Velocity-Dependent Suppression of Cutaneous Sensitivity during Movement

RONALD W. ANGEL AND ROBERT C. MALENKA[1]

*Department of Neurology, Veterans Administration Medical Center and Stanford
University School of Medicine, Palo Alto, California 94304*

Cutaneous sensory thresholds were measured at the index fingertip of eight normal
subjects. Electric shocks were applied with the finger at rest or tracking a target,
which oscillated at one of three frequencies. For each subject, the sensory threshold
was positively correlated with the frequency of oscillation. The correlations between
sensory suppression and speed of movement agree with previous findings obtained
using experimental animals and somatosensory-evoked responses. Possible mecha-
nisms are discussed.

INTRODUCTION

Several lines of investigation have shown that sensory responsiveness is
reduced during voluntary movement. The effect of movement has been
demonstrated at numerous sites along the sensory pathways, including the
medial lemniscus (5, 8), the thalamus (13), and the somatosensory cortex
(1). In humans, the ability to perceive an electric shock is reduced
during movement of the stimulated part, and this alteration of the sensory
threshold is accompanied by changes of the somatosensory-evoked
response (9–11).

The phenomenon of sensory suppression during movement raises a num-
ber of theoretical and practical questions. At what level of the nervous
system does the interaction between motor and sensory processes occur?
Is it mediated by a specific neurotransmitter? Can drugs be used to enhance
or mimic the phenomenon? Is it relevant to the management of pain?

Investigation of these questions, particularly in human subjects, will

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require a practical method for measuring sensory thresholds during movement and must take account of all variables that might influence the threshold, including the speed of movement. In cats, there is a negative correlation between the amplitude of the lemniscal response to radial nerve stimulation and the velocity of forelimb movement (8). In monkeys, kinesthetic afferent fibers projecting on cortical motor neurons are depressed during ballistic movement, but they remain intense during small, controlled movement (6). The purpose of the present study was to define the relationship between sensory suppression and the rate of voluntary movement in humans.

Previous work in this laboratory (7) showed that the ability to detect an electric shock on the forefinger is impaired during flexion or extension of the digit. In the present study, electric shocks were applied to the right forefinger, which was either held stationary or moved at one of three velocities. Psychophysical methods were used to determine the sensory threshold under each of the four test conditions. The findings demonstrated a positive correlation between the degree of sensory suppression and the speed of finger movement.

METHODS

The subjects were four men and four women, 23 to 58 years of age. All were in good health, with no signs or symptoms of neurological disease. Before testing, only two subjects (RA and RM) were aware of the relationship between movement and sensory threshold. The other subjects soon recognized, however, that shocks were more difficult to perceive during movement of the finger. Hence, none of the subjects can be classified as "naive."

Stimuli were applied by means of Beckman electrodes coated with a conductive electrolyte and fastened to the volar surface of the right forefinger by adhesive collars. The anode was placed on the terminal phalanx and the cathode on the second phalanx. To insure firm contact, each electrode was bound tightly to the skin with adhesive tape. The stimuli consisted of 100-μs pulses, produced by a Nicolet stimulus pulse generator (NIC-502) and current stimulator (NIC-1003). The apparatus delivered a standard current pulse, regardless of possible changes in electrode or skin resistance.

For each test, the subject was seated with the right hand resting on a table grasping a vertical bar, which was 9 cm from a cathode ray tube. The forefinger was extended toward a vertical line displayed on the cathode ray tube. On some trials, the target line was stationary; on others, it was moved alternately to the right and left by means of a function generator (Hewlett Packard Model 202A), which produced a triangular wave form. The lateral excursion of the target was 5 cm, corresponding to slightly

more than 0.5 radians of rotation at the metacarpophalangeal joint. Tests were conducted under each of four experimental conditions: F_0, target stationary; F_1, target oscillating at 1 Hz; F_2, target oscillating at 2 Hz; F_3, target oscillating at 3 Hz. The speed of target motion was 10 cm/s, 20 cm/s, and 30 cm/s under conditions F_1, F_2, and F_3, respectively.

The subject was instructed to track the target line as accurately as possible by alternate flexion and extension of the finger at the metacarpophalangeal joint. Controlled tracking was possible under condition F_1 but difficult or impossible under F_2 and F_3. When the target moved too rapidly for tracking, the subject was required to oscillate the finger at the same frequency as the target oscillation. Because tracking was imperfect, the position of the finger did not necessarily match that of the target. Therefore, we shall refer to the frequency of oscillation, which can be specified more exactly than finger velocity.

Sensory threshold was defined as the current strength at which the probability of perceiving the shock was 0.5. This was determined by the method of constant stimuli, which is based on the probability of perceiving the stimulus at each of several fixed intensities (14). Prior to each test, the experimenter determined the weakest current that was perceptible to the subject when the finger was motionless. This was labeled as intensity A. The experimenter then determined the weakest shock intensity that the subject could perceive while flexing and extending the finger as rapidly as possible. This was labeled as intensity E. Levels B, C, and D were evenly spaced between A and E. Thus, for subject number 1, levels A, B, C, D and E were 2, 3, 4, 5, and 6 mA, respectively.

The test protocol was designed to rule out any effects that might be attributed to the order of testing, such as fatigue, attentiveness, learning, or changes of skin resistance. The initial test condition was selected at random. Eight stimuli were then presented under this condition, the intensity being varied from shock to shock according to a preset, random schedule. After this block of eight stimuli, another test condition was selected at random, and again eight more stimuli of various intensities were delivered. This rotation was continued until the subject had received eight shocks under each of the four test conditions. The entire procedure was then repeated, the sequence of the four test conditions again being chosen randomly. The alternation of test conditions was continued until the subject had received 160 shocks (four test conditions $\times$ five shock intensities $\times$ eight shocks at each intensity).

The subjects were not informed about the intensity of the stimulus being applied. Even if the protocol required two successive shocks at the same intensity, the experimenter would go through the motions of changing the intensity, so that subjects would not be able to predict the shock intensity.

To minimize false positive responses, the stimuli were delivered at random times after the stimulator was switched on. With the switch in the "off" position, the experimenter set the stimulus to the prescribed intensity. The subject then began to track the target with his finger tip, and the experimenter turned on the stimulator, which was set to deliver shocks at 0.3 Hz. Hence, the shock occurred at some unpredictable time ranging from 0 to 3.33 s after the switch was thrown. A light flash, invisible to the subject, indicated the time when the shock occurred. The subject responded verbally to each perceptible shock. By comparing the times of the light flash and the verbal response, the experimenter could recognize responses that occurred before the stimulus or after a delay of more than 2 s. These were counted as negative.

When the finger was oscillating, its velocity was changing continually. Some of the shocks were delivered while the finger was flexing, some while extending, and probably some while it was changing direction, i.e., motionless. Hence, it would be impossible to state whether the finger velocity was positive, negative, or zero at the time when a given shock occurred. Also, it would be impossible to separate the effects of shocks delivered during flexion or extension. Therefore, the results were analyzed in terms of frequency (Hz), rather than velocity of movement.

To determine the sensory threshold under a given experimental condition, the number of shocks perceived at a given current strength was divided by 8, giving the probability of detection, which was converted to a z value by means of a standard table [(14), p. 206]. An $s - z$ plot was then constructed, showing z as a function of stimulus intensity, and a straight line was fitted to the data points by the method of least squares. The value of s corresponding to $z = 0$ was the strength at which the probability of detecting the shock was 0.5.

RESULTS

For the group as a whole, the ability to detect a test stimulus was inversely related to the speed of finger movement. Of the 320 shocks delivered under condition F_0 (finger stationary), 245 (77%) were perceived by the subjects. Under conditions F_1, F_2, and F_3, the corresponding numbers were 196 (61%), 180 (56%), and 141 (44%), respectively. Thus, every increase in the speed of finger movement was associated with a decrease in the percentage of shocks that were perceptible to the subjects. The group figures were consistent with the data for individual thresholds.

With the finger stationary, the sensory thresholds were about 1.5 to 11 mA (Table 1). The mean for the group was 4.40 mA $\pm$ 1.03 (SE). During oscillation of the finger at 1 Hz, the threshold increased in six cases and decreased very slightly in the other two. The group mean for condition F_1

TABLE 1

Sensory Thresholds (mA) during Movement

Subject	Frequency of movement (Hz)							
	0	1	Δ[a]	2	Δ[a]	3	Δ[a]	r[b]
RA	3.09	3.16	0.07	3.98	0.89	4.3	1.21	.96[c]
JR	4.47	4.46	−0.01	4.53	0.06	5.2	0.73	.81[c]
RM	5.02	6.56	1.54	7.28	2.26	7.46	2.44	.93[c]
JA	10.85	11.86	1.01	12.98	2.13	14.03	3.18	.99[c]
PR	3.27	3.22	−0.05	3.25	−0.02	3.36	0.09	.64
MS	4.92	5.08	0.16	5.06	0.14	5.46	0.54	.89[c]
MK	1.49	1.67	0.18	1.66	0.17	1.88	0.39	.94[c]
VW	2.08	3.20	1.12	3.70	1.62	3.50	1.42	.85[c]
Mean	4.40	4.90	0.50	5.31	0.91	5.65	1.25	
SE	1.03	1.12	0.22	1.23	0.34	1.33	0.38	

[a] Threshold minus threshold when finger stationary. To avoid rounding errors, numbers are given to two decimal points. Numbers are not accurate beyond two significant figures.

[b] Coefficient of correlation between frequency of oscillation and threshold.

[c] Significant at $P < 0.05$.

was 4.90 mA ± 1.12. Averaged for all subjects, the mean change was an increase of 0.50 ± 0.22 compared with condition F_0 ($P < 0.05$, t test for paired measurements). During movement of the finger at 2 Hz, seven of the eight subjects had an increased sensory thresold, compared with the resting condition. The mean threshold was 5.31 mA ± 1.23, and the mean change from condition F_0 was an increase of 0.91 mA ± 0.34 ($P < 0.05$). During movement at 3 Hz, all eight subjects showed a higher threshold than under condition F_0. The mean value for condition F_3 was 5.65 mA ± 1.33, and the mean change from condition F_0 was 1.25 mA ± 0.38 ($P < 0.02$). In Fig. 1, the changes in threshold are graphed as a function of the frequency of oscillation.

For each subject, we determined the coefficient of correlation between threshold and rate of oscillation. The values were all positive, from 0.64 to 0.99 (Table 1). By the sign test, the probability of obtaining this result by chance was 0.004. A test for the significance of the correlation coefficient showed that seven of the eight correlations were significant at $P < 0.05$.

DISCUSSION

The principal results of this study were to confirm the elevation of sensory thresholds during movement and to establish the positive correlations be-
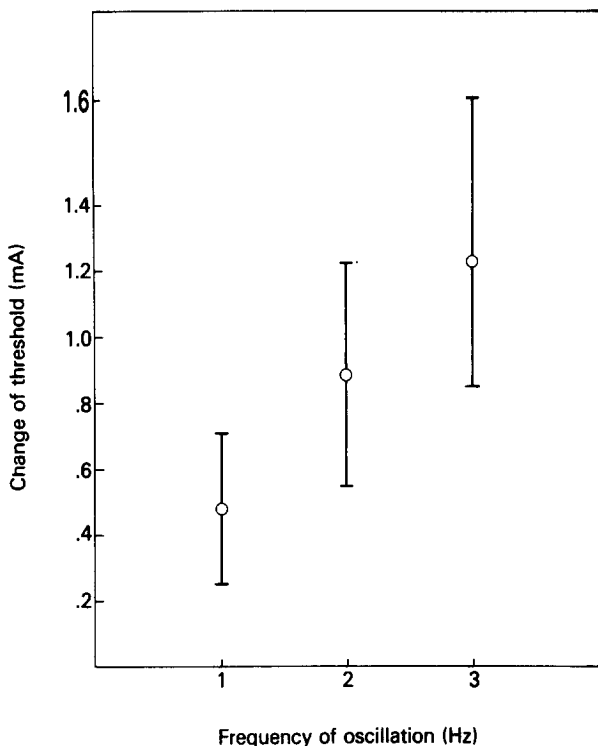
FIG. 1. Increase of cutaneous sensory threshold while tracking a target with the right forefinger. Each ordinate is the mean increase of sensory threshold at the given frequency of target oscillation, compared with the threshold when target is stationary. Vertical bars indicate standard errors. The amount of threshold elevation increases with the rate of finger movement.

tween sensory suppression and speed of movement. In our subjects, the sensory thresholds to electrical shocks at the fingertip were about 1.5 to 11.0 mA. The variance between subjects appears to deserve further attention, but it is not germane to the present study, which concerns the effect of movement on sensory thresholds. To confirm this effect, we used the t test for paired measurements, comparing thresholds at each rate of finger oscillation with those obtained at rest. We also determined the correlation between threshold and rate of oscillation for each subject individually. As noted above, all correlations were positive, and seven of eight were statistically significant.

These results agree with previous studies showing that movement alters the transmission of sensory impulses at several points along the afferent pathways. In the cat, stimulation of the sensorimotor cortex can depress the peripherally evoked activity of neurons on the dorsal column nuclei (12), and transmission of somatosensory volleys to the medial lemniscus is diminished during voluntary movement (5, 8). Ghez and Pisa (8) sug-

gested that pre- and postsynaptic inhibition in the cuneate nucleus may contribute to the attenuation of the lemniscal response. Coulter (5) showed that the lemniscal response is depressed both during and preceding voluntary movement of the contralateral forelimb.

Modulation of the somatosensory input during movement was also demonstrated in the extralemniscal pathways. Ciancia *et al.* (2) recorded the potentials evoked at three levels of the extralemniscal system by stimulation of the skin during rest and during movement. In the bulbar nucleus gigantocellularis, the centrum medianum of the thalamus, and the anterior suprasylvian gyrus of the cortex, the evoked potentials were found to be reduced during limb movements.

Sensory transmission through the ventrobasal complex of the thalamus is also modulated by activity in the motor pathways. In the cat, collaterals of the pyramidal tract (PT) neurons are connected monosynaptically with the thalamic relay cells, and repetitive shocks to the PT fibers can suppress the thalamic responses to stimulation of the medial lemniscus (13). The PT-induced inhibition of sensory units was found to increase as their receptive fields shifted from the trunk toward the digits. This observation may be relevant to the suppression of information of the moving digit, as found in the present study.

Single cells of the somatosensory cortex also respond differently to cutaneous stimulation during movement. Chapin and Woodward (1) showed that this suppression of sensory responsiveness is related to the movement itself, rather than the associated arousal or attentiveness.

In humans, the effect of movement on sensory transmission is manifested in two ways: by an increase of the sensory threshold (4, 7) and by alterations of the somatosensory-evoked responses (SERs) (3, 9, 10). Coquery (3) found that evoked potentials start to decrease in the first 100 ms after EMG onset and are abolished in the subsequent 100 to 200 ms. However, passive movements or even touching the stimulated area could also attenuate the SERs. Rushton *et al.* (11) also found that passive movement was almost as effective as active movement in suppressing the secondary complex of the SER. They concluded that some part of the afferent activity that accompanies an active or passive movement is important to controlling the processing of the SER.

The data from animal and human experiments suggest that both "outflow" and "inflow" mechanisms are important in the modulation of sensory feedback during movement. According to the "outflow" hypothesis, efferent impulses from the upper motor neurons are delivered to sensory relay nuclei, where they inhibit the transmission of sensory information during movement. This proposal is supported by (a) the known suppression of thalamic neurons by collaterals of the PT neurons (13), and (b) the fact that lem-

niscal responses are suppressed before the onset of voluntary movement (5). According to the "inflow" hypothesis, afferent impulses generated by the movement itself are responsible for the inhibition of sensory relay neurons. This proposal is supported by the fact that passive movement is also active in suppressing sensory responses (11). Further studies are needed to assess the relative importance of "outflow" and "inflow" mechanisms.

A new point to emerge from this study was the positive correlation between the sensory threshold and the intended rate of finger movement, a finding that agrees with the results of animal studies. Attempting to define the parameters of movement to which the change in lemniscal transmission might be related, Ghez and Pisa (8) found that there was a negative linear correlation between the amplitude of the lemniscal response and the logarithm of the velocity of the movement at the time the stimulus was delivered. Their observations showed that inhibitory processes alter the transmission of somatosensory volleys through the lemniscal system particularly during rapid movements. They conclude that rapid or ballistic movements, during which afferent impulses are suppressed, may be centrally programmed, i.e., relatively independent of feedback from the periphery.

This conclusion is supported by the experiments of Evarts and Fromm (6), who suggested that sensory feedback modulates the motor cortex responses during precisely controlled movements, whereas the modulation is much weaker during ballistic movement. Of course, the inputs to primary motor cortex are unlikely to have a direct effect on somatosensory perception. Nevertheless, it is interesting to observe that subjects were more likely to perceive stimuli during slow movements than during rapid ones. When the target moved back and forth at 1 Hz, most subjects were able to track its movements rather easily, and the thresholds were relatively low. When the target moved at 3 Hz, precise tracking was nearly impossible, and the finger was merely flung back and forth at a frequency approximating that of the target. Thus, the thresholds were higher during these "ballistic" movements than during the slower, more accurate performance.

Our results also agree with the reported effects of movement on the SER. Rushton et al. (11) showed that the degree of suppression is directly related to the speed of movement. Evidently, the afferent pathways of the SER are velocity sensitive and capable of distinguishing between 10 deg/s and 20 deg/s of flexion velocity at the distal phalanx of the thumb.

The decrease of sensory transmission during movement is now a well established phenomenon, but its neuronal mechanism and biologic significance are still uncertain. Coquery (3) suggested that it serves to screen out irrelevant signals generated by the movement, thus improving the signal-to-noise ratio. On this hypothesis, afferent signals would be more "rel-

evant" to slow, controlled movements than to ballistic movements, during which the sensory suppression appears to be maximal.

REFERENCES

1. CHAPIN, J. K., AND D. J. WOODWARD. 1981. Modulation of sensory responsiveness of single somatosensory cortical cells during movement and arousal behaviors. *Exp. Neurol.* **72**: 164–178.
2. CIANCIA, F., M. MAITTE., AND J-M. COQUERY. 1980. Reduction during movement of the evoked potentials recorded along the extralemniscal pathways of the cat. *Electroencephalogr. Clin. Neurophysiol.* **48**: 197–202.
3. COQUERY, J-M. 1978. Role of active movement in control of afferent input from skin in cat and man. Pages 161–169 in G. GORDON, Ed., *Active Touch*. Pergamon, Elmsford, N.Y.
4. COQUERY, J-M., AND N. VITTON. 1972. Altérations des potentiels évoqués sur le cortex somesthésique du chat durant un mouvement conditionné. *Physiol. Behav.* **8**: 963–967.
5. COULTER, J. D. 1973. Sensory transmission through lemniscal pathway during voluntary movement in the cat. *J. Neurophysiol.* **37**: 831–845.
6. EVARTS, E. V., AND C. FROMM. 1977. Sensory responses in motor cortex neurons during precise motor control. *Neurosci. Lett.* **5**: 267–272.
7. GARLAND, H. T., AND R. W. ANGEL. 1974. Modulation of tactile sensitivity during movement. *Neurology (New York)* **24**: 361.
8. GHEZ, C., AND M. PISA. 1972. Inhibition of afferent transmission in cuneate nucleus during voluntary movement in the cat. *Brain Res.* **40**: 145–151.
9. GIBLIN, D. R. 1964. Somatosensory evoked potentials in healthy subjects and in patients with lesions of the nervous system. *Ann. N.Y. Acad. Sci.* **112**: 93–142.
10. LEE, R. G., AND D. G. WHITE. 1974. Modification of the human somatosensory evoked response during voluntary movement. *Electroencephalogr. Clin. Neurophysiol.* **36**: 53–62.
11. RUSHTON, D. N., J. C. ROTHWELL, AND M. D. CRAGGO. 1981. Gating of somatosensory evoked potentials during different kinds of movement in man. *Brain* **104**: 465–491.
12. TOWE, A., AND S. J. JABBUR. 1961. Cortical inhibition of neurons in dorsal column nuclei of cat. *J. Neurophysiol.* **24**: 488–498.
13. TSUMOTO, T., S. NAKAMURA, AND K. IWAMA. 1975. Pyramidal tract control over cutaneous and kinesthetic sensory transmission in the cat thalamus. *Exp. Brain Res.* **22**: 281–294.
14. WOODWORTH, R. S., AND H. SCHLOSBERG. 1954. Chapter 8 in *Experimental Psychology*. Holt, New York.