

Gating of tactile input from the hand

I. Effects of finger movement

R.F. Schmidt¹, W.J.L. Schady², and H.E. Torebjörk¹

¹ Department of Clinical Neurophysiology, University Hospital, S-751 85 Uppsala, Sweden

² Department of Neurology, Manchester Royal Infirmary, Manchester M13 9WL, UK

Summary. Intraneural microstimulation within the median nerve of alert healthy subjects was used to evoke tactile sensations at threshold for conscious detection. The effect of movement on these sensations was studied by asking the subjects to estimate their magnitude before, during and after movement of the appropriate finger at different speeds. It was found that sensations of flutter and pressure were both attenuated by movement, as was the magnitude of spontaneous paraesthesiae. The degree of sensory inhibition correlated positively with speed of movement and was comparable to the previously reported reduction in cortical somatosensory evoked potentials by movement, using suprathreshold stimuli. These results indicate that (i) movement inhibits tactile sensations of different qualities, (ii) such inhibition is velocity-dependent, and (iii) threshold sensations are amenable to central modulation short of their abolition. It is likely that the mechanisms of inhibition of exteroceptive inputs during movement are contingent upon the character of the sensory stimulus and the nature of the motor task.

Key words: Sensory gating – Finger movement – Cutaneous mechanoreceptors – Microneurography – Intraneural microstimulation

Introduction

Movement is known to attenuate cutaneous percepts from the moved part. This inhibition is often termed “gating” (Papakostopoulos et al. 1975; Coquery 1978; Rushton et al. 1981). Several studies have been devoted to the subject but the site of

interaction and the mechanisms involved are not well understood. In the course of previous work on sensations evoked by delivering small electrical pulses through microelectrodes placed within the human median nerve (intraneural microstimulation, INMS), we have observed that tactile sensations are often suppressed during movement (Schady and Torebjörk 1983). Intraneural microstimulation offers several advantages for the study of gating. Since INMS bypasses peripheral receptors it ensures that any observed effect must occur proximally to the stimulation site in the nerve trunk. It permits stable delivery of identical trains of electrical stimuli, even when the limb is moving. Furthermore, the evoked tactile percepts can be subjectively divided into submodalities of pure flutter or pressure. It is also possible to deliver reproducible stimuli to sensory units supplying skin completely anaesthetised by peripheral nerve block (Schmidt et al. 1989).

The present study was designed to quantify the effect of movement on liminal tactile sensations evoked by intraneural electrical stimulation. The results allow us to draw some conclusions regarding mechanisms of sensory “gating” during movement.

Material and methods

General procedure for intraneural microstimulation

Intraneural microstimulation was carried out in 94 experimental sessions on 10 healthy subjects of both sexes aged 20–38 years. The procedure has been described elsewhere (Torebjörk and Ochoa 1980; Ochoa and Torebjörk 1983; Vallbo et al. 1984). Briefly, a lacquer-insulated tungsten microelectrode (shaft diameter 0.2mm, tip diameter 1–5µm) was inserted percutaneously into a skin nerve fascicle of the median nerve in the upper arm. A similar reference electrode was inserted in the subcutaneous tissue about 1 cm outside the nerve. The microneurographic technique (Vallbo and Hagbarth 1968) allowed recording of multi-unit mechanoreceptive activity from the glabrous skin of the hand, but attempts to obtain single afferent unit recordings

were not always pursued. The electrodes could be connected, by means of a switch in the preamplifier, to the output from a constant voltage Grass S48 stimulator with a stimulus isolation unit. Square wave pulses of 0.25 ms duration were delivered in 2s trains at 30 Hz, repeated every seventh second. The position of the electrode within the nerve and the intensity of the pulses were carefully adjusted until a discrete tactile sensation was induced at threshold for conscious detection.

Such threshold sensations were described by the subjects as either intermittent frequency-dependent flutter or steady pressure, and were projected to small areas of skin on the digits or palm. If pain was elicited the electrode was repositioned. Sensations were only accepted for further study if (i) their quality and projection were consistent in several trials, (ii) the stimulus intensity required to evoke them remained stable, (iii) increases in stimulus intensity beyond threshold resulted in the orderly recruitment of other sensations projected elsewhere in the hand, rather than in any alteration of the magnitude or projected field of the original sensation, and (iv) a clear step in stimulus intensity was observed between recruitment of the first and successive sensations. The stimulus intensity was then set at threshold for conscious detection and remained unchanged thereafter. Thus, only the first recruited threshold sensation was used for further study.

Magnitude estimation

Having identified the quality of the sensation at the outset, subjects were asked to rate its magnitude after each stimulus train on an open numerical scale (method of magnitude estimation, Stevens 1975). Most chose 10 as a convenient baseline rating. Magnitude ratings relative to this baseline were then obtained before, during and after controlled movements of the appropriate digit. Subjects were also asked to report if anything other than the magnitude of the sensation changed. In a few control experiments they were encouraged to concentrate on possible changes in frequency or projection area of the sensation.

Subjects were instructed to make alternating flexion-extension finger movements at a slow (1 Hz), moderate (2–3 Hz) or fast (4–5 Hz) rate. Natural movements which involved all the finger joints were used. The total range of movement of the fingertip in relation to the metacarpal head was 45–60°. Although subjects were asked to move only the finger to which the induced sensation was projected, small movements in neighbouring fingers also occurred. For sensations located in the palm of the hand a combined movement of all fingers was used. In most experiments a sine wave with the desired movement frequency was displayed on an oscilloscope in front of the subject and the speed of the actual movement was monitored by a transducer applied to the back of the finger.

A test run consisted of 15 stimulus trains (Fig. 1). A light bulb out of sight of the subject informed the experimenter when the trains occurred. The subject made a magnitude rating immediately after each one. Four trains were given while the finger was stationary in order to ensure stable baseline ratings. The subject was then instructed to begin finger movements and four further trains were given. After the eighth train finger movements were stopped and seven additional trains were delivered. When possible, several test runs at different finger speeds were undertaken at any one intraneural site.

Exclusion criteria

Out of 179 threshold sensations evoked by INMS, 130 were excluded because they did not fulfill the criteria i-iv listed above. Another 10 sensations were excluded because there was variation of more than 30% among the first four ratings or because

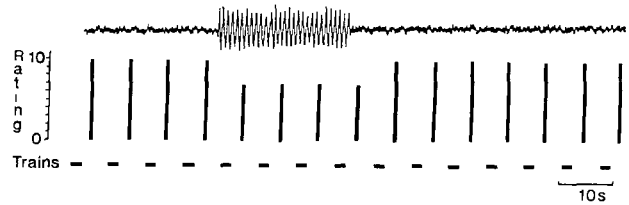


Fig. 1. Experimental procedure in a sample test run. The top tracing is an accelerometer recording before, during and after finger movement. Horizontal bars at the bottom of the figure represent 2s intraneural stimulation trains repeated every 7th second. Vertical bars show the subjects' magnitude ratings immediately after each stimulus train

the ratings failed to return to resting value $\pm 30\%$ after the movements had stopped. The most common reason for exclusion was unstable electrode position, resulting in a change of the evoked sensation. The remaining 39 sensations reported here constitute 22% of the initial threshold sensations collected during the study period.

Data analysis

Each standard test run was normalised to a starting value of 10. The mean value of ratings during ongoing finger movement divided by the mean of the four values preceding and the four values following movement formed a ratio (R) which was used to compare magnitude of sensation during movement and at rest. An R value of less than 1 therefore implied inhibition of sensation by movement, while a value greater than 1 signified enhancement. When several test runs were done at the same finger speed in the same subject, only the first one was included in the analysis of the effect of movement. Others were used to establish the degree of intrasubject variability inherent in the test.

Results were analysed, on the one hand, by comparing R values for flutter and pressure at different finger speeds, but also by pooling all ratings at each point in the testing sequence and comparing median rating values before, during and after movement. Comparison of ratings at rest and during movement (Fig. 3) was by the Mann Whitney U test. Comparison of R values at different finger speeds (Fig. 4) was by Wilcoxon's signed rank test for paired samples.

Results

The mean stimulus intensity required to elicit a sensation by intraneural microstimulation (INMS) was 0.22V (SD 0.13). Most sensations were projected to the fingertips and pulps (Fig. 2), and their projection field characteristics were similar to those previously described (Schady and Torebjörk 1983). The effects of finger movement were studied for 31 sensations of flutter evoked by INMS. Of these, 15 were studied at more than one finger speed, giving a total of 51 test runs. Eight intraneurally evoked sensations of pressure were studied, 3 of them at more than one finger speed. In 4 cases single FA1 (RA) units could be recorded at sites where INMS at threshold evoked flutter, and an SA1 unit could be recorded at a site where INMS induced pressure.

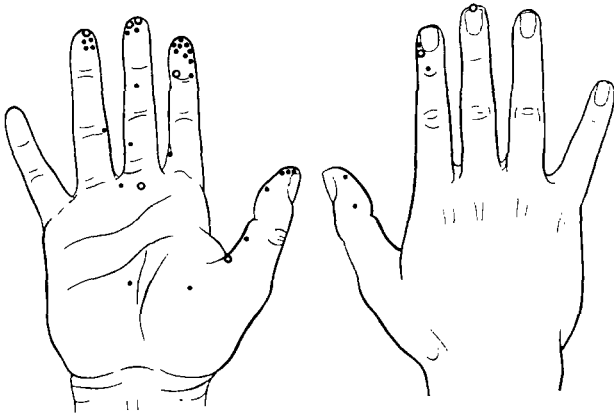


Fig. 2. Location of intraneurally evoked sensations of flutter (filled circles) and pressure (open circles) for the 39 preparations studied with intermittent INMS

The receptive fields of these units coincided with the projection areas of the evoked sensations. Finally, in one instance it was possible to study the effect of finger movement on spontaneous paraesthesiae.

Flutter

Eleven sensations of flutter were studied at slow finger speeds (1 Hz). In 2 there was no evident change in the magnitude of the sensation when the finger was moved. In the remainder, ratings dropped during movement (Fig. 3A). The median R value at this speed was 0.87 (quartiles 0.73 and 0.96). 21 sensations were studied at medium finger speeds of 2–3 Hz (Fig. 3B). There was a fall in ratings during movement in all but one. The median R value in this group was 0.69 (quartiles 0.55 and 0.86). As seen in Fig. 3C, a slightly larger drop in magnitude ratings occurred during fast finger movements (4–5 Hz).

The median R value for the 19 sensations studied at this finger speed was 0.59 (quartiles 0.4 and 0.85). The fall in ratings during movement was statistically significant for all finger speeds ($P < 0.005$). In four test runs (1 at slow, 2 at medium and 1 at fast finger speeds) none of the stimulus trains during finger movement were felt by the subject. The R value in these cases was evidently 0. There was no appreciable enhancement of sensation during movement in any of the trials at different speeds. The highest R values obtained were 1.04 (medium finger speed), 1.02 and 1.00 (slow speed). Figure 3 shows that suppression of sensation was not uniform throughout the period of finger movement and that inter-subject variability in rating was greater during movement than at rest.

Recovery of ratings usually occurred shortly after the movement stopped. However, in 7 out of 51 stimulation runs, recovery of the sensation was not complete but reached no less than 75% of the pre-movement rating. Overshoot was seen in only 4 experiments, when the first post-movement rating was up to 20% above that preceding movement.

No subject reported any change in the frequency of perceived flutter, as opposed to its magnitude, during finger movement. Equally, there were no reports of an effect of movement on the location or area of the sensory projection, although the latter was not studied systematically.

Pressure

Four sensations of steady pressure were studied at slow finger speeds, 4 at medium and 4 at fast finger speeds. Median R values were 0.70 (quartiles 0.50 and 0.88), 0.62 (0.41, 0.83) and 0.21 (0.03, 0.54). The lowest R value was 0.0 and the highest 1.02. The

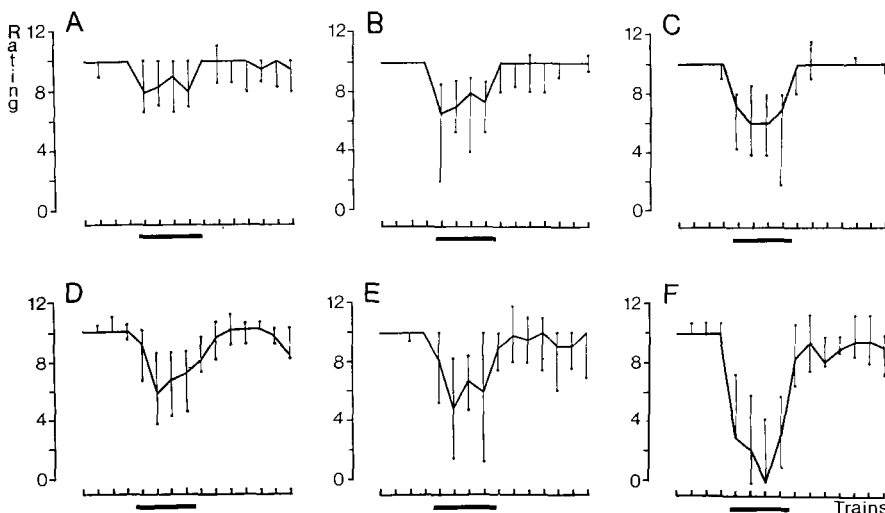


Fig. 3A–F. Median rating curves for sensations of flutter (upper panels) and pressure (lower panels) before, during and after finger movements. A, D correspond to slow movements, B, E to medium and C, F to fast finger movements. Subjects' magnitude ratings have been normalised to an initial value of 10 and each point in the curve corresponds to the median rating after a stimulus train with 25th and 75th percentiles given below and above. Medians and quartiles were calculated from sensations rather than subjects, so some subjects are represented more than once in the figure. A horizontal bar at the bottom of each panel illustrates the period of finger movement

average drop in magnitude ratings during movement was thus even more pronounced than for flutter (Fig. 3D to F), although in view of the small numbers involved such comparisons should be treated with caution.

As with flutter, there was uneven suppression of sensation by movement. One subject reported that during movement the margins of the projected field of pressure became more distinct. The period of recovery after movement also varied, but estimated magnitudes of sensation post-movement returned to baseline values in all but two cases, when it reached 80% of the mean pre-movement rating.

Eighteen sensations of either flutter or pressure were studied at more than one finger speed during the same experimental session. It is evident from the data in Fig. 4 that there was greater inhibition of sensation the faster the movement ($P < 0.01$).

Paraesthesiae

In one experiment stable spontaneous paraesthesiae were reported by the subject and were studied in the same manner as the intraneurally evoked sensations described above. They were felt as short bursts of vibration projected to a small area of the thumb and recurring at roughly 1 s intervals. The subject was asked to rate the magnitude of every fourth burst before, during and after thumb movement. At 1 Hz, 3 Hz and 5 Hz corresponding R values were 0, 0.12 and 0.12.

Variability of ratings

The mean intrasubject variability for the R ratio when repeated runs were carried out in the same subject at the same finger speed was 16%. Inter-subject differences were difficult to quantify but were also in evidence. Certain subjects consistently gave lower magnitude ratings during movement than others, regardless of finger speed. One subject, for instance, had a median R value for all his test runs of 0.29 (quartiles 0.0 and 0.57), while another of the same sex and similar age had a median R value of 0.86 (quartiles 0.6 and 0.93). By chance, the latter subject, who was relatively resistant to sensory suppression by movement, participated in a disproportionate number of early experimental sessions, when only fast finger speeds were used. This may have resulted in a spuriously modest degree of sensory suppression by movement at this speed when pooled data are presented as in Fig. 3. Figure 4 illustrates better the difference in response to various finger speeds when each subject is used as his own control.

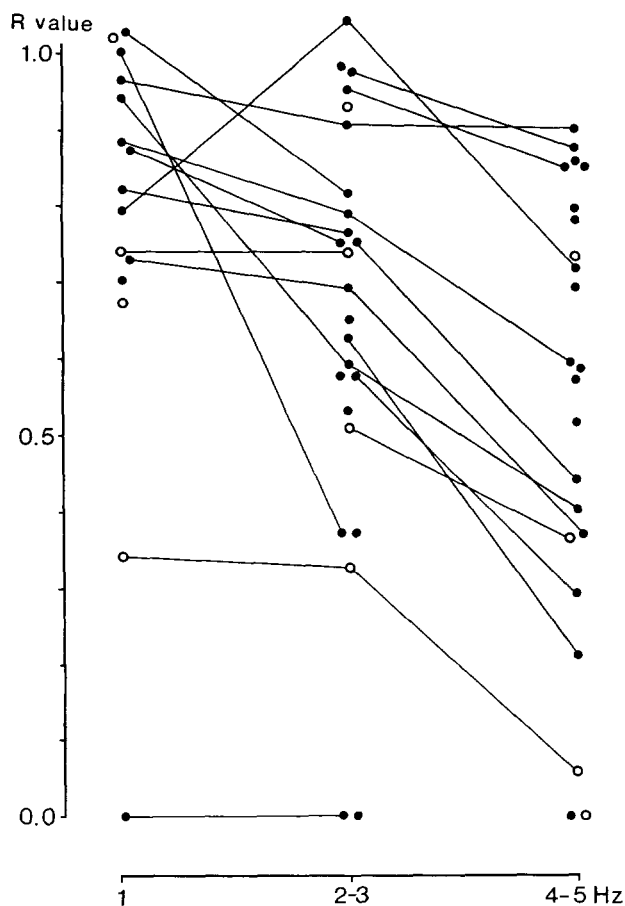


Fig. 4. Ratio (R value) of estimated magnitude of sensation during movement at 1, 2–3 and 4–5 Hz relative to the baseline rating. R values for flutter sensations are represented as filled circles, those for pressure as open circles. Lines join values obtained for the same preparation at more than one speed of finger movement

Discussion

It is obvious that supraliminal intraneural electrical stimulation can easily coactivate many nerve fibers, leading to complex paraesthetic or electric sensations. Strict selection criteria were applied in this study to minimise the likelihood of multiunit activation by intraneural microstimulation, resulting in an exclusion rate of almost 80%. The remaining sensations had definable characteristics in terms of quality, temporal profile and projection territory equivalent to the “elementary sensations” thought to correspond to activation of single mechanoreceptive units (Ochoa and Torebjörk 1983; Vallbo et al. 1984; Torebjörk et al. 1987). Furthermore, when single unit recordings were obtained, the qualitative and spatial attributes of sensations evoked from stimulation at the same intraneural site showed correspondences with mechanoreceptive unit types

and receptive fields, as described previously (Ochoa and Torebjörk 1983). Thus, we have reasons to believe that the sensations studied here are the result of stimulation of FA1 (Meissner) units for flutter, and SA1 (Merkel) units for pressure.

Our study reveals that the magnitude of tactile elementary sensations induced by intraneural stimulation is liable to incremental changes dependent upon central modulation. Subjects often used steps of as little as one tenth of the baseline magnitude estimate to rate changes during finger movement, and sensations were abolished in an all-or-none manner in only 10% of cases. This need not imply that elementary sensations are the composite result of coactivating several afferent units, since the size and location of their cutaneous projections remained unchanged. It merely indicates that graded inhibition of inputs from single mechanoreceptive units does not necessarily result in complete abolition of the evoked tactile sensations.

Nevertheless, even in the event that some of the sensations described by our subjects resulted from coactivation of more than one unit, three main conclusions can be drawn from our results, namely that cutaneous sensation is suppressed by movement, that such suppression is velocity-dependent, and that it applies both to flutter and to pressure. The return of ratings to baseline after movement and the consistent quality and projection of sensations before and after movement suggest that electrode shift was not responsible for these phenomena. The fact that spontaneous tactile paraesthesiae, too, could be inhibited by movement argues in favour of an inherent effect of motor performance on cutaneous sensation.

The mechanism for such inhibition is at present unclear. It is noteworthy that our subjects did not report a reduction in frequency but in magnitude of flutter. This would indicate that the periodicity content from the peripheral afferent message was retained in spite of magnitude suppression. Our observation is in line with the findings of Bystrycka et al. (1977), who showed that, while cuneate neurones in the cat may be inhibited by tactile stimuli, their ability to code information about the frequency of the cutaneous input is preserved.

There are previous reports to the effect that movement may suppress sensations arising in the moved part (Garland and Angel 1974; Papakostopoulos et al. 1975; Coquery 1978) and that such suppression correlates with speed of movement (Angel and Malenka 1982). Moreover, there is velocity-dependent attenuation of somatosensory evoked potentials (SEPs) corresponding to the increase in the sensory perception threshold (Giblin

1964; Conquery et al. 1972; Abbruzzese et al. 1981; Angel et al. 1984; Rauch et al. 1985; Seyal et al. 1987). Our study shows that this apparent gating of afferent information during movement applies to barely detectable sensations of different kinds and that it may be quantified even under these circumstances. The mean drop in ratings during slow, medium and rapid finger movements was 13%, 31% and 41%, respectively for flutter and 30%, 38% and 79%, respectively for pressure. This may be compared with the previously reported reduction in cortical SEPs, using far stronger test stimuli, of 30-80% (Abbruzzese et al. 1981; Cohen and Starr 1985; Rauch et al. 1985; Seyal et al. 1987).

Variability in our subjects' ratings during and after movement was considerable. This is not surprising, bearing in mind the exceedingly weak nature of the sensations even prior to movement. The amplitude of finger movements was not fully controlled, resulting in likely differences within test runs and between subjects. Finally, the rating scale may have been used differently by various subjects. Such sources of error may have resulted in an underestimate of the effect of rapid movements on flutter but should not affect the validity of our conclusions. Laskin and Spencer (1979) also reported substantial intersubject variability in the interactions between conditioning and test tactile stimuli to the skin.

Under resting conditions light touch activating only a few low threshold mechanoreceptors is readily felt (Johansson and Vallbo 1979). By contrast, voluntary isotonic finger movements activate a large number of low threshold mechanoreceptive units of various types supplying that finger (Hulliger et al. 1979), and yet movement is not accompanied by strong sensations. This implies that there must be inhibition of most exteroceptive inputs concomitant with movement. It is unlikely that this sensory input is simply wasted. More probably it is prevented from reaching consciousness, where it would serve no useful purpose, but is redirected to provide information on the occurrence, direction and speed of movement, thereby assisting in motor performance (Hulliger et al. 1979; Moberg 1983).

It may be asked why suppression of weak cutaneous sensations, only barely above threshold, is not complete during movement. The reason for the persistence during movement, albeit dulled, of most of the elementary sensations in our subjects may lie in their anomalous and artificial generation. Unlike movement-induced sensory input, intraneurally induced sensations constitute an additional input which is both unexpected and foreign. An insect alighting on a moving finger might similarly be felt, though perhaps less clearly than on a static finger.

Naturally, the speed and character of the movement are also important variables. In our experiments, the degree of sensory gating during movement correlated positively with finger speed. This may simply be a reflection of variable afferent coactivation during movement. A more functional interpretation of our data might be that rapid ballistic movements of the fingers strongly suppress cutaneous signals because they are regarded largely as "noise", whereas slow searching movements require much more feedback and hence cause less gating of cutaneous input. The latter hypothesis would be consistent with Chapin and Woodward's (1982) finding that somatosensory cortical neurones in the rat respond more briskly to cutaneous stimuli if the animal is engaged in exploration of the environment than in the course of regular locomotion. Equally, kinaesthetic afferents projecting upon cortical motor neurones in monkeys are depressed during ballistic movements but discharge intensely during small precisely controlled movements (Fromm and Evarts 1978).

Acknowledgements. Supported by grants from the Swedish Medical Research Council (B89-14X-05206) and British North West Regional Research fund (A 539).

References

- Abbruzzese G, Ratto S, Favale E, Abbruzzese M (1981) Proprioceptive modulation of somatosensory evoked potentials during active or passive finger movements in man. *J Neurol Neurosurg Psychiatr* 44: 942-949
- Angel RW, Malenka RC (1982) Velocity-dependent suppression of cutaneous sensitivity during movement. *Exp Neurol* 72: 266-274
- Angel RW, Boylls CC, Weinrich M (1984) Cerebral evoked potentials and somatosensory perception. *Neurology* 34: 123-126
- Bystrzycka E, Nail BS, Rowe M (1977) Inhibition of cuneate neurones: its afferent source and influence on dynamically sensitive 'tactile' neurones. *J Physiol (Lond)* 268: 251-270
- Chapin JK, Woodward DJ (1982) Somatic sensory transmission to the cortex during movement: gating of single cell responses to touch. *Exp Neurol* 78: 654-669.
- Cohen LG, Starr A (1985) Vibration and muscle contraction affect somatosensory evoked potentials. *Neurology* 35: 691-698
- Coquery J-M (1978) Role of active movement in control of afferent input from skin in cat and man. In: Gordon G (ed) *Active touch*. Pergamon Press, Oxford New York, pp 161-169
- Coquery J-M, Coulmance M, Leron M-C (1972) Modifications des potentiels évoqués corticaux somesthésiques durant des mouvements actifs et passifs chez l'homme. *Electroencephalogr Clin Neurophysiol* 33: 269-276
- Fromm C, Evarts EV (1978) Motor cortex responses to kinaesthetic inputs during postural stability, precise fine movements and ballistic movements in the conscious monkey. In: Gordon G (ed) *Active touch*. Pergamon Press, Oxford New York, pp 105-118
- Garland HT, Angel RW (1974) Modulation of tactile sensitivity during movement. *Neurology* 24: 361
- Giblin DR (1964) Somatosensory evoked potentials in healthy subjects and in patients with lesions of the nervous system. *Ann NY Acad Sci* 112: 93-142
- Hulliger M, Nordh E, Thelin A-E, Vallbo ÅB (1979) The responses of afferent fibres from the glabrous skin of the hand during voluntary finger movements in man. *J Physiol (Lond)* 291: 233-249
- Johansson RS, Vallbo ÅB (1979) Detection of tactile stimuli: thresholds of afferent units related to psychophysical thresholds in the human hand. *J Physiol (Lond)* 297: 405-422
- Laskin SE, Spencer WA (1979) Cutaneous masking. I. Psychophysical observations on interactions of multipoint stimuli in man. *J Neurophysiol* 42: 1048-1060
- Moberg E (1983) The role of cutaneous afferents in position sense, kinaesthesia, and motor function of the hand. *Brain* 106: 1-19
- Ochoa J, Torebjörk E (1983) Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand. *J Physiol (Lond)* 342: 633-654
- Papakostopoulos D, Cooper R, Crow HJ (1975) Inhibition of cortical evoked potentials and sensation by self-initiated movement in man. *Nature* 258: 321-324
- Rauch R, Angel RW, Boylls CC (1985) Velocity-dependent suppression of somatosensory evoked potentials during movement. *Electroencephalogr Clin Neurophysiol* 62: 421-425
- Rushton DN, Rothwell JC, Craggs MD (1981) Gating of somatosensory evoked potentials during different kinds of movement in man. *Brain* 104: 465-491
- Seyal M, Ortstadt JL, Kraft LW, Gabor AJ (1987) Effect of movement on human spinal and subcortical somatosensory evoked potentials. *Neurology* 37: 650-655
- Schady WJL, Torebjörk HE (1983) Projected and receptive fields: a comparison of projected areas of sensations evoked by intraneural stimulation of mechanoreceptive units, and their innervation territories. *Acta Physiol Scand* 119: 267-275
- Schmidt RF, Torebjörk HE, Schady WJL (1989) Gating of tactile input from the hand. II. Effects of remote movements and anaesthesia. *Exp Brain Res* 79: 103-108
- Stevens SS (1975) *Psychophysics: introduction to its perceptual, neural and social prospects*. Wiley, New York
- Torebjörk HE, Ochoa JL (1980) Specific sensations evoked by activity in single identified sensory units in man. *Acta Physiol Scand* 110: 445-447
- Torebjörk HE, Vallbo ÅB, Ochoa JL (1987) Intraneural microstimulation in man. *Brain* 110: 1509-1529
- Vallbo ÅB, Hagbarth K-E (1968) Activity from skin mechanoreceptors recorded percutaneously in awake human subjects. *Exp Neurol* 21: 270-289
- Vallbo ÅB, Olsson KÅ, Westberg K-G, Clark FJ (1984) Microstimulation of single tactile afferents from the human hand: sensory attributes related to unit type and properties of receptive fields. *Brain* 107: 727-749

Received November 14, 1988 / Accepted July 27, 1989