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Short Communications

Pyramidal modulation of responses of spinal neurons to natural stimulation of cutaneous receptors

Modulation of cutaneous input at the spinal level by pyramidal and other supraspinal systems has been demonstrated in studies of evoked slow potentials in which electrical nerve stimulation was used[1,8,9] and in single unit studies in which gross natural or electrical skin stimulation was employed[4–6,13,14]. Little attention has been given to whether and to how these supraspinal effects are related to types of cutaneous afferent systems[2,3]. Recently, the Type I afferents, innervating epidermal mechanoreceptors (tactile pads), have been shown to activate central cells of the dorsal gray in decerebrate and spinal cats[11,12]. Because the receptive field characteristics and the stimulus–response properties of the tactile pad receptor system have been particularly well defined[7,10], pyramidal modulation of postsynaptic discharges produced by stimulation of this cutaneous system has been emphasized in this study.

In 14 decerebrated anesthetic-free cats, the pyramids were exposed by a ventral approach and stimulated with bipolar electrodes using five 0.1 msec duration pulses at 500 c/sec. The stimulating position and threshold intensity were found by observing small visible muscle contractions in contralateral hind limb. Subsequently, the animals were rigidly mounted, paralyzed with gallamine triethiodide and artificially respired. The spinal cord was exposed by a laminectomy from S_1 to L_5 and the slow potential evoked by pyramidal stimulation was monitored with a surface macroelectrode at the

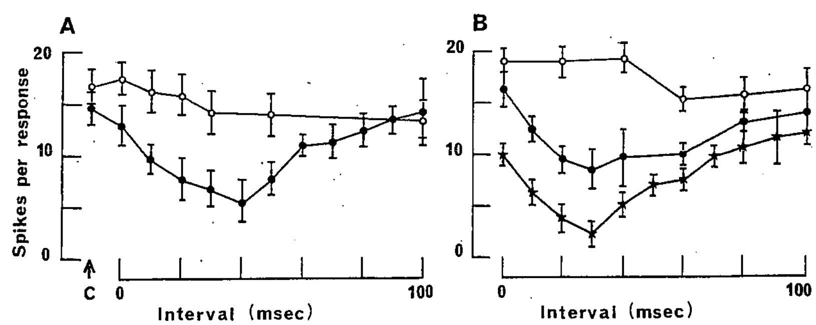

Fig. 1. Pyramidal inhibition of Type I afferent input into the spinal gray. A, Control (C) and conditioned responses of two units in the same preparation: a Type I primary afferent axon (open circles) and a postsynaptic cell (closed circles). The pyramidal stimulus intensity was 4 times threshold and threshold, respectively. Values in this and following graphs represent means and standard deviations. B, Increase in pyramidal inhibition of on-pad response at greater stimulus intensity. The control responses (open circles) at delays indicated were not preceded by conditioning pyramidal volleys. The conditioned responses of the postsynaptic cell were inhibited less by pyramidal volleys at threshold intensity (closed circles) than at 2 times threshold intensity (stars).

lumbar enlargement. Single unit activity in the dorsal gray was extracellularly recorded with tungsten microelectrodes, amplified and displayed on a storage oscilloscope. The tactile pad receptors and structures in adjacent depilated skin were activated by linearly rising ramp displacements (most often 10 μm/msec, final displacement: 250 μm). This stimulus format was chosen since the tactile pads are slowly-adapting and stimuli applied to adjacent skin (off-pad) do not elicit discharges from these specific receptors[10]. Pyramidal and/or peripheral stimuli were delivered at 1/10 sec. The pyramidal stimulation (conditioning stimulus) preceded the peripheral stimulation (control or test stimulus) at intervals of 0–300 msec, in increasing order. The control and conditioned responses consisted of spike trains which lasted for approximately 50 msec, from which an average number of action potentials was computed for 10 trials at each condition.

Two of the 24 units studied were primary afferent axons as judged by the lack of spontaneous activity, latency of response and receptive field characteristics. They responded only to stimulation of one and 4 tactile pads, respectively, and their discharges were not influenced by conditioning pyramidal volleys (Fig. 1A). The postsynaptic units were spontaneously active ($<$ 1–15/sec) and had larger receptive fields (1.5–44 sq. cm) than the primary afferents. One postsynaptic unit, with very low spontaneous activity, received only tactile pad input, *i.e.* it was not excited by off-pad stimuli. All other postsynaptic units received tactile pad and other cutaneous input. The pyramidal effects on spontaneous activity were varied: 4 units (each in different preparation) were not affected; 6 units (in 3 preparations) were excited and 12 units (in 11 preparations) were inhibited.

In contrast to other reports[4], the modulating effect of the pyramidal volley on the postsynaptic unit discharges that were produced by peripheral input was not always the same as the effect on spontaneous activity. The response of 19 of these units

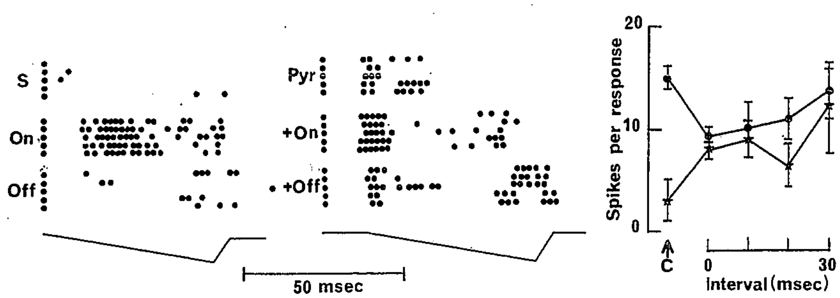

Fig. 2. Pyramidal inhibition of Type I afferent input and facilitation of other cutaneous input to the same central cell. Action potential trains from the cell are shown as horizontal rows of dots in which the first dot marks the synchronizing pulse for the trial. Five trials under each condition are represented as 5 rows of dots. The solid line under the dot patterns indicates the ramp displacement applied (5 μm/msec, final displacement: 250 μm). Pyramidal stimulation (Pyr) delivered at the synchronizing pulse, excited this cell over its spontaneous rate of discharge (S); its response to Type I input from a tactile pad (On) was inhibited by conditioning stimulus (+On) but its response to other cutaneous input (Off) was facilitated by identical volleys (+Off). The graph of averaged data shows that the control (C) on-pad responses were also inhibited (closed circles) and the off-pad responses were facilitated (stars) at other conditioning intervals than the 10 msec interval illustrated by the dot patterns.

to stimulation of tactile pad receptors was inhibited by conditioning pyramidal volleys at threshold and/or higher intensities; the response of 3 units was unaltered. The time course of this inhibition for two intensities of pyramidal stimulation is shown in Fig. 1B.

The responses of the central cells to off-pad stimulation were also often inhibited by conditioning pyramidal volleys, however in 3 units (in 2 preparations) facilitation of the off-pad response was observed although the discharge in response to on-pad stimulation was inhibited and the ongoing activity was enhanced or reduced, depending on the unit. As illustrated in Fig. 2, the discharge in response to tactile pad stimulation was inhibited while the response of the same central cell to stimulation of skin just adjacent to the pad was facilitated. The effects were qualitatively the same at two intensities of pyramidal stimulus.

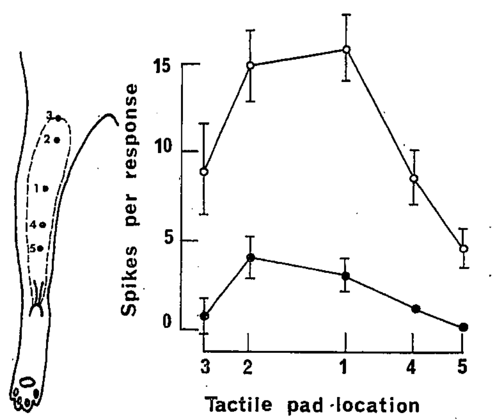

Fig. 3. Variation of the pyramidal effect across the receptive field. The magnitude of pyramidal inhibition of the on-pad responses across the receptive field is seen as the difference between the control responses (open circles) and the maximally inhibited responses (closed circles).

The time course and magnitude of the pyramidal effects on peripherally evoked response varied with the stimulus site within the receptive field of the postsynaptic unit (Fig. 3). Responses from tactile pads located more peripherally in the receptive field were inhibited at short intervals even if the peripheral locus was also more distal on the limb, *i.e.* apparently independent of conduction distance. Off-pad responses were similarly inhibited but to a slightly greater degree. The absolute difference between the number of impulses in the control on-pad response and the maximally inhibited response increased towards the center of the receptive field.

Evidence has been presented in this report that pyramidal modulation of cutaneous input depends to a significant extent upon which afferent system activates the central cell: the discharge of the unit in response to stimulation of different, but closely neighboring, skin receptors may be differentially influenced; and the effects vary from one portion of the receptive field to another.

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

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

1 ANDERSEN, P., ECCLES, J. C., AND SEARS, T. A., Cortically evoked depolarization of primary afferent fibers in the spinal cord, *J. Neurophysiol.*, 27 (1964) 63–77.
2 BURGESS, P. R., PETIT, D., AND WARREN, M., Receptor types in cat hairy skin supplied by myelinated fibers, *J. Neurophysiol.*, 31 (1968) 833–848.
3 BROWN, A. G., AND IGGO, A., A quantitative study of cutaneous receptors and afferent fibers in the cat and rabbit, *J. Physiol. (Lond.)*, 193 (1967) 707–733.
4 FETZ, E. E., Pyramidal tract effect on interneurons in the cat lumbar dorsal horn, *J. Neurophysiol.*, 31 (1968) 69–80.
5 HAGBARTH, K. E., AND FEX, J., Centrifugal influences on single unit activity in spinal sensory paths, *J. Neurophysiol.*, 22 (1959) 321–338.
6 HILLMAN, P., AND WALL, P. D., Inhibitory and excitatory factors influencing the receptive fields of lamina 5 spinal cord cells, *Exp. Brain Res.*, 9 (1969) 284–306.
7 IGGO, A., AND MUIR, A. R., The structure and function of a slowly adapting touch corpuscle in hairy skin, *J. Physiol. (Lond.)*, 200 (1969) 763–796.
8 LINDBLOM, U. F., AND OTTOSSON, J. O., Influence of pyramidal stimulation upon the relay of course cutaneous afferents in the dorsal horn, *Acta physiol. scand.*, 38 (1957) 309–318.
9 MAGNI, F., AND OSCARSSON, O., Cerebral control of transmission to the ventral spino-cerebellar tract, *Arch. ital. Biol.*, 99 (1961) 369–396.
10 TAPPER, D. N., Stimulus-response relationships in the cutaneous slowly-adapting mechanoreceptor in hairy skin of the cat, *Exp. Neurol.*, 13 (1965) 364–385.
11 TAPPER, D. N., AND MANN, M. D., Single presynaptic impulse evokes postsynaptic discharge, *Brain Research*, 11 (1968) 688–690.
12 TAPPER, D. N., MANN, M. D., AND KASPRZAK, H., Projection of skin afferents on neurons of dorsal spinal gray, *Fed. Proc.*, 28 (1969) 2930.
13 TAUB, A., Local, segmental and supraspinal interaction with dorsolateral spinal cutaneous afferent system, *Exp. Neurol.*, 10 (1964) 357–374.
14 WALL, P. D., The laminar organization of dorsal horn and effects of descending impulses, *J. Physiol. (Lond.)*, 188 (1967) 403–423.

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