Visual Discriminations of Cats with Cortical and Tectal Lesions

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ABSTRACT Fourteen cats were trained on three visual discrimination tasks: light vs. dark, horizontal vs. vertical stripes, and upright vs. inverted triangles. Four of the cats then underwent large, bilateral occipito-temporal cortex ablations; postoperatively, they demonstrated little or no visually guided orienting behavior and could solve only the brightness task and not the preoperatively learned pattern discriminations. Six other cats underwent the same cortical ablations plus a transection of the commissure of the superior colliculus; postoperatively, they demonstrated good visually guided orienting behavior (i.e., the Sprague effect) but still could solve only the brightness task. The final four cats were controls and underwent no surgery; they demonstrated good retention of the pattern task despite an extensive idle period corresponding to the postoperative period before retesting in the above ten cats. These data indicate that, while a transection of the collicular commissure after visual decortication dramatically improves visual orienting, it does not obviously improve visual discrimination abilities.

Sprague's ('66a,b; see also review by Sprague et al., '73) studies in the cat have emphasized the potential importance of the superior colliculus in visually guided behavior. For example, he found that, whereas large occipito-temporal ablations of cortex rendered a cat incapable of visually guided orienting behavior, a subsequent split of the commissure of the superior colliculus or removal of one colliculus dramatically restored much of this behavior. These results have been substantially confirmed (Sherman, '74, '77). Although the mechanism underlying this phenomenon is not understood, Sprague ('66b) suggested that, in the absence of cortex, the colliculi functionally suppress one another, and this prevents their participation in visually guided behavior; removal of the suppression by destroying its source (i.e., one colliculus) or interrupting its pathway (i.e., the collicular commissure) restores collicular participation in this behavior (also Sherman, '74, '77).

This finding, that cats rendered practically blind by cortical ablation demonstrate certain kinds of visually guided behavior after subsequent tectal surgery, raises questions regarding their abilities on learned, visual discrimination problems. That is, the literature is replete with evidence that sufficiently large bilateral cortical lesions in the cat produce profound impairment in the animal's ability either to perform previously learned discriminations or to learn new ones except, perhaps, for light/dark discriminations (Smith, '38; Spear and Braun, '69; Winans, '71; Doty, '71; Wood et al., '74). It may be that the suppressed tectum in such a cat is unable to function as it normally might, and recent evidence (see review in Sprague et al., '73) suggests considerable tectal participation in visual discrimination behavior. The present investigation was designed to determine if a transection of the collicular commissure in a cat with a large, bilateral, visual cortex ablation would improve its performance on a series of discrimination tasks. We found that, although these cats with commissure splits demonstrated clear visually guided orienting behavior, whereas cats with cortical lesions and no commissure split did not, both groups showed equally profound losses in the ability to perform visual pattern discriminations.

MATERIALS AND METHODS

Subjects

Fourteen cats, purchased as normal adults (2-4 kg weight), were studied. They were housed in individual cages with a 12-hour light/dark cycle for the duration of the study. Each cat was reduced to 80% of its free feed weight and maintained at that level of food deprivation throughout behavioral testing. During the preoperative week and for up to 12 weeks postoperatively before retesting, free access to food was permitted. Cats which received no surgery (as a control for spontaneous losses of learned discriminations not related to the lesions) were given equivalent periods of free access to food during their retention intervals.

The cats were placed into three groups. (1) Four cats (C6, C14, C15, C22), after preoperative training, received a large, one-stage, bilateral ablation of occipito-temporal cortex. The lesions included all known projection zones of the lateral geniculate nucleus, as well as projections of the medial, lateral and inferior divisions of the pulvinar nucleus (Niimi et al., '74; Sprague et al., '73).[1] After postoperative recovery periods of six to ten weeks, they were retested. (2) Six other cats received a large, bilateral ablation of the occipito-temporal cortex, as described above, plus a midsagittal transection of the commissure of the superior colliculus during the same operation. Five of the cats (C13, C18, C19, C20, C21) underwent preoperative training, and one (C23) did not. Testing commenced postoperatively after 7 to 12 weeks. (3) Finally, four "retention" cats (R1, R2, R3, R4) underwent training to criteria described below. Following this, they were returned to free food and not tested for periods equivalent to the postoperative intervals in the cats with neural lesions. They were then retested for their retention of the previously learned discriminations.

Other behavioral data from these cats with neural lesions have already been published, and thus the details of the surgical procedures are described elsewhere (Sherman, '77). Briefly, the lesions were performed in barbiturate-anesthetized cats by gentle subpial suction for the cortical removal and by insertion of a fine knife under visual control for the collicular commissure split.

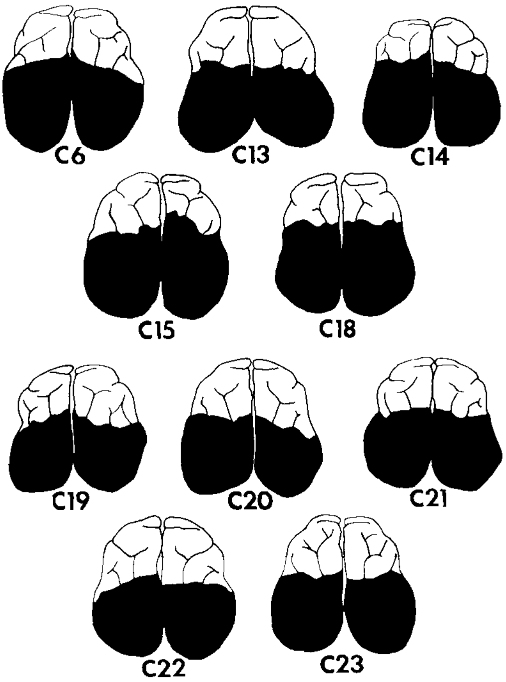

Fig. 1 Dorsal view of reconstructed cortical lesions redrawn from Sherman ('77). These lesions involved all known cortical projection zones of the lateral geniculate nucleus as well as those of the medial, lateral and inferior divisions of the pulvinar. More detailed reconstructions for these lesions plus the collicular commissure transections in cats C13, C18, C19, C20, C21, and C23 were published separately (Sherman, '77).

Behavioral methods

Apparatus. The behavioral apparatus was modeled after that of Berkley ('70; also Loop and Sherman, '77a) and consisted of an operant conditioning box with a head chamber at one end into which the cat thrust its head. The square head chamber was made of black plexiglass with a clear plexiglass top. The chamber contained two clear plastic response keys (3.75 × 6.25 cm; centers separated by 5.0 cm), 1.5 cm behind which were located two small in-line projectors (BRS/LVE Model 111-06; Technical Services Inc.). Between and 1.0 cm below the response keys, reinforcement (a small squirt of dilute beef baby food) was delivered from a solenoid feeder through a hole in the wall.

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[1] This terminology for the pulvinar nucleus (Niimi et al., '74) corresponds to older nomenclature as follows: medial pulvinar represents the lateral posterior nucleus of Rioch; lateral pulvinar represents the pulvinar of Rioch; and inferior pulvinar represents the nucleus posterior of Rioch. The cortical lesions, therefore, involved all of the known visual projection zones of the thalamus.

A total of four discrimination problems were utilized in the following order: (1) "light" vs. "dark" (1.5 × 1.5 cm square, average luminance 36.3 cd/m^2 vs. 1.1 cd/m^2); (2) horizontal vs. vertical stripes (two cycles of a square wave grating; the stripes were 3 mm wide by 22 mm long; bright stripes were 36.6 cd/m^2 luminance, dark stripes were 1.1 cd/m^2); (3) solid upright (base down) vs. inverted (base up) isosceles triangles (1.0 cm sides, 36.3 cd/m^2 luminance against a dark 1.1 cd/m^2 background; and (4) outlined upright vs. inverted isosceles triangles (1.0 cm sides, 36.3 cd/m^2 lines 1 mm thick against a 1.1 cd/m^2 background; thus the triangles appeared as a bright outline on a dark background). All experimental contingencies and data collection were accomplished with conventional electromechanical devices.

Training schedule. Each cat was trained to press the response keys with its nose by a method of successive approximation (Berkley, '70). The light/dark stimuli were present during shaping, and each of the 30 initial responses were reinforced. The day after the cats made 30 responses within a 30-minute period, discrimination training was begun and each cat was given 125 trials/day, 5-7 days/week. A response to the correct stimulus was immediately reinforced and followed by a 3-second intertrial interval during which both stimuli were off. A response to the incorrect stimulus was not reinforced, and it was followed by a longer intertrial interval which was gradually increased from 3 seconds to a maximum of 12 seconds. During the intertrial interval, both stimuli were off, and all responses reset the interval to the duration

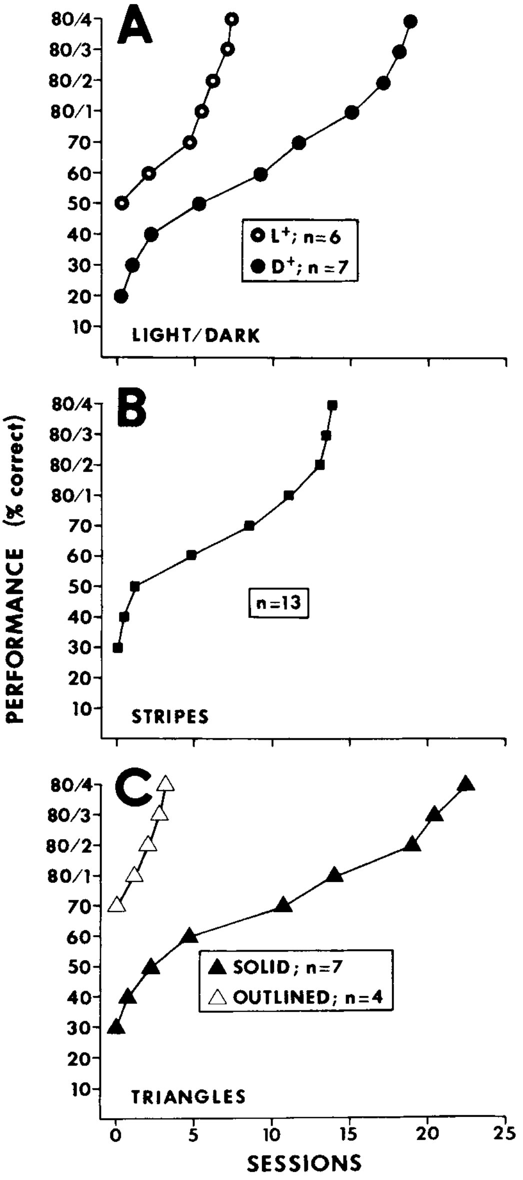

Figure 2

Fig. 2 Preoperative learning curves. Plotted are the mean number of daily test sessions required to reach a perticular performance level (i.e., percent correct). The performance levels are plotted in intervals of 10%. Unless otherwise specified, there were no appreciable differences among cats on any individual task, and thus intersubject data are pooled. Consequently, the data points represent the mean number of daily test sessions (abscissa) required to reach a particular performance level (ordinate). Criterion performance was defined as four consecutive days at ⩾80% correct, or two at ⩾90% (see text). The curves were drawn so that 80/1 represents the first session at ⩾80% correct, 80/2 represents the second *consecutive* session at ⩾80% correct, etc. For simplicity, ⩾90% correct is plotted as two consecutive days at ⩾80% correct. A. Preoperative learning curves for light/dark discrimination. The mean curve for the six cats trained to light positive (L+) is shown separately from that for the seven cats trained to dark positive (D+), because cats consistently learned the former discrimination more quickly. B. Preoperative learning curve for the horizontal versus vertical stripe discrimination. Seven cats were trained to horizontal positive, and the rest, to vertical positive. The data were pooled and averaged although there was a reliable but slight tendency for the cats which were trained on horizontal positive to reach criterion sooner than those trained on vertical positive. C. Preoperative learning curves for seven of the cats trained to discriminate upright from inverted triangles. Data were pooled from four of these cats which were trained on upright positive and the three trained on inverted positive, since there were no reliable differences between groups. The cats first were trained on solid figures, then four were transferred to outlined figures with the same positive target orientation for each (2 upright; 2 inverted). Considerable savings were evident in the transfer (see text).

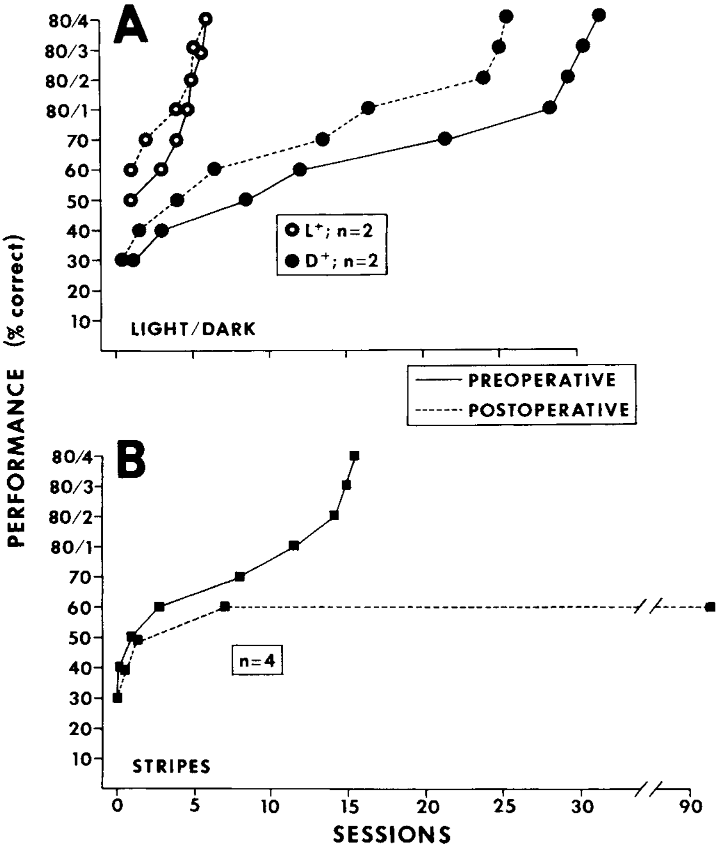

Fig. 3 Pre- and postoperative learning curves for the cats with cortical, but not tectal, lesions (C6, C14, C15, C22). Preoperative learning is represented by the solid curves; postoperative, by the dashed curves. The curves are plotted in the same manner as those in figure 2. A. Pre- and postoperative 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.

preselected for incorrect responses. The left/right position of the correct stimulus was determined initially by a Gellerman series (Gellerman, '33). After the first day of light/dark training, a modification of the Gellerman series was used. That is, a correction procedure was introduced whereby only a correct response advanced the sequence to the next position and this advancement was controlled by a Gellerman series. This proved a powerful deterrent to the cat's initial and recurrent habit of responding predominantly to one key.[2] Criterion performance was taken as either four consecutive days at $\geq 80\%$ correct or two consecutive days at $\geq 90\%$ correct. One day at $\geq 90\%$ correct was considered equivalent to two consecutive days at $\geq 80\%$ correct. Even if chance were the maximum attainable with the correction procedure (i.e., 67% — see footnote 2), this criterion level represents a highly significant result ($p < 10^{-6}$). When the cats were tested postoperatively, they were always given the same positive stimulus as

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[2] This correction procedure has two potential effects on the animal's performance, both of which tend to establish chance levels different from 50%. First, if the animal persists in responding to a particular key, levels of less than 50% will obtain. Second, the cat could improve upon a 50% chance score by learning the correction procedure (i.e., after a response to an incorrect key, it could always respond to the other key on the next trial); this could lead to chance scores of up to 67%. However, diagnosis of either of the above strategies is straightforward. If a trial is correct, then the ensuing percent correct represents a true estimate of the response level; if a trial is incorrect, then the difference between 50% and the ensuing percent correct indicates the direction and magnitude of the correction procedure. When present, these influences have been further controlled by introducing an insoluble light/light discrimination (RESULTS; and Wood et al., '74), and the response level obtained is an estimate of chance performance for that cat. This was done for each cat in the study.

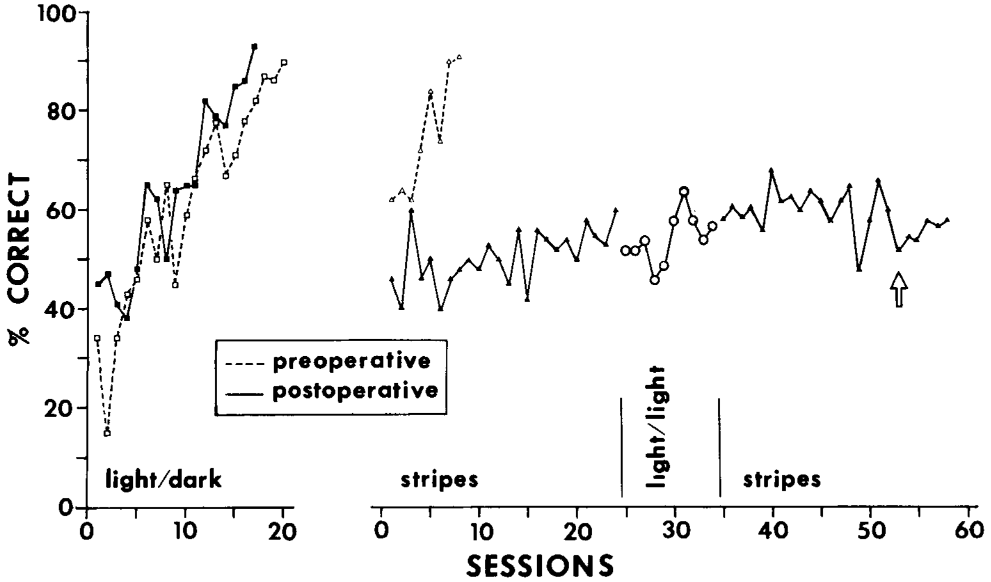

Fig. 4 Pre- and postoperative learning curves for cat C14; preoperative learning represented by the solid curves; postoperative, by the dashed curves. These curves are plotted somewhat differently from those in figures 2, 3. Here, every test session is indicated on the abscissa, and its percent correct, on the ordinate. Postoperatively on the stripe orientation problem, cat C14 consistently achieved 50-65% correct with the correction procedure. When switched to an insoluble (light/light) problem on sessions 25-34, no change in response level was evident. When the correction procedure was eliminated (session 53, arrow), there again was little effect on the response level.

preoperatively. Also, postoperative training was continued on a given task until the cats either reached criterion or were given six times the number of preoperative training sessions.

In addition to discrimination testing, these cats were also tested pre- and postoperatively for visually guided orienting behavior. The methods and results for these cats have been published in detail (Sherman, '77). The test chiefly consisted of judging the cat's ability to orient to various visual objects presented in limited portions of the visual field. This allowed an assessment of the extent of visual field. All discrimination testing was done binocularly (i.e., with both of the cat's eyes open), and visual field testing was done both binocularly and monocularly.

Histology

After each cat completed its testing regimen, histological controls were obtained. Routine procedures were used first to photograph the brains and then to prepare 40-μm thick coronal brain sections alternatively stained with cresylecht violet or the Mahon method for fibers (see Sherman, '77, for details of the procedures on these cats). From this material, the extent of the brain lesions was reconstructed.

RESULTS

Histology

Each of the lesions was analyzed by using the brain photographs plus serial reconstructions from the histological sections. 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 were ablated. As intended, each of the cortical lesions destroyed essentially all of the known projection zones of the lateral geniculate nucleus plus the medial, lateral, and inferior divisions of the pulvinar nucleus (Sprague et al., '73; Niimi et al., '74). Retrograde degeneration was evident throughout the lateral geniculate nucleus with no surviving patches of non-degenerated neurons, but such degeneration was difficult to assess in the pulvinar nuclear divisions.

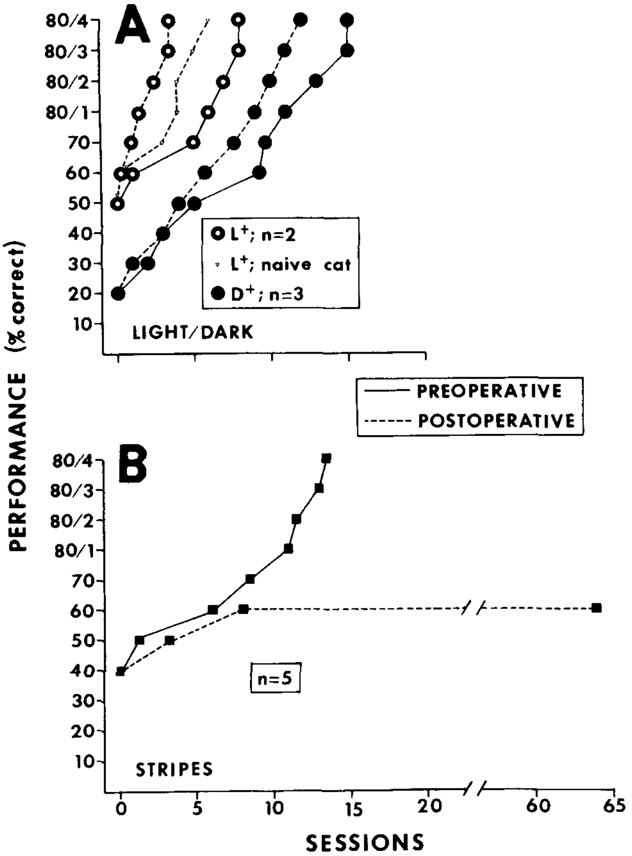

Fig. 5 Pre- and postoperative learning curves for the cats with cortical and tectal lesions (C13, C18, C19, C20, C21, C23); conventions as in figure 3. A. Pre- and postoperative learning curves for the light/dark discrimination. For cat C23 ("naive cat") no preoperative training was obtained. B. Pre- and postoperative learning curves for the stripe orientation discrimination (C23 was not tested on this task). None of the cats postoperatively exceeded chance levels on the correction procedure.

Figure 1 shows a dorsal reconstruction of each cortical lesion. All of the collicular commissure transections were complete except for a few fibers at the anterior and posterior limits of the commissure. Minimal or no detectable damage was evident in either the superior collicular laminae, the central gray, or the tegmentum. Further details of the lesions in these cats, were previously illustrated (Sherman, '77).

Behavioral results

The behavioral data are represented by learning curves which plot the number of daily training sessions required to reach a particular performance level (Horel et al., '66). This form was chosen, rather than the more common plots of mean performance level as a function of the number of sessions, because it was felt that different learning curves could be more conveniently compared in this manner (see legend for fig. 2).

Preoperative training. All of the cats except for C23 were trained preoperatively on the light/dark and stripe orientation discriminations. Seven of the cats (R1, R2, C6, C13, C14, C18, and C20) were also trained preoperatively on the solid triangle discrimination, and all of these except cats C6, C18, and C20 were transferred to the outline triangle discrimination with the same triangle orientation being positive. Since there was no detectable intergroup difference on any of these tests except as noted, these preoperative data are pooled in figure 2. Note that, on the brightness task, the cats learned light posi-

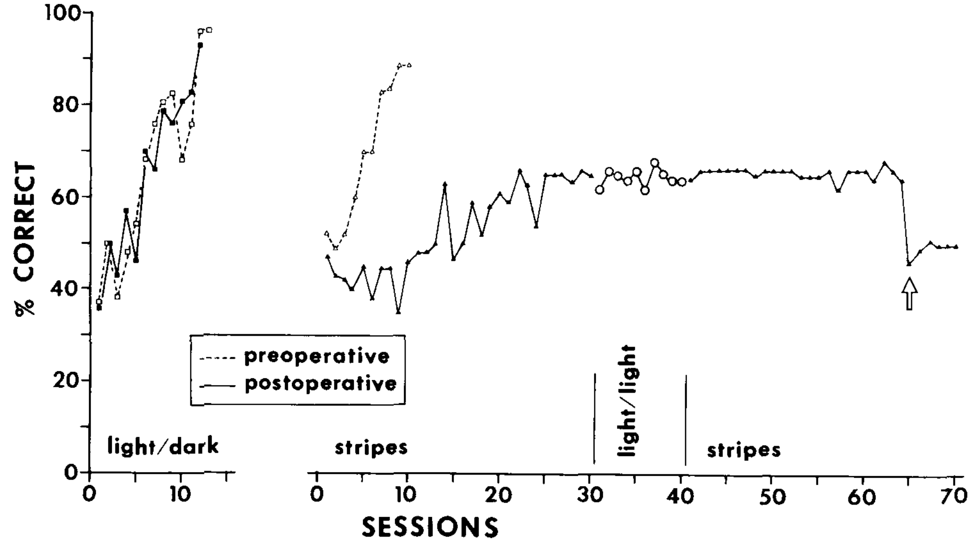

Fig. 6 Pre- and postoperative learning curves for cat C18; conventions as in figure 4. Postoperatively on the stripe orientation problem, this cat reached a stable 60-65% correct with the correction procedure. When switched to an insoluble (light/light) problem on sessions 31-40, no change in response level was evident. When the correction procedure was eliminated (session 65, arrow), the response level dropped precipitously from about 65% correct to about 50% correct.

tive more quickly than dark positive (fig. 2A). This presumably reflects an initial preference for "light" over "dark" by the cats in this testing paradigm (see also comments in Fischman and Meikle, '65; Berlucchi et al., '72). Note also that the cats which were trained on both triangle discriminations readily transferred from solid to outline figures (fig. 2C). At this point, the cats were divided into three groups (MATERIALS AND METHODS). One group received large, bilateral visual cortex lesions, and after a several week recovery period, were again tested on the discrimination problems. The second group received similarly large, bilateral, visual cortex lesions plus a transection of the collicular commissure; after a similar postoperative period, they were retested. The final group were the "retention" control cats which were held before retesting for a period equivalent to the postoperative recovery periods of the above cats.

Cortical lesions without tectal surgery. None of these cats (C6, C14, C15, and C22) demonstrated detectable visually guided orienting behavior on the visual field test (Sherman, '77). They were first retested for light/dark discrimination. Figure 3A illustrates the two main results for light/dark discrimination. (1) None of the cats showed any evidence of having fully retained the discrimination, although the two cats trained to dark positive required fewer sessions to reach criterion. (2) All of the cats relearned the discrimination in approximately the preoperative rate, and still the dark positive task took considerably longer. Visual decortication, then, did not appreciably alter the cats' apparent positive phototaxis. These data are consistent with numerous studies which report that visual decortication in cats eliminated previously learned light/dark discrimination, but does not interfere with reacquisition of these discriminations (see review of this literature in Sprague et al., '73).

These cats were next retested on the stripe orientation problem. As figure 3B illustrates, none of the cats achieved better than chance scores (i.e., 67% for the correction procedure) despite six times the number of training sessions as preoperatively. With the correction procedure, these cats achieved virtually identical scores on the stripe orientation problem and an insoluble light/light task. This is illustrated for a typical case (cat C14) in figure 4. Since none of the cats showed any evidence of discriminating between horizontal and vertical stripes, we did not formally test them on either of the triangle discriminations, but

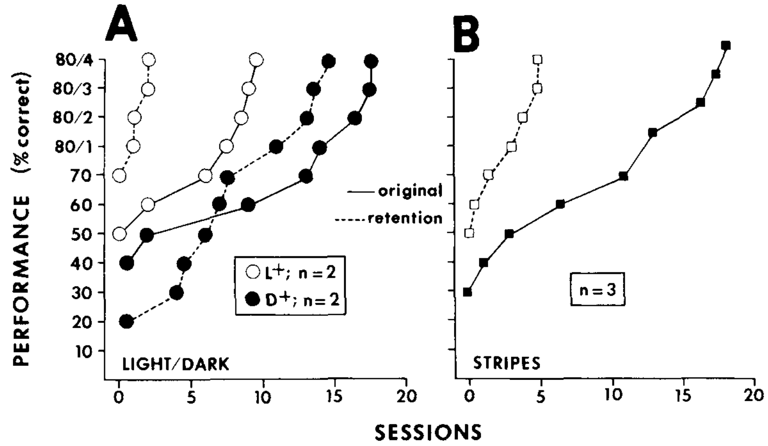

Fig. 7 Learning curves for the "retention" cats (R1, R2, R3, R4). The curves are plotted as in figure 2. Original learning is indicated by the solid curve; retention of these same discriminations after an idle period of 7 to 12 weeks is indicated by the dashed curves. A. Original learning and retention of the light/dark discriminations. Retention of light positive was good, but retention of dark positive was poor. B. Original learning and retention of the stripe orientation discrimination. Retention of this discrimination was good for each cat.

limited testing with fewer sessions indicated no ability to master these discriminations, either.

Cortical lesions and collicular commissure splits. Five of these cats (C13, C18, C19, C20, and C21) were trained similarly to those in the previous group. Unlike the previous group, all of these cats had reduced but still good postoperative visually guided behavior on the visual field test (Sherman, '77). However, the two groups postoperatively performed very similarly on tests of visual discrimination.

Figure 5A shows that, with the cortical and tectal surgery, the cats could relearn the light/dark task, with possibly some savings for dark positive and nearly complete savings for light positive. Next these cats were retested for their stripe orientation discrimination abilities, and as did the previous group, none of these cats scored better than chance (fig. 5B). Like the previous group, these cats performed equally well with the correction procedure on an insoluble light/light problem as on the stripe orientation problem, and this is illustrated for a typical case (cat C18) in figure 6. Limited testing indicated no ability to discriminate upright versus inverted triangles.

Cat C23 was trained on the light/dark task (light positive) as a naive animal after receiving the same cortical and tectal lesions as the other cats in this group. It, too, demonstrated clear but reduced visual orienting (Sherman, '77). We wished to determine whether the postoperative abilities to discriminate light from dark critically depended upon preoperative training. Figure 5A shows that this cat performed the task within the expected time and preoperative training was thus not required.

Retention control. The above data suggest that many cats which have learned to discriminate light from dark need to relearn this after large, visual cortex lesions. Since the cats learned other visual discriminations which may have interfered with or superceded their light/dark training, and since the postoperative recovery period was extensive, it may be that they simply lost the discrimination independently of the cortical ablation. As a control for this, cats R1, R2, R3, and R4 underwent training equivalent to the preoperative training of the above cats, and then were simply not tested for periods equivalent to the postoperative recovery periods (MATERIALS AND METHODS). Figure 7A shows that, when they were then retested for light/dark discriminations, the two cats trained on light positive showed perfect retention, but the two trained on dark positive needed considerable retraining to achieve criterion. The results are unfortunately ambiguous and suggest that some cats (at least some of those trained on a dark positive task) can lose the discrimination. Therefore, the need for many of the cats in this study with cortical lesions to relearn this discrimination may not be related to the surgery *per se.* On the other hand, figure 7B shows that, for the stripe orientation discrimination, retention was quite good. Therefore, the deficits seen after cortical lesions on this task were presumably due to the surgery. Retention for the triangle discriminations was not tested for these cats, although their original training included triangle discriminations and is used as control data for the following paper (Loop and Sherman, '77b).

DISCUSSION

Previous studies (Sprague, '66b; Sherman, '74, '77) have shown that a cat with a large bilateral ablation of the occipito-temporal cortex demonstrates little or no detectable visually guided behavior. However, if the commissure of the superior colliculus is transected before or after the cortical ablation, the cat demonstrates clear visual orienting (Sherman, '77). This commissure transection, therefore, qualitatively improves the visually decorticate cat's vision, at least on some behavioral tests.

The present study was designed to determine if this phenomenon applied to other tasks, such as learned visual discriminations. We found no evidence that discrimination behavior is in any way qualitatively affected by a collicular commissure split in visually decorticate cats. That is, cats with large posterior decortication demonstrated poor visual orienting and could not discriminate horizontal from vertical stripes. Cats with a collicular commissure split in addition to the cortical ablation demonstrated good visual orienting but still could not solve the stripe orientation problem. This failure to find an improvement due to the commissure split must be viewed with reservation. It may be that the use of different discrimination targets, different reinforcement contingencies, different training schedules, etc., may well demonstrate such an improvement. We tentatively conclude, however, that a collicular commissure split in visually decorticate cats does not qualitatively alter the cats' visual discrimination abilities.

The apparent dissociation between visual orienting and discrimination in cats with the combined cortical/tectal surgery is quite striking and reminiscent of Schneider's ('69) work on the hamster. Visual cortex ablations in the hamster yield an animal with good visual orienting but very little ability to discriminate visual patterns. While the colliculus may be important to visual discrimination in the cat (Sprague et al., '73), perhaps through tecto-pulvinar-cortical pathways, the present study offers no evidence that, in the absence of cortex, it can subserve pattern discriminations as it can subserve visually guided orienting behavior. Further comparisons between cat and hamster are considered in the following paper (Loop and Sherman, '77b).

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