Activity from Skin Mechanoreceptors Recorded Percutaneously in Awake Human Subjects

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A technique is described which allows recording of multi-fiber discharge and single-unit activity from intact peripheral nerves of awake human subjects. A tungsten electrode with a tip diameter of 5-15 μ was driven manually through skin, subcutaneous tissues and nerve sheath. From many recording sites in mixed nerve trunks neural impulses with an amplitude of 40 μv were recorded in response to peripheral mechanical stimuli. It was possible to judge when afferent nerve fibers of cutaneous origin lay close to the electrode tip by the quality of the insertion paresthesias and the type of peripheral stimuli required to induce afferent responses. Examples are presented of fast and slowly adapting mass discharge induced by mechanical stimuli on glabrous and nonglabrous skin areas. When single-unit activity was discriminated it was often possible to determine the site of the cutaneous end organ, the discharge characteristics of the unit, and the conduction velocity of the nerve fiber. Ten such single-unit recordings are described.

Introduction

As pointed out by Hensel and Boman (11) our present knowledge of cutaneous sensibility is largely based upon two quite different types of information: those obtained from neurophysiological investigations on animals, and those derived from psychophysical experiments on human subjects. A method which allows recording of afferent impulses in man with intact sensation implies a possibility to establish a connection between these two types of information in at least two different ways. First, it would be possible to define the physiological properties of human cutaneous receptors and to determine whether or not the human skin is supplied with the same type of receptors as other mammals. Second, it would be possible to relate the afferent nerve activity to the sensations experienced by the subject during the experiment.

Compound action potentials evoked by electrical stimuli can be recorded from human peripheral nerves with surface electrodes or needle electrodes inserted in the vicinity of the nerve (e.g., 1, 3). It has also been shown

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that the nerve discharge elicited by a tap on a finger nail can be recorded with this technique (17), but on the whole it seems that nerve activity induced by natural stimuli is too dispersed in time to be detected by such crude methods (6). In some investigations dispersed activity in human nerves has been studied by recording from the cut end of a peripheral nerve (4, 5, 11). However, the surgery required limits the practical value of such recording methods in man. In the present paper a simple method is described which allows percutaneous recording of dispersed sensory nerve impulses evoked by physiological stimuli in subjects with preserved sensation of the peripheral events. The technique is described in some detail. Activity from skin afferents in response to various types of mechanical stimuli is shown and some psychophysical aspects of the findings are considered. A microelectrode technique for percutaneous recording of nerve impulses in man has been described (15) since some of the preliminary results obtained in the present series of investigations were first reported (7, 20).

Methods

Thirty-three experiments have been performed in this series of investigations on two healthy male adults (the authors). Activity was recorded from the following nerves: the peroneal nerve at the knee joint level, the tibial nerve in the popliteal fossa, the ulnar nerve at the elbow, the median nerve about 5 cm proximal to the elbow, and the superficial branch of the radial nerve about 2 cm proximal to the wrist. In all, about one thousand penetrations have been made of these various nerves and activity has been studied from approximately 130 recording sites. Cutaneous mechanoreceptor activity was analysed from 40 recording sites. Such activity was encountered in another 50–100 recording sites, but in these cases it was not investigated in detail because the signal-to-noise ratio was too low. Activity in muscle nerves will be described in other papers (9, 21).

Recording Electrodes. Electrodes were made of 0.2-mm diameter tungsten wires, pointed electrolytically (13) to a tip diameter of 5–15 μ. The length of the taper was at least 4 mm. Electrodes with shorter taper were found to give more painful paresthesias. Insulating lacquer (Voltalac 435) was applied according to the method suggested by the manufacturers. This involved dipping the electrode in the lacquer six or eight times and baking at 200 C for successively longer periods (15–60 min). Several other lacquers were tried, but they were not found suitable since the coating did not resist the mechanical strain during the experiment but broke at the tip. The insulation was checked by applying 3.5-v alternating current to the electrode immersed in 0.9% sodium chloride solution

\(^2\) Voltalac 435 was kindly supplied by Standard Varnish AB, Gothenburg, Sweden.
containing a small amount of detergent. A stream of gas bubbles indicated uncoated areas. Many of the electrodes did not have a bare tip after the coating and in these cases the lacquer was removed from the distal portion of the tip by forcing 6.0–8.0 V alternating current through the electrode for a few seconds. The impedance of the electrodes at 1000 Hz was 10–50 kohm. A similar tungsten needle coated to within 3 mm from the tip was used as the indifferent electrode. A 0.2-mm diameter insulated copper wire was soldered onto the tungsten electrode for connection with the amplifier.

**Recording and Display System.** The recording electrodes were connected to the inputs of an a-c differential preamplifier with an input resistance of 10 Mohm (Tektronix 122). The band width was limited to 300 Hz–10 kHz (−3 db). The grid current was checked occasionally and kept to a minimum. The signals from the preamplifier were fed into a tape recorder, an oscilloscope, and an audioamplifier connected to a loudspeaker. The tape recorder (Precision type 6204) had three data channels with direct and FM recording systems selectable and one channel for voice recording which was used for comments and protocol. Nerve activity was recorded with the direct system which had a frequency response of 50 Hz–10 kHz while the frequency response of the FM system was dc–1 kHz at the tape speed used (95 mm/sec). After the experiment the signals stored on the tape were displayed on an oscilloscope screen (Tektronix 502 A or 565 with one four-beam chopper plug-in unit 3A74 and one plug-in unit 2A63). The tape recorder gave some noise mainly of low frequency which was eliminated by a RC-filter. The events displayed on the oscilloscope were photographed with a Grass camera (Model C 4).

**Mechanical Stimulations.** Local taps and pressure were exerted with the point of a small cone or the flat end of a cylindric rod with a diameter of 4 mm, both made of Perspex. These probes were attached to a small mechano-electrical transducer with two strain gauges connected to a carrier amplifier. The experimenter held the transducer by a handle and mechanical stimuli were conveniently applied to any skin area while an analogue signal of the force was obtained. The system had the disadvantage that it was difficult to apply successive stimuli on exactly the same point and it was not possible to reproduce accurately a stimulus with respect to force and time course. Two types of mechanical vibrator were used. One was a dental vibrator: a small hammer (1 mm diameter) at the end of a mouthpiece was beating at a maximum frequency of 800 cycle/sec. The amplitude of the vibrations varied to some extent with the force by which the mouthpiece was pressed against the tissues, but it did not exceed 0.3 mm. Vibrations of higher amplitude (up to 1 mm) and lower frequency (maximum 200 cycle/sec) were obtained by exchanging the
hammer for a ball-bearing attached excentrically to the rotating axis at the mouthpiece. The contact area between the ball-bearing and the skin was about 1 cm². Several other types of mechanical stimuli were used such as light strokings with a piece of cotton wool, v. Frey hairs and light air puffs. The skin area from which the recorded nerve signals originated was mapped with mechanical stimuli. The weakest possible stimulus was used in each case in order to avoid error due to spread of skin deformation. However, the aim was to obtain a fair estimate of the area but not to define its exact borderlines. The term "innervation zone" will be used to denote the area determined by such tests.

**Electrical Stimulations.** Pulses for electrical stimulation of nerve trunks were delivered from a commercial stimulator (Disa type 13G04). Surface or needle electrodes were used. The former consisted of two felt cushions 1.8 cm apart soaked in sodium chloride solution. The needle electrodes were similar to the recording electrodes, but about 3 mm of the tip was free from insulation. The surface electrodes described above were also used for electrical stimulations of nerve fibers within the innervation zones.

**General Procedure.** The subject was lying down or sitting in a resting position with firm support under the limb to be exploited. No special arrangements were used for fixation of the limb. The position of the nerve was determined as carefully as possible by palpation and electrical stimulation with surface electrodes. The recording electrode was inserted manually, the conductor of the experiment holding the electrode between his finger tips or with a pair of tongs. Micromanipulators or other special mechanical devices were not used. When the nerve to be studied was situated deeply below the skin—e.g., the tibial nerve in the popliteal fossa—a needle electrode was inserted for electrical stimulations and the optimum position was determined. The recording electrode was then introduced in parallel with the stimulating needle and to the same depth. The recording electrode was left in its position without support except from the surrounding tissue. This simple arrangement proved adequate; occasionally single-unit recordings were maintained for up to 1 hour. Muscle activity picked up by the electrode was easily recognized by the comparatively long duration of the individual discharges.

**Precautions.** The subjects had a full vaccination protection against poliomyelitis. The electrodes were kept at 200 C for an hour after the final coating, and afterwards they were not touched before the experiment. The skin surface and the electrodes were cleaned immediately before the experiment started with 99% alcohol to which 0.1% iodide was added.

**Results**

When inserting the needle electrode into the ulnar nerve at the elbow, one could easily feel when the electrode tip penetrated through the dense
nerve sheath, and at that moment the subject usually experienced sudden paresthesias within some restricted area of the ulnar nerve receptive field. When searching for other nerves, not surrounded by such dense fibrous structures, one was mainly guided by the paresthesias which obviously occurred when nerve fibers were mechanically irritated by the electrode tip. The paresthesias lasted only a few seconds. At the very moment when they were noticed the tracing on the oscilloscope screen broadened (Fig. 1, cf. A and B) and the sound from the loudspeaker increased abruptly to a new level indicating a change of the situation at the electrode tip. Sometimes the movement of the electrode induced distinct injury bursts of short duration or a few fasciculations which could be seen through the skin, or both. Attention was paid to all these signs—paresthesias, fasciculations, and the signals from the amplifier—and the electrode position was adjusted accordingly. Still, it was a tedious task to attain a good and reasonably stable recording situation, and quite often the electrode unexpectedly slipped out of a promising position.

The paresthesias were of two different types. Either there was a distinct sensation of pin pricks superficially in the skin within a rather well defined area, or there was a dull aching sensation in deeper structures. In the latter case the area could not be as well defined, but a region of maximum intensity could usually be determined. As a rule, activity from skin mechanoreceptors could be picked up when movement of the electrode had elicited distinct paresthesias of the superficial type whereas activity from muscle receptors was seen in the other case. However, several factors were considered before it was finally decided which type of activity was present: (a) the character of the paresthesias and the occurrence of fasciculations, as mentioned above; (b) the nerve response to air puffs, light touch and pressure on the skin; (c) the neural events accompanying muscle contractions and passive joint movements; (d) the spontaneous activity. When spontaneous activity was seen in skin nerves it was found to be continuous and nonperiodic (Fig. 1 B), whereas a periodic, spontaneous activity was present in practically all recordings from muscle nerves as will be described in another report (8). In some cases it was still not possible to ascertain whether the activity originated exclusively from deep structures and sometimes activity of both types was clearly recorded simultaneously. However, in the 40 recordings upon which the present study is based there was no doubt that the induced activity originated from receptors in the skin or closely beneath the skin?

The nerve activity appeared in most cases as a dense succession of deflections of various amplitudes with the most conspicuous phase in negative direction (downward deflections in the figures). Examples are shown in Figs. 1-3 and 6. It was not possible to identify repetitive impulses from a
single nerve fiber in this type of recordings. The signals presumably represent impulses recorded extracellularly from a large number of intact nerve fibers and this type of activity will be referred to as “mass discharge.” There was a considerable variation in signal-to-noise ratio from one recording to the other. The maximum peak-to-peak amplitude of mass discharge recordings was about 40 μv.

Occasionally another type of nerve signal was encountered which consisted of diphasic deflections with the first and the most conspicuous phase in positive direction. Examples are shown in Figs. 4, 5, and 7. The deflections were fairly uniform in size and shape, and the number of such deflections per unit time was usually less than in case of mass discharge recordings. The amplitude was generally greater although the maximum amplitudes encountered were about the same in the two types of record. The polarity and the shape of these signals suggest that they represent impulses from fibers which had been damaged by the electrode tip. In many cases, when this type of activity appeared, repetitive impulses from a single nerve fiber could be identified and studied: the size and the shape of the deflections were as uniform as can be expected considering the noise level and the spike intervals were regular or smoothly changing with the stimulus (Figs. 4, 5,). However, during the course of the experiment the spike amplitude often decreased continuously (Fig. 5) until finally the unit disappeared in the mass discharge. This type of recording will be referred to as “single-unit” discharge.

The innervation zones, as defined in methods, were 20–40 cm² in case of mass discharge recordings on the nonglabrous skin. Two examples are shown in Figs. 1 and 6. The innervation zones on the glabrous skin were often somewhat smaller. In typical cases, activity was picked up from the distal two-thirds of the volar surface of two or three digits. The innervation zone was always but a part of the total area supplied by the nerve. The area from which single-unit activity could be elicited by threshold stimuli was considerably smaller (0.25–2.0 cm²) than the innervation zones in case of mass discharge recordings.

Mass Discharge. This type of activity is illustrated by the recordings shown in Figs. 1, 2, and 3 which are all taken from the same experiment and recording site in a cutaneous nerve bundle in the popliteal fossa. Signal to noise ratio was unusually high in this case. The innervation zone, indicated by the black area in Fig. 1, was situated on the dorsal aspect of the leg over the calf muscles and the size of this area was approximately 40 cm². In Fig. 1 A is shown the noise of the total recording and display system in this experiment. The two needle electrodes had been inserted through the skin and their uncoated tips were in the subcutaneous tissues. It can be seen that the peak-to-peak amplitude of the
FIG. 1. Nerve activity recorded percutaneously from a cutaneous nerve bundle in the popliteal fossa. A: Noise of the recording and display system. Electrode tip in the tissues surrounding the nerve. B: Spontaneous activity. Electrode tip inside the nerve sheath. C: Activity induced by two light puffs of air. D: Activity induced by four light strokings with cotton wool on the epidermal hairs. Black area indicates innervation zone and small circle the point of remote stimulations (see text and legend Fig. 3). The downward deflections indicate negative signals at the intraneural electrode in this and all other figures. Records in Figs. 1, 2, and 3 from the same experiment and recording site. Calibrations. Nerve signal amplitude: 20 μv, applies to A-D. Time: 5 sec for A and B; 1 sec for C and D.

noise was about 10 μv. In Fig. 1 B, is shown a recording taken while the indifferent electrode was in the same position as before whereas the other electrode had been driven through the nerve sheath. This recording was made about 10 min after penetration of the nerve sheath when the subject experienced no paresthesias. It can be seen that the peak-to-peak amplitude is greater in B (about 20 μv) than in A, and, further, that the downward deflections (negative signals) are more prominent than the upward deflections, indicating that the record is composed of some signals and not merely random noise. The same assymmetry was found when there was
definite evidence of nerve activity induced by mechanical stimulations (e.g., Fig. 1 C). It therefore seems justified to conclude that nerve impulses were recorded in B. This activity was continuous, there were not any appreciable fluctuations with time, and it was present without stimulation of any kind being exerted. Furthermore, the subject did not experience any particular sensation within the innervation zone such as chill, heat, or mechanical strain; i.e., the situation was completely indifferent from the perceptive point of view. We have therefore used the term “spontaneous” nerve activity. This activity could be affected by a preceding mechanical stimulation. This can be seen most clearly in Fig. 2 B, left. Immediately after the period of heavy discharge induced by vibratory stimuli the spontaneous activity was much less prominent than in Fig. 1 B which shows the spontaneous activity on the same time scale. A rough test of

![Graphs showing nerve activity and stimuli](image-url)
the effect of temperature was done several times. The skin was heated with a microscope lamp or a burning match by which the skin temperature was increased quite rapidly up to or just below the pain threshold. This was not associated with any clear change of the spontaneous activity.

A spontaneous activity of this type was seen clearly just in two experiments (illustrated in Figs. 1–3 and 6), in which recordings were done from nonglabrous skin and the signal-to-noise ratio was particularly high. It was never observed when recording from the glabrous skin. However, in practically all experiments the tracing on the oscilloscope screen was broader when the electrode tip was in the nerve than when it was in the surrounding tissues. The difference was often small and an asymmetry in the record, as described above, could not be seen. It therefore could not be finally determined whether the important factor was simply a change of the noise level or if, in fact, a spontaneous nerve activity was present in most cases.

Both fast and slowly adapting mass discharge could be induced by mechanical stimuli on nonglabrous skin areas. However, the fast adapting activity was particularly striking, and the slowly adapting discharge could be studied only when the signal-to-noise ratio was high as in the experiment illustrated in Figs. 1, 2 and 3. In this case, pronounced discharge appeared in response to very light stimuli, which did not give any skin deformation, such as merely the rapid bending of the hairs with light air puffs and light strokings with a piece of cotton wool (Fig. 1 C and D). A short burst of impulses appeared when a single hair was briefly bent (Fig. 2 C, left). The stimulus is indicated diagrammatically by the horizontal bars below the tracing of the nerve activity. Thus it is obvious that activity could be recorded from hair-follicle units. It could not be shown whether these units adapted quickly to zero frequency as in other mammals, but they were clearly very sensitive to hair movements; i.e., they had a high dynamic sensitivity. Tapping of the skin surface elicited distinct bursts of nerve impulses, whereas sustained pressure induced a continuous activity with marked on- and off-discharges (Fig. 2 A). The sustained activity in response to a hard pressure was not more intense than the phasic discharge elicited by light air puffs (cf. Fig. 2 A, right, and Fig. 1 C). The activity shown in Fig. 2 B, left, was induced by vibratory stimuli applied to an area of about 1 cm² in the center of the innervation zone. The frequency of the vibrations was 100–200 cycle/sec. and the amplitude 0.5–1.0 mm. It seems that vibrations of this type must be quite an effective stimulus for fast adapting, low-threshold mechanoreceptors, and in fact, the response recorded from the nerve trunk was the most pronounced activity seen in this experiment. The response was quite powerful also from the perceptive point of view: the subject had an intense
experience of vibration over an area corresponding roughly to the whole innervation zone as indicated in Fig. 1. The activity shown in Fig. 2 B right, appeared when the vibrator was held 2–3 mm above the skin surface. This induced movements of hairs mainly through direct contact with the vibrator but to some extent also from air currents around the rotating ball-bearing. The sensation was of course much less intense in this case and it was of quite a different quality compared to the sensation induced by vibrations on the skin surface. It is seen that the neural response was moderate compared to the discharge shown in Fig. 2 B, left. This test seems to indicate that much of the activity in Fig. 2 B, left, originated from hair receptors. The innervation zone, indicated in Fig. 1, was mapped by lightly stroking the epidermal hairs with a piece of cotton wool. The receptive field for taps and pressure of moderate intensity was much larger. It included the major part of the calf as well as the lower part of the thigh. It was observed that such stimuli were efficient only when the deformation of the tissues at the point of stimulation was large enough to cause a visible stretching of the skin within the innervation zone. Examples of activity induced by such remote stimuli are given in Fig. 3, which shows response to taps and sustained pressure on a point (indicated by the small circle in Fig. 1) about 10 cm distal to the margin of the innervation zone. Both fast and slowly adapting activity is apparent. The most pronounced response to such distant stimuli was seen when the skin on the anterior surface of the leg was pulled slightly sideways. In addition, passive or active movements of the ankle joint induced a discharge presumably due to a small skin displacement in the upper calf region (Fig. 2 C, right). Obviously the receptors initiating this type of activity were extremely sensitive to skin stretching and at least some of them were slowly adapting.
For the subject himself, it was striking to note that, whereas he could easily feel and localize the weakest touch stimuli within the innervation zone as well as the remote mechanical impacts, he could not determine whether these remote impacts were accompanied by a mechanical change within the innervation zone. This aspect will be further considered below (p. 283).

Mass discharge from glabrous skin areas induced by mechanical stimuli was similar to that from nonglabrous skin, but activity induced by remote stimuli was not observed, nor was spontaneous activity—of the type described above—apparent.

**Single Unit Recordings.** Activity from single nerve fibers could often be discriminated, but in the majority of such cases the recording situation deteriorated within a minute or less. It was therefore not possible to obtain much information about the receptor. Sometimes, however, single units could be studied for a period long enough to determine the site of the end organ, the discharge characteristics of the unit, and the conduction velocity of the nerve fibers. It was possible to make more detailed analyses of ten sensory units with receptors located in the skin or closely beneath the skin.

Two of these units will be described in some detail. The discharge of a fast adapting unit from the end phalanx of the index is shown in Fig. 4. Taps and sustained pressure evoked pure phasic responses and a fast decrease of the local pressure was almost as effective as an increase. Vibratory stimuli applied to the most sensitive spot could drive this unit with a maximum frequency of about 300 impulse/sec and a minimum regular frequency of about 50 impulse/sec (Fig. 4 C). About the same maximum discharge frequency could be evoked by a single tap. The sensitivity of this unit was not extremely high: the receptor was not activated by the minimum stimulus which could be perceived by the subject and it can be seen that a single impulse was elicited by a stimulus which reached a peak of approximately 0.05 newton (Fig. 4 A). The stimulus was effective within a fairly small area and remote stimuli or vibrations did not activate this receptor (16). In the upper record of Fig. 4 D one of the mechanically evoked impulses is displayed on an extended time scale. A single impulse of the same shape could be induced by an electric shock on the skin overlying the receptor (lower record in D). Furthermore, no other positive spikes appeared from this recording site and it seems justified therefore to conclude that in this case impulses were recorded from only one nerve fiber. The conduction velocity was calculated from the interval between the electric shock and the impulse. It was in this case 53 m/sec.

An example of a slowly adapting single unit is shown in Fig. 5. The end organ was located in the palm of the hand as indicated by the black dot. The unit fired with a moderate frequency when the fourth finger was
Fig. 4. Impulses of a single nerve fiber. Fast-adapting receptor. Left median nerve. A: Taps. B: Sustained pressure. Stimulus force and time course are indicated by lower trace in A and B. Note that time and stimulus-force calibrations are not equivalent in A and B. C: Vibratory stimuli. Maximum discharge frequency to the left, and minimum to the right. D, upper trace: Mechanically induced impulse. D, lower trace: Electrically induced impulse. Receptor site indicated by black dot. Conduction velocity 53 m/sec. Calibrations. Stimulus force: lower bar opposite A, 0.75 newton; bar opposite B, 3.0 newton. Nerve signal amplitude: upper bar opposite A, 40 μV, applies to A and B; bar opposite C, 40 μV, applies to C. Time: bar below C, 1 sec for B; 0.25 sec for A and C; bar below D, 10 msec.

extended passively to its extreme position (Fig. 5 A). It was noticed during the experiment that this stimulus gave rise to some stretching of the skin at the receptor site. The unit was not activated by isometric contraction of the muscles of the hand. Local pressure was a much more effective stimulus than extension of the digits. The frequency range in response to sustained local deformation was fairly high: the minimum steady frequency was as low as 3.0 impulse/sec and the maximum was about 60
Fig. 5. Impulses of a single nerve fiber. Left median nerve. Slowly adapting receptor. A: Slow passive stretching of the fourth digit to over-extension of the base joint. B: Local pressure. Left: slowly rising and sustained stimulus. About 2 sec omitted at gap. Short record at right: fast rising stimulus. Stimulus force and time course indicated by lower trace. C: Frequency range to sustained stimulus. Receptor site indicated by black dot. Conduction velocity 40 m/sec. Calibrations. Nerve signal amplitude: 20 μV, applies to all records. Stimulus force: 10.0 newton. Time: 1 sec. Stimulus in C was in upper left, passive stretching of the fourth finger (as in A); in the other records, local pressure; force 5.4 newton in upper right; 7.7 newton in lower left; and more than 15.0 newton in lower right.

The impulse/sec (Fig. 5 C). The forces involved when this unit was activated were quite high (see legend, Fig. 5). The impulse frequency in response to a rapidly increasing pressure did not exceed 25 impulse/sec (Fig. 5 B, right). Thus, the dynamic sensitivity was quite poor. The notion that the end organ was located superficially is strongly supported by the fact that this unit could be stimulated by an electric shock of moderate intensity through a surface electrode on the most sensitive spot for mechanical stimuli. The conduction velocity of the nerve fiber determined from the latency of the electrically evoked impulse was 40 m/sec.

The main findings obtained in the ten single unit recordings can be summarized as follows: The end organs of seven of the ten units were
located on the volar or the lateral-volar surface of the end phalanx of the fingers. Three of these pulp units were fast adapting, whereas four of them were slowly adapting. The other three receptors were located, one distally on the dorsal aspect of the fourth toe (fast adapting), one (slowly adapting) in the palm of the hand (Fig. 5) and one (fast adapting) on the ventrolateral aspect of the leg, over the anterior tibial muscle. Thus, five of the ten units were fast adapting and five were slowly adapting. The dynamic sensitivity of four of the slowly adapting units was fairly pronounced. The unit illustrated in Fig. 5 had a considerably lower dynamic sensitivity than all the other units tested. The maximum discharge frequency seen in the whole investigation was about 300 impulse/sec (Fig. 4 C) (11) and the minimum steady frequency was about 3.0 impulse/sec (Fig. 5 C). None of the single units was spontaneously active (11). Activity was not encountered from single units which had an extremely high sensitivity to vibrations and remote stimuli as the receptor described by Lindblom and Lund (16) in the monkey foot, and none of the single units were excited by the minimum mechanical stimulus which could be perceived (11). The nerve conduction velocity of three single sensory units was determined. Two of these were described in detail (Figs. 4 and 5). Another fast adapting unit with the end organ in the pulp of the fourth finger had a conduction velocity of 45 m/sec.

Neural Response and Perception. In most cases there was a fair correspondence between the intensity of the induced neural response and the intensity of the subjective experience of the peripheral events. Thus, a slight sustained pressure, which was relatively difficult to perceive, evoked a weak mass discharge, while the pronounced neural responses to taps were accompanied by more distinct experiences. Further, light strokings within the receptive field resulted in a comparatively heavy discharge in the nerve and such a stimulus was also more clearly perceived than sustained touch and pressure of moderate intensity. However, when activity from nonglabrous skin was recorded there was not always such a correspondence between the neural discharge from a particular skin area and the subject's experience from the same area. A pronounced activity could sometimes be recorded when a mechanical stimulus was applied at a point some distance from the innervation zone provided the stimulus was strong enough to give some stretching of the skin within this zone. In many such cases the subject did not have any experience whatsoever from the innervation zone even when his attention was directed to this area. Figures 2 C, right, and 3 show examples of nerve activity which was not associated with any psychological experience from the innervation zone. The stimuli were active flexions and extensions of the ankle joint (Fig. 2 C), and taps and sustained pressure at a point 10 cm from the border of the innervation zone.
(Fig. 3). The point of local stimulation is indicated by the small circle in Fig. 1. These neural responses might be compared with the discharge evoked when one of the hairs in the middle of the innervation zone was suddenly bent (Fig. 2 C, left). In this case the discharge was quite small, but the sensation was rather distinct and the stimulus could be quite well localized. Figure 6 C presents another example of intense discharge in a skin nerve, not associated with any distinct cutaneous sensation. The recording was obtained from the superficial branch of the radial nerve at the wrist, the innervation zone being an area on the dorsum of the hand, the thumb and the index. Activity in response to taps and weak strokings within this area was pronounced (Fig. 6 A and B) and these peripheral stimuli were easily perceived. Quite substantial discharges were evoked also by fast, active flexions and extensions of the base joint of the fingers (Fig. 6 C). Such maneuvers caused distinct movements of the skin.

Fig. 6. Activity from the superficial branch of the left radial nerve. A: Spontaneous activity and response to taps applied to a 12 mm² area. Stimulus force and time course indicated by lower trace. B: Light strokings with fingertips within the innervation zone. C: Fast voluntary flexion and extension of the metacarpo-phalangeal joint. Innervation zone indicated by hatched area. Calibrations. Stimulus force: bar opposite A, 1.0 newton. Nerve signal amplitude: bar opposite B, 20 μv, applies to all records. Time: 0.5 sec.
MECHANORECEPTORS

Fig. 7. Activity from left median nerve. Fast-adapting receptor response to different surface textures. A: Strokings with the smooth surface of a match-box. B: Similar strokings with the abrasive surface of a match-box. Innervation zone about 10 mm² on dorsolateral aspect of the end phalanx of the index. Calibrations. Nerve signal amplitude: 20 µv. Time: 1 sec.

within the innervation zone, but the nerve discharges were not associated with any definite sensations from the skin. It is possible that deep receptors participated in these neural responses (18, 19), but the findings stress that afferent activity in skin nerves is not necessarily associated with distinct sensation from the skin.

It seemed that it would be of interest to correlate the neural discharge with the sensory experience in response to a situation which is common in everyday life although the stimulus is difficult to define in physical terms. An example of this kind of test is shown in Fig. 7. The neural response of a group of fast adapting receptors in a finger pulp was recorded. In A, the stimulus was light strokings with the smooth surface of a match box, and in B, strokings of a similar rate and pressure with the abrasive surface. It is seen that the receptor response was much more pronounced in the latter case. The difference in texture could be very well distinguished by the subject in this test.

Discussion

The method described in the present investigation was developed to achieve a means of recording dispersed activity from peripheral nerves in awake human subjects without surgical procedures or significant injury to
the nerve. Furthermore, it was considered essential that the technique should be simple, that the procedures involved were not too painful for the subject and that recordings could be done from many nerves, not merely from one or two which were readily accessible. It seemed that percutaneous insertion of a needle electrode would be the only method which could possibly satisfy these requirements.

One of the major problems—expected and encountered—was to insert an electrode with a small tip diameter through the tissues without serious damage to the point. If the point of the electrode was smaller than 5-15 μ it was easily broken or bent. Several insulating lacquers were tried. Most of them did not stick to the tungsten surface well enough, but broke at the tip when the electrode was driven through the tissues. The penetration of the skin, subcutis, and nerve sheath was done in the simplest possible way. However, the electrode tip, both metal point and insulating lacquer, was not always sufficiently tenacious to withstand this treatment, and it was frequently found that the tip had been damaged during the experiment. A few attempts were made with a slightly different technique involving penetration of the skin and the subcutaneous tissues with a hypodermic needle surrounding and protecting the electrode tip. However, this introduced several technical problems and made the experimental procedure more complicated, which was a great disadvantage.

Another major problem was the sensitivity of the system to movement. Systems involving rigid fixation of the microelectrode to an external point, e.g. by means of a micromanipulator, were not tried. On the contrary, the idea was that the electrode should be floating in the tissues, which would in principle allow movements of the limb with reference to the surroundings. As the connection to the amplifier, a very light copper wire was used in order to minimize the tendency of electrode tilting. It was found in preliminary tests that tungsten electrodes were very sensitive to any movement between the tissues and the uncoated electrode tip: such movements gave rise to large artifacts in the recordings. This effect was quite prominent when rigid tungsten needles were used (diameter about 0.5 mm), but not when the needle was more flexible. The reason for this was probably that the electrode shaft did bend to some extent when there were movements between the superficial and deeper layers of the tissues. Associated with the flexibility of the electrode was one disadvantage, however: the route of the electrode tip through the tissues was often slightly curved and it was, therefore, more difficult to judge the position of the tip and to make the correct adjustment. Thus, the size of the electrode was a compromise with respect to both tip and shaft diameter.

It seems that the method of recording from intact limb nerves in awake human subjects opens—in principle at least—two new and significant
possibilities: one is to relate afferent discharge to sensations, and the other, is to study proprioceptive inflow in an intact preparation during various types of complex motor behavior. In practice, the usefulness of the method is highly dependent upon such factors as the stability of the experimental situation and the sensitivity to mechanical disturbances. It was found in the present investigation that activity could be recorded continuously from one recording site for several hours if movements were avoided as much as possible. As a rule the experimental situation also allowed various kinds of mechanical stimulations as well as joint movements. A few examples of cutaneous activity induced by joint movements are given in the present investigation and it will be shown in subsequent papers what kind of information can be obtained concerning proprioceptive activity (9, 21).

It seems that the technique would be more useful if the signal-to-noise ratio could be improved and especially if activity from single nerve fibers could be discriminated more easily. Modifications of the method in order to approach such aims probably require systematic studies of various technical problems concerning, e.g., the structures mainly responsible for the effective recording resistance, electrode characteristics favoring single unit recordings etc. It was recently shown by Knutsson and Widén (15) that metal microelectrodes with a tip diameter of about 1 μ can be driven percutaneously into human nerves by means of a micromanipulator and it seems that the signal-to-noise ratio is higher with this technique. The report in which the method is described does not, however, give a very clear picture of the possibilities offered by this technique.

No serious complications have occurred and no enduring symptoms of neuropathy have been noted during the 2 years since this series of investigations started (October, 1965). Moderate temporary paresthesias occurred during 1 or 2 weeks following an experiment. The paresthesias appeared especially when the nerve was stretched or when local pressure was applied on the point where the needle had been inserted. EMG-recordings have revealed no signs of denervation. The absence of serious complications so far does, of course, not mean that the over-all risks are negligible. The experience is probably still too limited to exclude that, e.g., intraneural bleeding or infections might occasionally occur.

A conspicuous spontaneous activity was seen in some recordings from nonglabrous skin. In animal experiments it has been shown that at least two types of cutaneous sensory unit may be spontaneously active: one type is temperature receptors (10, 12), the other is a mechanoreceptor described by Iggo (14), and Chambers and Iggo (2), and designated type II slowly adapting mechanoreceptor. Spontaneously active temperature receptors have also been found in human skin (11). It was shown in the present investigation that the spontaneous activity could be modified by
mechanical stimulation. The activity was less pronounced immediately after a period of heavy discharge induced by mechanical vibrations, whereas—as judged by a somewhat crude test—it was not affected by temperature changes. It seems justified therefore to conclude that the spontaneous activity originated mainly from mechanoreceptors. The type II slowly adapting mechanoreceptors (2, 14) are very sensitive to stretching of the skin and to remote mechanical stimuli, they are slowly adapting and have a high dynamic sensitivity. In the present investigation a pronounced discharge could be induced by remote mechanical stimuli—stretching of the skin being particularly effective. The discharge consisted of both sustained activity and bursts at the start and the end of the stimulus. The spontaneous activity as well as the response to remote stimuli may thus well be explained as impulses from type II slowly adapting mechanoreceptors. However, it should be pointed out that there is no direct evidence in the present investigation that the spontaneous activity and the phasic and tonic response originated from the same type of receptors. The view proposed here is merely a way of arranging the information in a simple pattern that fits with the findings from animal experiments.

The mechanoreceptor activity associated with remote stimuli did not necessarily give rise to any sensation even when the nerve activity was fairly pronounced. It remains to be shown whether activity from a certain type of mechanoreceptor does not give rise to any sensation, or whether a central regulation of sensory transmission, such as surround inhibition, might be a significant mechanism behind these findings.

The neural response of a group of fast-adapting mechanoreceptors in a finger tip to stroking of the skin with the smooth surface of a matchbox was compared with the response to similar stroking with the abrasive surface. The difference in surface texture was clearly distinguished by the subject. The neural response was also quite different in the two cases and it seems likely that the impulses from these receptors were significant for the perception of the stimulus. In every-day life mechanical stimuli often include movements between the skin surface and an object. In fact, the ability to appreciate a surface texture is very poor when there is no such movement, whereas it is remarkably improved when there is a sliding between the two surfaces. The findings described above illustrate that fast-adapting mechanoreceptors may be of paramount importance for the information obtained in such everyday situations.

References