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Effects of Serial Lesions of Somatosensory Cortex and Further Neodecortication on Tactile Retention in Rats*

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Summary. Four groups of rats with bilateral lesions of somatosensory cortex and one of animals sustaining only sham operations were tested for retention of a difficult tactile discrimination. Two of the lesion groups had serial ablations, in one case with interoperative testing, and two had one-stage lesions. Bilateral ablations of somatosensory cortex severely retarded retention in all lesion groups relative to the control group and serial and one-stage groups did not differ from each other. The sham operated rats then experienced lesions of cortex anterior and posterior to the somatosensory areas. These lesions only marginally affected retention. Somatosensory cortex then was ablated and severe performance decrements were seen. Removal of additional neocortex in animals that previously had relearned the discrimination after somatosensory cortex lesions also resulted in very poor retention. These data demonstrate the importance of the somatosensory cortex in mediating tactile discriminations and suggest that non-somatosensory cortex may play a role in recovery after somatosensory cortical lesions.

Key words: Somatosensory — Tactile — Cortex — Serial lesions — Ablation

Introduction

The importance of the electrophysiologically defined somatosensory areas of the cortex in tactile performance in rats has been demonstrated in several experiments employing extirpation techniques (Finger *et al.*, 1972; Finger and Frommer, 1968a, b; Zubek, 1951a, 1952a). These studies have shown that damage to somatic cortex areas 1 and 2, alone or together, generally results in marked deficits in postoperative performance on rough-smooth and some tactile form discriminations.

Recent experiments, however, have revealed that rats with extensive damage to cortical somatosensory areas may perform as well as sham operated animals under certain conditions. Finger *et al.* (1971b) observed little or no impairment in the acquisition of tactile discriminations in rats that had sustained bilateral somatic cortex damage in two sequential operations. Further, Weese *et al.* (1973) found that some postoperative performance deficits could be circumvented with preoperative overtraining.

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Several experimenters have investigated the relationship between serial surgery and training variables in retention of black-white discriminations in the rat. The results of these studies have been found to vary with parameters such as lesion size and the nature and complexity of the task (Kircher *et al.*, 1970; Meyer *et al.*, 1958; Petrinovich and Carew, 1969). Analogous retention studies involving serial lesions in the somatosensory system have not been conducted. Hence, the first experiment was undertaken to investigate the effects of serial lesions with and without interoperative training on retention of a difficult ridge-smooth discrimination. It was predicted that serial ablation of somatosensory cortex would result in less severe performance deficits than comparable lesions produced in a single operation and that interoperative training would further enhance retention.

Experiment 1

Methods

Subjects

Thirty-five naive male rats derived from the Sprague-Dawley strain (Bio-Labs, White Bear, Minnesota) were used in the study. The animals were approximately 90 days old at the beginning of the investigation and weighed approximately 250 gms. They were housed by threes in 30.5 × 35.6 × 17.7 cm plastic cages under constant illumination. Water was available *ad libitum*, although food (Purina Rat Chow mixed with water) was restricted to a 15 min period at the end of each test session.

Apparatus

The animals were tested for the ability to discriminate between two tactile surfaces in the *T*-maze that had been used in previous experiments conducted in this laboratory (e.g., Finger *et al.*, 1971a, b, 1972). The maze was constructed from plywood and the startbox measured 35.6 cm long, while each maze alley was 57.2 cm in length. The walls of the maze stood 21.6 cm high and were spaced 10.2 cm apart. A single sheet-metal guillotine door in the shape of an inverted "T" separated the start box from the two wings of the maze and the wings from each other.

Two aluminum plates (one smooth and the other milled) covered the floors of the wings of the maze and served as the discriminanda. The plates extended 43.0 cm from the choice point in the maze to the food cups. Previous testing has shown that the use of aluminum plates circumvents an olfactory confounding which could be present when sandpaper stimuli are used (Finger *et al.*, 1970a). Furthermore, earlier studies (e.g., Finger and Frommer, 1968b) which frequently involved inserting a probe into the ear and damaging the eardrum and associated structures as an auditory control have not provided data different from those in later studies (e.g., Finger *et al.*, 1971b) in which this procedure was abandoned. Thus, differential auditory cues either are not available or can not be used by the animals in the maze. The surfaces, taken from the set first described by Finger and Frommer (1968b), are shown in cross section in Fig. 1.

Preliminary Surgery and Testing

The animals were anesthetized with ether and blinded by enucleation 2 weeks prior to the start of testing. This was done to eliminate the possible use of visual cues in the maze. Ten days later the rats were introduced to the 15 min feeding schedule and were handled for 5 min/day until testing began.

The blinded rats were assigned at random to two squads to facilitate testing and three experimenters alternated testing these squads. Each rat was given 5 trials per day (7 days/week), and individual animals within each squad were run in random order on each of the 5 successive trials.

The ridged plated was designated as the positive stimulus for half of the animals while the smooth plate served as the correct stimulus for the remaining animals. The position of the positive stimulus in either the right or left wing of the maze was determined by a random

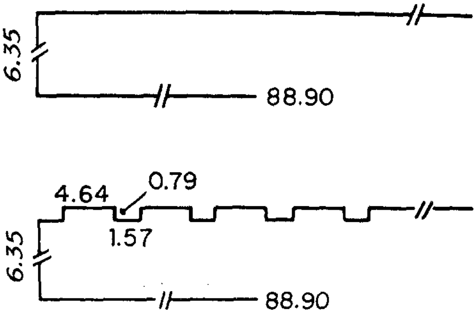

Fig. 1. The tactile discriminanda in cross-section. Dimensions given in millimeters (see text)

procedure with the restriction that it would not appear in the same wing more than three consecutive times for any animal on a given day. Olfactory cues were balanced by placing Purina Rat Chow mixed with water in a food cup at the end of each discriminandum. A sheet-metal barrier blocked the food cup in the wing containing the incorrect stimulus. A non-corrective method of training was used; that is, the guillotine door was lowered to prevent retracing as soon as the animal extended its body past the choice point and placed all four paws on one of the surfaces. Animals were left in the maze for 20 sec regardless of whether a choice was correct or incorrect. The discriminanda were scrubbed with a Lysol solution after the group completed each trial to minimize odor trials.

Following the procedure used by Weese *et al.* (1973), an *a priori* criterion of no errors on two consecutive days was chosen to define learning. Subjects were removed from testing after meeting this criterion. Operations were performed no less than three and no more than 5 days later.

Surgery

Animals were assigned to one of five experimental groups as they met criterion. An attempt was made to have fast and slow learners distributed evenly among these groups. The groups underwent the following surgical procedures: a) two control (sham) operations (*C-C*); b) a sham operation followed by one-stage bilateral lesions of somatosensory cortex areas 1 and 2 with retraining to criterion interposed between operations (C^t-*SS*); c) one-stage lesions of the same areas followed by a sham operation (*SS-C*); d) successive unilateral lesions of the somatosensory areas ($^1/_2SS$-$^1/_2SS$); and e) successive unilateral lesions of the somatosensory areas with retraining to criterion interposed between operations ($^1/_2SS^t$-$^1/_2SS$). A 30 day interoperative period was used for groups *C-C*, *SS-C*, and $^1/_2SS$-$^1/_2SS$. This was determined by adding the mean number of days for retraining rats in groups C^t-*SS* and $^1/_2SS^t$-$^1/_2SS$ to criterion during the interoperative interval (11.13 days) to both the preceding recovery period of 14 days and to the mean home cage duration of slightly more than 4 days just preceding the second surgery.

All surgery was conducted under pentobarbital sodium anesthesia (Diabutal, 60 mg/kg, IP). Cortical extirpations were accomplished by aspiration and lesion placement was based on previously constructed electrophysiological maps of the rat cortex (Welker, 1971; Zubek, 1951 b). A mid-line incision exposing the dorsal surface of the skull constituted the sham condition. Wounds were sutured with silk thread and rats were treated with 100000 U benzathine penicillin G (Bicillin, Wyeth) before being placed in cages for recovery. Ten days of *ad libitum* feeding constituted the first part of the recovery period for both interoperative and postoperative testing. After this the animals were placed on a 15 min feeding schedule for 4 days to enhance motivated running.

Postoperative Testing

All rats were tested for retention of the same ridge-smooth discrimination that was used in the original training sessions. The choice of the plate (ridged or smooth) was not changed and mastery was determined according to the same criterion used for preoperative training. The first and thereafter every third animal that mastered the problem in groups C^t-*SS*, $^1/_2SS^t$-$^1/_2SS$ and $^1/_2SS$-$^1/_2SS$ was sacrified for histological study. Sixty days was considered a suitable cut-off point for postoperative testing in the absence of learning as this was 3 standard deviations from the preoperative mean. Each animal that failed to master the problem within 60 days (300 trials) received its cumulative error score plus a conservative maximum day score of 63 days to criterion and also was sacrificed. All remaining animals were advanced to the next experiment (see Experiment 2 below). This included all rats without lesions (*C*-*C*) and all *SS*-*C* subjects that reached criterion. No animals that learned the problem in the latter condition were sacrificed because only two rats in this group met criterion within the allotted time.

Histological Procedure

Animals to be sacrificed were deeply anesthetized with pentobarbital sodium and were perfused with 0.9% saline followed by 10% Formalin solution injected through the aorta. The dorsal and two lateral surfaces of the brains were photographed. Coronal sections were cut at 50 micra on a freezing microtome after preparation in Formalin solution, and every third section was saved and stained with cresyl-violet acetate. The extirpations were studied with a low power microscope to confirm the location and extent of neural damage and drawings of the surface lesions were made with aid of the photographs.

Results

Non-parametric statistical tests were applied to all of the data since the assumptions underlying parametric tests (e.g., homogeneity of variance) were not met on many of the comparisons (Siegel, 1956). Further, for all statistical tests, animals rewarded on the smooth surface were pooled with rats rewarded on the milled surface since this factor did not appear to affect the behavior of the animals in any of the groups.

Statistical analyses first were conducted on the preoperative scores to confirm group equivalence prior to surgery. These error scores are seen in Fig. 2. Significant differences between the five experimental groups were not found on errors to criterion or on days to criterion prior to surgery indicating that fast and slow learners were distributed equally among the various conditions (Kruskal-Wallis one-way ANOVA: $H = 1.40$, $p > 0.05$).

Figure 3 shows the results of testing during the interoperative period for animals in groups C^t-*SS* and $^1/_2SS^t$-$^1/_2SS$. Rats with unilateral somatic cortex lesions did not differ from the sham-operated animals in errors or days to criterion, or on error and day difference scores (Mann-Whitney U tests, one-tail, all $p > 0.05$).

The interoperative performance of $^1/_2SS^t$-$^1/_2SS$ animals was compared to the postoperative performance of *SS*-*C* animals since both groups had an equivalent amount of training prior to this comparison. One-tailed Mann-Whitney tests on the various performance scores showed that bilateral insult resulted in significantly worse retention than did unilateral damage (all $p < 0.05$). Hence, although the data revealed no significant impairments after unilateral ablations, the bilateral lesions precipitated pronounced deficits.

Figure 4 shows the results of all testing after the second surgery. A one-way analysis of variance by ranks revealed a significant difference among the groups (Kruskal-Wallis, $H = 12.67$, $p < 0.02$). One-tailed Mann-Whitney U tests showed that the two groups of serial animals did not differ from each other; that the two groups of one-stage animals did not differ from each other; and that the pooled

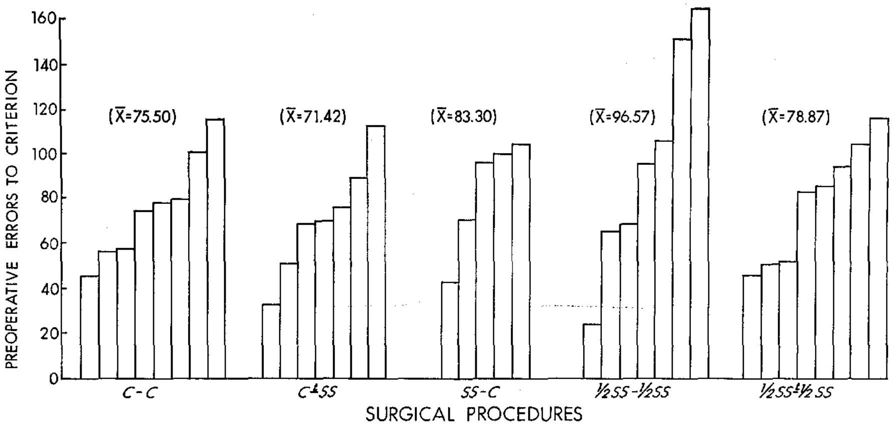

Fig. 2. Individual performance scores of rats prior to cortical surgery. Each column shows the preoperative error scores of an individual subject. Group means are presented in brackets above columns

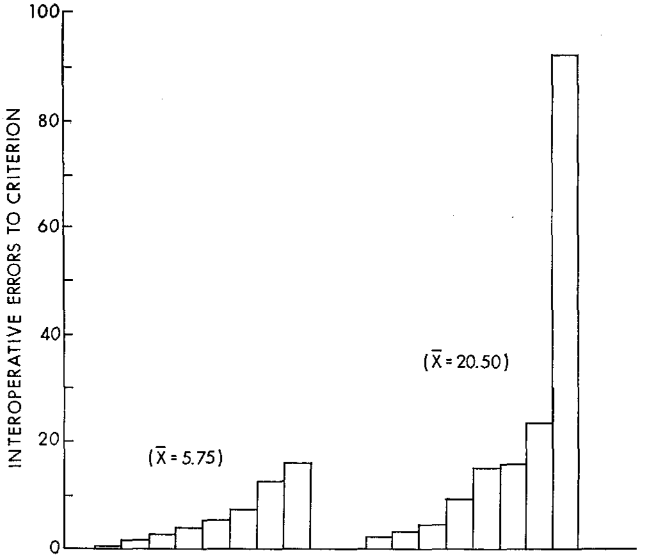

Fig. 3. Performance of rats in groups C^t-SS and $^1/_2SS^t$-$^1/_2SS$ after the first of two operations. Each column shows the interoperative error score of one subject. Group means are presented in brackets above columns

serial animals did not differ from the pooled one-stage animals ($p > 0.05$ for each comparison). Both the combined serial group and the pooled one-stage group differed from the control group at the 0.001 level. Further, a significantly smaller proportion of animals sustaining bilateral somatic cortex lesions remastered the problem within the alloted time in comparison to animals with two sham operations ($\chi^2 = 4.72$, $df = 1$, $p < 0.05$).

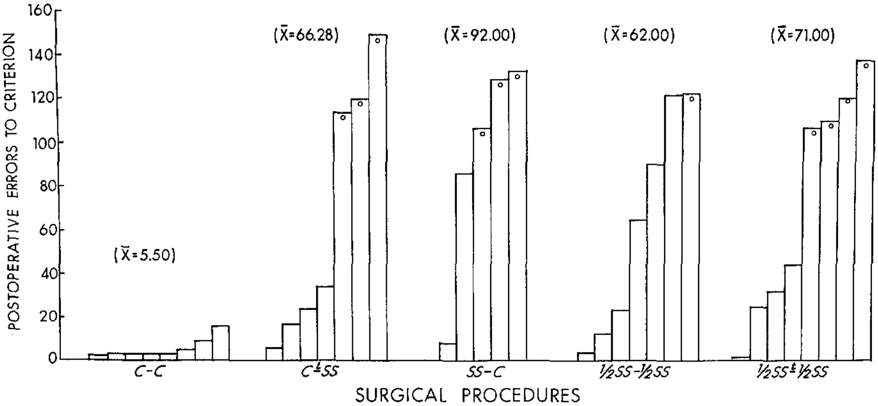

Fig. 4. Postoperative performance scores of rats following successive or simultaneous lesions of somatosensory cortex or two sham operation. Subjects in two of the lesion groups received training to criterion during the interoperative period (Fig. 2). Each column shows the error score of one subject and a dot indicates that the problem was not mastered within the 60 day time limit for learning. Group means are presented in brackets above the columns

Examination of preoperative and postoperative performance scores revealed that no *C-C* animals had negative day or error difference scores whereas the percentages of negative scores were 80, 29, 60 and 43% for groups C^t-SS, SS-C, $^1/_2SS$-$^1/_2SS$ and $^1/_2SS^t$-$^1/_2SS$, respectively. When two Kruskal-Wallis one-way analyses of variance were performed on these scores, significant differences between the groups were found ($p < 0.05$). Again, these differences reflected the fact that the sham-operated rats relearned the discrimination faster than did the animals with somatic cortex lesions (Mann-Whitney U tests, all $p < 0.05$).

Examination of individual performance scores obtained by the 11 rats that failed to reach criterion following bilateral destruction of somatosensory cortex revealed that nine of the animals performed above chance on the 300 trials (Binomial tests, $p < 0.05$). However, none of these rats performed above chance when only the last five days of testing were examined (Binomial tests, p, > 0.05). These data suggest that discriminative performance was impaired but not entirely abolished in most animals that failed to reach criterion.

No consistent differences in terms of lesions size and placement were found between the brains of animals that failed to remaster the problem and those that reached criterion and subsequently were sacrificed for comparison purposes. The brains of the 16 animals in the four lesion groups closely resembled those described in earlier publications (Finger *et al.*, 1970b, 1971a, b) and are presented in Fig. 5. While some sparing of tissue occurred in the second somatic area, most lesions were large and encompassed both paw and facial areas in the two somatosensory areas of the cortex (see Welker, 1971; Zubek, 1951b, for cortical maps). Although the lesions frequently extended to and involved the corpus callosum, no animals showed septal or hippocampal damage or direct insult to the thalamic nuclei. Motor cortex damage also appeared to be minimal. Retrograde degeneration was seen scattered throughout the ventrobasal thalamus and typically appeared heaviest in the dorsolateral parts of the complex.

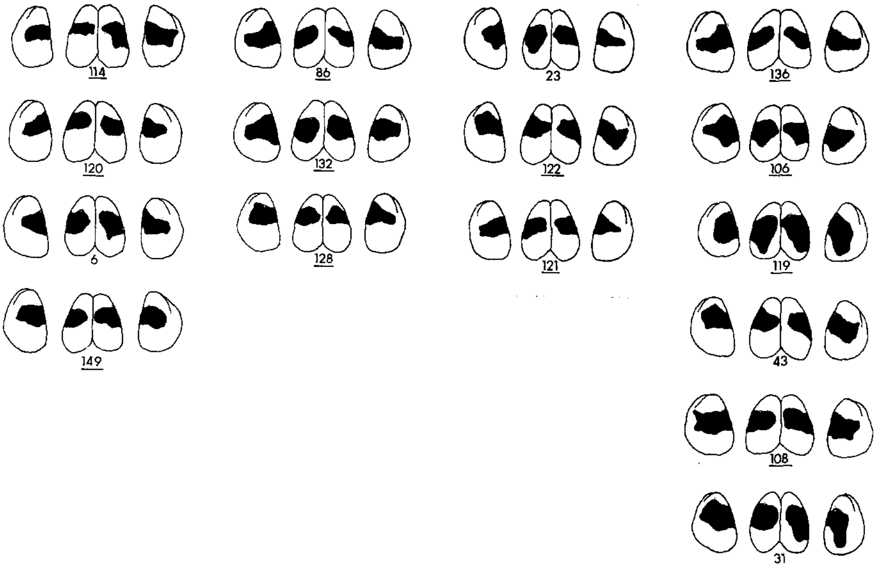

Fig. 5. Drawings showing the surface areas of the lesions of those rats in groups C^t-SS (Column 1), SS-C (Column 2), $^1/_2SS$-$^1/_2SS$ (Column 3) and $^1/_2SS^t$-$^1/_2SS$ (Column 4) that were sacrificed in Experiment 1 (see text). The number under each brain signifies errors to criterion after the second operation. A line under this number indicates that the animal was unable to master the problem within the allotted time (see text)

Experiment 2

In Experiment 1 it was found that bilateral damage to the somatosensory cortex resulted in severe deficits in tactile retention even when the ablations were accomplished in two operations and when training was permitted between surgeries. Some of these animals, however, did relearn the discrimination and this is consistent with most reports on the effects of these ablations on the retention of tactile discriminations by rats (Finger *et al.*, 1971a; Weese *et al.*, 1973; Zubek, 1951a). Units that respond to tactile stimulation of the body are known to exist in neocortical areas outside the somatosensory projection zones (e.g., Buser and Imbert, 1961), suggesting that non-somatosensory cortex may play a role in learning or recovery.

Experiment 2 was designed to investigate the effects of placing lesions in cortical areas anterior and posterior to the somatosensory projection zones in animals that demonstrated learning in Experiment 1. It was hypothesized that these lesions would have little effect on animals with somatosensory cortex intact, but that they would markedly affect those rats that previously had experienced cortical extirpations.

Methods

Subjects

Nineteen of the 24 animals that had performed to criterion in Experiment 1 served as subjects in the second experiment. They included 8 animals from group C-C and 11 animals that had sustained successive or simultaneous bilateral removal of somatic cortex areas 1 and 2. Specifically, groups C^t-SS, SS-C, $^1/_2SS$-$^1/_2SS$ and $^1/_2SS^t$-$^1/_2SS$ contributed 3, 2, 4 and 2 animals, respectively.

General Procedures

Surgery was conducted 3—5 days after an animal had successfully completed postoperative testing in Experiment 1. Subjects that previously had experienced bilateral removal of somatic cortex areas 1 and 2 received bilateral cortical lesions both anterior and posterior to the somatosensory projection zones in a single operation. Animals in the sham operated condition ($C\text{-}C$) underwent the same neocortical surgery designed to leave only somatic cortex areas 1 and 2 intact. The rats then were tested for retention of the same ridge-smooth discrimination that was learned in the first experiment. This testing began two weeks after surgery.

Animals in groups $C\text{-}SS$, $SS^t\text{-}C$, $^1/_2SS\text{-}^1/_2SS$ and $^1/_2SS^t\text{-}^1/_2SS$ were sacrificed after relearning the problem or, alternatively, after 60 days of testing. Six animals in group $C\text{-}C$ were subjected to bilateral removal of somatic cortex areas 1 and 2 after relearning the problem and 15 days later were retested to criterion or to the 60 day limit on the same discrimination. Thus, all five groups of animals had extensive portions of somatosensory, frontal and occipital cortex ablated by the end of this experiment.

The surgical, behavioral and histological procedures used in Experiment 2 were identical to those employed in Experiment 1. An attempt was made to leave a ridge of bone above the sagital sinus and a ridge just anterior and posterior to the somatic cortex in each preparation. Only one animal ($C\text{-}C$) died while undergoing these surgeries. Two other rats, however, were discarded from this part of the experiment upon showing signs of infection ($C\text{-}C$, $C^t\text{-}SS$). The remaining animals, while showing some signs of spasticity, appeared strong and eagerly ran and ate in the maze.

Results

The results of the second experiment are summarized in Fig. 6. Animals in groups $C^t\text{-}SS$, $SS\text{-}C$, $^1/_2SS\text{-}^1/_2SS$ and $^1/_2SS^t\text{-}^1/_2SS$ that previously had learned the discrimination in the absence of somatic cortex areas 1 and 2 were severely impaired following ablation of frontal and occipital cortex and only 40% of the rats were able to relearn the habit. Examination of individual scores revealed that the four rats that were able to remaster the discrimination were from the two serial lesion groups. None of the rats from the original one-stage lesion groups reached criterion. This difference between one-stage and two-stage animals was found to be marginal but not statistically significant (Fisher Exact Probability Test, $p < 0.071$; Mann-Whitney U Test, $p < 0.057$), in part reflecting the small number of subjects involved.

All 6 rats that failed to reach criterion performed above chance levels on the 300 trials (Binomial tests, $p < 0.05$) but not on the last 25 trials of testing (Binomial tests, $p > 0.05$). The performance of the 10 animals as a group was significantly worse than that of animals in group $C\text{-}C$ who now had experienced removal of frontal and occipital cortex (Mann-Whitney test, $p < 0.01$).

Figure 6 also presents the error scores obtained by group $C\text{-}C$ animals as they progressed through three experimental conditions. All of these rats readily remastered the problem with the cortex intact (Experiment 1). Removal of frontal and occipital cortex had a negligible effect on performance as determined by a Sign test ($p > 0.05$). Following ablation of somatic cortex areas 1 and 2, 3 of the 5 remaining animals were unable to relearn the habit within the allotted time. Sign tests on the repeated measures showed poorer performance here than in the two preceding conditions (both $p < 0.05$).

Mann-Whitney U tests on errors and days to criterion showed that rats that had somatic cortex extirpated after ablation of frontal and occipital cortex performed as poorly as did rats in groups $C^t\text{-}SS$, $SS\text{-}C$, $^1/_2SS\text{-}^1/_2SS$, and $^1/_2SS^t\text{-}^1/_2SS$ that had occipital and frontal cortex removed after somatic cortex lesions

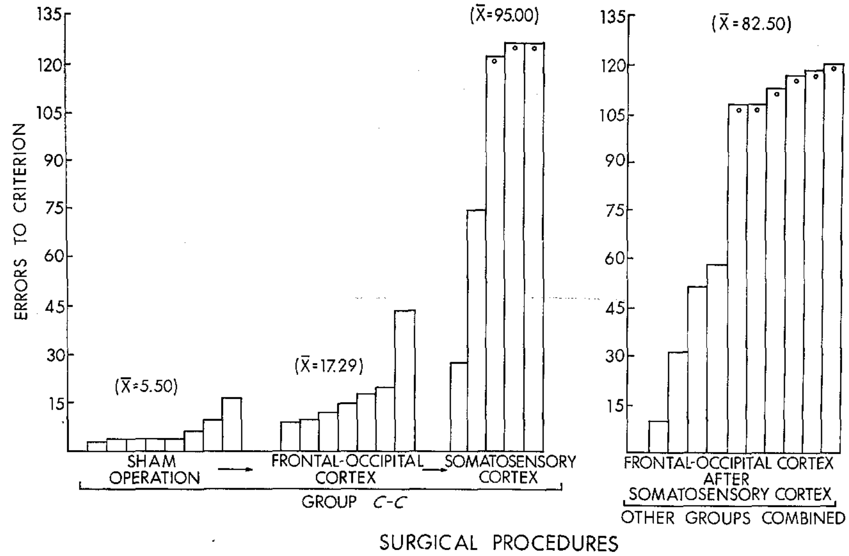

Fig. 6. The diagrams on the left show the error scores of rats in group *C-C* following each of three surgical procedures. Upon reaching criterion after two sham operations these animals experienced destruction of cortex anterior and posterior to the somatosensory zones. They then were retrained to criterion. Next they were subjected to lesions of the somatosensory cortex and tested one more time. The diagram to the right shows the performance scores of 10 rats that relearned the tactile discrimination after large lesions of the somatosensory cortex in Experiment 1 and subsequently were tested after experiencing lesions anterior and posterior to the original destruction. A dot indicates that the problem was not mastered within the 60 day time limit for learning. Group means are presented in brackets above the columns

($p > 0.05$). Further, these two divisions were approximately equal in terms of the proportion of animal that failed to relearn the discrimination problem. Hence, animals in all groups were impaired after removal of large portions of somatic, frontal and occipital cortex, regardless of the sequence in which the ablations were performed.

Drawings of the surface lesions of animals that experienced anterior and posterior neocortex ablations in addition to somatic cortex lesions are presented in Fig. 7. All rats sustained extensive damage to neocortex above the rhinal fissure. However, in most animals islands of tissue were noted immediately anterior and posterior to the somatic cortex as well as just anterior to the cerebellum. In addition, most lesions of non-somatosensory cortex failed to extend to the rhinal fissure. The serial sections showed that there was no direct damage to the hippocampus, septum or thalamus in any brain. However, as in Experiment 1, many of the lesions did extend to and involve portions of the corpus callosum. There were no apparent differences in terms of lesion size or locus among those animals that performed satisfactorily and those that did not.In fact, the two rats (both *SS-C*) with the smallest lesions were among those who failed to learn the discrimination.

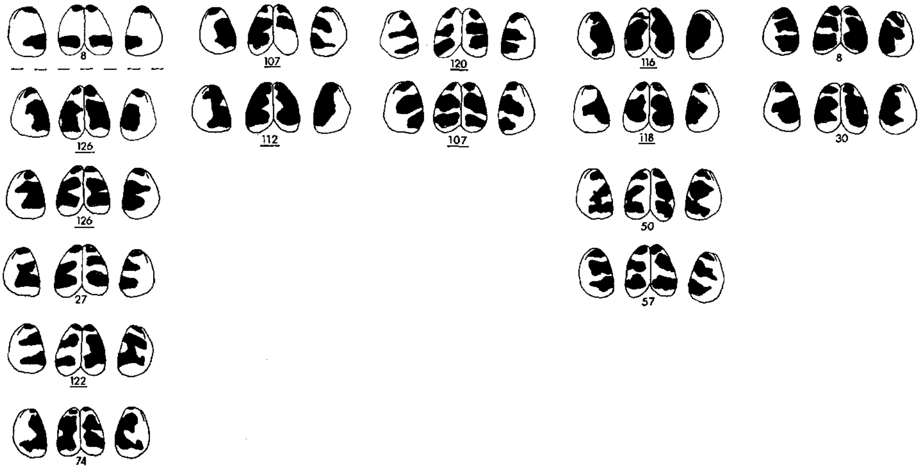

Fig. 7. Diagrams showing the surface topography of the ablations of 15 rats that had lesions of frontal, occipital and somatic cortex. Animals in group *C-C* (Column 1) had frontal and occipital cortex damage prior to ablation of somatosensory cortex, while animals in groups C^t-SS, SS-C, $^1/_2SS$-$^1/_2SS$ and $^1/_2SS^t$-$^1/_2SS$ (Columns 2, 3, 4 and 5, respectively) experienced frontal and occipital cortex lesions after ablations of somatosensory cortex. The reconstruction in the upper left-hand corner shows the brain of one *C-C* rat that was sacrificed for comparison purposes after only sustaining frontal and occipital cortex lesions

Discussion

The poor performance of animals sustaining bilateral damage involving the somatosensory cortex demonstrates the importance of these cortical areas in ridge-smooth discrimination in the rat. Tactile retention deficits also have been observed in cats (Zubek, 1952b), dogs (Allen, 1947; Norrsell, 1967, 1971) and monkeys (Orback and Chow, 1959) following insult to the somatosensory cortex, although considerable recovery has been witnessed under some conditions (e.g., Schwartzman, 1972; Weese *et al.*, 1973). Further, the observation that extensive lesions sparing the somatosensory cortex did not result in deficits (unless somatosensory cortex was removed previously) parallels Zubek's (1952a) finding that the somatosensory areas are sufficient by themselves to maintain previously learned tactile discriminations (see also Sperry, 1959).

The observation that the serial animals were as impaired as their one-stage counterparts (Experiment 1) stands in marked contrast to the results of an earlier experiment conducted in this laboratory in which rats with two-stage cortical lesions acquired a series of five tactile discriminations as rapidly as did sham operated animals (Finger *et al.*, 1971b). Differences in lesion size and locus cannot explain these divergent results since most ablations in the present study resembled those described previously. In addition, the change in the paradigm (retention vs. acquisition) would not explain the differences inasmuch as better performance typically follows preoperative training (see Weese *et al.*, 1973). In contrast, the divergent results could be attributed to the different learning histories of the animals. In the present investigation the rats were tested only on the fourth problem of the battery of five problems used in the earlier study. Serially operated and even normal control animals are known to have difficulty learning this problem if not first exposed to easier tactile discriminations (Walbran, 1974). Thus, if capacity differences among the lesion groups did exist in the present experiment, they may have been obscured by the testing procedure in association with the physical stimuli; i. e., limited previous training may have made this particular discrimination too difficult for the brain damaged animals. This conclusion would appear to be supported by the results of one part of a follow-up retention experiment involving an easier tactile discrimination (rough vs. smooth) than that used here (Simons, Finger and Baldinger, 1975). Animals with one-stage lesions performed worse than rats with two-stage lesions in the more recent study, although rats in both groups were able to relearn the discrimination within a reasonable period of time.

Failure to find serial sparing under conditions in which specific formal training was imposed during the interlesion interval conflicts with some reports involving two-choice visual discriminations in rats with lesions of the posterior neocortex (Petrinovich and Carew, 1969; Thompson, 1960). The results of the present experiment suggest that such interpolated practice may not always enhance retention with successive unilateral lesions in the somatosensory system. The data, however, do parallel those of Glendenning (1972) who reported, among other things, that limited overtraining administered prior to simultaneous removal of cortical tissue may not protect a previously learned visual habit.

The excellent retention by rats in group *C-C* following extensive damage restricted to non-somatosensory cortex argues strongly that the tactile retention deficits observed after somatic cortex lesions cannot be attributed to general cortical damage (*vide*, Semmes, 1973). In addition, the lesion effects do not appear to be applicable to all somesthetic submodalities since ablations similar to those described here do not impair acquisition or retention of temperature discriminations in rats (Downer and Zubek, 1954; Finger *et al.*, 1970b). Nevertheless, since these stimuli demanded complex exploratory movements, the impairments could have been multiple in nature and it cannot be assumed that the scores demonstrated by the animals in the different experimental groups reflect the same underlying deficits (see Finger, 1974). Specifically, while it can be claimed that the animals were not able to use visual, auditory or olfactory cues in the maze, the possibility that animals in the different experimental groups were using different strategies (simultaneous vs. successive sampling of the discriminanda) and/or different mechanoreceptors (vibrissae vs. paws) in the experiment cannot be excluded. However, in this context it should be emphasized that most of the animals in each of the groups appeared to be relying heavily on their paws for making the discrimination and that consistent differences did not appear among the groups with regard to the lesions which almost always encompassed both paw and facial afferents in the two somatosensory areas.

The poor performance of animals in groups SS-C, C^t-SS, $^1/_2SS$-$^1/_2SS$ and $^1/_2SS^t$-$^1/_2SS$ after anterior and posterior neocortical damage implies that non-somatosensory cortex may be involved in relearning the tactile habit following damage to the somatosensory areas. Spared fragments of functional tissue in the presence of otherwise complete somatic cortex lesions also may play a role in the relearning process (Diamond *et al.*, 1962; Galambos *et al.*, 1967; Lashley, 1939). The suggestion (Experiment 2) that serial animals may be better able to learn than one-stage animals following additional neocortical insult should be explored further. If confirmed, the behavioral data would raise the interesting theoretical possibility that the substrates underlying recovery are not necessarily the same after one-stage and two-stage lesions.

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