

Somatosensory Function and Cortical Unit Activity in Cats with only Dorsal Column Fibers

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Summary. Cats received lesions that transected the entire thoracic cord except for partial sparing of the dorsal columns. The cats were required to discriminate the side on which they were touched, the size of simultaneously presented discs, or the direction their fur was stroked to obtain food reward. All cats found by anatomical and/or electrophysiological criteria to have any functional continuity in the dorsal columns were able to master the first of these tasks; some responded above chance on the second. Performance was at chance on blank trials, and cats with complete cord transection failed to discriminate. Lesioned cats did not orient or otherwise react to any nonrewarded stimulus below the level of the lesion. A total of 532 units were recorded under light barbiturate anesthesia from the hind paw projection near the tip of the ansate sulcus in these and other similarly prepared cats. Three-fourths of the units found before and acutely after the cord lesions were made were driven by hind limb stimulation. Only 27% of the units recorded 10 or more days afterwards could be driven. Of these driven units, 15 (38%) responded to foreleg stimulation, 13 exclusively so. No such units were found in intact or acutely lesioned cats.

Key words: Dorsal columns – Tactile discrimination – Cortical units

The widely held view that the dorsal columns mediate fine tactile, joint position, and vibratory sensory function has been challenged by the results of several workers. Cook and Browder (1965) reported that rare clinical cases in which lesions were restricted to the dorsal columns showed little or no deficit in tactile or kinesthetic modalities. Wall and Dubner (1972) reviewed the experimental literature and concluded that dorsal column lesions alone resulted in only limited loss in performance of fine tactile discriminations. In this laboratory, Dobry and Casey (1972a, b) found that very large lesions of the cervical dorsal columns were necessary to affect reliably roughness discrimination or cortical neurophysiology in the cat. One common interpretation of this general finding is in terms of redundancy due to the presence of parallel systems. Wall (1970) rejected this explanation because he found that rats with

thoracic spinal cord lesions sparing only the dorsal columns usually failed to orient promptly to stimuli below the level of the lesion. He proposed that the dorsal column system regulates parallel somatosensory afferent pathways in their analysis of incoming somatosensory information. Melzack and Bridges (1971) have suggested a related hypothesis: namely, that the dorsal column system mediates the evaluation of the outcome of response strategies. Beck (1976), Dubrovsky et al. (1971), Dubrovsky and Garcia-Rill (1973), Gilman and Denny-Brown (1966), and Melzack and Southmayd (1974) have presented data supporting similar concepts.

Recent investigations have suggested that the dorsal column system mediates complex somatosensory functions involving analysis of spatial or temporal patterns. Lesions of the dorsal columns of monkeys produced a severe and lasting deficit in discriminations requiring active exploration of excavated patterns (Azulay and Schwartz, 1975) or detection of different sequences of stimulating two points on the skin, the separation of which was progressively reduced (Viereck, 1974).

The purpose of the present research is to pursue further Wall's strategy of determining the functions the intact dorsal columns can mediate in the absence of any other parallel system. Wall (1970) used overt behavioral orientation towards brushing, pin pricks, and mild electrical stimulation to the body as a measure of sensory function. Myers et al. (1974) have recently used a discrimination task to evaluate sensory functioning following such a lesion. They showed that cats continued successfully to detect direct electrical stimulation of cutaneous afferents below the level of such cord lesions. The present research has confirmed and extended this finding by using natural cutaneous stimuli in a somewhat different discrimination task and by examining in these same cats changes in cortical electrophysiology following the spinal lesions.

Methods

Subjects

A total of 12 adult mongrel cats weighing between 2.0 and 3.7 kg were used in these experiments. Behavioral data were obtained from 8, and electrophysiological records were obtained from 11 including 7 of those in the behavioral experiments.

Apparatus

Behavioral testing took place while the cat held its head through a diamond-shaped opening in the center of a 44 cm square screen made of Masonite (Fig. 1). Two clear plastic food cups, illuminated from within by rheostatically controlled lamps, were mounted 6 cm in front of the screen below and equidistant from the center of the hole. The approach of the cat's head over either illuminated food cup was detected by a photocell. An electromechanical programming circuit controlled the delivery of 3–5 ml portions of a liquid diet.

Four kinds of somatic stimuli were used in behavioral testing. Light tactile stimuli were produced by a flexible coil spring which required about 4 g of force to bend it enough to close a circuit and initiate a trial. A stronger tactile stimulus was produced by a contactor vibrating at 60 Hz pressed firmly against the skin of the cat's hindlegs. The device was made of a table tennis ball glued to the voice coil of a 4 Ω loudspeaker modified to minimize the effect of varying load. The

amplitude of vibration was about 0.25 mm peak to peak without load. Stimuli for size discrimination were plastic discs ranging from 6.4 mm (1/4") to 50.8 mm (2") in diameter mounted on the end of plastic rods by which they were manually pressed against the animals' thighs.

Surgery

Cord Lesions. Cats were anesthetized with pentobarbital (35 mg/kg i.p.), and a laminectomy was performed for several segments on either side of T7. The dorsal lateral sulcus was identified and suture was passed at the level of T7 under the cord and then back through the cord under the dorsal columns and in 3 cats under the dorsal lateral columns as well. Thus, the suture was looped around all of the spinal cord except the dorsal fiber tracts which were to be spared. The loop was tightened to sever the cord except for those tracts, the cord was covered with absorbable gelatin sponge (Gelfoam), and the wound was closed in layers. The cats received 50 mg of sulfadimethoxine (Bactrovet) and 25 mg of oxytetracycline (Liquamycin) twice daily for 5 days postoperatively. The bowels and bladder were manually expressed at least twice daily for the survival period of the animals.

Implantation for Unit Recording. In order to permit repeated unit recording sessions from each cat a nylon cylinder with a silicone rubber dam fixed across the bottom was implanted over the hind paw projection of somatic area I. The cats were anesthetized with pentobarbital, the pericruciate cortex was exposed, and the dura was reflected. The nylon cylinders were stereotaxically positioned just anterior to the tip of the ansate sulcus and cemented in place. A notch on the top of one of the cylinders served as the stereotaxic reference mark. The cats received a course of antibiotics for 5 days postoperatively.

Procedure

Behavioral Testing. Six cats were trained prior to the placement of the cord lesion; 2 were trained only afterwards. The cats were deprived of food and were trained to approach the illuminated food cups and to drink the liquid diet from them. The start of each trial throughout training and testing was signaled by illuminating the food cups. The first task was a simple brightness discrimination to teach the cats the nature of the response required in subsequent tactile discriminations. The luminances of the correct and the incorrect cups were set to about 10^4 and 10^3 cd/m² respectively, as measured with a SEI photometer positioned approximately where the cat's head would normally be. When the cat's approach to one of the food cups was detected the lamps went out; if the correct (brighter) cup was approached, liquid diet was delivered to that cup. Twenty-four trials were administered daily, the position of the correct cup being determined by sequences described by Fellows (1967). As training continued the cat was required to remain still and face straight ahead before a trial was initiated to minimize responses based on head position. The cats were soon able to hold this posture for 5 sec though this requirement was subsequently not stringently enforced. After 7–12 days of training on this brightness discrimination task the 4 g tactile stimulus was made part of the discriminative stimulus by presenting it on the same side as the brighter (correct) cup (Fig. 1). Trials were initiated by applying the 4 g tactile stimulus to the cat's body. The negative visual discriminative stimulus was eliminated by increasing its intensity in 2 stages to equal that of the positive stimulus (10^4 cd/m²), leaving only somatosensory discriminative stimuli to guide behavior. Five cats were trained with the tactile stimuli on the hind legs; the remaining 3, including the 2 trained only after the cord lesions had been made, received the stimuli on the shoulders. Subsequent changes in stimulus conditions were usually introduced after the cat reached a minimum criterion of 90% correct or better on 3 of 4 consecutive days.

After reaching criterion on the 4 g tactile discrimination the 6 animals trained before cord surgery were switched to 1 of 3 tasks. Valid data were obtained on a size discrimination between a smaller plastic disc on the correct side and a larger one on the incorrect side and on a direction-location discrimination on the right thigh between the 4 g tactile stimulus moving from the posterior edge anteriorly (left cup correct) and the same stimulus moving from the anterior edge posteriorly (right cup correct). Four of the 6 cats trained before the cord lesion was made were also tested with 4–6 blank trials per day on which no tactile stimulus was delivered. Chance performance on

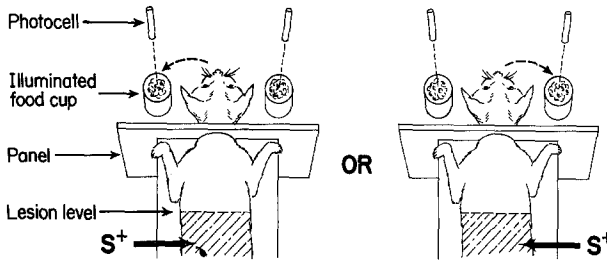


Fig. 1. Semi-diagrammatic representation of behavioral training situation and basic testing task. Cat must hold head through a diamond-shaped opening in the panel and approach the illuminated food cup on the side on which the positive tactile discriminative stimulus (S^+) is presented

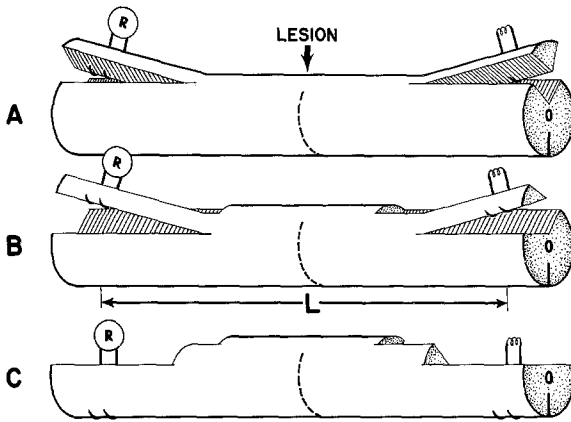


Fig. 2A-C. Diagrammatic representation of preparation for terminal electrophysiological verification of conduction through the area of the lesions in the dorsal columns, the dorsal lateral columns, and the ventral cord. **A** Dissected dorsal columns are lifted onto stimulating and recording electrodes. **B** Dorsal columns are cut away, and dissected dorsal lateral columns are lifted onto electrodes. **C** Dorsal lateral columns are dissected away, and electrodes rest on intact ventral cord

these trials demonstrated that the cats were in fact using somatosensory cues to guide their behavior. In addition, 3 of these 6 cats were tested for stimulus generalization between thigh and shoulder prior to placement of the cord lesion. This change had no effect on their performance.

Cord lesions were placed 1–31 days after behavioral training was completed, and testing resumed 10–21 days later. The 6 previously trained cats were initially retrained with the 4 g tactile stimulus applied to the shoulders. When criterion was achieved on this task, sensory function below the level of the lesions was tested.

Unit Recordings. The 9 cats prepared with the nylon cylinders over the cortical hind paw projection in somatosensory area I were anesthetized with pentobarbital and placed in a stereotaxic device periodically before, during, and after the period of behavioral testing. Before the first penetration, the impedance of the steel microelectrodes measured at 100 Hz was usually about 8 M Ω . The signals were amplified and displayed on a CRO and an audio monitor. In addition, the signal could be sent to an averaging instrument (Mnenotron CAT 400) and to a spike height discriminator and post-stimulus histogram system which could also be used as a counter (Spears et al., 1970). Shocks were delivered 1/sec through bipolar needles inserted in the footpads. Averages of 20 cortical evoked responses were collected usually at 0.5 mm intervals along each electrode track. Permanent records were made on an X-Y plotter.

As many properties as possible were recorded for each isolated unit, including micrometer depth of the microelectrode, amplitude and polarity of the impulse, location and size of the receptive field, adequate stimulus, spontaneous rate, latency and post-stimulus response pattern to electric shocks, and responses to repetitive electrical stimulation. Recording sessions lasted for 8–16 hrs. Because no surgical trauma was involved the level of anesthesia could be allowed to become and remain very light, and behavioral testing could be resumed the next day.

Terminal Verification of Cord Lesion. The functional continuity of the different components of the spinal cord was tested electrophysiologically in 6 cats with cord lesions and in 3 intact control animals. The cats were deeply anesthetized with pentobarbital and fixed in a Kopf spinal investigation unit. An extensive laminectomy was performed several cm rostral and caudal to the site of the lesion. The animal was paralyzed with gallamine triethiodide (Flaxedil), artificial respiration was begun, and expired CO₂ was periodically monitored. It remained at about 4.5% throughout recording. The depth of anesthesia at the start of paralysis and the brevity (2–3 hrs.) of the recording period insured that the cats remained under anesthesia for their survival. Bipolar silver wire electrodes were placed on the surface of the exposed cord. Shocks were delivered caudal and responses recorded rostral to the lesion. In addition, the dorsal columns, the dorsal lateral fasciculus, and the ventral cord were tested for conduction independently by dissecting free the former two and placing the 3 components individually in contact with the stimulating and recording electrodes in an overlying mineral oil pool (Fig. 2).

After recordings were completed the cats were perfused by intracardiac infusion with saline followed by 10% formalin. The entire spinal cord was dissected free, and the lesion area was examined grossly before the cord was fixed in 10% formalin prior to histological verification of the extent of the lesions. Frozen sections were cut at 30 or 60 μ and stained with Weil and Nissl stains. Before dissecting the brain from the skull a hypodermic needle was stereotaxically driven through the center of the silicone rubber dam over the somatic cortex. A radio frequency lesion was made to serve as a reference for identifying the approximate position of the microelectrode tracks on the sensorimotor cortex.

Results

Verification of Cord Lesion

Both the anatomical reconstructions of the lesions (Fig. 3) and the terminal electrophysiological tests for functional continuity showed that all pathways ventral to the dorsal columns were severed as intended. No conduction was observed in any animal in the ventral cord with any available stimulus intensity (150 V, maximum) despite the fact that these intensities were adequate to stimulate the normal tracts rostral to the lesion by current spread over a distance of several mm. Histological evidence for sparing of some fibers lateral to the dorsal lateral sulcus could not be confirmed by the electrophysiological test for functional continuity of the dorsal lateral fasciculus.

Conduction in the dorsal columns was found to be significantly modified and in 2 cats completely abolished. In 2 unlesioned control cats the conduction velocities in the dorsal columns were 60 and 66 m/sec, and the amplitude of the compound action potential was 1.5–2 mV (Fig. 4; 1). In the lesioned animals whose dorsal columns remained functional, the conduction velocity ranged from 21 to 40 m/sec, the compound action potential was prolonged, and the maximum amplitude of the response was only 200 μ V (Figs. 4; 4–6). This finding was consistent with the histological findings (Fig. 3). In most instances the dorsal columns in the region of the lesion were only partially spared, showed gliosis and meningeal fibrosis with scattered patches of degenerating fibers, and were sometimes severely distorted by the scarring. The cortical electrophysiology described below also reflected the incomplete sparing of the dorsal columns.

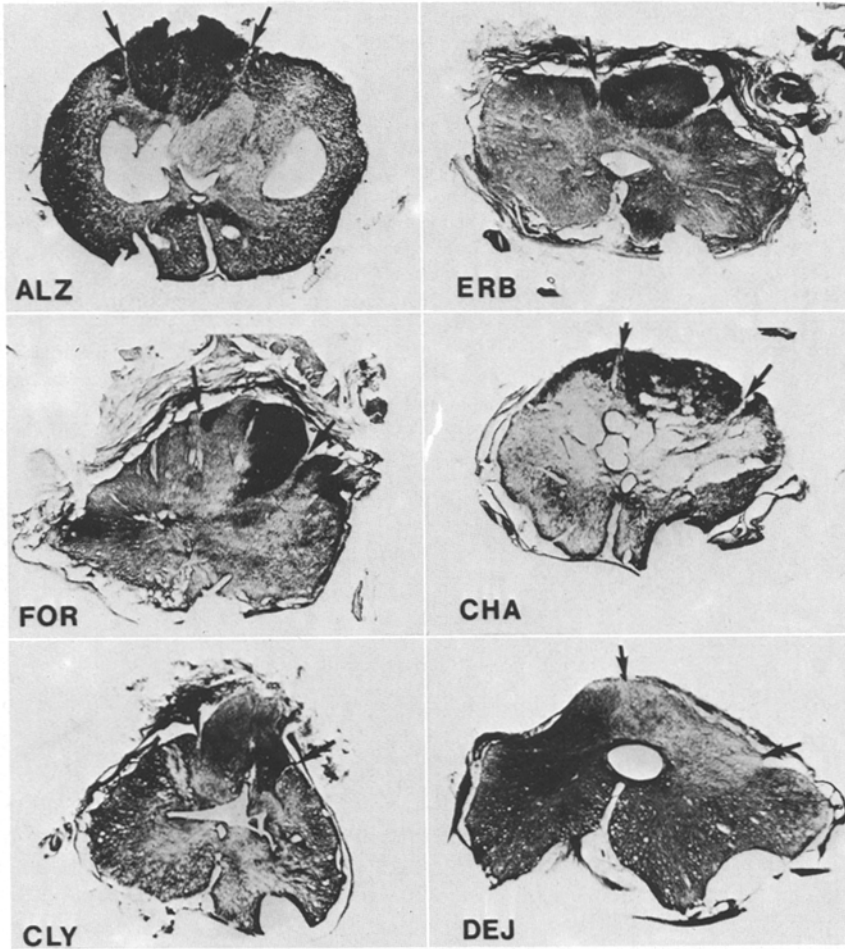


Fig. 3. Weil stained sections from the spinal cord of 6 of the cats, slightly rostral to the area of maximum damage. Arrows indicate position of dorsal lateral sulcus

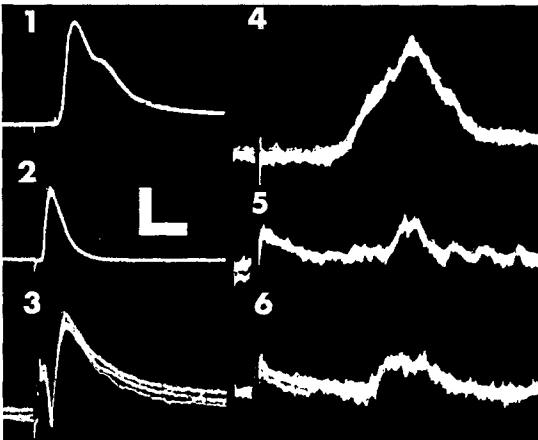


Fig. 4. Evoked potentials recorded terminally from spinal cord. (1-3) Intact control cat. 1 Dorsal columns. 2 Dorsal lateral columns. 3 Ventral cord. 4-6 Dorsal columns from lesioned cats (ALZ, ERB, and FOR respectively). Calibration: 1.0 msec; (1, 2) 0.5 mV. (3) 0.1 mV. (4-6) 50 μ V

Behavioral Training under Control Conditions

All 8 cats learned the touch discrimination, 2 learned and 1 performed above chance on the direction discrimination, and 2 learned to discriminate between different sized discs. The results of formal behavioral testing are presented for each cat in Figures 5a and 5b together with a diagrammatic reconstruction of the cord lesions. Data from the early training period are not shown. The 6 cats trained prior to cord surgery reached criterion 10–23 days after the tactile stimulus was introduced. The 2 cats trained after cord surgery with stimuli delivered to the shoulders learned in 6 (JOE) and 13 (CLY) days. Cats BAB and ERB eventually mastered the direction-position task, showing clear evidence of being able to make the discrimination in about 20 and 5 days, respectively. A third cat, DEJ, also performed above chance on this discrimination but failed to reach criterion in the 38 days she was trained on it. The remaining 2 cats, CHA and FOR, were trained on the size discrimination, initially between a 50.8 mm (2") diameter (–) and a 6.3 mm (1/4") diameter (+) disc. CHA eventually mastered the discrimination between 6.3 mm diameter and 25.4 mm diameter, and FOR had almost mastered the same discrimination when training was terminated to place the lesion.

Postoperative Performance

All 6 cats subsequently shown to have some intact dorsal column fibers were able to make consistent discriminative responses to hindlimb somatic stimuli. One of these animals had no preoperative training. The 2 cats with complete cord transections showed no evidence of ability to detect hindlimb stimuli (Fig. 5b).

The cats with preoperative training were retrained with the 4 g tactile stimuli delivered to the shoulders above the sensory level. They all showed either a very rapid rise to criterion performance or an almost immediate and complete generalization from their pre-lesion training on the hind legs. One cat (ALZ), subsequently shown to have the most extensive dorsal cord sparing, showed excellent retention of the 4 g tactile discrimination on the hind leg, but did take 17 days to return to criterion performance. Training was then begun on the size discrimination which she was able to perform above chance when the positive stimulus was 50.8 mm (2") in diameter and the negative was 6.3 mm (1/4"). As the diameter of the positive stimulus was progressively decreased, her performance deteriorated, but it recovered when the 50.8 mm stimulus was reintroduced. Chance performance on blank trials showed she was using the somatic stimuli to guide her behavior. A second cat (ERB) also showed evidence of retention of the light touch discrimination when first tested on the hindlimbs 19 days after the lesion had been placed. Her performance was, however, quite erratic, probably because of abdominal skin lesions resulting from paroxysmal licking and biting. When the skin lesions were heavily protected and allowed to heal, her performance stabilized and finally reached criterion. Subsequent performance on the retention test for the direction-location discrimination was erratic for the 25 days available for testing. This cat had less dorsal cord sparing than did ALZ.

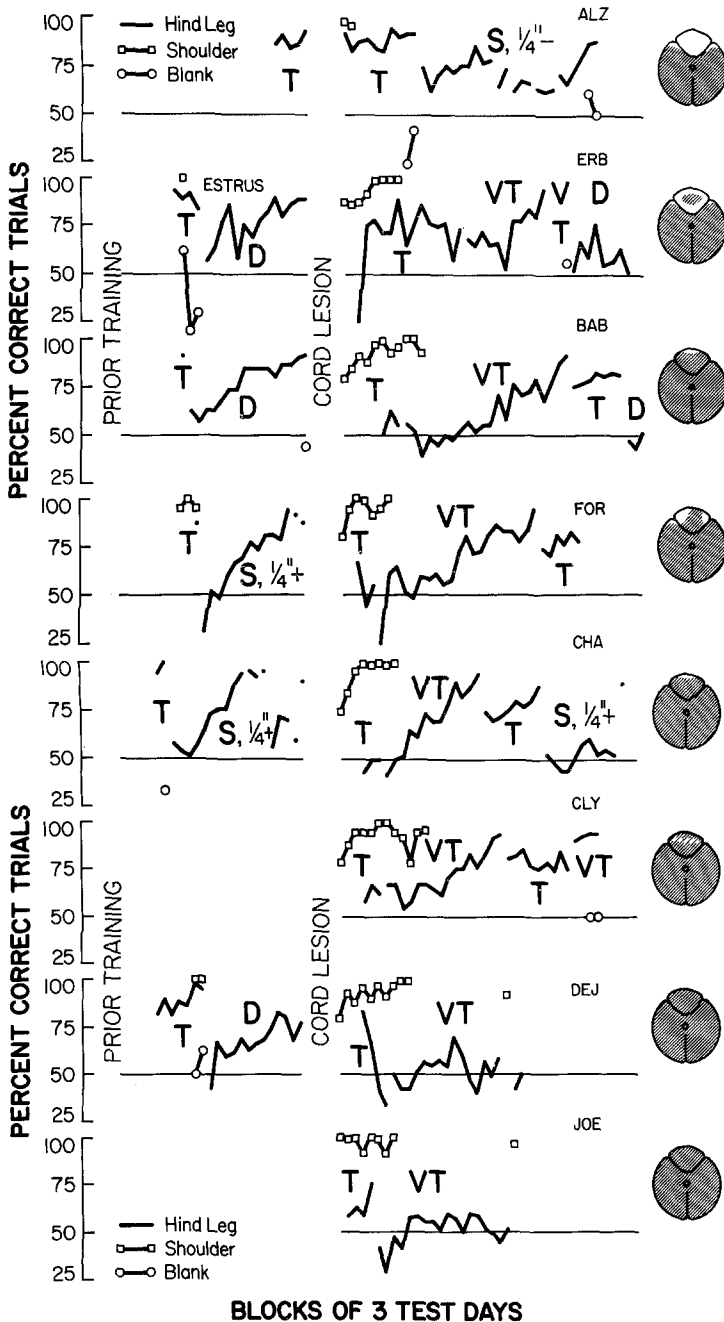


Fig. 5. Behavioral discrimination performance and diagrammatic representation of maximum cord lesions. Breaks in lines represent change in test condition. Each point making up the lines is the average of 3 days, except a few points at the start or end of a condition when data were averaged over 2 or 4 days. (T) 4 g tactile stimulus. (VT) Vibrating tactile stimulus. (D) Direction-position discrimination between 4 g stimulus moving rostrally and caudally over the thigh. (S) Size discrimination between 6.3 mm (1/4") diameter disc and a larger disc, initially 50.8 mm in diameter and successively reduced to 38.1, 25.4, and, in two cases, to 12.7 mm. Preliminary training for all cats and an unsuccessful effort to train discrimination between a vibrating and a stationary stimulus in *ALZ* and *BAB* are not shown

The remaining 4 cats in this group showed chance performance when first tested with the 4 g spring. When the vibrating contactor was used in place of the 4 g spring, however, 3 (BAB, FOR and CHA) eventually demonstrated somatosensory functioning below the level of the lesion. Their performance on the vibrating touch detection started to be consistently above chance 53 (BAB), 40 (FOR), and 27 (CHA) days after hindleg stimuli were first introduced postoperatively. All 3 eventually reached criterion when the vibrating contactor was used as the discriminative stimulus. When the 4 g touch stimulus was reintroduced the performance of all 3 cats declined and failed to return to criterion in the allotted testing period, though it did consistently remain above chance. Neither BAB nor CHA showed any retention of the more difficult tasks which they had mastered before the lesions had been placed, though the test period was limited. Terminal anatomical and electro-physiological examination of the spinal cords of BAB, FOR and CHA showed partial sparing of ascending fibers across the lesion, restricted in each case to the dorsal columns. The performance of the fourth cat (DEJ) varied little from 50% correct throughout the 55 days of testing with somatosensory stimuli on the hind legs. Histological and electrophysiological evidence showed that conduction in her cord had been abolished.

Two cats were trained only after the cord lesions had been placed. Cat JOE showed no sign of discriminating stimuli below the level of the lesion on any test used, and anatomical and physiological evidence showed that the cord was completely severed. Cat CLY failed for 26 test days to discriminate reliably stimuli delivered to the hind legs on 4 test trials interspaced among 20 trials on which the discriminative stimuli were delivered to the shoulder. However, 5 days after the vibrating contactor was applied to the hind legs on all 24 daily trials, his performance went reliably above chance and finally reached criterion on the twenty-seventh day on this task. Performance declined but remained well above chance for the next 26 test days on which the 4 g touch stimulus was used as the discriminative stimulus, and returned to criterion level when the vibratory stimulus was reintroduced. Anatomical reconstruction of the cord lesion showed small patches of stained fibers restricted to the dorsal columns.

Additional Behavioral Observations

After the cord lesions were placed none of the animals responded by orienting to light jabs with a needle or to any other stimulus below the mid-thoracic level throughout their survival period. However, they did paroxysmally lick and in 2 cases bite themselves for brief periods at specific sites below the level of the lesion. This behavior first appeared several weeks after the cord lesion had been made. Two cats (ALZ and ERB) showed the phenomenon in a particularly striking fashion. The former attacked her paws and the latter her abdomen vigorously and often enough to leave open wounds which had to be bandaged and heavily taped for protection. Between these brief paroxysms, all cats appeared to be in no distress for they ate, groomed above the level of the lesion, and responded to handling normally.

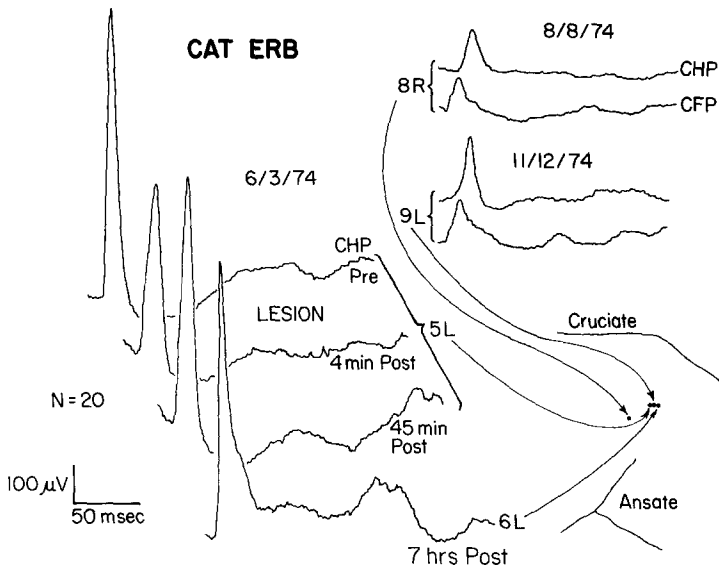


Fig. 6. Sums of 20 evoked potentials recorded from hindpaw projection in somatosensory cortex I near the tip of ansate sulcus. (*Left*) Evoked potentials in response to contralateral hindpaw (CHP) shocks recorded before lesion was made and up to 7 hrs afterwards. (*Right*) Evoked potentials recorded chronically after lesions were made in response to contralateral hindpaw (CHP) and forepaw (CFP) shocks. Approximate location of tracks from which responses were recorded are shown in relation to cortical sulci at bottom right

Cortical Electrophysiology

Before placement of the cord lesions, cortical evoked potentials elicited by contralateral hind paw (CHP) stimuli exhibited the normal surface positive-negative configuration with amplitudes up to several hundred microvolts (Fig. 6, top left). Unit responses appeared only after the evoked potential reversed polarity on deeper penetration. Electrical stimulation of the contralateral forepaw in one intact control cat elicited only small evoked potentials ($\bar{X} = 53 \mu\text{V}$, p-p) ordinarily detectable only with signal averaging.

Immediately after cord lesions were placed, evoked potentials elicited by contralateral hind paw shocks recovered to or remained within the normal range for several hours (Fig. 6, left). No data were obtained on response to forepaw shocks at this time. Comparable records obtained from neighboring tracks on subsequent recording sessions in the chronic phase showed a marked decline in the amplitude of the responses elicited by hind paw stimulation (Fig. 6, right). Responses to contralateral forepaw (CFP) shocks tended to be larger than in the intact control averaging $\approx 153 \mu\text{V}$, p-p. The 2 cats which terminally were found to have completely transected cords exhibited neither evoked responses nor drivable units in response to hind leg stimulation within a few tenths of a mm of tracks which prior to lesioning had shown both. The 5 cats that successfully discriminated somatosensory stimuli below the level of

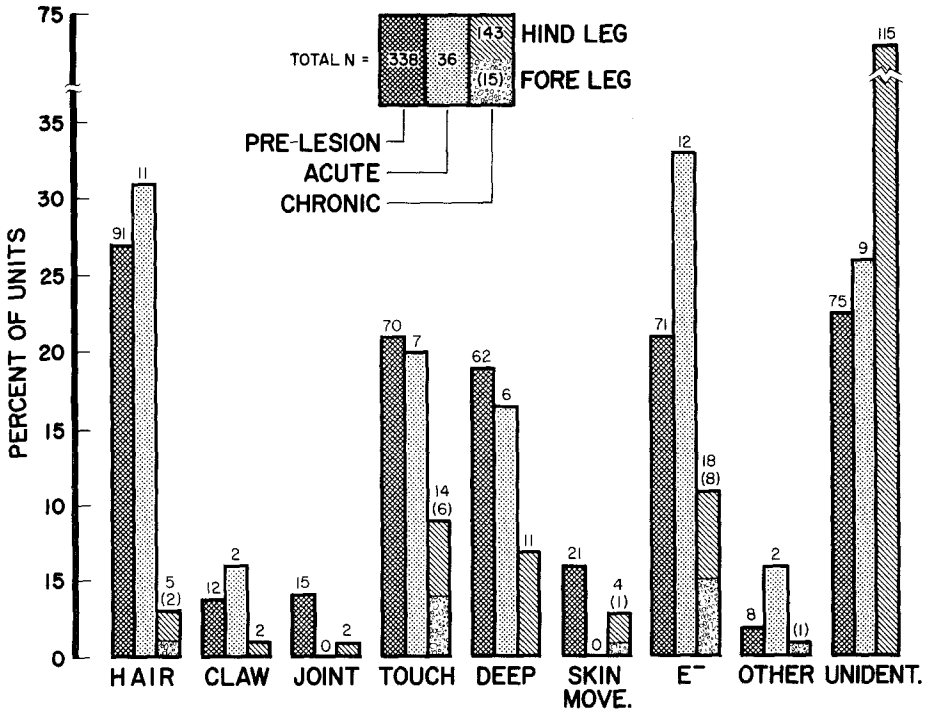


Fig. 7. Percentage and number of cells recorded before cord lesion was made (Pre-lesion), up to several hrs afterwards (Acute), and 10 or more days afterwards (Chronic) divided according to driving stimulus. Data from chronic condition are divided according to location of receptive field on hind leg (cross hatching and numbers without parentheses) or on foreleg (speckling and numbers in parentheses). 102 cells were driven by more than one class of stimuli, electrical (E^-) usually being one. Only 23 of these were driven by more than one natural stimulus. Unident. refers to spontaneously active units not driven by any of the stimuli with which they were tested

the lesion and for which cortical electrophysiological data are available all showed some cortical electrical activity in response to stimuli below the level of the lesion. However, except for the immediate post-lesion period the evoked potentials were attenuated and in many locations undetectable despite averaging 20 responses or more.

Properties of the population of units recorded in the chronic post-lesion condition also differed markedly from those of the populations obtained from intact cats and from lesioned cats in the first few hours after the lesions were made. Figure 7 presents the percentages and number of units excited by various types of peripheral stimuli in the 3 recording conditions. The test stimuli included gentle hair movement, gentle pressure to the skin, movement of claws, muscles, skin, and joints, and electric shocks through bipolar needle electrodes thrust into the skin. Approximately 75% of the units recorded before lesions of the cord were placed or in the first few hours afterwards were excited by one of the stimuli tested. In contrast, only about 25% of the units re-



Fig. 8A-D. Cortical unit responses to shocks delivered through needle electrodes thrust into the plantar surface of the paw. **A** Normal cord (GLO). **B-D** Chronically lesioned cord (ERB). **A-C** Responses to hindpaw stimulation. **D** Forepaw stimulation. **C** and **D** were recorded within a few minutes of each other without moving the electrode and show the same unit driven by fore and hind leg stimulation. Calibration: 5 msec; 0.1 mV

corded in the chronic post-lesion condition were excited by any stimulus. Very few drivable units were located, even in tracks placed within a few tenths of a mm of preoperative tracks with a high yield of excitable cells.

Units responding to hair stimulation were most profoundly affected by the lesions. The first 6 submodality categories showed no significant difference in the proportion of decline between categories, ($\chi^2 = 6.86$, $df = 5$, $p > 0.20$), but a test on the 3 categories of natural stimulation with the largest sample sizes showed that the Hair category suffered a significantly larger decline than did the Touch and Deep categories ($\chi^2 = 6.63$, $df = 2$, $p < 0.05$).

Several other features of the 3 populations can be compared. The mean number of units/track (including non-drivable, spontaneously active ones) for all control tracks were 4.83, for acute tracks, 4.00, and for chronic tracks, 2.93. All 7 animals on which data are available from both the control and chronic survival periods showed a decline in the number of units/track ($t = 5.0$, $df = 6$, $p < 0.01$). The number of units/track obtained acutely after the lesion was made was usually between the number for control and for chronic lesions, but the small number of cats ($N = 5$) from which these data are available makes the differences unreliable statistically. The median latency of 62 units recorded before the cord lesion was made was 18 msec. It was 27.5 msec for 9 units recorded acutely after the lesion was made, and 30.1 msec for 10 units from the

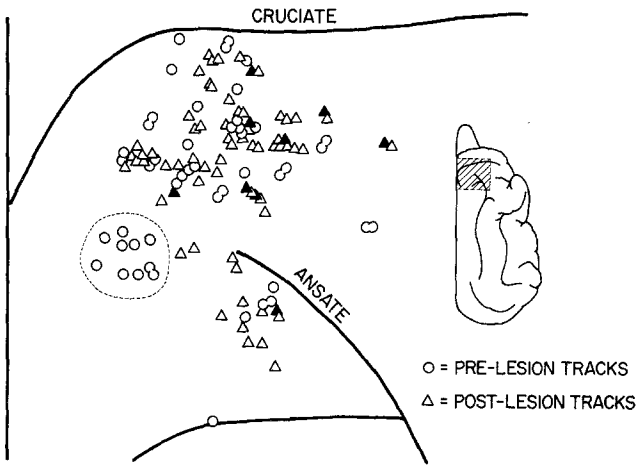


Fig. 9. Approximate location of electrode tracks in relation to cortical sulci. Filled symbols represent tracks from which units driven by forepaw stimulation were found. Symbols enclosed by broken line represent the tracks in the control cat dedicated to the systematic search for foreleg driving

chronic recordings. However, these differences approached statistical reliability only when the acute and chronic post-operative data were pooled to increase the sample size (Kolmogorov-Smirnov two-sample test, $D|\max| = 0.37$, $p = 0.05$ [Segal, 1956]). In all 3 conditions the sizes of the receptive fields varied as a function of position on the leg, showing the systematic decline proceeding from proximal to distal loci that has repeatedly been demonstrated at all levels of the lemniscal system. More units recorded in the chronic post-lesion condition had receptive fields located proximal to the feet than on feet and toes, while the opposite relation held for units recorded in the control and acute post-lesion conditions. However, this difference was not statistically reliable. The distribution of sizes of receptive fields and the spontaneous rate of firing also were not reliably different among the 3 conditions.

A total of 15 units observed in the chronic post-lesion condition was driven by foreleg stimulation. Two responded to both fore- and hindleg stimulation as shown in the bottom 2 traces of Figure 8. The remaining 13 responded only to foreleg stimulation. No units recorded in any cat before the lesions were made could be driven by foreleg stimulation despite a careful search during several sessions on 1 cat devoted to this question. Although the tracks in this cat lay somewhat more medially than did most, the units recorded from them exhibited the normal properties of hindleg units. These tracks are enclosed by the broken line in Figure 9 which presents the approximate location of the electrode tracks relative to the cortical sulci. All were located on the posterior sigmoid gyrus in the immediate vicinity of the tip of the ansate sulcus. Tracks in which units driven from the foreleg were found (solid triangles) are intermingled with other tracks obtained both before and after cord lesions were made.

Discussion

The present experiments show that cats with ascending somatosensory pathways limited to the impaired dorsal columns are capable of using natural tactile stimuli below the level of the lesion as discriminative stimuli. This result extends the finding of Myers et al. (1974) that cats with similar sparing could utilize electrical stimulation in the same manner. Several lines of evidence showed that the cats used tactile cues: chance performance on blank trials, decline in performance following increased difficulty of the discrimination, improvement when the discrimination was made easier, consistently high level of performance in response to tactile stimuli rostral to the level of the lesion, and failure of the 2 cats with anatomically and physiologically verified complete transections of the cord to show any sign of discrimination of stimuli below the level of the lesion.

Only a fraction of the fibers in the dorsal columns were functional. Conduction in these was slowed, but nonetheless sufficient to mediate somatosensory function. Similar findings have been reported in the visual system (Galambos et al., 1967; Chow, 1968), the auditory system (Goldberg and Neff, 1961), and in the somatosensory system (Dobry and Casey, 1972a; Schwartz et al., 1972; Frommer, unpublished observation). This finding does not affect the interpretation of the behavioral results except to suggest that more sparing of function would likely have been observed had dorsal column sparing been more complete.

The cats in this study retained or recovered somatosensory discriminative function in spite of profoundly disturbed electrophysiology of hindlimb somatosensory cortex. Cortical responses of the cats in the present experiment were unaffected acutely by the lesion, confirming an evoked potential study on kittens by Andersson and Leissner (1972) and 3 acutely prepared cats reported by Levitt and Levitt (1968b). However, 10 days or more after the lesion was placed, recordings from the hindleg area of somatosensory cortex I were markedly altered. The amplitude of evoked potentials elicited by hindpaw stimulation, the number of units isolated per electrode track, and the proportion of driven units were markedly reduced.

The chronic spinal lesions were also associated with an apparent increase in the number of forepaw-activated units. This phenomenon became apparent after all lesions were placed, so our control sample is limited to a systematic search for forepaw driving in 10 microelectrode penetrations of the hindlimb cortex of an intact cat. Units with wide field or off-focus driving have been recorded from other areas of somatosensory cortex (Baker et al., 1971; Towe et al., 1968) and ventrobasal thalamus (Bava et al., 1966b; Harris, 1970; Jabbur et al., 1972; Mallart et al., 1961; Shimazu et al., 1965), but we found no forepaw driving in our control sample of 67 units. Under similar conditions of pentobarbital anesthesia, Levitt and Levitt (1968a) also failed to find a single forepaw-activated unit in their sample of 588 units taken from a wider area of hindlimb cortex. A similar restriction of receptive field is found in the coronal forepaw focus (S1) of unanesthetized (Baker et al., 1971) or chloralose-anesthetized cats (Towe et al., 1968).

It is not clear whether the decrease in responsiveness to hindpaw stimulation and the apparent increase in responsiveness to forepaw stimulation was a result of the complete loss of ventral cord pathways or of interference with dorsal column conduction. The latter interpretation is supported by several studies on animals with dorsal cord lesions. Changes in somatosensory electrophysiology in the cortex (Eidelberg et al., 1975; Levitt and Levitt, 1968b, 1974a,b), thalamus (Andersson and Leissner, 1973; Bava et al., 1966a; Bowsher, 1971; Wall and Egger, 1971) and spinal cord (Millar et al., 1976) are similar to the effects reported here. These data were interpreted in terms of axonal sprouting (Wall and Egger, 1971) or release of "normally silent" inputs (Eidelberg et al., 1975; Millar et al., 1976; Merrill and Wall, 1972).

Despite their capacity to make a learned response guided by tactile stimuli below the level of the lesion, the cats failed to orient towards or show any sign of arousal to nonrewarded stimuli below the level of the lesion. Thus, the behavior of our cats is consistent both with Myers et al.'s (1974) finding of a sparing of cue function following such lesions and with Wall's (1970) report that rats failed to orient or otherwise react to stimuli below the level of similar lesions. The absence of orienting or arousal may have been due to an insufficient number of dorsal column afferents remaining functional. However, the slight movement of a few hairs on a normal cat's back activates only a few fibers and is sufficient to initiate arousal and orientation. It seems equally possible that the dorsal column system alone is incapable of activating supraspinal mechanisms essential for arousal and orientation. Consistent with this possibility is the absence of anatomical evidence for collaterals from the dorsal column-medial lemniscal pathway to the reticular formation (Bowsher, 1958; Lund and Webster, 1967; Matzke, 1951) and the failure of afferent impulses restricted to the dorsal columns to evoke activity in the reticular formation (Morrillo and Baylor, 1963, see however Mallart and Petit, 1963) or to modify EEG synchrony or desynchrony (Andersson, 1967; Pompeiano and Swett, 1962). Noxious (and hence presumably motivating) stimuli can activate long, second-order neurons in the dorsal columns (Angaut-Petit, 1975). If they were functioning in any of our cats, they would appear not to mediate the motivating aspect of nociception.

Wall and Dubner (1972) used Wall's (1970) findings to attack the concept that the dorsal column system is "redundant" with some other component of the somatosensory system in the cord. Our current knowledge of the physiology and anatomy of the ascending somatosensory pathways indicates that unique and complex functions are probably mediated by each. In the present experiment, however, all that is required to make the basic discrimination is the detection of any difference in the neural activity arising when one or the other side of the body is touched. On the basis of known electrophysiological properties of their central connections, such an elementary code is present in both the dorsal columns and other ascending somatosensory pathways.

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Note Added in Proof: Recently, Doetsch and Towe (*Exp. Neurol.* **53**, 520–547 (1976)) have reported that approximately one third of the units they isolated in the hind paw projection in somatosensory area I of cats under chloralose anesthesia were driven by off focus stimulation.

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