Brain Research, 85 (1975) 59–63

Cells of origin of the cutaneous subdivision of the dorsal spinocerebellar tract

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(Accepted November 15th, 1974)

The cutaneous subdivision of the dorsal spinocerebellar tract (DSCT), which has now received considerable attention[4–6,8,9], is known to originate from cells rostral to the fifth lumbar segment (L_5) of the spinal cord[4]. There is a relatively complete agreement among anatomists that the DSCT arises from Clarke's column, a nucleus extending from cervical regions down to the third or fourth lumbar segments[7]. The adequacy of this definition of the tract has been brought into question by some physiological studies from several laboratories. Indeed, somata of some of these cutaneous DSCT cells have been located within Clarke's column at the L_2–L_3 level[5], but identification of these cells as DSCT cells simply on the basis of antidromic response to stimulation of the dorsolateral funiculus (DLF) at T_2 would be dubious[4,6], were it not for the histological demonstration that they were located within Clarke's nucleus. Kuno *et al.*[5] examined the question of whether cutaneous cells of the DSCT may have their somata outside Clarke's nucleus, but unfortunately, although they looked lateral to the nucleus, they failed to search caudal to it. Mann *et al.*[8] examined a small sample of neurons in laminae III–VI[10] of the L_6–S_1 segments of the spinal cord and found that none of the neurons could be driven antidromically from the inferior cerebellar brachium (ICB). On the other hand, Hongo *et al.*[3] did find DSCT cells responding to group I and flexor afferents in the L_4–L_6 segments. Neurons caudal to Clarke's nucleus, but located within the same region of the dorsal horn, are known to convey group I muscle afferent activity from hindlimbs as far as the C_1 segment, possibly to the cerebellum[1]. The present report illustrates that there are DSCT neurons, connected to cutaneous afferent fibers, found in the dorsal gray column of the spinal cord, and that these neurons are located caudal to and outside of the region of Clarke's column.

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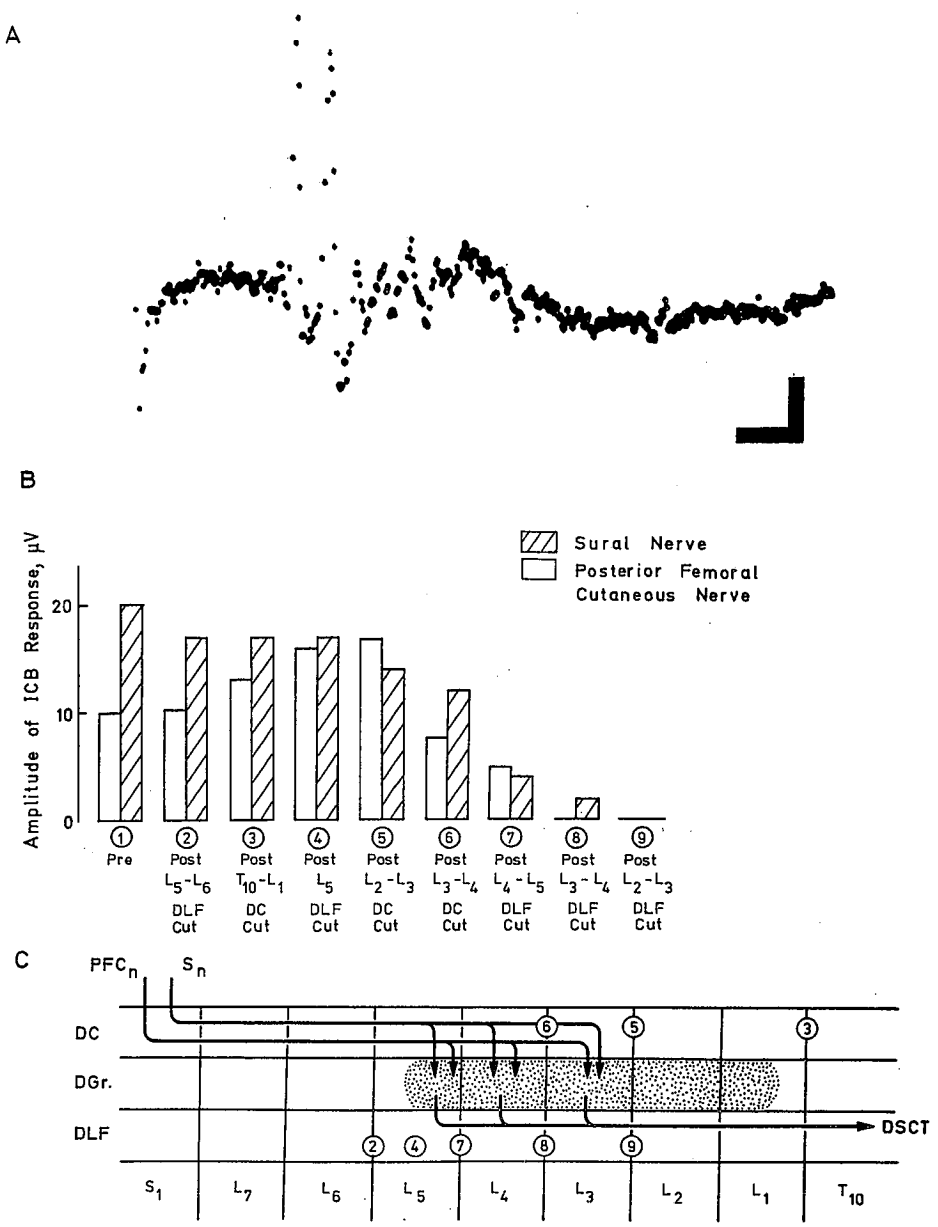

Fig. 1. A: average evoked response due to supramaximal stimulation of the ipsilateral sural nerve recorded in the ICB. The early response that occurs with a latency of 6–7 msec represents activity in the DSCT. An average of 100 stimuli delivered at 1/3 sec. Calibrations: 3 msec, 5 μV. Positivity is upward. B: amplitude of the ICB response evoked by stimulation of the sural nerve (hatched bars) and the posterior femoral cutaneous nerve (open bars) prior to and following the sequence of transections performed in the order from left to right. Circled numbers correspond to those locations indicated in C. C: model of the location of the cutaneous DSCT somata in the dorsal gray matter (DGr.) as determined by the transection experiments.

Experiments were performed on adult cats, using either pentobarbital sodium anesthesia or decerebrate–decerebellate preparations. For the latter, halothane anesthesia was used during surgery. In the first series of 5 animals, the sural and posterior femoral cutaneous nerves were prepared for bipolar electrical stimulation. The spinal cord was exposed by dorsal laminectomy and longitudinal incision of the dura mater from the second sacral (S_2) to the first lumbar (L_1) segment. The mass potential evoked by supramaximal stimulation of the cutaneous nerves was recorded either by an electrode stereotaxically placed in the ipsilateral ICB, or by a surface electrode placed in the same region after removal of the cerebellum. A computer of average transients was used to average the responses to stimuli applied to either nerve. The level of the somata of the neurons which responded was localized by observing alterations in amplitude of the response following a sequence of selective transections of the ipsilateral dorsal column (DC) and the DLF at various spinal cord levels. In the second series of 3 animals, extracellular unit activity was recorded at sites in the dorsal horn at the L_4–L_5 level. Units were included as DSCT cells if they could be activated antidromically using electrical stimulation of ICB. Units that followed 200 cycles/sec with no change in latency were assumed to be antidromically activated. The receptive fields of these neurons were located and the types of mechanoreceptors that excited the neurons were determined. Following such analyses, current was passed through the stainless steel microelectrode to deposit iron at the recording site. The sites were later located on histological sections using the Prussian blue reaction[2]. The lesions produced by spinal cord transections were reconstructed and the location of stimulating electrodes within the ICB verified from histological sections.

Fig. 1 illustrates the results of the first series of experiments. The averaged evoked ICB potential produced by 100 electrical stimuli of the sural nerve is shown in Fig. 1A. The short latency discharge (6–7 msec) represents the direct DSCT inflow, whereas the longer latency peaks probably reflect indirect spinocerebellar activity, *i.e.* by multisynaptic pathways. The changes in amplitude of the positive going phase of the short latency discharge produced by selective interruption of DC and DLF are graphed in Fig. 1B. The sequence of transections progressed from (2) through (9). No significant reduction in ICB response to stimulation of either sural or posterior femoral cutaneous nerve occurred after each of the first 4 transections, *i.e.*, DC at L_1, L_1–L_2, DLF at L_5–L_6 and mid-L_5, respectively. In fact, the response to posterior femoral cutaneous nerve stimulation increases, perhaps due to release of relay cells from inhibition. When the DC was transected at L_3–L_4, the response to posterior femoral cutaneous nerve stimulation was substantially reduced. This suggests that a significant portion of the somata of cutaneous DSCT neurons connected to that nerve lies in the L_3 segment. There was also a slight reduction in the response to sural nerve stimulation. When the DLF was sectioned at L_4–L_5, both responses declined, suggesting that a major portion of the somata lies in rostral L_5. Section of the DLF at L_3–L_4 abolished the response to posterior femoral cutaneous nerve stimulation, whereas a lesion at L_2–L_3 of DLF was required to abolish the response to sural nerve stimulation. A similar sequence of response changes was observed for the longer latency waves, suggesting that the neurons initiating these responses either are the same neurons, or

that they reside in the same segments of the spinal cord. Inferences from these observations lead to the summary diagram shown in Fig. 1C.

Direct confirmation of the location of the cutaneous DSCT somata was obtained by single unit recordings in L_4 and rostral L_5 segments. Three types of units activated by both hindlimb skin receptors and ICB stimulation were encountered: (1) those antidromically activated by ICB stimulation, (2) those orthodromically activated from ICB, and (3) those activated with a fixed latency, but unable to follow above 100 cycles/sec. The latter units had impulses that appeared to be soma spikes and were, therefore, possibly also cutaneous DSCT neurons that for some reason were not reliably invaded antidromically. Nonetheless, these cells were not included as DSCT neurons in the present study. In addition, antidromically and orthodromically activated cells with no apparent peripheral receptive fields[6] and cells whose activity was elicited by deep stimuli were found. The receptive field characteristics of the cutaneous DSCT units were the same as those previously reported[6]. The 5 neurons antidromically activated by ICB stimulation were all located in laminae IV and V caudal to Clarke's column. They were each connected to several of the rapidly- and slowly-adapting afferent fiber systems of hairy skin such as the guard, down, type I and type II fiber systems.

These observations indicate that cutaneous DSCT somata may lie outside of Clarke's nucleus, at least in segments L_4–L_6; for these segments do not contain an identifiable Clarke's nucleus. The sample of neurons reported, while admittedly small, probably does not represent an anomalous set since they were found with little difficulty in each animal studied. This implies that in fact the numbers of such neurons may be quite large. The reason why these neurons were not discovered by Lundberg and Oscarsson[4] may lie partly in their adoption of the anatomical notion that the DSCT arises solely from Clarke's column.

There appear to be no differences in receptive field characteristics or course through the lateral columns[6] between those cells with somata inside or outside Clarke's column. Also, no differences in function of their projections within the cerebellum have thus far been ascertained. Therefore, it seems more profitable at this time to define the DSCT in terms of the pathway traversed by its axons and their terminations rather than to split the projection into components according to the location of the cell bodies.

This study was supported by U.S. Public Health Service Grants NS 07505 and 1-F2-NS 30, 383 NSRA.

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