

Modulation of Sensory Transmission in Cat Lemniscal System during Voluntary Movement*

C. GHEZ and G. L. LENZI

Istituto di Fisiologia Umana, Cattedra II, Università di Pisa, Italia

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Summary. Adult cats were trained to lift their forepaw, depress a lever and then replace their paw on the ground. The potential recorded in the medial lemniscus to stimulation of the superficial radial nerve in the forelimb involved in the movement is depressed both prior to and during displacement of the limb. These changes did not result from movement of the stimulating electrode. The timing of the suppression in lemniscal transmission suggests a central origin of this effect.

Key-Words: Operant Conditioning — Voluntary Movement — Cutaneous Nerve Stimulation — Evoked Potential — Medial Lemniscus.

Schlüsselwörter: Konditionierung — Willkürbewegungen — Hautnervenstimulation — Evozierte Potentiale — Lemniscus Medialis.

Several studies have demonstrated that transmission through the dorsal column nuclei and other relay stations contributing to the medial lemniscus may be modified by stimulation of structures within the central nervous system [2, 9, 12, 13]. Both excitatory as well as inhibitory effects have been observed [2, 6—9, 11—14]. That such effects may also occur under physiological conditions is suggested by the studies of sensory transmission during the different phases of sleep [3]. Indeed, during the phase of rapid eye movements, transmission through the cuneate nucleus is depressed at a time when there is increased activity of pyramidal tract neurons [4]. Furthermore decreased unit responses in the region of the cuneate nucleus have been reported to accompany periods of activity in free-moving rats [1].

Among the structures capable of modulating sensory transmission in the lemniscal system are the sensorimotor cortex [2, 7, 8, 13] and other regions [6, 11, 12] which are also presumed to be concerned with the genesis of voluntary movement [5]. The present study was therefore undertaken to determine the changes in transmission of somatosensory volleys to the medial lemniscus during a conditioned voluntary movement.

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Seven adult cats were trained to lift their right forepaw and depress a lever at the onset of a tone while otherwise remaining immobile in a sitting position. Such a movement was rewarded with a cat-food milk mix and a second reward given when the animal replaced its paw in a specified position on the ground. Pairs of metal grids, made of interdigitating combs through which passed a low current (less than $5 \mu\text{A}$) driving a regenerative switch, were placed on the ground and on the bar. The grid circuits were shorted by contact with the animal's paw and the output of the regenerative switch was used for monitoring purposes and to trigger a stimulating unit.

When the animals responded reliably to the tone with a smooth and uninterrupted lifting and releasing movement, stimulating and recording electrodes were implanted under pentobarbital anesthesia. These consisted of stimulating cuff electrodes placed around the right superficial radial nerve, and bipolar stainless steel electrodes placed stereotaxically in the contralateral medial lemniscus. Recording sessions started one to two days after the surgical procedure.

Responses in the medial lemniscus to stimulation of the superficial radial nerve (0.05 msec rectangular pulses from 1.5 to 3 times threshold) were displayed on an oscilloscope and photographed. The output of the grid circuits and stimulus artifacts were recorded on the same pen of a polygraph while the other pens recorded a pulse for the duration of the tone and a time marker (100 msec). Stimuli were delivered either every two seconds (recurrent) or triggered at set intervals following the tone or the opening of the grid circuits. The stimuli did not interfere with the animals' normal behavior or pattern of movement. Since the interval between trials and the duration of each trial were variable, recurrent stimuli occurred at random in relation to the movements. Typical potentials were evoked in the medial lemniscus with latencies of 2.8 to 3.6 msec (Fig. 1). The amplitudes of the potentials were measured and grouped according to the time interval in which the stimulus occurred in relation to the various phases of the movement (ground, lift, bar-press, and release). Means, standard deviations and standard errors were computed for each group and two-by-two comparisons among these groups using the T-test were performed for each recording session by means of a computer. An uninterrupted lifting movement, which was predominantly flexor in nature, commonly took 200 to 400 msec from opening of the ground grid circuit to contact with the bar. Releasing movements were often somewhat slower (300 to 700 msec) and mainly extensor as the cat replaced its paw on the ground. Movements lasting longer than 500 msec were discarded.

In all animals studied there was a significant depression of lemniscal responses during active movement (Fig. 1, 2A). This was most marked during the lifting phase when the average responses were reduced by 20 to 35% of control values obtained while the cat rested its paw on the

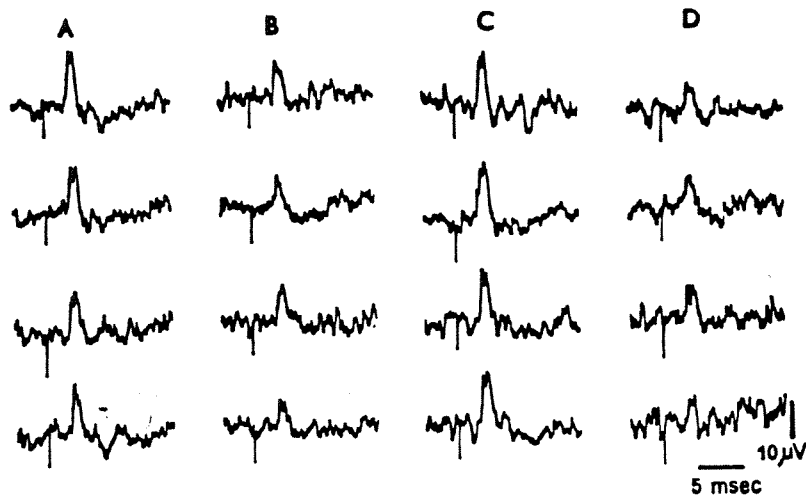


Fig. 1 A—D. Potentials evoked in medial lemniscus during movement by stimulation of the superficial radial nerve. A: controls obtained while the animal remained still with both paws on the ground. B: lifting movement; C: postural fixation, the animal depressing the bar; D: release of the bar

ground (Fig. 2A), ($P < 0.01$). Release of the bar was likewise associated with a reduction of the lemniscal potential, however this was invariably of a lesser degree (15 to 20% of controls) ($P < 0.01$).

The onset of the depression was satisfactorily evaluated in six experiments performed on three cats. This was done both using recurrent stimuli and, in animals with reasonably constant reaction times (200 to 400 msec), by triggering the stimulus after the tone. The latter permitted a larger number of responses (10 to 15) to be obtained even for 100 msec intervals into which they were grouped preceding the onset of movement. Both methods gave similar results (Fig. 2B) and indicated that the first detectable depression of the lemniscal response occurred between 100 and 200 msec prior to a lifting movement. In order to assess the changes in lemniscal transmission during the course of the movement itself, stimuli were triggered at set intervals from 0 to 300 msec from the opening of the ground grid circuits. In no case was any significant difference found between the mean amplitude of the responses elicited at the different times after the movement had been initiated.

From about 250 msec following contact with the bar grid circuit and during the period of postural fixation while depressing the bar, lemniscal responses remained at stable levels which were not statistically different from control values.

The onset of the depression prior to release of the bar occurred earlier than the corresponding depression prior to lift, and preceded opening of the bar grid by 200 to 300 msec. This finding undoubtedly resulted from

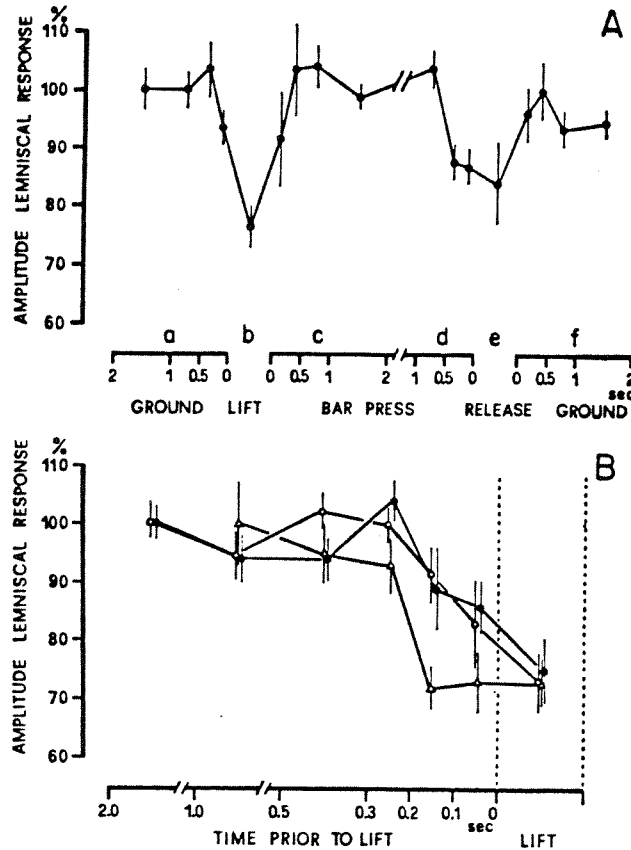


Fig. 2A and B. Time course of the changes in lemniscal evoked potentials in relation to movement. A: complete cycle of movement. The data were obtained using recurrent stimuli delivered every 2 sec. Time is represented in the abscissa and referred in *a* and *d* to the opening and in *c* and *f* to the closure of the ground and bar grid circuits respectively. The duration of the interval in *b* and *e* varied from trial to trial between 0.2 and 0.5 sec. Mean amplitudes of lemniscal potentials are plotted in the ordinate and expressed as percentages of the mean during the control interval, arbitrarily designated as 1 to 2 sec before a lifting movement. Vertical lines are standard errors of the means. Responses are grouped into intervals of 250 msec for the first 500 msec, 500 msec between 500 and 1000 msec and 1 sec between 1 and 2 sec both preceding opening and closure of the grid circuits. B: changes preceding lift. Results obtained from a different animal. The filled circles represent the mean amplitudes of lemniscal responses to recurrent stimuli with the animal retrained to bar press without the tone as a conditioned stimulus. Empty circles and triangles were derived from separate recording sessions in which stimuli were delivered at set intervals following the onset of the tone. In the latter, mean amplitudes are expressed as percentages of the mean in the interval furthest removed from the onset of movement obtained in that session

the fact that movement of the limb started before the opening of the bar grid. Responses returned to control levels within 100 to 200 msec after the cat replaced its paw on the ground. In the present series of experiments, the angle of the bar and force exerted were not monitored, therefore no systematic investigation of the changes during the lowering of the bar could be made.

The effect of the conditioned stimulus (tone) on lemniscal transmission was evaluated in four cats (seven experiments). In two experiments, stimuli were delivered following the tone and after the animal was satiated and remained immobile. In four experiments, the cat was retrained so that the reward was given following the tone only if the animal remained quiet. In no case was any depression in lemniscal responses found to be associated with the tone. Furthermore, one animal was retrained during the recording session itself so that an aliquot of food was delivered upon depression of the bar without a preceding tone. In this case (Fig. 2B, filled circles) the sequence of changes affecting the evoked potentials was not different from what was found using the tone as a conditioned stimulus (Fig. 2B, empty circles and triangles).

Controls were performed in three animals to ensure that the changes observed did not result from movement of the stimulating electrodes. In these cases a second bipolar cuff electrode was placed around the superficial radial nerve distal to the stimulating electrode to record the direct antidromic neurogram. Variation in stimulus intensity resulting from movement of the stimulating electrode would be detected as well with this arrangement as with a central recording electrode. Such a central electrode was undesirable in our experiments because of possible mechanical damage of the nerve. Although small differences were occasionally seen in the mean amplitudes of the compound nerve action potential at different times, even at rest, there was no relation between variation in nerve and lemniscal potentials.

These observations indicate that transmission of cutaneous volleys in the lemniscal system is partially suppressed during voluntary movement in the cat. Presynaptic and/or postsynaptic inhibitory mechanisms may contribute to this depression.

In so far as the depression precedes actual movement of the limb, it is most likely to be principally determined by descending influences upon the relay stations contributing to the medial lemniscus. Indeed there was no delay in the grid circuits employed to detect movement of the limb. Consequently, for the most part, any change in afferent activity preceding displacement of the limb would be due to the activation of muscle afferents in an initial isometric phase of movement. In this regard there is evidence that muscle afferents, particularly the Ia fraction, are well represented in the cuneate nucleus, nevertheless they do not cause substantial inhibition of transmission of cutaneous volleys [10].

Two explanations may be considered for the more pronounced attenuation observed during flexor (lift) rather than extensor (release) movements other than the slight differences in velocity. On the one hand, the central pathways mediating flexion, *i.e.*, pyramidal and rubral, may exert a more powerful inhibitory effect on the lemniscal system. Alternatively, our fixed stimulus to the superficial radial nerve, innervating the physiologically flexor surface of the forepaw, may have selected a specific population of neurons differentially affected during flexor movements.

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Dr. C. Ghez
Istituto di Fisiologia Umana, Cattedra II
Università di Pisa
Via S. Zeno, 31
I-56100 Pisa, Italia