

The Effect of Superior Colliculus Lesions upon the Visual Fields of Cats with Cortical Ablations

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ABSTRACT The visual fields of 18 cats were measured before and after various lesions. Preoperatively, all cats had identical fields. With both eyes open, they saw from 90° left to 90° right; with one eye, from 90° ipsilateral to 45° contralateral. Thus the field for nasal retina extends from 90° ipsilateral through to the midline; for temporal retina, from the midline through to 45° contralateral.

In summary, postoperative testing led to two major conclusions. (1) Large occipito-temporal cortical lesions produce a stable field blindness, but the blindness is alleviated by a transection of the commissure of the superior colliculus (or a unilateral collicular ablation). This transection yields the same result whether it occurs in an operation before, during, or after the cortical lesion. These data confirm and extend the Sprague effect. (2) Cats made dependent upon retinotectal pathways due to cortical ablations responded much better to stimulation of nasal retina than to stimulation of temporal retina. This presumably is related to the preponderance of nasal retina as a source of the retinotectal pathway. Since even smaller cortical lesions limited to areas 17, 18, and 19 produce this nasal/temporal retinal difference, it is concluded that integrity of the geniculocortical pathways is necessary for good temporal retinal vision as determined by these methods.

In a remarkable series of studies, Sprague and Meikle ('65) and Sprague ('66a) demonstrated that much of the cat's visually guided behavior is subserved by interactions involving midbrain and cortical pathways. Sprague ('66b) then reported that the hemianopia that is produced contralateral to a large, posterior cortical lesion could be at least partially alleviated either by an ablation of the superior colliculus contralateral to the cortical lesion or by a transection of the commissure of the superior colliculus.

The neural basis of this dramatic phenomenon remains unresolved, but Sprague's ('66b) suggestion follows. Each colliculus normally may receive a balanced set of inputs, including a form of functional facilitation from the ipsilateral cortex and suppression from the other colliculus via the commissure. Destruction of cortex leads to an imbalance due to surplus suppression playing on the ipsilateral collicu-

lus, and this interferes with its potential functioning. This functioning can be at least partially restored by destroying either the source of excess suppression (i.e., the contralateral colliculus) or its pathway (i.e., the collicular commissure).

Despite the profound significance of this study by Sprague ('66b), it has, to my knowledge, neither been confirmed nor reported in detail. The purpose of the present study was to confirm the Sprague effect and extend our knowledge of it. This was found to be a robust and repeatable phenomenon in cats, and details are added in this paper. A brief preliminary report of these results was recently published (Sherman, '74b).

MATERIALS AND METHODS

Subjects and surgical procedures

Eighteen cats, purchased as normal adults, were studied. They were housed in individual cages with a 12-hour light/dark

cycle for the duration of this experiment. Most of these cats were also studied for visual discriminations of patterned stimuli, but these data will be presented separately (Loop and Sherman, '77, submitted).

Each cat underwent one or a series of brain lesions consisting of cortical ablation, midsagittal transection of the commissure of the superior colliculus, collicular ablation, and/or midsagittal transection of the optic chiasm. The cats were anesthetized with barbiturate, and routine aseptic precautions were taken. All surgery was performed under visual control aided by an operating microscope with co-axial illumination.

Cortical lesions were created by gentle subpial suction. The smaller ablations were bilateral and were designed to remove the lateral gyrus dorsally and all cortex medially above the splenial sulcus; thus all of areas 17 and 18 plus most of area 19 was ablated. The larger ablations were also bilateral (with the exception of the left cortical lesion in cat C5) and were designed to remove nearly all of the occipito-temporal cortex. Thus all known cortical projection areas of the "visual" thalamus (including the lateral geniculate nucleus plus the inferior, medial and lateral divisions of the pulvinar nucleus¹) were ablated (see Sprague et al., '73, for a review of these pathways; also Kawamura, '74; Niimi et al., '74).

The collicular commissure was transected by inserting a fine knife between the colliculi to a depth of approximately 2 mm, and the collicular ablation in cat C5 was achieved by gentle subpial suction. The tectum was commonly approached by first removing the bony tentorium and retracting the *dura mater* between the cortex and cerebellum. For some of the commissure sections, the tectum was approached through a small gap placed in the back of the corpus callosum (only after extensive, bilateral occipito-temporal cortex removal), the knife being guided under the tentorium. Except for the first few tectal operations, intravenous mannitol (50 ml; 30%) was routinely administered proper-

ately to achieve shrinkage of the hemispheres. This greatly facilitated exposure of the tectum.

Cat C4 had its optic chiasm midsagittally sectioned by gentle suction, the approach being through the roof of the mouth.

Every cat was tested before and after each surgical procedure. A two to four week postoperative recovery period was allowed before testing, and testing continued for at least three to four months postoperatively in order to assess final, stable performance. Table 1 summarizes the surgical procedures for each cat.

Behavioral testing

These cats were tested with techniques which have been previously described in detail (Sherman, '73, '74a), and these methods will be briefly outlined. Each cat was food-deprived and tested on a table marked off into sixteen 15° sectors by intersecting guidelines designated 120°L, 105°L, . . . , etc. . . . , 0°, 15°R, . . . etc. . . . , 120°R (cf. fig. 1). The cat was restrained so that its lateral canthi were aligned with the 90° guidelines and its nose pointed along 0°. It was pretrained to fixate to visual and/or auditory cues provided by a piece of dry cat food held in forceps and tapped on the table at 0° and approximately 50 cm in front of the cat's nose; this was the *fixation object*. While the cat was thus fixating, a *novel stimulus* (food in forceps or a 1 cm diameter red cardboard circle at the end of a long, stiff wire) was presented vertically 20-40 cm from the cat's nose along one of the guidelines. The cat was then immediately released from restraint and its behavior noted. A clear and immediate orienting response to the novel stimulus was scored as a positive trial, and any other behavior, as negative. Negative trials nearly always (>95%) consisted of ignoring the novel stimulus and moving towards the fixation object. The cat was fed a small

¹ To facilitate comparisons with primates, I have chosen the terminology of Niimi et al. ('74) for these thalamic nuclei in cats. The correspondence to older nomenclature is: inferior pulvinar represents the nucleus posterior of Rioch, the medial pulvinar represents the lateral posterior nucleus of Rioch, and the lateral pulvinar represents the pulvinar of Rioch.

TABLE 1

Cat	Surgery
C5	1. Remove left occipito-temporal cortex. 2. After 7 months, remove right superior colliculus. Sacrifice after 7 additional months.
C22	1. Remove occipito-temporal cortex bilaterally. Sacrifice after 12 months.
C6, C14, C15	1. Remove occipito-temporal cortex bilaterally. 2. After 8 to 9 months, split collicular commissure. Sacrifice after 6 to 12 months.
C3, C7, C13, C17, C18, C19, C20, C21, C23	1. Remove occipito-temporal cortex bilaterally and split the collicular commissure. Sacrifice after 6 to 16 months.
C8	1. Split the collicular commissure. 2. After 7 months, remove occipito-temporal cortex bilaterally. Sacrifice after 5 additional months.
C4	1. Split the optic chiasm. 2. After 3 months, remove occipito-temporal cortex bilaterally and split the collicular commissure. Sacrifice after 15 additional months.
C10, C11	1. Remove areas 17, 18 and most of 19 bilaterally. Sacrifice after 3 months.

piece of food regardless of its response. Because novel stimuli at 0° elicited no turning responses, trials for the 0° guideline were scored differently as follows: on positive trials the cat stopped short of the novel stimulus to explore it; on negative trials, the cat ignored the novel stimulus until tactile contact was made and a distinct startle response resulted; the few (<10%) of these responses which could not be clearly classified were scored separately and are not considered further.

The cats were tested with both eyes open or with one eye occluded by means of an opaque, contact occluder covering the cornea. Every 15° guideline was tested in this fashion at least 50 to 100 times for binocular, right monocular, and left monocular viewing. The assistant holding the fixation object determined that no detectable (i.e., >15°; Sherman, '73) eye movements occurred except during orientations to the novel stimulus.

As a control, the proportion of orientations for each 15° guideline was compared to a baseline of spontaneous orientations that obtained without a novel stimulus. These have been termed "blank" trials (Sherman, '74a), and at least 100 were run at random throughout each viewing condition (i.e., binocular and monocular). Unless

otherwise indicated in RESULTS, the final response levels for each guideline and for each viewing condition have been normalized against these spontaneous response levels during blank trials (Sherman, '74a). That is, if the spontaneous response level during blank trials for a particular viewing condition is B%, and the raw positive score for a particular guideline is G%, then the "normalized" score for positive orientations becomes $(G-B)/(100-B)\%$ if $G > B$, and is zero if $B \geq G$. These spontaneous orientations during blank trials occurred never more than 20%, and usually between 5% and 10%; they are considered more fully in RESULTS. For the general assumptions underlying this test, see Sherman ('73).

Histology

Histological controls were obtained for each cat at the completion of the final training procedures. The cats were anesthetized and perfused intracardially with saline followed by 10% formol saline. The brains were blocked stereotaxically, allowed to harden in 10% formol saline for seven days, removed, photographed, embedded in egg yolk, and cut frozen in the coronal plane at 40 μ m. These sections were alternately stained with cresylecht

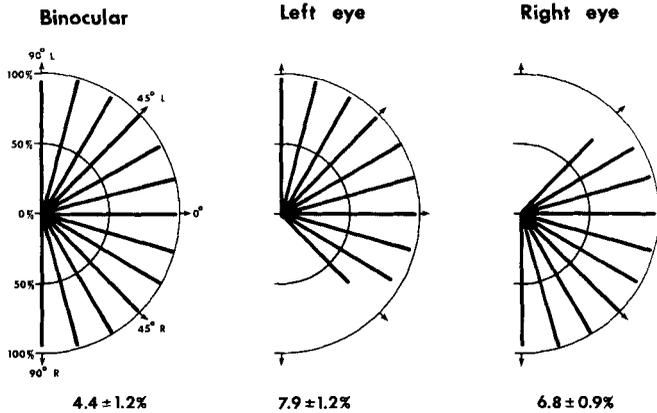


Fig. 1 Typical visual fields for normal cats. The plots in polar coordinates represent the normalized response levels for each 15° sector of visual field, and the two semicircles represent the 50% and 100% response levels. For each sector, each response level represents an average of the separate values computed for the 18 cats preoperatively. Computed in this manner, the standard errors for the 45° sector contralateral to the open eye during monocular viewing are 2-3%, and for all other sectors during monocular and binocular viewing, the standard errors are less than 1.5%. The numbers below each plot represent the level of spontaneous orienting (mean \pm standard error). Spontaneous levels were computed in the same way as were the response levels shown in the plots. The sectors of visual field beyond 90° were also routinely tested, but stimuli placed there elicited responses so rarely that they have been omitted from this and succeeding figures.

violet and the Mahon method for myelinated fibers. In addition to direct reconstruction of lesions, the total retrograde degeneration throughout laminae A and A1 of the lateral geniculate nucleus indicated that in all cases areas 17 and 18 were completely removed (see also legend for fig. 2).

RESULTS

Visual fields of normal cats

The binocular and monocular visual fields were assessed for each of the 18 cats before any surgery, and an impressive interanimal consistency obtained. Figure 1 illustrates the pooled data from these cats. The response level for each 15° sector represents the average of the 18 separate response levels. Each cat responded to stimuli from 90° right to 90° left with both eyes and from 90° ipsilateral to 45° contralateral with one eye (fig. 1). Even the response levels within the functional visual fields indicate little variability among the cats. If the percent response for each 15° sector is considered an average based on 18 data points (one for each cat), then the standard errors for each response level are 2-3% for

the 45° sector contralateral to the open eye during monocular viewing, and less than 1.5% for all other sectors during monocular or binocular viewing. The extent of these fields is consistent with conclusions based on optical considerations of the cat's eye (Hughes, '76). Finally, with monocular viewing, these cats could continuously follow horizontally moving objects in either lateral direction across the midline, presumably because the monocular visual fields extend to both sides of the fixation point.

Histological controls

The brain photographs plus serial reconstructions of the histological sections provided a detailed analysis for each lesion.

Occipito-temporal cortical lesions

Sixteen of the cats underwent large occipito-temporal cortical lesions (table 1). In every case, all of the cortex on the medial surface above the splenial sulcus was ablated with variable damage to the cingulate gyrus; on the dorsal surface, all of the posterior two-thirds of the lateral, suprasylvian and most of the ectosylvian gyri

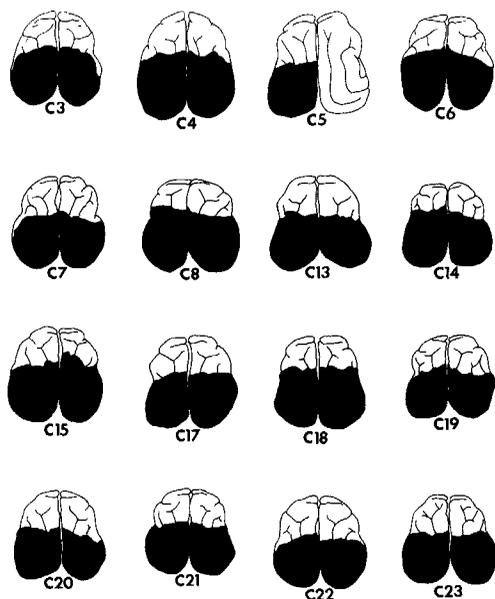


Fig. 2. Summary of occipito-temporal cortex ablations as seen in dorsal view. There was relatively little variability in lesion size. An attempt was made to assess retrograde degeneration in the thalamus, but the bilateral lesions in all cases except cat C5 made this difficult since a control side was unavailable for comparison. However, the laminated portion of the lateral geniculate nucleus was clearly degenerated throughout in all cases, and no surviving patches of larger cells were detected in the lateral geniculate or pulvinar nuclei. Therefore, it appears that all cortex receiving from "visual" thalamus (see text) was ablated. In cat C5, all of the lateral geniculate plus the lateral, medial, and inferior divisions of pulvinar nuclei appeared degenerated on the lesioned side. In figure 3, the lesions for cats C5 and C18 are reconstructed in more detail.

were ablated. Figure 2 provides a superficial reconstruction of these lesions from a dorsal view, and figure 3 provides a more detailed reconstruction of two typical occipito-temporal lesions (C5 and C18). Therefore, in every case, essentially all of the cortical recipient zones for the lateral geniculate nucleus plus the inferior, medial and lateral portions of the pulvinar nucleus were destroyed (Sprague et al., '73; Niimi et al., '74).

Lesions of areas 17, 18, and 19

In cats C10 and C11, bilateral cortical lesions were limited to areas 17, 18, and 19. These are reconstructed in figure 4. In both

cases, most of the cortical recipient zone for the lateral geniculate nucleus was destroyed; only the relatively sparse projection of the medial interlaminar nuclear subdivision to the suprasylvian gyrus was left intact (Rosenquist et al., '74). On the other hand, most of the cortical zones which are recipients of the retino-tecto-thalamic relay were spared (Sprague et al., '73; Kawamura, '74; Niimi et al., '74).

Transections of the commissure of the superior colliculus

Collicular commissure splits were done in 15 of the cats, and they were assessed chiefly by the myelin stained sections. In every case all of the crossing fibers were cut with the exception of very few at the anterior and posterior limits of the commissure. Little detectable damage was done to the collicular gray matter, and the cuts extended down or near to the cerebral aqueduct. Figure 5 shows a reconstruction of four typical commissure splits plus tracings of an unoperated midbrain for comparison.

Other lesions

The ablation of the right superior colliculus in C5 is reconstructed in figure 6. Nearly all of the right colliculus was ablated and minimal damage was evident in either the tegmentum or the left colliculus. The optic chiasm section in C4 was complete as judged both by gross observation of the unsectioned brain and also from myelin stained sections.

Postoperative visual fields

Postoperative testing of the cats with various lesions led to the following general conclusions: (1) As Sprague ('66b) observed, decorticate cats are capable of visual orienting providing appropriate tectal manipulations are performed. (2) The decorticate cats, presumably using retinotectal pathways, orient to stimulation of nasal retina more briskly than to stimulation of temporal retina. These results are described below for cats grouped according to the types of lesions they suffered.

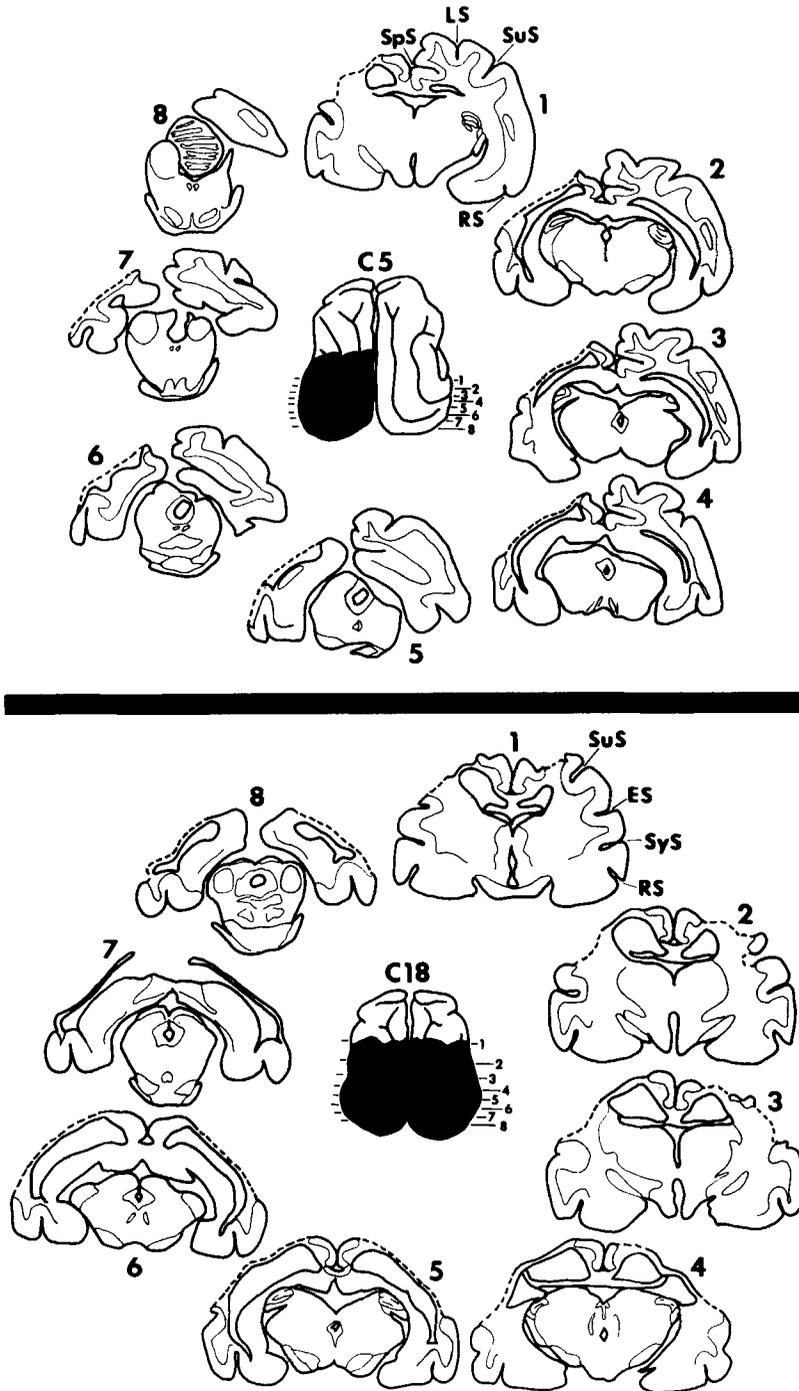


Fig. 3 Reconstruction of cortical ablations in cats C5 (upper) and C18 (lower). These were chosen as representative lesions for the series of figure 2. The cortical ablations for cats C3 and C7 are reconstructed in Sherman ('74a). Abbreviations: ES, ectosylvian sulcus; LS, lateral sulcus; RS, rhinal sulcus; SpS, splenic sulcus; SuS, suprasylvian sulcus; SyS, sylvian sulcus.

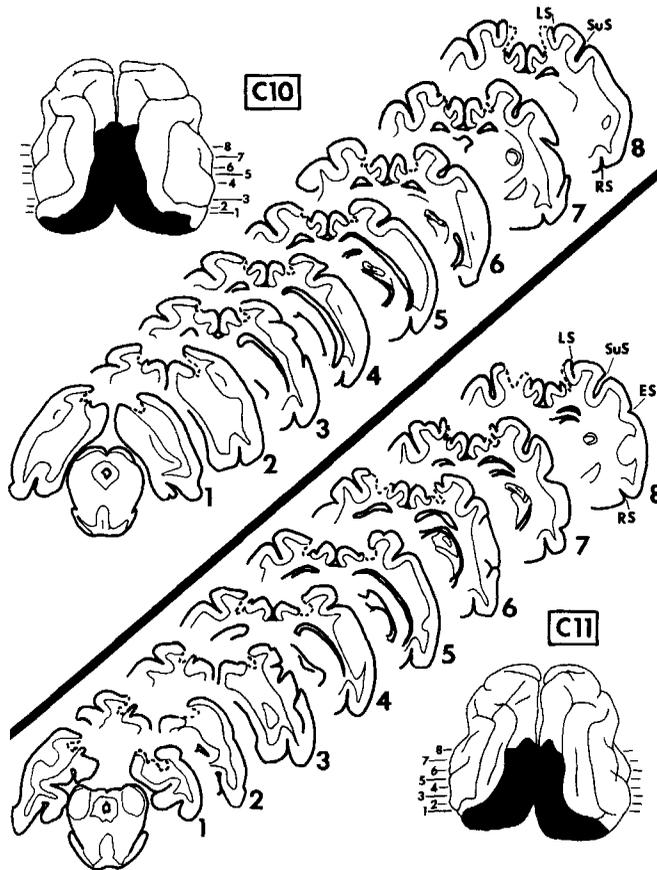


Fig. 4 Reconstruction of cortical ablations in cats C10 (upper) and C11 (lower). In both cats, neurons throughout laminae A and A1 of the lateral geniculate nuclei showed retrograde degeneration. This was clear even throughout the caudal tail of the nucleus as it extends dorsally. This suggests that some surviving gray matter in caudal striate cortex evident in both brains (see the sections numbered 1) was undercut, a conclusion also supported by the fiber-stained sections. Abbreviations as in figure 3.

Cat C5

As figure 7 shows, data from cat C5 confirm and somewhat extend Sprague's ('66b) findings. The left occipito-temporal cortical ablation resulted in a right hemianopia that persisted stably for seven months (fig. 7B). The cat simply ignored all stimuli to the right of the fixation object.

Following the 7-month period, the cat's right superior colliculus was ablated (fig. 6). During the weeks postoperative to the collicular lesion, the cat tended to circle noticeably to the right (Sprague and Meikle, '65; Sprague, '66b) which made visual field testing extremely difficult. After two to

three months, this circling tendency nearly disappeared, and figure 7C shows the fields after this time. Visual orientation was dramatically restored for stimuli throughout the right hemifield, although responses to the right were noticeably less brisk and accurate than those to the left (cf. Sprague, '66b). Presumably, the right hemifield was now dependent upon retinotectal pathways; the left, upon cortical pathways.

Figure 7C also demonstrates an interocular asymmetry in the visual fields. The right eye had a full field of view, but the left saw clearly only in its ipsilateral hemifield. That is, the collicular lesion restored vision

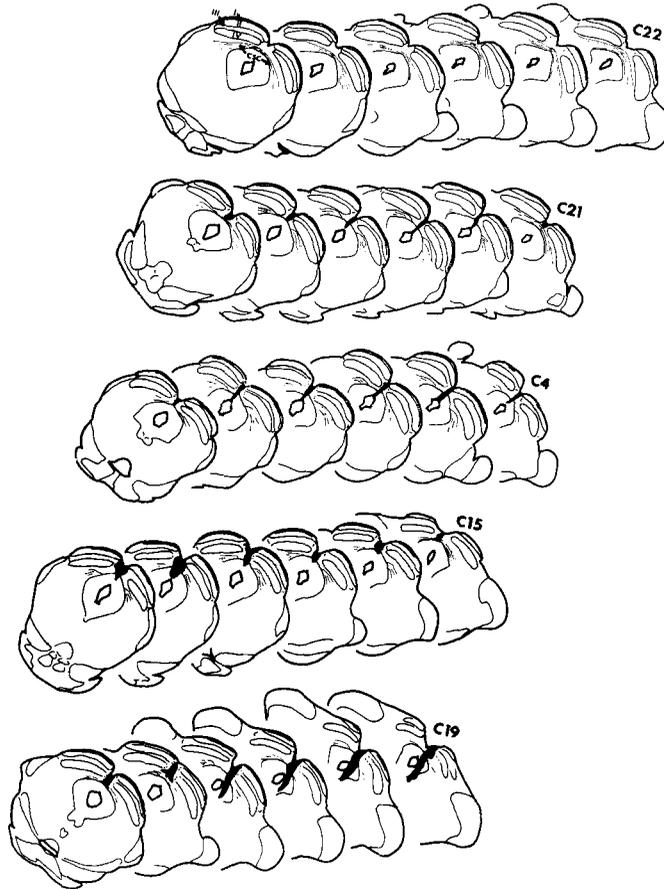


Fig. 5 Reconstruction of collicular commissure transections for cats C4, C15, C19, and C21. The knife cut and lesioned area is in black. These are representative of the transections not illustrated for the other cats receiving such surgery (table 1). For each cat, drawings are from evenly spaced sections moving from posterior at the bottom left to anterior at the top right. Collicular commissure transections for C3 and C7 are reconstructed in Sherman ('74a). Drawings through the midbrain are shown at the top for C22 to illustrate the unsectioned collicular commissure. CSC indicates the commissure of the superior colliculus, and the collicular layers are shown as I, II, III, and IV according to Kanaseki and Sprague ('74). The relationship to older terminology is: I, stratum zonale; II, stratum griseum superficiale; III, stratum opticum; IV, stratum griseum intermediale.

for the right nasal retina much more dramatically than for the left temporal retina. In fact, there was no evidence that with the left eye the cat could orient to stimuli falling upon temporal retina, but there may have been some vision there for the following reason. With left-monocular viewing, C5 had a much higher spontaneous response level (MATERIALS AND METHODS and fig. 7C). However, this higher level obtained nearly exclusively because of spontaneous orientations towards the *right* as if the cat

were scanning the amblyopic field, although this could also represent the circling due to the collicular ablation. This high spontaneous level obscured orientations evoked by stimuli presented from 0° to 45° right, and thus a genuine but low response level might be obscured by the spontaneous orientations (fig. 7D). This point is elaborated again in the next section.

This asymmetry between monocular visual fields in C5 was seen in another way.

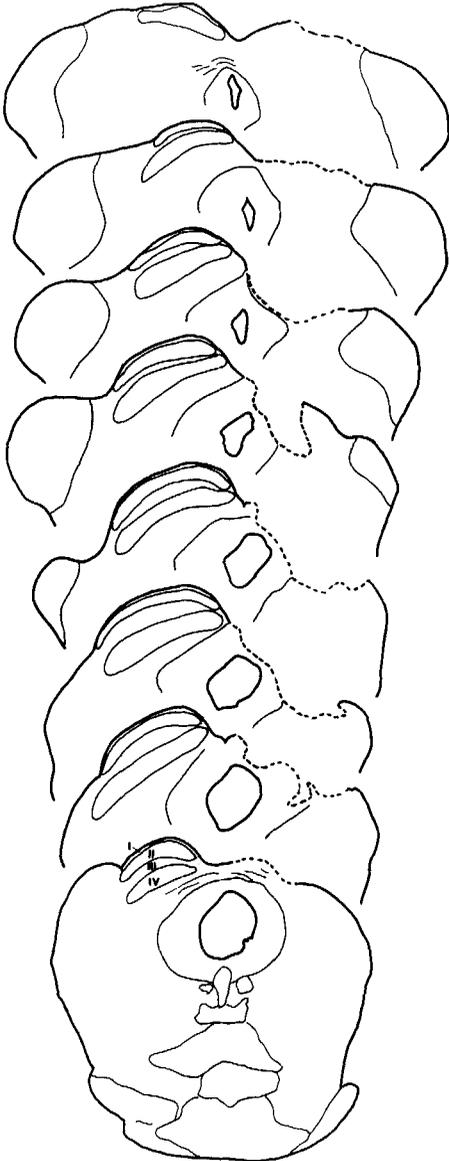


Fig. 6 Reconstruction of ablation of right superior colliculus in cat C5. Conventions and abbreviations are the same as in figure 5.

During right-monocular viewing, C5 would follow objects circling in either direction around it in an apparently normal fashion (i.e., much like normal cats; see above). However, with left-monocular viewing, the cat would continue tracking only objects circling to the left; for a rightward moving stimulus, C5 soon lost it, apparently when

the stimulus fell onto the temporal retina. Note that this asymmetry cannot be explained by residual circling caused by the collicular lesion, since such circling was directed to the right.

Cats C6, C14, C15, C22

The first operation in each of these cats was a large bilateral occipito-temporal cortex ablation. All four cats reacted in an identical fashion: they appeared blind on the visual field test, although C14, C15, and C22 were able to learn a brightness discrimination (Loop and Sherman, '77, submitted).² C22 appeared blind on the visual field test for the remaining 12 months, at which time it was sacrificed. C6, C14, and C15 showed no signs of orienting responses throughout the 8 to 9-month period between operations (fig. 8B). At this point, the collicular commissure was split during a second operation in these three cats, and within the first four postoperative weeks each of these cats showed dramatic recovery of orienting responses. Figure 8C shows this for C15, and virtually identical results obtained in C6 and C14. The responses, while clearly evident, were sluggish and relatively poorly directed; they in all ways resembled the final responses of C5 to stimuli in its right hemifield after its collicular ablation. With monocular viewing, figure 8C shows that C15 clearly oriented only to stimuli in the ipsilateral hemifield (i.e., to stimuli falling on the nasal retina), but again responses to stimuli in the contralateral 45° of visual field could have been obscured by the relatively high rate of spontaneous orientation towards the amblyopic, contralateral hemifield (fig. 8D). As was seen for C5, most (>90%) of the spontaneous responses were in this direction, but this cannot be explained by an overall tendency for the cat to orient spontaneously left or right: with the right eye these spontaneous turnings were to the left; with the left eye, to the right. C6 and

² It is emphasized that cats which fail to demonstrate visual orientations on this visual field task may well demonstrate visually guided behavior, such as brightness discrimination, on other tasks with different visuo-motor requirements.

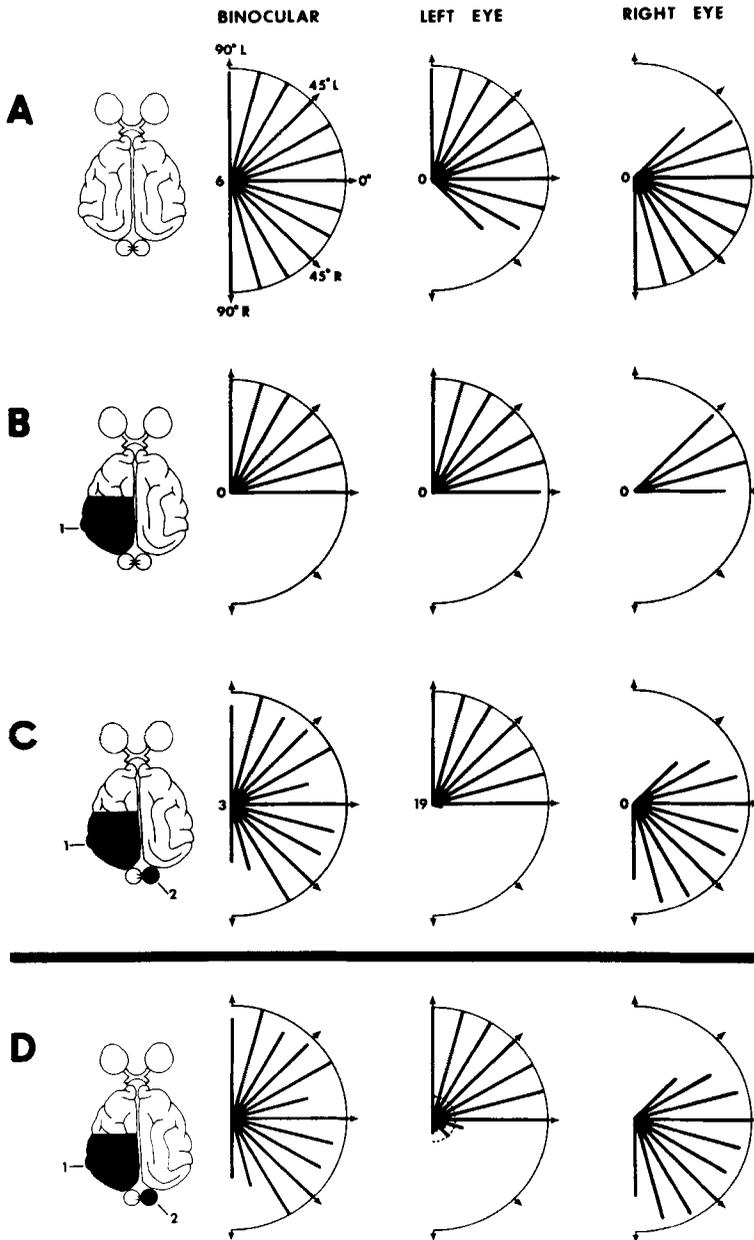


Fig. 7 Visual fields for cat C5. The conventions for the polar plots are the same as in figure 1. A, B, C represent normalized scoring (MATERIALS AND METHODS) and the number next to each origin indicates the percent level of spontaneous orientation. A. Preoperative fields. B. Fields following the left cortical ablation. C5 now had a stable, right hemianopia. C. Fields following the right collicular ablation. Orienting to the right hemifield returned, but not for left monocular viewing. D. Same fields as in C, but without normalized scoring. The dashed semicircle for the left eye field indicates the level of spontaneous orientations, nearly all of which were directed to the right (see text). The spontaneous level was too low (3%) to be indicated in binocular viewing, and with the right eye, there were no spontaneous orientations.

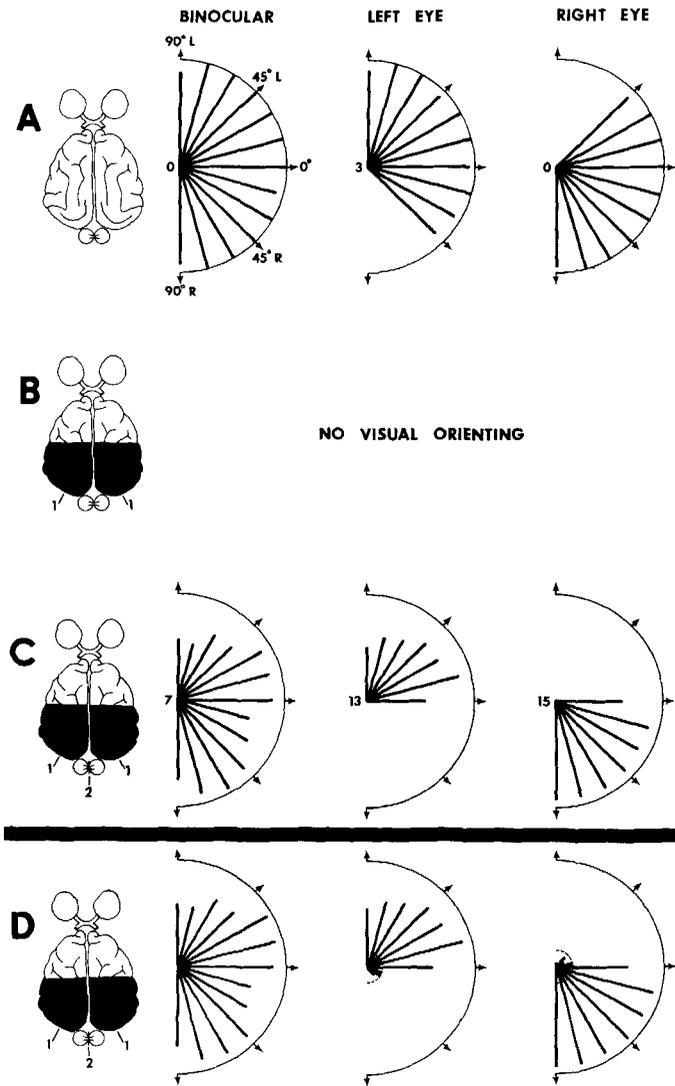


Fig. 8 Visual fields for cat C15. Conventions as in figure 7. A, B, C, are normalized scoring; D is not. A. Preoperative fields. B. After the bilateral cortical ablation, the animal failed to orient to visual stimuli. C. Fields after the subsequent collicular commissure transection. Visual orienting returned, but mainly or only to stimulation of nasal retina. D. Same fields as in C, but without normalized scoring.

C14 showed the same pattern. Also, all three cats with monocular viewing continuously followed objects moving only in the ipsiversive direction (i.e., moving in a temporal direction in the hemifield), but lost them if they moved across the midline in the other direction. As in cat C5, moving targets could not be consistently tracked into the amblyopic hemifield despite the

spontaneous turning in that direction. The monocular visual fields for C6, C14, and C15 were consequently in all ways like the left-monocular field for C5.

Cats C3, C7, C13, C18, C19, C20, C21, C23

Each of these cats had a one stage operation in which a large bilateral occipito-

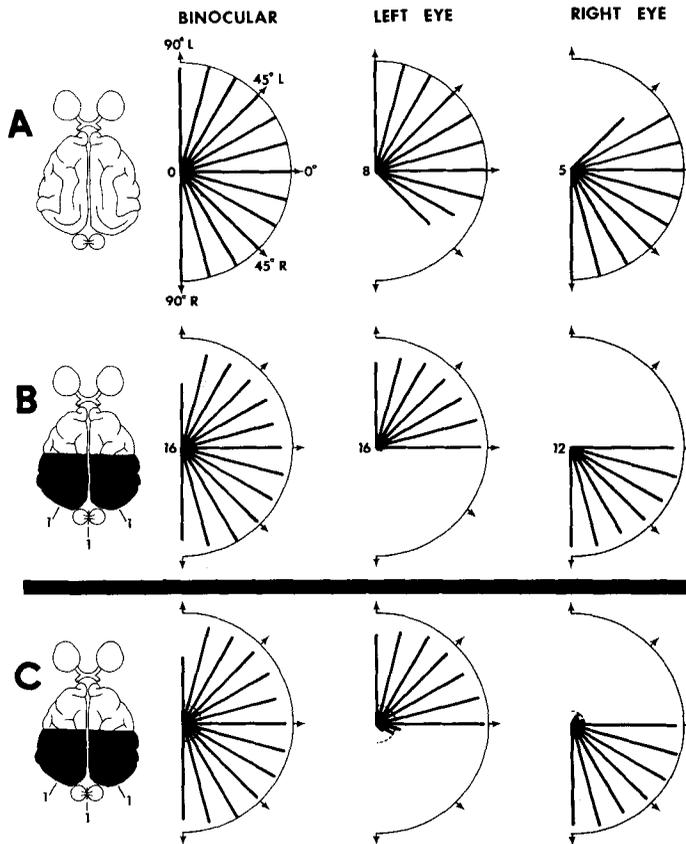


Fig. 9 Visual fields for cat C13. Conventions as in figure 7. A, B are normalized scoring; C is not. A. Preoperative fields. B. Fields after the bilateral cortex ablation plus a transection of the collicular commissure. Orienting was limited mainly or only to stimulation of nasal retina. C. Same fields as in B, but without normalized scoring.

temporal cortex ablation and a split of the commissure of the superior colliculus were made. All of these cats reacted identically, and figure 9 illustrates the typical and representative results from C13. Within three to eight weeks postoperatively, these cats showed behavior which was indistinguishable from the performance of C14, C15, and C22 after their collicular commissure transection (fig. 9B). Even the pattern of postoperative spontaneous orientations with monocular viewing was the same (fig. 9C), as was the following of moving targets.

Cat C17

This cat had the same surgery as the previous group of eight cats (i.e., one stage

cortical ablation plus collicular commissure transection) but its postoperative behavior differed. For the entire 16-month postoperative period before sacrifice, C17 could not be tested for its visual fields because it would not consistently fixate forward. Overall, its postoperative visual ability seemed considerably poorer than that of the above eight cats. It did, however, occasionally demonstrate, with either eye, the ability to locate and even briefly follow objects moving in its presumptive field of view. In addition to its apparently poorer visual ability, this cat showed neurological signs not evident in any other cat: namely, it was hyperexcitable and had several *grand mal* seizures. On the basis of available histology, however, the cortical lesions

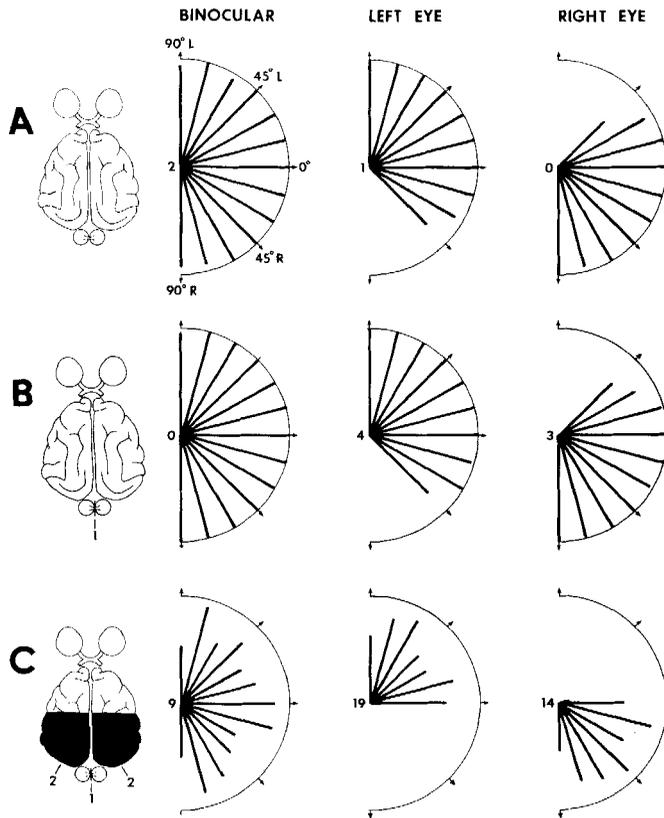


Fig. 10 Visual fields for cat C8; conventions as in figure 7 with normalized scoring throughout. A. Preoperative fields B. Fields following the mid-sagittal transection of the commissure of the superior colliculus. C. Fields after the subsequent bilateral cortical ablation.

were within the limits of the other occipito-temporal decorticate cats, and no obvious damage was seen in the midbrain other than the transection of the collicular commissure. The poor vision of this cat relative to the others with similar lesions could be due to two factors: (1) There may be considerable variability among cats in the potential to demonstrate the Sprague effect, but even if so, certainly the great preponderance of cats shows the effect. (2) A more likely explanation is that other neural tissue (i.e., cortical, midbrain, etc.) was damaged but such damage could not be ascertained with the available histological material.

Cat C8

Since a split of the collicular commissure after cortical lesions greatly enhanced

visually guided behavior, this lesion alone could affect visual fields in a cat. Thus cat C8 had only its collicular commissure transected during its first operation. Figure 10B shows that this surgery had no observable effect on the visual fields, nor did it affect any obvious aspect of the cat's behavior (including visual discrimination learning; Loop and Sherman, '77, submitted). During the second operation seven months later, occipito-temporal cortex was bilaterally removed. Figure 10C shows that the final fields were identical in every respect to those of other cats with such cortical and midbrain lesions, and thus the order of the lesions is not crucial.

Cat 4

From the above, it appears that cats dependent upon retinotectal pathways de-

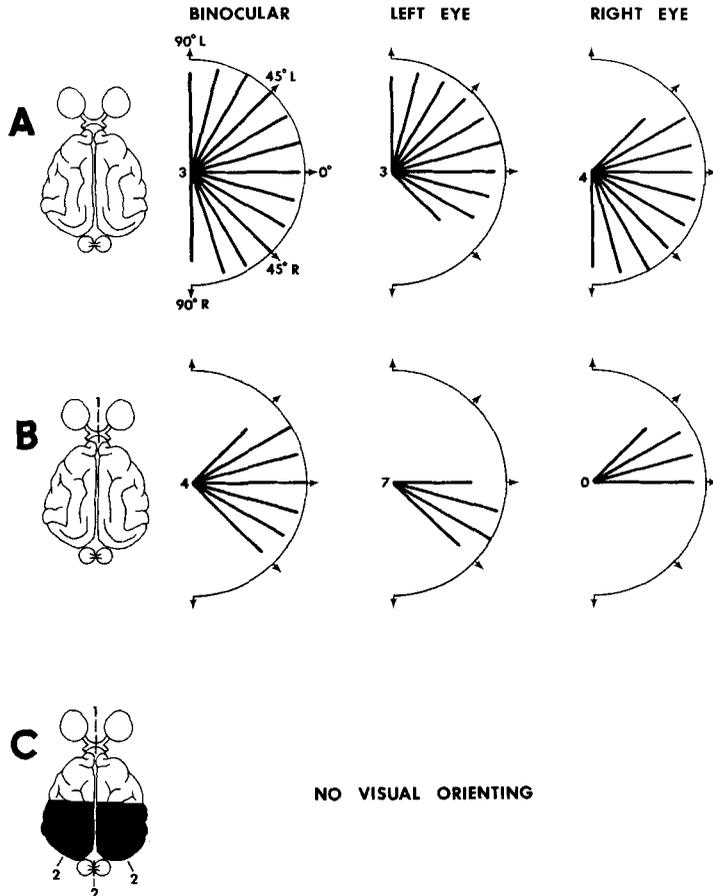


Fig. 11 Visual fields for cat C4. Conventions as in figure 7 with normalized scoring throughout. A. Preoperative fields. B. Fields following the mid-sagittal transection of the optic chiasm. The cat oriented only to stimulation of temporal retina. C. After the subsequent bilateral cortical ablation plus a transection of the collicular commissure, the cat failed to orient to any visual stimulus.

velop fairly good visual responses for stimuli falling upon the nasal retina and poor or no responses to stimulation of the temporal retina. Responses related to the temporal retina were further studied in C4 after first destroying nasal retinal connections by a mid-sagittal transection of the optic chiasm. This led to the classic bitemporal hemianopia illustrated in figure 11B. A second operation two months later removed occipito-temporal cortex bilaterally and split the collicular commissure. For the remaining 15-month postoperative period, C4 appeared blind on the behavioral tests applied in this study. It attended to the fixation object, presumably due to the

auditory cues, and would move toward it when unrestrained, but the cat consistently ignored all of the visual test stimuli. Stimuli placed in its path yielded a distinct startle response when the cat contacted them. Unlike the previously described cats with similar cortical and midbrain lesions, this cat showed very few spontaneous orientations (7%).

C10, C11

All of the above results suggest that a cat dependent upon retinotectal pathways responds much better to stimulation of nasal retina than to stimulation of temporal retina. Evidently the visual fields normally

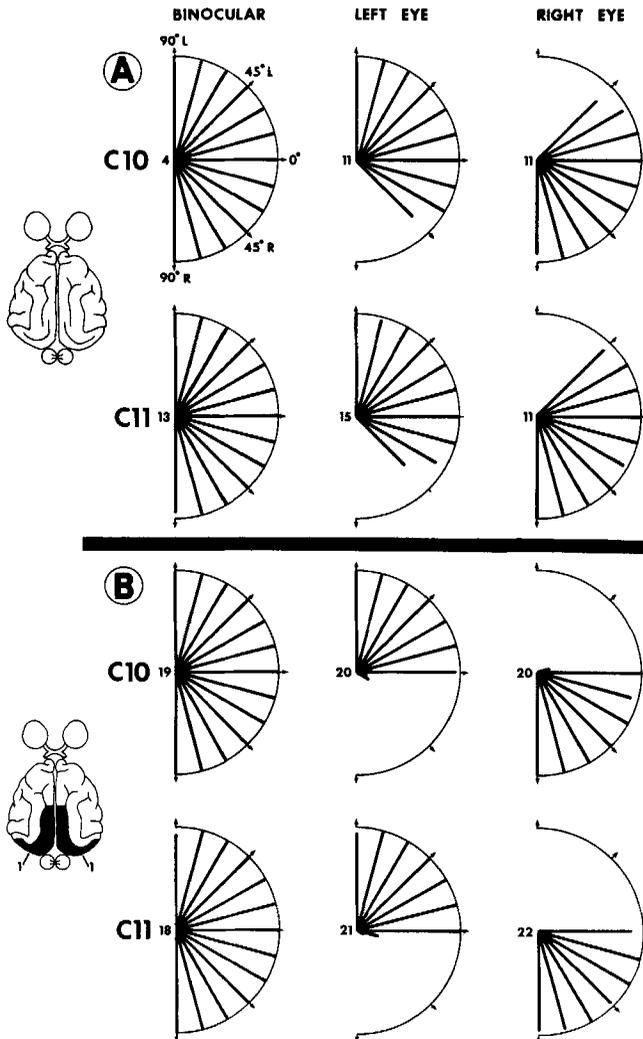


Fig. 12 Visual fields for cats C10 and C11; conventions as in figure 7 with normalized scoring throughout. A. Preoperative fields. B. Fields following the bilateral cortical lesion of areas 17, 18 and most of 19.

mapped for temporal retina depend upon retinofugal pathways other than retinotectal, and the most likely are the retinogeniculo-cortical. For C10 and C11, areas 17, 18 and most of 19 were removed bilaterally to disrupt this pathway. Thus the remaining visual cortex was mostly dependent on retinotectal pathways via the inferior, medial and lateral divisions of the pulvinar (Sprague et al., '73; Kawamura, '74; Niimi et al., '74). Figure 12B indicates that these cats postoperatively showed

clear visual fields for nasal retina and much reduced responsiveness to stimuli impinging upon temporal retina. Like the previously described cats, C10 and C11 during monocular viewing showed more spontaneous orientations into the amblyopic region. Unlike the cats with larger cortical lesions, C10 and C11 showed normally brisk and accurate responses to stimulation of nasal retina. With monocular viewing they could follow fast stimuli only if moved ipsiversively. They could, however, follow

very slowly moving targets ($<5^\circ/\text{sec}$) in the opposite direction.

DISCUSSION

With the possible exception of cat C17, these cats provided data consistent with two conclusions. First, decorticate cats have considerable visually guided behavior if intercollicular influences are abolished, either by ablation of one colliculus or transection of the collicular commissure. Without such tectal surgery, a permanent and total deficit in orienting ensues. This is precisely the effect that Sprague ('66b) described. Second, while dependent upon retinotectal pathways, the cat sees much better with nasal than with temporal retina. With intact geniculo-cortical pathways, no such difference between nasal and temporal retina is evident.

Basis for the Sprague effect

Given the potential importance of this effect, it is somewhat surprising that so little has been written about it in the past ten years (e.g., for the cat: Wood, '73, '75; for the rat: Cooper et al., '70; Goodale, '73). At the single neuron level, many changes occur among collicular neuronal properties after cortical ablations (e.g., Rosenquist and Palmer, '71; Wickelgren and Sterling, '69). Perhaps the most striking result of decortication is the total loss of visual responses among multimodal neurons in deeper collicular layers (Schiller et al., '74; Stein and Arigbede, '72). It is possible that some of these changes underly the Sprague effect, but if so, then a collicular commissure split or contralateral collicular lesion should reduce or reverse these changes. Unfortunately, such data are as yet unavailable, and the specific neuronal correlates of the Sprague effect remain unknown. Our understanding of the phenomenon consequently remains at the level of Sprague's ('66b) general suggestion that collicular function is somehow affected by the balance of global facilitatory (corticotectal) and suppressive (colliculo-collicular) influences. In this context, the pres-

ent results add some details to our knowledge of the phenomenon.

A decorticate cat will demonstrate clear visually guided orienting behavior providing the colliculi are functionally disconnected. The order of these lesions is irrelevant (see, however, Wood, '75). In cats C5, C6, C14, and C15, collicular disconnection followed decortication (in C5 this disconnection was achieved by removing a source, the right colliculus). In cats C3, C7, C13, C18, C19, C20 and C23, the cortical ablation and collicular commissure transection were done simultaneously. In cat C8, the collicular commissure transection preceded decortication. Yet all of these cats provided consistent behavioral data, and the final behavior in no way correlated with the order of the lesions.

If, as Sprague ('66b) suggested, collicular function is depressed by decortication, then one might expect the depressed colliculus to be unable to suppress the other colliculus. If so, then one might expect a balanced, bilateral cortical ablation (without transection of the collicular commissure) to permit better visually guided behavior than seen in the hemifield contralateral to a unilateral cortical ablation. This was not the case. After bilateral, occipito-temporal cortical ablations, cats C6, C14, C15 and C22 appeared just as blind as did cat C5 in its right hemifield after its left cortical ablation. Therefore, any colliculo-collicular suppression crossing in the commissure is not dependent upon facilitatory influences descending from cortex.

A final point, illustrated by cat C5 and also made by Sprague ('66b), is that a cat has the potential for good visually guided orienting behavior providing either the cortical or collicular pathways are intact. That is, after the collicular ablation in C5, orientations to targets in the right hemifield presumably depended upon retinotectal pathways while those in the left hemifield depended upon retino-geniculo-cortical pathways. This would seem different from conclusions in the hamster (Schnei-

der, '69), rat (Kirvel et al., '74), and tree shrew (Casagrande and Diamond, '74). In these animals, visually guided orienting appears dependent upon retinotectal pathways. In the absence of these pathways, but with functional retino-geniculo-cortical pathways, these animals cannot visually orient. Differences between the cat and the other mammalian species regarding potential cortical participation in visual orienting could be an important inter-species difference. On the other hand, these differences could obtain from different testing procedures.

Contents of the collicular commissure

The commissure of the superior colliculus is anatomically complex. Not only does it contain fibers interconnecting the colliculi, many in a homo-typical fashion, but it also includes many decussating fibers heading to the superior colliculus from other regions or vice-versa (Antonetty and Webster, '75; Edwards, '77; Powell, '76). Therefore, the commissure transections described in this study probably interfered with many or all of the above-mentioned fiber systems, and at present it is not possible to determine which of these systems is related to the Sprague effect.

Consistency of the Sprague effect

Clear evidence for the Sprague effect was seen in 13 cats (C3, C5, C6, C7, C8, C13, C14, C15, C18, C19, C20, C21, and C23), and only one cat, C17, failed to demonstrate the effect. Of the cats that did show it, an impressive consistency of final behavior was noted. Given the difficulty of the surgery, especially the commissure transection, this consistency is surprising and suggests that the phenomenon is a powerful one that can survive minor surgical variations. While it is possible that not every cat has the potential for the full-blown phenomenon, certainly the overwhelming majority do. It is most likely that the one failure, C17, was due to extra, uncontrolled neural damage.

Temporal versus nasal retinal stimulation

The behavior of cats showing the Sprague effect seems largely dependent on retinotectal pathways (Sprague and Miele, '65; Sprague, '66a). Whereas a normal cat demonstrates good visually guided orienting behavior for stimulation of the entire retina (fig. 1, and Hughes, '76), cats without cortex demonstrate good vision on these tests for nasal retina but poor or no vision for temporal retina. The question as to whether any orienting behavior in decorticate cats is specifically evoked by stimulation of temporal retina is not possible to answer from these data because of the curious spontaneous scanning of this region of visual field; but clearly, stimulation of nasal retina is considerably more effective in eliciting fairly accurate orienting than is stimulation of temporal retina. It should be noted that the spontaneous scanning of amblyopic portions of visual field seen in these cats was not seen in other cats with partial field defects. Thus, optic chiasm section (C4), unilateral cortical lesion (C5), and monocular or binocular deprivation (Sherman, '73, '74a; see also the following paper, Sherman, '77), do not produce this scanning in the region of the field defect.

This retinal asymmetry would suggest that the retino-geniculo-cortical pathways necessary for this behavior receive roughly equal functional inputs from corresponding parts of nasal and temporal retina; but the analogous retino-tectal pathways receive functional inputs predominantly from nasal retina. This suggestion has an anatomical basis. In the cat, the retino-geniculate pathways representing binocular portions of the visual fields are nearly equal in terms of fibers from nasal and temporal retina, whereas the retinotectal pathways are predominantly crossed from nasal retina (Sprague, '66b; Wickelgren and Sterling, '69; Rosenquist and Palmer, '71; Sterling, '73; see, however, Graybiel, '75; Harting and Guillery, '76). Some fibers from tem-

poral retina also cross to terminate anteriorly in the superior colliculus (Harting and Guillery, '76), but their function is unclear. Presumably this asymmetry between nasal and temporal retinal projections to colliculus underlies the behavioral asymmetry seen in the decorticate cats. Cat C5 clearly exemplifies this. With the right eye, it has a full field of view, because the right temporal retina projects into the undamaged geniculocortical system, and the right nasal retina projects to the undamaged left colliculus. With the left eye, the field of view is largely limited to the left hemifield. This presumably obtains because the nasal retina projects contralaterally to the intact geniculocortical system while temporal fibers have only a small projection to ipsilateral colliculus and their large input through the lateral geniculate nucleus to the cortex has been destroyed by the cortical lesion. Good visual responses for stimulation of temporal retina, then, depend upon the integrity of the retino-geniculocortical pathways, and destruction of these (as in cats C10 and C11) can lead to the relatively poor, or absent, behavioral responses for the temporal retinal stimulation described in this paper.

This postoperative asymmetry related to nasal and temporal retina raises a question about the virtue of the split-brain preparation (i.e., after transections of both optic chiasm and commissures such as the corpus callosum). The preparation is frequently used for intrasubject control: each eye is connected strictly to the ipsilateral half of brain; and if lesions are limited to one side, the behavioral capacity related to the lesioned eye/brain combination is compared to that of the other, control combination (cf. Berlucchi et al., '72; Wood, '73, '75). However, the transected optic chiasm itself largely denervates the superior colliculus since only ipsilaterally directed fibers from temporal retina survive the transection. Studies of functions in any way dependent upon retinotectal pathways in split-brain animals could consequently provide misleading data.

CONCLUSIONS

On the basis of the behavior described in this paper, it is clear that the Sprague effect is a robust phenomenon in cats. That is, visual behavior dependent upon retinotectal pathways after large cortical lesions can be unmasked if the superior colliculi are functionally disconnected. In such a preparation, one could perhaps more accurately assess the visual capacity of decorticate cats. For instance, it may be that, in a wide range of testing conditions, transection of the collicular commissure allows for visual behavior which is considerably better than has been previously reported for decorticate cats, and perhaps other mammals (Kirvel et al., '74).

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