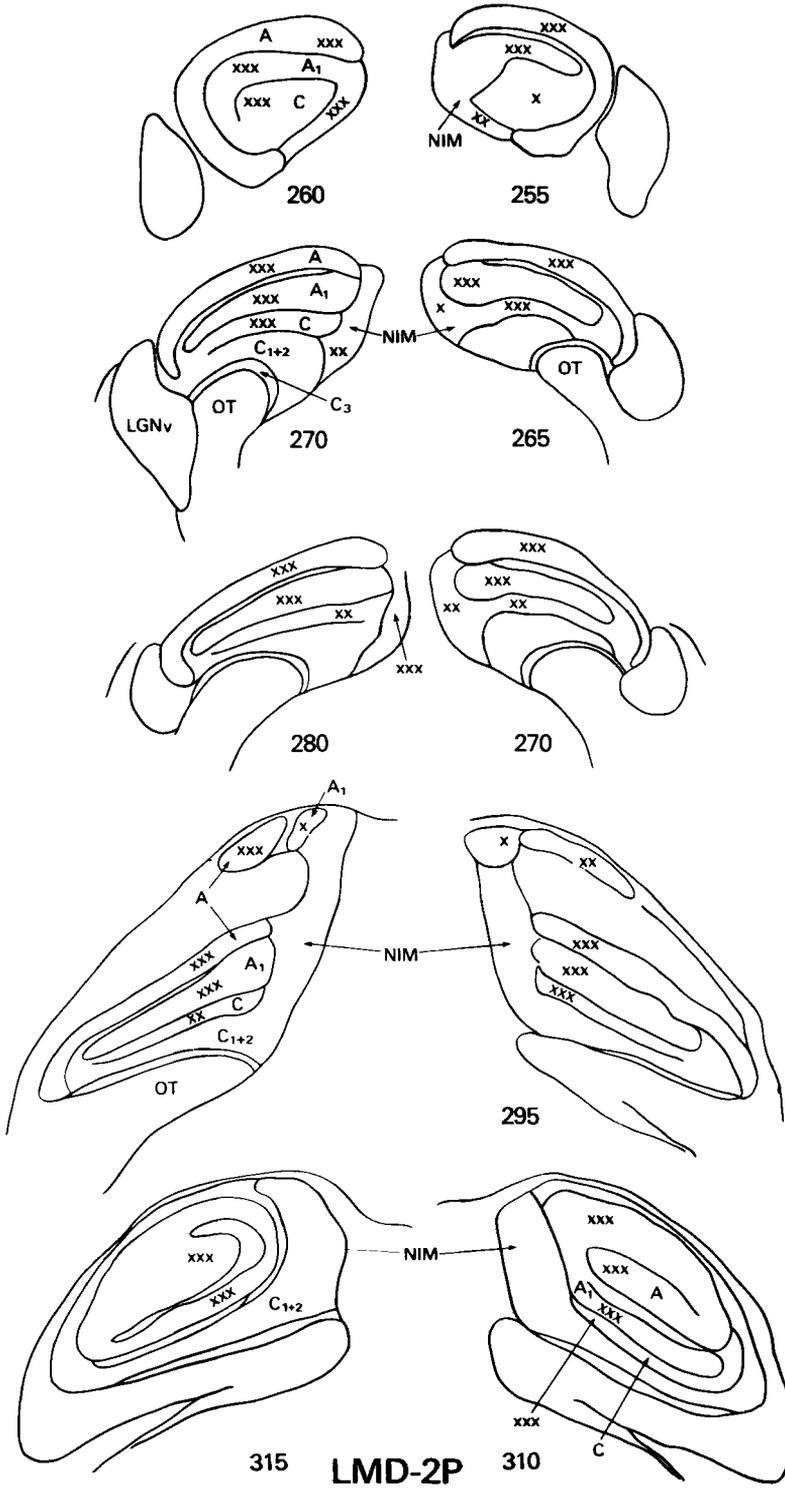


Fig. 4 Selected coronal sections through the dorsal lateral geniculate nucleus of cat LMD2P, showing extent of retrograde atrophy. The symbols and abbreviations are as in figure 3, except LGN_v, ventral lateral geniculate nucleus.

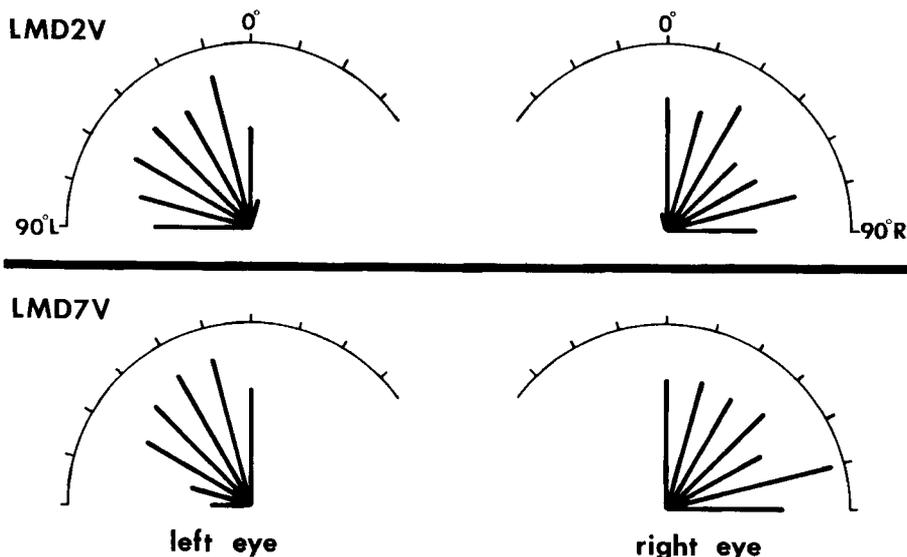


Fig. 5 Monocular fields following extensive bilateral removal of occipitotemporal cortex and a transection of the commissure of the superior colliculus; conventions as in figure 1. The deprived eye for both cats was the left, and the preoperative fields of both nondeprived and deprived eyes were similar to those represented in figure 1.

the behavior for cats LMD2V and LMD7V following a 1-stage, bilateral ablation of occipitotemporal cortex and a midsagittal split of the collicular commissure (see Sherman, '74c, for a previous description of this experimental result). As in all figures of postoperative behavior, figure 5 shows the stable behavior following at least a 2- to 4-week recovery period. While preoperatively there was considerable difference in the extent of visual field seen by the deprived and nondeprived eye (cf. fig. 1); postoperatively, there was little or no difference. Each eye responded to targets throughout its ipsilateral hemifield, as if nasal, but not temporal, retina subserved the behavior. The postoperative responses, however, were notably sluggish and imprecise, as they are for normally reared cats following similar surgery (Sherman, '74b, '77a). Also, as in normally reared cats following similar surgery, there was a pronounced tendency for the cat with monocular viewing to scan spontaneously the hemifield contralateral to the open eye as if searching the blind hemifield. That is, practically all "blank" responses (METHODS) were in this direction: rightward with the left eye open and leftward with the right eye open.

Nonetheless, this pattern of postoperative behavior represents a dramatic increase in the deprived eye's visual field. It was previously

suggested (Sherman, '74c) that the cortical and tectal surgery allowed expression of the retinotectal pathways, which are fairly normal for the deprived eye (Hoffmann and Sherman, '74). This explains both the lack of obvious interocular differences, as well as vision limited to nasal retina (cf. Sherman, '74b, '77a), because the cat's retinotectal pathways are dominated by the contralateral, nasal retina (Wickelgren and Sterling, '69a; Rosenquist and Palmer, '71; Sterling, '73; Kanaseki and Sprague, '74; however, see Graybiel, '75; Harting and Guillery, '76). In monocularly sutured cats, evidently cortex must first be removed to permit expression of the retinotectal capabilities (Wickelgren and Sterling, '69b).

The postoperative behavior of cat RMD1V is illustrated in figure 6. After a right occipitotemporal ablation (fig. 6A), responses to stimuli through the left hemifield were completely lost for the left eye. That is, the left eye saw only from 0° to 45° right; the right eye continued to respond to stimuli in its monocular segment. As expected, responses with the left (nondeprived) eye remained brisker and better localized than those with the right (deprived) eye. However, following the subsequent ablation of the left superior colliculus (fig. 6B), responses to targets in the left hemifield returned for the left (nondeprived) eye as in normal cats (Sprague, '66b; Sher-

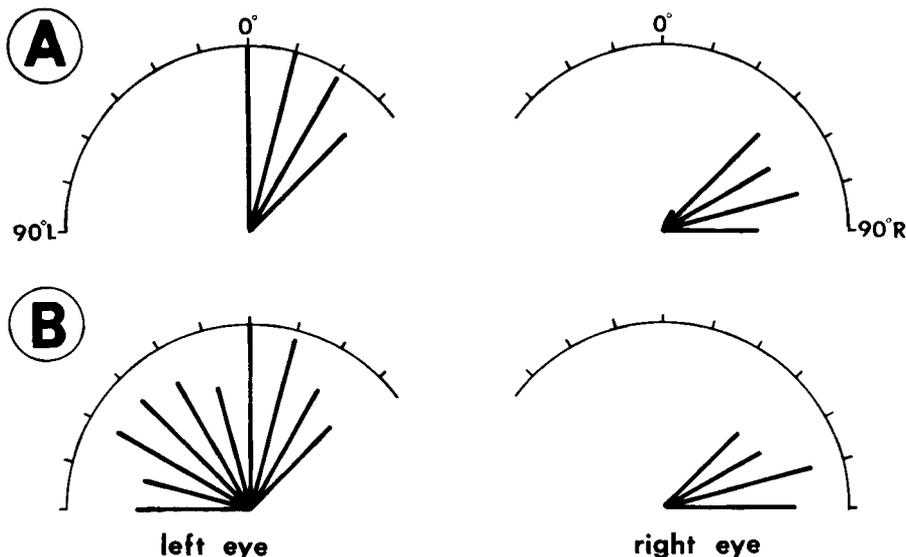


Fig. 6 Postoperative fields of cat RMD1V; conventions as in figure 1. The right eye was deprived, and the preoperative fields of both eyes were similar to those represented in figure 1.

- A Fields following right occipitotemporal cortex ablation.
 B Fields following subsequent ablation of left superior colliculus.

man, '77a), and the right (deprived) eye continued to respond only to stimuli in the monocular segment. As in normal cats with similar lesions (Sherman, '77a) the responses of cat RMD1V via the nondeprived eye's nasal retina evidently are mediated by way of the contralateral retinotectal pathways, and those via the temporal retina, by way of ipsilateral geniculocortical pathways. The deprived eye's responses in the monocular segment apparently can be mediated by contralateral cortical pathways in the absence of the colliculus, and no expansion of its useful visual field is seen with this pattern of lesions. Therefore, behavior with the deprived eye can involve cortical pathways and is not limited to tectal pathways (cf. Hoffmann et al., '78).

Cats RMD8V, RMD11V, RMD16V, RMD3P, and RMD5P. These cats had medium-sized cortical lesions aimed at areas 17, 18, and 19. Several of these cats also had collicular lesions. The behavioral effect of the cortical lesions was fairly consistent among the animals, although some quantitative differences were noted, especially for responses with the nondeprived eye. These cortical lesions, like the larger occipitotemporal lesions, resulted in an expansion of the deprived eye's visual field to include most or all of the ipsilateral hemifield. In several cats, the field

of the nondeprived eye remained unchanged by the cortical removal (90° ipsilateral to 45° contralateral); in others, responses were restricted to the ipsilateral hemifield. Orienting responses of the nondeprived eye were somewhat less brisk, and tracking responses of moving stimuli were much slower, than they were preoperatively. Visual placing remained, as did the animal's ability to locate stationary objects on a white surface. Apart from the expansion of visual field, responses using the deprived eye were changed little by the decortication in contrast to changes observed for the nondeprived eye. Finally, these cats postoperatively displayed exaggerated spontaneous scanning movements on blank trials. For some cats, these were consistently directed towards the hemifield contralateral to the eye open during testing; for others, towards the hemifield ipsilateral to the deprived eye.

Figure 7 shows the postoperative behavior for the Virginia cats (RMD8V, RMD11V, RMD16V). A bilateral lesion of areas 17, 18, and 19 (figs. 7A,B) in these cats produced fields very similar to those seen after occipitotemporal lesions combined with a transection of the collicular commissure, except that responses for the nondeprived eye remained relatively brisk after the smaller ablation. As in normal cats (Sprague, '66a,b; Sher-

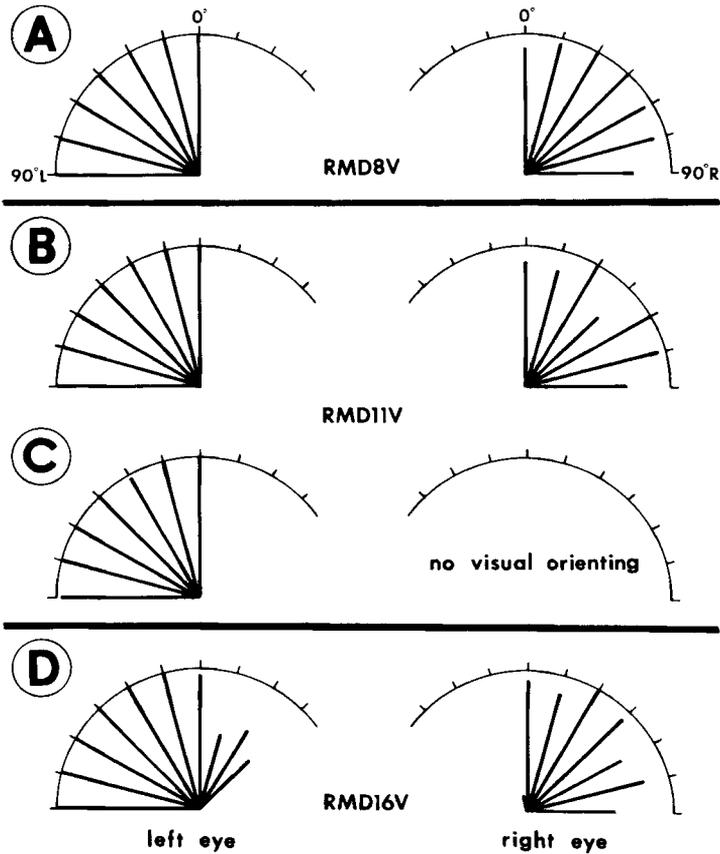


Fig. 7. Monocular fields following lesions in cortical areas 17, 18, and 19; conventions as in figure 1. The right eye in each cat was deprived, and the preoperative fields of both eyes were similar to those in figure 1.

- A Fields for RMD8V after bilateral ablation of areas 17, 18, and 19.
 B Fields for RMD11V after bilateral ablation of areas 17, 18, and 19.
 C Fields for RMD11V after subsequent ablation of left superior colliculus. The right eye seemed blind.
 D Fields for RMD16V after unilateral ablation of left areas 17, 18, and 19.

man, '77a), lesions here that did not extend significantly lateral to area 19 did not require collicular lesions to permit visually guided orienting behavior. In figures 7A,B, each eye responded throughout the ipsilateral hemifield, and little or no interocular asymmetry between eyes was evident. This represented an increase of the deprived eye's field with a roughly equal decrease of the nondeprived eye's field. That the deprived eye's behavior was now due to retinotectal pathways is suggested by figure 7C. In this case, a subsequent ablation of the left superior colliculus in cat RMD11V has rendered the right, deprived eye essentially blind without noticeably affecting the extent of visual field for the left, nondeprived eye. Also, figure 7D shows for cat

RMD16V that a left, unilateral cortical lesion of areas 17, 18, and 19 contralateral to the right, deprived eye is sufficient to expand the eye's field of view to include the entire hemifield without affecting behavior using the left, nondeprived eye.

Note that cat RMD16V, as well as others described below (fig. 8), had substantially overlapping monocular visual fields. This occurred presumably because the cortical lesion was not extensive enough to abolish orienting to stimulation of the left (nondeprived) temporal retina. That is, perhaps enough temporal retina was represented in the spared geniculocortical pathways to sustain orienting to targets directed at this retina. However, this cat's orienting while using the left, nondeprived eye

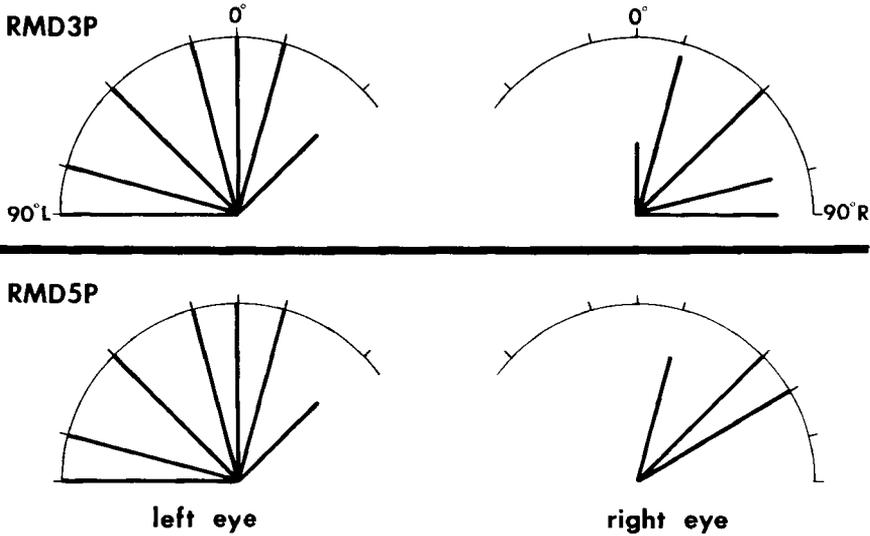


Fig. 8 Monocular fields following bilateral ablations of cortical areas 17, 18, and much of 19; conventions as in figure 3. The right eye in each cat was deprived, and the preoperative field of both eyes were similar to those depicted in figure 1.

was clearly brisker, more accurate, and more frequent to targets presented in the ipsilateral hemifield (nasal retina) than to targets in the contralateral hemifield (temporal retina). It is not clear why seemingly comparable lesions in cats RMD8V and RMD11V or in some normal cats (Sherman, '77a) seem to abolish the responsiveness to stimulation of temporal retina more completely than in cat RMD16V. Perhaps this results from individual variability among cats or from certain differences in the size of cortical ablations. For example, some of the lesions spared parts of area 19 (lying in the posterior suprasylvian gyrus) in which the upper visual fields are represented. If this tissue was functional and represented a region through which the novel stimulus passed, orientation to the stimulus could have occurred. In our test procedures, the novel stimuli were introduced from above (METHODS).

Postoperative behavior for the Pennsylvania cats (RMD3P, RMD5P) is illustrated in figure 8. Both of these animals had bilateral ablations of areas 17, 18, and 19, with sparing of the peripheral, upper field representation in all three areas bilaterally in RMD3P and in the right hemisphere of RMD5P. Postoperatively, responsiveness for the deprived eye in both cats extended significantly towards the midline. For cat RMD3P postoperatively, as

with the above Virginia cats, the deprived eye's field of view included the entire ipsilateral hemifield. Curiously, the postoperative responses of cat RMD5P to more peripheral stimuli ($>70^\circ$) were lost. Except for the possibility of inadvertent and unknown damage of neural areas necessary for responses to targets in more peripheral visual field, we cannot explain this unexpected result. Figure 8 also shows that the postoperative visual field for the nondeprived eye in both cats extends beyond the midline. However, it was clear for cat RMD5P (but not for cat RMD3P) that the responses with this eye were considerably brisker and more accurate to ipsilateral (nasal retina) than to contralateral (temporal retina) stimuli. Therefore, it seems that for many cats with bilateral ablation of cortical areas 17, 18, and 19, the nondeprived eye responds better to ipsilateral than to contralateral stimuli, but this difference was more complete for the Virginia cats than for the Pennsylvania cats. Subtle differences in testing and/or lesion size might account for these differences between groups.

Cats LMD2P, RMD12V, RMD1P, and RMD8P. It has been previously shown that transection of the tectal commissure releases function of the retinotectal pathways after cortical ablations (Sprague, '66b; Sherman, '74b, '77a). Since the expansion of visual field

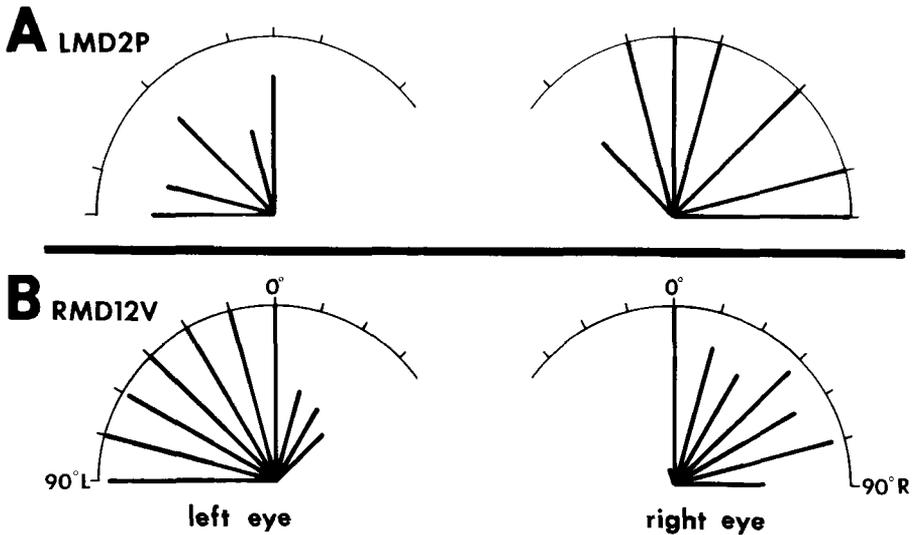


Fig. 9 Monocular fields following lesions limited to cortical areas 17 and 18; conventions and preoperative fields as in figure 1.

A Fields for LMD2P following bilateral removal of areas 17 and 18. The left eye was deprived.

B Fields for RMD12V following unilateral removal of left areas 17 and 18. The right eye was deprived.

for the deprived eye seen in the present study following cortical lesions is considered to result from expression of retinotectal pathways (Sherman, '74c), it was thought that a transection of the collicular commissure alone might result in such a behavioral change. However, this surgery in cat LMD2P was without observable effect on visual orienting. This is not surprising, since similar surgery in normally reared cats is also without observable effect (Sherman, '77a).

Cortical lesions in these cats (virtually limited to areas 17 and 18) were designed to elucidate the smallest cortical ablation that could produce an expansion of the deprived eye's field of view. The surgery in LMD2P and RMD8P completely removed area 17 and most of 18 bilaterally with no detectable damage to 19 (cf. figs. 3 and 4). RMD1P had minor sparing in area 17 only in the left splenial sulcus; area 18 was partly spared, and area 19 partly involved on the left side. RMD12V had some sparing of 18 caudally (periphery of upper visual fields) and some damage in area 19 rostrally. Figure 9A shows the monocular fields for cat LMD2P following the tectal split and bilateral removal of areas 17 and 18 in two stages (table 1). Expansion of the visual field of the deprived eye did not occur until roughly one year after the final lesion, and there was

no noticeable change in the nondeprived eye's field. However, unilateral ablation of areas 17 and 18 contralateral to the deprived eye of cat RMD12V (fig. 9B), as well as bilateral removal of these areas in cat RMD8P, produced a similar behavioral result: the deprived eye's field enlarged to include the entire ipsilateral hemifield, while the nondeprived eye's field remained unchanged. Thus, it would appear that lesions restricted to areas 17 and 18 will result in enlargement of the visual field of the deprived eye, and this effect can be induced by the lesion limited to the cortex contralateral to the deprived eye.

Optic chiasm section

Cat LMD1V. Figure 10 illustrates this cat's monocular fields before (fig. 10A) and after (fig. 10B) the optic chiasm transection. Such a transection effectively cuts all fibers from nasal retina, thus destroying retinal connections in the monocular segment, but spares the majority of fibers from temporal retina, thus leaving most connections in this portion of the binocular segment intact. Postoperatively, the cat displayed the expected visual behavior with the nondeprived eye, since a complete field for the temporal retina was evident. On the other hand, the cat seemed totally blind when using the deprived eye. No vis-

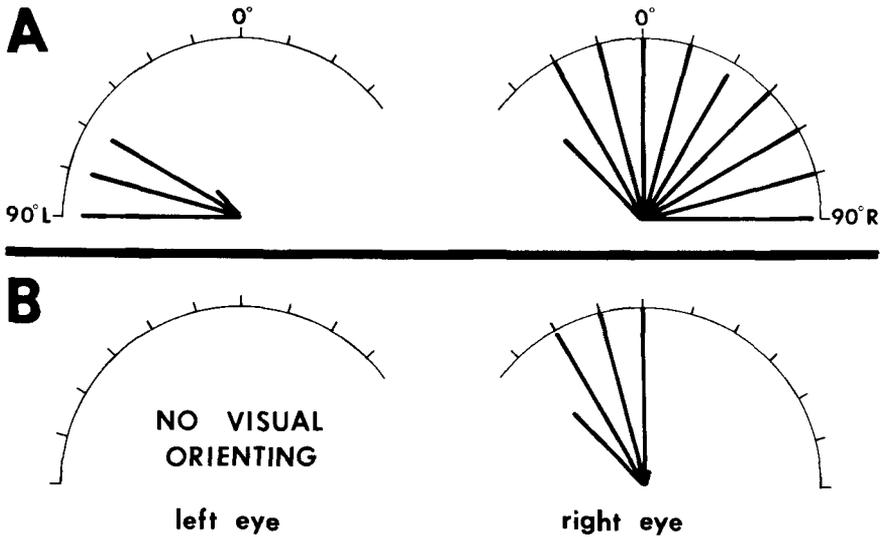


Fig. 10 Monocular fields for LMD1V; conventions as in figure 1, and the left eye was deprived.
 A Preoperative fields.
 B Fields following midsagittal transection of the optic chiasm. The left eye seemed blind.

ually guided behavior could be elicited on any of our tests (i.e., orienting, placing, following, etc.). It might be expected that any vision associated with the remaining binocular segment would be most easily seen after destruction of the clearer visual responsiveness of the monocular segment. However, we emphasize that, although postoperatively cat LMD1V seemed blind with its deprived eye on these visually guided tasks, it may well have shown visual responsiveness on other tasks, such as a brightness discrimination.

DISCUSSION

These studies show that the visual field of the deprived eye of a cat reared with monocular closure can be dramatically increased by appropriate lesions of visual cortex. Preoperatively, using the deprived eye, these cats oriented predictably only to targets placed in a monocular segment of the visual field; postoperatively, they could orient to targets throughout the hemifield ipsilateral to the deprived eye. This represents roughly a doubling of the functional visual field for the deprived eye.

Preoperative behavior

We found that if the lid closures were complete during rearing (or if small apertures

were limited to the medial canthus and thus did not expose the cornea), these cats while using the deprived eye oriented fairly briskly only to targets in the monocular segment. Some animals appeared to orient occasionally to targets in the binocular segment, but most did not, and given the limitations of the test procedure, we cannot be certain of the visual capacities of the deprived eye in the binocular segment. Rather, we feel that these results clearly indicate dramatically better vision for the deprived eye in the monocular than in the binocular segment. This behavioral result can be related to studies of the central visual pathways of these cats which also indicate less severe effects of monocular deprivation upon the monocular than upon the binocular segments (Guillery and Stelzner, '70; Sherman et al., '74; Wilson and Sherman, '77). Taken together, these observations are consistent with the notion that some form of binocular competition guides visual development in these cats (Wiesel and Hubel, '65; Guillery, '72; Sherman et al., '74).

We emphasize that these conclusions of visual behavior are based strictly upon a specific orienting task, which measures visual attention and orientation of head, eyes, and body to a moving target. Other tests of the deprived eye's visual capacity, such as pattern and form discriminations, may or may not disclose dif-

ferential deprivation effects upon the binocular and monocular segments.⁴

The visual fields of the two cats (RMD4P and LMD6P) raised with incompletely closed lids were somewhat different. Such an animal with the deprived eye could effectively orient to targets throughout the hemifield ipsilateral to that eye, and thus a considerable part of the binocular segment seemed as functionally useful as was the monocular segment. The status of the central pathways in such animals has not, to our knowledge, ever been studied, except perhaps unwittingly. The importance of this point is that subtle differences in rearing conditions (such as the presence or absence of a very small lid aperture exposing the cornea) can lead to quite different developmental processes.

Comparison with other studies

The basic results reported for these cats preoperatively have been reported for several other species. Monocularly deprived dogs (Sherman and Wilson, '75) and bushbabies (Joseph and Casagrande, '78), while using the deprived eye, orient nearly exclusively to targets presented in the monocular segment. Likewise, informal testing of monocularly deprived tree shrews suggest a similar result (see discussion in Norton et al., '77).

However, van Hof-van Duin ('77) and Heitländer and Hoffmann ('78), in careful studies of monocularly deprived cats, have described a somewhat different result from that presented in this paper. Using the deprived eye, their cats responded to targets throughout the hemifield ipsilateral to that eye, although in many cases responses were somewhat better for targets in the monocular than in the binocular segment. Two main possibilities, which are differences in testing procedures and/or animals, are considered in detail as possible explanations for these apparently conflicting results.

Different testing procedures. In our experience, cats using the deprived eye tend to scan compulsively the ipsilateral hemifield of that eye. If this scanning is uncontrolled, it is conceivable that a functional field actually limited to the monocular segment could be estimated as a full hemifield. Although blank trials were used in the other studies (van Hof-van Duin, '77; Heitländer and Hoffmann, '78), neither study mentioned this spontaneous scanning that seemed so obvious to us.

The most common method of testing em-

ployed by van Hof-van Duin ('77) was considerably different from ours in many important details. First of all, a stationary instead of a moving novel stimulus was used. This 1° to 2°-stimulus was randomly placed in any one of six positions within the field while the cat's eyes were covered by an investigator, and when the eyes were exposed, the cat was then expected to locate this target. Our animals, which had no special training that may have been employed by van Hof-van Duin ('77), were unable to locate such stationary targets. That scanning must have occurred in the van Hof-van Duin testing paradigm is seen in the fact that responses are reported out to 120° ipsilateral to the open eye. This position is well beyond the extent of the retina. From optical considerations of the cat's eye, Hughes ('76) calculates 94° as the extreme theoretical limit of the temporal visual field, and this is in close agreement with our behavioral estimates (cf. Sprague and Meikle, '65; Sherman, '73, '74a,b, '77a). As stated above, uncontrolled eye movements which cause an estimate of the temporal border of the field to be 30° too far could well cause an equally large error in the estimate of the nasal border.

Van Hof-van Duin ('77) has repeated the field testing in seven monocularly deprived cats with methods much closer to ours. Heitländer and Hoffmann ('78) also employed methods very similar to ours. With these methods, the deprived eye's field still occupied a full hemifield, but the monocular segment seemed generally more responsive than did the binocular segment. More recently, Hoffmann et al. ('78) have emphasized the greater visual responsiveness to targets in the deprived monocular segment compared to the deprived binocular segment. Many uncontrolled, subtle differences in stimuli or training paradigms could cause targets in the deprived binocular segment to be subthreshold for evoking a visual response (such as in our cats) or suprathreshold (i.e., Hoffmann et al., '78).

⁴ It is possible, if unlikely, that the poor form discriminations shown by a monocularly deprived cat via its deprived eye can be explained by relatively normal performance for the monocular segment and practical blindness in the binocular segment. Unfortunately, none of the form discrimination experiments were designed to control or assess precisely the retinal region used to analyze the discriminanda. Nonetheless, informal comments in some reports (cf. van Hof-van Duin, '76) suggest that for most cats, the deprived eye is directed straight ahead during discrimination performance, and thus, the binocular segment is used. Some studies (Rizzolatti and Tradardi, '71; van Hof-van Duin, '76), on the other hand, report that some of these cats employ large head and/or eye movements during deprived eye testing, and these movements could be used to bring the discriminanda onto the monocular segment.

Different cats. Cats used in these studies could differ either due to genetic factors or subtle differences in rearing procedures. The possibility of genetic differences may be not so far fetched, given the differences in central visual pathways reported between "Boston" and "Midwestern" Siamese cats (Kaas and Guillery, '73; Shatz, '77).⁵ It seems plausible that, if deprived retinotectal pathways can be used behaviorally, good orienting by the cat with its deprived eye would be elicited by targets throughout the eye's ipsilateral hemifield (Sherman, '74c; see also below). It is interesting in this context that Berman and Sterling ('76), on the basis of electrophysiological criteria, found three of nine monocularly deprived cats in which the retinotectal pathways from the deprived eye seemed to influence superior collicular neurons fairly normally. Perhaps such cats were unavailable to us but common to the pool used by European workers (van Hof-van Duin, '77; Heitländer and Hoffmann, '78; Hoffmann et al., '78). It should also be noted that the postdeprivation treatment of their cats, unlike ours, typically involved suturing or even removal of the non-deprived eye, often in conjunction with an enriched visual environment for the deprived eye. This, too, could have favored expression of deprived pathways in their cats but not in ours.

Perhaps related to this are the recurring and disturbing observations which suggest that some monocularly deprived cats exhibit roughly equal deficits in deprived geniculate laminae A and A1, while other cats display much more pronounced deficits for deprived lamina A1 than for A. Most anatomical (Wiesel and Hubel, '63a; Guillery and Stelzner, '70) and physiological (Sherman et al., '72; Lehmkuhle et al., '78) studies have emphasized the former pattern, but the physiological studies of Sireteanu and Hoffmann ('79) point to the latter. Their cats, with minimal deficits for deprived lamina A, and thus the deprived nasal retina, might indeed be expected to demonstrate appreciable visual behavior for targets falling within that entire retinal portion. Recent anatomical studies (T. L. Hickey, personal communication) tend to support this possibility: most monocularly deprived cats had abnormally small cells distributed equally in deprived laminae A and A1, but 10-20% of the cats displayed abnormally small cells only in deprived lamina A1.

The data are insufficient to establish such

different developmental responses to monocular deprivation among cats (i.e., retinotectal and/or geniculate development), but the possibility exists and could well explain some of the discrepancies in the literature. In any case, the type of cat commonly studied by us seems to be one for which monocular deprivation creates roughly equal anomalies in laminae A and A1 and little expression of the retinotectal pathway from the deprived eye.

Postoperative behavior and electrophysiological correlates

Whether or not the deprived eye's responsiveness to targets in the binocular segment is dependent upon behavioral methodology, the environmental or genetic history of the cats, or other factors, it seems clear from the present study that, given our animals and behavioral techniques, a dramatic increase in the extent of functional visual field for the deprived eye was consistently achieved following visual cortex lesions. Large occipitotemporal cortical ablations, which removed all known areas of cortex activated by visual stimuli, produce this effect. The questions as to which cortical area(s) or what is the minimum cortical volume that must be ablated to achieve this visual field expansion remain open. Our smallest lesion, essentially limited to areas 17 and 18 contralateral to the deprived eye, was sufficient to increase the deprived eye's field, and this suggests a partial answer to these questions.

The most parsimonious (but not only) explanation for the expansion of visual field after cortical ablations is that it represents the behavioral counterpart to the electrophysiological data of Wickelgren and Sterling ('69b; also Hoffmann and Sherman, '74). In studies of superior collicular neurons in monocularly deprived cats, these authors reported that most cells could be activated only by stimulation of the nondeprived eye, much like the pattern seen in striate cortex (Wiesel and Hubel, '63b). However, within an hour after large lesions of visual cortex in these cats, neurons in each colliculus are equally dominated by its contralateral eye (whether deprived or non-deprived), and this is the pattern seen in

⁵ There is no reason to believe that these suggested genetic differences between types of Siamese cats in any way relates to the variable results in studies of lid sutured, common cats. Rather, we wish to suggest only that significant neural differences of presumably genetic origin can exist among animals. This has been appreciated for many years, and for an older example outside the visual system, Edinger and Wallenberg ('02) observed differences among rabbits in the structure of their fornices.

normally reared cats after cortical lesions (Wickelgren and Sterling, '69a; Rosenquist and Palmer, '71). In the colliculus contralateral to the deprived eye, this postoperative pattern represents an enormous increase of cells responsive to that eye. Our interpretation of these data is that normal retinotectal input from the deprived eye is somehow suppressed in the colliculus by activity in corticotectal pathways which, in turn, reflect the expected dominance for the nondeprived eye. Removal of these corticotectal pathways by cortical ablation permits expression of the retinotectal input. Finally, the smallest cortical lesions we employed (areas 17 and 18) would be expected to create the necessary ocular dominance shifts in superior colliculus, since such small lesions are effective in this regard in normal cats (Rosenquist and Palmer, '71).⁶

Regardless of the electrophysiological interpretation, these data suggest the neural basis for the behavioral phenomenon described in the present paper. It is known that in normally reared cats following visual cortex ablation, the retinotectal pathways can subserve the orienting behavior tested here (Sprague, '66b; Sherman, '74b, '77a). Therefore, if preoperatively, the collicular and cortical neurons in the binocular segment are less responsive than those in the monocular segment to visual stimulation of the deprived eye (Hoffmann and Sherman, '74; Wilson and Sherman, '77), it is not surprising that the animal using that eye orients poorly, if at all, to targets presented in the binocular segment. If, however, after visual cortical lesions, the collicular neurons contralateral to the deprived eye are dominated by that eye, the cat should be able to use those retinotectal pathways for orientation to targets falling anywhere on the deprived eye's nasal retina. This suggestion is supported by the observation that after the phenomenon was observed in cat RMD11V, a subsequent ablation of the left superior colliculus rendered the right, deprived eye blind on this orienting task (fig. 7C) for the remaining five months prior to sacrifice.

CONCLUSIONS

Given our cats and testing procedures, two conclusions seem clear. First, rearing with monocular suture produces certain visual deficits in cats which are more pronounced for the binocular than for the monocular segments of the deprived eye's visual field. This observation, as well as analogous observations

based on morphological and electrophysiological studies, is consistent with the hypothesis that some form of binocular competition controls visual development in these cats (Guillery and Stelzner, '70; Guillery, '72; Sherman et al., '72, '74, '75; Wilson and Sherman, '77). However, the differential effects of monocular deprivation, seen as better visual orienting to stimuli within a larger functional visual field while using the nondeprived eye than while using the deprived eye, are diminished after visual cortical lesions. This is consistent with the hypothesis that deprivation deficits develop primarily within the cortical pathways, and that deficits seen in the superior colliculus are secondary manifestations of an abnormal corticotectal input. With smaller lesions (areas 17 and 18 or 17, 18, and 19), the difference in orienting capacity between the nondeprived and deprived eyes is diminished but not abolished. After removal of all known visual cortical areas (and thus the total primary site of the deprivation deficits), no discernible asymmetry remains between the visual fields and capabilities of the two eyes.

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⁶One possible criticism of this physiological explanation of the visual field enlargement is that the neurological changes are found within an hour after the cortical lesion. The behavioral responses, however, cannot be reliably tested until all effects of anesthesia, edema, and shock from the cortical insult have dissipated. Thus, we waited at least two postoperative weeks until testing was resumed. Nonetheless, in most cases, clear evidence of visual field expansion was seen during the first postoperative test sessions.

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