

# The Effect of Cortical Lesions upon Visual Discriminations in Binocularly Deprived Cats

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**ABSTRACT** Four cats were raised with binocular eyelid suture and, after their eyes were opened, were trained on a series of discrimination tasks. They performed at normal rates on the brightness task but indicated some difficulty with the pattern tasks. They then received large, bilateral occipito-temporal cortex ablations. Postoperatively, this in no observable way affected their visually guided orienting behavior, but it did destroy their capacity to perform the preoperatively learned pattern tasks. Postoperative performance on the brightness task remained good. These data indicate that, in these deprived cats, there is little or no cortical development for visual orienting, but cortex is necessary for visual discrimination learning.

Cats raised with binocular eyelid suture develop a number of well defined abnormalities in their central visual pathways (Wiesel and Hubel, '65; Sherman et al., '72; Hoffman and Sherman, '75). Correlated with this is the finding that these cats have relatively poor, although clearly evident, visually guided behavior (Chow and Stewart, '72; Ganz et al., '72; Sherman, '73, '74a).

In an analysis of the visually guided orienting behavior of such binocularly sutured cats, Sherman ('77b) concluded that visual cortex was not appreciably involved. This followed from two observations. First, the visual orienting of the binocularly deprived cats was virtually identical to that of normally reared cats with bilateral occipito-temporal cortex ablations (Sherman, '74b, '77a). Second, whereas large visual cortical ablations clearly change a normally reared cat's visual orienting (Sprague, '66; Sherman, '74b, '77a), they do not substantially affect this behavior in a cat raised with binocular lid suture (Sherman, '77b).

This raises the possibility that early binocular lid suture prevents the development of cortical pathways which would normally contribute to visual behavior. The implication would be that the visually guided orienting behavior of these cats depends upon relatively normal development of the subcortical visual centers. The present experiment was designed to test this possibility further by studying the

visual discrimination behavior of binocularly deprived cats before and after large, bilateral, visual cortex lesions. We found that, while these lesions did not appreciably alter visual orienting, they virtually abolished pattern discriminations.

## MATERIALS AND METHODS

### *Subjects*

Four adult cats (BD5, BD11, BD12, and BD18) were studied in this experiment. They were born and reared in the laboratory. On the eighth postnatal day (at or before the time of natural eye-opening), each had the lids of both eyes sutured together. Care was taken to insure that no openings occurred in the lids until they were parted for behavioral testing at 9 to 16 months postnatal.

### *Methods*

The cats in this experiment were studied concurrently with those reported in the preceding paper, and consequently, all of the surgical, histological, and behavioral methods were identical to those previously described (Loop and Sherman, '77; also Sherman, '77a,b). Each of the cats had virtually identical, bilateral occipito-temporal cortex ablations, and none of the cats underwent mid-brain surgery.

Preoperatively, all of the cats learned a light/dark and horizontal versus vertical stripe discrimination; all but cat BD12 were

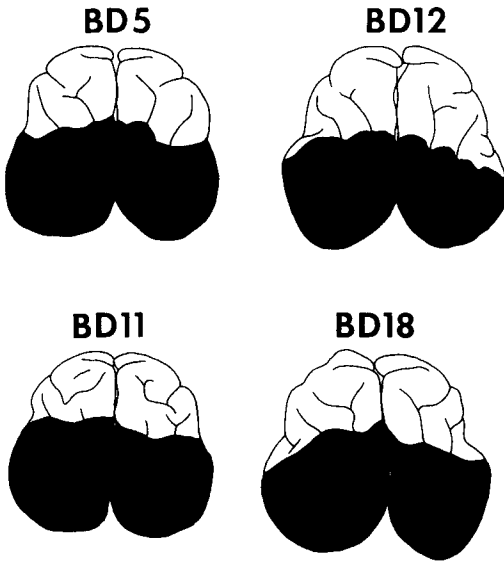


Fig. 1 Dorsal view of reconstructed cortical lesions redrawn from Sherman ('77b). These lesions involved all known cortical projection zones of the lateral geniculate nucleus as well as those of the medial, lateral and inferior divisions of the pulvinar (see Sherman, '77b, for details).

trained to discriminate upright versus inverted triangles (both solid and outlined figures). Postoperatively, after a 3 to 9-week recovery period, the cats were retested on these discriminations. Always, the same target of the pair was positive pre- and postoperatively for each cat. Postoperative testing was continued until a cat achieved criterion or completed three (BD12) or six (BD5, BD11, BD18) times the number of sessions required to master the task preoperatively. These cats were also tested pre- and postoperatively for visually guided orienting behavior, and details of both methodology and results have been previously published (Sherman, '77b). All discrimination testing was done binocularly (i.e., the cats had both eyes open), whereas the orienting behavior was tested both binocularly and monocularly.

## RESULTS

### *Histology*

Details of the histological reconstructions for these cats have been published (Sherman, '77b), and a dorsal view of the lesions is provided in figure 1. In summary, the ablations involved the posterior two-thirds of cortex. Medially, all cortex superior to the splenial

sulcus was removed; and dorsally, all of the lateral, suprasylvian, and some of the ectosylvian gyri were ablated. Thus all known recipient zones of the "visual" thalamus (i.e., the lateral geniculate nucleus and medial, lateral, and inferior divisions of the pulvinar nucleus) were ablated (see footnote 1 of the preceding paper, Loop and Sherman, '77, for terminology; also Sherman, '77a,b). In each cat, retrograde degeneration was evident throughout these thalamic nuclei.

### *Preoperative testing*

On tests of visually guided orienting behavior, these binocularly deprived cats readily oriented to small objects placed within their visual fields. In this way, the visual fields were measured to be from 90° left to 90° right with both eyes open, and from the midline to 90° ipsilateral to the open eye with monocular viewing (for details, see Sherman, '77b).

All four cats quickly learned the basic motor skills necessary to perform the discrimination tasks. They did not require any special handling such as has been previously reported for binocularly deprived cats (Chow and Stewart, '72). Figure 2 summarizes the preoperative learning of these cats. In general, the cats exhibited qualitatively normal performance on these tasks, although in several cases they took abnormally long to fulfill criterion.

The discrimination rate of light versus dark was within normal bounds and, as in normal cats (Loop and Sherman, '77), light positive was more readily learned than was dark positive (fig. 2A). Figure 2B shows that these cats also learned the stripe orientation task. Three of the cats (BD5, BD11 and BD18) learned this in 10 to 13 sessions, which was the rate achieved by normal cats (Loop and Sherman, '77). The fourth cat, BD12, required 89 sessions to achieve criterion; subsequently, this cat was not trained preoperatively on the triangle discrimination tasks. Figure 2C summarizes the results of testing cats BD5, BD11, and BD18 on these triangle tasks, and all required more training than did normals to achieve criterion on the solid figures (Loop and Sherman, '77). In fact, cat BD18 never achieved criterion during its 121 sessions, although it did perform at better than chance levels (i.e., "chance" being 67%;  $p < 10^{-6}$ ; see Loop and Sherman, '77), and it did occasionally reach 80% correct. All of the cats, including BD18, transferred to the outlined triangles

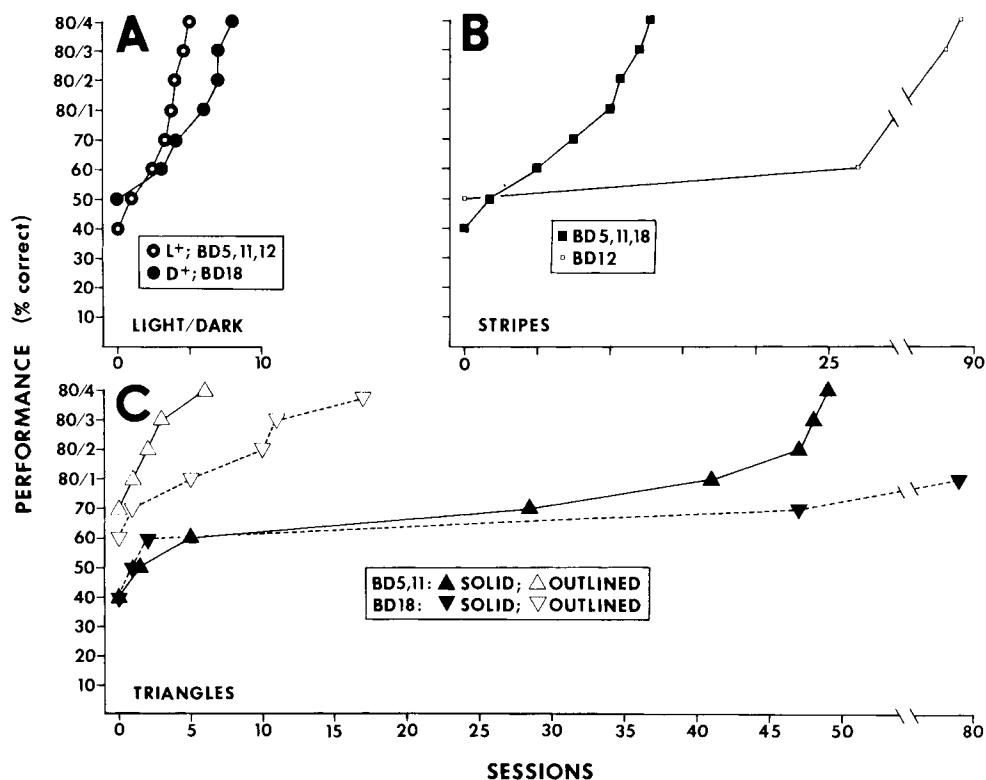


Fig. 2 Preoperative learning curves. Plotted are the mean number of daily test sessions (abscissa) required to pass a particular performance level (ordinate). This method of plotting is detailed in the preceding paper (Loop and Sherman, '77). A. Preoperative learning curves for the light/dark discrimination. Cats BD5, BD11 and BD12 were trained to light positive; Cat BD18, to dark positive. B. Preoperative learning curves for the stripe orientation problem. Cats BD5, BD11 and BD18 learned this within the normal number of sessions, but BD12 required an abnormally high number of sessions and was thus not trained on the triangle discriminations. Although not clear from the figure, BD12 remained at chance levels for at least 28 sessions and improved gradually and sporadically to reach criterion on the eighty-ninth session. C. Preoperative learning curves for discrimination of upright vs. inverted triangles. For solid figures, cats BD5 and BD11 learned the problem readily and they quickly transferred to the outlined task. Cat BD18 never achieved criterion performance on the solid figure task. However, this cat achieved performance levels significantly better than chance, and after transfer to outlined figures, soon reached criterion performance.

with considerable savings, and they quickly achieved criterion.

#### Postoperative testing

These cats all had large, bilateral occipito-temporal cortical lesions as described above. After a 3 to 9-week recovery period, behavioral testing resumed. These cortical lesions in no observable way affected the cats' visually guided orienting behavior (Sherman, '77b), yet it did affect their visual discrimination abilities.

Postoperatively, each of the cats immediately began responding in the discrimination apparatus, and figure 3 summarizes these re-

sults. Figure 3A shows that the light/dark task was rapidly reacquired, and substantial savings were evident for the three cats trained to light positive; conversely, the cat trained to dark positive required more trials to achieve criterion than it did preoperatively. Figure 3B shows that none of the cats were able postoperatively to discriminate horizontal from vertical stripes. Cats BD5, BD11, and BD18 were trained for six times the number of sessions they required preoperatively to achieve criterion; because of its many preoperative sessions, cat BD12 was tested postoperatively for only three times its preoperative number of sessions. Each of the cats hov-

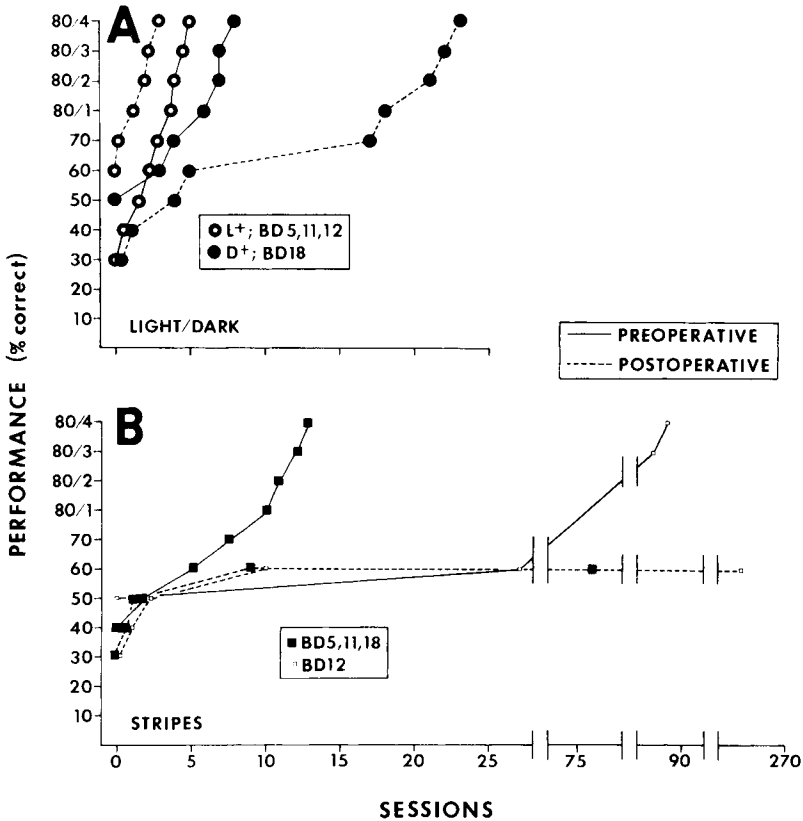


Fig. 3 Pre- and postoperative learning curves. Preoperative learning is represented by the solid curves; postoperative, by the dashed curves. The curves are plotted in the same manner as those in figure 2. A. Pre- and postoperative learning curves for the light/dark discrimination. B. Pre- and postoperative learning curves for the stripe orientation discrimination. None of the cats postoperatively exceeded chance levels on the correction procedure.

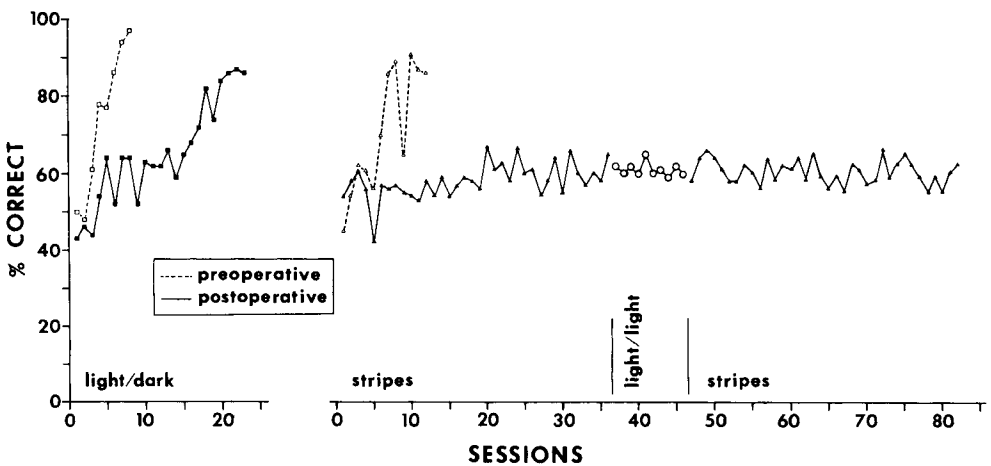


Fig. 4 Pre- and postoperative learning scores for cat BD18. Preoperative learning is represented by the dashed curves; postoperative, by the solid curves. The curves are plotted somewhat differently from those in figures 2, 3. Here, every test session is indicated on the abscissa, and its percent correct, on the ordinate. Postoperatively on the stripe orientation problem, this cat soon achieved a stable performance level of approximately 60% correct. This same level was maintained while an insoluble (light/light) problem was inserted on sessions 37-46.

ered at a daily performance rate of near 67% (i.e., chance), and each did virtually the same on the insoluble light/light task. This illustrated in figure 4 for BD18, and these results were typical for all of the cats.

#### DISCUSSION

Although the four binocularly deprived cats were generally capable of learning the discrimination tasks preoperatively, they seemed to have difficulty with those tasks based on differences in the spatial distribution of light (i.e., stripe and triangle orientation). This finding is in accord with previous studies (Chow and Stewart, '72; Ganz et al., '72).

Furthermore, the visual cortical ablations, which did not appreciably affect these cats' orienting behavior, seriously interfered with their discrimination performance. The earlier conclusion that cortical pathways do not develop in binocularly deprived kittens for visual orienting behavior (Sherman, '77b) does not seem applicable to visual discrimination behavior. Clearly some visual cortical development occurs despite the binocular suture. However, from the present data, which include massive cortical ablations, it is not clear which cortical areas are responsible for this behavior in the deprived cats. For example, it is possible that, in these cats, geniculocortical pathways (involving mostly areas 17 and 18) fail to develop participation in this behavior, and the discrimination behavior is dependent upon other thalamocortical pathways (such as area 19, suprasylvian cortex, etc.). It appears that normally reared cats with lesions limited to the geniculocortical pathways are capable of good, albeit reduced, discrimination behavior (Berkley et al., '76; Doty, '71; Winans, '71). The behavioral capacities of such cats may be closely comparable to those of binocularly sutured cats. Therefore, while the present data indicate clear cortical involvement in the visual discrimination performance of binocularly deprived cats, they do not allow conclusions regarding the involvement of separate cortical areas. More work is needed to reach such conclusions.

A final point concerns an interspecies comparison. Schneider ('69) reports that, in the hamster, lesions of visual cortex interfere with visual discrimination behavior, but not with visual orienting; conversely, lesions of the superior colliculus interfere with visual orienting, but not with visual discrimination behavior. Thus he concludes that the hamster

cortex is necessary for visual pattern discrimination; the colliculus, for visual orienting. In contrast, the normally reared cat has considerable cortical participation in visual orienting since cortical lesions affect this behavior and collicular lesions do not entirely abolish it (Sprague, '66; Sherman, '77a). Yet a cat raised with binocular lid suture is more like a hamster in this regard; both animals require cortex for visual pattern discrimination, and both require colliculus for visual orienting (Schneider, '69; Sherman, '77b). It is interesting to speculate that something which fails to develop normally in the binocularly deprived cat (e.g., the geniculocortical Y-cells; see Sherman et al., '72; Hoffman and Sherman, '75), is not normally a major component of the hamster visual pathways.

#### ACKNOWLEDGMENTS

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