Reprinted from
Brain Research
Elsevier Publishing Company, Amsterdam
Printed in the Netherlands

Ascending dorsolateral pathways relaying type I afferent activity

A variety of cutaneous receptor systems has been described in the cat hairy skin[3,5]. Two ascending pathways for these afferents have been examined in detail: the spinocervical tract (SCT) and the dorsal column (DC) system. The fibers of the SCT have been found to be activated by combinations of cutaneous receptors exclusive of type I afferents associated with tactile pad receptors[2] (see also ref. 13). Evidence for the presence of type I afferent collaterals in the DC is contradictory[1,10]. Recent electrophysiological experiments in our laboratory indicate that the dorsolateral tracts are responsible for relaying tactile pad input to the brain (in preparation), which is consistent with lesion data from behavioral experiments[12]. In this communication we provide further evidence that tactile pad input is relayed in the dorsolateral funiculus (DLF), *i.e.*, in the dorsal spinocerebellar tract (DSCT) and possibly in the SCT.

Nembutal anesthetized and anesthetic-free decerebrated cats were used. Postsynaptic unit activity was recorded extracellularly with stainless steel microelectrodes in the spinal gray at L_6–S_1 level in 10 experiments and in the DLF at L_1 level in 23 experiments. Locations of the units studied were histologically determined by depositing iron from the microelectrode tip[6]. The units were tested for cutaneous activation from hind quarters by brushing the clipped fur and depilated skin. Those so activated, were further tested for type I afferent activation by stimulating tactile pads in the receptive field with a hand-held probe or a precisely controlled mechanical stimulator[11]. Many of the tactile pads that were chosen for quantitative mechanical stimulation were not associated with tylotrich hairs[3]. Brief mechanical stimuli applied to tactile pads were effective in eliciting a discharge in the cells under study while the same stimuli applied to structures adjacent to the pad were generally ineffective. The amplitudes of such stimuli were small enough to only excite the type I afferent[4]. Maintained displacements of tactile pads often evoked a sustained discharge in the central cells. Similar stimuli applied directly to down, guard or tylotrich hairs either produced no response, or when effective, only evoked a transient response. These units were unresponsive to stretch of the skin or steady indentation of regions adjacent to the pad, confirming that activity in type II afferents was not involved in evoking the discharge. The DSCT units were physiologically identified by antidromic activation from the inferior cerebellar brachium. The stimulating electrode in the brachium was stereotaxically placed and its location was confirmed histologically. The population of units at L_6–S_1 level was also tested for DLF activation from a stimulating silver-ball electrode at L_3, a stimulation which produced a slow potential at the inferior brachium electrode.

Fig. 1A illustrates the receptive field and histological location of a unit antidromically activated by DLF stimulation which, however, was not antidromically activated by inferior brachium stimulation. The unit was activated by several receptor types in its receptive field, including tactile pads. Of the 27 postsynaptic units in L_6–S_1 spinal gray, 11 were antidromically activated by DLF stimulation and had cutaneous receptive fields. Of these 11, 7 units were more effectively excited by stimuli delivered to the tactile pads than by similar stimuli delivered to the neighboring skin.

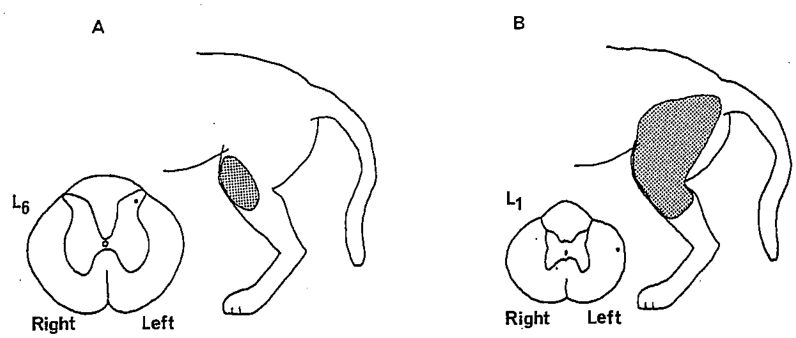

Fig. 1. Histological locations and ipsilateral receptive fields of two representative units activated by type I afferents and projecting in the DLF. A, Postsynaptic unit in rostral L_6 segment antidromically activated by DLF but not inferior brachium stimulation. Conduction velocity was 40 m/sec. B, DSCT axon in DLF at L_1 which was antidromically activated by inferior brachium stimulation, with conduction velocity of 45 m/sec.

None of the units recorded at L_6–S_1 level were antidromically activated by inferior brachium stimulation, including those activated by DLF stimulation.

Fig. 1B illustrates the receptive field and histological location of a unit recorded in the DLF at L_1 in a decerebrate cat. This unit, because it followed brachial stimulation at frequencies over 200/sec and showed no jitter in response latency at threshold stimulus intensities, was classified as a DSCT axon. The unit was activated only from stimuli applied directly to the tactile pads; stimulation anywhere else within the locus of active receptors could not elicit a response even at displacements above 200 μm. In this case there were 113 tactile pads from which activity could be elicited. Out of 279 DSCT units 6 were found with properties as illustrated above, 23 were found which responded to stimulation of hair receptors as well as tactile pads, and 7 were found which responded to stimulation of hair receptors, tactile pads and deep receptors (*i.e.*, muscle, joint or other subcutaneous structure).

There is no doubt that the latter group is part of the cutaneous subdivision of the DSCT described by Lundberg and Oscarsson[8]. However, there is no evidence that the former group, units with cell bodies in L_6–S_1, is part of the spinocervical tract. Since deep structures may also have activated these units but were not always adequately tested, there is the possibility that some of these cells were part of the non-DSCT, flexor reflex afferent-activated pathway in the DLF[9] or some other 'propriospinal' pathway. Since the latter cells had much smaller receptive fields than DSCT units studied, it is possible that they converge onto the cells of origin of the cutaneous subdivision of DSCT and are thus intersegmental interneurons in the spinocerebellar pathway. The absence of tactile pad activity in the spinocervical tract as shown by Brown and Franz[2] may not hold for all sources of input into the lateral cervical nucleus (LCN). Notably, Ha and Liu[7] suggest that DSCT and ventral spinocerebellar tract axons may send collaterals into LCN, a conjecture for which there are as yet no physiological data. It is clear that the type I afferent activity is present in DLF and that some at least has its ultimate termination in the cerebellum; it is also clear that some fibers in DLF excited by type I activity do not go to the cerebellum.

This study was supported by U.S. Public Health Service Grants NS 07505, 1-F2-NS 30, 383 NSRA and GM 00223.

Department of Physical Biology,
New York State Veterinary College, and
Section of Neurobiology and Behavior,
Cornell University, Ithaca, N.Y. 14850 (U.S.A.)

M. D. MANN
H. KASPRZAK
D. N. TAPPER

1 BROWN, A. G., Cutaneous afferent fibre collaterals in the dorsal column of the cat, *Exp. Brain Res.*, 5 (1968) 293–305.
2 BROWN, A. G., AND FRANZ, D. N., Responses of spinocervical tract neurones to natural stimulation of identified cutaneous receptors, *Exp. Brain Res.*, 7 (1969) 231–249.
3 BROWN, A. G., AND IGGO, A., A quantitative study of cutaneous receptors and afferent fibres in the cat and rabbit, *J. Physiol. (Lond.)*, 193 (1967) 707–733.
4 BROWN, P. B., AND TAPPER, D. N., Applications of signal averaging to dorsal root recording, *Brain Research*, 25 (1971) 87–102.
5 BURGESS, P. R., PETIT, D., AND WARREN, R. M., Receptor types in cat hairy skin supplied by myelinated fibers, *J. Neurophysiol.*, 31 (1968) 833–848.
6 GREEN, J. D., A simple microelectrode for recording from the central nervous system, *Nature (Lond.)*, 182 (1958) 962.
7 HA, H., AND LIU, C. N., Organization of the spino-cervico-thalamic system, *J. comp. Neurol.*, 127 (1966) 445–470.
8 LUNDBERG, A., AND OSCARSSON, O., Functional organization of the dorsal spinocerebellar tract in the cat. VII. Identification of units by antidromic activation from the cerebellar cortex with recognition of five functional subdivisions, *Acta physiol. scand.*, 50 (1960) 356–374.
9 LUNDBERG, A., AND OSCARSSON, O., Three ascending spinal pathways in the dorsal part of the lateral funiculus, *Acta physiol. scand.*, 51 (1961) 1–16.
10 PETIT, D., AND BURGESS, P. R., Dorsal column projection of receptors in cat hairy skin supplied by myelinated fibers, *J. Neurophysiol.*, 31 (1968) 849–855.
11 TAPPER, D. N., Stimulus–response relationships in the cutaneous slowly-adapting mechanoreceptor in hairy skin of the cat, *Exp. Neurol.*, 13 (1965) 364–385.
12 TAPPER, D. N., Behavioral evaluation of the tactile pad receptor system in hairy skin of the cat, *Exp. Neurol.*, 26 (1970) 447–459.
13 TAUB, A., Local, segmental and supraspinal interaction with a dorsolateral spinal cutaneous afferent system, *Exp. Neurol.*, 10 (1964) 357–374.

(Accepted January 4th, 1971)