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Responses of Mechanoreceptive Afferent Units in the Glabrous Skin of the Human Hand to Sinusoidal Skin Displacements

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The impulse responses to perpendicular sinusoidal skin displacements were recorded from 4 different types of mechanoreceptive afferent units innervating the glabrous skin of the human hand. The cycle responses, defined as the number of impulses evoked per sine wave cycle, were studied at a wide range of frequencies (0.5–400 Hz) and amplitudes (0.001–1 mm). The rapidly adapting units (RA) were most easily excited at stimulus frequencies between 8 and 64 Hz, whereas the corresponding frequencies for the Pacinian units (PC) were above 64 Hz. However, at high stimulus amplitudes, the RA and the PC units showed quite similar response profiles within the range of frequencies tested. The sensitivities of the slowly adapting unit types (SA I and SA II) were greatest at lower frequencies. A characteristic finding for all 4 types of units was that the higher the amplitude, the lower the frequency at which the cycle response was maximal.

INTRODUCTION

In contrast to the well documented response properties of the low threshold mechanoreceptive afferent units in the glabrous skin area of the human hand to ramp indentations[10,13,16,17], virtually nothing has been published on the responses to sinusoidal displacements of the skin. Such data may be of particular interest since several important findings regarding tactile mechanisms have emerged from psychophysical studies with sinusoidal skin displacements delivered to this area of skin[29,30]. The psychophysical findings have often been interpreted on the basis of the assumption that man and subhuman mammals are equipped with mechanoreceptive units which respond similarly to sinusoids[2]. Likewise, the fundamental work on psychoneuronal correlates in the perception of 'flutter-vibration' was largely based on psychophysical data collected during stimulation of the glabrous skin of the human hand and neurophysiological data extracted from tactile afferent units in monkeys innervating the corresponding skin area[27].

The purpose of the present experiments was to obtain a survey of the responses of the tactile afferent units in the glabrous skin of the human hand to sinusoidal skin displacements of a wide range of amplitudes and frequencies. It has been shown that 4 kinds of low threshold mechanoreceptive units can be distinguished in this area[10,18]. Two types adapt quickly, the RA (rapidly adapting) units and the PC (Pacinian) units. They respond to skin indentation only as long as the stimulus is in motion. The other two types are slowly adapting, the SA I and the SA II units. They are sensitive to moving stimuli but exhibit also a response related to the amplitude of maintained skin indentation. The RA units and the SA I units are characterized by small and well defined receptive fields. In contrast, the PC and SA II units have large receptive fields

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with obscure boundaries and are sensitive to remote stimuli. The PC units are particularly sensitive to remote transient mechanical events, whereas the SA II units are sensitive to directional skin stretch.

METHODS

Experiments were carried out on 17 healthy subjects, 9 females and 8 males, of ages 20–40 years. The subject sat comfortably in a dentist's chair with the right arm extended laterally and supported by a vacuum cast. To avoid movements, the dorsum of the hand was embedded in a Plasticine (Colman) mold with the fingers moderately flexed. Occasionally, finger clamps were used for additional fixation. The surface temperature of the skin in the palm was measured as 25–33 °C.

Recordings of single afferent mechanoreceptive units were obtained with tungsten needle electrodes inserted percutaneously into the median nerve about 10 cm proximal to the elbow[28]. The units were classified in accordance with criteria described previously[12,16–18]. The extent of the receptive field was assessed with von Frey hairs at 4–5 times the threshold of the unit and the receptive field boundary was marked on the skin with a sharp ink pen. The sample of units studied was representative of larger samples described earlier with regard to the sizes of the receptive fields and mechanical thresholds determined with von Frey hairs[14,15].

When a unit had been isolated and classified, sinusoidal skin displacements were delivered through a small perspex probe which was driven by a feedback controlled moving coil stimulator[31]. The probe movement was monitored by the optical position transducer of the stimulator (DC, 1.8 Hz), whose linearity was $\pm$ 0.2% and the standard deviation of its total noise (normally distributed) corresponded to $\pm$ 0.05 μm. The input waveforms to the stimulator were derived from a programmable function generator. The stimulator was adjusted so that the probe movement was perpendicular to the skin surface at the center of the receptive field. The contact surface of the cylindrical probe was flat with a diameter of 6, 8 or 10 mm. For each unit the diameter of the probe used was selected on the basis of the size of the previously defined receptive field, with the aim of symmetrically covering the field with a clearance of at least 0.5 mm. This condition was fulfilled for the RA and SA I units, and most of these were studied with the 6 mm probe. The large fields of the PC and SA II units could not be completely covered by the 10 mm probe for most units. In these cases the 8 or 10 mm probe was used and positioned over the zone of maximal sensitivity. To obtain a stable mechanical coupling between the probe and the skin surface, a static indentation of 0.5–0.7 mm beyond minimal skin contact was used, upon which mechanical sinusoids were superimposed. With this preindentation, the flat surface of the stimulus probe was completely in contact with the skin at all probe locations.

The test stimuli were delivered as a sequence of sine wave bursts and were superimposed on the preindentation in such a manner that the negative peaks (minimal indentation) coincided with the level of the preindentation (Fig. 1). The bursts consisted of 5 sine wave cycles which started and stopped at the level of the preindentation (Fig. 1). A test sequence consisted of a series of consecutive bursts of constant amplitude but of different frequencies in the following order: 0.5, 1, 2, 4, 8, 16, 32, 64, 128, 256, 400, 256, 128, 64, 32, 16, 8, 4, 2, 1 Hz. The extreme test frequencies, 0.5 and 400 Hz, were executed only once. The time intervals between the bursts was 1 s. During these intervals, the probe was held constant in the preindentation position. The amplitude was varied between test sequences, starting with 1 mm peak to peak. All amplitudes are expressed in decibels (dB) relative to this amplitude. A stepwise attenuation by 6 dB (i.e. by a factor of 0.5) was performed until the unit did not respond to any of the tests in the sequence. For amplitudes less than —36 dB the steps were 8 dB. The pauses between the test sequences were ca. 10 s, and the time from the initial preindentation to the start of the first test sequence was, in most cases, 10–30 s. The size of the preindentation was controlled during some of these pauses. As to the accuracy of the mechanical stimulation, the actual movement of the probe was within 0 dB to —3 dB of the programmed value. However, for tests at high amplitudes (nominally 0 dB and —6 dB) and high frequencies (400 and 256 Hz) the probe movement was occasionally attenuated more than 3 dB. These tests were excluded from the analysis.

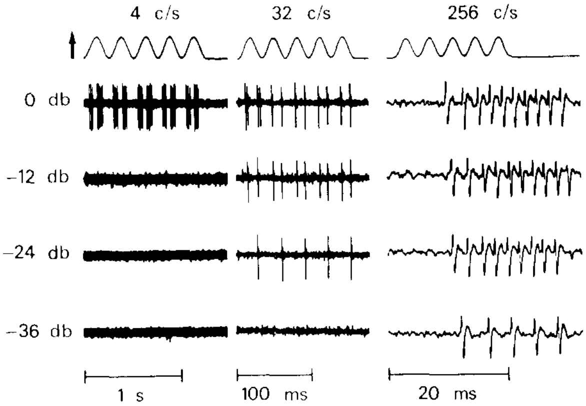

Fig. 1. Examples of discharge patterns of an individual unit (PC) at 4 different sine wave amplitudes and 3 different frequencies. The uppermost row shows the time course of the skin displacements which were superimposeed on a 0.5 mm preindentation. Arrow indicates the direction of skin indentation. Lower rows show the neuronal impulse discharge. Each column refers to a single stimulus frequency and each row to a constant amplitude given in dB relative to 1 mm peak to peak skin displacement. Note the different time scales. The time lag between the occurrence of the mechanical stimulus and the appearance of nerve impulses was accounted for mainly by the conduction time of the peripheral nerve and by the time required for the excitation of the nerve ending.

The neuronal discharges together with the output of the position transducer that monitored the mechanical displacement of the probe, and the timing pulses were recorded on tape. After the experiment the tape records were filmed. Fig. 1 shows examples of the discharge patterns of a single mechanoreceptive unit at 9 different amplitude–frequency combinations. The average number of impulses evoked per cycle of the sine wave bursts, denoted the *cycle response*, was calculated from the film records. The data from the same stimulus frequencies of the ascending and the descending part of the test sequence were pooled in this calculation. This seemed justifiable as the cycle responses obtained at the same frequencies during these two parts of the test sequence revealed no systematic difference except for two units. The exceptions concerned two of the PC units for which the cycle response was slightly higher during the descending part of the test sequence.

RESULTS

Twenty-five mechanoreceptive units (out of 60 initially isolated at random) were stable long enough to be tested according to the complete schedule as described in Methods. These units (8 RA, 4 PC, 4 SA I, 8 SA II), all had their receptive fields in the glabrous skin area of the hand.

Quickly adapting units

RA units. The average cycle responses of the RA units within a frequency range of 0.5–400 Hz and at various stimulus amplitudes are shown in Fig. 2A, and the corresponding results from an individual RA unit are shown in Fig. 2B. Considering low stimulus amplitudes close to the absolute threshold amplitudes of the units, the RA units were most easily excited within a frequency range of about 8–64 Hz. At higher stimulus amplitudes, the effective frequency range was broader, as found in other studies. A characteristic finding was that the higher the stimulus amplitude, the lower the frequency at which the cycle response was maximal. This was true for all the units studied. Data from individual units also indicated that the higher the sensitivity of the unit, the lower the stimulus frequency which elicited the peak cycle response at a given stimulus amplitude. To illustrate the variability among the RA units, Fig. 2C shows the cycle response at 3 amplitude levels for individual units superimposed in the same graphs. It can be seen that some of the RA units were sensitive to a wide frequency range and responded with about one impulse per stimulus cycle up to 400 Hz even at an amplitude as low as —24 dB. The most sensitive RA units in the sample responded between 4 and 400 Hz at —30 dB, and showed a cycle response of 1 imp./cycle in the range 8–32 Hz at this amplitude, which was about 6 dB above the absolute threshold of the unit at its 'best' frequency (32 Hz). (For further data on absolute thresholds of RA units, see ref. 11.)

PC units. The mean cycle responses for the PC units is shown in Fig. 3A. It can be seen that the PC units were most easily excited at frequencies above 64 Hz with a maximal sensitivity between 128 and 400 Hz. At 256 Hz ('best' frequency) the minimal stimulus amplitude required for eliciting a discharge was as low as —60 dB (1 μm peak to peak) for 3 out of 4 PC units. Thus, the amplitude threshold of the PC units was 20–30 dB below that for the RA units. As for the RA units, stimulations at higher amplitudes broadened the frequency range within which

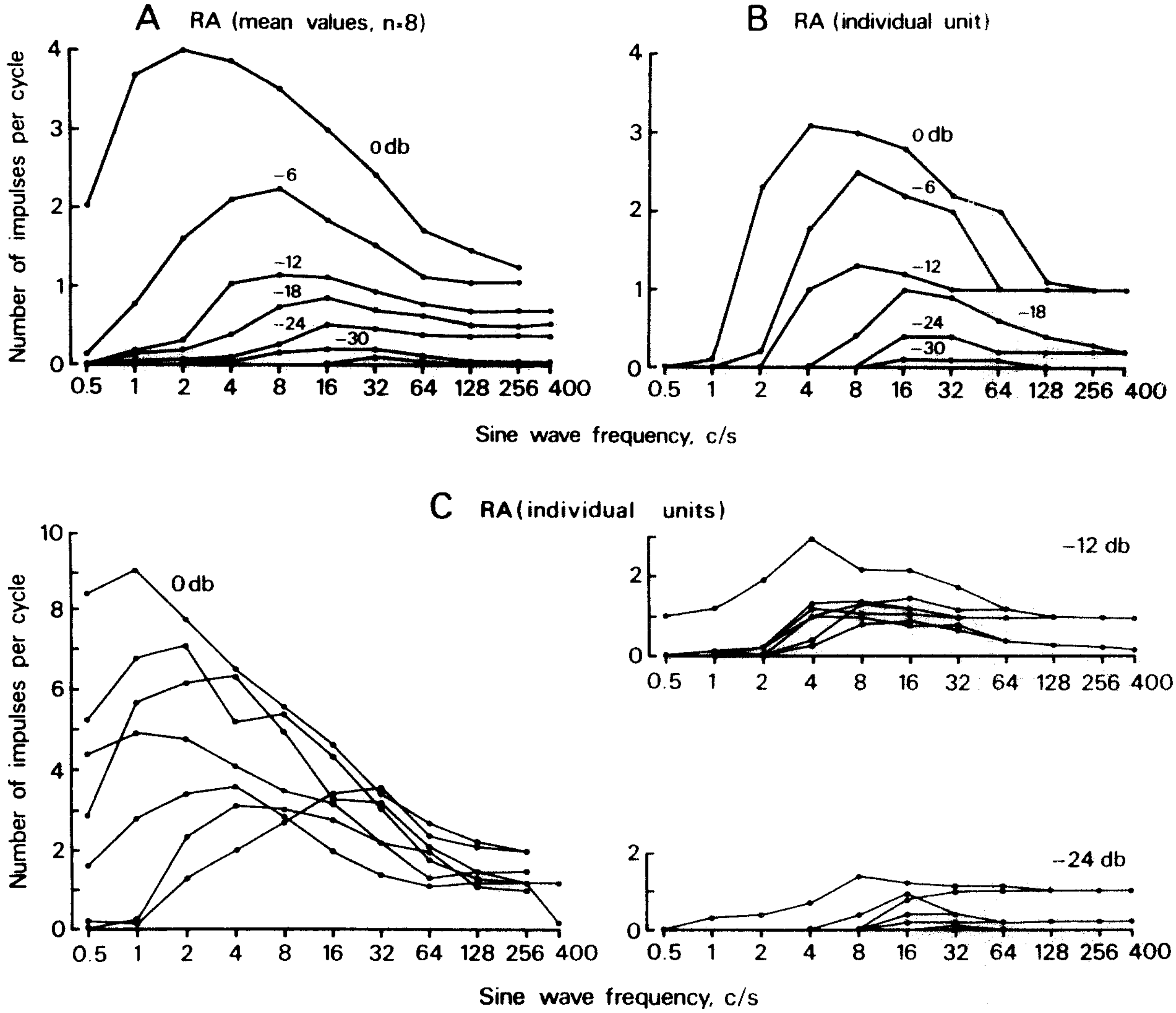

Fig. 2. Relation between cycle response and stimulus frequency for RA units. Note the logarithmic abscissae. A: mean values of 8 units. B: individual unit. The individual curves in A and B refer to different stimulus amplitudes. Curve without amplitude label in A refers to —36 dB. C: relation between cycle response and stimulus frequency for separate RA units at 3 different stimulus amplitudes. In A, B and C, all data points are shown except those referring to 0 imp./cycle where only the points at which the curves first reached this discharge level are shown. All amplitudes are given in dB relative to 1 mm peak to peak skin displacement.

the PC units were excited. A striking finding was that the peak cycle response was displaced considerably towards lower values with increasing amplitude of the sine wave. The large size of this displacement is illustrated by the fact that, at high stimulus amplitudes (0 and 6 dB), the RA and PC units were fairly similar with regard to the magnitude of the mean cycle response throughout the tested frequency range (cf. Figs. 2A and 3A). Fig. 3B shows the cycle response as a function of frequency at 3 different sine wave amplitudes for individual PC units. It can be seen that there was a large variability in size of cycle responses between the units at low frequencies, whereas at higher frequencies the cycle response tended to be either 2 imp./cycle at higher stimulus amplitudes or 1 imp./cycle at lower amplitudes.

A characteristic feature of the RA and PC units was their tendency to discharge impulses both on the indentation phase and the retraction phase of the skin displacement (Fig. 1). For the RA units, the number of impulses at the retraction phase was always lower than at the indentation phase, and decreased to zero much earlier when the stimulus

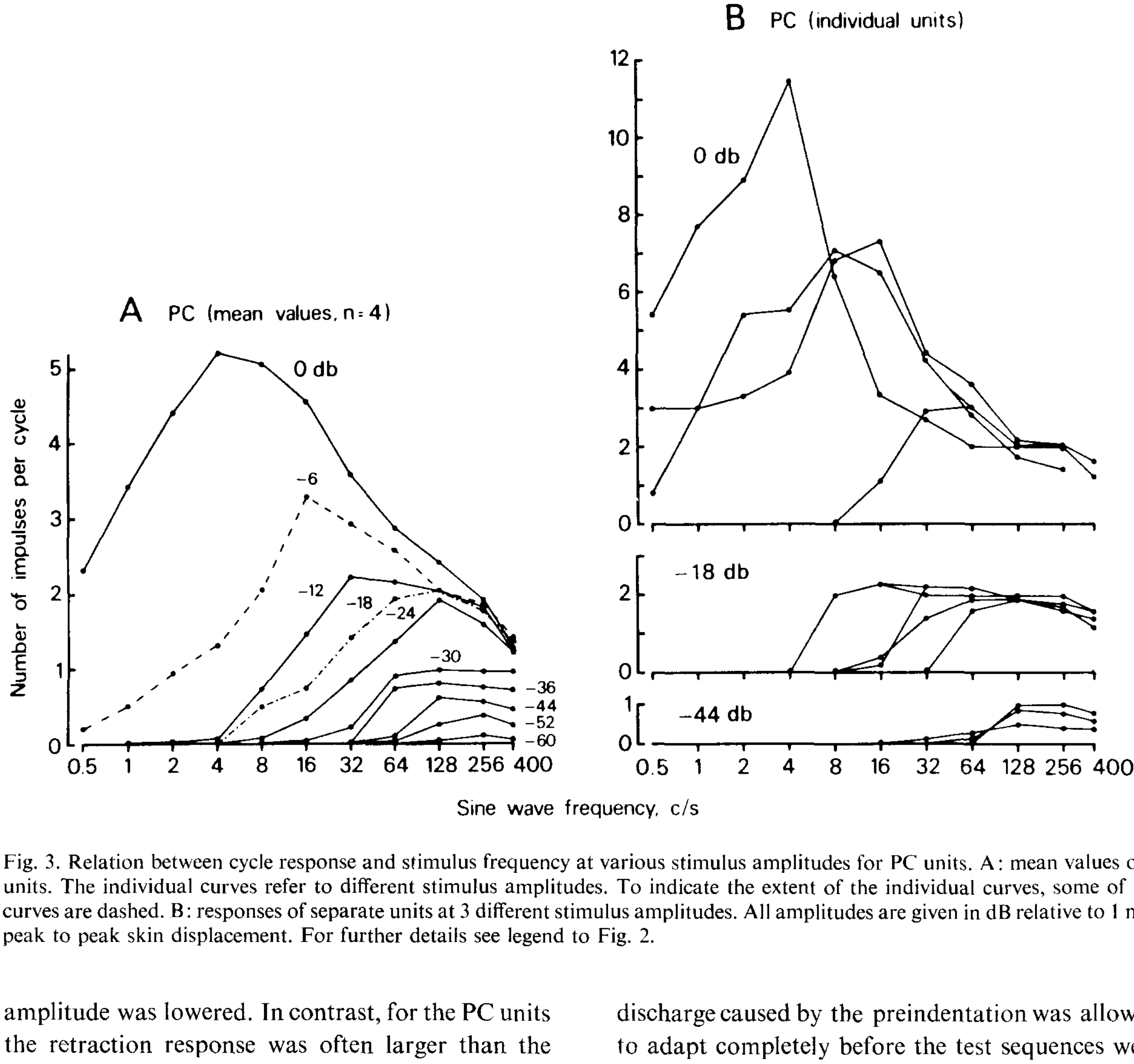

Fig. 3. Relation between cycle response and stimulus frequency at various stimulus amplitudes for PC units. A: mean values of 4 units. The individual curves refer to different stimulus amplitudes. To indicate the extent of the individual curves, some of the curves are dashed. B: responses of separate units at 3 different stimulus amplitudes. All amplitudes are given in dB relative to 1 mm peak to peak skin displacement. For further details see legend to Fig. 2.

amplitude was lowered. In contrast, for the PC units the retraction response was often larger than the response to the indentation phase. For the initial few cycles out of 5 in the test, and particularly for the very first cycle, the RA and PC units tended to respond with a higher number of impulses compared to cycles later in the tests (cf. Fig. 1). However, it also occurred that the impulse discharge was one and occasionally two impulses for all cycles in the test. Such a regular impulse response persisted sometimes even when the stimulus amplitude was changed 6 dB or more (cf. 'tuning plateau' in ref. 27) (e.g. Fig. 1 and Fig. 2B). This plateau phenomenon was more pronounced the higher the stimulus frequency.

Slowly adapting units

SA I units. For all the SA I units, the static discharge caused by the preindentation was allowed to adapt completely before the test sequences were delivered. The time required for complete silence varied between the SA I units and was maximally ca. 50 s.

The mean cycle response of the SA I units as a function of stimulus frequency at various stimulus amplitudes is shown in Fig. 4A, whereas Fig. 4C shows the cycle response for individual SA I units at 3 amplitude levels. It can be seen that the SA I units were particularly sensitive at very low stimulus frequencies. The range of frequencies within which the SA I units could be excited most easily was from 2 to 32 Hz. As for the RA and PC units, the frequency at which the cycle response was maximal decreased with the amplitude of stimulation. However, for most SA I units this could only be appreciated at relatively low stimulus amplitudes as the

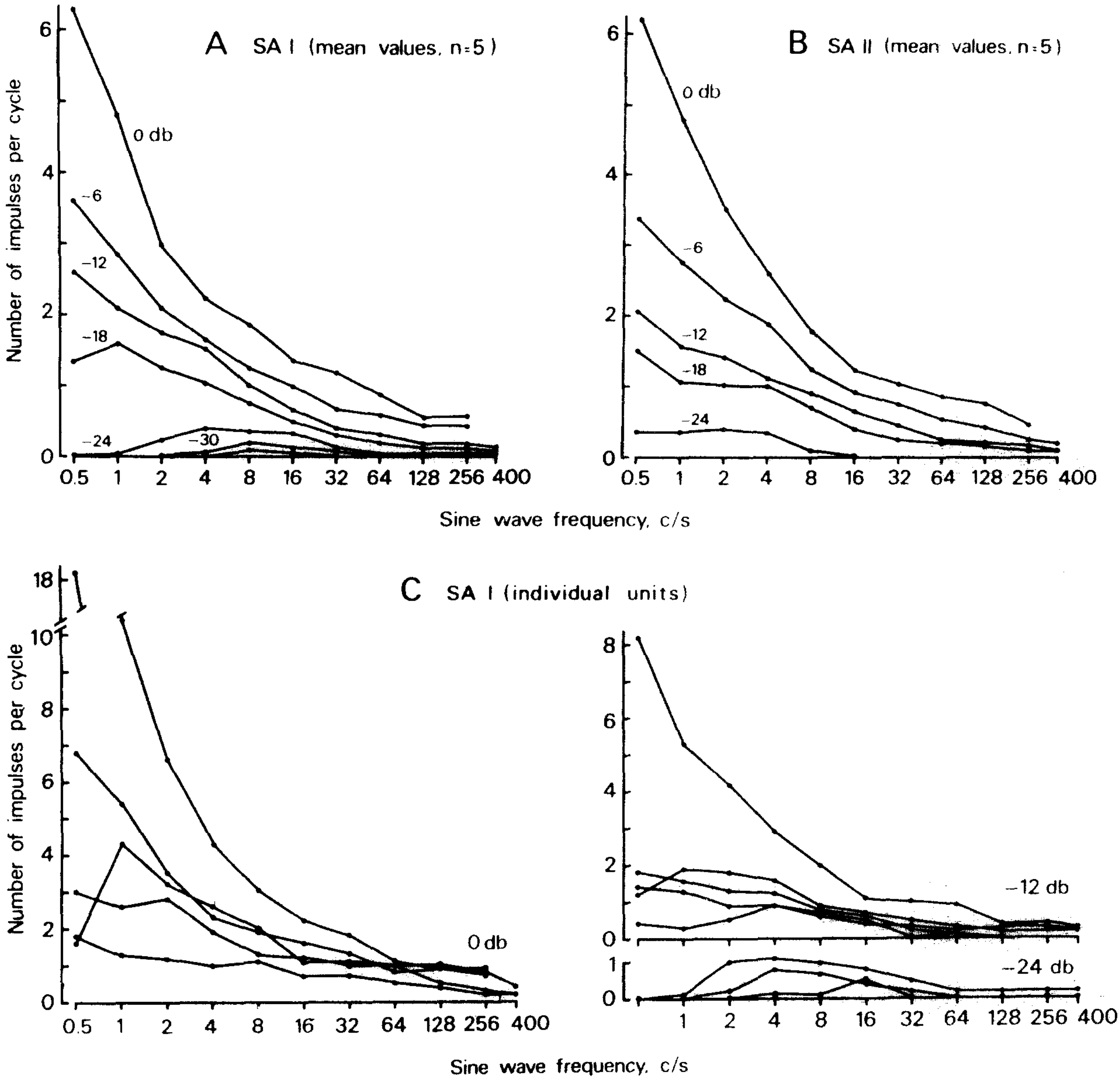

Fig. 4. Relation between cycle response and stimulus frequency at different stimulus amplitudes for slowly adapting units. A: mean values of 5 SA I units. B: mean values of 5 SA II units which exhibited no static background discharge. The individual curves in A and B refer to different stimulus amplitudes. C: responses of separate SA I units at 3 different stimulus amplitudes. All amplitudes are given in dB relative to 1 mm peak to peak skin displacement. For further details see legend to Fig. 2.

peak cycle response at higher amplitudes coincided with the lowest test frequency (0.5 Hz) (Fig. 4A and C). As to the absolute sensitivity of the SA I units, all of the units studied responded to stimuli at an amplitude of —18 dB whereas 3 out of 5 SA I units could be excited by a stimulus amplitude of —24 dB (Fig. 4C). One of the SA I units responded to an amplitude as low as —36 dB with a cycle response of about 0.5 at the 'best' frequencies (8 and 16 Hz). (For further data on the absolute thresholds of the SA I units, see ref. 11.)

SA II units. Three out of 8 SA II units exhibited a very stable sustained background discharge during the entire period of preindentation. The remaining 5 SA II units were either not excited by the preindentation or had completely adapted as the SA I units.

Fig. 4B shows the mean cycle response at various stimulus amplitudes for the 5 SA II units which did not exhibit any background discharge during the test sequences. A comparison between the cycle responses of the SA I and the SA II units revealed large similarities (cf. Fig. 4A and B). There was, however, one main difference: the frequencies at which the SA II units were most easily excited was lower than for the SA I units. Their maximal sensitivity was at frequencies below 8 Hz, and the maximal cycle response coincided with the lowest test frequency (0.5 Hz) even at very low stimulus amplitudes. The lowest amplitude at which the 3 most sensitive SA II units with no background discharge responded was —24 dB.

Concerning the 3 SA II units which exhibited a sustained background discharge, the response to the sine wave stimulation was mainly an increase in activity rather than a pure frequency modulation of the sustained discharge[27]. The net contribution to the total neuronal discharge accounted for by the sine wave stimulation was estimated by calculating the difference between the total number of impulses which appeared duiing each of the tests and the expected number of impulses which would have appeared if only the sustained discharge had existed. It turned out that a main difference between the SA II units with and without background discharge was a much higher cycle response at stimulus frequencies mainly below 8 Hz for the units which showed the background discharge. In average the cycle response at 0.5 Hz was ca. 3 times higher for units with background discharge.

In contrast to the RA and PC units, the slowly adapting unit types responded principally only to the indentation phase of the skin displacements. However, at high amplitudes and very low stimulus frequencies, it was quite common, particularly among the SA II units, that there was a response also at the positive peak of the sine wave when the velocity of indentation was zero and at the beginning of the probe retraction when the velocity of the indentation was negative. This reflects the high position sensitivity of the SA II units in relation to their sensitivity to velocity[1]. Like the rapidly adapting unit types, the slowly adapting unit types could discharge in a regular fashion with an integer cycle response. However, the tendency of the slowly adapting units to show a constant cycle response when the stimulus amplitude was varied was not at all as pronounced as with the rapidly adapting unit types. Although the SA II as well as the SA I units had their highest sensitivity at low stimulus frequencies, they responded to all test frequencies including 256 and 400 Hz (Fig. 4). The most sensitive SA I and SA II units responded to these high frequencies at amplitudes as low as —24 dB and —18 dB respectively. At low stimulus amplitudes the responses at high frequencies were generally accounted for by a single impulse elicited during the very first cycle in the 5 cycle tests. The maximal frequency at which the most sensitive SA I and SA II units responded with at least 1 imp./cycle, as determined with the maximal amplitude used (1 mm peak to peak), was 128 Hz for both types of units.

DISCUSSION

The present study clearly shows that the 4 types of low threshold mechanoreceptive afferent units in the glabrous skin of the human hand exhibit different response properties to perpendicular sinusoidal skin displacements of frequencies between 0.5 and 400 Hz. The frequencies at which the RA units were most easily excited (8–64 Hz) are in agreement with previous findings regarding rapidly adapting units with intradermal endings in the glabrous skin of monkey and cat[7,24,27]. Units with similar response properties have also been described in the dorsum of the human hand[9,20]. The sensitivity of the human PC units to sine wave stimuli at high frequencies (above ca. 64 Hz) was very similar to the sensitivity of previously described Pacinian corpuscle units in the cat's leg, foot paw and mesentery[5–8,26] and in the skin of monkeys[22–24,27].

Most of the results obtained for the slowly adapting units cannot easily be compared with the response properties to mechanical sinusoids of slowly adapting units described in earlier studies, since the responses accounted for by sine wave stimulation in these studies was allowed to interfere with an already existing background discharge caused by the preindentation[20,23,27]. However, it seems clear that the slowly adapting units in both man and subhuman primates are most sensitive to mechanical sinusoids of low frequencies. The fact that most of the slowly adapting units in the present study completely adapted to the employed preindentation is in agreement with earlier investigations of static thresholds of SA I and SA II units in the glabrous skin of man[17]. As to the consequences of adaptation, it has been shown in studies of the SA I and SA II units in cat that adaptation does not induce a decrease in receptor sensitivity, but rather a slight increase in sensitivity to both threshold and suprathreshold stimuli superimposed on a preindentation[4]. Another factor which is known to influence the magnitude of the obtained cycle response of the SA I as well as the RA units is whether the contact surface of the stimulus probe covers the receptive field completely or only partially. When the probe edge cuts through the receptive field the response is often enhanced[11]. However, in the present experiments no such edge effects occurred since the probe covered the whole receptive field of the unit.

A consistent finding in the present study was that the frequency range within which the units responded increased rapidly with stimulus amplitude. Moreover, the frequency at which the cycle response had its maximal value decreased considerably when the stimulus amplitude was increased. This decrease was roughly 1 octave per 10 dB for the RA and PC units. These factors together with the high sensitivity of the PC units, implied that there was a considerable overlap between the frequency ranges within which the RA and the PC units responded already at stimulus amplitudes above —30 dB. Likewise, the magnitude of the cycle responses were quite similar for the RA and the PC units at the highest stimulus amplitudes used throughout the studied frequency range. The pronounced responsiveness of the PC units to low stimulus frequencies has not been pointed out in earlier animal studies. The slowly adapting units had their maximal sensitivity at frequencies lower than those of the rapidly adapting unit types. However, at all amplitudes to which the units responded, there was a considerable overlap between the slowly adapting units, particularly the SA I units, and the RA units with regard to the frequency ranges at which the responses occurred.

On the basis of these considerations, it may be concluded that the possibilities to selectively stimulate the different types of units simply by selecting particular stimulus frequencies are limited, particularly when suprathreshold stimuli are applied. To selectively stimulate one type of unit, the stimulus amplitude has to be very close to the thresholds of the most sensitive units of this type except for the PC units. As soon as high stimulus amplitudes are employed e.g. in psychophysical magnitude estimation tasks, more than one type of unit will be brought into play.

The present results are compatible with the idea that the detection of mechanical sinusoids delivered to the glabrous skin of the human hand depends on afferent activity in at least two populations of mechanoreceptive units[21,24,27,29]: the detection of sinusoids at frequencies above ca. 40 Hz, i.e. frequencies eliciting the sense of diffuse vibration, is related to neuronal activity in Pacinian corpuscles, whereas the intradermal rapidly adapting units (RA units) most probably account for the detection and frequency discrimination at lower frequencies, i.e. the frequency range evoking 'flutter' sensation. As to the slowly adapting units, it has been emphasized that they do not contribute to the detection of sine wave skin displacements[20,23,27]. In contrast, evidence has been produced that these units play a part in the sensation of cutaneous pressure[3,19,25]. On the basis of certain preliminary psychophysical results (unpublished observations, J. Löfvenberg and R. S. Johansson) we believe, however, that the SA I units contribute to detection of frequencies at which the sensitivity of the SA I units is higher than for the RA and PC units, i.e. at frequencies below about 4 Hz.

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