BEHAVIORAL CUES AND BRAIN AREAS INVOLVED IN FUNCTIONAL RECOVERY AFTER REMOVAL OF VISUAL CORTEX IN THE CAT

by

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EXPERIMENT I

After removal of visual cortex (VC) (i.e., areas 17, 18 and 19) animals show a great degree of visual pattern and form discrimination ability, even when total luminous flux cues have been eliminated. Cats, rats and monkeys lacking VC can make discriminations based on differences in pattern (Spear & Braun, 1969; Wood, Spear & Braun, 1974; Baumann & Spear, 1975; Spear & Barbas, 1975; Cowey & Weiskrantz, 1971; Weiskrantz & Passingham, 1975), form (Winans, 1967, 1971; Adler & Meikle, 1975; Baumann & Spear, 1975; Mize, Wetzel & Thompson, 1971; Pasik, Pasik & Schilder, 1969; Schilder, Pasik & Pasik, 1971, 1972), amount of contour (Winans, 1967, 1971; Mize, et. al., 1971; Weiskrantz, 1963; Pasik, Pasik & Schilder, 1969; Schilder, et. al., 1971, 1972) and brightness (Spear & Braun, 1969; Baumann & Spear, 1975; Lewellyn, et. al., 1969; Weiskrantz, 1963; Pasik, et. al., 1969; Schilder, et. al., 1971, 1972). In the cat, evidence suggests that after VC removal the suprasylvian gyrus (SSG) plays an important role in the recovery of pattern discrimination ability (Wood, et. al., 1974), though it plays only a minimal role in the intact animal (Wood, et. al., 1974; Hara & Warren, 1961a, b; Hara, 1962; Warren, Warren & Akert, 1961).

The SSG is not a unitary structure, but rather it has been divided into several different anatomical areas: posterior suprasylvian sulcus (PSS), lateral suprasylvian

area (LS), areas 7, 20, and 21 (see figure 1). Based on anatomical and physiological findings, however, only the LS area is predominantly a visual area. Anatomically, LS is the only subdivision of the SSG which receives primarily visual input from the cortex. Ipsilaterally, LS receives input from areas 17, 18 and 19 and contralaterally from 17, 18, 19 and LS (Garey, Jones & Powell, 1968; Heath & Jones, 1970, 1971; Shoumura, 1972, 1974; Diamond, Jones & Powell, 1968). It is important to point out that LS is the only SSG area that receives extensive input from areas 17 and 18 (Heath & Jones, 1970, 1971; Shoumura, 1972, 1974; Diamond, Jones & Powell, 1968), the two areas which receive direct retino-thalamic input via the dorsal lateral geniculate (DLGN) (Rosenquist, Edwards & Palmer, 1974; Maciewicz, 1974; Heath & Jones, 1971). Thalamic projections to LS include a direct retino-thalamic input via the medial interlaminar nucleus (MIN) of the DLGN (Rosenquist, et. al., 1974; Maciewicz, 1974) and from the lateral posterior nucleus (LP) and posterior nucleus (PN) (Graybiel, 1970, 1972a; Maciewicz, 1974; Rosenquist, et. al., 1974) which receive projections from the superior colliculus (SC) (Graybiel, 1972b) and areas 17, 18 and 19 (Garey, et. al., 1968; Graybiel, 1972b, c).

Although areas on the crown of the gyrus receive little (Garey, et. al., 1968) or no (Heath & Jones, 1970, 1971; Shoumura, 1972, 1974; Diamond, Jones & Powell, 1968) cortical input from areas 17 or 18 these SSG areas receive visual

input from cortical areas 19 and LS (Heath & Jones, 1970, 1971). Thalamic inputs to these areas include afferents from the pulvinar (PUL) and LP (Graybiel, 1970, 1972a; Heath & Jones, 1971; Rosenquist, et, al., 1974).

Recent electrophysiological studies have shown that LS cells have very specific visual stimulus requirements (Wright, 1969; Hubel & Wiesel, 1969; Spear & Baumann, 1975a). In addition, LS is the only SSG area shown to have a visuotopic organization (Wright, 1969; Hubel & Wiesel, 1969; Spear & Baumann, 1975a). After bilateral removal of VC the responsive cells are still present though their stimulus requirements have drastically changed (Spear & Baumann, 1975b). That responsive cells are still present is important in showing that this area could support visually guided behaviors after complete VC ablation.

Early evoked potential work by Thompson, Johnson and Hoopes (1963) and Dubner and Rutledge (1964) showed that both the anterior middle suprasylvian area (AMS) and the posterior middle suprasylvian area (PMS), both of which are probably located in area 7, are responsive to visual stimuli and that these responses could not be abolished by removal of all primary sensory cortex. Single unit studies of AMS have shown the cells to be quite specific in their stimulus requirements and that they continue to respond following removal of VC (Dow & Dubner, 1969, 1971; Dubner & Brown, 1968). Therefore, it is also possible that areas on the crown of the SSG are also involved in

behavioral recovery following removal of VC.

The present experiment investigated which of the SSG subareas are involved in recovery following VC removal, with special attention paid to the LS area. Eight cats were trained preoperatively on brightness, pattern and form discriminations followed by bilateral removal of VC. After retraining and retention periods half of the animals received bilateral ablation of the LS area and half received ablation of all the SSG except the LS area (CROWN). Each animal was then tested for retention of the previously learned tasks.

METHODS

Subjects

Eight experimentally naive adult cats were used for this study. All animals were housed in a large room in group cages and were on a 12 hour light-dark schedule.

Apparatus

A two-choice discrimination apparatus similar to that described by Spear and Braun (1969) was used for visual discrimination training and testing. At one end of a rectangular box (150cm long x 50cm wide x 28cm high) was centered a hinged 28 x 13cm translucent plastic panel (start panel) which was illuminated at 27 millilamberts (mL). At the opposite end of the box were two 28 x 13cm choice panels which were symmetrically placed with their centers 6cm from the floor and 28cm apart. In all three panels the stimulus area consisted of a 16.5 x 11cm rectan-

gular area which was 3cm from the bottom of the panels and 8.5cm from the top. The surrounding area on each panel was covered with black construction paper and was illuminated at .10mL (surround). Behind each choice panel there was a small cup into which approximately 1.5ml of liquid reward (powdered milk or powdered milk mixed 3:1 with clam juice) could be automatically delivered. Visual stimuli were rear-projected by two Kodak "Carousal" projectors directly onto the choice panels from outside the rectangular box. These projectors were specially wired to allow bulb intensity to be varied independently for use in brightness discrimination.

Three discrimination tasks were employed: brightness discrimination (L-D), vertical versus horizontal stripes (H-V) and upright versus inverted isoceles triangles (TRI). For the L-D discrimination the light choice panel was illuminated at 270mL and the dark panel at 34mL. For the H-V discrimination the horizontal stimulus consisted of 18 1.5cm wide x 11cm long stripes and the vertical stimulus consisted of 13 1.5cm wide x 16.5cm long stripes. Therefore, total luminous flux and total contour length were equal for the two stimuli. Luminance of the bright stripes was 140mL and the darker stripes 8.6mL. Since each stimulus had an even number of stripes a light stripe was always present on one edge and a dark stripe on the other. It was therefore possible to eliminate consistent trial to trial local luminous flux cues by reversing the position of the light and dark edges of the two stimuli from trial

to trial according to a Gellermann series. For the triangles discrimination the stimuli consisted of two isoceles triangles with a base of 4.5cm and a height of 9.5cm. The luminance of the triangles was 140mL on a background of 8.6mL.

Position of the S^+ and S^- stimuli on the right and left choice panels were varied from trial to trial according to separate Gellermann series. Four different sequences of stimulus presentation for each task were used with no two sequences on consecutive days being the same. A masking noise was present throughout training and testing. All events were recorded on an Esterline Angus event recorder.

Discrimination Training and Testing

Following a 4-7 day period of adaptation to a food or food and water deprivation schedule each cat received a shaping procedure similar to that described in detail by Spear and Braun (1969). Each discrimination trial began with illumination of the start panel. When the cat pressed this door the light went out and the choice panels were illuminated. The cat then walked to the choice panels and pushed one or the other door open with his head or paw. If an incorrect choice was made the door would not open and the choice panels remained illuminated until the correct choice was made. When the correct choice was made the door opened and the reward was delivered. Also, as the correct door was opened the choice panels were turned off and a 15 second intertrial interval began. At the end

of the interval the start panel was turned on and the sequence was repeated. All animals were trained 5-7 days per week and received 40 trials per day. Training was continued until a criterion of 36 correct out of 40 (90%) was reached on two consecutive days.

After each training or testing session animals were allowed ad lib food and water for 1-2 hours and then returned to their home cages. Vitamin supplements were given as necessary for continued health. Thus, the cats were food or food and water deprived 22-23 hours at the time of each training or testing session.

Cats were trained and tested on the three tasks in the following order: L-D, H-V and TRI. The correct stimulus for each of the three tasks was assigned randomly for each cat preoperatively. Six cats were trained with L^+, four with H^+ and two with the upright triangle as the S^+.

After reaching criterion on the H-V and after the TRI tasks all cats were tested for two days with an indiscriminable task (blanks) to insure that no extraneous nonvisual cues were being used in making the discriminations. Both choice panels were illuminated at 140mL for 20 trials followed by 20 trials of stimuli (i.e., H-V or TRI).

Design and Procedure

Table 1 shows the experimental sequence for all cats in the present experiment. Seven cats were first trained to criterion on all three discriminations. One cat was trained and tested only on the L-D and H-V tasks. A 6-10 day period of ad lib food and water was given prior to all

surgeries. All cats then received bilateral removal of VC. After a 23-25 day recovery period, which followed all surgeries, cats were placed back on the food and water deprivation schedule and 5-7 days later retraining on the three discriminations began. After reaching criterion on all three discriminations after the VC lesion, four of the cats received control retention periods for 40 days during which no training was administered. These cats were then retrained to criterion on all tasks. This provided a measure of the amount of forgetting that would be expected from cats with VC lesions over the same time period spanned by surgery and recovery.

The eight cats were assigned to one oftwo groups matched as closely as possible for preoperative and postoperative trials to criterion, S^+ on each of the three tasks and retention period versus no retention period. The first group received a lesion intended to include LS bilaterally and the second group received a lesion intended to include all SSC except LS. After the standard recovery period all animals were then tested for retention of the previously learned tasks.

Following the final lesion testing on the L-D discrimination was continued for each cat for as long as it required in original learning or for 15 days (the approximate number of days required by all cats in original learning), whichever was longer. Similarly, H-V testing continued for 10 days and triangles for 15 days or for as many days as

required in original learning, whichever was longer.

Surgery and Histology

All surgery was performed under aseptic conditions. Animals were given 0.25mg atropine sulfate and then anesthetized with pentobarbital sodium (Nembutal, 40mg/kg), both drugs given intraperitoneally. Ablation was performed by aspiration after retraction of the overlying meninges. The VC lesions were intended to be identical to those described by Spear and Braun (1969), including the marginal gyrus, posteromarginal gyrus, dorsoposterior genu of the middle suprasylvian gyrus, and suprasplenial and splenial gyri bilaterally. This lesion was thus intended to include areas 17, 18 and 19 (Otsuka & Hassler, 1962). The LS lesion included the entire medial wall of the middle suprasylvian sulcus and approximately 6-7mm of the posterior extent of the caudal wall of the posterior suprasylvian sulcus. For two animals in this group the lesion extended slightly up the lateral wall of the middle suprasylvian sulcus near the posterior genu of the ectosylvian gyrus, in accord with the anatomical limits of LS as defined by Heath and Jones (1971). The second group's lesion (CROWN) consisted of all middle and posterior SSG except the LS area. Postoperatively, all animals were given a single dose of a broad-band antibiotic (Bicillin, 300,000 units).

For histological preparation animals were given a lethal dose of pentobarbital sodium and profused through the heart with 0.9% saline followed by 10% formol-saline. Brains

were blocked, removed from the skull and stored in 10% formol-saline. After embedding in celloidin, all brains were sectioned at 40μm. Every fifth section through the posterior thalamus and every fifteenth section through the cortical lesion was mounted and stained with cresyl violet. The extent of the cortical lesions was assessed for each animal by examination of the serial stained sections. Lesion reconstructions were made at 1mm intervals on surface maps adapted from the atlas of Reinoso-Suarez (1961). Detailed analysis of the retrograde degeneration of the DLGN, LP, PN and PUL was assessed.

RESULTS

Histology

Although the SSG lesions were intended to fall into two groups, LS and CROWN, histological analysis indicates that the lesions actually fell into three groups: LS only, CROWN only and LS + CROWN (due to undercutting during the LS lesion in two cats). Figure 2 shows surface reconstructions and coronal sections through the cortical lesions together with projection drawings of anterior, middle and posterior sections through the left and right DLGN for a representative cat in each group. Laminae of the DLGN are labeled in figure 2 according to the terminology of Thuma (1928) and Guillery (1970): the main laminae A, A1 and C and the central and medial interlaminar nuclei, CIN and MIN, respectively. The sublayers within layer C are not indicated. Retrograde degeneration in the DLGN was interpreted accordin

to the results of Garey and Powell (1967), Niimi and Sprague (1970) and Burrows and Hayhow (1971). Combined damage to areas 17, 18 and 19 results in severe degeneration of the main laminae of the DLGN and of the CIN and only moderate degeneration (i.e., several scattered healthy cells) in the MIN, possibly due to its remaining projection to the LS area (Garey & Powell, 1967; Burrow & Hayhow, 1971; Rosenquist, et. al., 1974). Undegenerated areas in the MIN are considered to indicate the presence of remaining cortical tissue in both areas 18 and 19. Lesions of 18 and 19 but with 17 spared results in marked degeneration in the MIN and CIN and little or no degeneration in the main laminae. LP, PUL, and PN were also assessed for retrograde degeneration.

Histological analysis for six of the cats is presented below. Two additional cats in the CROWN group (SL-1 and SL-10) received a third lesion including the LS cortex. Histological analysis for these animals will not be available for several months.

LS Group

The surface reconstructions and coronal sections in figure 2a indicate that the VC lesion for SL-7 was incomplete with sparing of area 17 on the medial wall of the hemisphere and a small portion of area 19 in the depths of the lateral sulcus. In accord with the sparing of area 17 the most posterior sections of the DLGN showed areas of sparing.

The SSG lesion consisted of bilateral removal of from

50 to 100% of the dorso-ventral extent of LS with no damage to the crown of the gyrus. A total of 70-80% of LS was removed. The posterior genu of the ectosylvian gyrus was also damaged, moreso on the right than the left. PSS was spared bilaterally. LP showed moderate to severe degeneration throughout its entire extent while PUL showed little or no degeneration. PN was severely degenerated (i.e., few, if any healthy cells present) but MIN only moderatly so, probably reflecting the minimal sparing of both areas 19 and LS.

The VC lesion of SL-12 was almost identical to that of SL-7 except that slightly more of area 17 on the medial wall was spared. The degeneration in the DLGN was similar to that of SL-7 with sparing in the most posterior sections.

The SSG lesion was also similar to that of SL-7 with the addition of damage to the anterior middle portion of the crown of the gyrus on the left side. Degeneration in LP, MIN and PN was similar to that of SL-7. PUL on the left showed moderate to severe degeneration reflecting the damage to the crown of the SSG on that side. The right PUL showed little or no degeneration.

CROWN Group

The surface diagrams in figure 2b show that the extent of the VC removal in SL-5 included all of areas 18 and 19 and most of area 17. There was apparent sparing of area 17 posteroventrally on the medial wall of both hemispheres. However, only the right DLGN showed localized regions of

sparing in the main laminae in the posterior sections. The left DLGN was severely degenerated throughout its entire extent with only a few scattered large cells present.

The SSG lesion included the crown of the gyrus with only minimal sparing of area 20. PSS and LS were spared bilaterally, as shown by the coronal sections in figure 2b. PUL was severely degenerated throughout its entire extent with only small crescents of normal healthy cells in the dorsal extremities. LP showed mild degeneration in its anterior portions and otherwise appeared normal. MIN and PN showed only moderate degeneration throughout.

The VC lesion for SL-6 included all of areas 17, 18 and 19. The main laminae of the DLGN showed severe degeneration throughout their entire extent.

The SSG lesion included all of the middle SSG crown and up to 60% of the dorso-ventral extent of LS bilaterally, with the average involvement being 40-50%. The areas of LS that were spared are known to represent the central visual field, while the areas removed contain a representation of the peripheral visual field (Spear & Baumann, 1975a; Hubel & Wiesel, 1969; Wright, 1969). Posteriorly, area 20, and PSS were spared. There was also slight damage to ectosylvian gyrus bilaterally. Only the anterodorsal sections of the LP showed any signs of degeneration and both MIN and PN showed moderate degeneration. PUL was severely degenerated.

LS + CROWN Group

The surface reconstructions in figure 2c show that the extent of VC removal in SL-4 included all of areas 17, 18 and 19. There was no localized sparing in any of the main laminae of the DLGN.

LS was removed bilaterally with only minimal sparing on the left as indicated by the coronal sections in figure 2c. Though the crown of the gyrus was not damaged it was severely undercut throughout its entire extent with only 30-40% of the crown apparently intact. Correspondingly, there was moderate degeneration throughout the entire extent of PUL with localized sparing only in its dorsal portions. MIN and PN were more severely degenerated than in SL-5 though there was some localized sparing posteriorly in the left PN. LP showed moderate degeneration throughout its entire extent.

The VC lesion of SL-2 was complete as intended, including all of areas 17, 18 and 19. There were no localized regions of spared cells in any of the main laminae of the DLGN.

The SSG lesion included the entire crown of the gyrus but with only partial damage to PSS bilaterally. The LS and PSS areas were spared bilaterally but on the left these areas were markedly shrunken with extensive chromatolysis present. This was reflected in the conspicuous lack of healthy cells in both MIN and PN and by the moderate degeneration of LP throughout the left posterior sections. MIN and PN on the right showed only moderate degeneration.

LP showed only slight degeneration in its most anterior portions. PUL was severely degenerated.

Behavioral

Figures 3 and 4 present median percent correct on the three discriminations as a function of successive blocks of 40 trials at different stages of the experiment. Group curves were constructed by computing a group median for each successive block of trials from the individual percent correct scores for each cat. Since training was discontinued after a given cat had reached the 90% correct criterion on two successive days, a score of 90% was given to each cat after criterion had been reached for purposes of computing the group curves. Tables 2, 3 and 4 summarize the performance of all cats following the first lesion (VC), retention period after the VC lesion and second lesions (SSG) respectively.

For purposes of analyzing the data prior to the second lesion the eight cats were divided into two groups on the basis of the extent of the second lesion: one group with damage to the SSG crown and little or no damage of LS (CROWN), and one group which showed damage or degeneration of LS either alone (LS) or in addition to the SSG crown (LS + CROWN). Table 4 shows the cats that fell into each group.

Original Learning

The median number of blocks to criterion for all cats in this experiment for the L-D, H-V and TRI tasks were 13, 5 and 12, respectively, and the median number of errors for

the three tasks were 149, 36 and 137 respectively. (Number of errors were calculated for the first 15, 10 and 15 days of training for the L-D, H-V and TRI tasks respectively. These are the same number of days used for calculating errors after the second lesion.) T tests for independent groups showed that there were no significant differences between the two groups for error scores or blocks to criterion on any of the tasks in preoperative learning (p .05).

VC Lesions

Table 2 shows ranges and median number of blocks to criterion, number of cats performing significantly above chance on the first post VC day of training and number of cats with positive savings scores for each of the three tasks. T tests for independent groups showed that there were no significant differences between the two groups on any of the three tasks for post VC performance (p .05). That all three discriminations were disrupted as a result of the VC lesion is indicated by the fact that all but one cat on the H-V task and one on the TRI task performed within chance levels on the first postoperative day of retraining. While all cats were able to relearn all three discriminations they required more trials than in original learning as indicated in figure 3. There was no correlation between amount of sparing of 17, 18 or 19 and savings following the VC lesion.

All cats dropped to within chance levels of performance when tested with blanks after reaching criterion on the H-V task and after the TRI task, indicating that no extraneous

nonvisual cues were being used in making the discrimination.

VC Lesion ± Retention Period

Table 3 presents percent correct on the first day of training, performance and number of errors after 15, 10 and 15 days of training for the L-D, H-V and TRI tasks for each cat that received a retention period following the VC lesion. Performance following the retention period for the three tasks is shown by open triangles in figure 4. For the L-D discrimination all animals showed an initial drop in performance but subsequently returned to criterion in 5 to 20 blocks of retraining. There was only a minimal drop in initial performance for the H-V task and all animals returned to criterion in four or less days of retraining. For the TRI task there was an initial drop in performance and a subsequent return to criterion in 3 to 9 blocks of trials. Again, all cats dropped to within chance levels of performance when tested with blanks. There was no correlation between amount of VC sparing and retention performance.

Lesions of VC and different areas of the SSG

Table 4 summarizes the cortical areas remaining following the second lesion, performance on the first and last day of testing and the number of errors during the testing period for each cat on the three tasks. SL-1 and SL-10 are not available for histological analysis at the present time. Their intended lesions included the crown of the SSG in addition to the initial VC lesion.

Figure 4 presents median percent correct as a function

of blocks of 40 trials for the three groups on each task. T tests showed that there was no significant difference between the two main groups on the L-D task for any of the measures taken (i.e., first day performance, final day performance and number of errors during testing) and neither of the two groups differed from performance following a retention period after a VC lesion ($p < .05$). However, t tests indicate that cats lacking LS plus portions of the SSG crown are more deficient on a L-D task than cats with either damage to LS alone or the SSG alone. Comparing the LS and the LS + CROWN groups reveals that the LS + CROWN cats were significantly lower than the LS cats on the final level of performance ($p < .05$) and had a marginally greater number of errors ($p < .075$). Furthermore, the performance of the LS group was not different from that of the CROWN group or performance after a VC retention period ($p < .05$). The final level of performance of the LS + CROWN group on the other hand, was significantly worse than that of the CROWN group and performance after a VC retention period ($p < .05$). Also, the LS + CROWN group had a significantly greater number of errors than animals after a VC retention period ($p < .05$).

After the allotted 15 days of testing on the L-D task those cats which were not at criterion were placed on a new L-D discrimination with the bright stimulus increased in intensity from 270mL to 583mL. This was to insure that all cats were performing at a criterion level before

proceeding to the next task. Only one cat in the CROWN group was placed on this discrimination whereas three in the LS and LS + CROWN groups required such training. All animals reached criterion in 2-7 days after being placed on this task.

Randomization tests showed that the two main groups were significantly different on all three measures of performance for the H-V task ($p < .05$). All animals in the CROWN group reached criterion within the number of days allotted for testing as indicated in table 3. Furthermore, for these cats randomization tests indicate that there was no significant difference between performance following a retention period after a VC lesion, which is apparent from figure 4 ($p > .05$). On the other hand, only one cat (SL-7) in the LS or LS + CROWN groups reached criterion on the H-V task, and its performance resembled that of animals following a retention period after a VC lesion. The three cats with LS damage that did not reach criterion on the task performed significantly better than chance after the second lesion (sign test, $p < .05$). The LS and LS + CROWN groups performed worse than animals following a VC lesion and retention period on all measures of performance (randomization tests, $p < .05$). When presented with blanks all animals dropped to chance or below chance performance indicating that they were discriminating on the basis of visual cues.

Using randomization tests the two main groups were significantly different on all measures of performance for

the TRI task (p .05). All cats in the CROWN group reached criterion within the number of days allotted for testing and the performance of these animals was not different from performance following a retention period after a VC lesion (p .05). No cats with LS or LS + CROWN damage were able to reach criterion and all of these cats were performing within the 95% confidence interval for chance performance on the final day of testing. The LS and LS + CROWN groups performed significantly worse than animals following a VC lesion and retention period on all measures of performance (p .05). A sign test indicated that over the testing period these cats performed consistently above the 50% correct level (p .05). When tested with blanks all cats dropped to 50% correct or below.

DISCUSSION

Performance after VC removal and after a retention period following VC removal

The results of the present experiment agree with previous reports that removal of areas 17, 18 and 19 produces a complete loss of preoperatively learned pattern and form discriminations (Spear & Braun, 1969; Wood, et. al., 1974; Winans, 1967, 1971). However, for an H-V discrimination, Spear and Braun (1969) and Wood, et. al., (1974) report that their animals required a much greater number of trials to reach criterion for both preoperative and post VC learning

than required in the present experiment. On the other hand, Winans (1967, 1971) results for a triangle discrimination are similar to those of the present study in terms of amount of training to reach criterion, both pre- and postoperatively. The differences may be due to the task the cat was required to perform. In the Spear and Braun (1969) and Wood, et. al. (1974) studies the cats were required to push the correct door with their paw and received reward in a food cup beneath the door. In Winans' (1967, 1971) and the present study the cat was required to push open a door with his head or paw and received the reward behind the door he had pushed open. Furthermore, the animal was required to hold the door open so that he would have access to the reward cup. The latter case provides for greater stimulus-reward contiguity than that of the Spear and Braun (1969) or Wood, et. al. (1974) studies and this could possibly account for the difference in learning speeds.

The performance of cats following a retention period after VC removal indicates that there was a considerable loss on the L-D and TRI discriminations and only a minimal loss on the H-V task. Wood, et. al. (1974) report a much greater loss on an H-V task after a VC retention period than in the present study. Their two cats returned to criterion after 11 and 19 days of retraining which is approximately 3 to 5 times longer than required by animals in the present study. Unfortunately, number of errors or first day

performance are not reported by Wood, et. al. (1974) making a more thorough comparison with the present study impossible. However, the differences in the experimental situations discussed above may account for this difference in relearning times.

The role of LS after VC removal

The results of the present experiment indicate that LS is the SSG area important for functional recovery of pattern and form discrimination following removal of VC. For the L-D discrimination however, a deficit was produced only when both LS and the SSG crown were damaged. The two animals with such damage were performing at 60 and 67% levels at the end of testing. All other animals however, were performing at or near criterion level at the end of testing and they showed no loss other than that expected from a retention deficit. That both animals returned to criterion after the bright stimulus was increased in intensity may suggest that there was a change in their difference threshold as a result of the damage to LS and the crown, thus making the original discrimination more difficult.

Removal of LS consistently resulted in a discrimination loss on the H-V and TRI tasks as compared with the retention period. That SL-2 with unilateral LS damage showed a deficit while SL-6 with bilateral damage of approximately 40-50% of LS did not might seem inconsistent with such an interpretation. However, the portion of LS that was removed

in SL-6 contained a representation of the peripheral visual field (Spear & Baumann, 1975a; Hubel & Wiesel, 1969). That is, the LS cortex representing the central visual field was left intact bilaterally. SL-2 on the other hand, had unilateral damage to the cortex representing the entire visual field which could conceiveably be responsible for the discrimination loss.

The role of other SSG areas and remnants of area 17 after VC removal

Although the eight cats were dichotomized into two groups on the basis of presence or absence of LS damage, cats in both groups frequently had area 20, PSS and medial 17 remaining. There was no correlation between the amount of recovery after VC removal and the amount of area 17 that was spared, which is consistent with previous reports (Spear & Braun, 1969; Winans, 1971). Furthermore, the presence or absence of any of these areas does not correlate well with the presence or absence of a discrimination loss in the same manner as the presence or absence of LS does. For example, SL-5 had unilateral sparing of medial 17, bilateral sparing of PSS and an intact LS and showed no loss whereas SL-7 and SL-12 had these same areas remaining but without LS and showed a loss. Therefore it seems reasonable to conclude that the portions of medial 17 and SSG areas other than LS that remained are not involved in functional recovery, at least not to the extent that LS appears to be.

It is clear from the differences between the two

main groups that LS is involved in recovery after VC removal but the presence of PSS in both CROWN cats with available histology does not permit the conclusion that LS is the only area involved in recovery. That is, it may be that both LS and PSS are important in functional recovery. Although Heath and Jones (1971) suggest an anatomical distinction between these areas they express several reservations about this conclusion and state that LS could extend onto the dorsal portion of the caudal bank of the posterior suprasylvian sulcus. Thus, sulcal PSS may be a continuation of LS.

Possible role of the SC and SSG

The superior colliculus (SC) has been implicated in recovery of function after VC removal the same as the SSG has. Since the SC is indirectly connected to the SSG via posterior thalamic nuclei it might be suggested that SC removal produces an effect due to its indirect cortical projections, especially to LS. Initial removal of either the SC or LS produces little or no deficit in preoperatively learned tasks (Wood, et. al., 1974; Hara & Warren, 1961a,b; Hara, 1962; Warren, Warren & Akert, 1961; Berlucchi, Sprague, Levy & DiBerardino, 1972; Adler & Meikle, 1975). If however, the SC or LS is lesioned in addition to VC profound deficits occur (Wood, et. al., 1974; the present study; Adler & Meikle, 1975; Fischman & Meikle, 1965; Urbaitis & Meikle, 1968). Nevertheless, a recent study indicates that the SC is not totally dependent on its indirect cortical projections

for its effects. Adler and Meikle (1975) showed that combined lesions of VC and SC produce a greater deficit in original learning of a form discrimination than a combined VC and SSG lesion. This may possibly be due to the fact that SC lesions produce deficits in original postoperative learning (Berlucchi, et. al., 1972; Adler & Meikle, 1975). No data are currently available concerning initial learning after a SSG lesion.

No data concerning the SC address the issue of recovery of pattern and form discriminations after a VC lesion. For a brightness discrimination however, similar results have been obtained for the SC and the SSG. Fischman and Meikle (1965) showed a second loss on an L-D task after a secondary SC lesion following a VC lesion and postoperative retraining. Similar results were obtained in the present experiment with a secondary lesion of the SSG. No data are available for secondary lesions using pattern and form discriminations and hence no statements can be made concerning which area is more involved in functional recovery, LS, SC or both, following VC removal.

TABLE 1 SEQUENCE OF LESIONS AND RETENTION PERIODS

SL-1	TR	VC	RETR	RET	RETR	CROWN	TEST
SL-10	TR	VC	RETR	RET	RETR	CROWN	TEST
SL-5	TR	VC	RETR	---	----	CROWN	TEST
SL-6	TR	VC	RETR	RET	RETR	CROWN	TEST
SL-7	TR	VC	RETR	RET	RETR	LS	TEST
SL-12	TR	VC	RETR	---	----	LS	TEST
SL-2	TR	VC	RETR	---	----	LS+CR	TEST
SL-4	TR	VC	RETR	---	----	LS+CR	TEST

TR-Preoperative training to criterion on all three tasks
VC-Visual cortex lesion
RETR-Postoperative retraining on all three tasks
RET-Forty day retention period
CROWN-Cats receiving a second lesion of the SSG crown
LS-Cats receiving a second lesion of LS alone
LS+CR-Cats receiving a second lesion of LS + the crown of the SSG

TABLE 2 PERFORMANCE FOLLOWING THE VC LESION

GROUP	N	TASK	MDN # BLOCKS TO CRITERION	RANGE OF BLOCKS TO CRITERION	# Ss SIGNIFICANTLY ABOVE CHANCE ON DAY 1	# Ss WITH + SAVINGS
CROWN	4	L-D	26	10-37	0	1
		H-V	9	4-25	1	0
		TRI	10	6-76	2	2
LS	2	L-D	19	15-22	0	0
		H-V	16	11-21	0	0
		TRI	29	29	0	0
LS + CROWN	2	L-D	15	13-16	0	0
		H-V	25	7-43	0	0
		TRI	18	18	0	0

TABLE 3 PERFORMANCE FOLLOWING A VC RETENTION PERIOD

CAT	% CORRECT ON DAY 1			PERFORMANCE ON NTH DAY OF TESTING			# ERRORS		
	L-D	H-V	TRI	L-D	H-V	TRI	L-D	H-V	TRI
SL-1	72	65	65	C	C	C	145	31	60
SL-10	62	87	77	C	C	C	49	8	12
SL-6	60	90	65	70	C	C	201	8	96
SL-7	65	77	67	C	C	C	103	17	38

C-Criterion level performance (i.e., 90% correct on two consecutive days)

Number of errors and performance on "Nth" day of testing were determined for 15, 10 and 15 days of training for the L-D, H-V and TRI tasks respectively.

TABLE 4 PERFORMANCE FOR EACH CAT AFTER THE SECOND LESION

GROUP	CAT	AREAS REMAINING	% CORRECT ON DAY 1			PERFORMANCE ON LAST DAY OF TESTING			# ERRORS		
			L-D	H-V	TRI	L-D	H-V	TRI	L-D	H-V	TRI
CROWN	SL-1	**	75	72	72	70	C	C	179	34	60
	SL-10	**	65	97	70	C	C	C	139	2	46
	SL-5	Med. 17(U), LS, PSS	55	90	80	C	C	C	61	8	21
	SL-6	20, PSS, 50% LS	52	67	62	C	C	C	137	53	50
LS	SL-7	PMS, AMS, 20, 21, PSS, Med. 17, 19	70	82	47	80	C	60	142	53	249
	SL-12	PSS, PMS, AMS(U), 20, 21, Med. 17	70	65	--	C	57	--	66	152	--
LS + CROWN	SL-2	LS(U), PSS(U)	50	67	52	67	65	60	190	129	227
	SL-4	Minimal AMS, PMS	65	50	50	60	67	55	201	132	258

(U)-Indicates that the brain area listed as remaining is present only on one side, i.e., unilaterally.

Med.-Medial

C-Criterion level performance (i.e, 90% correct on two consecutive days)

Number of errors and scores for the last day of testing were determined for 15, 10 and 15 days of testing for the L-D, H-V and TRI tasks respectively.

FIGURE CAPTIONS

Figure 1

Dorsal view of the cat brain showing the different anatomical divisions of the lateral and suprasylvian gyri according to Otsuka and Hassler (1962) and Heath and Jones (1971). Areas 7, 17, 18, 19, 20 and 21 are as indicated. PSS-posterior suprasylvian sulcus; LS-lateral suprasylvian area.

Figure 2

Upper left: Surface reconstructions showing a dorsal view and the medial surface of the left and right hemispheres are presented for three cats. These three cats were chosen to show representative lesions for each of the three groups. The retracted splenial sulcus on the medial surface allows representation of the extent of the lesion along the dorsal bank of the sulcus. Stippling indicates cortex that was removed and stripes indicates cortex that was undercut. A-dorsal lip of the splenial sulcus; B-fundus of the splenial sulcus. Right: Projection drawings of coronal sections through the lesion at positions indicated by the lines extending through the surface reconstructions. The number above each section indicates its stereotaxic coordinates in millimeters anterior (+) or posterior (-) from the interaural zero plane. Lower left: Projection drawings of coronal sections through the left and right DLGN at three different levels through the nuclei. VLGN-ventral lateral geniculate nucleus; MIN-medial interlaminar nucleus; CIN-

central interlaminar nucleus; A, Al and C indicate the three major laminae of the main body of the DLGN. Dots indicate the presence of healthy, large principle cells.

Figure 3

Median percent correct plotted as a function of blocks of 40 trials for preoperative (open circles) and post VC (filled circles) learning on each of the three discrimination tasks for all cats in the present experiment.

Figure 4.

Median percent correct plotted as a function of blocks of 40 trials for performance following lesions of VC + SSG crown (open circles), VC + LS (filled circles) VC + SSG crown + LS (filled triangles) and VC + a retention period (open triangles) for each of the three discrimination tasks. The dashed line indicates the upper limit of the 95% confidence interval around the chance level of performance which is indicated by a solid line at 50% correct. The vertical line at 15 days for the L-D task indicates the point at which the bright stimulus was increased in intensity. See text for details.

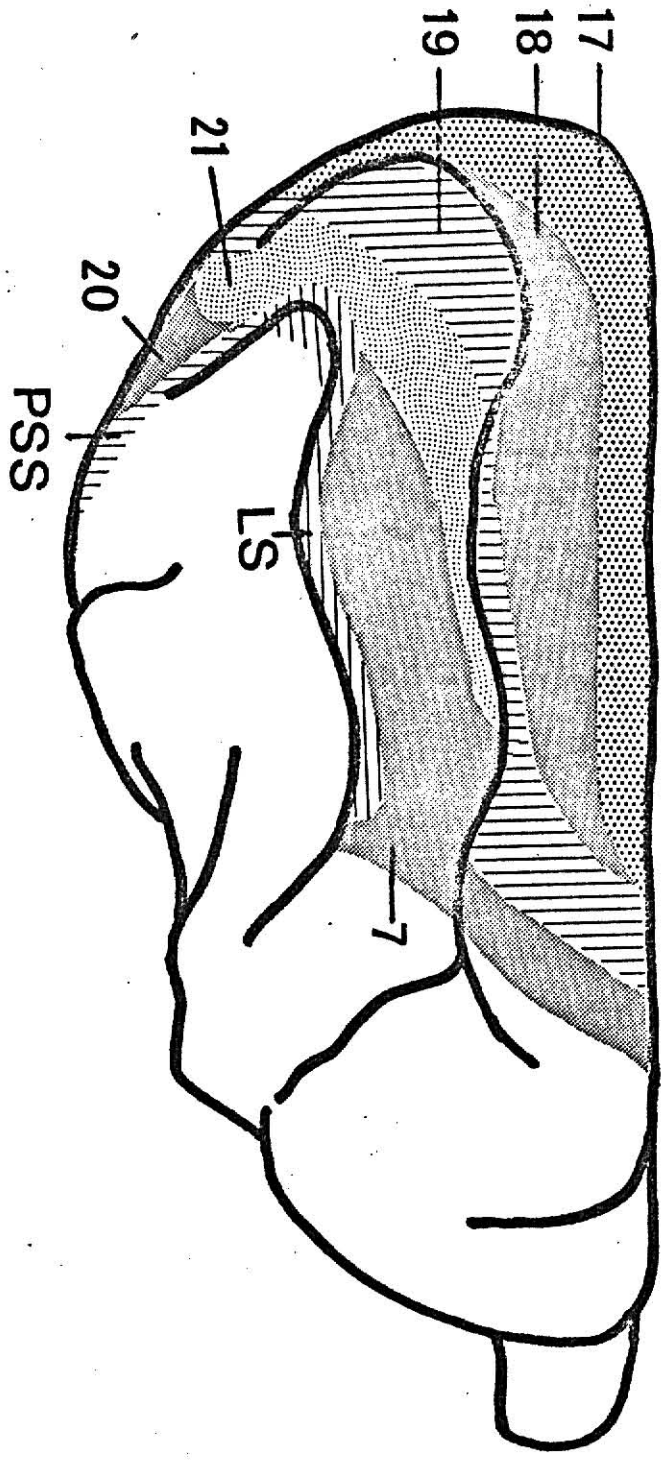

FIGURE 1

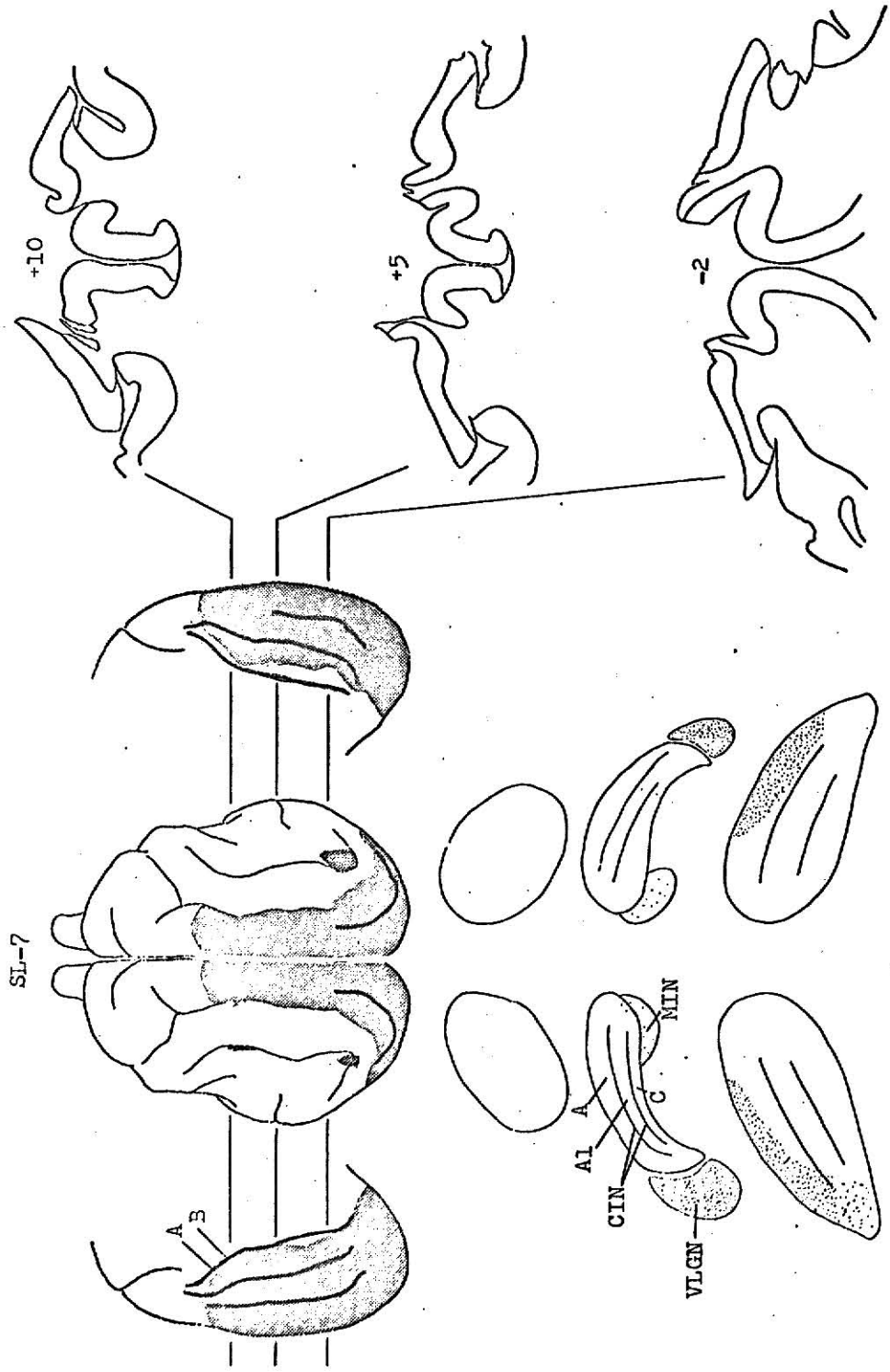

FIGURE 2a

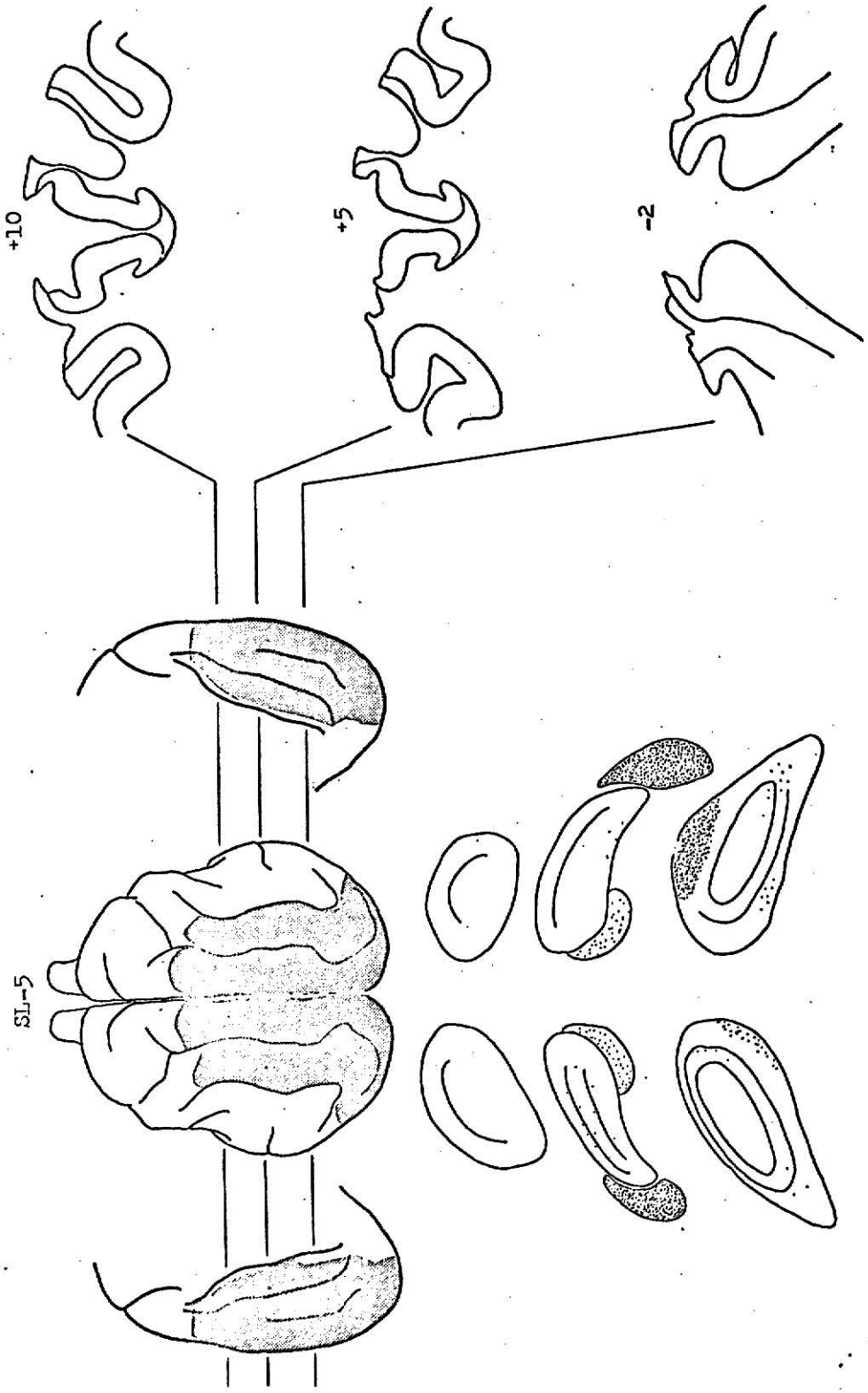

FIGURE 2b

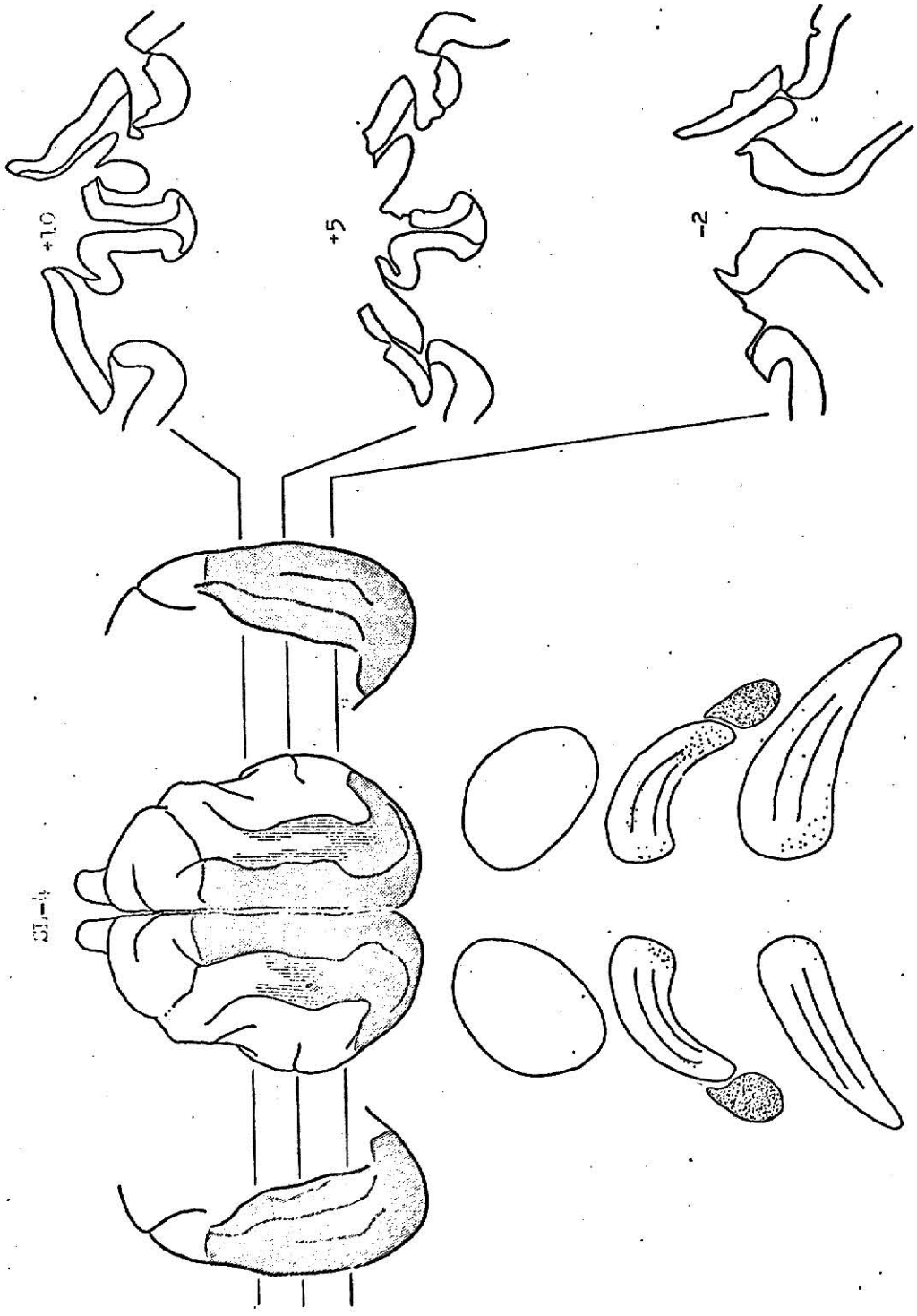

FIGURE 2c

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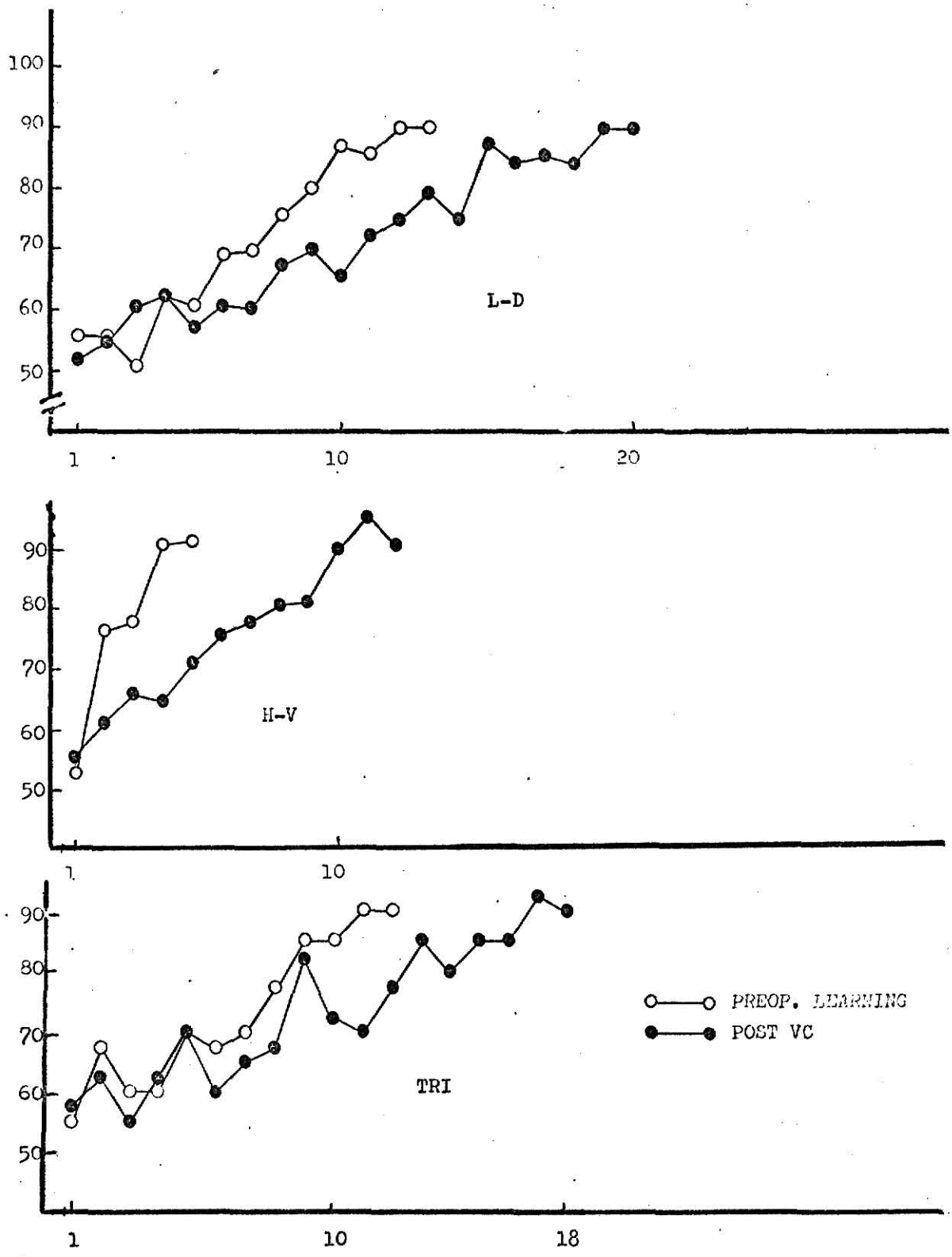
100
90
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L-D
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TRI
1
10
18
PREOP. LEARNING
POST VC
BLOCKS OF 40 TRIALS

FIGURE 3

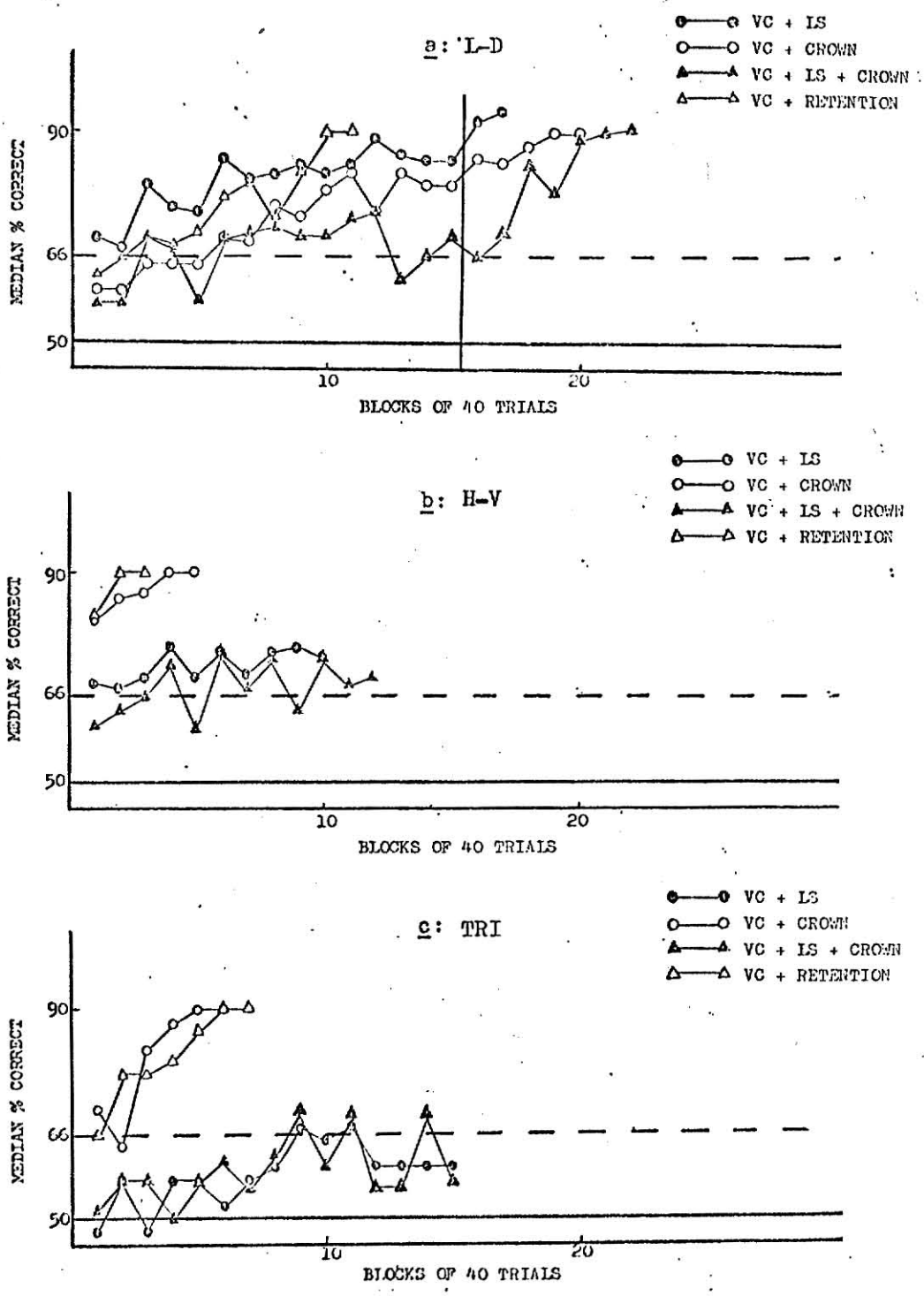
a: L-D
VC + LS
VC + CROWN
VC + LS + CROWN
VC + RETENTION
MEDIAN % CORRECT
90
66
50
10
20
BLOCKS OF 40 TRIALS
b: H-V
VC + LS
VC + CROWN
VC + LS + CROWN
VC + RETENTION
MEDIAN % CORRECT
90
66
50
10
20
BLOCKS OF 40 TRIALS
c: TRI
VC + LS
VC + CROWN
VC + LS + CROWN
VC + RETENTION
MEDIAN % CORRECT
90
66
50
10
20
BLOCKS OF 40 TRIALS

FIGURE 4

EXPERIMENT II

Animals lacking visual cortex (VC) can discriminate stimuli that have been equated for total luminous flux if there are differences in amount of contour (Mize, Wetzel & Thompson, 1971; Wetzel, 1969; Weiskrantz, 1963), local luminous flux (Winans, 1967, 1971), brightness and/or size (Pasik, Pasik & Schilder, 1969; Schilder, Pasik & Pasik, 1971). However, even when such cues are eliminated discriminations are still possible. For example, cats lacking all of areas 17, 18 and 19 can discriminate between horizontal-vertical striped stimuli (H-V) which are equated for total luminous flux and contour length and in which consistent trial-to-trial local luminous flux cues have been eliminated (Spear & Braun, 1969; Wood, Spear & Braun, 1974). It has been suggested that in this case animals lacking VC are not discriminating on the basis of the spatial aspects of the stimuli as such, but rather are using behavioral strategies to produce discriminable cues (Spear & Braun, 1969; Wood, et al., 1974; Ward & Masterson, 1970; Ware, Diamond & Casagrande, 1972). It is known that animals lacking VC show optokinetic nystagmus elicited by moving vertical stripes (Baden, Urbaitis & Meikle, 1965; Smith, 1937; Spear & Braun, 1969; Wood, Spear & Braun, 1973) and can discriminate intermittent photic stimulation from steady light (Schwartz & Cheney, 1966; Taravella & Clark, 1963). Such cues are potentially present in a horizontal-vertical stripes discrimination.

For example, up and down head or eye movements would produce a series of on-off signals for the H stimulus but not for the V stimulus. The animal could then discriminate on the basis of the differential flicker rates.

One approach to answering the question of whether or not VC animals are using such flicker cues is to experimentally produce flicker which should disrupt any flicker cues the animal itself is generating.

METHODS

Subjects

Six adult cats of both sexes were used. Four of these also served as subjects in Experiment I. All animals were housed in a large room in group cages and were on a 12 hour light-dark schedule.

Apparatus

The apparatus used in the present experiment was the same as that used in Experiment I with the addition of two rotary motors which were placed between the projectors and the choice panels for use in stimulus flicker testing (see below). A Grass model PS2E Photostimulator was used for background flicker testing (see below).

Two discrimination tasks were employed: brightness discrimination (L-D) and vertical versus horizontal stripes. For the L-D discrimination two animals were trained with the bright choice panel illuminated at 538mL and the dark panel at 34mL. Four animals were trained with the bright stimulus at 270mL and the dark stimulus at 34mL.

The H-V discrimination was the same as that used in Experiment I.

Discrimination Training

For details of discrimination training see Experiment I.

The correct stimulus for the L-D and H-V tasks was assigned randomly for each cat preoperatively. Five cats were trained with the bright and one cat with the dark stimulus correct; three cats were trained with H correct and three with V correct.

Design and Procedure

Four of the cats were trained on both discrimination tasks and two received only the brightness discrimination training before surgery. One animal received flicker testing prior to surgery (see below). After a 6-10 day period of ad lib food and water all cats underwent bilateral removal of VC. Following a 23-25 day recovery period all cats were placed back on the food and water deprivation schedule. Five to seven days later they were trained to criterion on the brightness and H-V discriminations in that order. After reaching criterion on the H-V task five of the cats were tested with three different types of flicker (see below). One additional cat was retrained to criterion and then received a second lesion involving the crown of the suprasylvian gyrus (SSG). After recovery, this animal then received flicker testing.

For the first type of flicker, stimulus presentation remained constant but the background illumination flickered

(background flicker). The effect of the background flicker was to reduce the contrast of the stimuli while the background light was "on". Two different intensities of background flicker were employed. For the brighter level, the luminance of the bright stripe became 320mL and the dark stripe became 126mL. For the dimmer flicker the light and dark stripes were illuminated at 240mL and 86mL respectively. For the brighter intensity the following flicker rates were tested: 5, 10, 20, 30, 40, 50, 60, and 70hz. For the dimmer flicker the rates tested were: 5, 10, 15, 20, 30, 40, and 50hz. The duration of flashes for both types of flicker was .01sec. These ranges of frequencies adequately exceed the CFF for cats with VC lesions (Schwartz & Cheney, 1966).

For the second type of flicker testing the stimuli themselves flashed on and off by means of the two rotary motors placed between the projectors and the choice panels (two-stimulus flicker). Background illumination remained constant. Flicker rates of 10 and 20hz were tested. On and off durations were 50msec. at 10hz and 25msec. at 20hz respectively.

If the cats are making the discrimination on the basis of the presence or absence of flicker in one of the stimuli then flickering both stimuli or flickering the background illumination should disrupt performance. However, this is not the case if they are making the discrimination on the basis of a relative difference in flicker rates between the

two stimuli. That is, with both stimuli flickering at the same rate or with the background flickering the cat could still make the discrimination on the basis of a relative difference in flicker rates the animal itself would be generating. For example, he may always choose the stimulus with the slower or faster flicker rate. The third type of flicker testing was designed to disrupt any relative difference in flicker rates that the animal may be using to make the discrimination. Only one stimulus flickered for this test (one-stimulus flicker). That is, only the H or V stimulus flashed on and off while the other stimulus remained constant for all trials in a test session. Flicker rates and durations were the same as those used for the two stimulus flicker.

Each type or rate of flicker was tested for a block of 20 trials. Typically, two blocks of different types and/or rates of flicker were given on the same day. The different rates and types of flicker were presented in a random order. Following the flicker testing, or interspersed between 20 trial blocks of flicker, all animals were tested with two blocks of 20 trials with an indiscriminable brightness task (blanks) to insure that no extraneous nonvisual cues were used in making the H-V discrimination. On such days both choice panels were illuminated at 140mL for 20 trials followed by 20 trials of stimuli, either flickering or stationary.

Surgery and Histology

See Experiment I for descriptions of the VC and SOG

crown lesions and for histological procedures.

RESULTS

Histology

Surface reconstructions for the cortical lesions together with projection drawings of anterior, middle and posterior sections through the right and left DLGN are shown for two representative cats in figure 1. These cats were selected to show the largest and smallest lesions of all cats in the present experiment. See Experiment I for details of procedure for lesion reconstructions.

For the cats that also served in Experiment I it is impossible to distinguish histologically between tissue removed or damaged as a result of the VC lesion or as a result of any subsequent SSG lesion, particularly with regard to areas 18 and 19. Damage to area 17 should not be confounded as a result of any subsequent lesion. The cats from Experiment I that were also used for the present study were: SL-5, SL-7, SL-10 and SL-12. Histological analysis for the two cats not included in Experiment I are presented below.

AVC-42

Figure 1a shows that the VC lesion for this cat was complete, including all of areas 17, 18 and 19. In addition, the right middle suprasylvian gyrus was severely undercut and degenerated. There was no localized sparing in any of the main laminae of the DLGN. MIN on the left showed moderate degeneration (i.e., several scattered healthy cells).

The MIN on the right however, showed more severe degeneration reflecting not only the damage to areas 18 and 19 but also the shrinkage of the lateral suprasylvian area. Also on the right, the pulvinar and the lateral portions of the lateral posterior nucleus showed severe degeneration as a result of the damage to the SSG.

AVC-14

The VC lesion for this cat was clearly incomplete, with bilateral sparing of area 17 on the medial wall of the hemisphere particularly on the right, as indicated in figure 1b. Portions of area 19 were also spared in the depths of the lateral sulcus. There were large regions of spared normal, healthy cells in the intermediate, lateral portions of the DLGN on the left and throughout the intermediate and posterior sections of the right DLGN. MIN showed only slight degeneration, in accord with the sparing of area 19.

Behavioral

Cats trained preoperatively on the H-V task showed zero or negative savings when retrained postoperatively, which is consistent with previous reports (Wood, et. al., 1974; Spear & Braun, 1969). Postoperative trials to criterion for animals not trained preoperatively were within the range of postoperative scores obtained for animals which also received preoperative training.

Figure 2a-b presents the ranges and median percent correct for the different types of flicker as a function

of frequency (hz). Group curves were constructed by computing a group median for each successive block of trials from the individual percent correct scores for each cat. Scores for the one cah which was tested following removal of both VC and the SSG crown are included in this graph since the animal's performance was not different from that of animals lacking only VC. There was no significant effect of flicker, as all medians are significantly above chance ($p < .05$, binomial test). In addition, no animal's performance dropped to within the 95% confidence interval for any type or rate of flicker on any given day. However, performance did frequently drop from the 90% criterion level and on six occassions scores of 75% were recorded, though these did not occur systematically.

Although only rates of 10 and 20hz were used for the stimulus flicker the speed with which the discrimination was made on any given trial suggests that animals were not generating flicker rates lower than approximately 10hz. It typically took the animals less than 1.50sec. from the time the start panel was pushed to the time a choice was made. The discrimination actually took less time than that since there was a 1.10sec. interval between the pushing of the start panel and the presentation of the stimuli on the choice panels.

Figure 3 presents individual animal's performance for days on which blanks were presented. No scores for either stationary or flickering stimuli fell within the

95% confidence interval, whereas all animals performed within this range when blanks were presented.

Performance of the one cat tested preoperatively was similar to that of the lesioned animals.

DISCUSSION

The present results show that background flicker, two and one-stimulus flicker do not disrupt the performance of cats lacking VC on an H-V discrimination in which the stimuli have been equated for total luminous flux and contour length and in which consistent trial-to-trial local luminous flux cues have been eliminated. The fact that performance frequently dropped from the criterion level is probably due to a general disruption effect of the flickering stimuli or background illumination rather than a disruption of any artificial flicker cues the animal is generating. That such drops were in no way systematic and that such drops also occured for the animal tested preoperatively supports this explanation. Also, no animal ever dropped to within chance levels of performance.

It is conceiveable that with either the background illumination or with both stimuli flickering the animal could still discriminate on the basis of relative differences in self-generated flicker cues. However, with only one stimulus flickering, performance should be disrupted even if the animal is using relative differences in flicker. Furthermore, such disruption should occur regardless if the animal is making vertical or horizontal head or eye

movements since both stimuli were flickered separately. Though it cannot be positively concluded from these results that animals are not using flicker they strongly suggest that cats lacking VC are not discriminating on the basis of self-generated flicker cues, rather it appears that they are discriminating on the basis of the spatial aspects of the stimuli.

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FIGURE CAPTIONS

Figure 1

Left: dorsal and medial surface diagrams of the lesions of two cats, illustrating the largest (AVC-42) and smallest (AVC-14) lesions in the present experiment. Cortical removal is shown by cross-hatching and undercutting by straight lines. Splenial sulcus as in Figure 2, Experiment I. Bottom: projection drawings of representative anterior, middle and posterior sections through the DLGN of each cat. Different laminae and nuclei as in Figure 2, Experiment I.

Figure 2a-b

Ranges and median percent correct are plotted as a function of frequency for the different types of flicker presented for cats with VC ablation. The dashed line indicates the upper limit of the 95% confidence interval around the chance level of performance which is indicated by a solid line at 50% correct. 2a. Dim and bright background illumination flicker. 2b. Stimulus flicker with background illumination constant. Double, both stimuli flickering; Single (H), horizontal stimulus only flickering; Single (V), vertical stimulus only flickering.

Figure 3

Percent correct for each cat on blocks of trials during which blanks were presented. Blanks were presented first followed by stimuli. Filled circles indicate cats which received blanks testing interspersed between blocks of flickering stimuli. Open circles indicate cats which

received blanks interspersed between blocks of stationary stimuli. All blocks consisted of 20 trials for both blanks and patterned stimuli. Details as in figure 2.

AVC-42

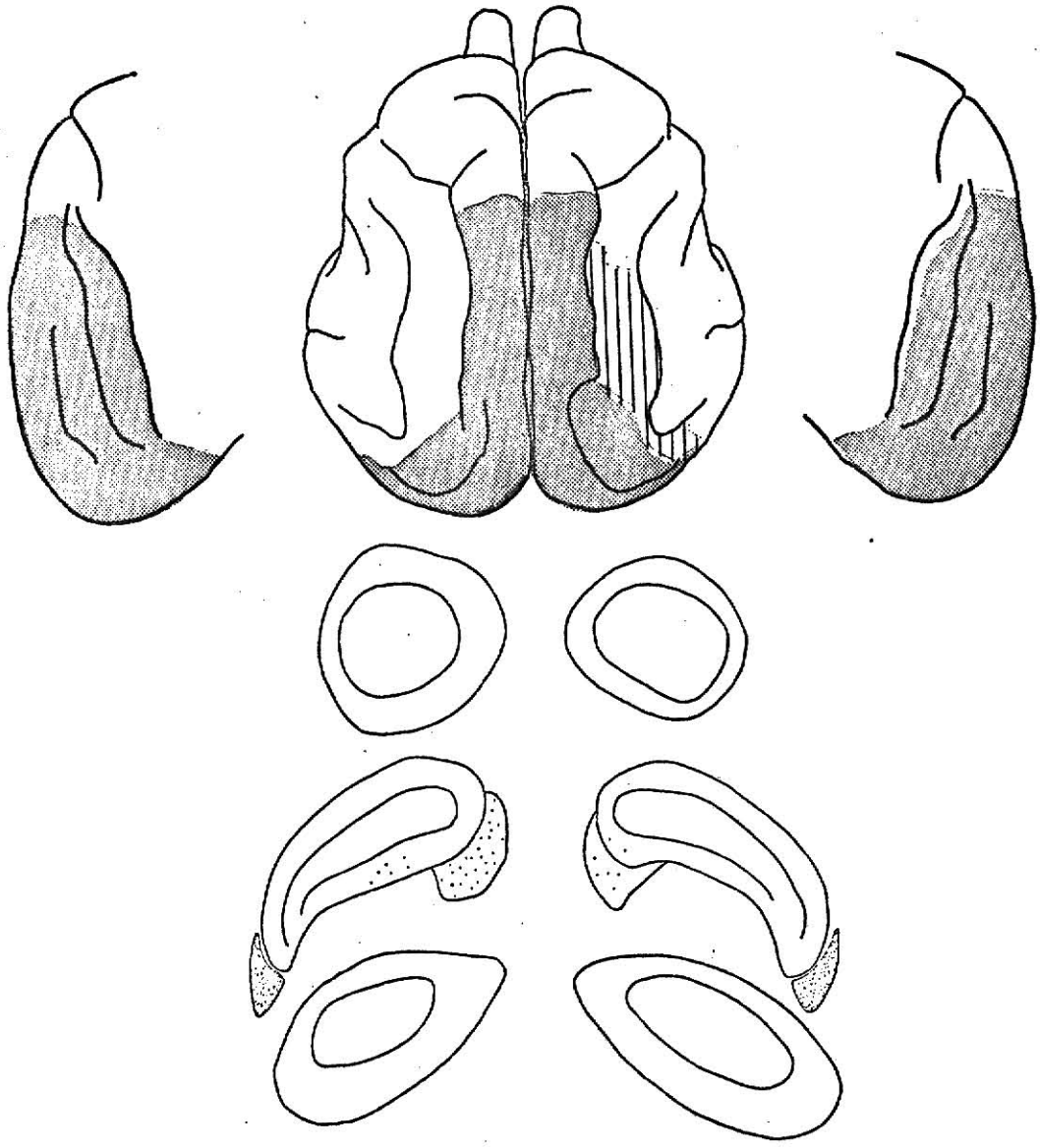

FIGURE 1a

AVC-14

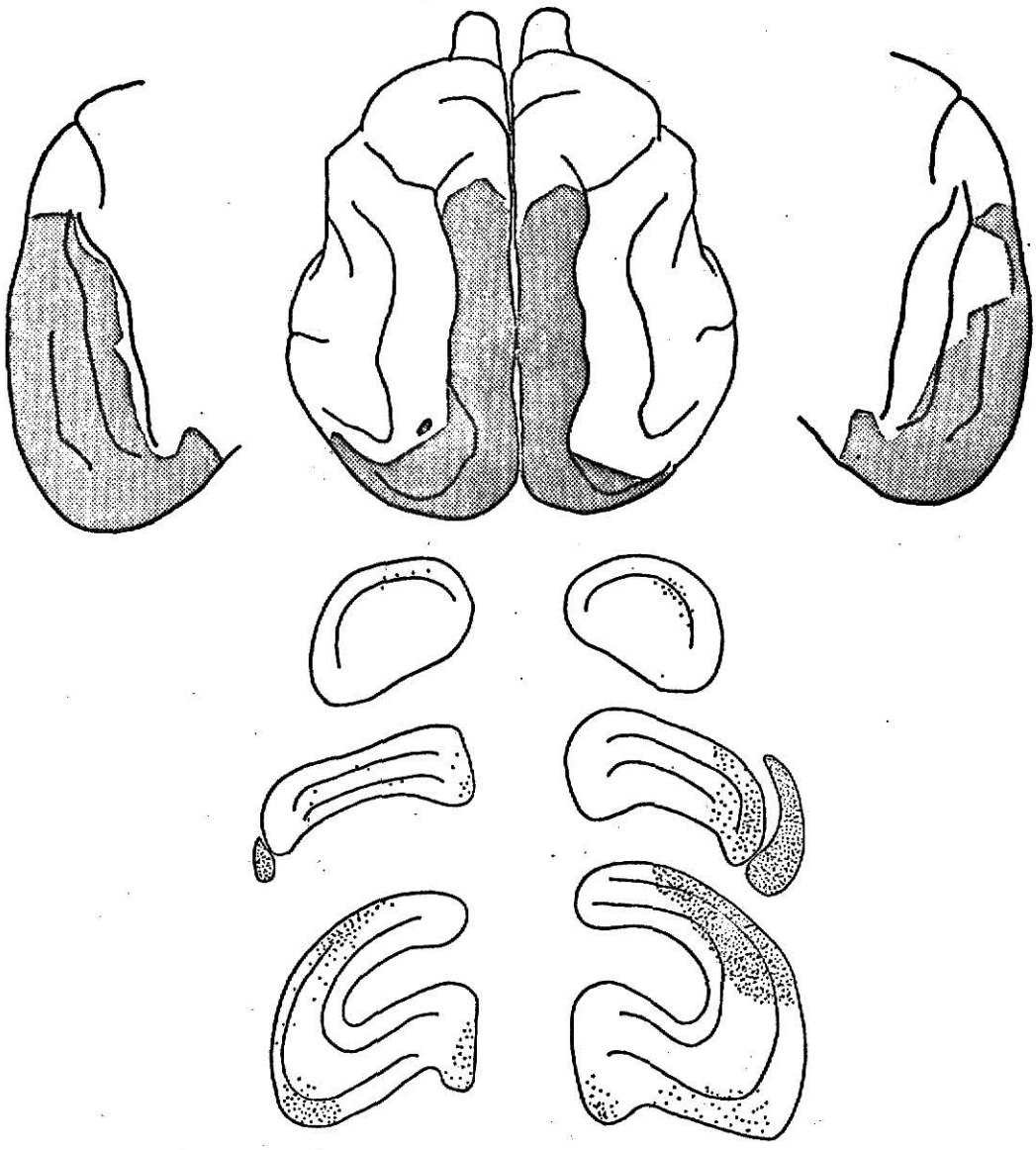

FIGURE 1b

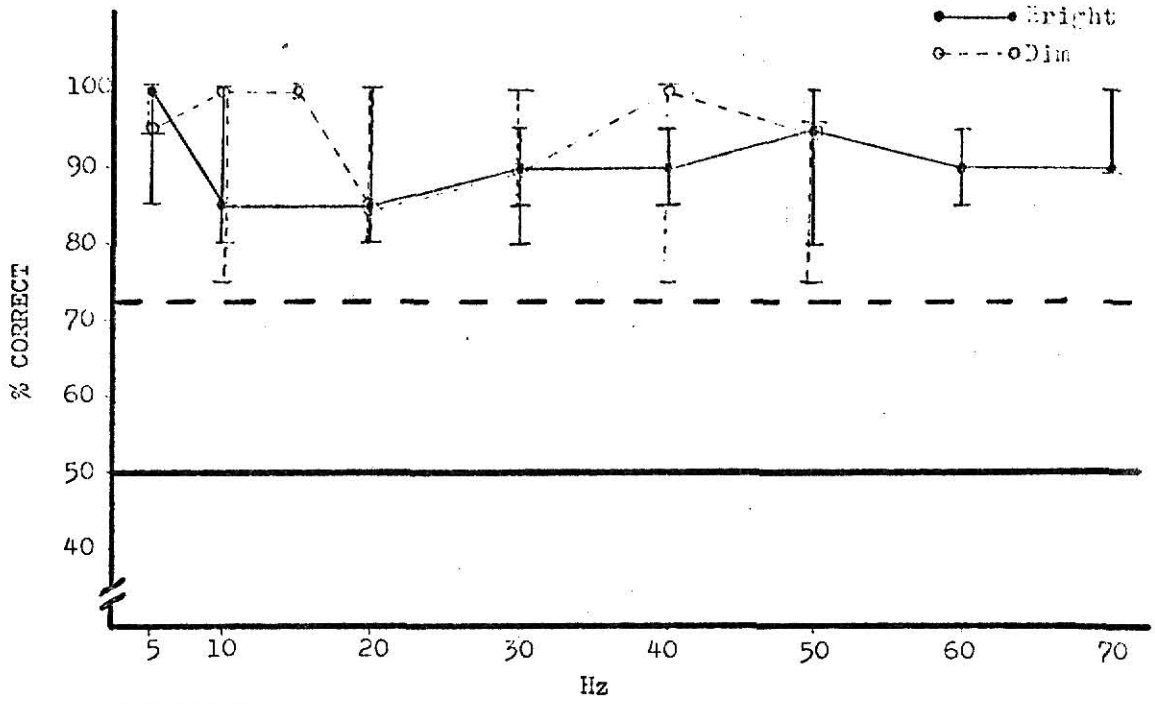

FIGURE 2a

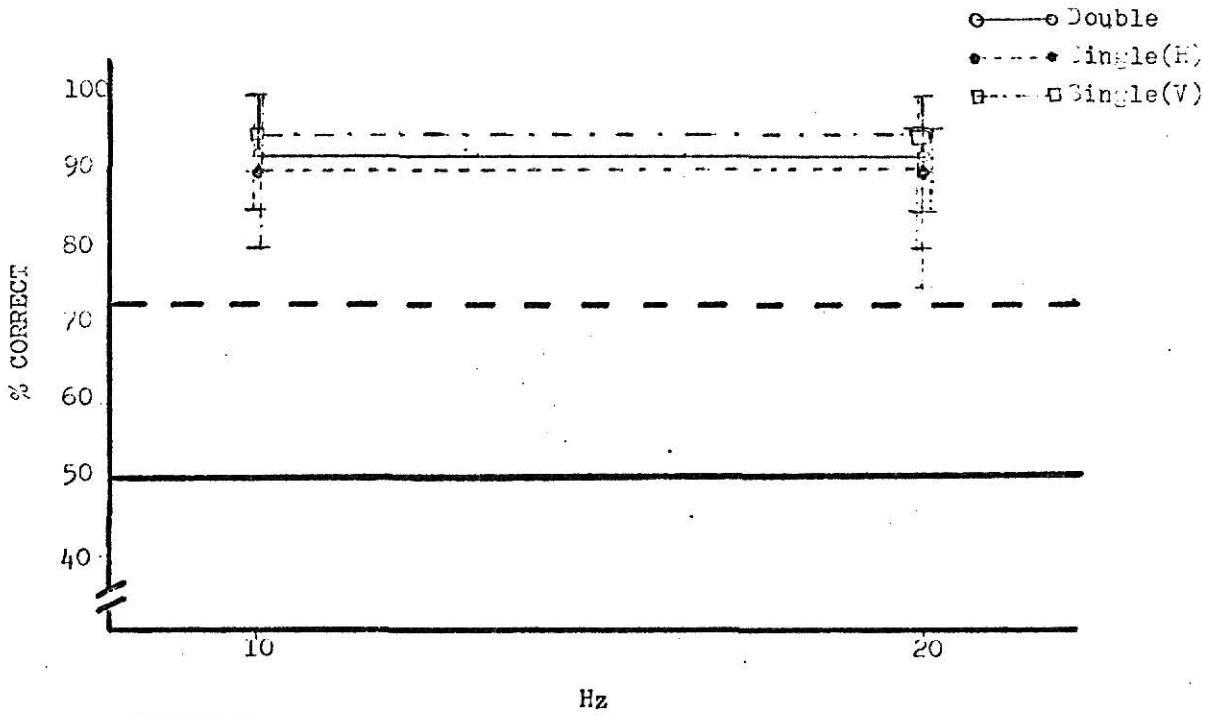

FIGURE 2b

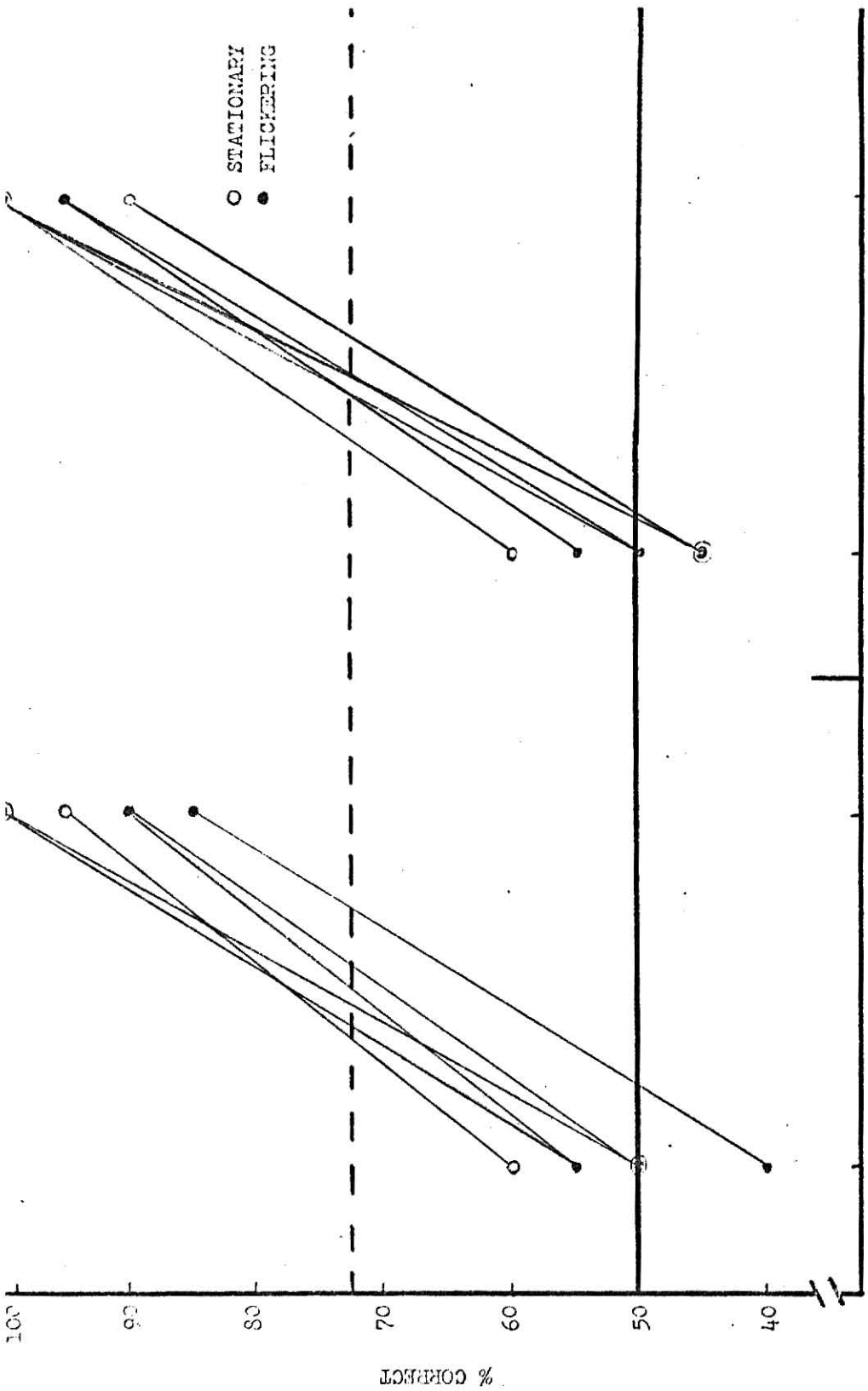
STATIONARY
FLICKERING
% CORRECT
100
90
80
70
60
50
40
BLANKS
STIMULI
BLANKS
STIMULI
DAY 1
DAY 2

FIGURE 3

BEHAVIORAL CUES AND BRAIN AREAS INVOLVED IN FUNCTIONAL RECOVERY AFTER REMOVAL OF VISUAL CORTEX IN THE CAT

by

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Two experiments were conducted concerning 1) areas involved in functional recovery following visual cortex (VC) removal (areas 17, 18 and 19) and 2) the possibility that animals lacking VC generate discriminable cues by different behavioral strategies. In Experiment I eight cats were trained on brightness, pattern and form discriminations then received bilateral removal of VC. After retraining to criterion four of these cats received control retention periods to determine the amount of forgetting of the visual tasks that occurs over time. After being retrained to criterion the eight cats were assigned to one of two groups. One group received second lesions of the lateral suprasylvian area (LS), and one group received lesions of all of the suprasylvian gyrus (SSG) except for the LS area. All cats were then tested for retention of the three visual tasks. Histological analysis of the lesions indicated that in addition to the VC lesion two cats had damage to both LS and the crown of the SSG, two had damage to LS alone and four had damage confined chiefly to the crown of the SSG. Behavioral results show that there was no loss of a brightness discrimination other than that due to forgetting unless both LS and the crown of the SSG were damaged. For the pattern and form discrimination however, damage to LS alone was sufficient to produce a loss greater than that due to a retention deficit and additional damage to the crown of the gyrus did not increase the size of the loss. Performance of cats with only crown damage was not different

from cats following a VC retention period.

In Experiment II six cats lacking VC were trained to criterion on brightness and pattern discriminations. The pattern discrimination consisted of horizontal versus vertical striped stimuli that were equated for total luminous flux and contour length and in which consistent trial-to-trial local luminous flux cues were eliminated. It has been previously argued that cats lacking VC generate discriminable flicker cues through head or eye movements to solve a pattern discrimination. After reaching criterion the cats were given three tests which attempted to disrupt any behavioral flicker cues the animals were generating. For the first test background illumination flashed on and off while stimulus presentation remained constant. In the second test both patterned stimuli themselves were made to flash on and off while background illumination remained constant. The third test consisted of having only one stimulus flash on and off while the other remained constant. The results showed that none of the three tests caused a drop in performance to chance levels. Though it cannot be positively concluded that cats were not discriminating on the basis of self-generated flicker cues, these results strongly suggest that cats lacking VC discriminate on the basis of the spatial aspects of the stimuli.