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Effects of Serial Lesions of Somatosensory Cortex and Further Neodecortication on Retention of a Rough-Smooth Discrimination in Rats

S. Finger and D. Simons

Department of Psychology, Washington University, St. Louis, Missouri 63130 (USA)

Summary. Five groups of rats with bilateral lesions of the somatosensory cortex and one of animals sustaining only sham operations were tested for retention of a rough-smooth discrimination. Two of the lesion groups had sequential unilateral ablations, in one case with interoperative testing, and three groups had one-stage bilateral lesions. The two groups of animals with serial lesions did not differ from each other or from sham operates in relearning the task. Rats with one-stage lesions and preoperative overtraining also performed well, but the other one-stage groups showed deficits relative to control and serial lesion groups. In the second experiment the sham operated rats from Experiment 1 experienced lesions anterior and posterior to the somatosensory zones. These lesions did not affect retention. Somatosensory cortex then was ablated in one operation and severe performance decrements were seen. Removal of additional neocortex in a sample of animals that had relearned the discrimination after one-stage somatosensory cortex lesions (Exp. 1) also affected retention. In contrast, retention was not impaired on some of the measures in those animals that originally had two-stage ablations. The findings from these two experiments show that some ablation effects can be circumvented with overtraining or serial lesion techniques. The data also indicate that non-somatosensory cortex may play a role in recovery after somatic cortex lesions, but that the substrates underlying recovery might not be the same after one-stage and two-stage ablations.

Key words: Somatosensory – Lesion – Somesthesis – Somatic Cortex – Discrimination – Serial Lesions – Learning – Recovery of Function.

Introduction

Animals with brain lesions resulting from a number of operations often perform better than conspecifics with matched lesions of the same structure(s) produced in a single operation. This phenomenon, usually referred to as the serial lesion effect, has been observed after damage to sensory systems, motor systems, the reticular formation, and the limbic system (cf. Finger *et al.*, 1973).

Nevertheless, in some investigations animals with multi-stage lesions have performed as poorly as animals with one-stage surgery involving the same structures (e.g., Isaacson and Schmaltz, 1968; Kircher *et al.*, 1970; LeVere, 1969). Examination of these studies and of subsequent experiments designed to explore serial lesion phenomena suggests a number of variables upon which the serial lesion effect is at least in part dependent. Some of these factors are the length of the inter-lesion interval (Glick and Zimmerberg, 1972; Stewart and Ades, 1959), age at the time of surgery (Stein and Firl, 1974; Walbran, in press), and the nature of the homecage environment during the interoperative period (Meyer *et al.*, 1958; Petrinovich and Bliss, 1966).

Task difficulty, a factor dependent upon both the physical dimensions of stimuli and the previous experience of the subjects, also may be important in serial lesion experiments. However, this variable has received little systematic attention in the past. In one recent study animals with serial lesions of the somatosensory cortex exhibited severe and prolonged deficits in retention of a single tactile form discrimination (Simons *et al.*, 1975). This finding was interpreted in the context of task difficulty since it had been shown that other rats with serial cortical lesions could *acquire* the identical problem as rapidly as sham operated animals if first exposed to a series of easier but related tactile discriminations (Finger *et al.*, 1971).

The present study is a replication of the Simons *et al.* (1975) retention experiment with one additional group and one modification. In this investigation the single retention problem is a less difficult tactile discrimination (rough-smooth) which even animals with one-stage lesions of the somatosensory cortex are capable of relearning relatively soon after surgery. It was hypothesized that with the single, relatively easy tactile discrimination the serial lesion effect would be demonstrated for the first time in a tactile retention experiment. In the context of earlier ablation studies from this laboratory (Finger *et al.*, 1971; Simons *et al.*, 1975; Walbran, in press) it was hoped that this study would further clarify the role of task difficulty in serial lesion research.

Experiment 1

Methods

Animals

Forty-eight naive male rats derived from the Sprague-Dawley strain (Bio-Labs, White Bear, Minnesota) were used in the study. The animals were 90 days old at the beginning of the investigation and were fed and housed identically to the animals of Simons *et al.* (1975).

Apparatus

The rats were tested for the ability to discriminate between a rough and a smooth surface in the same *T*-maze that had been used in the earlier experiments (e.g., Simons *et al.*, 1975). The interchangeable aluminum plates that covered the floors of the wings of the maze are shown in cross section in Fig. 1 and were taken from the set first described by Finger and Frommer (1968). On the basis of

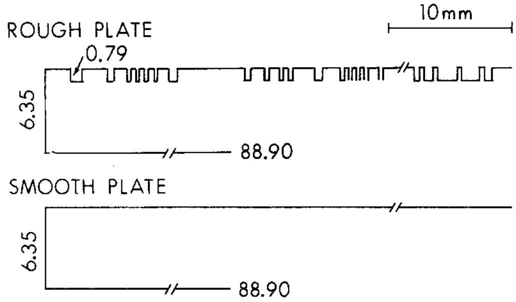


Fig. 1. The tactile discriminanda in cross section. Ridges and grooves, made with a flying cutter, interweave with each other along the length of the top plate in such a way that cross-sectional representations at different points may differ considerably from each other. The overall configuration is described as being that of a "rough" surface. Dimensions given in millimeters (see text)

previous testing it was known that these tactile stimuli would be mastered by naive rats much more rapidly than the discriminanda used by Simons *et al.* (1975).

Preliminary Surgery and Testing

The testing procedures in the present study were identical to those described in the previous experiment (Simons *et al.*, 1975). Testing began 2 weeks after enucleation and animals were rewarded with food for traversing the wing of the maze containing the correct surface. Animals were given 5 trials per day until they mastered the problem (two consecutive sessions without an error), and surgery was performed no less than 3 and no more than 5 days later.

Surgical Procedures

Animals were assigned to one of six groups upon mastery of the problem. 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 areas 1 and 2 with retraining to criterion interposed between operations ($C^{1}SS$); c) one-stage lesions of the same areas followed by a sham operation (*SS-C*); d) a sham operation followed by one-stage bilateral lesions of the somatosensory areas (*C-SS*); e) successive unilateral lesions of the somatosensory areas ($^1/_2SS$-$^1/_2SS$); f) successive unilateral lesions of the somatosensory areas with retraining to criterion interposed between operations ($^1/_2SS^{1\,1}/_2SS$).

A 27 day interoperative period was used for rats in groups *C-C, SS-C, C-SS* and $^1/_2SS$-$^1/_2SS$. This was determined by estimating (from preliminary data) the mean number of days for retraining rats in groups $C^{1}SS$ and $^1/_2SS^{1\,1}/_2SS$ to criterion during the interoperative period (8 days), and adding the estimate to both the preceding recovery period (14 days) and mean home cage duration after learning and preceding the second surgery (approximately 4.5 days). Since interoperative testing actually averaged 7 days for rats in group $^1/_2SS^{1\,1}/_2SS$ and approximately 6 days for $C^{1}SS$ animals, their respective interoperative intervals averaged 1 and 2 days less than those of the other animals.

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). A midline incision exposing the dorsal surface of the skull constituted the sham condition. All rats were treated with 100,000 U Benzathine penicillin G (Bicillin, Wyeth) postoperatively. Ten days of *ad libitum* feeding constituted the first part of the recovery period. The animals were then 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 rough-smooth discrimination that was used in the original training sessions. The choice of the rewarded plate (rough or smooth) was not changed and mastery was determined according to the same criterion as that used for preoperative training. Two animals were unable to relearn the problem within 40 days (more than 7 times the control group mean). These rats were removed from testing and assigned conservative scores of 43 days to criterion for the statistical analyses on days to relearn the discrimination. Since both of these rats were from group *SS-C*, the remaining rats in this group were saved for Experiment 2. In contrast, a sample of the first and approximately every fourth animal that learned the problem from groups *C-SS*, $^1/_2SS$-$^1/_2SS$ and $C^{t}SS$ were sacrificed at this time. Group $^1/_2 SS^{t1}/_2SS$ contributed more subjects to histological study than did the other groups since the decision to save animals for Experiment 2 was made after many of these rats had completed testing.

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 of the entire brain were cut at 40 micra after fixation in formalin solution, and every sixth frozen 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. Reconstructions of the surface lesions were made with aid of the photographs.

Results

Non-parametric statistical tests were used to analyze the data. This choice was dictated by the wide range of scores noted within some of the groups during postoperative testing as well as by a desire to treat the data identically to those of the preceding experiment in this series (Simons *et al.*, 1975). Since days to criterion and errors to criterion yielded the same results, only the error scores are given below. For both sets of statistics, however, animals rewarded on the rough plate were pooled with rats rewarded on the smooth plate since this factor did not affect performance within any of the groups.

Figure 2 shows the error scores of the animals in the different groups prior to aspirative ablations. A Kruskal-Wallis one-way ANOVA (Siegel, 1956) revealed no significant differences between the groups ($K = 2.66$; $p > 0.05$). Thus, fast and slow learners were distributed equally among the groups prior to cortical surgery.

Two of the six groups received training after the first operation ($C^{t}SS$, $^1/_2SS^{t1}/_2SS$) and most of the animals relearned the problem within 5 days. Their error scores are presented in Fig. 3 (note change in ordinate). It was found that rats with unilateral somatosensory cortex lesions did not differ from sham operated rats in errors to criterion during the interoperative period (One-tailed Mann-Whitney U test; $p > 0.05$). This was expected given the bilateral nature of the task and the healthy status of the animals.

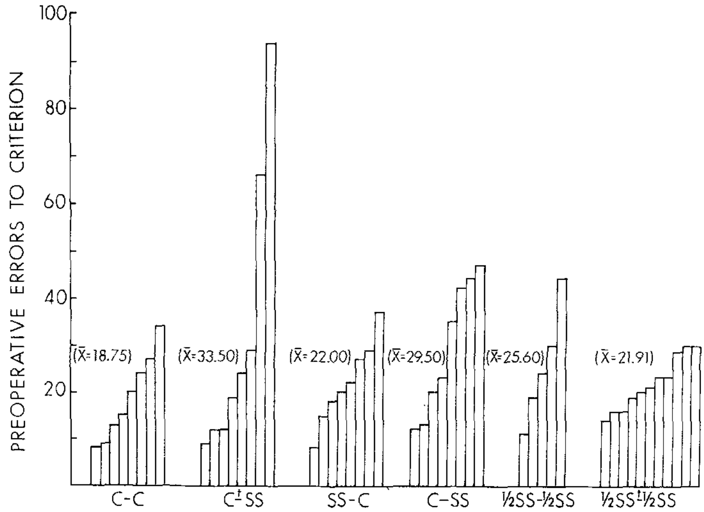


Fig. 2. Individual performance scores of rats after enucleation but prior to cortical or sham operations. Each column shows the preoperative error score of an individual subject. Group means are presented in brackets above columns

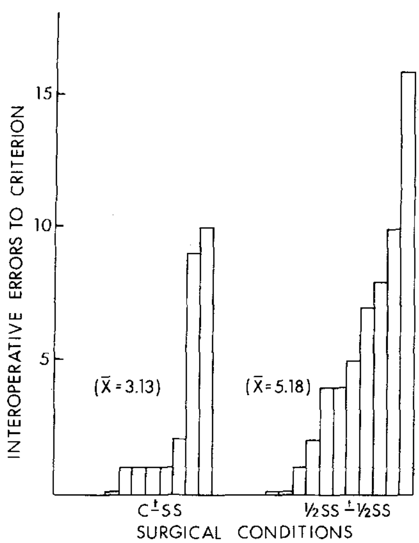


Fig. 3. Performance scores of rats in groups *C±SS* and *½SS±½SS* after the first of two operations. Each column shows the interoperative error score of one subject. Group means are presented in brackets above columns

Figure 4 shows the results of all testing after the second surgery. It illustrates that 62.5% of the animals with one-stage lesions and no overtraining (*SS-C*, *C-SS*) had scores outside the range of control group performance, while 64–88% of the animals in the other groups ($\bar{X}$ = 75%) performed within the range of the control animals. A Kruskal-Wallis one-way ANOVA on the data

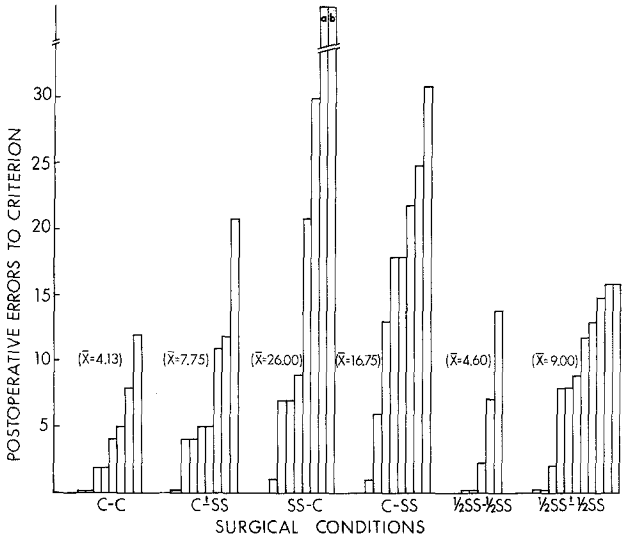


Fig. 4. Postoperative performance scores of rats following successive or simultaneous lesions of somatosensory cortex or two sham operations. Subjects in two of the lesion groups received training to criterion during the interoperative period (Fig. 3). Each column shows the error score of one subject and letters indicate that the problem was not mastered within the 40 day time limit for learning (a = 51 errors; b = 82 errors). Group means are presented in brackets above columns

confirmed the observation that the six groups were no longer performing equivalently ($K = 12.85$; $p < 0.05$).

A series of one-tailed Mann-Whitney U tests was conducted to compare selected groups on the basis of the experimental hypotheses of this study. No statistical difference was found between the scores of the animals with serial lesions and interoperative training and those with serial lesions without such training ($^1/_2SS$-$^1/_2SS$ vs $^1/_2SS^{t\,1}/_2SS$; $p > 0.05$). Further, when the two serial lesion groups were pooled, their scores did not differ significantly from those of the control animals ($p > 0.05$). As for the remaining animals, the length of the postoperative recovery period after one-stage lesions (no interoperative training) was not a significant factor in retention (*C-SS* vs *SS-C*; $p > 0.05$). Overtraining, however, did statistically improve performance in the one-stage lesion conditions (C^tSS vs *C-SS*; $p < 0.05$). When pooled, the one-stage animals were found to be worse than the control animals at the 0.01 level, and worse than the pooled serial animals at the 0.05 level, even though the two overtrained groups did not differ from each other ($^1/_2SS^{t\,1}/_2SS$ vs C^tSS; $p > 0.05$).

Examination of individual scores revealed that only two rats failed to reach criterion within the allotted amount of time. Both animals came from group *SS-C*. Although one of the two rats performed at better than chance expectancy (errors/trials) when all 40 days on the problem were examined (Binomial test; $p < 0.01$) both animals were performing at chance levels on the last 5 days of testing. The preoperative scores of these animals (13 and 16 days to criterion) fell

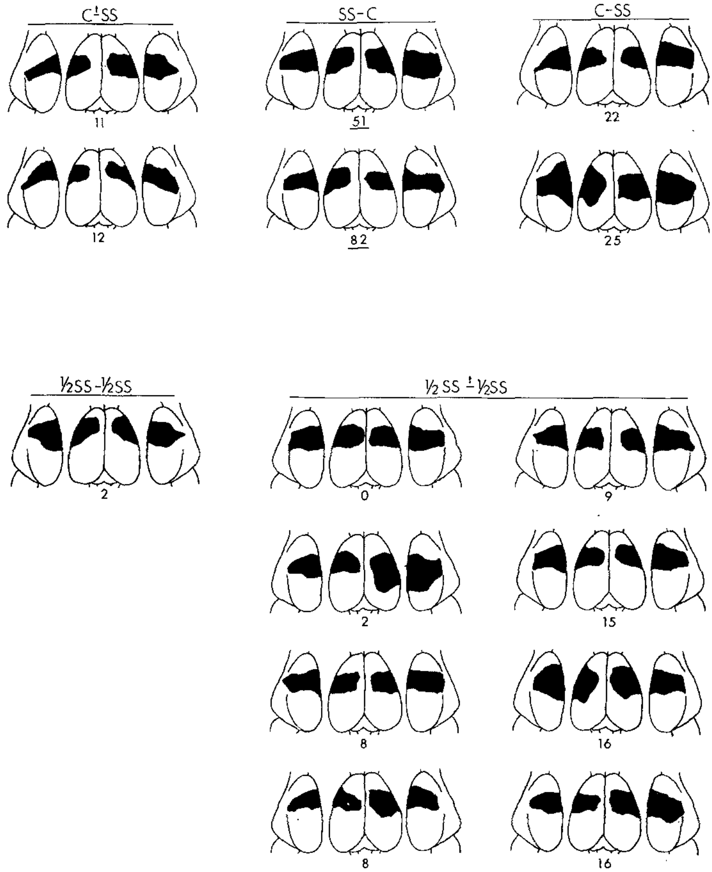


Fig. 5. Drawings showing the surface areas of the lesions of those rats that were sacrificed at the end of Experiment 1 (see text). The number under each brain signifies errors to criterion after the second operation. A line under this number indicates that the animal was unable to master the problem within the alloted time (see text)

within 1 standard deviation of the preoperative group mean (15.5 days) suggesting that their poor postoperative performance scores could not be attributed to the fact that these animals were slow learners. In addition, their lesions (Fig. 5) were not distinguishable from the lesions of the other animals in this group (see Figs. 7–8). In the light of this finding it should be stressed that individual animals with postoperative scores outside the control group range also were seen in the lesion groups that performed well. Thus, for reasons which are not understood on the basis of the available data, these ablations increased the variability of the scores within the different groups regardless of each group's mean postoperative performance.

Reconstruction of the brains of the animals sacrificed at the end of Experiment 1 are presented in Fig. 5. All of the lesions severely damaged both somatosensory areas of the cortex bilaterally (Welker, 1971; Zubek, 1951) and so closely resembled each other that it was not possible to detect any differences among the groups on the basis of these samples. Although some of the ablations extended to and involved the corpus callosum, no animals showed septal or hippocampal damage or direct insult to the thalamic nuclei.

Eperiment 2

In Experiment 1 it was found that animals with serial lesions performed statistically better than animals with one-stage lesions of the somatosensory cortex (although most rats in group *C±SS* performed well). It also was seen that the scores of animals with serial lesions were not significantly different from those of rats with sham operations. The finding that all but two of the animals with lesions were able to relearn the discrimination within the allotted time suggests that non-somatosensory cortex may play a role in learning or recovery. This hypothesis is supported by the data of Simons *et al.* (1975) who noted that lesions placed anterior and posterior to the somatosensory cortical zones severely impaired retention in animals that had previously relearned the problem after somatic cortex lesions. The same surgeries did not significantly affect the performance scores of animals who had intact somatosensory cortices.

Experiment 2 utilizes the paradigm of Simons *et al.* (1975) with the relatively easier discrimination used in the present Experiment 1. Specifically, it investigates the effects of placing lesions in cortical areas anterior and posterior to the somatosensory projection zones in a sample of animals that demonstrated learning in the first experiment. In the context of the earlier study it was hypothesized that these lesions would not affect performance scores of animals with somatic cortex intact. However, it also was predicted that while all animals with somatic cortex lesions would be impaired to some degree after these surgeries, rats who had originally sustained serial ablations of the somatosensory cortices would perform better than animals that had originally experienced similar lesions in one sitting.

Methods

Animals

Thirty-three animals from Experiment 1 served in the second experiment. Excluding one operative death (*C-C*), this included 7 animals from group *C-C* and 25 animals that had sustained successive or simultaneous removal of somatic cortex areas 1 and 2. Specifically, groups *C-SS*, *C±SS*, *SS-C*, $^1/_2SS$-$^1/_2SS$, and $^1/_2SS$±$^1/_2SS$ contributed 6, 6, 6, 4 and 3 animals respectively.

General Procedures

Surgery was conducted 3–5 days after an animal had successfully completed postoperative testing in Experiment 1. Animals 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

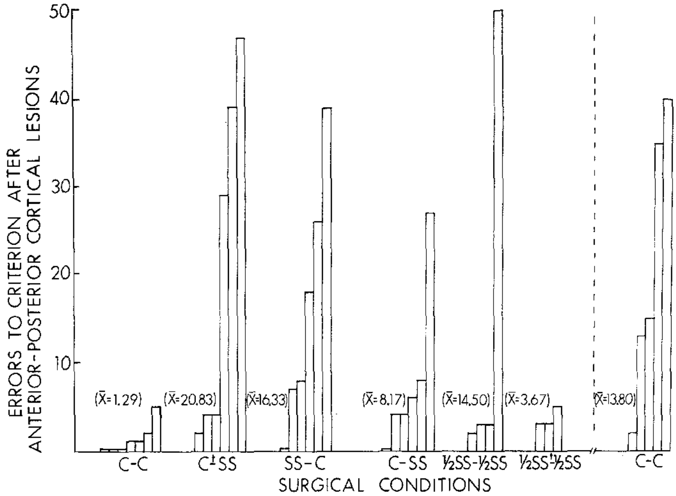


Fig. 6. Performance scores of rats after lesions anterior and posterior to the somatosensory cortex areas. Group *C-C* is shown twice; first (far left) with somatosensory cortex intact, and then (far right) following somatosensory cortex ablations (see text). Group means are presented in brackets above columns, each of which signifies the error score of an individual animal

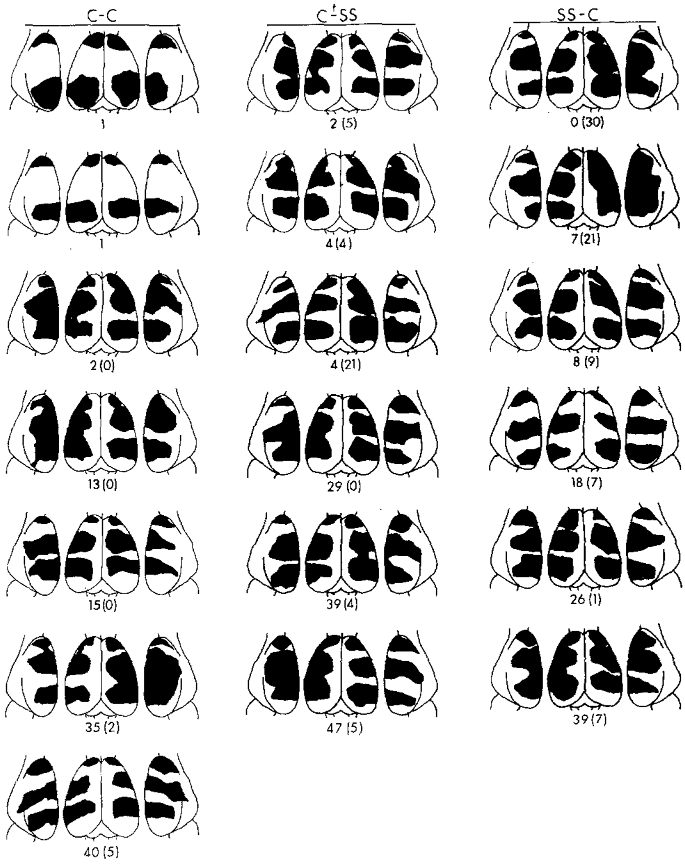
zones in a single operation. Animals in the sham operated condition (*C-C*) underwent the same neocortical surgery designed to leave only somatic cortex areas 1 and 2 intact. The rats then were tested for retention of the same rough-smooth discrimination that they learned in the first experiment. This testing began 2 weeks after surgery.

All animals in groups *C-SS*, $C^{\underline{t}}SS$, *SS-C*, $^1/_2SS$-$^1/_2SS$ and $^1/_2SS^{\underline{t}}\,^1/_2SS$ were sacrificed after relearning the problem. Two rats in group *C-C* were sacrificed for histological comparison. The remaining five animals in group *C-C* were subjected to bilateral removal of somatic cortex areas 1 and 2 after relearning the discrimination and 15 days later began retesting to criterion on the same problem. Thus, animals in all six groups 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 saggital sinus and a ridge just anterior and posterior to the somatic cortex in each preparation.

Results

The results of Experiment 2 are presented in Fig. 6. A Kruskal-Wallis one-way ANOVA on the error scores following lesions anterior and posterior to the somatosensory areas (SS cortex intact in Group *C-C*) resulted in a borderline probability ($p < 0.052$). Thus, Mann-Whitney U tests were used to analyze the error scores more carefully. These comparisons showed that both the pooled one-stage lesion group and the pooled two-stage lesion group differed significantly from the control group which had experienced cortical lesions sparing the somatosensory zones ($p < 0.001$; $p < 0.01$, respectively). These tests did not,



Figs. 7 and 8. Diagrams showing the surface topography of the ablations of the rats that had lesions of frontal, occipital and somatic cortex in Experiment 2. Animals in group *C-C* had frontal and occipital cortex damage prior to ablation of somatosensory cortex, while other animals experienced frontal and occipital cortex damage after somatosensory cortex lesions. The first two reconstructions in the colum marked *C-C* show the brains of two rats that were sacrificed for purposes of comparison after only sustaining frontal and occipital cortex ablations

however, demonstrate a statistically significant difference between animals with one-stage ablations and animals with two-stage lesions ($p > 0.05$).

In contrast to Experiment 1, different results were obtained when days to criterion were analyzed. In this case the scores of rats with two-stage lesions did not differ significantly from those of the control animals ($p > 0.05$). Again it was found that one-stage animals performed more poorly than rats with somatosensory cortex intact ($p < 0.01$). Nevertheless, the scores of the pooled one-stage and two-stage lesion groups still did not differ significantly from each other ($p > 0.05$).

Examination of individual scores showed that only one animal with a serial lesion of the somatosensory cortex had difficulty with the discrimination follow-

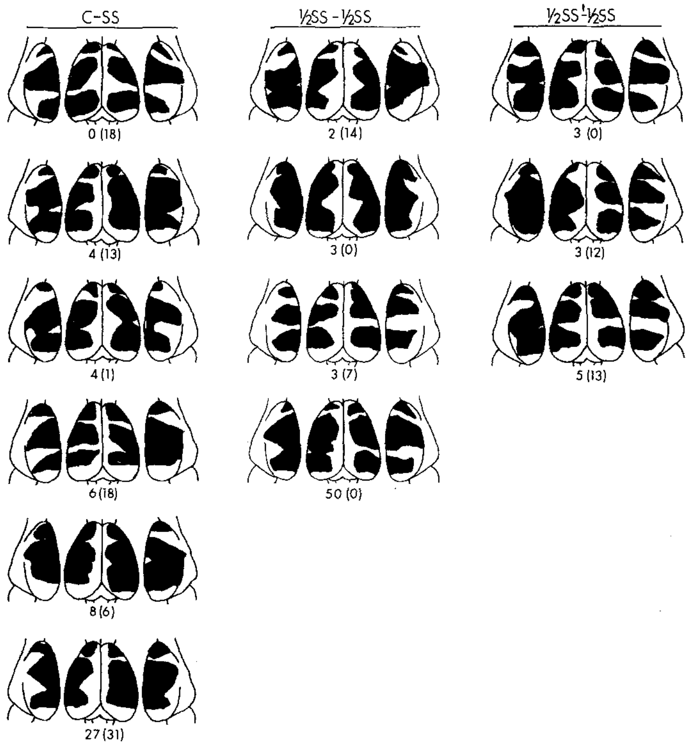


Fig. 8

ing anterior-posterior cortical lesions (group $^1/_2SS$-$^1/_2SS$) and that all other animals with serial lesions displayed excellent retention on the discrimination. In contrast, a large proportion of rats with one-stage lesions had difficulty relearning the retention problem and less than 40% of these animals had scores within the range of control group performance. A Fisher Exact Probability Test revealed that this difference between one-stage and two-stage rats was significant at the 0.05 level.

Sign tests on the repeated measures obtained by rats in Group *C-C* showed that non-somatosensory cortex lesions (Experiment 2) did not impair performance relative to the sham condition (Experiment 1) ($p > 0.05$). However, following bilateral ablation of somatic cortex these animals were unable to relearn the habit as rapidly as they did following only frontal and occipital cortex lesions ($p < 0.05$).

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 did not differ significantly from the one-stage animals (pooled) that had frontal and occipital cortex removed after somatic cortex lesions (both $p > 0.05$). Hence, whether the one-stage somatosensory cortical ablations were made before or after frontal-occipital cortex lesions was not a key factor in performance during final testing.

Drawings of the surface lesions of the animals that experienced anterior and posterior neocortical ablations in addition to somatic cortex lesions are presented in Figs. 7 and 8. All rats sustained severe damage to the somatic cortex as was noted in Experiment 1 plus extensive damage to the remaining neocortex. However, in most cases islands of tissue were found anterior and/or posterior to the somatic cortex and in the most posterior region of the occipital cortex. Because there was considerable anatomical variability within and between surgical conditions it was not possible to note any systematic differences among the groups in terms of lesion size and locus. Nor did there appear to be any significant relationships between lesion characteristics and performance within these groups. As in Experiment 1 many lesions were found to involve the corpus callosum. Limbic and thalamic nuclei were not directly involved in the aspirative damage.

Discussion

Some but not all of the hypotheses proposed in the present experiments were confirmed by the data. In the first study animals with one-stage lesions of the somatosensory cortex performed statistically worse than rats with two-stage lesions of the same structures as had been predicted. The presence or absence of interoperative training did not, however, differentiate the scores of the two groups of animals with serial lesions. In contrast, additional training prior to one-stage lesions of the somatosensory cortex was found to be effective in statistically minimizing this lesion effect. This confirms the findings of Weese *et al.* (1973) who previously reported an overtraining effect in rats with one-stage lesions of the somatic cortex. Interestingly, preoperative overtraining may not play an important role in rats with one-stage lesions of the visual cortex (see Glendenning, 1972). Interoperative overtraining, on the other hand, appears to be necessary for good performance scores under some conditions where the visual cortex of the rat is serially damaged (Glendenning, 1972; Kircher *et al.*, 1970; Petrinovich and Carew, 1969; Thompson, 1960). Inherent differences between the two sensory systems, task difficulty (see Simons *et al.*, 1975), and the amount of overtraining are three factors which might account for these divergent results.

In the second experiment it had been proposed that rats with cortical lesions sparing the somatosensory areas would demonstrate essentially normal performance and this was confirmed (see also Simons *et al.*, 1975; Sperry, 1959; Zubek, 1952). In addition, there was some support for the hypothesis that the performance scores of rats with two-stage lesions would be less affected by additional neocortical insult than those of one-stage animals. The evidence for a difference between the two groups comes in part from the observation that while the one-stage animals performed worse than control animals on both errors and days to criterion, the two-stage rats performed significantly worse than the control group only on the error index. Further, although the one-stage and two-stage groups failed to differ significantly from each other on the above measures, this was found to be attributable to one deviant animal with a serial lesion who performed very poorly on the problem. All of the remaining animals with serial lesions relearned the discrimination rapidly and with little variability (Fig. 6). The strongest evidence for a difference, however, comes from the fact that significantly more two-stage rats than one-stage animals had scores that fell into the control group range. In the context of these findings it should be noted that scores indicating better performance by the original two-stage animals were also seen in Experiment 2 of the previous study although these data failed to attain statistical significance ($p < 0.057$; $p < 0.071$; Simons *et al.*, 1975). The emergence of the same trend after additional neocortical damage in two independent cases would suggest that this effect is real and that it could have been more convincingly demonstrated in both experiments had more animals been tested.

The major reason for conducting the present investigation was to examine in some detail the role of task difficulty in serial lesion research. Since this study is directly comparable to the previous investigation (Simons *et al.*, 1975) in terms of experimental design, animals, lesion characteristics and apparatus, and significantly different only in terms of the choice of tactile stimuli, the observed differences appear to be related to task difficulty. In the earlier invesigation the tactile form discrimination was one which took naive rats approximately 40 days to learn, and one which 50% of the rats with one-stage lesions of the somatosensory cortex and 33% with serial lesions could not relearn within 60 days. The task used in the present study was acquired by the naive rats in approximately 15 days, and it was relearned postoperatively by all but a few animals in less than 18 days. Although rats having one-stage lesions without overtraining performed poorly compared to control subjects in both studies, the groups of animals with serial lesions of the somatosensory cortex performed better than the one-stage animals and did not differ significantly from the sham operates only in the present instance. Further, after ablation of somatosensory cortex plus tissue anterior and posterior to these areas all of the animals in this experiment relearned the problem. Sixty percent of comparable subjects in the earlier study failed to show such relearning within an even longer retest period. Hence, it can be concluded that task difficulty is an important factor in serial lesion studies as well as in more traditional lesion experiments. This variable can be manipulated by altering the physical characteristics of the stimuli as was done here, or by varying the nature and amount of training prior to exposure to the discrimination in question. The latter possibility is illustrated by comparing the performance of the serially lesioned rats on the same "difficult" tactile discrimination in two separate experiments (Finger *et al.*, 1971; Simons *et al.*, 1975). In the former, a series of progressively more difficult tasks preceded the critical test and the serial animals performed well. In the latter, the animals were placed directly onto the problem and those with serial lesions were as impaired as the one-stage subjects.

The data from these retention studies suggest that roughness thresholds may be temporarily elevated following ablations of the somatosensory cortex. Threshold alterations have been reported in a variety of other laboratory animals following analogous lesions (cf., Semmes, 1973). However, because the precise nature of this threshold shift in rats is not understood (Finger, 1974), it is unclear what relationship exists between recovery after serial lesions and recovery after simultaneous ablations. The trends noted in the scores of the one-stage and two-stage animals with additional neocortical lesions in this and in the pervious experiment show that the serial animals may be less affected by later cortical insult. This would imply that the substrates underlying recovery might not be the same in animals that experience ablations in two sittings as opposed to one. In the context of this hypothesis the importance of task difficulty may in part be explained by postulating the existence of related but not identical parallel systems that either remain functional or become so after the somatic cortex ablations. Surgical procedures may determine which systems become available postoperatively and to what extent the animal is able to use them, although training variables and the potential for using alternate behavioral strategies cannot be discounted as interacting factors in the recovery process. Future studies in which both the physical stimuli and the learning histories of the animals are varied could cast further light on the nature of the serial lesion effect and on the effects of ablation *per se*.

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