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# Facilitation of Afferent Sensory Transmission in the Cuneate Nucleus of Rat during Locomotor Movement

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**=ABSTRACT=**

**Single neuronal activities were recorded in the cuneate nucleus of awake rats during rest and running behavior. Movement-induced changes in somatic sensory transmission were tested by generating post-stimulus time histograms of these neurons' responses to stimulation through electrodes chronically implanted under the skin of the forepaw, during control resting behavior and during two standardized speeds of locomotor movement: slow (1.0 steps/s), fast (2.0 steps/s).**

**The magnitudes of firing during these responses were measured and normalized as percentage increases over background firing. The averaged evoked unit responses were facilitated by +59.3 ±12.5% and +25.6±5.4% (SEM) as compared with resting behavior, during slow and fast movement respectively. This is to be compared with the movement-induced sensory suppressions observed previously in the ventrobasal thalamus (−31.0%±1.9%) and in the primary somatosensory cortex (−71.2%±3.8%) of slowly running rats. These results suggest that afferent somatosensory information may be uniquely modulated at each sensory relay, such that it may be facilitated at brainstem level and then subjected to suppression at higher somatosensory nuclei during movement.**

**Key Words:** Somatosensory, Cuneate nucleus, Afferent modulation, Locomotion

## INTRODUCTION

The dorsal column-medial lemniscal somatosensory system, which conducts to the primary somatosensory (SI) cortex, is known for its submodal specificity and reliability of transmission, especially in anesthetized animals (Poggio & Mountcastle, 1963; Jones, 1981). However, there are much evidences suggesting that afferent transmission through this system may be significantly modulated, especially during active movements (Coulter, 1974; Chapin & Woodward, 1982a,b; Nelson & Douglas, 1989). In particular, we have demonstrated that sensory responses of single neurons recorded in the forepaw area of the VPL thalamus are suppressed during movement, but to a lesser extent than in the SI cortex (Shin and Chapin, 1990a,b; Shin et al, 1993; 1994). Unfortunately, the question of the presence of movement-induced afferent sensory modulation in the brainstem somatosensory nuclei has not been studied. Thus, the current study was carried out to test whether movement-induced modulation of afferent somatosensory transmission may also occur in the cuneate nucleus of awake rats and, if present, to characterize its polarity and magnitude.

## MATERIALS AND METHODS

Long-Evans (hooded) rats (n=13, 250-30 g) were habituated to handling and treadmill running (30~60 min/day, for 3-7 days). These animals were then surgically implanted with bipolar stimulating electrodes in the paw, and with recording microwire electrodes (25 $\mu$m stainless steel teflon coated, California Fine Wire, Grover City, CA) in the rostral and middle cuneate nucleus (1.0 mm lateral from midline, 1.0 mm rostral ~0.5 mm caudal to obex, 0.5~1.0 mm deep). Further detailed methods for surgery and the recording of single neurons are described elsewhere (Shin & Chapin, 1990a,b; Shin et al, 1992; 1993; 1994).

A computer was used to access and display on-line post-stimulus time histograms of the unit responses to natural touch of the forepaw and to electrical stimulation (single 0.1 ms pulses, 2.0 Hz) through indwelling electrodes. Stimulation currents were typically set to about 50 $\mu$A above the threshold for the smallest statistically detectable responses in the cuneate neurons. These currents were generally between 50 and 200 $\mu$A, and were far subthreshold for elicitation of flexion reflexes (> 500 $\mu$A). To provide a controlled behavioral situation allowing testing of afferent responses during movement and rest, the same parameters of electrical forepaw stimulation were applied during two standardized speeds of locomotor movement: slow (1.0 footfalls/s) and fast (2.0 steps/s). The treadmill was turned on and off at 10 s intervals. Post-stimulus time histograms were used to quantitate cuneate neuronal responsiveness to forepaw stimulation. Changes in neuronal responsiveness to paw stimuli during movement, as opposed to resting control, were quantitated by using these histograms to measure the average number of neuronal spike discharge which occurred during a specified post-stimulus excitatory response epoch. The following formula was used to calculate the average firing rate during such a response epoch: (No. of spikes/No. of sweeps)$\times$(1000 /No. of milliseconds in epoch).

## RESULTS

Simultaneous recordings of many single neurons were obtained from the cuneate nucleus in freely moving rats (n=13) using implanted arrays of 25 $\mu$m microwire electrodes. Neuronal activity recorded from a single microwire was not considered to be from the same unit observed in previous experimental sessions unless discharge characteristics (during rest and running, excitatory responses evoked by forepaw electrical stimulation) and somatosensory receptive field properties were identical. A total of 28 units were examined in this study. All neurons used in this study possessed cutaneous receptive fields on the palm of the ipsilateral forepaw.

The major result of this study was the demonstration that afferent responses in the cuneate nucleus were facilitated during movement as compared with resting behavior. As a typical example, Fig. 1A-C illustrate data from an experiment in which a cuneate neuron was recorded during rest and running. The peri-event histogram in Fig. 1A indicates the firing rate of this neuron over 60 cycles of treadmill movement (each cycle 10 s ON, 10 s OFF). Peristimulus histograms (Fig. 1B, C) show the averaged responses of this neuron to forepaw stimulation (2 Hz) during the resting (B) and running (C) periods of this experiment. In this cuneate neuron, the magnitude of the excitatory response to forepaw stimulation (arrow) was facilitated (by 35.1%)

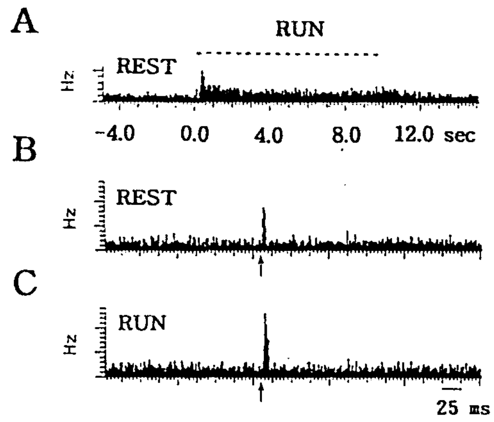


*Fig. 1. Effects of movement on discharge rates and sensory responses of a cuneate neuron. A: peri-event histogram of averaged activity across the treadmill ON/OFF cycle for 10 min, Y-axis ticks = 10 spikes/s, Small X-axis ticks = 200 ms, B,C: peri-stimulus time histograms triggered by electrical paw stimulation during rest (B) and treadmill running (C). For both, the magnitude of the evoked unit response was calculated as the average discharge frequency (in spikes/s) during the excitatory response epoch (3~7 ms post-stimulus). Background discharge was calculated as the average firing rate measured between 25 and 175 ms prestimulus. Vertical scales are normalized for constant instantaneous firing rate per bin, Vertical scale: 50 spikes/s/tick, Horizontal scale: 5 ms/tick, bin size: 1.0 ms. Arrow indicates the time when the forepaw was stimulated.*

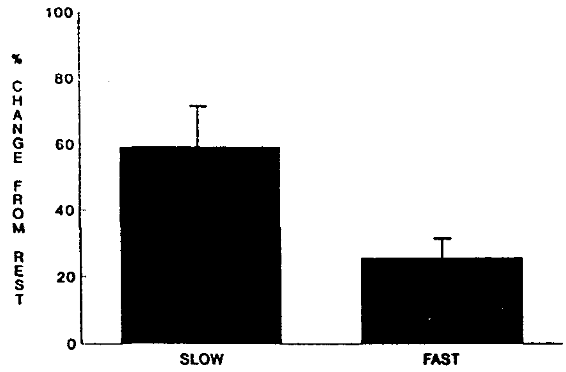


*Fig. 2. Mean percent changes of evoked unit responses of cuneate neurons during two speeds (slow: 1.0 footfalls/s, n=12; fast: 2.0 footfalls/s, n =16) of locomotor movement on the treadmill.*

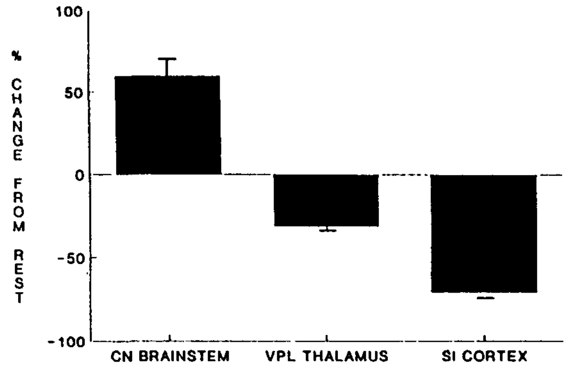


*Fig. 3. Comparison of the mean percent changes of slow (1.0 footfalls/s) movement-induced modual -tions of afferent sensory transmission among cuneate (n=12), VPL thalamic (n=135) and SI cortical neurons (n=108).*

during running as compared with rest.

As is depicted graphically in Fig. 2, the averaged evoked unit responses (EURs) of these cuneate neurons were facilitated by means of +59.3±12.5% (n=12) and +25.6±5. 4% (n=16, SEM) during slow (1.0 footfalls/s) and fast (2.0 footfalls/s) locomotor limb movement, respectively, as compared with resting behavior. This result can be compared with the reductions of afferent sensory transmission which we have measured in the SI cortical ( -71.2±3.8%) and in the VPL thalamic (-31.0±1.9%) forepaw area neurons in similar experiments (slow movement: 1 footfall/s) reported previously (Fig. 3, Chapin & Woodward, 1982a; Shin & Chapin, 1990a).

## DISCUSSION

The results of this study demonstrate that sensory transmission through the middle and rostral cuneate nucleus is subject to an overall facilitatory influence during locomotor limb movements as compared with non-moving controls. It is possible that this facilitation of evoked unit responses may merely represent an elevated excitability of the cuneate neurons due to increased afferent input during running. However, this cannot explain the result that movement-induced facilitations of evoked unit responses were reduced when the rat was subjected to faster locomotor movement (Fig. 2).

The enhancement of afferent sensory transmission in the neurons recorded in the middle and rostral regions of the cuneate nucleus of awake, moving rats in this study is consistent with our previous study, where we have reported the effects of motor cortex (MI) stimulation on afferent sensory transmission in the cuneate nucleus of anesthetized rats (Shin & Chapin, 1989).

A relatively strong and consistent mean afferent inhibition (13~37%) was found in the caudal region (0.5~1.5 mm caudal from obex) of the cuneate nucleus. By contrast, short latency (6~10 msec) mean facilitations (8~20%) were observed in the rostral and middle cuneate nucleus (1.0 mm rostral - 0.4 mm caudal to obex). In the cat, Towe and Jabbur (1961) reported that motor cortical stimulation was able to inhibit 61% and facilitate 30% of cuneate neurons. Levitt et al. (1964) found that SI cortex stimulation excites neurons in the dorsal column nuclei in cat, whereas MI cortex inhibits them.

Neuroanatomically, projections to the DCN from the motor cortex are rare, and projections from the somatosensory cortex mainly reach the 'reticular zones' in the rostral cuneate and in the deep part of the middle and caudal cuneate (Wall, 1970; Weisberg & Rustioni, 1979). The mesencephalic reticular formation has also been reported to be involved in the facilitation of DCN neurons by cortical stimulation (Vierck, 1978). It is thus conceivable that the motor cortex may exert facilitatory influence on the rostral and middle cuneate neurons indirectly through SI cortex or mesencephalic reticular formation during movement.

The fact that movement-induced facilitation of afferent transmission in the cuneate nucleus was reduced during faster locomotion suggests that both facilitatory and inhibitory modulations may be present in the cuneate nucleus during movement. Although the facilitation of afferent sensory inflow may be predominant during both slower and faster movement states, stronger inhibitory influence, which may originate from the motor cortex, may reduce the overall facilitation of afferent transmission in the cuneate nucleus during faster movement.

Gibson (1962) has suggested that active sampling may be a general strategy employed by the brain in cognitive processing in all senses. In this model, sensory information is interpreted in the light of the external movements in which the information was gained. A number of lesion studies suggested that the lemniscal system may play an important role in evaluation of somatic sensation gained during active exploratory searching movements and manipulation of objects in extrapersonal space (Wall, 1970; Hick & D'Amato, 1975). In these viewpoints, the net facilitation of the sensory transmission in the middle and rostral cuneate nucleus may suggest either a lowered threshold for cutaneous information at the first processing station of the dorsal column lemniscal system or a phasic gating-in of afferent sensory information during certain time period of the repetitive, regular locomotor step cycle. Thus, this sensory facilitation in the cuneate nucleus, which is the first relay station of the dorsal column-medial lemniscal somatosensory system, may function to reduce the loss of afferent information or to ensure sufficient afferent inflow to the VPL thalamus and the SI cortex, where phasic transmission of only meaningful feedback signals is allowed by successive suppressions of the afferent sensory transmission during movement (Chapin & Woodward, 1982b; Shin & Chapin, 1990b,c, Shin et al, 1993; 1994).

The major conclusion to be drawn from this study is that movement produces a rather complex pattern of modulation of somatosensory information as it ascends from the cuneate nucleus to the VPL thalamus, and within the SI cortex. Incoming afferent somatosensory information may be first facilitated at the brainstem level and then subjected to progressive inhibitions while ascending to the VPL thalamus and finally to the SI cortex.

## ACKNOWLEDGEMENT

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