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Psychophysical Tuning Curves in Vibrotaction

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PSYCHOPHYSICAL TUNING CURVES IN VIBROTACTION

by

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VITA

The author, Sharon Marie Labs, is the daughter of Edward John Labs, Jr. and Miriam (Johnson) Labs. She was born April 2, 1954, in Syracuse, New York.

Her elementary education was obtained in the Fayetteville-Manlius school system, Manlius New York. Her secondary education was obtained at Kalani High School, Honolulu, Hawaii and Fayetteville-Manlius High School, where she graduated in June, 1972.

In September, 1972, she entered the College of the Holy Cross, Worcester, Massachusetts, and in May, 1976 received the degree of Bachelor of Arts, awarded magna cum laude, with a major in psychology. While attending Holy Cross, she was awarded a summer research grant in 1975 to study psychosomatic symptom choice with Dr. Seymour Fisher, chairman of the Department of Psychiatry Research, Upstate Medical Center, Syracuse, New York. In 1975, she was elected to Psi Chi, the national honor society in psychology, and Alpha Sigma Nu, the national honor society of Jesuit colleges and universities. She was elected to Phi Beta Kappa in 1976.

In September, 1976, she entered the Experimental Psychology Program at Loyola University, Chicago, Illinois. She was granted a research assistantship in visual psychophysics in January, 1977. In September, 1977, she was invited to conduct her thesis research in cutaneous psychophysics with Dr. George A. Gescheider, chairman of the Psychology Department, Hamilton College, Clinton, New York.

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INTRODUCTION

Investigations of human vibrotactile sensitivity as a function of frequency, duration, location of stimulation, and contactor size have led to the formulation of the duplex model of mechanoreception (Verrillo, 1968). It has been proposed that two receptor systems, differing in their frequency response and in their ability to integrate stimulus energy spatially and temporally, mediate the perception of mechanical disturbance in the skin.

The relationship between vibrotactile thresholds and stimulus frequency has been established by a number of investigators. The studies utilizing extremely small contactors reported vibratory displacement thresholds which were independent of frequency (Geldard, 1940; Sherrick, 1960). However, pronounced frequency effects were reported in studies employing large contactors (Békésy, 1939; Gilmer, 1935; Hugony, 1935; Knudsen, 1928; Setzepfand, 1935; Sherrick, 1953). In examining the joint effects of contactor size (range: .005 to 5.1 cm^2) and stimulus frequency on the human vibrotactile threshold function, Verrillo (1963) found two distinct modes of psychophysical response, as is illustrated in Fig. 1. For all but the smallest contactors, the threshold function had two distinct segments. At high frequencies, the function was U-shaped with lowest threshold at approximately 250 Hz. At

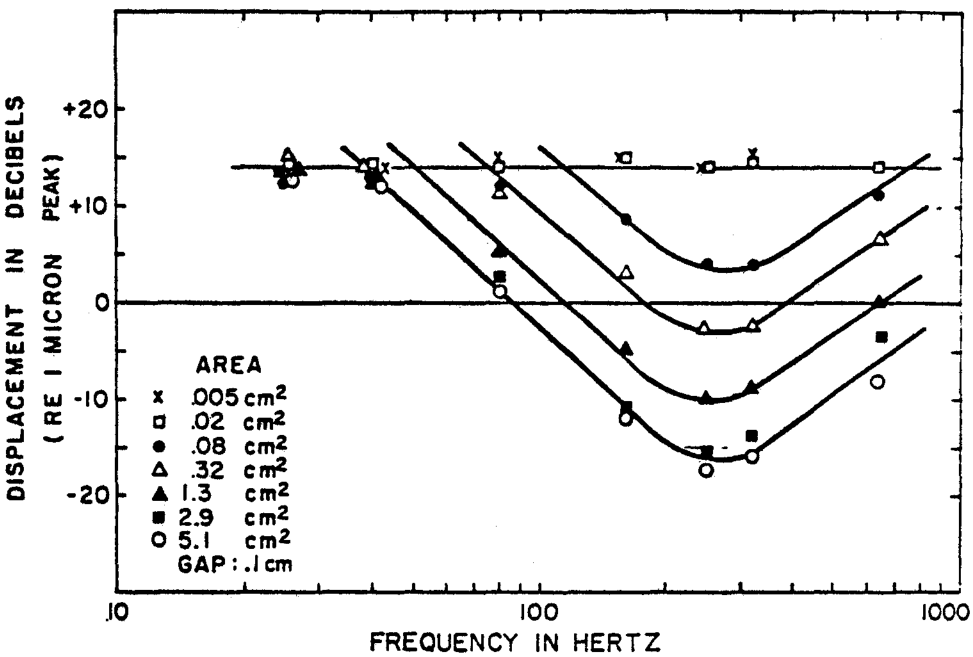

Figure 1. Vibrotactile thresholds as a function of frequency of vibration. The two modes of response are shown by the flat function drawn through the data for the smallest contactors (.005 cm^2 and .02 cm^2) and the U-shaped curves described by the data of the larger contactors. Taken from Fig. 7, Verrillo, R. T., Journal of the Acoustical Society of America, 1963, 35, 1962.

lower frequencies, the function tended to be flat. For frequencies above 40 Hz, and for contactors greater than .02 cm^2, a doubling of contactor area resulted in an approximate 3 dB decrease in the displacement amplitude required for the detection of vibration, indicating complete spatial summation of stimulus energy. For frequencies below 40 Hz, or for contactor areas of .02 cm^2 or smaller, vibrotactile threshold was independent of contactor size. In addition, threshold for the smallest contactors was a constant value for all frequencies in the measured range (25-640 Hz). Recently, Gescheider (1976) has repeated and confirmed Verrillo's measurements and Verrillo and Gescheider (1977) have found that the flat, low-frequency portion of the threshold function extends to frequencies as low as 10 Hz.

Verrillo (1963) concluded from his findings that at least two functionally independent populations of receptors were responsible for vibrotactile sensitivity in the human. This notion that two processes may be involved in vibrotaction was originally suggested by Békésy (1939). Verrillo (1966a) was able to compare his psychophysical findings with the electrophysiological data of Sato (1961), who recorded frequency-response characteristics of Pacinian corpuscles in the cat. The relationship between the human vibrotactile frequency-response function measured psychophysically and the frequency-response function of Pacinian corpuscles suggests a possible mechanism mediating vibratory sensitivity. The slope of both functions between 40-250 Hz is approximately -12 dB per doubling of stimulus frequency, with each curve exhibiting maximum sensitivity between 250-300 Hz. From this comparison, Verrillo (1966b) suggested that the Pacinian corpuscle mediated the detection of higher frequencies of vibration in the human and was responsible for the U-shaped portion of the human vibrotactile threshold function.

Investigations by Verrillo (1965) concerning the effects of stimulus duration and contactor area on vibrotactile threshold again revealed a duality of psychophysical response, as is evident in Fig. 2 which shows vibrotactile threshold shift as a function of stimulus duration. For contactor areas greater than .02 cm^2, threshold decreased as stimulus duration increased to a maximum of 1.0 sec. No temporal summation was evident when contactor area was reduced to .02 cm^2 or smaller. Gescheider (1976) found no temporal summation for low-frequency stimuli.

To further clarify the relationship between the response characteristics of the two receptor systems and the spatial and temporal characteristics of cutaneous input channels, a series of studies was conducted by Verrillo (1968) comparing frequency, spatial, and temporal characteristics of skin surfaces known to contain Pacinian corpuscles (the thenar eminence of the hand, the ventral surface of the tongue, the volar forearm) and those areas known to be devoid of such receptors (the dorsal surface of the tongue). Vibrotactile

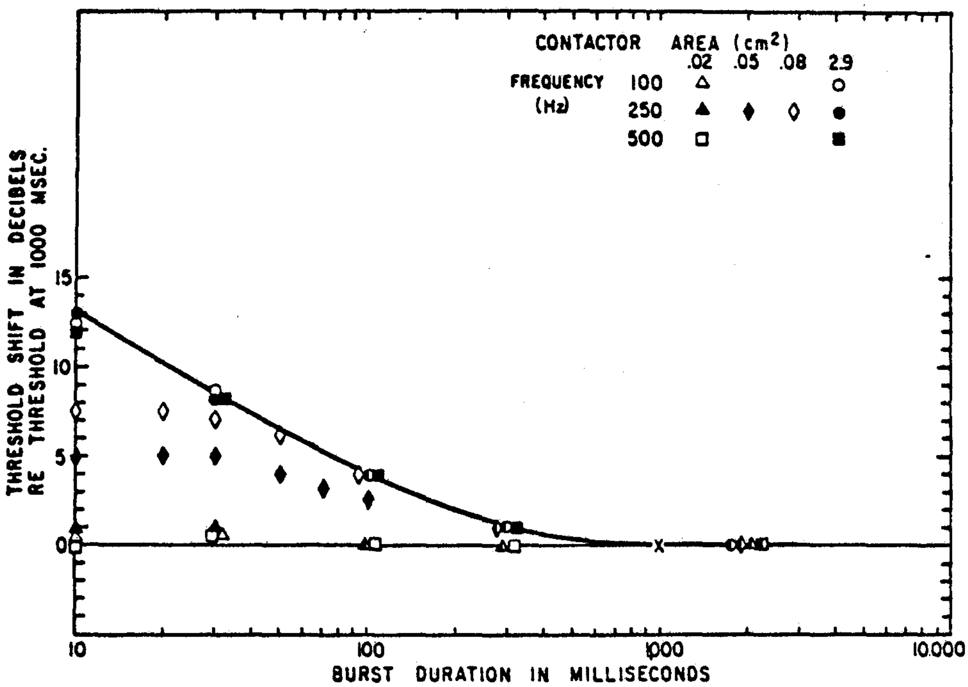

Figure 2. Vibrotactile threshold shift as a function of burst duration. The curve is theoretical. The effect of temporal summation decreases with the size of the contactor. Taken from Fig. 4, Verrillo, R. T., Journal of the Acoustical Society of America, 1965, 37, 843.

thresholds measured from body sites innervated by Pacinian corpuscles were found to be dependent on stimulus frequency, duration, and contactor area, whereas thresholds obtained from sites devoid of Pacinian receptors were independent of these three stimulus parameters. These results lend support to Verrillo's proposal that there are at least two separate systems for the detection of vibration in humans: the system identified with the Pacinian corpuscle is governed by a U-shaped threshold versus frequency function and exhibits both spatial and temporal summation; the other presumably non-Pacinian system, which has not yet been positively identified with a specific receptor, has a flat frequency response, and exhibits neither spatial nor temporal summation.

The work of Lindblom (1965), Lindblom and Lund (1966), and Mountcastle and his associates (Mountcastle, LaMotte, & Carli, 1972; Talbot, Darian-Smith, Kornhuber, & Mountcastle, 1968) has indicated a strong correlation between physiological responses of low-frequency and high-frequency sensitive mechanoreceptive afferents innervating the hand of the monkey as is illustrated in Fig. 3, and the vibrotactile threshold function measured from the glabrous skin of the human hand. The Mountcastle group has consistently found two populations of quickly-adapting fibers. One population has a U-shaped frequency-response function, with optimal sensitivity around 250 Hz, and is thought to be associated with Pacinian corpuscles. The other population, with optimal sensitivity between 30-40 Hz,

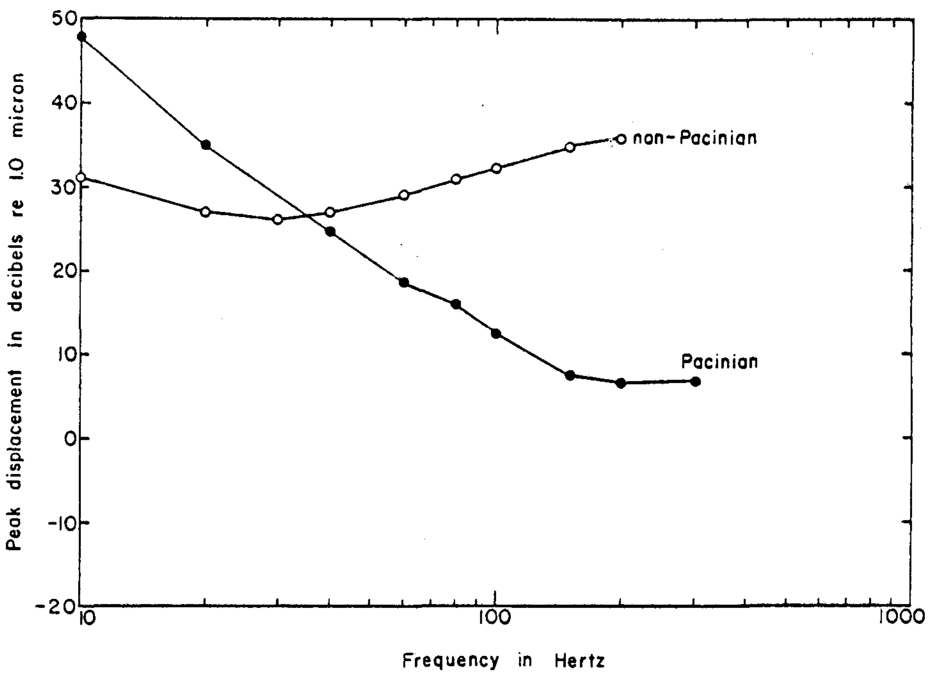

Figure 3. Median thresholds as a function of frequency of vibration measured electrophysiologically from the single-fiber afferents innervating the Pacinian and non-Pacinian receptors in the monkey hand (Talbot et al., 1968). Measurements were made without a rigid surround. These curves are identical to the Mountcastle et al. (1972) recordings except in sensitivity level. (Data averaging courtesy of R. Hamer.)

is thought to be associated with Meissner corpuscles.

Attempts to psychophysically isolate the frequency-response characteristics of the two systems in humans have met with limited success. Electrophysiological recordings from Pacinian corpuscles (Merzenich & Harrington, 1969; Sato, 1961; Talbot et al., 1968) indicate that the U-shaped threshold curve for single fibers extends to frequencies as low as 10 Hz. Furthermore, thresholds for Pacinian fibers at frequencies below approximately 40 Hz are higher than the thresholds for non-Pacinian fibers (see Fig. 3). This finding suggests that a low-frequency stimulus, when sufficiently above the psychophysical threshold can activate the Pacinian as well as the non-Pacinian system. Hamer and Verrillo (1975) predicted that a masker below 40 Hz would not interfere with the detection of a test signal above 40 Hz until its intensity level was raised to exceed the theoretical extension of the Pacinian threshold function illustrated in Fig. 4. This is based on the assumption that psychophysical thresholds are mediated by the receptor system with the lower threshold. Hamer and Verrillo determined that shifts in threshold response to a 250 Hz signal occurred as a function of masker frequency. Continuous maskers of 20, 30, and 40 Hz failed to elevate the threshold response of a pulsed 250 Hz signal until masker intensities were increased to 22.5 dB SL, 15.5 dB SL, and 13.0 dB SL, respectively. Above these intensity levels, breakpoints occurred in the masking function and test threshold rose linearly

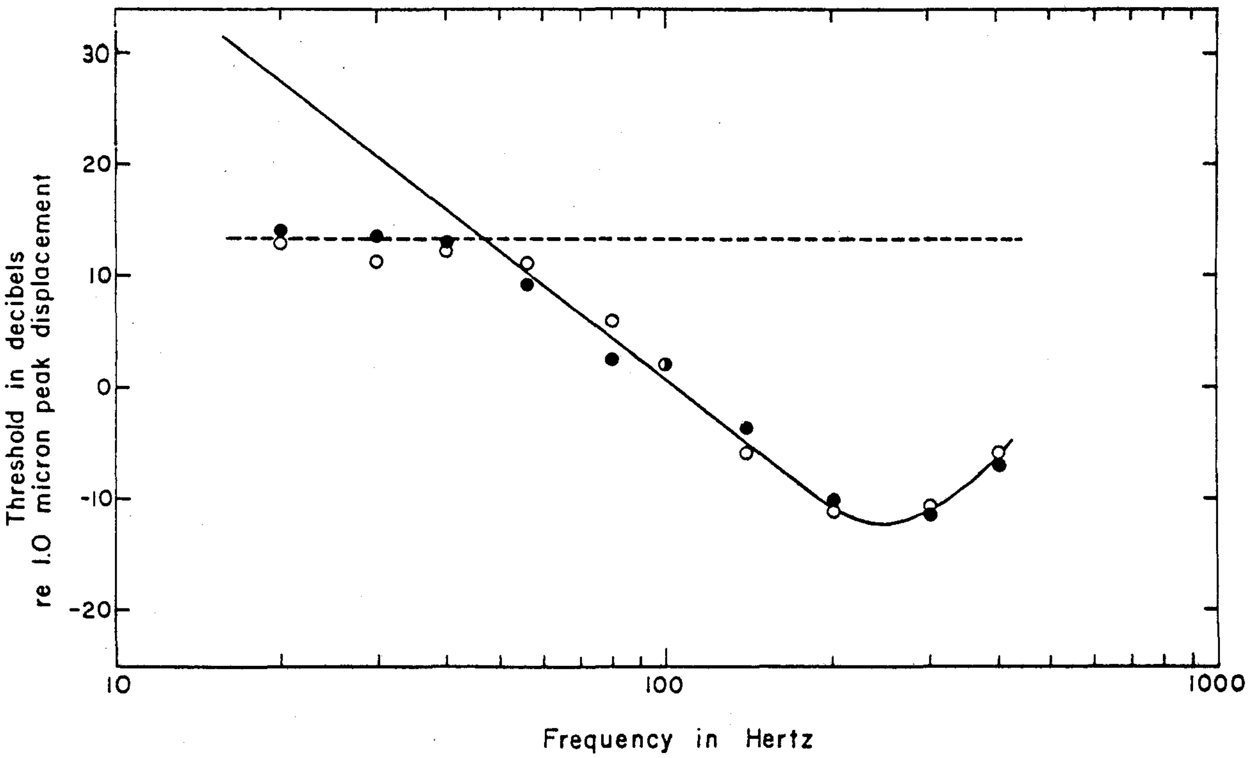

Figure 4. Hypothetical extensions of the psychophysical threshold functions of the Pacinian (solid line) and non-Pacinian (dotted line) systems based on electrophysiological recordings of Talbot et al. (1968) and Mountcastle et al. (1972). Open and closed circles represent data from two subjects obtained using a .75 cm^2 contactor.

with further increases in masker intensity. Although the breakpoint intensities were approximately 10-12 dB above predicted thresholds of the Pacinian system, the results were interpreted as indicating independent processing of the two mechanoreceptive channels below breakpoint intensity.

Verrillo and Gescheider (1977) have approached the problem of psychophysically isolating the frequency-response characteristics of the two systems through a selective adaptation paradigm. The threshold of the low-frequency system was elevated with a 10 Hz conditioning stimulus to the extent that it was higher at all frequencies than the threshold of the high-frequency system. The threshold of the unadapted high-frequency system was then measured, yielding a U-shaped psychophysical function with a constant slope of -12 dB/octave, down to 15 Hz. These results indicated that the 10 Hz conditioning stimulus, when raised to a maximum intensity of 30 dB SL, had no effect on the detection of high-frequency stimuli (40-250 Hz), as detection of these frequencies was mediated solely by the unadapted high-frequency system. However, at test frequencies below 40 Hz, the effects of the conditioning stimulus were substantial and the decrease in sensitivity of the low frequency system was proportional to the intensity of the conditioning stimulus.

Recently, Gescheider, Capraro, Frisina, Hamer, and Verrillo (in press) have employed the selective adaptation procedure to examine the low-frequency branch of the threshold function. A 250 Hz conditioning stimulus was shown to uniformly elevate the Pacinian branch of the threshold function by approximately 11 dB, while leaving the sensitivity of the non-Pacinian system unaffected. Selective adaptation of the Pacinian system had the effect of extending the flat portion of the curve out to higher frequencies. The entire curve for the low-frequency system could not be measured, however, because adapting the Pacinian branch of the curve by more than about 12 dB was associated with corresponding elevations in threshold along the flat portion of the curve.

The purpose of the present investigation was to isolate and psychophysically measure the frequency-response characteristics of the two vibrotactile systems using a masking paradigm adopted from auditory research. Both physiological and psychophysical paradigms have been utilized to study the frequency-response characteristics of hypothetical channels in the auditory system. One electrophysiological procedure established in mammals (e.g. Kiang, Watanabe, Thomas & Clark, 1965) entails measuring the intensity (SPL) of a single-frequency tone burst necessary to bring the response of a single eighth-nerve fiber to a constant spike rate above spontaneous activity. A graphic plot of tone intensity required to produce criterion rate of firing in a specific auditory unit as a function of tone frequency yields a characteristic V-shaped tuning curve for that unit. The lowest point of the curve indicates the frequency at which the single unit is most sensitive. It has been further demonstrated that a tonotopic organization of frequency-tuned units exists at several levels in the auditory system, indicating frequency selectivity throughout the system (Aitkins, Anderson & Brugge, 1970; Békésy, 1960; Rose, Greenwood, Goldberg & Hind, 1963; Tsuchitani & Boudreau, 1966).

Psychophysical equivalents of neural tuning curves have been established in humans (Christovich, 1971; Zwicker, 1974) and in animals (Fay, Ahroon & Orawski, 1978; McGee, Ryan & Dallos, 1976). Zwicker points out that to produce psychoacoustical analogs of electrophysiological tuning curves, equivalents of four parameters must be made. These are: tone frequency, tone intensity, response criterion, and single unit fiber. Although tone intensity and frequency can be controlled precisely, and response criterion established as the psychophysical threshold measurement, there is no direct psychophysical equivalent of the single auditory fiber. However, it has been speculated that a sinusoidal tone with a frequency corresponding to a unit's characteristic frequency, presented at an intensity level near threshold, produces a psychoacoustic approximation of that unit's sensitivity. In employing a psychoacoustical paradigm to measure tuning curves, a probe or signal of fixed frequency and intensity replaces the microelectrode. From the electrophysiological data, it is presumed that a single-frequency test stimulus stimulates the one auditory channel which is most sensitive to that frequency. A masker stimulus (replacing the tonal signal of the electrophysiological experiment) which is close in frequency to the test stimulus will, therefore, require less intensity to interfere with the detection of the test stimulus than a masker of a widely-divergent frequency because a single channel is utilized in the processing of both stimuli. Although the neural mechanisms involved in masking are not completely understood, psychoacoustical analogs of single-unit tuning curves can be established and the frequency-selective filter characteristics of the system examined by measuring the intensity of a masker tone required to just mask a test tone of a given frequency and intensity (near threshold) over a wide range of masker frequencies.

Although the duplex model of mechanoreception suggests that the cutaneous system is much more limited in its ability to perform a spatial or "labeled-lines" analysis of frequency by proposing the existence of only two frequency-selective input channels, it is suggested that the response characteristics of these channels may be examined psychophysically through the implementation of the psychoacoustic tuning curve paradigm. It is predicted from Verrillo's model that if the locus and area of stimulation is chosen to activate Pacinian (high-frequency-sensitive) and non-Pacinian (low-frequency-sensitive) channels, and if the test stimulus is near threshold intensity, detection of the test stimulus will be mediated by one or the other receptor system, depending on test frequency.

Similar to frequency processing in the auditory system, it is assumed that the test stimulus is detected by a single input channel. A single exception is at the transition frequency where the threshold of both systems is approximately equal. When the test stimulus is detected in a single channel, it is assumed that the masking effects will be evident only when the masker, depending on its frequency and intensity, stimulates the same response area as the test stimulus. When the test stimulus, because of its frequency, affects both systems, a complex function revealing the operation of both channels is anticipated.

EXPERIMENT 1

In the first experiment, a simultaneous (signal-on-signal) masking paradigm adopted from the auditory literature (Christovich, 1957, 1971; Small, 1959; Zwicker, 1974) was employed in determining the intensity level of masker necessary to mask a test stimulus as a function of masker frequency. Vibrotactile masking functions (tuning curves) were measured for five test frequencies, and a rigid surround was used to confine the vibratory stimulus to the area of the contactor. Two low-frequency test stimuli (15 Hz and 25 Hz) were selected to isolate the tuning characteristics of the non-Pacinian system. Two high-frequency test stimuli (250 Hz and 400 Hz) were chosen to isolate the tuning characteristics of the Pacinian system. These psychophysical functions were expected to be U-shaped, exhibiting a slope of -12 dB/octave between frequencies of 15-250 Hz. An intermediate freauency of 100 Hz was also selected for testing.

METHOD

SUBJECTS

Four male undergraduates (ages: 19-22 years) with no previous experience in psychophysical experiments, and a 41-year-old male with extensive experience as a psychophysical observer were employed as Ss. Prior to the experiment, each subject was given extensive practice in tracking the threshold of vibrotactile stimuli applied to the thenar eminence.

APPARATUS

A block diagram of the apparatus is illustrated in Fig. 5. In both the test-stimulus channel (channel II) and the masker channel (channel I), sinusoidal electrical signals of variable frequency were generated by two Krohn-Hite Model 5200 A function generators, separately passed through two Grason-Stadler Model 1287 B electric switches, and then amplified by two Crown D-60 amplifiers. The amplified signals in the masker channel were passed through a Békésy recording attenuator and a Hewlett-Packard Model 3500-D decade attenuator. The amplified signals in the test-stimulus channel were passed through an identical decade attenuator. In order that their intensities could be independently varied, signals from masker and test channels were mixed in a mixer network. The signals were further amplified by a Crown DC-300 amplifier before being applied simultaneously to a Ling 203 vibrator.

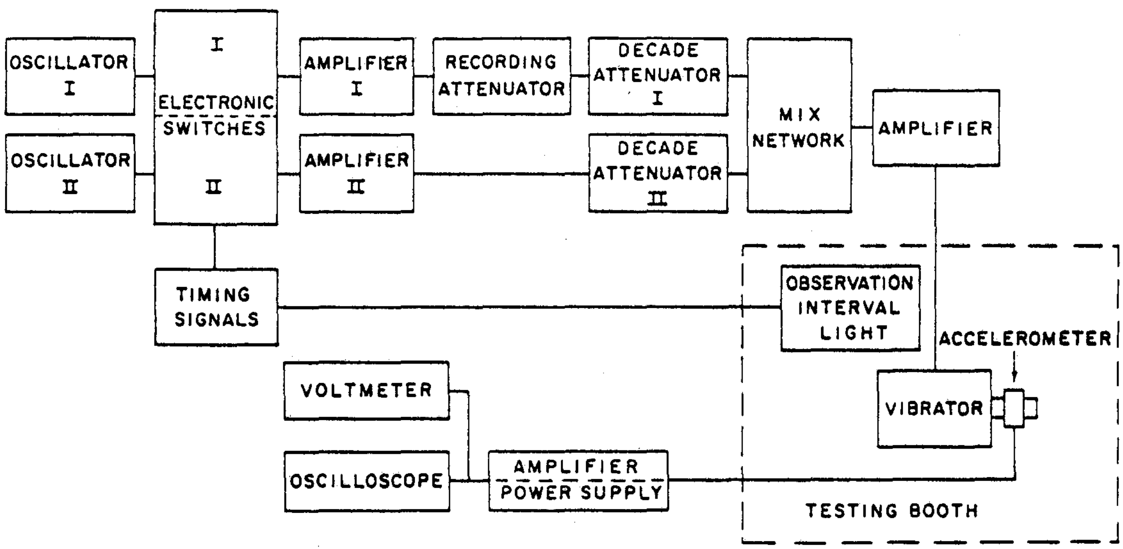

Figure 5. Block diagram of the apparatus.

Electronic switch II was adjusted to provide the test stimulus with a 50 msec rise-decay time. Test stimulus duration of 200 msec at half-power points was regulated by a 10-v dc pulse of 200 msec duration from a Tektronix Type 161 pulse generator which was applied to the gating circuit of electronic switch II. The 2.75 sec repetition rate of the test stimulus was controlled by a Tektronix Type 162 waveform generator which determined the pulse rate from the pulse generator. The continuous maskers were presented by applying 10 volts dc to electronic switch I for the duration of the trial. In order to determine the absolute threshold of the test stimulus, it was necessary to use the masker channel for the purpose of threshold tracking by the Békésy method. A 10-v dc pulse of 200 msec duration from the Tektronix Type 161 pulse generator was applied to the gating circuit of electronic switch I and the 2.75 sec repetition rate of the test stimulus was controlled by the Tektronix Type 162 waveform generator.

Observation intervals were signaled by means of a light-emitting diode (l.e.d.). A 200 msec flash was adjusted to be temporally contiguous with the test stimulus. A second 200 msec observation interval containing no stimulus was presented 500 msec after the presentation of the first. The timing of the observation intervals was regulated by Tektronix Type 161 pulse generators. The timing relationship of the test and masker stimuli, and observation light employed in the simultaneous masking paradigm (Experiments 1, 2) is illustrated in

Fig. 6.

The S was located in a sound-attenuated booth that isolated him from extraneous sound and vibration. Narrow-band noise centered around the freouency of the vibrotactile stimuli was presented through earphones to mask the sound of the vibrator.

A diagram of the vibratory assembly, previously illustrated by Verrillo (1966a), is given in Fig. 7. The vibrator was positioned on the platen of a drill press which could be raised and lowered to precisely regulate the depression of the contactor into the S's hand. The contactor of the vibrator protruded through a hole in the table to make contact with the thenar eminence of the S's right hand. The point of initial contact with the skin was determined by adjusting the height of the vibrator assembly until a non-infinite electrical resistance could be read from an ohmmeter that was connected in series with the S's skin and the metal contactor. The vibrator was then raised 1.0 mm to insure the maintenance of constant mechanical coupling between the skin and the contactor throughout the test session.

Contactor size was .75 cm^2. A 1.0 mm gap between the contactor and the rigid surface of the table was maintained throughout the first experiment. Eijkman and Vendrick (1960) have demonstrated that such a gap effectively limits vibratory stimulation to the locus of the contactor. Vibration amplitude was measured with a calibrated Endevco Model 2221 D

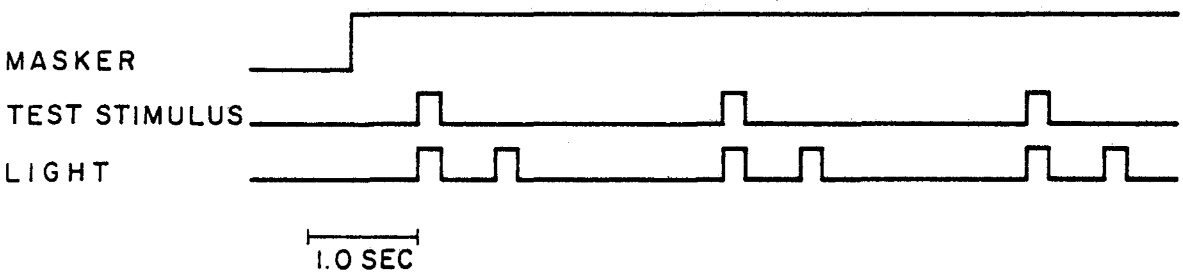

Figure 6. Timing relationship of test and masker stimuli and observation light employed in the simultaneous masking paradigm (Experiments 1, 2).

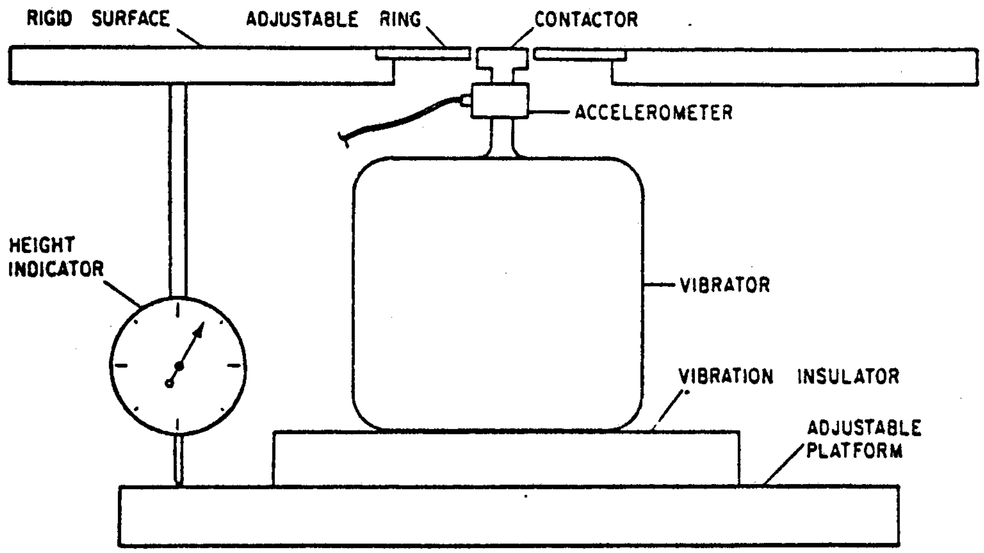

Figure 7. Diagram of the vibrator assembly. Taken from Fig. 1, Verrillo, R. T., Journal of Experimental Psychology, 1966a, 71, 570.

accelerometer mounted directly on the moving element of the vibrator. The accelerometer unit also included an Endevco Model 4206 power supply and an Endevco Model 2614 C amplifier. All measurements were made during stimulation of the skin and are expressed in decibels re 1.0 mm peak displacement of the vibrator. The time relationships and wave forms of the test and masker stimuli and the observation interval light were monitored on a Tektronix 5103 N oscilloscope. When the mechanical stimuli were very intense, wave forms occasionally became non-sinusoidal due to mechanical distortion of the vibrator response or to distortion of electrical signals to the vibrator. When such distortion was observed, psychophysical measurements were not made.

PROCEDURE

Vibrotactile thresholds were measured using an SN-N tracking procedure. This procedure, a modification of the Békésy tracking method, was designed by Gescheider, Herman, and Phillips (1970) to reduce criterion shifting during cutaneous contralateral masking. In SN-N tracking, a stimulus is presented during the first of two successive observation intervals (signal-plus-noise) and no stimulus is presented during the second observation interval (noise). During absolute threshold tracking, the Ss were able to directly compare the sensation of the pulsed test stimulus with the sensation produced by physiological noise alone. The SN-N tracking procedure was adapted for use in the masking paradigm. In the case of the simultaneous masking paradigm, the Ss directly compared the sensation of the masker alone with the sensation of the masker plus the test stimulus. For the threshold tracking of the test stimulus, the Ss were instructed to decrease stimulus intensity if the observation in the first interval was more intense than the one in the second interval, and to increase stimulus intensity if the observation in the first interval containing the test stimulus was equal to or less intense than the observation in the second interval containing no test stimulus. In this masking paradigm, Ss were instructed to adjust the intensity of the masker so that they could just detect a weak test stimulus. For both threshold tracking of the test stimulus and masking, Ss tracked for a duration of one to two minutes by controlling a hand switch connected to the recording attenuator. When the switch was depressed, stimulus intensity decreased continuously at a rate of 1 dB/sec, and when it was released stimulus intensity increased at the same rate. The S's manipulation of the intensity level was recorded graphically by the recording attenuator. Thresholds or masker levels were derived by fitting a horizontal line through the middle of each S's record. The voltage output of the accelerometer was measured for this value during stimulation of the skin and was converted to decibels re 1.0 mm peak displacement of the vibrator. Masking functions were determined for five test frequencies: 15, 25, 100, 250, and 400 Hz. For each test frequency, ten masker frequencies ranging from 10-505 Hz were employed in a simultaneous masking paradigm. To minimize interaction between the test and masker stimuli, and to reduce potential beating, test intensity was kept low (10 dB SL) and masker frequencies were chosen to avoid harmonics (Small, 1959).

During each trial, the S first tracked the threshold of the test stimulus. From this result, the intensity level of the test stimulus presented in channel II could be precisely adjusted to 10 dB SL. Prior to the simultaneous presentation of the pulsed test stimulus and the continuous masker, the S confirmed his perception of the test stimulus presented alone. This procedure served as a safeguard against commencing a trial before the cutaneous receptor recovered from adaptation resulting from a preceding trial. The time needed between trials for complete recovery of sensation ranged from a few seconds for weak maskers to approximately 1.0 min for the most intense maskers.

Within a session, one masking function was obtained for a single frequency of the test stimulus. The order in which maskers were administered within a session was random, as was the order in which test frequencies were chosen between sessions. A total of three masking functions for each test frequency was obtained from each S.

RESULTS AND DISCUSSION

Absolute thresholds and psychophysical tuning curves measured with a simultaneous masking paradigm and a rigid surround for test stimulus frequencies of: 15, 25, 250, and 400 Hz are shown in Fig. 8. The data for individual subjects were in close agreement and, therefore, it is appropriate to examine the median data for the five subjects (Fig. 9). The tuning curve procedure appeared to be highly successful in psychophysically isolating the frequency-response characteristics of the Pacinian system. The tuning curves for test stimulus frequencies of 250 Hz and 400 Hz were highly similar, both in the individual and in the median data. Both curves exhibited the characteristic U-shaped function of the Pacinian system and exhibited a slope of approximately -13 dB/octave between 15-250 Hz. These data are in agreement with the psychophysical functions of the Pacinian system obtained by selective adaptation (Verrillo & Gescheider, 1977) and with the electrophysiological data recorded from the single-fiber afferents connected to the Pacinian receptors (Mountcastle et al., 1972; Sato, 1961; Talbot et al., 1968). In these studies, the threshold functions of the Pacinian system were U-shaped, exhibiting a slope of -12 dB/octave between 15-250 Hz. In the present study, the threshold function of the Pacinian system exhibited a slope of approximately -11 dB/octave between

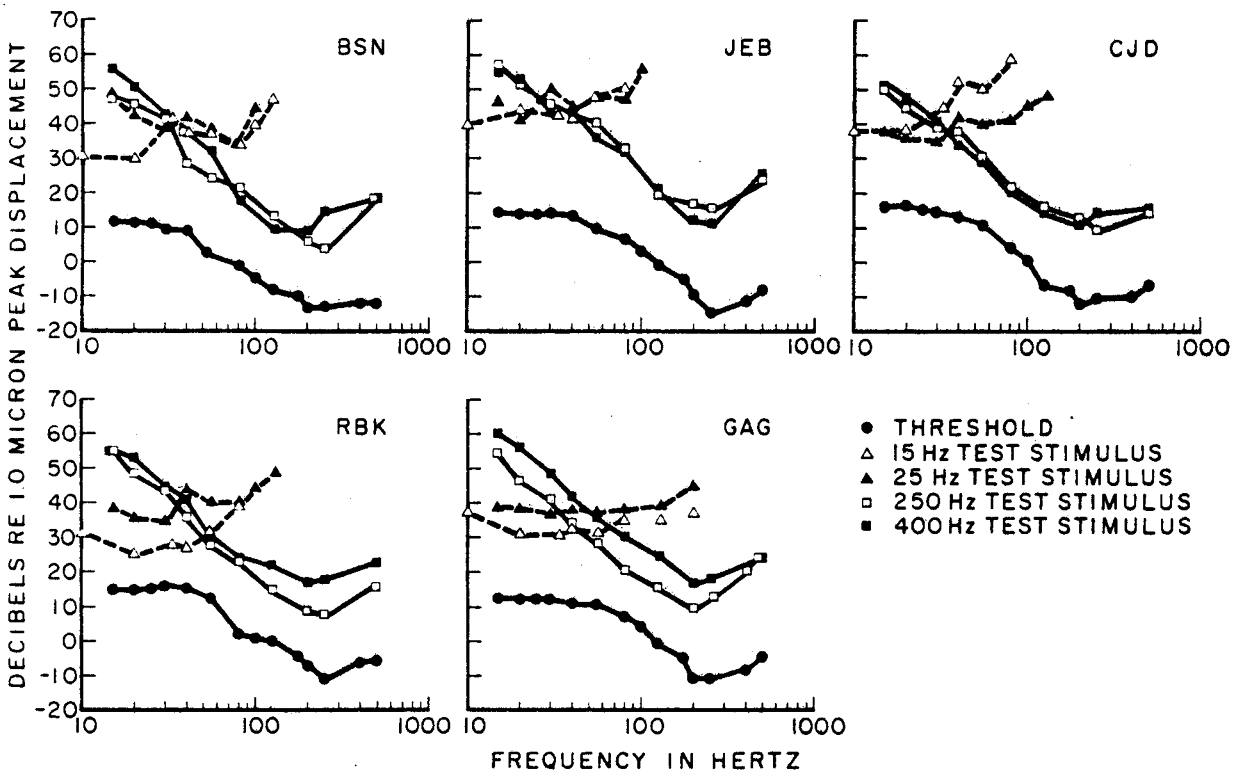

Figure 8. Cutaneous psychophysical tuning curves measured with a rigid surround for test stimulus frequencies of: 15, 25, 250, and 400 Hz, using a simultaneous masking paradigm. Absolute thresholds are included for comparison. Each point is a mean of three thresholds.

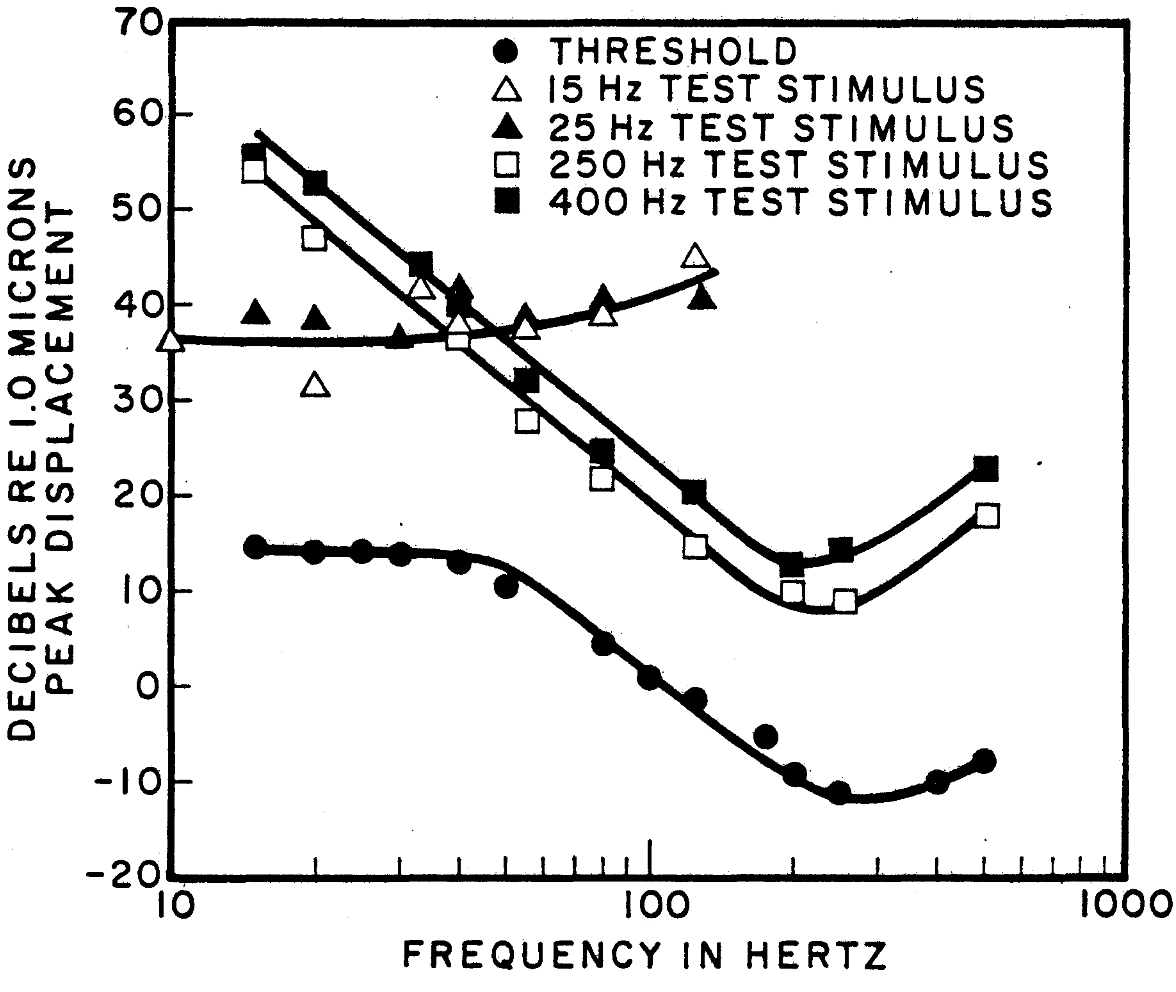

Figure 9. Median cutaneous psychophysical tuning curves measured with a rigid surround for test stimulus frequencies of: 15, 25, 250, and 400 Hz, using a simultaneous masking paradigm. The median threshold function is included.

15-250 Hz.

The tuning curve procedure employed in this experiment achieved only partial success in isolating the frequency-response characteristics of the non-Pacinian system. The tuning curves for the 15 Hz and 25 Hz test stimuli were similar in both the individual and median data. Both functions were relatively flat between 10-55 Hz, with gradually increasing slopes beyond approximately 55 Hz. Intensity limitations of the vibrator and distortion of the masking stimulus at approximately 60 dB made it impossible to obtain accurate measurements of the non-Pacinian system beyond 125 Hz for most subjects. A measurement of 37.75 dB intensity level of masker (200 Hz) required to just mask a 15 Hz test stimulus was obtained for subject GAG. In addition, with the 25 Hz test stimulus, a measurement of 45.58 dB intensity level of masker (205 Hz) was obtained for subject GAG. The Mountcastle group (Mountcastle et al., 1972; Talbot et al., 1968) have physiologically measured the frequency-response characteristics of the non-Pacinian system to a maximum frequency of 200 Hz. The physiological function (Fig. 3) and the psychophysical functions of the non-Pacinian system obtained in this study appear comparable, although it must be noted that in the physiological studies, no rigid surround was employed to confine the vibratory disturbance to the locus of stimulation. Experiment 2 was conducted to observe the effects of surround removal on the tuning characteristics of the two major functions obtained in the present study.

With the implementation of the tuning curve paradigm in auditory and, presently, vibrotactile research, comparisons can be made between the psychophysical characteristics of the auditory and cutaneous systems. Physiological and psychophysical procedures have indicated that the human auditory system is provided with a great number of narrowly-tuned, frequency-selective filters, spanning a frequency range of approximately 10-10,000 Hz. The tuning curve paradigm employed in this experiment has indicated that the cutaneous system is much more limited in its ability to process frequency information spatially. Coincident with the duplex model of mechanoreception (Verrillo, 1968), the tuning curve paradigm has indicated the existence of two, widely-tuned filters in the glabrous skin of the thenar eminence.

The masking function for the 100 Hz test stimulus for each subject is shown in Fig. 10. The data for subjects: BSN, JEB, RBK, and GAG were similar, and it is appropriate to examine the median function for these four subjects. The median function shown in Fig. 11 exhibited two distinct segments. Between 13-40 Hz, the function exhibited a slope of about -11 dB/octave, suggesting activation of the Pacinian system. Beyond 40 Hz, the function became relatively flat, suggesting activation of the non-Pacinian system. Breakpoints in the absolute threshold function, from the flat response of the non-Pacinian system to the U-shaped response of

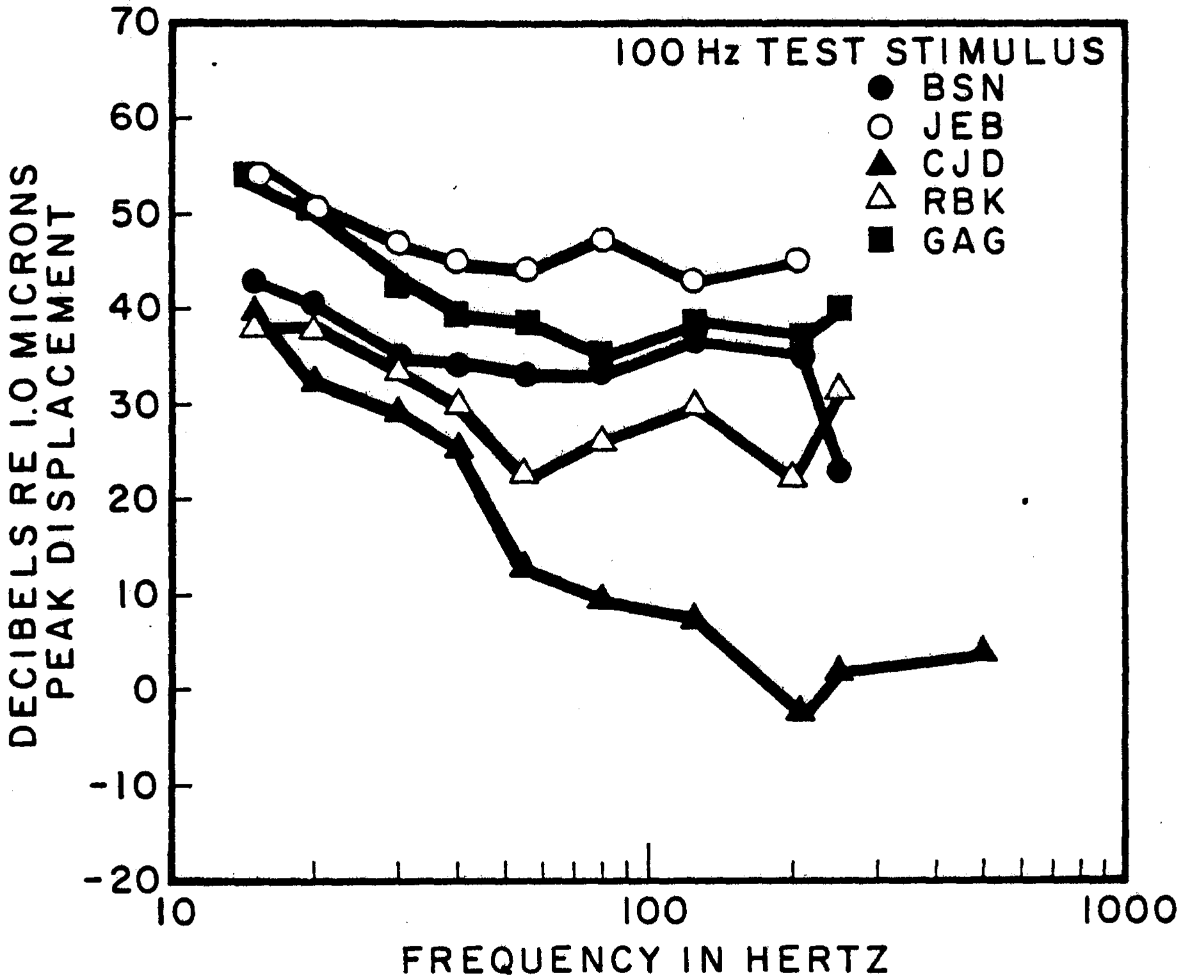

Figure 10. Cutaneous pseudo-tuning curves measured with a rigid surround for test stimulus frequency of 100 Hz, using a simultaneous masking paradigm (BSN, JEB, RBK, GAG). These functions are a composite of Pacinian and non-Pacinian mediation. The function for CJD is mediated by the Pacinian system as a result of this subject's high non-Pacinian threshold (see Fig. 8) and a relatively low Pacinian threshold at 100 Hz (0.63 dB). Each point is a mean of three thresholds.

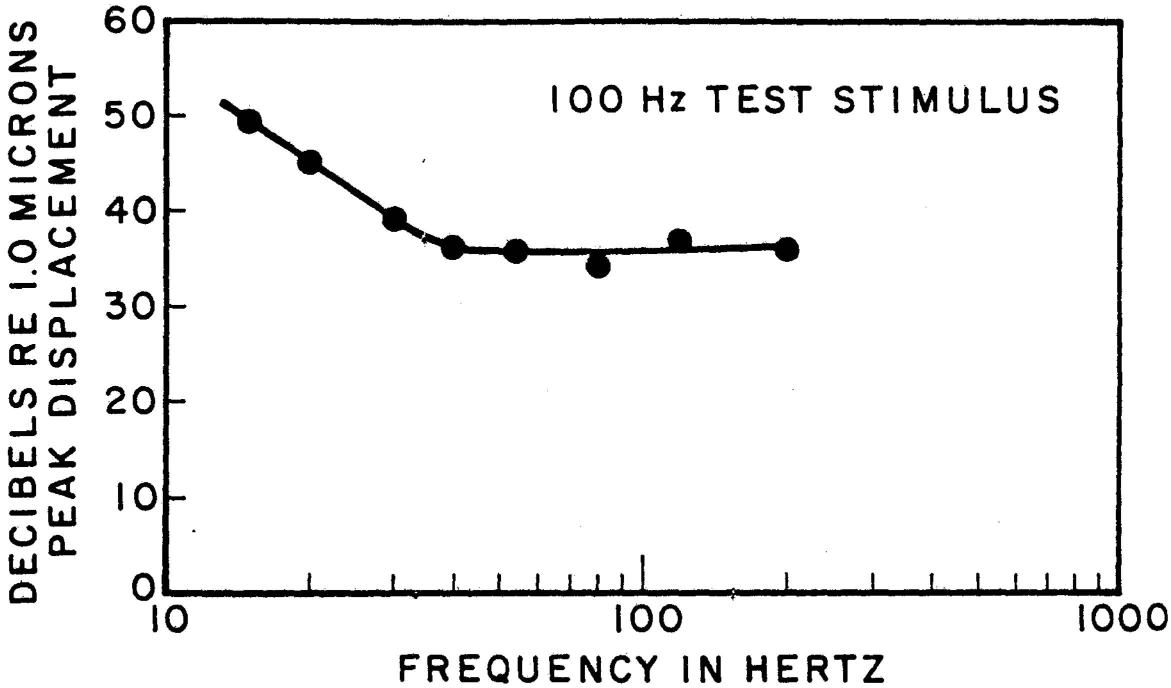

Figure 11. Median cutaneous pseudo-tuning curve measured with a rigid surround for test stimulus frequency of 100 Hz, using a simultaneous masking paradigm for subjects: BSN, JEB, RBK, and GAG.

the Pacinian system, occurred for all subjects between 40-60 Hz. The median absolute threshold at 100 Hz was 0.5 dB. When the intensity of the test stimulus is raised 10 dB SL (median intensity: 10.5 dB), it is reasonable to expect that the 100 Hz test stimulus could activate both Pacinian and non-Pacinian systems. For frequencies below the breakpoint on the threshold curve, the masker first masks the non-Pacinian system and then the Pacinian system as masker intensity is increased. The test stimulus is felt as long as one system remains unmasked. For frequencies above the breakpoint threshold, the masker must first mask the Pacinian system and then, with a further increase in masker intensity, the non-Pacinian system. It is suggested that the masking function obtained using a test stimulus frequency of 100 Hz for these four subjects is a pseudo-tuning curve, and does not reflect a third psychophysical filter, but rather reflects a composite of the operation of the Pacinian and non-Pacinian systems. Similar behavior and interpretations have been reported for psychophysical tuning curves measured in the goldfish auditory system (Fay, Ahroon, & Orawski, 1978).

The masking function produced by the 100 Hz test stimulus for subject CJD appeared to yield a complete Pacinian curve, as opposed to a composite of the operation of both cutaneous systems. This function could be expected, as this subject had a high non-Pacinian threshold and a relatively low Pacinian threshold at 100 Hz (0.6 dB). In this case, when the intensity of the 100 Hz test stimulus is raised 10 dB SL (approximately 10.6 dB), the threshold of the test stimulus is still below the threshold of the non-Pacinian, and a Pacinian function is therefore measured.

Further investigation is needed to examine the masking effects produced by test stimulus frequencies which are intermediary to both receptor systems. One such experiment currently in progress in this lab has shown composite, pseudo-tuning curves, identical to the results obtained in this study, for test stimulus frequencies of 65 Hz (breakpoint threshold) and 100 Hz. It appears that such a composite function will be obtained as long as both receptor systems are stimulated by the test stimulus frequency.

EXPERIMENT 2

In the second experiment, the simultaneous masking paradigm employed in Experiment 1 was utilized to determine masking functions for two test frequencies, 15 Hz and 250 Hz, measured without a rigid surround. A rigid surround serves to confine the vibratory disturbance to the area of the contactor; its removal allows the vibration to spread across the surface of the skin. Gescheider et al. (in press) have shown that removal of the rigid surround results in a reduction of thresholds along the Pacinian branch of the threshold function and an elevation of thresholds along the non-Pacinian branch. Furthermore, when the rigid surround was employed, the non-Pacinian system had a flat frequency response, but when the surround was removed, the threshold function for this system was elevated and had a slope of -6 dB/octave measured out to 50 Hz. These psychophysical results were directly comparable to the frequency-response functions recorded without surround from the quickly-adapting afferents, believed to innervate Meissner corpuscles and Pacinian corpuscles, and the psychophysical thresholds, also measured without surround in monkeys and in humans (Mountcastle et al., 1972; Talbot et al., 1968).

The use of the tuning curve paradigm in this experiment without a rigid surround was an attempt to determine more completely the frequency response of the non-Pacinian system by a psychophysical procedure.

METHOD

SUBJECTS

The subjects were five male adults ranging in age from 19 to 41 years. All subjects had served in Experiment 1.

APPARATUS

The apparatus was the same as that used in Experiment 1 except for the removal of the rigid surround. The contactor was applied to the skin through a 28.3 cm^2 hole in the table. This modification allowed vibration to spread over the thenar eminence, while providing sufficient support for the hand and insuring stable mechanical coupling between the contactor and the skin.

PROCEDURE

A simultaneous masking paradigm described in Experiment 1 was used to measure masking functions for test frequency stimuli of 15 Hz and 250 Hz. For each S, three measurements of the intensity the masker needed to mask the 10 dB SL test stimuli were obtained for a wide range of masker frequencies. All measurements were expressed in decibels re 1.0 micron peak displacement of the vibrator.

RESULTS AND DISCUSSION

Absolute thresholds and psychophysical tuning curves measured with a simultaneous masking paradigm and without a rigid surround for test frequencies of 15 Hz and 250 Hz are shown in Fig. 12. The data for individual subjects were in close agreement, and therefore it is appropriate to examine the median function for the five subjects (Fig. 13). As in Experiment 1, the tuning curve paradigm appeared to be highly successful in psychophysically isolating the frequency-response characteristics of the Pacinian system. The individual and median functions for the 250 Hz test stimulus were all U-shaped. The slope of the median curve was approximately -14 dB/octave between 15-250 Hz. The Pacinian branch of the median threshold curve exhibited a slope of approximately -14 dB/octave between 35-200 Hz.

The median tuning curves produced by the 250 Hz test stimulus in Experiments 1 (Fig. 9) and 2 (Fig. 13) were identical in shape and slope. The sensitivity level of these two functions was highly similar, differing on the average by approximately 2 dB. In accordance with the Gescheider et al. study (in press), removal of the rigid surround did not appear to significantly affect the threshold or the tuning characteristics of the Pacinian system. Only when a relatively small contactor (0.2 cm^2) was used, were the thresholds of the

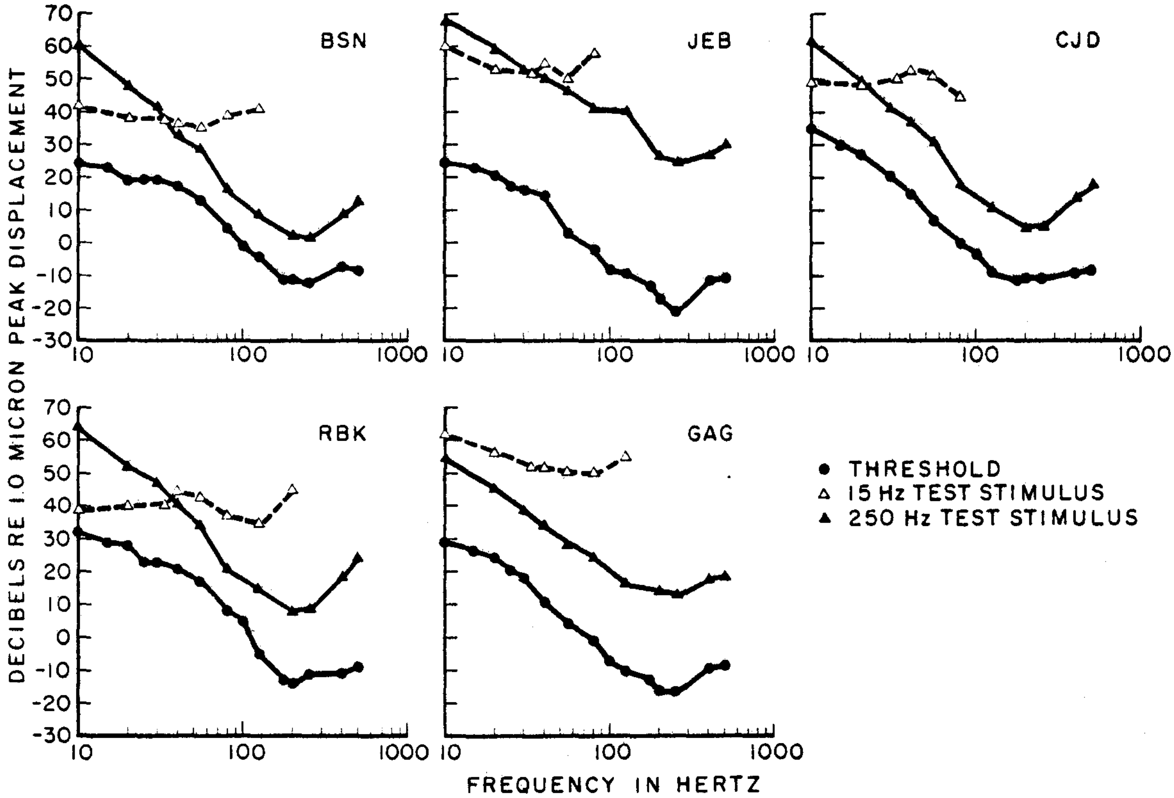

Figure 12. Cutaneous psychophysical tuning curves measured without a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a simultaneous masking paradigm. Absolute threshold functions are included for comparison. Each point is a mean of three thresholds.

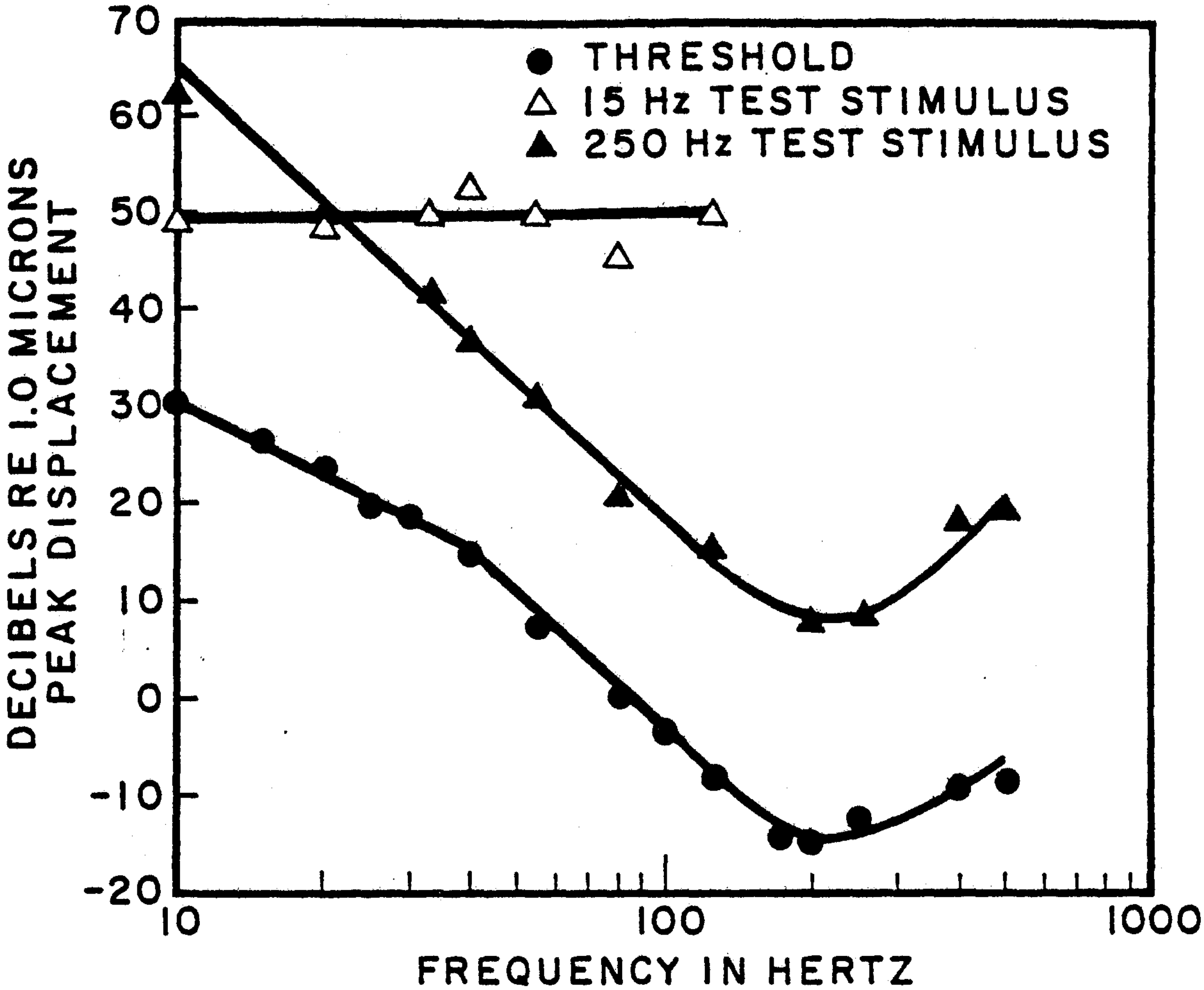

Figure 13. Median cutaneous psychophysical tuning curves measured without a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a simultaneous masking paradigm. The median threshold function is included for comparison.

U-shaped portion of the curve appreciably affected by removal of the surround.

Again, the data produced by the 250 Hz test stimulus are in agreement with the psychophysical functions of the Pacinian system obtained by selective adaptation (Verrillo & Gescheider, 1977) and the electrophysiological recordings from single-fiber afferents innervating the Pacinian receptors (Talbot et al., 1968).

As in Experiment 1, the tuning curve procedure employed in this experiment was only partially successful in psychophysically determining the frequency-response characteristics of the non-Pacinian system. The median function produced by the 15 Hz test stimulus was relatively flat between 10-80 Hz. Intensity limitations of the vibrator and distortion of the masking stimulus at approximately 60 dB made it impossible to obtain accurate measurements of the non-Pacinian system beyond 80 Hz for subjects JEB and CJD, and beyond 125 Hz for subjects BSN and GAG.

A comparison of the tuning curves produced by the 15 Hz test stimulus in Experiment 1 (Fig. 9) and 2 (Fig. 13) indicated that removal of the rigid surround elevates the threshold of the non-Pacinian system by about 12.6 dB on the average. This agrees with the Gescheider et al. (in press) finding that removal of the surround elevates the threshold of the non-Pacinian curve, and changes the shape of the threshold function from flat to sloping (-6 dB/octave). A comparison of the threshold functions of Experiments 1 and 2 shows that this finding was replicated in the present study.

For three of the five subjects, the tuning characteristics of the psychophysical masking function measured for the 15 Hz test stimulus without a rigid surround are comparable to the frequency-response characteristics of the non-Pacinian system measured to a maximum frequency of 200 Hz electrophysiologically without a rigid surround by Mountcastle et al. (1972) and Talbot et al. (1968; see Fig. 3). The other two subjects have flat curves. The tuning curves for these two subjects do not account well for their low-frequency thresholds (no 6 dB/octave slope).

Interest concerning the shape and slope of the non-Pacinian function beyond 80-125 Hz led to the formulation of Experiments 3 and 4 in which a forward masking paradigm was employed to measure the tuning characteristics of both the Pacinian and non-Pacinian systems. Thus, comparison of the simultaneous and forward masking data provides an opportunity to evaluate the possible effects of physical interaction of the masker and test stimuli on the shape of the tuning curves.

EXPERIMENT 3

A forward masking paradigm was employed in determining masking functions for test stimulus frequencies of 15 Hz and 250 Hz, measured with a rigid surround. In this procedure, since the test stimulus and masker were applied to the skin at different times, the results could not be explained in terms of a complex interaction between the two stimuli, as in the first two experiments in which a simultaneous masking paradigm was employed. It was thus anticipated that the forward masking procedure might be more effective in isolating the frequency-response characteristics of both cutaneous systems than the simultaneous masking procedure. Recent evidence by Hamer (unpublished dissertation, 1978) has shown that the threshold for a 23 Hz test stimulus is almost unchanged when a simultaneous 250 Hz masker is presented at an intensity level of 34 dB SL than when no masker is presented. However, current investigations in this lab have shown that the threshold of a 15 Hz test stimulus is reduced by 10 dB when a simultaneous 250 Hz masker is presented at 30-40 dB SL. In this case, the subject may be detecting the low-frequency stimulus by the Pacinian system because the test stimulus disrupts the entrainment of neural firing in this system, resulting in detectable cues. Separating the test stimulus and the masker in time may have the consequence of allowing the measurement of the actual neural tuning curve at high frequencies.

METHOD

SUBJECTS

Three male undergraduates (ages: 19-21 years) with no previous experience in psychophysical experiments, and the 41-year-old male who served in the first two experiments were employed as Ss. Prior to the experiment, each S was given extensive practice in tracking the threshold of vibrotactile stimuli applied to the thenar eminence.

APPARATUS

The apparatus employed in the first two experiments was modified to provide the new timing relationships of the masker and observation intervals illustrated in Fig. 14. A 500 msec, 10-v dc pulse from a Tektronix Type 161 pulse generator was applied to the gating circuit of electronic switch I. The resulting masker stimulus was 500 msec in duration at half-power points, with a rise-decay time of 50 msec. A second 500 msec pulse, occurring 650 msec after the first was followed by a 1,100 msec delay before the pair of 500 msec stimuli was repeated in a continuous train. The timing of the masker stimulus was regulated by a Tektronix Type 162 waveform generator which determined the pulse rate from the pulse generator.

Test stimuli of 200 msec duration were controlled by a 10-v dc, 200 msec pulse from a Tektronix Type 161 pulse

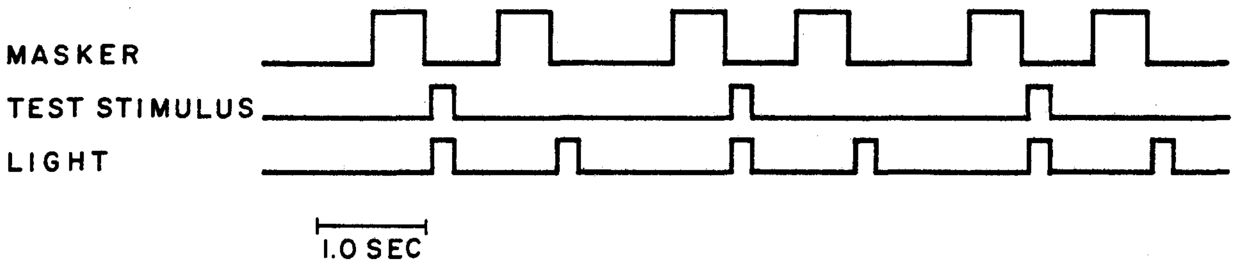

Figure 14. Timing relationship of test and masker stimuli and observation light employed in the forward masking paradigm (Experiments 3, 4).

generator which was applied to the gating circuit of electronic switch II. The 2.75 sec repetition rate of the test stimulus was controlled by a Tektronix Type 162 waveform generator. The onset of the test stimulus occurred 25 msec after the offset of the masker to provide a momentary break of sensation between test stimulus and masker.

Observation intervals were signaled by a light-emitting diode. A 200 msec flash was adjusted to be temporally contiguous with the test stimulus. A second 200 msec observation interval containing no stimulus was presented 50 msec after the presentation of the second 500 msec masker. The S could make a direct comparison of observation intervals containing the stimulus with an observation interval not containing the stimulus when both observation intervals came immediately after the masking stimulus.

PROCEDURE

A forward masking paradigm was employed to determine masking functions for test frequencies of 15 Hz and 250 Hz measured by the SN-N tracking procedure described in Experiment 1. For each test frequency, ten masker frequencies ranging from 10-500 Hz were utilized.

During each trial, the S first tracked the threshold of the test stimulus. From this result, the intensity level of the test stimulus presented in channel II could be precisely adjusted to 10 dB SL. The time between trials was sufficiently long to allow for the recovery from any adaptation that may occur during testing. The time required for recovery of sensation ranged from a few seconds to approximately 1.0 min, depending upon masker intensity.

Witnin a session, one masking function was obtained for a single frequency of the test stimulus. A total of three masking functions for each test frequency was obtained for each S.

RESULTS AND DISCUSSION

Absolute thresholds and psychophysical tuning curves measured with a forward masking paradigm and a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz are shown in Fig. 15. The data for individual subjects were in close agreement and it is therefore appropriate to examine the median function of the three subjects (Fig. 16). The forward masking procedure was successful in psychophysically isolating the frequency-response characteristics of both the Pacinian and non-Pacinian systems.

The median masking function produced by the 250 Hz test stimulus was U-shaped, with a slope of approximately -11 dB/octave between 15-250 Hz, indicating Pacinian mediation for the detection of the test stimulus. The slope of the median threshold function between 80-250 Hz was approximately -11 dB/octave.

A comparison of the tuning curves produced by the 250 Hz test stimulus in Experiment 1 (Fig. 9), in which a simultaneous masking paradigm was employed and in the present experiment (Fig. 16) revealed a noteworthy difference in sensitivity. The simultaneous masking paradigm appeared to be a more effective procedure to mask the 250 Hz test stimulus consistently across the frequency range of masking stimuli (15-505 Hz) than the forward masking paradigm. In the present

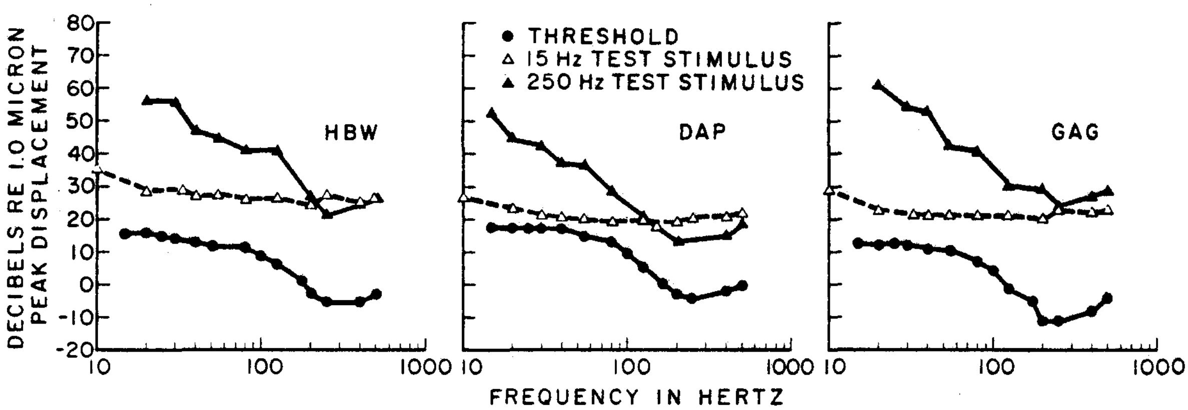

Figure 15. Cutaneous psychophysical tuning curves measured with a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a forward masking paradigm. Absolute threshold functions are included for comparison. Each point is a mean of three thresholds.

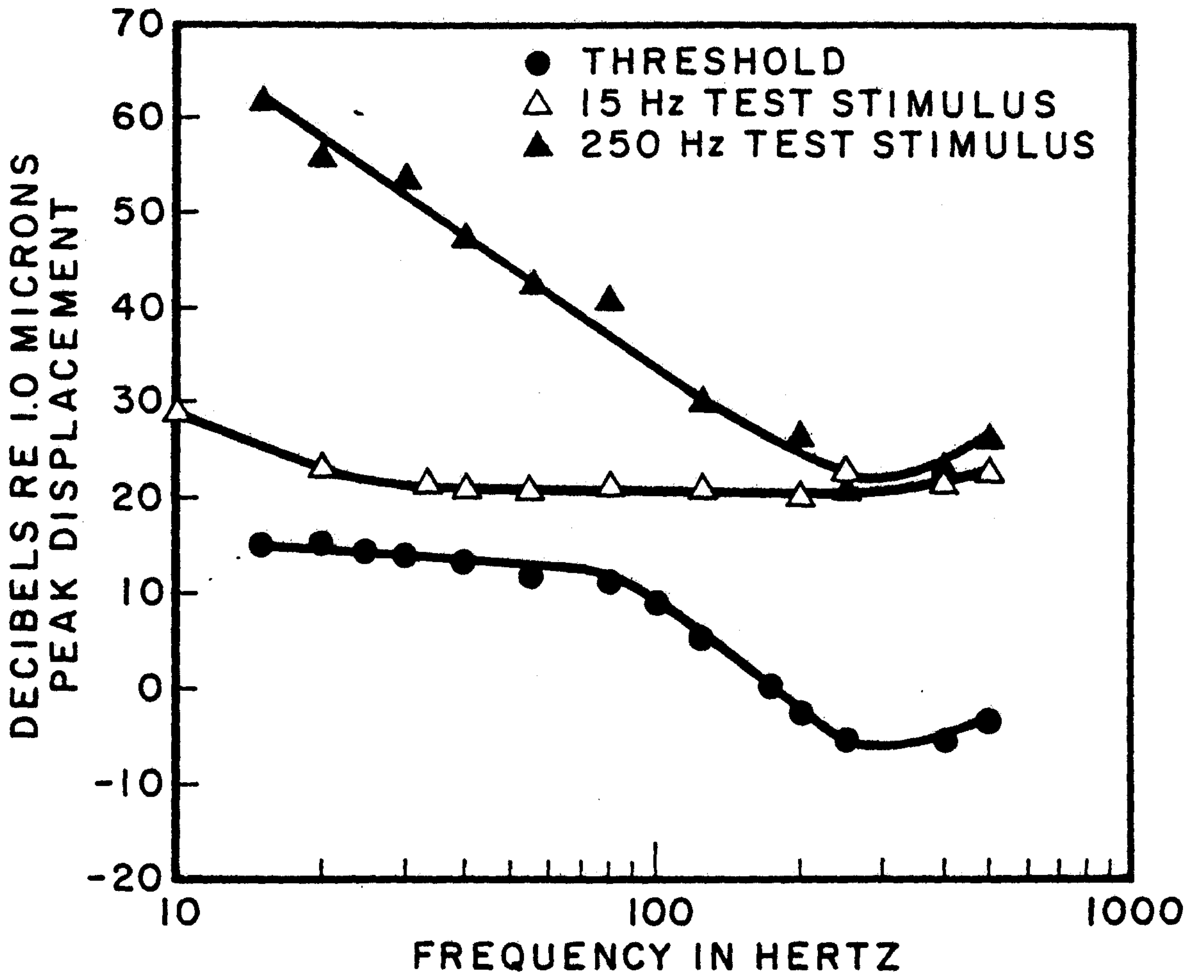

Figure 16. Median cutaneous psychophysical tuning curves measured with a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a forward masking paradigm. The median threshold curve is included for comparison.

experiment, masker intensity was required to be, on the average, 12 dB higher to mask detection of the 250 test stimulus than the masker intensity in the simultaneous masking procedure (Experiment 1). The finding that simultaneous masking is more effective than forward masking has also been demonstrated by Sherrick (1964) who found that thresholds are progressively elevated as the time interval between the test stimulus and the masking stimulus is decreased.

The median tuning curve produced by the 15 Hz test stimulus was relatively flat between 20-500 Hz. There was a gradual slope in the function between 10-20 Hz. The electrophysiological function of the non-Pacinian, quickly-adapting fibers system, measured without surround (Talbot et al., 1968) was relatively flat between 10-40 Hz, with a gradual slope of approximately -4 dB/octave between 10-20 Hz, and a slope of approximately +6 dB/octave between 40-200 Hz (Fig. 3, open circles). This is not seen in the tuning curve and, in fact, the nearly flat tuning curve looks more like the flat psychophysical threshold curves obtained with surround at low frequencies for large contactors and at all frequencies for the smallest contactors. Further physiological investigations in which recordings are made both with and without rigid surround are needed to determine whether the tuning characteristics of cutaneous receptors are altered under these two conditions. From the tuning curve data, we would predict that the frequency response of the receptors would be flatter with than without surround.

The tuning curves produced by the 15 Hz test stimulus in the simultaneous masking study (Experiment 1, Fig. 9) and in the forward masking study (Experiment 2, Fig. 13), both measured with surrounds, differed in sensitivity level. The non-Pacinian masking function in which forward masking was employed was, on the average, 16 dB lower than the non-Pacinian masking function measured by the simultaneous masking procedure. The fact that the threshold of the non-Pacinian system could be measured out to 500 Hz in the present investigation suggests that a forward masking procedure appeared to be a more effective means to determine the psychophysical tuning characteristics of the non-Pacinian system than the simultaneous masking procedure.

It is interesting to note that in the present experiment, the median masking function of the Pacinian system is higher at all frequencies than the function of the non-Pacinian system, with the exception of a single point at 255 Hz. The data from subject GAG showed this general pattern, with all points comprising the Pacinian function above those of the non-Pacinian system. The data from the other two subjects, HBN and DAP, indicated that a portion of the Pacinian function above 200 Hz and 175 Hz, respectively, was below the non-Pacinian function.

A comparison of the results of Experiments 1 (Fig. 9) and 3 (Fig. 16) appeared to indicate that a forward masking procedure is more effective in masking a 15 Hz test stimulus, across masker frequencies, than a simultaneous masking procedure. However, it also appeared that a simultaneous masking procedure is, in general, more effective in masking a 250 Hz test stimulus across masker frequencies than a forward masking procedure. Further investigations are indicated to account for these findings.

Experiment 4 was conducted to investigate the effects of surround removal on the tuning characteristics of the Pacinian and non-Pacinian systems, as measured by a forward masking paradigm.

EXPERIMENT 4

In the fourth experiment, the forward masking procedure outlined in Experiment 3 was employed to determine masking functions for test stimuli of 15 Hz and 250 Hz, measured without a rigid surround. It was previously explained in Experiment 2 that removal of the rigid surround allows vibration to spread over the surface of the skin. This procedure has been shown to elevate the threshold of the non-Pacinian system to a slope of approximately -6 dB/octave measured to 50 Hz, and to lower the U-shaped threshold of the Pacinian system (Gescheider et al., in press).

The forward masking paradigm was employed to determine the form of Pacinian and non-Pacinian tuning curves obtained in the absence of a rigid surround under conditions in which the results could not be contaminated by the effects of physical interaction between masker and test stimulus.

METHOD

SUBJECTS

The subjects were three male adults ranging in age from 19 to 41 years. All subjects had served in Experiment 3.

APPARATUS

The apparatus was the same as that used in Experiment 3, except for the removal of the rigid surround. The .75 cm^2 contactor was applied to the skin of the thenar eminence through a 28.3 cm^2 hole in the table. This arrangement allowed the vibration to spread over a wide range or skin while providing sufficient support for the hand and constant mechanical coupling between the contactor and the skin.

PROCEDURE

The forward masking procedure described in Experiment 3 was used to measure masking functions for test frequency stimuli: 15 Hz and 250 Hz. For each S, three measurements of masker threshold were obtained at each test frequency. All measurements were expressed in decibels re 1.0 micron peak displacement of the vibrator.

RESULTS AND DISCUSSION

Absolute thresholds and masking functions measured with a forward masking paradigm and a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz are shown in Fig. 17. A median function was determined for the three subjects and appears in Fig. 18.

As in Experiment 3, the forward masking procedure provided an effective means to psychophysically isolate the frequency-response characteristics of the Pacinian and non-Pacinian systems. The median masking function produced by the 250 Hz test stimulus exhibited a U shape, characteristic of the Pacinian function, and had a slope of approximately -14 dB/octave between 15-250 Hz. The slope of the median absolute threshold function was -13 dB/octave between 40-255 Hz. Although there were differences in sensitivity level, the shape of the 250 Hz masking functions for the three subjects were in fairly close agreement. Considerable variability in the 200 Hz and 255 Hz data points for subject HBW rendered their accuracy somewhat questionable. It is speculated that the subject was tracking the ringing produced by the intense masking stimulus, rather than tracking the test stimulus. A close inspection of the data for subject DAP revealed a 10.3 dB difference between the mean of the absolute threshold for 250 Hz (-7.92 dB), determined prior to Experiment 3, and the

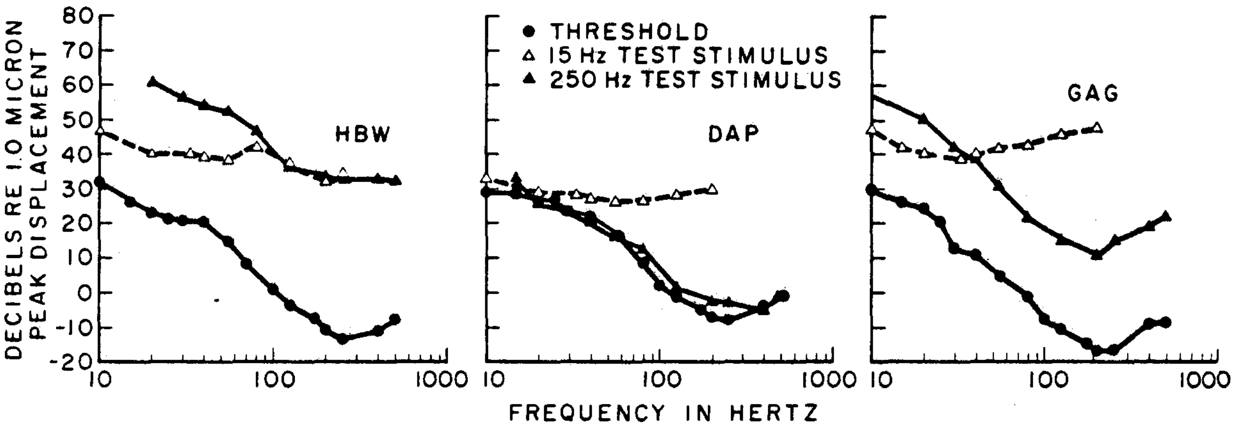

Figure 17. Cutaneous psychophysical tuning curves measured without a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a forward masking paradigm. Absolute threshold functions are included for comparison. Each point is a median of three thresholds.

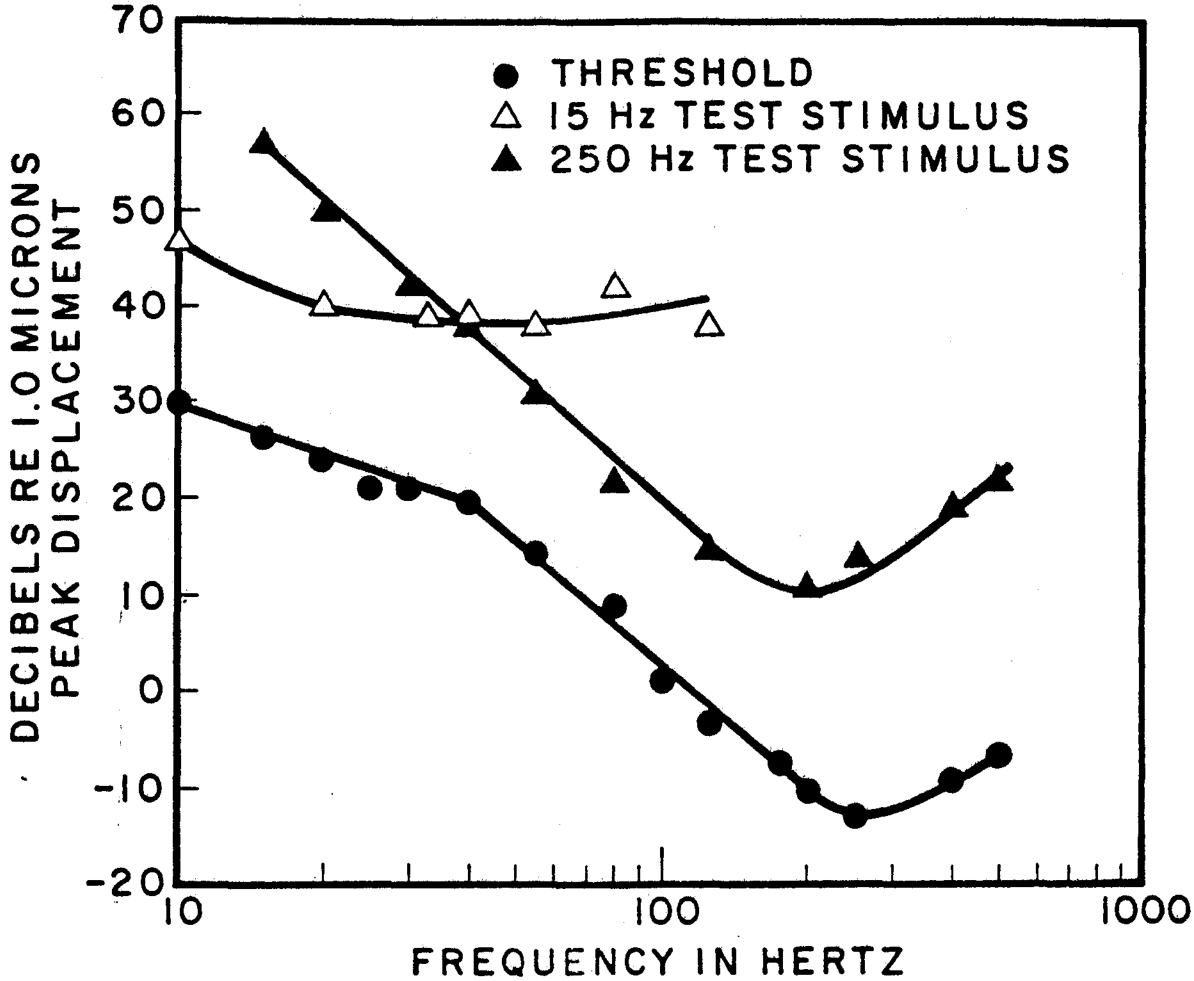

Figure 18. Median cutaneous psychophysical tuning curves measured without a rigid surround for test stimulus frequencies of 15 Hz and 250 Hz, using a forward masking paradigm. The median threshold curve is included for comparison.

threshold of the 250 Hz test stimulus (-18.25 dB), from which the intensity level was set at 10 dB SL for the masking procedure. Because of this unexpected shift in sensitivity, the amount of masking produced in this experiment can not be accurately determined by comparing the absolute threshold function with the masking function for 250 Hz for subject DAP.

Removal of the rigid surround in the present experiment lowered the Pacinian portion of the absolute threshold function between 80-505 Hz by an average of 7.5 dB. Under these conditions, removal of the rigid surround appeared to produce results equivalent to those obtained with a large contactor. Gescheider et al. (in press) have shown that the Pacinian system is capable of summating stimulus energy across space; however, the non-Pacinian system is incapable of spatial summation, and instead, responds to gradients. With the rigid surround removed, there is no sharply defined gradient and, therefore, more stimulus intensity is required to attain threshold level. The 250 Hz masking function was also lowered by an average of 9.8 dB from Experiment 3 (Fig. 16), as a result of surround removal. The net result appeared to indicate an approximately equivalent amount of masking produced under conditions of surround and no surround, using a forward masking paradigm, as was found in Experiments 1 and 2, in which a simultaneous masking paradigm was employed.

The masking function produced by the 250 Hz test stimulus and measured with the simultaneous masking paradigm

(Experiment 1, Fig. 9) and the forward masking paradigm (Experiment 3, Fig. 16), both with surrounds, are identical in shape, slope, and sensitivity level. Both procedures appeared equally effective in measuring the tuning characteristics of the Pacinian system.

The median masking function produced by the 15 Hz test stimulus in the present experiment was relatively flat between 20-55 Hz, with a slope of about 7 dB/octave between 10-20 Hz, and a gradually increasing slope beyond 55 Hz. Intensity limitations of the vibrator and distortion problems beyond masker intensities of 60 dB rendered measurements beyond about 200 Hz impossible.

Using the forward masking procedure, removal of the rigid surround appeared to elevate the threshold of the non-Pacinian function by an average of 13 dB. This finding is in accordance with the Gescheider et al. finding (in press) that surround removal elevated the threshold function of the non-Pacinian system.

A comparison of the psychophysical functions of the non-Pacinian system measured without a surround, employing a simultaneous procedure (Experiment 2, Fig. 13) and employing a forward masking procedure (Experiment 4, Fig. 18) indicated that a forward masking stimulus, across the frequency range of 15-200 Hz, is generally more effective at masking a 15 Hz test stimulus than a simultaneous masking stimulus. Further investigations must address the problem of explaining this phenomenon.

GENERAL DISCUSSION

The previous four experiments have attempted to: 1) isolate and psychophysically measure the frequency-response (tuning) characteristics of the Pacinian and non-Pacinian systems in the glabrous skin of the thenar eminence, 2) compare the efficacy of a simultaneous masking paradigm and a forward masking paradigm in achieving these measurements, 3) compare the tuning characteristics of the cutaneous systems measured under conditions with and without rigid surround with established psychophysical and electrophysiological data, and 4) compare and contrast the processing of frequency stimuli in the cutaneous and auditory systems.

Both simultaneous and forward masking procedures were highly successful in measuring the frequency-response characteristics of the Pacinian system. The tuning curves produced by a 250 Hz test stimulus, measured both with and without rigid surrounds, were similar in shape and slope to the electrophysiological functions measured from single-fiber afferents innervating the Pacinian receptors (Talbot et al., 1968) and the psychophysical functions obtained through selective adaptation (Verrillo & Gescheider, 1977). In general, the simultaneous and the forward masking procedures were found to be equally effective in measuring the tuning characteristics of the Pacinian system, measured in conditions where rigid surrounds were and were not employed. A noteworthy exception to this finding was found in comparing the results of Experiment 1 (Fig. 9), in which a simultaneous masking paradigm was employed, with the results of Experiment 3 (Fig. 16), in which a forward masking paradigm was employed. In both experiments, rigid surrounds were employed during measurement. A simultaneous masker, across the frequency range of masking stimuli (15-505 Hz) was found to be a more effective masker than a forward masking stimulus. Further investigations are necessary to evaluate the effects of reducing the time interval between the offset of the masker and the onset of the test stimulus. Instead of employing an inter-stimulus interval of 25 msec between the masker and the test stimulus, the interval could be reduced so that no time gap existed between stimuli. It was recently found in measuring psychoacoustic tuning curves (Moore, 1978) that this procedure served to render a more effective forward masking stimulus.

Removal of the rigid surround did not significantly affect the tuning characteristics (shape, slope) of the tuning curve of the Pacinian system, measured with both a simultaneous and a forward masking paradigm. Removing the surround did affect the sensitivity level of the Pacinian function only under the forward masking paradigm. The sensitivity levels of the Pacinian curves, measured with and without surrounds, using a simultaneous masking paradigm were virtually identical. It was proposed that the decrease in the threshold of the Pacinian branch of the absolute threshold function and in the 250 Hz masking function measured in Experiment 4 (Fig. 18) was due to the capacity of the Pacinian system for spatial summation. Removal of the surround appeared to be equivalent to employing a large contactor under these conditions.

The simultaneous and forward masking procedures were only partially successful in measuring the psychophysical tuning characteristics of the non-Pacinian system. A number of factors including intensity limitations of the vibrator and distortion of the masking stimulus at approximately 60 dB made accurate measurements of the non-Pacinian system beyond 125-200 Hz impossible. One solution to these problems might be to lower the intensity of the test stimulus. Pilot data prior to this study were obtained using a test stimulus of 5 dB SL intensity. As was found in Moore's (1978) psychoacoustic tuning curve study, this intensity level of the test stimulus was difficult for the subjects to perceive, easily adapted, and resulted in highly variable data, mainly due to the day-to-day fluctuations in absolute sensitivity. The intensity level of the test stimulus for this study was set at 10 dB SL in order that the stimulus be clearly above threshold, and easily detectable to the subject. However, at this intensity level, it was necessary to increase the intensity of the masking stimulus to levels at which ringing and distortion occurred before masking was observed. If the masker intensity could be reduced, either by reducing the intensity of the test stimulus, or employing a more effective masking stimulus, it might be possible to psychophysically measure the entire non-Pacinian tuning curve. Further investigations might consider using a test stimulus of 7 dB SL intensity level.

In the conditions where rigid surrounds were employed (Figs. 9 and 16) and surrounds were not employed (Figs. 13 and 18), the forward masking procedure produced tuning curves which were of lower intensity than when measured by the simultaneous masking procedure. Further investigations are indicated to explain why forward masking is more effective than simultaneous masking for low frequency stimuli.

Removal of the rigid surround in Experiment 2 (simultaneous masking) and Experiment 4 (forward masking) resulted in an elevation of the non-Pacinian branch of the absolute threshold function, as was observed by Gescheider et al. (in press); however, a corresponding change in the tuning characteristics of the non-Pacinian system was not observed in the resulting masking function (see Figs. 13 and 18). The tuning curves produced by the 15 Hz test stimulus, measured without surround were comparable to the frequency response characteristics of the non-Pacinian system, measured to a maximum frequency of 200 Hz, electrophysiologically, without a rigid surround by Mountcastle et al. (1972) and Talbot et al. (1968). The tuning curves produced by the 15 Hz test stimulus with a rigid surround are comparable to these electrophysiological functions; however, a complete comparison cannot be assessed until electrophysiological data are obtained from the non-Pacinian system, employing a rigid surround to confine the stimulus energy to the locus of stimulation.

With the implementation of the tuning curve paradigm in auditory, and presently in vibrotactile research, comparisons can be made between the psychophysical and neurophysiological characteristics of the auditory and cutaneous systems. Physiological and psychophysical procedures have indicated that the human auditory system is provided with a great number of narrowly-tuned, frequency-sensitive filters, spanning a frequency range of approximately 10-10,000 Hz. The tuning curve paradigm employed in this investigation has indicated that the cutaneous system is much more limited in its ability to process frequency information via a spatial or "labeled-lines" code. In support of the duplex model of mechanoreception (Gescheider, 1976; Verrillo, 1968), the tuning curve paradigm (both simultaneous and forward masking) employed in this study has indicated the existence of two, widely-tuned filters in the glabrous skin of the thenar eminence, each with a characteristic shape and range of frequency-sensitivity. The pseudo-tuning curves obtained for the 100 Hz test stimulus lent further support for this model, as it was indicated that the curve was a composite function of Pacinian and non-Pacinian mediation.

The psychophysical and physiological tuning characteristics of the receptor systems in the ear and the skin represent major differences in the two sensory systems. Moore (1978) recently demonstrated that the tuning characteristics of the auditory system change, depending on whether the functions are measured with a forward masking or a simultaneous masking paradigm. When measured with a forward masking paradigm, the V-shaped psychoacoustic functions are more finely-tuned, show steeper slopes, particularly on the high-frequency side, and tip bandwidths which are more narrow than those measured with a simultaneous masking paradigm. Moore (1978) suggested that in simultaneous masking, the threshold of the test stimulus may be influenced by lateral suppression (inhibition). The masking stimulus may suppress the activity evoked by the test without itself producing an excitatory effect in the channels responding to the test stimulus. Thus, Moore (1978) suggested that the simultaneous masking function will not be analogous to the neural tuning curve, will be more broadly-tuned, and will represent the boundaries of the "suppression areas".

In the cutaneous system, the tuning characteristics of the Pacinian and non-Pacinian systems did not appear to change when measured by a simultaneous or by a forward masking procedure. The notion of lateral suppression suggested by Moore (1978) does not appear to operate in the cutaneous system as it does in the auditory system, because frequency processing in the skin is not analogous to the cochlear model proposed by Békésy (1960). It would be interesting to experimentally induce a cochlear model of vibrotaction by placing a masking stimulus at varying distances on the skin from a fixed test stimulus and observing the effects on the tuning characteristics of the two cutaneous systems.

In conclusion, the use of the tuning curve paradigm, adopted from auditory literature and applied to the study of mechanoreception, has proven to be a new method by which the characteristics of the cutaneous systems may be examined. The "psychocutaneous" tuning curves measured by the simultaneous and forward masking procedures lend support to the duplex model of mechanoreception, and have provided some insight into the mechanisms involved in human vibrotaction.

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The thesis is therefore accepted in partial fulfillment of the requirements for the degree of Master of Arts.

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