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EFFECTS ON VISUAL DISCRIMINATION OF CROSSHATCHING AND UNDERCUTTING THE INFEROTEMPORAL CORTEX OF MONKEYS[1]

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Original learning and postoperative retention of 12 rhesus monkeys, trained on a visual pattern discrimination before or after bilateral crosshatching or undercutting of their inferotemporal cortices, were compared with that of 4 normal Ss. Crosshatching produced no deficit in learning or retention even on a difficult 5-alternative discrimination, while undercutting led to a deficit in both. The results reopen the issue as to whether the various sectors of the posterior intrinsic "association" cortex contribute to discrimination performance by acting on information received through transcortical fibers from the respective primary sensory areas, or whether these intrinsic areas act corticofugally to modify activity in the primary sensory pathways.

It has been repeatedly demonstrated that partial ablations of posterior intrinsic "association" cortex result in sensory-modality-specific deficits in the performance of discriminations. The particular sensory modality affected is dependent upon the locus of the lesion. For example, visual discriminations are disturbed by inferotemporal lesions, auditory discriminations by midtemporal lesions (Pribram, 1954), and so on.

One conception of the function of these areas is that they each receive input from one primary sensory area and that they perform some operation on it which is crucial for discrimination. Pribram (1958) has suggested an alternative to this view, namely, that the various posterior intrinsic "association" areas act via corticofugal, efferent fibers which alter the activity of the primary sensory pathways. The inferotemporal cortex in this case would selectively affect the primary visual system. Evidence for this position comes from the finding that circumsection of the primary visual striate cortex or interruption of thalamo-cortical input to the inferotemporal area does not generally disrupt visual discrimination performance (Chow, 1952, 1954). In addition, Spinelli and Pribram (1966) have recently shown that stimulation of the inferotemporal area can selectively alter the recovery function of evoked responses in the striate cortex to pairs of flashes—recovery of the response to the second flash was slowed by concurrent electrical stimulation of the inferotemporal cortex. Conversely, recovery of the response in the primary auditory system to the second of two clicks is speeded up (as far peripheral as the cochlear nucleus) by ablation of the auditory intrinsic association area (Dewson, Nobel, & Pribram, 1966). These findings demonstrate the existence of an efferent effect of intrinsic association cortex on incoming sensory signals.

If the essential operation of the inferotemporal cortex depended on the organization of transcortical fibers over which information could be relayed from striate and prestriate locations to inferotemporal cortex, interruption of these fibers should be as effective as ablation in disrupting discrimination performance. A corticofugal mechanism, however, would not be disrupted by this manipulation. The existence of transcortical fibers is not in dispute here; multisynaptic connections have been found by many investigators, most recently by Kuypers, Szwarcbart, Mishkin, and Rosvold (1965). The question asked is whether they are essential for discrimination.

In the present study, therefore, rhesus monkeys were prepared with thin vertical cuts throughout their inferotemporal cortices. In another group, the same cortex was "undercut," that is, the fibers coming

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and leaving perpendicular to it were severed. These surgically prepared *S*s (and a control group of monkeys) were tested postoperatively for original learning as well as for performance of a previously learned visual discrimination. The results of similar experiments were reported by Chow (1961). In this study Chow concludes that, contrary to the implications of his earlier work (1952, 1954), the transcortical organization of fibers is important to visual discrimination. This discrepancy has not been adequately explored and was deemed sufficiently important to warrant reinvestigation.

METHOD

Subjects

The *S*s were 16 preadolescent rhesus monkeys weighing 2.5–3.8 kg. at the start of training.

Apparatus

All testing was carried out in the automated apparatus for discrete trial analysis (Pribram, Gardner, Pressman, & Bagshaw, 1962), an apparatus for programmed stimulus presentation and automatic response recording. The *S* sat in a transport cage facing a 4 × 4 array of 16 plastic panels onto which up to 12 stimulus patterns could be projected from the rear. When *S* pressed any panel displaying a pattern, a microswitch was activated and the stimuli vanished for 6 sec., after which they reappeared on another randomly chosen set of panels. If the stimulus chosen was the correct one, a peanut was delivered into a cup in the center of the array. If an incorrect response was made, no peanut was given. Responses to nonilluminated panels caused no change in the display. Presentation of stimuli was controlled from an adjacent room and the responses (position, identity, and correctness of the stimulus chosen) were recorded on punched tape. An overhead light provided illumination in the testing cage, and the noise of a blower masked extraneous sound.

Pretraining

The *S*s were trained to enter transport cages from their home cages and were gradually shaped in the testing apparatus to press any panel on which an illuminated pattern appeared. The pattern used for pretraining was the numeral 1. The number of lighted 1's was gradually reduced from 12 to 1, and shaping continued until *S* responded about 60 times over 2 consecutive days to a single 1.

Throughout testing *S*s were fed 8–10 standard lab pellets per day and an occasional orange in addition to the peanuts they obtained during testing.

Training

Fifty trials were given per day in all phases of the experiment, with the exception of the first day of original learning and the few days on which an *S* refused to complete testing.

Original learning. Twelve of the *S*s were divided into three groups, equated as nearly as possible on the basis of pretraining scores: normal *S*s, *S*s whose inferotemporal cortex was crosshatched, and *S*s in whom it was undercut. Following preoperative testing of their pretraining responses, surgery was performed on 8 of the *S*s. After a recovery period of at least 2 wk., all 12 *S*s were trained to discriminate between the numbers 3 and 8 (3 being rewarded) to a criterion of 90% correct over 2 consecutive days or to a maximum of 1,000 trials. They were then switched to a simpler discrimination between a red and a green spot, 1 in. in diameter, and trained to the same 90% criterion. Red was rewarded.

Retention. The remaining 4 *S*s were trained preoperatively to criterion on 3 vs. 8 and then were divided into two groups equated as nearly as possible on the basis of learning scores (mean trials to criterion, inclusive, were 450 and 250, respectively). In 2 *S*s the inferotemporal cortex was crosshatched and in 2 it was undercut. Just before surgery *S*s were again tested on the 3 vs. 8 discrimination and all required only the minimum of 100 trials necessary to pass the criterion.

After the 2-wk. recovery period, *S*s were tested for retention of the previously learned 3 vs. 8 discrimination, by being run to the same criterion of 90% correct over 2 days or to a maximum of 500 trials. All 4 *S*s were then switched to the red-green problem and trained to criterion.

Multiple-stimulus discrimination. The 4 normal and 6 crosshatched *S*s from both earlier phases were trained to criterion on a multiple-stimulus discrimination: *S*s were asked to discriminate between the letters A, H, K, N, and M, with the M rewarded.

Surgery

All operations were single-stage, bilateral surgical procedures carried out under intravenously administered Diabutal anesthesia; they required 2–3 hr. each. Entrance to the inferotemporal area was made by removing portions of the temporal bone. Before opening the second side a 10-cc injection of 50% sucrose was given to reduce the possibility of edema on that side, which was especially likely as a result of the undercutting procedure. To undercut the cortex, the superior temporal fissure was gently opened and a fine curved ophthalmic knife was inserted into its ventral bank, lowered to the base of the skull in the region of the vein of Labbé, withdrawn about 2 mm., and pivoted anteriorly and posteriorly to cut the fibers reaching the middle and inferior temporal gyri. To make each of the crosshatches, the knife was inserted at one point through the pia and then drawn at a depth of 3 mm. within the cortex under the pial vessels. Three or four cuts were made running the length of the inferotemporal area and shorter cuts crossing these at about 2–3-mm. intervals.

Postoperative recovery was generally uneventful, except for the first undercut *S*'s (No. 181) remaining comatose for 24 hr. after surgery and requiring special care and tube feeding for about a week. For 1–3 wk. it appeared to be unable to see, but this disability disappeared gradually until at the time of testing there was no evidence of inability to see the stimuli. This complication was attributed to the marked edema which developed immediately after the first undercutting and became more acute after the second. The wound could be closed only after considerable damage to the inferotemporal cortex had occurred.

Histological Procedures

All brains were perfused, fixed, cut, and stained according to the procedure described by Sherer and Pribram (1962). Serial reconstructions of the lesions were then made on graph paper. Figure 1 shows the crosshatches; however, these were difficult to establish with any exactness since scarring, degeneration, or other untoward permanent effects were minimal. Figure 2 shows the undercuts; *S* 181 had a large bilateral cortical defect and so is not shown, and *S* 158 died from intercurrent gastrointestinal disease before sacrifice and adequate perfusion could be instituted. Figure 2 also shows a composite of the sums of eight of the undercuts and the intersect between them; the brains of all *Ss* who failed to discriminate the 3 from the 8 within 1,000 trials and had minimal cortical damage were chosen to make this diagram. Figure 3 contains representative cross sections from a typical undercut animal; thalamic degeneration was limited to the posterior extremity of the inferior pulvinar in these brains.

RESULTS

Original Learning

The crosshatched and normal groups did not differ significantly (Mann-Whitney *U* test) in the number of trials taken to reach criterion on the 3 vs. 8 discrimination (Table 1). Of the undercut *Ss* only No. 167 reached criterion in the maximum of 1,000 trials, and this *S* required 120 trials more

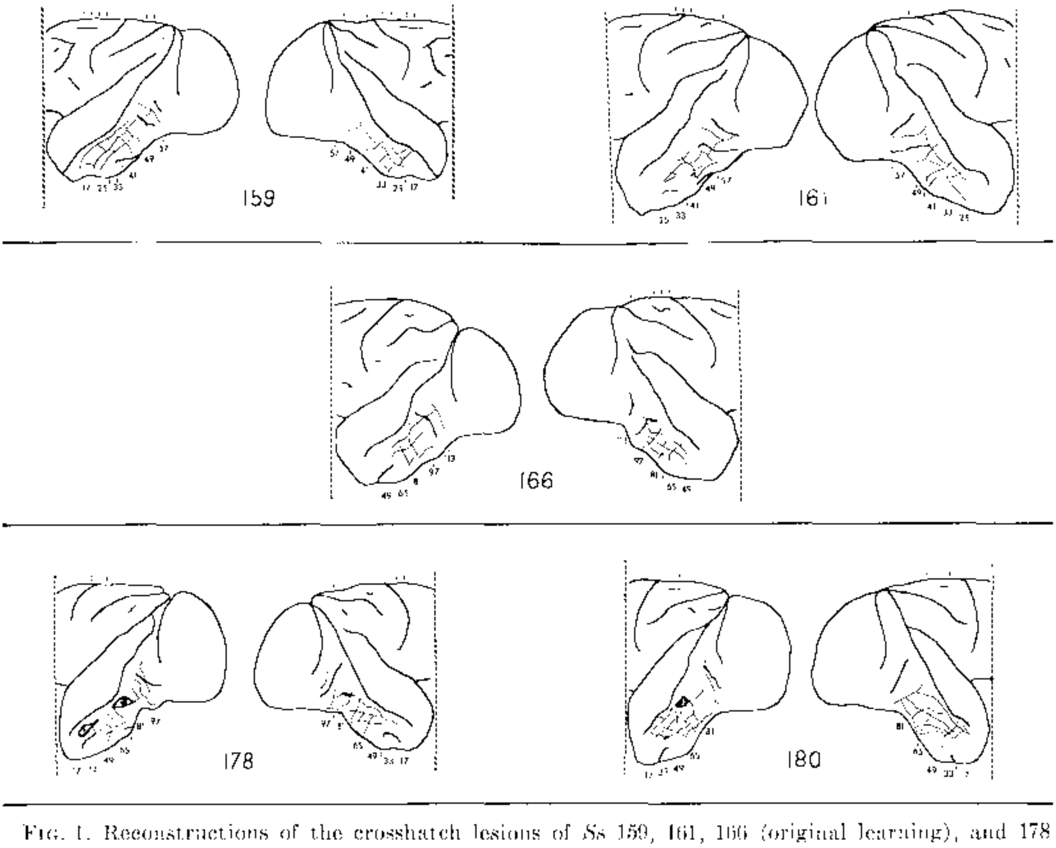

FIG. 1. Reconstructions of the crosshatch lesions of *Ss* 159, 161, 166 (original learning), and 178 (retention). (Fine lines indicate the lesions.)

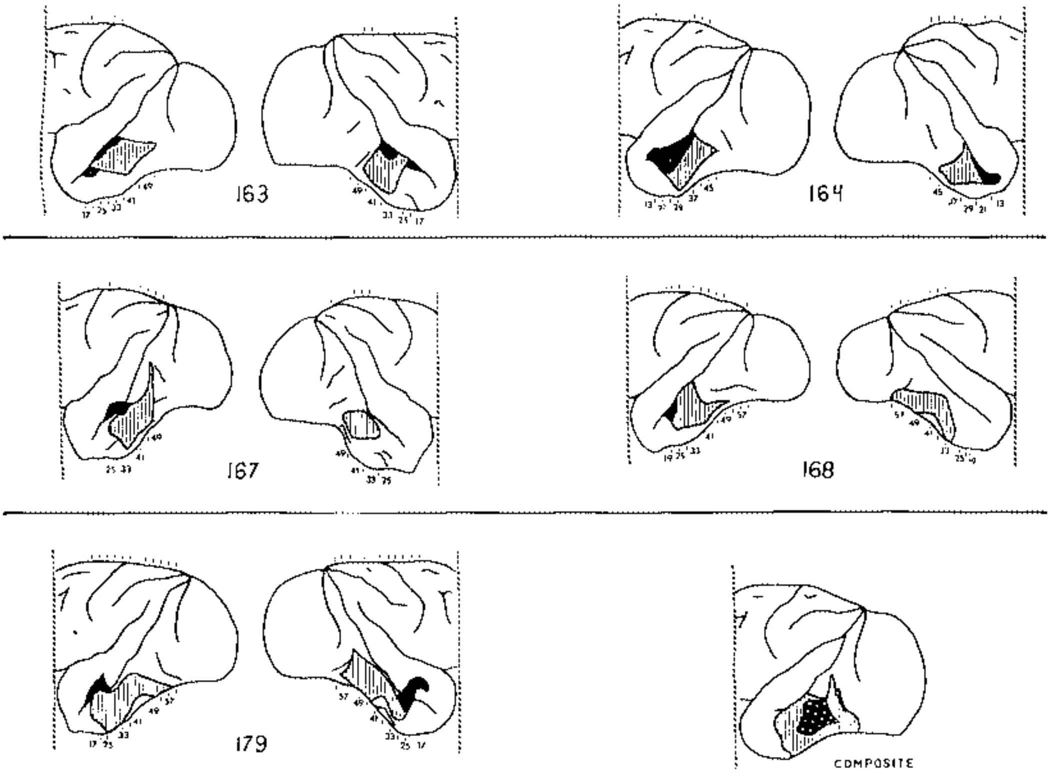

Fig. 2. Reconstructions of the undercut lesions of *S*s 163, 164, 167, 168 (original learning), and 179 (retention). (Black indicates superficial cortical damage; stripes indicate the deep lesion.)

than the nearest *S*. Choices of the 3 by those *S*s which did not reach criterion remained at 50% over the entire 1,000 trials. When, following training on the red vs. green discrimination, *S*s were returned to the 3 vs. 8 problem, those *S*s who had learned within the initial 1,000 trials maintained criterion performance without further training. Another undercut *S* (No. 163) learned after an additional 400 trials, while the remaining 2 *S*s continued to respond randomly for the entire 500 trials.

The undercut *S*s were not significantly retarded compared to the normal *S*s on the red vs. green discrimination, a result which is not unexpected since inferotemporal ablation has been found to impair discrimination proportional to the difficulty of the task for normal animals, and here these required only 100 trials prior to criterion to master the discrimination. Those *S*s whose cortices had been crosshatched were not significantly different from the normal *S*s.

The multiple-stimulus discrimination, on which only the normal and crosshatched *S*s were tested, produced no significant difference between the two groups.

Although there was no significant difference in trials to criterion between the normal and crosshatched *S*s, we were interested in determining whether there might be differences in the strategy by which the discriminations were attained. The analysis performed is reported in full in Blehert (1966). Briefly, it was found that both normal and crosshatched *S*s responded randomly among the stimuli for many trials (an average of 234 on the 3 vs. 8 discrimination and 206 on the multiple-stimulus discrimination) and only then began to eliminate one or more of the negative stimuli. In the multiple-stimulus problem, the A, H, and K were always eliminated as a group with no apparent discrimination between them. Responses were then divided randomly between the remaining stimuli for an

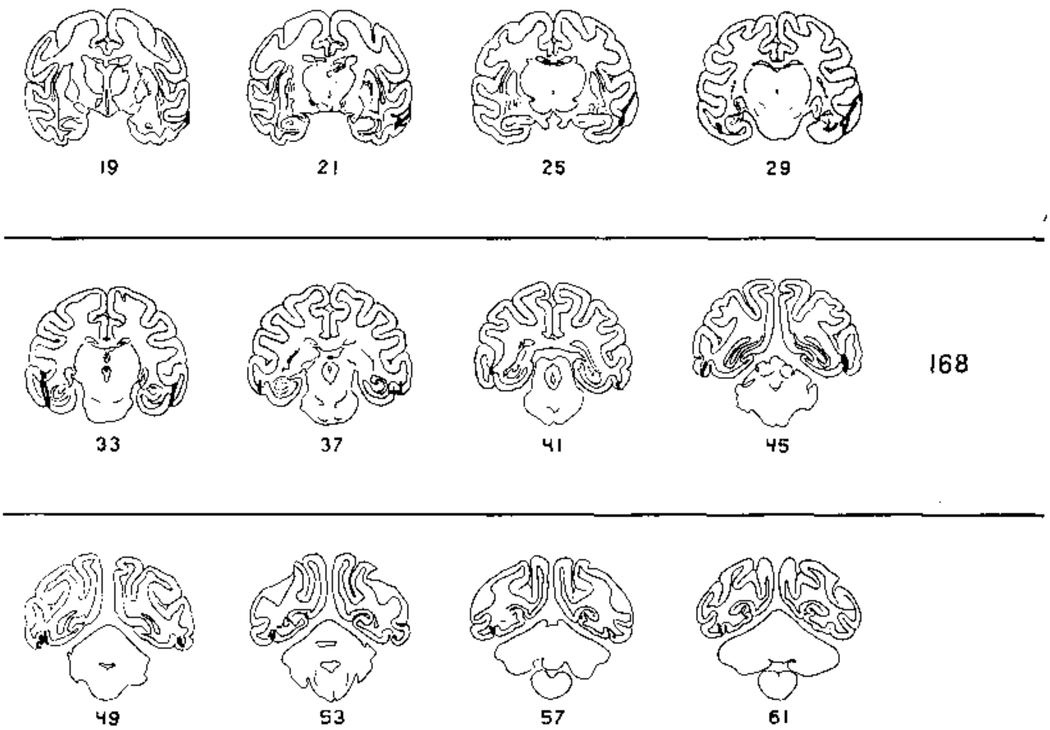

FIG. 3. Cross sections from a representative undercut (*S* 168) showing cortical and deep lesions in black.

average of 207 trials, after which the final stimulus, N, was dropped. It generally required about 100 trials for a stimulus to be completely eliminated once this began. There was no consistent difference between the two groups in either the length of the periods of random response or the rate at which stimuli were eliminated.

Retention

The 3 vs. 8 discrimination which had been learned preoperatively was retained perfectly by the two crosshatched *S*s (Nos. 178 and 180). The undercut *S*s failed to relearn the discrimination in 1,000 additional trials. Neither of the two lesioned groups was significantly retarded on the red-green discrimination. Subject 180 was within the normal limits for the multiple-stimulus problem. Subject 178 required more trials than any other *S*, but was also the slowest *S* on original learning of the 3-8 discrimination prior to surgery.

DISCUSSION

The results of these experiments are clear-cut: crosshatching the inferotemporal cortex does not affect visual discrimination learning or retention; undercutting the same cortex has devastating effects on such discriminations.

These results are opposite to those reported by Chow (1961), who was kind enough to make available to us some of his histological preparations; it is clear that the undercuts in his experiments were considerably less extensive than those performed in the present experiments. The extent and depth of the crosshatch procedure, on the other hand, was not essentially different in the two studies as far as we could determine. This leaves unexplained the

TABLE 1

TRIALS TO CRITERION FOR INDIVIDUAL *Ss* AND GROUP MEANS INCLUSIVE OF 100 CRITERION TRIALS

S	Preoperative	Postoperative			
	3 vs. 8	3 vs. 8	Red vs. green	3 vs. 8	Multiple
Original learning: control *Ss*					
160	—	380	200	100	800
162	—	280	200	100	400
165	—	380	200	100	550
170		450	200	100	700
M		372	200	100	612
Original learning: crosshatch *Ss*					
158		480	180	100	400
159		280	200	100	575
161	—	680	150	100	750
166	—	230	100	100	450
M		418	158	100	544
Original learning: undercut *Ss*					
163	—	1000+	200	400	—
164	—	1000+	300	500+	—
167	—	800	150	100	—
168	—	1000+	250	500+	—
M		—	225	—	
Retention: crosshatch *Ss*					
178	700	100	200		1050
180	200	100	200		750
M	450	100	200		900
Retention: undercut *Ss*					
179	250	1000+	150	—	—
181	250	1000+	400	—	—
M	250	—	275	—	—

production of a deficit by crosshatching in Chow's study while in our experiments no such effect was obtainable. However, our results are more in consonance with those obtained in an earlier study in which the crosshatching technique was employed (Sperry, Miner, & Meyers, 1955).

We interpret our results therefore as demonstrating the importance to visual discrimination of fibers entering or leaving the inferotemporal cortex. The location of the crucial fibers is shown in stippled black in Figure 2, the composite of the undercut lesions. If these fibers or any major portion thereof are spared, the effect is minimized (as for example in No. 167). The pathways in question may reach the inferotemporal cortex from the brainstem or, by way of U fibers, from other parts of the cerebral mantle including the striate cortex. In like manner, these pathways may contain fibers leaving the inferotemporal cortex to reach the brainstem or other cortical regions. Because of these multiple possibilities, the positive results of the present experiment do not critically answer the question as to whether the importance of the inferotemporal cortex to vision is due to its input or to its output, or both. But at least the question is reopened for investigation.

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