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Response of Rapidly and Slowly Adapting Mechanoreceptors and Vibratory Sensitivity in Human Hairy Skin* **

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Summary. Single unit activity was recorded percutaneously with microelectrodes from 38 rapidly adapting (RA) mechanoreceptors of the dorsal surface of the hand in 49 awake human subjects. Tuning characteristics were determined for 28 RA-fibers at various frequencies between 5 and 100 cps of sinusoidal mechanical stimulation. In separate experiments human thresholds of vibration perception were studied under comparable conditions.

Several RA-mechanoreceptive fibers were broadly tuned, showing no clearly defined best frequency in the range between 5 and 20 cps. Other RA-fibers had a minimum of sensitivity between 20 and 40 cps. For either lower or higher frequencies, stronger stimuli were required to elicit one nerve impulse per stimulus cycle. These RA-receptors may be related to the perception of low frequency oscillation (flutter). They cannot account for human vibration sensitivity in the higher frequency range, since tuning of the receptors required considerably higher amplitudes than perception.

Sixteen slowly adapting (SA) mechanoreceptors of Type I and II showed a frequency modulation in phase with low frequency mechanical oscillations of stimulus amplitudes far below human thresholds for perception of movement.

Key words: Microelectrodes – Human nerve fibers – Mechanoreceptor – Tuning curves – Vibration perception.

INTRODUCTION

During the last decade our knowledge of peripheral skin receptors in human beings has advanced considerably due to the application of electrophysiological techniques, particularly with the use of single-fiber preparations and microelectrode recording. Hensel and Boman (1960), using the microdissection technique, recorded action potentials from single cutaneous afferent nerve fibers in conscious human subjects when mechanical and thermal stimuli were applied to the skin. By use of percutaneously inserted microelectrodes (Vallbo and Hagbarth, 1967), several authors have studied in humans the relation between peripheral stimuli, neural activity, and perception (Vallbo and Hagbarth, 1968; Gybels and van Hees, 1971; van Hees and Gybels, 1972; Torebjörk and Hallin, 1972, 1974; Torebjörk, 1974; Konietzny and Hensel, 1975; Hensel, 1976).

An approximate estimate of the sensitivity of mechanoreceptors to vibratory stimuli in human glabrous skin has been reported by Knibestöl and Vallbo (1970). In more detailed investigations (Knibestöl, 1973, 1975), the response of slowly adapting (SA) and rapidly adapting (RA) single afferents to mechanical ramp stimuli applied to human hairy and glabrous skin has been analyzed. The latter publications are restricted to the relation between stimulus and neural response, no data about perception being available. The same holds for some recent observations of the vibratory sensitivity of RA-receptors in human hairy skin (Järvilehto et al., 1976).

The present investigation was undertaken to determine the response properties of single RA- and SA-mechanoreceptors in the hairy skin of the human hand to vibratory stimuli and to correlate the results with the sensations evoked by the same stimuli in separate experiments. The main questions were whether there are RA-fibers innervating the hairy skin of the human hand which could account for the perception at threshold of low-frequency (5–100 cps) mechanical sinusoids, and whether SA-mechanoreceptors also contribute to the sense of vibration.

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** A preliminary account of a part of these results was presented at the 47th Meeting of the German Physiological Society, Regensburg, 1976 (Konietzny and Hensel, 1976)

METHODS

Recording of Afferent Impulses. The investigations were performed in 49 healthy adults, 18 females and 31 males, aged between 19 and 27 years. The experiments took place in a large shielded cage, the temperature of which was controlled at 23° C, and each experiment usually lasted 4 h. The subjects were lying on a couch. The left arm was abducted and the forearm—radial side up—was embedded in a large block of plasticine. After the superficial branch of the left radial nerve had been located by palpation, the skin was cleaned with a sterilizing detergent (Kodan®) and Hostaflon TF® coated tungsten micro-needles (Konietzny and Hensel, 1974) sterilized in air at 200° C for 2 h, were then manually inserted through the skin into one of the nerve fascicles. No microdriver or any other device was used to further adjust the electrode within the nerve bundles. In most cases the electrode was supported by the surrounding tissues well enough to allow single fiber recordings for more than 1 h.

Another electrode with a tapered portion of about 2 mm, and placed subcutaneously beside the recording electrode, was used as a reference. Neural activity was picked up by a preamplifier with high input impedance, displayed on a storage oscilloscope, controlled by an audiomonitor, and fed into a 6-channel magnetic tape for subsequent processing.

The impedance of the electrodes, tested in physiological saline at 1000 cps, was about 1 MΩ. The conduction velocity of the afferent nerve fibers was calculated from the distance between stimulation and recording point and the time latency to electrical stimulation of the center of the receptive field.

Skin Stimulation. Once a single mechanoreceptive fiber was isolated, its identification in terms of stimulus parameters was carried out using wooden rods, thin steel needles and v. Frey hairs, and the receptive field size was marked on the skin. The device used for quantitative mechanical stimulation of the skin was a feedback-controlled moving coil vibrator[1] carrying on its moving coil a 1-mm-diameter Plexiglas probe with a flat tip. The operation principle was similar to that described by Werner and Mountcastle (1965), allowing load-independent mechanical stimulation with defined waveforms. A photoelectric transducer gave the feedback signal which was proportional to the displacement of the probe. The stimulator delivered ramp, square, and sine waves, or square waves with superimposed sine waves. The amplitude of the probe displacement was adjustable in 1-μm steps and the maximum displacement was 2 mm when operating in the square wave mode. The response of the system to a sine wave was 0—1000 cps. Fine control of the position of the tip of the probe relative to the skin surface was provided by an adjustable DC-voltage from a ten-turn potentiometer. The moment when the tip of the probe made contact with the skin was monitored by means of an additional electric circuit. The analogue output signal of the mechanical stimulator was stored on a separate channel on tape. By means of a micromanipulator the stimulator could be moved in all directions.

When a single mechanoreceptor was isolated, the stimulating probe was brought into contact with the skin, the flat surface of the tip being parallel with the skin surface and covering approximately the center of the receptive field. A sinusoidal displacement was superimposed on a stepwise indentation of the skin. The amplitude of the indentation was 500 μm and lasted 2000 ms, while the sinusoidal displacement began 200 ms after onset of the step indentation and lasted 1600 ms. The resting position of the probe was checked frequently and adjusted when necessary.

The sensitivity of mechanoreceptive fibers to mechanical oscillation within the frequency range of 5—100 cps was studied by determining their tuning curves. A tuning curve is defined as the relation between the amplitude of the sine wave necessary to elicit one nerve impulse per stimulus cycle and the frequency of the sine wave. The amplitude of the sine wave at which one nerve impulse locked in phase with each cycle throughout the full duration of the sinusoidal stimulation period was determined at 5, 10, 20, 30, 40, 60, 80, and 100 cps and measured by visual inspection of the record displayed on a storage oscilloscope.

Sensory Thresholds for Vibration. The vibratory threshold for 10 subjects (3 females and 7 males) was measured with sinusoidal mechanical stimuli delivered to the hairy skin of the left hand at 10, 20, 30, 40, 60, 80 and 100 cps. Of these subjects 5 (2 females and 3 males) had participated in the electrophysiological investigations and their sensory thresholds were determined after a recovery period of about 30 min following the electrophysiological experiments. None of the 10 subjects had had previous experience with the experiments. The 500 μm step indentation of the skin was constantly maintained for 60 s respectively, thus preventing loss of contact with the stimulating probe during the sinusoidal excursions. The time interval between onset of the step indentation and the superimposed sine wave was 1 s. The frequency of the sine wave was presented randomly while the amplitude could be adjusted continuously from 0—500 μm by means of a ten-turn potentiometer by the subject itself.

Estimation of stimulus threshold (*RL*) for oscillatory movement on the skin was achieved by the method of limits (Guilford, 1954). Within each frequency presented, 5 alternate ascending and descending series with respect to the amplitude of the sine wave were made and the threshold determined. The subject was instructed to stop the estimation either when he feels movement on the skin (ascending series) or no movement (descending series). Within a trial each pair of values, one from an ascending and one from the following descending series was averaged and then these averages were averaged. These final values appear in the graphs in Figure 3 (dashed line).

Usually the ascending and descending *RL* values may be different because of certain "constant errors", i.e. the error of "anticipation" (ascending series) and the error of "habituation" (descending series). The purpose of the alternate ascending and descending series is to average out either of these "constant errors" when it is present (Woodworth and Schlosberg, 1965).

RESULTS

In the present experiments a total of 38 units could be classified as RA-fibers. Of these 5 were best excited by stimuli moving across their receptive fields rather than by vibratory stimuli. The RA-receptors showed the classical on-off behavior, i.e. they responded with brief bursts of impulses at the onset of the step indentation of the skin and with 1 or 2 impulses upon its removal. No impulses were elicited during steady maintenance of the step indentation. Twenty-eight units of the total sample were stable enough to allow detailed quantitative studies of their tuning characteristics over the frequency range of 5—100 cps. Figure 1 illustrates the responses of an RA-receptor when an sine wave oscillation was superimposed on a step indentation of the skin at amplitudes required to produce one nerve impulse per cycle of sinusoid.

The locations of 26 units are shown in a schematic drawing in Figure 2. The receptive fields of 4 units not shown in the drawing were in the area between the

[1] We would like to express our appreciation to Dipl.-Phys. Dr. K. Meinzer for construction of the mechanostimulator

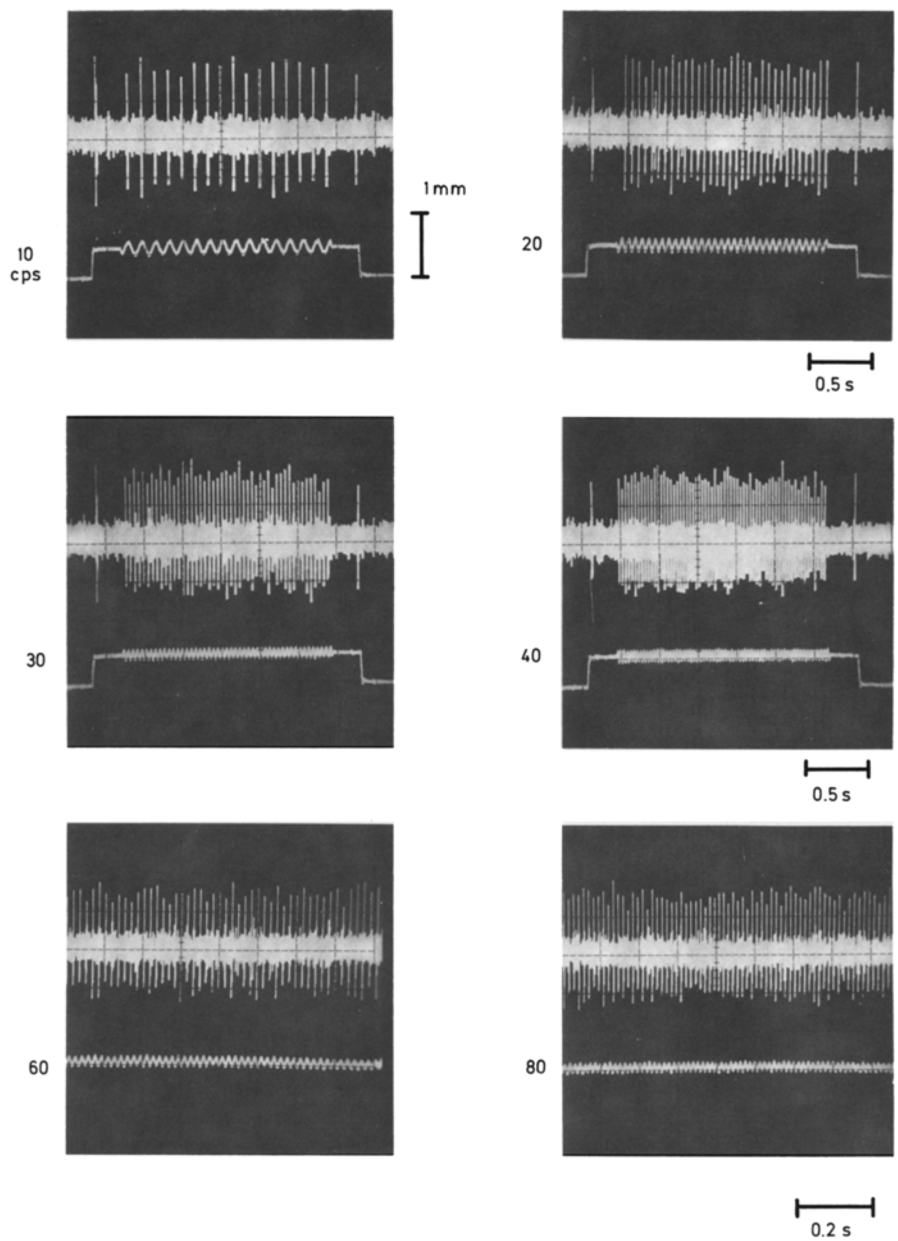

Fig. 1
Response of a rapidly adapting mechanoreceptor innervating hairy skin of the human hand to stimulation with stepwise indentations of the skin at amplitudes of the superimposed sine wave required to evoke a one-to-one following of the fiber at stimulation frequencies of 10, 20, 30, 40, 60 and 80 cps. The step indentation of the skin was 500 µm. The lower trace in each record is the analogue signal of the movement of the 1-mm-diameter tip of the stimulating probe. Note that the lowermost records do not show the step indentation

hairy and glabrous skin of the left index finger. So far, activity led off from Pacinian afferents in hairy skin has not been identified in our experiments.

The tuning curves of 12 RA-receptors are shown in Figure 3. Several fibers were very broadly tuned, being equally sensitive in the frequency range from 5–20 cps. As the frequency of the oscillation was increased, stronger stimuli were required to evoke one impulse per stimulus cycle. The mechanical thresholds of the more insensitive RA-fibers were about 5–8 times higher than those of the most sensitive ones. The curves have minima between 20 and 40 cps. For either lower or higher frequencies the tuning required higher amplitudes of the sine wave oscillation. Conduction velocities, measured in 4 units, ranged from 20–31 m/s, indicating that these fibers fall into the Aδ cutaneous group.

A survey of the response pattern of a sample of 16 slowly adapting mechanoreceptors in human hairy skin (both Type I and Type II; Knibestöl and Vallbo 1970; Chambers et al., 1972; Knibestöl, 1975) to low-frequency mechanical oscillations (5–20 cps) showed that frequency modulation occurred in phase with the sine wave when its amplitude increased slightly from zero to only a few micrometers. The records in Figure 4 demonstrate the typical behavior. The uppermost

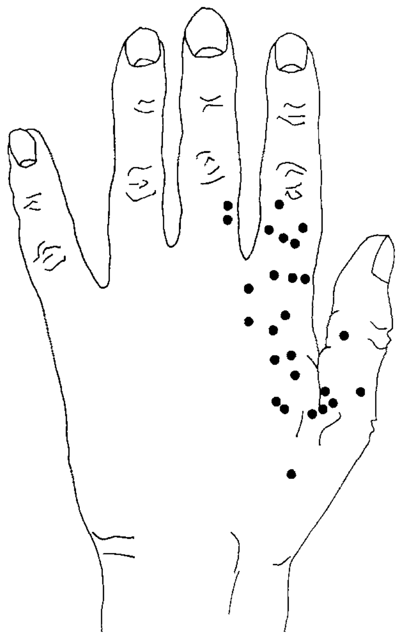

Fig. 2. Schematic drawing of the receptive field locations of 26 rapidly adapting mechanoreceptors in human hairy skin. Recordings were taken from the superficial branch of the left radial nerve

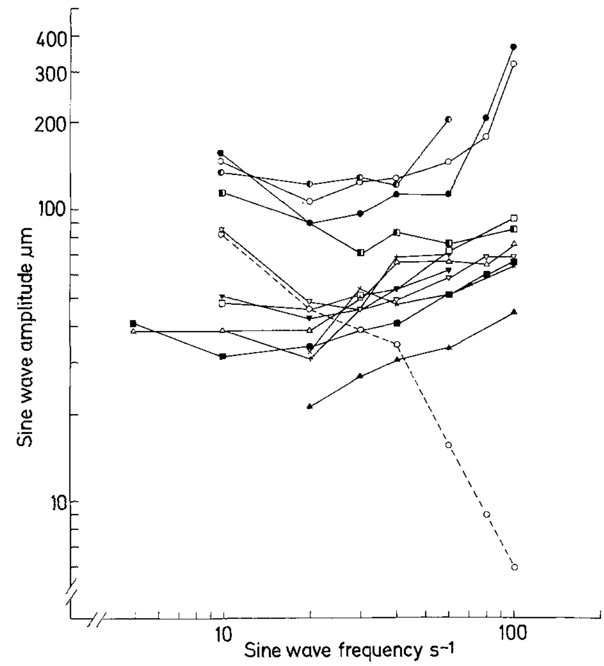

Fig. 3. Tuning curves for 12 rapidly adapting mechanoreceptors from the superficial branch of the left radial nerve in human subjects (solid lines) and the human threshold function for the perception of sine wave oscillation applied to the hairy skin of the hand (dashed line). A point in the latter curve represents the mean of 10 subjects. 5 determinations of thresholds were made in each subject

record was obtained from a Type I SA-receptor with a steady skin indentation of 500 µm with no superimposed oscillation. If a sine wave of 5 cps was superimposed onto the step indentation, as shown in the successively lower records, the continuous discharge is interrupted; here, frequency modulation is apparent at sine wave amplitudes below 20 µm and very marked at higher intensities.

The dashed line in Figure 3 shows the threshold of detection of oscillatory movement on the hairy skin of the hand at various frequencies of mechanical sine wave stimulation, as obtained in measurements of human performance. At each of the frequencies tested, 5 measurements were made in each subject, and the values given are the average of 10 subjects, The average threshold at 10 cps was 88 µm and, as the frequency rose, it fell progressively to about 6 µm at 100 cps. The standard error of mean was ± 26 µm for 10 cps and about ± 8 µm for the other frequencies.

The threshold curve can be described by two approximately linear functions with different slopes. The change of slope took place at about 40 cps, a frequency at which the subjects reported a remarkable change in the quality of the sensation.

Frequencies below 40 cps were felt as flutter, whereas frequencies above 60 cps were reported as vibration.

DISCUSSION

Our studies of the human capacity to detect vibratory stimuli, and of the response properties of RA-receptors in hairy skin, obtained under similar conditions, indicate that this class of afferent fibers, which appears to be best excited in the low-frequency range, may be related to the perception of low-frequency oscillation (flutter). On the other hand, since the threshold for tuning lies well above the sensory threshold, this class of cutaneous units cannot contribute to the higher frequency range of the human sensitivity curve (40 to 100 cps). The fact that the tuning curves of Pacinian afferents, like the threshold function for perception of skin movements in humans and monkeys, are U-shaped, with best frequencies at about 250 cps, is strong evidence that these fibers are concerned with vibratory sensibility (Talbot et al., 1968; Merzenich and Harrington, 1969; Harrington and Merzenich, 1970; Mountcastle et al., 1972). Since only a few conduction velocity measurements could be carried out, the question must be left open as to whether the fibers found in human hairy skin nerves fall into the two different fiber populations (alpha and delta distribution) seen in the hairy skin nerves of the Rhesus monkey (Merzenich and Harrington, 1969). Some results on the characteristics of human mechanoreceptors in hairy

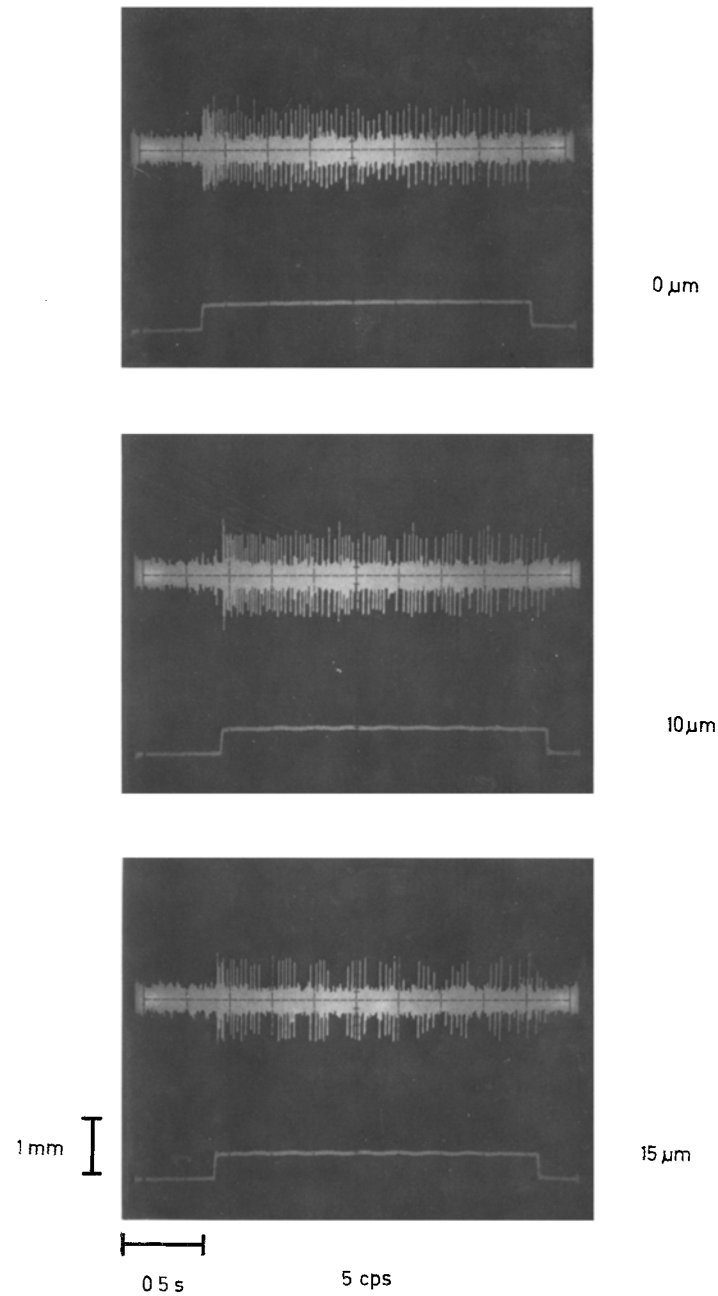

Fig. 4
Afferent discharges of a Type I slowly adapting mechanoreceptor from the superficial branch of the human radial nerve to a maintained skin indentation of 500 µm and to a 5 cps superimposed sine wave stimulus at amplitudes of 10 µm and 15 µm. The lower trace in each record is the analogue signal of the displacement of the stimulating probe

skin evoked by vibratory stimuli were recently published (Järvilehto et al., 1976). One unit was driven periodically at 40–400 cps and was extraordinarily sensitive at the higher frequencies, indicating that this fiber corresponds to a Pacinian corpuscle. Another unit showed a minimal threshold in the low frequency range, and 3 units were entrained at some of the frequencies between 20 and 200 cps. However, neither quantitative threshold values of these receptors nor sensory data were given.

The other question we were confronted with was: Do SA-receptors innervating the hairy skin of the human hand contribute to the capacity to detect oscillatory movements of the skin at frequencies well below 20 cps? From our findings it appears unlikely that these classes of cutaneous afferents play an essential role: Frequency modulation in phase with the sine wave was visible at amplitudes far below the human threshold for perception of movement. However, it cannot be excluded that low-threshold SA-receptors contribute to the sensation of low-frequency vibration because the threshold of central neurons might be higher than that of the peripheral SA-receptors.

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