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Axons of Dorsal Spinocerebellar Tract Which Respond to Activity in Cutaneous Receptors

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NOTIONS OF the cerebellum as an integrator exclusively of proprioceptive information have substantially changed and the role of cutaneous information in cerebellar function is now being explored. The importance of mossy fiber activity resulting from stimulation of cutaneous primary afferent fibers has recently been emphasized by the work of Eccles and his coworkers (9, 23, 24). They showed that evoked potentials produced by such activity are always of larger amplitude than those produced by stimulation of muscle nerves of comparable size (9) and that the potentials evoked by stimulation of the medial, central, and lateral branches of the plantar nerve are sufficiently localized to give information about the part of the foot receiving cutaneous stimulation (24).

The pathways by which this activity reaches the cerebellar cortex have received considerable attention (for a review of cerebellar afferent pathways see ref 40). Although several hindlimb spinocerebellar pathways end as mossy fibers, only the dorsal spinocerebellar tract (DSCT) has a low-threshold cutaneous component (32, 39, 40). That the DSCT is responsible for conduction of cutaneous activity to the cerebellar cortex is suggested by the similarity of discharges in DSCT axons and cerebellar granule cells (9) and the similarity of their receptive fields (55). An illuminating series of experiments by Swedish investigators demonstrated that the DSCT is a heterogeneous tract carrying activity from both proprioceptors and exteroceptors (14, 25–27, 30–32, 34). The proprioceptive subdivision consists of axons activated by stimulation of group Ia and II afferent fibers and axons activated by stimulation of group Ib afferent fibers (32, 34). The exteroceptive subdivision is composed of fibers activated by pressure on foot or toe pads, by touch and pressure in restricted receptive fields, or by touch, pressure, or pinch in larger receptive fields, as well as stimulation of high-threshold muscle afferent fibers.

The nature of receptors producing activity in the proprioceptive subdivision of the DSCT is well known, but we know only the nature of the stimuli which evoke responses in the cutaneous subdivision. Oscarsson (39) suggested that activity in both slowly and rapidly adapting cutaneous afferent fibers (5) is capable of causing discharge in DSCT axons, but did not specify whether this occurs in the same or different axons. Two studies to this point have been done (22, 59), but in neither study were the axons, located in the dorsolateral funiculus, explicitly shown to project to the cerebellar cortex. The importance of this verification was emphasized by Lundberg and Oscarsson (32) who demonstrated three tracts in the dorsolateral funiculus which do not project to the cerebellum (33).

This study is an attempt to identify the cutaneous receptor types, stimulation of which evokes discharges in DSCT axons identified by antidromic activation from the inferior brachium of the cerebellum. Receptor types studied were those associated with rapidly adapting afferent fibers, i.e., types D, G, and T, and one slowly adapting afferent fiber, type I, described by Brown and Iggo (5). A similar classification scheme suggested by Burgess et al. (7) is based more on conduction velocities of the afferent fibers; since these fibers were not observed directly in this study, a classi-

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fication based on receptor structure was employed.

A preliminary communication of some of this work and an abstract have been published previously (36, 37).

METHODS

Surgical preparation

Twenty-three adult cats, 2.5–3.5 kg in weight, were used in this study. The animals were initially anesthetized with pentobarbital sodium (Diabutal, Diamond Laboratories, 35 mg/kg) administered intravenously; throughout the experiment additional doses of 5–10 mg were given as necessary. In a few experiments the cats were initially anesthetized with halothane and decerebrated. The rectal temperature was constantly monitored through an indwelling thermistor and maintained at 37 ± 1 C through use of a d-c heating pad.

The fur of the left hindlimb and the lower abdomen was closely clipped, including the hairs which reside on and between the toes. Screws were driven into the shaft of each tibia for support of the legs in a position convenient for viewing. The T_{12}, L_3, and L_7 vertebrae were exposed and rigidly held by clamps applied to their spinous processes. The animal was placed in a stereotaxic holder and the head, body, and legs were raised off the table. A double pneumothorax was produced, the animal was artificially respired, and 20 mg gallamine triethiodide (Flaxedil, Davis & Geck) were administered intravenously. Supplementary doses were given as required.

A hole was drilled in the cranium just rostral to the external occipital protuberance. The dura covering the portion of the cerebellum underlying the hole was removed and a concentric, bipolar stimulating electrode was lowered at an angle of 22°, stereotaxically through the opening into the dorsomedial extremity of the inferior brachium of the cerebellum, the region shown by von Beusekom (1) and Busch (8) to contain a concentration of DSCT axons (Horsley-Clarke coordinates: F—8.5 mm, S5.5 mm, H—4.5 mm). At the end of each experiment 50 μa of current were passed through the stimulating electrode for 1 min and its position was verified in free-hand sections of formalin-fixed tissue as shown in Fig. 1.

Spinal cord segments T_{13}–L_2 were exposed by laminectomy and the exposed cord was covered with warm saline until recording was ready to begin. The saline was then removed from the spinal cord and, in an early preparation, a longitudinal incison was made in the dura. A silver ball electrode was lowered onto the dorsolateral funiculus and the slow wave evoked by 0.2-msec shocks to the inferior brachium was recorded. The voltage of the stimulus was adjusted to produce the maximal evoked wave. Stimulating current was usually maintained at ≤0.1 ma but never exceeded 0.2 ma. Occlusion of the venous circulation, swelling of the cord, and dimpling of the surface by the microelectrode have been shown to result from longitudinal incisions of the dura in this region (10). In order to avoid these difficulties, a small hole was made in the dura over each recording site and the electrode was lowered through the hole into the dorsolateral funiculus. This procedure was followed in all experiments from which data are reported here.

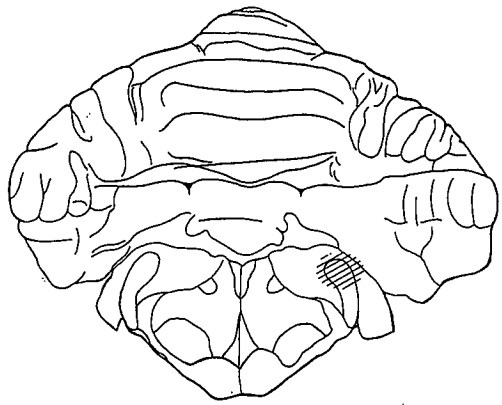

FIG. 1. Composite of locations of stimulating electrodes in the inferior brachium in all animals studied.

Recording and stimulation

Single-axon recordings were made in the dorsolateral funiculus at the L_1 segment using stainless steel microelectrodes fashioned by the procedure described by Green (12). The electrodes had tip diameters of 1–2 μ and impedances of 1–20 megohms in Kohlrausch's solution (46). When necessary, the impedance of an electrode was lowered without excessive increase in tip size by platinizing (46). Signals were led through a high-impedance probe into an a-c amplifier, displayed on a storage oscilloscope, and monitored over a loudspeaker.

The inferior brachium was stimulated once every 2 sec as the electrode was lowered into the spinal cord. The use of such a probe stimulus increased the likelihood of isolating DSCT axons preferentially. Therefore, the sample is representative of the DSCT but not necessarily of the dorsolateral funiculus. Once a unit was isolated, the antidromic character of its re-

sponse to brachial stimulation was determined by *1*) the lack of jitter in response latency to repeated stimulation at threshold intensity, or *2*) the ability to follow repeated stimulation in a 1:1 manner at or in excess of 200 pulses/sec (pps). Most units qualified under both criteria. Units were classified as DSCT axons if and only if they could be antidromically activated from the inferior brachium.

The conduction velocities of the axons were calculated from the antidromic latency and the conduction distance. The distance was measured by placing a string along the approximate conduction route and then measuring the length of string used.

A measure of the spontaneous activity of the DSCT units was obtained by averaging the number of responses in 10 1-sec sweeps of the oscilloscope trace in the absence of any applied stimulus.

Once it was determined whether a unit was a DSCT axon, the periphery was examined for a receptive field. Preliminary examination consisted of light brushing of the entire surface of the skin of the hindlimb and lower part of the ipsilateral trunk, light squeeze of all muscle groups, and movement of joints not held immovable by the mounting of the animal. Units which discharged in response to brushing or light touch of the skin but not to deep pressure, squeeze of muscles, or movement of joints were classified as cutaneous. Such units responded vigorously to touching skin after it had been carefully lifted away from underlying muscle and fascia.

Units which responded to light squeeze of a muscle group or more than one group, to rotation of a joint, or to deep pressure, but which gave no response to stimulation of the skin were classed as deep units. No attempt was made to divide this group further since stimulation methods did not allow distinction between muscle, joint, or subcutaneous receptors.

Cutaneous receptive fields were further characterized by stimulating specific cutaneous receptor structures lying within the field while observing through a dissecting microscope at 30× magnification. With fur closely clipped, hairs (down, guard, and tylotrich (5, 49, 50)) were carefully moved with fine jeweler's forceps. Care was taken to move only a single hair and not to cause large displacements of the skin surrounding the follicle. In many cases the hairs were pushed from side to side with one leg of the forceps.

Once hairs had been stimulated, the skin within the receptive field was depilated using a mild cosmetic depilatory agent. With the hair removed, tactile pads (20, 21, 48, 51) were easily stimulated with one foot of the jeweler's forceps or with a small glass probe. Some confusion of terminology exists with respect to cutaneous afferent fibers and their receptor structures. Terminology based on conduction velocities (29) is of little value for this sort of study and so the classes proposed by Brown and Iggo (5) were employed for lack of a better system. The receptor structure of the type I afferent fibers (not to be confused with the group I afferent of muscle) will be referred to as the "tactile pad," consistent with other papers from this laboratory (53). The same structure has been termed "Haarscheibe," "touch corpuscle," "Iggo corpuscle," "Pinkus corpuscle," and "Iggo-Pinkus dome" by other investigators (3–5, 7, 20, 21, 48–50).

On some occasions, precisely controlled, minute mechanical stimuli were applied to tactile pads and to hairs. A 200-μ-diameter probe attached to the cone of a high-impedance loudspeaker was placed just touching the structure to be stimulated. Displacements from this resting position were monitored using a double-photocell bridge. The stimulator and its mount have been described in detail elsewhere (53). Short-duration displacements consisted of pulses, 4 msec in duration, with a rise time to peak of 2 msec and amplitude variable between 1 or 2 and 200 μ, with a resolution of 1 μ on the monitor. Such small stimuli were used mainly to judge whether stimulation of a given receptor activated DSCT units. The group to which a unit was assigned did not differ whether "precisely controlled" or "hand held" stimuli were employed in its identification. For a few units, threshold displacements were determined using this stimulus.

Histological examinations

Depths of units were read from the micrometer scale of the micromanipulator carrying the electrode. After an electrode track had been explored, 4 μa of current were passed through the electrode for 25 sec at 2.0 and 2.5 mm depths; the microelectrode was an anode for this procedure. At the end of the experiment, the animal was sacrificed with an overdose of pentobarbital and perfused with a solution of 1% potassium ferrocyanide in 10% formalin (12). Eosin-stained sections of spinal cord were photographed and slides were projected onto paper. Outlines of the spinal cord and the gray matter were traced along with the position of the Prussian blue markers. Tracks were reconstructed through the center of each marker to the dorsal surface of the cord, axon loca-

tions were indicated along the track, and composites were constructed of the tracks.

RESULTS

A total of 279 DSCT axons were isolated in the dorsolateral funiculi of 23 cats. Units were held for a few seconds up to 2–3 hr with little change in amplitude. No excitatory fields were found contralateral to the recording electrode but, for units activated by stimulation of deep structures, contralateral inhibitory fields were common. Three basic types of DSCT fibers were distinguished—cutaneous, cutaneous-plus-deep, and deep units. Since the major focus of this investigation was the cutaneous subdivision of the DSCT, this class was further subdivided.

Fifty-three DSCT units (19% of all DSCT units studied) were activated by stimulation of the skin but not by stimulation of deep structures. The receptive fields of all of these units were located on the ipsilateral hindlimb and the trunk caudal to the rib cage. All the fields were continuous, i.e., two areas from which a response could be elicited were never completely separated by an area from which no response could be elicited. As suggested by Oscarsson (39), activity in both rapidly and slowly adapting afferent fibers evokes a discharge in the cutaneous subdivision of the DSCT, but not always in the same cell. In these experiments I found a group of fibers that responded to stimulation of both rapidly and slowly adapting receptors, but two other groups were also found: one which responded only to stimulation of tactile pads and another which responded only to stimulation of hairs (summary, Table 1).

DSCT cells activated by type I activity

Of the 41 cutaneous DSCT units for which receptive fields were carefully examined, 6 (15%) were found to respond only to stimulation of tactile pads. In all 6, stimuli applied just off the tactile pads or on any other visible structure produced no discharge of any kind. These units were not activated by stretching the skin in the area of the receptive field. The fields of these

TABLE 1. *Receptive field classes for all DSCT axons studied*

Type of Axon	No. Studied	Percent of Total DSCT
Cutaneous DSCT axons	53	19
Tactile pad (6)		
Hair (13)		
Guard hairs (3)		
Down, guard, and tylotrich hairs (5)		
Hair, type unknown (5)		
Tactile pad and hair (22)		
Tactile pad and down hair (1)		
Tactile pad and down and tylotrich hair (4)		
Tactile pad and down, guard and tylotrich hair (16)		
Tactile pad and hair, type unknown (1)		
Cutaneous, receptor type unknown (12)		
Cutaneous-plus-deep DSCT axons	22	8
Tactile pad (2)		
Tylotrich hair (1)		
Guard and tylotrich (1)		
Down, guard, and tylotrich hair (5)		
Tactile pad, down, guard, and tylotrich hair (4)		
Tactile pad, guard, and tylotrich hair (1)		
Hair, type unknown (2)		
Cutaneous, receptor type unknown (5)		
Deep DSCT axons	149	53
Mute DSCT axons	55	20
Total	279	100

Figures in parentheses are numbers of axons.

unimodal units were uniformly large, varying between 31 and 124 cm^2 in area, and all were located on the trunk, thigh, calf, and the upper part of the foot. The lower foot and toes were spared in spite of the presence of tactile pad receptors on these parts of the extremity. Some typical receptive fields are illustrated in Fig. 2*A*.

For one such unit (the unit whose receptive field is stippled in Fig. 2*A*), 113 tactile pads were counted from which activity could be elicited. The area formed by a line through the most peripheral of the 113 tactile pads included no pads from which activity could not be evoked. Tapper (51) reported a modal value of 3 tactile pads per type I afferent. Using this figure, it is clear that activity from at least 37 such afferents converged onto this particular DSCT cell. Although no counts of tactile pads were made for other tactile pad DSCT cells, there were some with even larger receptive fields and one with a field only half as large. Within any of these fields, stimulation of any tactile pad resulted in a discharge; however not necessarily the same discharge. Responses of these units tended to be slowly adapting, but the average frequency of discharge was less than in the type I afferent.

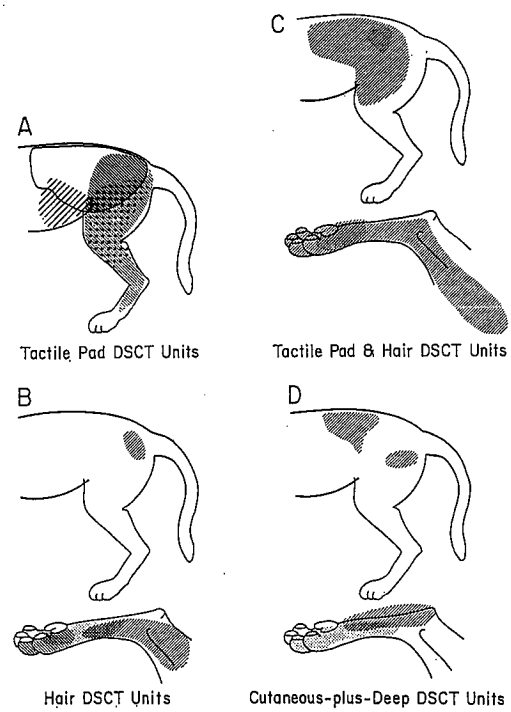

FIG. 2. Samples of cutaneous receptive fields of the various classes of DSCT cells. Units that responded to tactile pad stimulation (*A*), hair stimulation (*B*), tactile pad and hair stimulation (*C*), and cutaneous-plus-deep stimulation (*D*) are illustrated. Four fields are shown in each diagram.

Units activated by stimulation of hairs

Thirteen cutaneous DSCT units responded only to stimulation of hairs within the receptive field; stimulation of no other receptor, cutaneous or deep, caused a discharge. Small movements of down, guard, and tylotrich hairs activated five of the hair DSCT units. The discharges evoked by stimulation of different types of hairs were not compared quantitatively since it is difficult to stimulate hairs in a controlled manner.

Three of the hair DSCT units were activated only by stimulation of guard hairs. In the remaining five hair DSCT units, the receptor types were not identified because the units were lost during characterization. Typical receptive fields of hair DSCT units are illustrated in Fig. 2*B*. These receptive fields were located predominantly on the foot and toes. The areas ranged from 0.5 to 2 cm^2 on the toes to the entire surface of the foot, excluding the foot pad and the toe pads. The only exception to this localization on the foot was one found near the root of the tail. The size and position of hair DSCT receptive fields are very similar to those which have been described for the forelimb counterpart of the DSCT, the cuneocerebellar tract (16). Discharges in this type of unit were invariably rapidly adapting; usually when a single hair was displaced in one direction the discharge consisted of one or a few spikes.

Units activated by tactile pad and hair stimulation

Over half (54%) of the 41 fully studied cutaneous DSCT units responded to stimuli applied to tactile pads as well as hairs within their receptive fields. Of these, 16 cells responded to stimulation of down, guard, and tylotrich hairs in addition to tactile pads; 4 responded to stimulation of down and tylotrich hairs and tactile pads; and 1 to stimulation of down hairs and tactile pads. For 1 cell, the type of hair in-

volved was not identified, however, the unit was clearly activated by stimuli applied to hairs and tactile pads.

Typical receptive fields for this class of DSCT units are shown in Fig. 2*C*. The fields were located on the trunk, leg, and foot and had the appearance of a combination of the receptive fields of the tactile pad DSCT and hair DSCT units. Usually fields located on the foot were smaller in area than those on the leg and trunk, but there was no strong correlation between field size and location on the periphery.

The smallest receptive fields appeared to be uniform, i.e., if stimulation of a receptor of a certain type caused the axon to discharge, then stimulation of every receptor of that type within the field caused the axon to discharge. This was true for tactile pads as well as for hair receptors. These uniform fields were all located on one toe or a small area of skin near the toes. Larger receptive fields were usually heterogeneous. Stimulation of tactile pads in only part of the receptive field, often the center, elicited a discharge. Stimulation of tactile pads elsewhere in the field was ineffective; however in these areas stimulation of hairs caused a discharge. In some cases, stimuli applied to hairs and tactile pads within the same area caused a discharge. An example of a heterogeneous receptive field is shown in Fig. 3. Stimulation of tactile pads and hairs within the nonstippled area evoked a discharge in this unit, but stimulation of tactile pads in the stippled area evoked no discharge. Stimulation of hairs within the stippled area could evoke a discharge. For this particular unit, stimulation of depilated skin between tactile pads within the stippled area evoked a discharge. In general, no responses were observed from stimulation of the depilated skin next to a tactile pad, but in a few cells such responses were observed.

Four tactile pad and hair DSCT fibers also responded to stimulation of foot and toe pads. Usually only stimulation of the pad of one toe or one lobule of the central foot pad was effective, but in some cases stimuli applied to the entire central pad and all of the toe pads were effective in eliciting a discharge. The latter situation

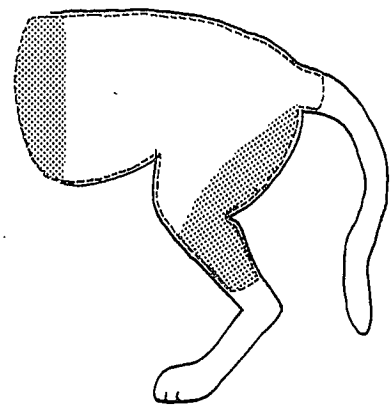

FIG. 3. Nonhomogeneous receptive field of a tactile pad and hair DSCT unit. The receptive field perimeter is indicated by the broken line. Tactile pad stimulation evoked activity in the unit only when applied within the nonstippled areas, whereas hair stimulation evoked DSCT discharges when applied throughout the receptive field. Stimulation of the skin between the tactile pads only within the stippled area evoked a discharge in this unit.

resulted if stimulation of skin between the toe and foot pads was also effective.

Quantitative stimulation was not employed in the study of any but tactile pad DSCT units. However, some observations on response properties of tactile pad and hair DSCT cells may still be made. Stimuli applied to hairs within the receptive fields caused a discharge similar to that in hair DSCT units. Stimuli applied to tactile pads, on the other hand, often evoked responses in these units which were greatly attenuated compared with the responses of type I afferents. In some units the response was so attenuated that it appeared to be phasic, whereas in other units the responses were more nearly like those of the afferent but perhaps less so than in tactile pad DSCT units.

Cutaneous-plus-deep subdivision of DSCT

Of all DSCT units, 8% responded to stimulation of both cutaneous and deep structures and were probably the FRA DSCT cells of Lundberg and Oscarsson (32). No attempt was made to identify the deep structure involved but the cutaneous component of the receptive field was examined in the same manner as above. In general, the cutaneous receptive fields resem-

bled those of purely cutaneous units, but there were some differences.

Four cutaneous-plus-deep DSCT units were activated by stimulation of tactile pads and by stimulation of down, guard, and tylotrich hairs. Two units were excited from tactile pads alone, and five others only by stimuli applied to the three types of hair. An additional unit was activated by stimulation of tactile pads, guard, and tylotrich hairs. The units described so far resembled, in every way examined, those units which had only the corresponding cutaneous receptive fields; however, unlike the purely cutaneous fibers, there were two fibers which responded to stimulation of tylotrich and guard hairs, and tylotrich hairs, respectively. The remainder of the cutaneous-plus-deep DSCT units were activated by stimulation of hairs and cutaneous structures, but specific receptors were not identified.

Examples of the cutaneous part of the cutaneous-plus-deep DSCT cell receptive fields are illustrated in Fig. 2*D*. No obvious consistent relationship was found between the cutaneous portion and the deep portion of fields either with respect to location or function (e.g., extensor or flexor).

Responses produced by stimulation of hairs in this type of unit were not different from those in hair DSCT units, as judged from stimulation with a hand-held probe. Stimuli applied to tactile pads did not elicit discharges like those in tactile pad DSCT units but, instead, the discharges were shorter and in some cases the responses were not slowly adapting. Stimulation of the skin next to the pad produced no response, demonstrating that the response was due to tactile pad activity.

Deep subdivision of DSCT

The majority of the DSCT fibers (149 or 53%) were activated by stimulation of deep structures only. These structures were located from the toes to the last thoracic segment; however, the majority of units were activated from the muscles of the leg, foot, and tail. Most deep DSCT units (72%) were activated by lightly squeezing the belly of one muscle or moving a single joint in one direction or another. A significant number were activated from more than one muscle group: 15% from two muscle groups, 3% from three muscle groups, and 6% from four muscle groups. The activation crossed functional groups, i.e., flexors or extensors, in many cases and remained within a functional group in many others, as summarized in Table 2.

Mute DSCT units

An additional 55 DSCT units were identified by antidromic activation but could not be activated by any stimulus employed

TABLE 2. *Summary of muscle groups in receptive fields of deep DSCT axons*

One Muscle Group	No.	Two Muscle Groups	No.	Three Muscle Groups	No.	Four Muscle Groups	No.
Knee extensor	21	Knee flexor + ankle extensor	5	Knee flexor + extensor + ankle extensor	2	Knee flexor + extensor + ankle flexor + extensor	8
Knee flexor	17	Knee flexor + ankle flexor	1	Knee flexor + ankle flexor + extensor	1	Knee flexor + extensor + ankle extensor + toe flex	1
Ankle extensor	13	Knee flexor + extensor	4	Knee flexor + ankle extensor + toe flex	1	Knee extensor + ankle flexor + extensor + toe flex	1
Ankle flexor	4	Knee extensor + ankle extensor	2	Ankle extensor + toe flex + tail	1		
Toe flex	10	Ankle flexor + extensor	2				
Tail	27	Ankle flexor + toe flex	2				
Hard ankle flexion	15	Ankle extensor + toe flex	7				
Total	107		23		5		10

on the periphery. In most cases the animal was searched for receptive fields on the forelimbs as well. About one-third of these mute units were spontaneously active; the remainder were activated only antidromically.

Inhibition of DSCT unit discharges

Although inhibitory effects on DSCT discharges were not systematically studied, such effects were evident for some cells. Four cutaneous DSCT cells were found which were inhibited by stimulation in a cutaneous receptive field eccentric to, but not surrounding the excitatory field. Like the excitatory fields, these inhibitory fields had irregular shapes. Inhibition was noted only in cells with spontaneous activity because it is difficult to manually stimulate both excitatory and inhibitory fields at the same time, but inhibition possibly also exists for cells which do not show spontaneous activity. Receptor types mediating the observed inhibition were not studied.

Inhibition of deep DSCT unit discharges was also observed following stimulation of deep and cutaneous receptors. Inhibition from deep structures frequently originated from antagonist muscle groups but was also observed following stimulation of other muscle groups of the ipsilateral as well as the contralateral hindlimb. Often inhibitory effects from contralateral muscles were very powerful, causing complete cessation of the high-frequency discharge evoked by a hard squeeze of the excitatory muscle.

Twelve deep DSCT units were inhibited by cutaneous stimulation, but controlled stimulation was not employed in the study of this phenomenon so that receptor types mediating such inhibition were not identified. Usually the effect was small, lasting 40–150 msec, but could be seen in oscilloscope sweeps triggered by electrical stimuli applied to the skin in the inhibitory area.

Conduction velocity

Conduction velocities of DSCT fibers ranged from a low of 20 m/sec to a high of 116 m/sec. The distribution of conduction velocities for each class of DSCT cell and for the total population of 279 axons are shown in Fig. 4*A*. The modal conduction velocity was between 71 and 75 m/sec for all DSCT axons considered together (lowest histogram), as well as for cutaneous, cutaneous-plus-deep, and deep axons considered separately (histograms 4–6). The range of conduction velocities is approximately the same for each class of cutaneous DSCT axons except for the tactile pad and hair axons which had a slightly wider range. However, the sample sizes are too small to imply significance for this small difference.

Spontaneous activity

Most of the DSCT units encountered were spontaneously active, i.e., they discharged in the absence of any applied stimulus. A summary of spontaneous discharge rates for 223 DSCT units is shown in Fig. 4*B*. The majority of units were only slightly active in the absence of stimulation; most discharged less than 10 spikes/sec, but a few units were extremely active, at rates up to 90 discharges/sec. The most active fibers were primarily deep DSCT units. More than 50% of the cutaneous units discharged at 1–10 spikes/sec, but three had spontaneous activity in excess of 20 spikes/sec.

Cutaneous DSCT units were of special interest since the cutaneous afferent fibers are not spontaneously active except for an occasional type D afferent (5, 51). Only two of the six tactile pad DSCT units had any spontaneous activity at all and those fired at a rate of less than 5 discharges/sec. There was spontaneous activity in about 50% of the units which responded to stimulation of hair afferent fibers. This spontaneous activity in cutaneous DSCT cells is possibly mediated by interneurons which have been described in the pathways to DSCT cells (14).

Anatomical location of DSCT axons

The locations of DSCT axons studied are shown in Fig. 5. It is immediately evident that axons which proceed from the L_1 spinal cord directly into the inferior brachium may be found throughout the dorsolateral funiculus. There is some sparing of the most dorsomedial part of the funiculus in agreement with the observations of Oscarsson (39). No DSCT

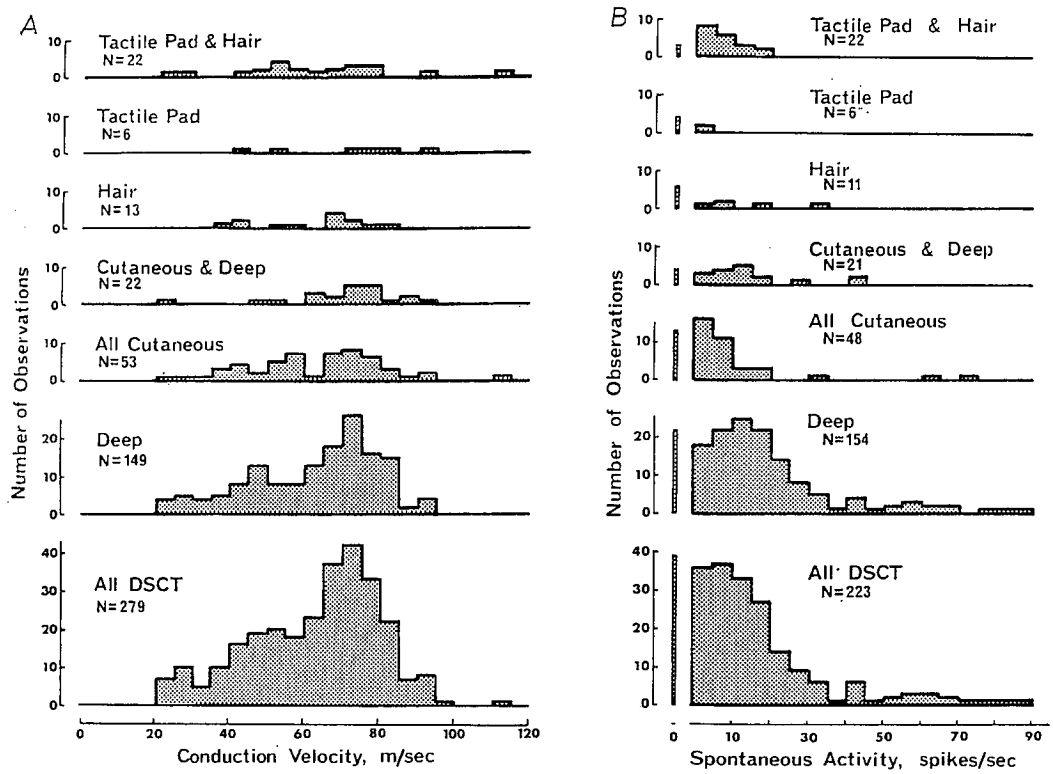

FIG. 4. Conduction velocities and spontaneous activity of DSCT axons. *A:* conduction velocities of DSCT axons sampled, shown for all DSCT cells considered together (lowest graph) and broken into cutaneous-plus-deep, cutaneous, and deep (graphs 4, 5 and 6, respectively). Conduction velocities of various classes of cutaneous DSCT cells shown in graphs 1–3. *B:* spontaneous activity of DSCT axons sampled, shown for all DSCT cells considered together (lowest graph) and broken into cutaneous-plus-deep, cutaneous, and deep (graphs 4, 5, and 6, respectively). Spontaneous activity of various classes of cutaneous DSCT cells shown in graphs 1–3.

axons were located below the level of the central canal, in the ventrolateral funiculus, even though the dorsal part of this area was probed extensively.

There is a tendency for the purely cutaneous units to be more lateral and the purely deep and mute fibers to be located more medially. In spite of these differences in the exact locations of axons of the various DSCT classes, there is considerable overlap. The separation suggested by the more caudal location of cutaneous cells in Clarke's column (17) and the addition of new fibers to the tract on its ventromedial aspect (35, 42, 47, 60) was not found.

Also shown in Fig. 5 are the locations of axons which did not go into the inferior brachium. These axons were isolated in all parts of the dorsolateral funiculus, even in the most dorsomedial part. Although the sample was not representative of the non-DSCT axons, nonetheless it is clear that cutaneous non-DSCT and deep non-DSCT axons enjoy a rather broad dispersion among the DSCT axons.

Similar composites were made for each DSCT subdivision and receptive-field location to determine whether any somatotopy could be observed. Cutaneous DSCT cells with receptive fields on the foot were encountered throughout the dorsolateral funiculus even medially where no other receptive-field locus was represented. Axons with receptive fields on the lateral and medial leg were located on the lateral edge of the dorsolateral funiculus, whereas axons with fields on the trunk had a slightly more medial distribution, but not as medial as those with fields on the foot (Fig. 6*A*). No somatotopy was discerned for the axons of cutaneous-plus-

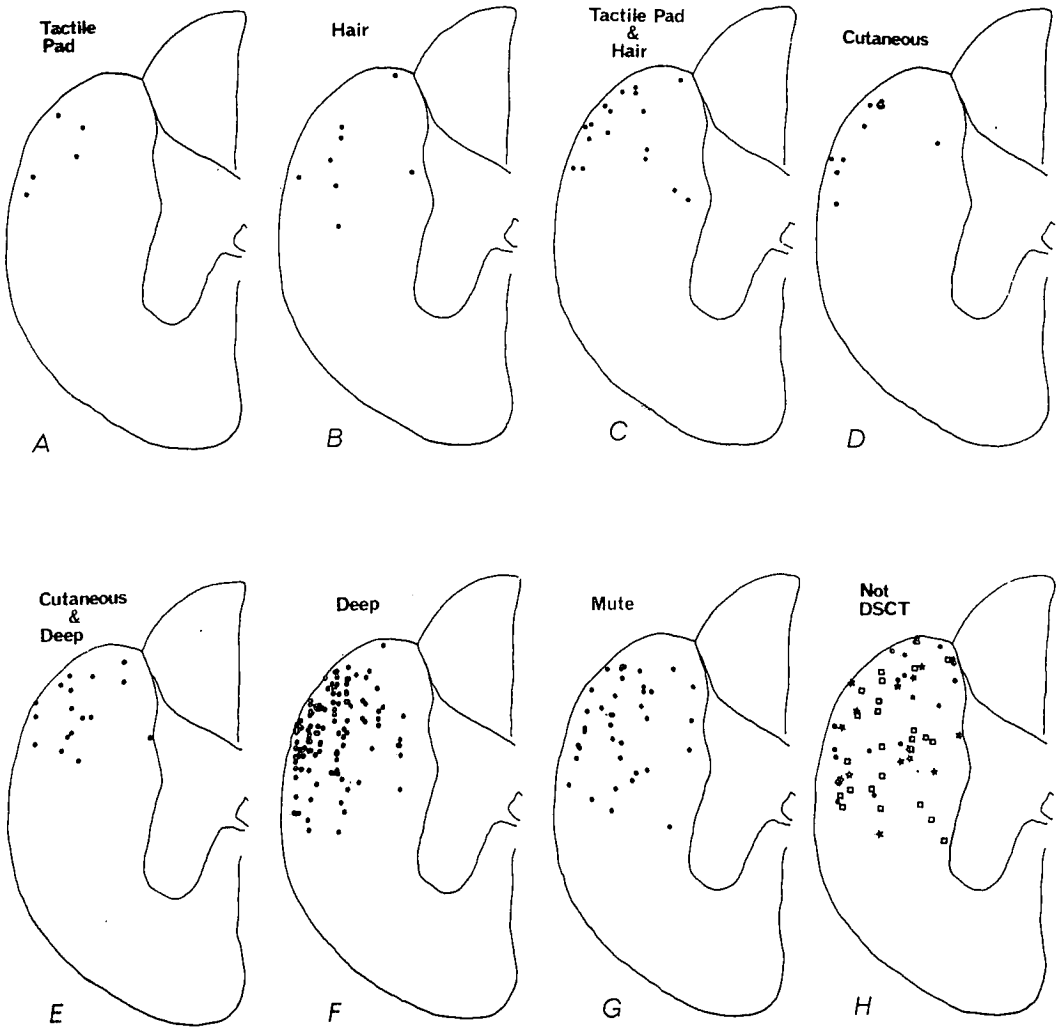

FIG. 5. Anatomical locations of DSCT and non-DSCT axons. Locations for DSCT axons are illustrated in *A–G* for classes indicated above each drawing. Axons indicated in *D* were activated by cutaneous stimulation but specific receptors were not identified. Non-DSCT cells (*H*) with cutaneous receptive fields are indicated by filled circles, with deep fields indicated by open squares, and with unidentified field composition indicated by filled stars. One tactile pad DSCT axon location was not marked; so only five are shown in *A*. Only locations of those hair DSCT axons for which receptors were identified are shown in *B*.

deep DSCT cells (with respect to cutaneous fields, Fig. 6*B*). Since somata of Clarke's cells connected to calf and foot muscles are located more caudally than those connected to thigh muscles (17), it was expected that DSCT axons activated from calf and foot muscles would be located more laterally and dorsally than those activated from thigh muscles. Evidence to support this prediction was not found. Rather a complete lack of somatotopy was observed for deep DSCT axons (Fig. 6*C*).

DISCUSSION

In the cutaneous subdivision of the DSCT there are axons which respond to stimulation of specific cutaneous receptors of only one type and of several types, i.e., there are unimodal and multimodal DSCT cells in the terminology employed by Tapper et al. (53). The significance of this dual representation of receptor types may be related to the two levels of coordination suggested by Kitai et al. (24). These investigators suggested that coordination occurs

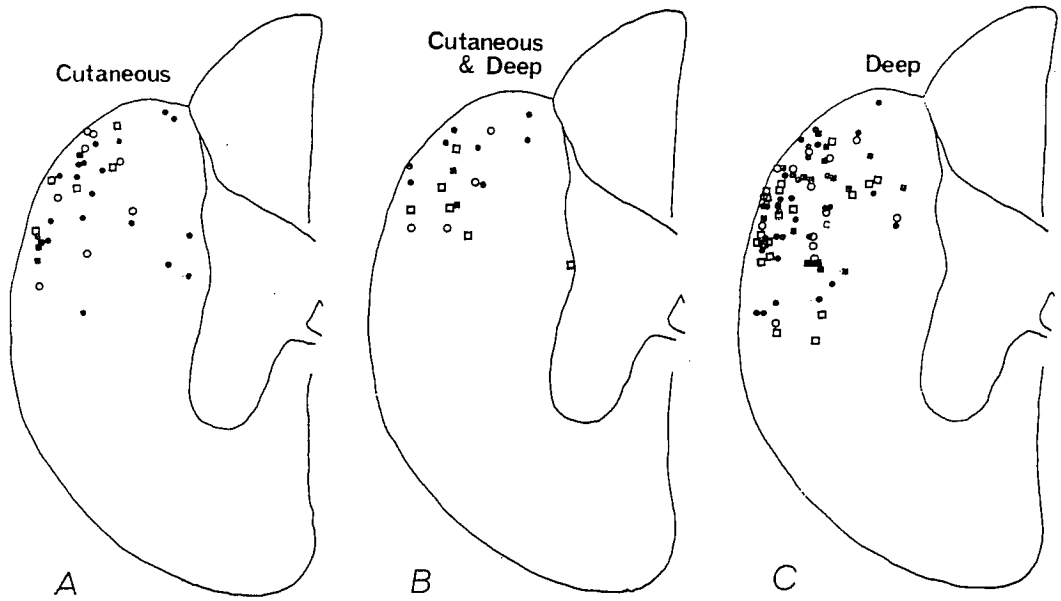

FIG. 6. Topographical distributions of cutaneous, cutaneous-plus-deep, and deep DSCT axons. Cutaneous receptive fields of cutaneous and cutaneous-plus-deep units (*A*, *B*) on the medial leg indicated by open squares, on the lateral leg by filled squares, on the trunk by open circles, and on the foot by filled circles. Deep DSCT axons activated from muscles of tail (open squares), thigh (filled squares), calf (open circles), and foot (filled circles) indicated in *C*. Locations of axons activated from one muscle group only are shown; locations of axons activated from two or more groups are omitted.

1) at the level of the whole body, i.e., coordination of head with tail with hindlimb; and *2*) at the level of a single limb or part of a limb, e.g., coordination of the flexors of the ankle and the extensors of the knee. It is possible that unimodal cells have a role in the coordination at the finer level where more exact information on the nature and extent of the stimulus is required and multimodal cells carry information for gross coordination. It might be expected that receptive fields of unimodal cells would be smaller in area than those of multimodal cells if this hypothesis is correct. In this study, the size of the field seemed to bear no particular relationship to modalities but, rather, was related more to the position on the limb (proximal fields were usually larger). However, specificity may be in terms of the stimulus information transmitted rather than area information. This notion has already been proposed for cells of the dorsal gray matter (53). Receptive fields were smallest in those areas of the body where spatial information would be most useful, on the toes, foot, and ankle.

The low-displacement thresholds (12–20 μ), determined for activation of two tactile pad DSCT and six tactile pad and hair DSCT cells when stimuli were applied to tactile pads, are well within the range of displacements shown by Brown and Tapper (6) to elicit single action potentials in type I afferent fibers, but produce no response in any other afferent fiber. This indicates that a single action potential in a single cutaneous fiber is capable of evoking a postsynaptic DSCT discharge. Eide et al. (11) suggested that two to three group I impulses were required to elicit a DSCT discharge. Apparently the cutaneous subdivision of the DSCT has an even more efficient transmission than the deep subdivision. It has been suggested that excitatory postsynaptic potentials in cutaneous DSCT cells are larger than those in deep DSCT cells (10), which may account for the more efficient transmission.

Similar potency of transmission has been shown for type I afferent activity to cells of the dorsal gray matter of the L_7 or S_1 spinal segments (52). It is possible that the cells of this level of the cord relay to

Clarke's nucleus, or wherever the cutaneous DSCT somata are located, since connecting fibers have been seen traversing some distance from the caudal levels of the cord to end in Clarke's column (45). Cells at the L_6 level of the spinal cord which send axons into the dorsolateral funiculus have been reported by Mann et al. (36), and furthermore axons have been reported leaving the funiculus to enter Clarke's nucleus (2). Possibly these are the same axons, but it seems unlikely that they are, since the excitabilities of cells at the L_6 level are depressed by pentobarbital while the excitabilities of DSCT cells are not. At any rate, the cells at the L_6 level described by Mann et al. (36) clearly do not give rise to the cutaneous DSCT because they are not activated antidromically by the same stimulus employed here.

There is a clear inconsistency between the results of this study and those of Yamamoto and Miyajima (59) and Kitai and Morin (22) concerning the frequency of occurrence of cell types. Both of these groups reported that 50% or more of their DSCT neurons were activated only by cutaneous stimulation, but in this study only 19% of the DSCT units were activated by cutaneous stimulation alone. Even if the cutaneous-plus-deep fibers are included, the cutaneous units only composed 28% of the total sample. Casual observations made in a few decerebrate cats suggested that cutaneous activity is more pronounced or deep activity is depressed. Such supraspinal depression of deep activity has been reported for the DSCT (15, 32). While this observation may explain part of the discrepancy with the results of Yamamoto and Miyajima (59), it does not explain the discrepancy with Kitai and Morin (22), who also used pentobarbital anesthesia. Three other reasons for this discrepancy are apparent. Yamamoto and Miyajima (59) suggested that part of their cutaneous rapidly adapting units could have been activated from rapidly adapting deep receptors which can be exquisitely sensitive to light pressure on the skin. Since, in the present investigation, the classification was independent of the adaptation of the responses, these units would have been classified as deep units. Both groups of investigators included in their samples a large proportion of forelimb fibers which were more frequently activated by cutaneous stimulation than deep; this would tend to overemphasize cutaneous fibers in their samples. Finally, since neither group explicitly indentified their units as DSCT axons, their samples undoubtedly included other sorts of fibers which have been shown to be located throughout the dorsolateral funiculus. Lundberg and Oscarsson (33) have described three cutaneous pathways in the funiculus which are not part of the DSCT. Any one or several of these tracts and propriospinal fibers could have contributed to the samples of both Yamamoto and Miyajima (59) and Kitai and Morin (22).

Receptive-field sizes observed in this experiment were not notably different from those of Yamamoto and Miyajima (59) or Lundberg and Oscarsson (32) but they were never as small as the "one hair receptive fields" of Kitai and Morin (22). Mute cells were also reported by Yamamoto and Miyajima (59). The significance of these cells is unclear, but perhaps they were connected to thermoreceptor afferents, to deep structures of the abdomen, to joints which could not be moved, or to receptors with thresholds too high to be activated by the stimuli employed. The frequency of occurrence of mute cells is too great to be dismissed as insignificant. Curiously few DSCT cells were located which responded exclusively to stimulation of foot pads, a frequently encountered class in the sample of Lundberg and Oscarsson (32). In contrast, many fibers were found which responded to stimulation of foot and toe pads in addition to deep or other receptors.

Lundberg and Oscarsson (32) noted that some cutaneous DSCT cells were activated by light touch in the center of their receptive fields, but required more intense stimuli on the periphery. It is possible that this difference in sensitivity is mediated by the inhomogeneity of receptive fields described here, but it is equally likely that there are differences in the ability of activity from receptors in the center and on the periphery of the fields to evoke DSCT discharges, similar to those which have

been described for cells of the dorsal gray matter (53).

While a slight difference in distributions was found for cutaneous DSCT and deep DSCT axons within the dorsolateral funiculus, there was still considerable overlap found in the locations, in agreement with the illustration presented by Yamamoto and Miyajima (59). DSCT axons were found throughout the dorsolateral funiculus, not just in a crescent-shaped portion on the dorsolateral border. At all points they were interspersed with axons of other, non-DSCT, cells (see also ref 33); in any electrode track one encounters DSCT fibers and non-DSCT fibers seemingly at random. This complicates interpretation of anatomical studies of the DSCT since complete transection of the DSCT inevitably involves a large number of non-DSCT fibers as well.

The question of sampling bias is always a valid one when microelectrode techniques are employed. Unfortunately we know no reliable function for the DSCT for conversion from conduction velocity to fiber diameter. A constant has been computed recently for the fibers of the pyramidal tract by Towe and Harding (56). If their value of 4.72 μ/m per sec (excluding myelin sheath) is applied to the velocities obtained in this study, the fiber diameters are estimated to be 6–40 μ (including myelin sheath). As stated by Towe and Harding (56), this estimate is too large for small fibers where the ratio of myelin thickness to axis cylinder diameter is greater, implying that the lower limit of fiber diameters probably should be depressed to 5 or 6 μ. Von Beusekom (1) showed that 2% of the DSCT axons reached diameters greater than 15 μ. Using the Towe-Harding constant, about 90% of the axons of this sample were computed to have diameters greater than 15 μ, suggesting that the entire spectrum of diameters (not just the smallest) has been shifted toward "too high" values.

It is clear that proportionality constants with values less than that discussed above will yield even more disharmonious results when applied to these data. A value of 6 μ/m per sec (including myelin sheath) was computed for peripheral nerve by Hursh (19). If we apply this value to the current data we obtain fiber diameters from 3 to 20 μ, more in line with histological measurements. Von Beusekom (1) reported that 56% of the fibers in Flechsig's fasciculus have diameters greater than 3 μ. If Hursh's constant were to apply to the DSCT, the current sample would be adequate for the larger 56% of the tract.

We can attempt to compute a new proportionality constant for the DSCT using the velocities reported here and the fiber spectrum of von Beusekom (1), even though his spectrum is not fine enough to allow a fitting like that done by Towe and Harding (56). Von Beusekom (1) reports that 17% of the fibers in Flechsig's fasciculus in the region of the DSCT had diameters less than 1.5 μ. The same percentage of the DSCT axon velocities will bring us to about 40 m/sec, suggesting a constant of 26 μ/m per sec, which corresponds with none suggested for any pathway and fits the fastest fibers very poorly. On the high end of the distribution, 2% of the fibers ought to be larger than 15 μ (1) which accounts for velocities down to about 93 m/sec. The constant calculated from these figures has the value 6.2 μ/m per sec, about that computed by Hursh (19).

Probably, then, Hursh's constant is a pretty good fit, at least for the larger diameter fibers and the sample here is adequate for at least 56% of the DSCT. Since the dorsolateral funiculus is a heterogeneous bundle of fibers, many of the fibers measured by von Beusekom (1) were undoubtedly not DSCT but spinocervical tract or other fibers (33). It is likely that the sample here was adequate for much more than the percentage above, but some small fibers probably were not detected. On the other hand, if the size of the axons is related to soma size, DSCT axons should all be of larger diameters since the small cells in Clarke's nucleus do not project into the dorsolateral funiculus (28, 47). A better estimate of the proportionality constant for the DSCT and a better estimate of the adequacy of the present sample wait on a more adequate fiber spectrum

ERRATA: The units of the parameters relating velocity to diameter referred to on page 1047 should read

"m/sec/μ".

and a knowledge of the bias of the recording electrode.

There is a curious paucity of type I activity in the ascending pathways of the spinal cord. The dorsal column is dominated by hair afferents, particularly in the dorsomedial portion (3, 43, 57). Responses to guard and tylotrich hair stimulation were observed in 44 and 39%, respectively, of the dorsal column fibers (3). All the type II but none of the type I afferent fibers project into the cervical dorsal columns (43) and D. N. Tapper (personal communication) failed to locate type I activity in either the gracile or the cuneate nucleus. Uddenberg (58) described second-order dorsal column fibers in which Petit et al. (44) found responses evoked by stimulation of hair and skin. In a later series of experiments, these investigators showed that the receptive fields of the cells in this group were not of homogeneous sensitivity and low-threshold points often corresponded to tactile pads (D. Petit, D. Lackner, and P. R. Burgess, personal communication).

Brown and Franz (4) found axons in the spinocervical tract which responded to stimulation of all three types of hair and some which responded to stimulation of hair and skin, but not to stimulation of tactile pads (see also ref 54). Cutaneous activity in the DSCT may contribute to the cervicothalamic pathway through the lateral cervical nucleus and thus reach the cerebral cortex. Degenerating fibers have been reported to leave the DSCT at cervical levels and enter the lateral cervical nucleus following lesions in Clarke's nucleus (13). Some receptive fields found by Oswaldo-Cruz and Kidd (41) for cells of the lateral cervical nucleus were similar in composition and area to hair DSCT units; others could have been formed by convergence of DSCT axons. This similarity between receptive fields of cells of the DSCT and the lateral cervical nucleus was also pointed out by Morin et al. (38). However, doubt that there is a significant connection between the DSCT and the lateral cervical nucleus has been cast by the failure of Horrobin (18) to activate any neurons of the nucleus by stimulation of the cerebellar cortex.

SUMMARY

Receptive-field properties of axons of the cutaneous subdivision of the dorsal spinocerebellar tract (DSCT) were studied in anesthetized cats. DSCT axons were identified by antidromic activation from the inferior brachium of the cerebellum which was stimulated through a bipolar electrode placed stereotaxically. Axons were located which responded to stimulation of a single type of receptor (unimodal): 15% to stimulation of tactile pads and 7% to stimulation of guard hairs. Others responded to stimulation of more than one type of receptor (multimodal): 12% to stimulation of down, guard, and tylotrich hairs, and 54% to stimulation of tactile pads, down, guard, and tylotrich hairs. The possible significance of this multiple representation of receptor type to cerebellar function is discussed.

In addition to cutaneous cells, there were DSCT axons activated by cutaneous-plus-deep, and deep stimulation (8 and 53% of all DSCT units studied). Cutaneous receptive fields of cutaneous-plus-deep DSCT cells were similar to those of purely cutaneous cells. Deep cells were activated by stimulation of one to four muscle groups, and inhibition from other muscle groups was common.

Histological examination showed that DSCT axons were located throughout the dorsolateral funiculus sparing only the most dorsomedial part, the position of the spinocervical tract. At every location, the DSCT axons were mixed with non-DSCT axons activated by both cutaneous and deep receptors. No somatotopic organization was found for either cutaneous-plus-deep or deep DSCT axons. A suggestion of somatotopy was noted for cutaneous DSCT axons but there was extensive overlap in locations of axons with receptive fields on foot, calf, and thigh. Similarly, there was a broad overlap of locations of different classes of cutaneous cells irrespective of field location.

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