Four channels mediate the mechanical aspects of touch

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Although previous physiological and anatomical experiments have identified four afferent fiber types (PC, RA, SA II, and SA I) in glabrous (nonhairy) skin of the human somatosensory periphery, only three have been shown to mediate tactile (mechanoreceptive) sensation. Psychophysical evidence that four channels (P, NP I, NP II, and NP III) do, indeed, participate in the perceptual process is presented. In a series of experiments involving selective masking of the various channels, modification of the skin-surface temperature, and testing cutaneous sensitivity down to very low-vibratory frequencies, the fourth psychophysical channel (NP III) is defined. Based on these experiments and previous work from our laboratory, it is concluded that the four channels work in conjunction at threshold to create an operating range for the perception of vibration that extends from at least 0.4 to greater than 500 Hz. Each of the four channels appears to mediate specific portions of the overall threshold-frequency characteristic. Selection of appropriate neural-response criteria from previously published physiological data and correlation of their derived frequency characteristics with the four psychophysical channels indicates that each channel has its own physiological substrate: P channel and PC fibers, NP I channel and RA fibers, NP II channel and SA II fibers, and NP III channel and SA I fibers. These channels partially overlap in their absolute sensitivities, making it likely that suprathreshold stimuli may activate two or more of the channels at the same time. Thus the perceptual qualities of touch may be determined by the combined inputs from four channels.

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INTRODUCTION

Microneurographic recordings from nerves innervating the glabrous skin of the human hand have isolated four groups of low-threshold, mechanoreceptive fibers: (a) rapidly adapting (RA) fibers; (b) type I, slowly adapting (SA I) fibers; (c) type II, slowly adapting (SA II) fibers; and (d) Pacinian corpuscle (PC) fibers (Johansson and Vallbo, 1979; for review, see Vallbo and Johansson, 1984). In addition to possessing different rates of adaptation in their responses to pulselike mechanical stimuli, the fiber types have other functional characteristics that help permit classification into the four categories. For example, PCs and SA IIs have large receptive fields that lack distinct borders, while the receptive fields of RAs and SA Is are smaller but better defined (Johansson, 1976, 1978). Furthermore, the different fiber types seem to have distinct capacities to respond to specific frequency ranges of vibratory stimuli, as displayed by the "tuning" properties of isoresponse contours (Johans-

son *et al.*, 1982a). This segregation of response characteristics is apparently present beyond the primary afferent level, extending even to cortical levels (for review, see Dykes, 1983).

In spite of the fact that there appear to be four separate classes of fibers presumably involved in mediating the non-painful aspects of taction, psychophysical experiments on the glabrous skin of human observers have assayed only three such information channels (Capraro *et al.*, 1979; Bolanowski and Verrillo, 1982; Gescheider *et al.*, 1985; Verrillo and Bolanowski, 1986). The P channel, as measured in threshold experiments, typically operates over the vibratory-frequency range of 40–800 Hz and possesses a U-shaped threshold-frequency characteristic with a maximum sensitivity near 300 Hz (for review, see Verrillo, 1975). This channel is highly sensitive to changes in skin-surface temperature (Bolanowski and Verrillo, 1982) and to changes in stimulus size and duration (Verrillo, 1962, 1963, 1966b). Since increases in both the size and duration of a stimulus preferentially activating the P channel produces decreases in threshold (Verrillo, 1965, 1968; Craig, 1968), it is conclud-

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ed that the P system is capable of spatial and temporal summation. The sensory attribute routinely ascribed to the P channel is that of "vibration" (Talbot et al., 1968). It is well documented that Pacinian corpuscle afferents are the inputs to the P channel (Verrillo, 1966a; Mountcastle et al., 1972; Bolanowski and Verrillo, 1982).

The non-Pacinian I (NP I) channel (Capraro et al., 1979) is less sensitive to changes in stimulus frequency (Verrillo, 1962, 1968; Gescheider, 1976; Verrillo and Bolanowski, 1986) than the P channel and has, at threshold, a relatively flat response across vibratory frequencies. The NP I channel possesses a nominal operating range of vibration frequencies between 10 and 100 Hz (Labs et al., 1978; Gescheider et al., 1985; Verrillo and Bolanowski, 1986). It appears not to be affected by variations in temperature (Verrillo and Bolanowski, 1986) nor does it display either temporal or spatial summation (Verrillo, 1965; Gescheider, 1976). The sensory attribute ascribed to this channel is that of "flutter" (Talbot et al., 1968). The physiological correlate of NP I is presumably the RA fibers (Lindblom and Lund, 1966; Talbot et al., 1968; Mountcastle et al., 1972), which are believed to innervate Meissner copuscles (Lindblom, 1965).

A second non-Pacinian channel, NP II, the existence of which was originally proposed by Capraro et al. (1979), has been shown by Gescheider et al. (1985) to operate in the vibratory-frequency range similar to the P channel (i.e., 15–400 Hz) but at a much lower sensitivity. In their study, the channel was defined by desensitizing the P channel through the use of a small stimulus area (i.e., minimizing spatial summation, see above) and by preventing NP I from contributing to the overall threshold-frequency characteristic through a masking paradigm (Gescheider et al., 1979; Gescheider et al., 1982; Gescheider et al., 1983). Verrillo and Bolanowski (1986) similarly have shown the existence of two separate NP channels in the glabrous skin by using a small stimulus probe to eliminate contributions to threshold by the P channel in conjunction with variations of skin-surface temperature. They found a differential effect of temperature on the threshold-frequency response of human observers, indicating two separate channels. At low frequencies (12–100 Hz), temperature changes had no effect on the average sensitivity as expected for the NP I channel. For stimulus frequencies above 100 Hz, however, temperature had a large effect on the threshold responses. Because of the stimulus configuration used in this study, the high-frequency system must have been NP II. In addition to being temperature sensitive, NP II is also capable of temporal summation (Gescheider et al., 1985). It is not known if NP II displays spatial summation. Neither the sensory attribute nor the physiological correlate of NP II is known presently, although it is highly likely that SA fibers are involved.

Prior to the present study, the psychophysical evidence that only three channels apparently contribute to vibrotactile sensation suggested that at least one of the four physiologically identified afferent groups does not contribute to somatosensory perception. This idea was supported by the work of Ochoa and Torebjörk (1983) who found that electrical activation of individual SA II fibers in human observers did not elicit a conscious perception. They pointed out, however, that perhaps several SA II fibers must be activated or recruited before a sensation can be elicited, a form of spatial summation. Alternatively, they suggest that the SA II fibers may be responsible, not for perception, but for proprioceptive feedback in motor control (see also, Knibestöl, 1975). Contrary to this latter idea are the results of Harrington and Merzenich (1970) who recorded from peripheral-nerve fibers in the hairy skin of the macaque. They concluded that SA II fibers are involved in mediating the intensity of tactile sensations. Unfortunately, the glabrous skin of the macaque contains only three types of response profiles (PC, RA, and SA; see, for example, Freeman and Johnson, 1982a,b, and Johnson, 1987), supporting the notion that perhaps only three channels transmit tactile information from the volar surface of the hand to the somatosensory cortex.

Interpretation of the physiological results relies heavily on assumptions regarding the neural code used for signaling peripheral events, but the code for somatosensation has not been adequately deciphered. It is possible that, even though afferent fibers may be rigorously excited, unless it is done with the precise code, the artificially induced activity may not enter into consciousness. It could then be erroneously concluded that the activated units play no role in mediating the sense of touch.

Rather than rely on physiological techniques that require assumptions of criterion response (Bolanowski and Verrillo, 1979), we have chosen to use psychophysical measurements to reassess whether a fourth, low-threshold mechanoreceptive channel can or does contribute to the sense of touch. Since the fourth channel, if present, might be obscured by other, more sensitive channels or may operate at vibratory frequencies not previously investigated, we have measured psychophysical thresholds from 0.4–500 Hz and have used a forward-masking paradigm, as well as variations in stimulus dimensions and temperature, to differentiate the various channels. Since electrical stimulation of SA I fibers apparently produces the sensation of "pressure" (Torebjörk and Ochoa, 1980; Vallbo, 1981; Ochoa and Torebjörk, 1983), a static or slowly changing experience, it was expected that a fourth channel would most likely operate at very low stimulus frequencies. This notion was also suggested by the frequency-response characteristics of SA fibers recorded in macaque peripheral nerve (Freeman and Johnson, 1982b) and by the results of Johansson et al. (1982a,b) who recorded activity of all four fiber types in man. Both groups of investigators found that SA fibers could be driven by low-frequency vibratory stimulation.

The results indicate that a fourth channel does indeed exist and operates in the vibratory frequency range between 0.4 and 100 Hz. The channel, which we call NP III, has a sensitivity comparable to that of the NP I channel and is affected by skin-surface temperature. NP III does not appear to have the capabilities of spatial summation. These facts, together with a reinterpretation of previously published psychophysical and physiological data, form the basis of a four-channel model for the sense of touch.

I. METHODS

The methods and procedures used in the present study were similar to those used previously in this laboratory (Verrillo, 1962, 1963, 1965, 1966a–c; Verrillo and Capraro, 1974; Verrillo and Gescheider, 1977; Bolanowski and Verrillo, 1982; Gescheider et al., 1985; Verrillo and Bolanowski, 1986). Sinusoidal, vibratory displacements of the skin were produced with a Goodman's 390A vibrator under computer control and applied to the thenar eminence. The displacements were produced around a static indentation of 0.5 mm and monitored with an electromagnetic, linear-voltage displacement transducer that senses the displacement of the moving element of the vibrator. Stimuli were applied with either of two circular contact surface areas, 0.008 and 2.9 cm^2 and were surrounded by a rigid surface (33 cm^2) that confines the deformations to the area of stimulation. The contactor surface and surround were separated by a 1-mm gap. The temperature of the skin surface underlying both the contactor and the surround was controlled during a given experimental series. The temperature was maintained by circulating water at the appropriate temperature through hollow chambers in both the aluminum contactor and surround. A Lauda/Brinkman K-2/R heating and refrigeration unit and pump controlled both the water temperature and the circulation flow rate. The contactor and surround were placed in series such that the water from the circulating unit first flowed through the contactor and then through the surround, eventually returning to the circulation unit. The size of the 0.008-cm^2 contactor did not permit water to be circulated through it, but, for both contactor sizes, the skin-surface temperature at both the contactor/skin interface and the surround/skin interface were always within 0.5 °C. This was monitored by small thermistors placed either at (2.9-cm^2 contactor) or next to (0.008 cm^2) the contactor/skin interface. The active surface of the thermistor touched the skin. To monitor the surround/skin temperature, an additional thermistor was also placed at that junction (see Bolanowski and Verrillo, 1982). Prior to each testing session, the subject's hand was allowed to adapt to the contactor/surround temperature for a period of no less than 10 min. In all, the effects of three skin-surface temperatures (15, 30, and 40 °C) were investigated.

In one group of experiments, sinusoidal bursts with durations calculated at the half-power points of 700 or 2400 ms were used as test stimuli. The rise–fall time at the onset and offset of the stimulus burst was 500 ms when the burst duration was 700 ms, and 1250 ms for the 2400-ms stimulus. These durations were chosen to ensure that most of the energy in the stimulus, regardless of the test frequency used, occurred at the fundamental frequency. This was particularly important since the vibratory-frequency range investigated extended from 0.4–500 Hz requiring fairly long-duration stimuli (see the Appendix). Threshold values are given in decibels (dB) referenced to 1-μm peak displacement. For a second group of experiments, only test stimuli of 700-ms duration were used, but a conditioning stimulus that produced forward masking (Gesheider et al., 1979, 1982, 1983) of the test stimulus was presented first. The masking stimulus was presented for 4 s (rise–fall times, 50 ms) and was followed by a period of 25 ms after which the test stimulus was presented. No stimulation was present during the 25-ms temporal gap. As shown by several investigators (Hamer, 1979; Gescheider et al., 1982; Hamer et al., 1983) masking occurs only when the masker and the test stimulus excite the same channel. It is thus possible, depending upon the masking- and test-stimulus frequencies, to differentiate between two channels by masking one of them without affecting the other. For example, if the frequency and intensity of the masking stimulus is such that it stimulates the same channel that the test stimulus activates, detection of the test stimulus will be impaired. The amount of masking depends upon the intensity of the masking stimulus (Gescheider et al., 1982). If, on the other hand, the masking and the test stimuli activate different channels, then no masking will occur. Masking is defined as a loss of sensitivity in detecting a test stimulus in the presence of a masker, and is expressed as a threshold shift relative to the unmasked threshold. By varying the intensity and frequency of the masking stimulus and the frequency of the test stimulus, it is possible to differentiate any underlying and independent channels. In our experiments, the intensities of the masking stimuli are expressed relative to the threshold of the masker, i.e., sensation level (SL), and are given in dB referenced to the masking-stimulus threshold level (dB SL). In each experimental session, the detection threshold of the masking stimulus was determined and the intensity of the masker was set in dB relative to that value. Thresholds were then measured for detecting the test stimulus alone. Finally, thresholds for detecting the test stimulus in the presence of the masking stimulus were measured. The masking experiments were conducted only at 30 °C.

Thresholds were measured by a two-alternative, forced-choice tracking procedure (Zwislocki et al., 1958) in which subjects judged which of two sequential intervals of time contained the test stimulus. Their judgments were signaled by depressing one of two switches, the response recorded by computer. The probability of the test stimulus occurring in one interval versus the other was 0.5. The intervals were separated in time by 1750 ms. The stimulus intensity was increased by 1 dB for every response error and decreased by 1 dB for every three correct responses. In this manner, the criterion used to determine threshold was 75% correct detection over a period of 3 min. The actual period of stimulation was considerably longer than this since the stimulus intensity was always a suprathreshold level prior to each test. Nominally, a period of 3–6 min was required before the subject reached the approximate threshold level at which time the 3-min period of 75% detection was started. Thresholds were expressed in dB referenced to 1-μm peak displacement. In the masking experiments, the masking stimulus was presented in each of the two observation intervals, and the subject was required to select the interval that also contained the test stimulus. Every subject was presented with each test condition three times over several sessions. A total of five subjects, two females (ages 20 and 27) and three males (ages 26, 36, and 49) were used. All were well experienced with this type of tactile experiment. Individual results closely follow the group averages. Because of this close cor-

II. RESULTS

A. The vibrotactile-frequency response

Figure 1 shows average psychophysical thresholds obtained for frequencies ranging from 0.4–500 Hz. Skin-surface temperature was held constant at 30 °C. Stimulus duration was 700 ms, and the contactor area was 2.9 cm². The masking stimulus was not used. The line through the data points has been fitted by eye with the error bars depicting the standard error of the means. Three segments of the curve can be discerned. First, there is a low-frequency portion extending between 0.4 and 3.0 Hz which appears frequency insensitive. Second, there appears to be a middle-frequency portion, which is frequency dependent, having a slope in displacement-frequency units of about − 5.0 dB/oct. Third, a U-shaped portion can be seen in the highest frequency range, between the frequencies of 40 and 500 Hz. The slope of the low-frequency portion of the U is − 12 dB/oct.

The high-frequency portion of the curve is produced by the P channel and has the expected shape, sensitivity, and location found in many other studies assessing the properties of this channel (see the Introduction). The middle-frequency portion is probably produced by the NP I channel. Although in previous work from this laboratory NP I appeared insensitive to frequency, this conclusion may have resulted from the fact that the lowest frequency investigated was only 12 Hz. Other investigators (Békésy, 1939; Mountcastle *et al.*, 1972) have used lower frequencies and have found an effect of stimulus frequency on sensitivity in this region. The fact that a breakpoint exists between the low- and middle-

frequency portions of the threshold-frequency characteristic suggests the presence of two separate channels, one for the low-frequency portion and a second, probably NP I, for the middle-frequency part. Since no previous studies have measured the response of NP I for frequencies lower than about 2 Hz, however, it is possible that the low-frequency region is also mediated by NP I. Masking experiments were conducted to determine if this was the case.

B. Effects of masking stimuli

In the masking experiments, a frequency of 0.7 Hz was used as the test stimulus since it falls in the middle of the low-frequency portion of the threshold-frequency characteristic of Fig. 1. The frequencies of the masking stimuli were chosen to selectively affect the other portions of the threshold-frequency characteristic. For example, in the first case to be presented, the masking stimulus was 40 Hz.

After measuring the threshold of the 0.7-Hz test and 40-Hz masking stimuli alone, the masking stimulus was presented at preselected SL levels, and the subject tracked the threshold for the test stimulus in the masking paradigm. Five subjects were tested in each condition during two sessions in which each test condition was presented twice. Skin-surface temperature was maintained at 30 °C. Figure 2 shows the average threshold shift as a function of masker intensity for the 40-Hz masking stimulus. In this and similar figures to follow, a least-squares analysis was used to fit the data points (see figure legends for the correlation coefficient *r* and slope *m*) affected by the masking stimulus. This was done to produce breakpoints between the two segments of the masking functions, since the exact position of the transition from no masking to the point of masking was not measured. In addition to using those points showing an effect by the masker, in the least-squares analysis, the highest point at which masking did not occur was also included. A horizon-
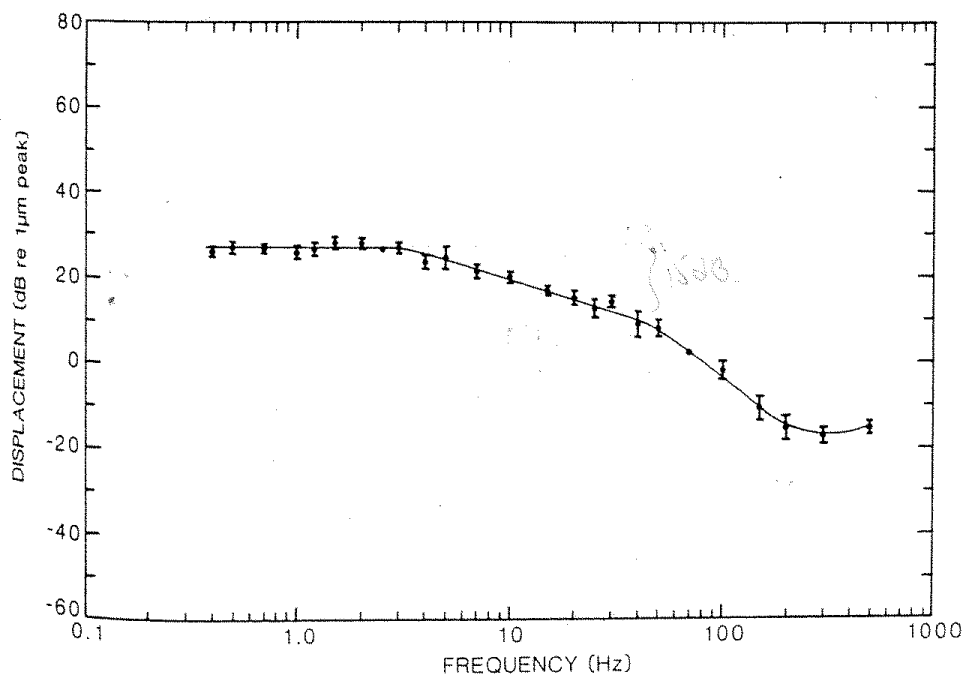

FIG. 1. Threshold-frequency characteristic relating stimulus intensity to stimulus frequency. The results are the averages of five observers. The error bars in this and the figures to follow signify the standard error of the means, their absence indicating that the error was too small to be depicted. Skin-surface temperature was maintained at 30 °C. Stimulus contactor size was 2.9 cm².
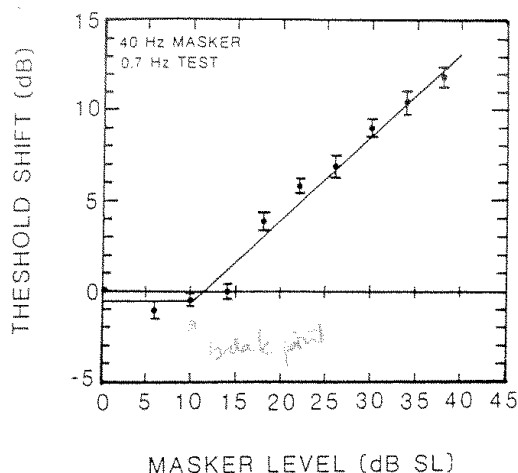
FIG. 2. The effects of a 40-Hz masking stimulus on the threshold of a 0.7-Hz test stimulus. The lines through the data points from 14- to 38-dB masker level have been fitted by linear regression ($r = 1.0$, $m = 0.46$).

FIG. 3. Masking functions obtained with various masker stimuli (10 Hz, ●, $r = 0.99$, $m = 0.41$; 20 Hz, ○, $r = 0.99$, $m = 0.43$; and 100 Hz, ▲, $r = 0.99$, $m = 0.46$) and with a test stimulus of 0.7 Hz. The breakpoints of these curves are plotted as ×'s in Fig. 4.

tal line was fitted to all of the data points that were unaffected by the masking stimulus, the point of intersection between the two straight-line segments thus obtained being referred to as the breakpoint. As shown in Fig. 2, masking levels of 0, 6, 10, and 14 dB SL produced no masking of the test stimulus. The horizontal line determined by the data points signifies this fact. This means that the masking stimulus was not affecting the channel mediating the 0.7-Hz test stimulus. For masking levels greater than 14 dB SL, however, the masking stimulus produced threshold elevations above the unmasked threshold of the test stimulus. The presence of masking above 14 dB SL indicates that the channel mediating the test stimulus was being affected by the masking stimulus. A least-squares analysis of the data from 14 dB SL and above indicates that the effect of the masking stimulus occurs with an efficiency (i.e., slope) of 0.46. The breakpoint at 10-dB SL masking level defines the approximate location of the threshold at 40 Hz of the channel mediating the 0.7-Hz test stimulus. Specifically, the channel mediating 0.7 Hz has a threshold at 40 Hz, which is 10 dB above the 30 °C curve shown in Fig. 1.

Additional masking experiments were performed at masking frequencies of 10, 20, and 100 Hz in order to determine the breakpoints for various masking functions. These breakpoints, as demonstrated in Fig. 2, define the location of the channel that in this case mediates the 0.7-Hz test stimulus, at the frequency of the masking stimulus. Average results from these experiments are shown in Fig. 3. Masking of the 0.7-Hz test stimulus begins to occur at various intensities of the masking stimulus, depending on the masker frequency. For example, masking stimuli at 100 Hz produce masking of the test stimulus only at masker levels greater than about 24 dB SL (as defined by the breakpoint). On the other hand, masking occurs at very low SL levels of the 10- and 20-Hz masking stimuli. In each instance, the efficiency of the masker as it masks the 0.7-Hz test stimulus is approximately the same (10 Hz, 0.41; 20 Hz, 0.43; and 100 Hz, 0.46) indicating commonality in the channel being masked. The
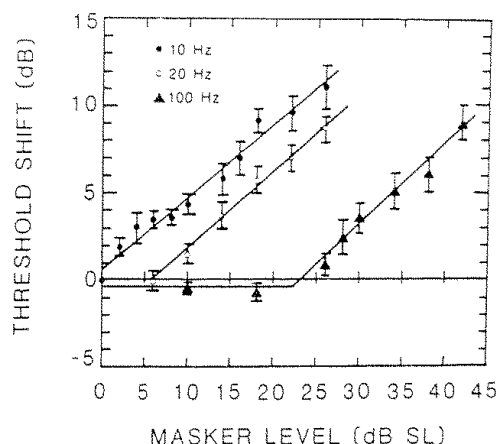
breakpoints of the masking functions shown in Figs. 2 and 3 were used to determine the thresholds of the channel mediating detection of the 0.7-Hz stimulus. Since the masking experiments were conducted only at 30 °C, we have replotted the threshold-frequency characteristic obtained at this temperature and described in Fig. 1 (i.e., unmasked threshold-frequency characteristic) into Fig. 4. In so doing, we have eliminated the data points for clarity. In addition, we have plotted the breakpoints of the masking functions shown in Figs. 2 and 3 into Fig. 4 and as shown by the ×'s. The dashed line (see Fig. 4) connecting the threshold values obtained at 0.7 Hz for the unmasked condition (and for the flat low-frequency region in general) with the masked thresholds given by the ×'s defines, to a first approximation, the functional characteristic of the channel mediating the 0.7-Hz test stimulus. Since the obtained curve does not follow the overall threshold-frequency characteristic, a different channel must be operating in the low-frequency part of the curve. Neither the P or the NP II channels can be mediating the low-frequency portion of the overall threshold-frequency characteristic since previous experiments (Gescheider *et al.*, 1983; Gescheider *et al.*, 1985) have shown that their sensitivities below 2.5 Hz are at least 27 dB above the unmasked threshold measured here.

To substantiate the independence of this low-frequency channel (Fig. 4, ---), a masking experiment was performed in which a 40-Hz masking stimulus was coupled with a 25-Hz test stimulus. Based on previous results (see the Introduction), it was reasonable to assume that the 25-Hz test stimulus would be detected by the NP I channel. The results are plotted in Fig. 5. Also shown is the masking function obtained with the same masking frequency but with the 0.7-Hz test stimulus, the results replotted from Fig. 2. Note that masking of the 25-Hz test stimulus occurs at masking intensities as low as 1 dB SL. In this particular case, the function is best fit by two segments, one for low-masking levels (least-squares fit from 0–8 dB) and a second for the higher levels (least-squares fit from 8–30 dB). Neither segment operates
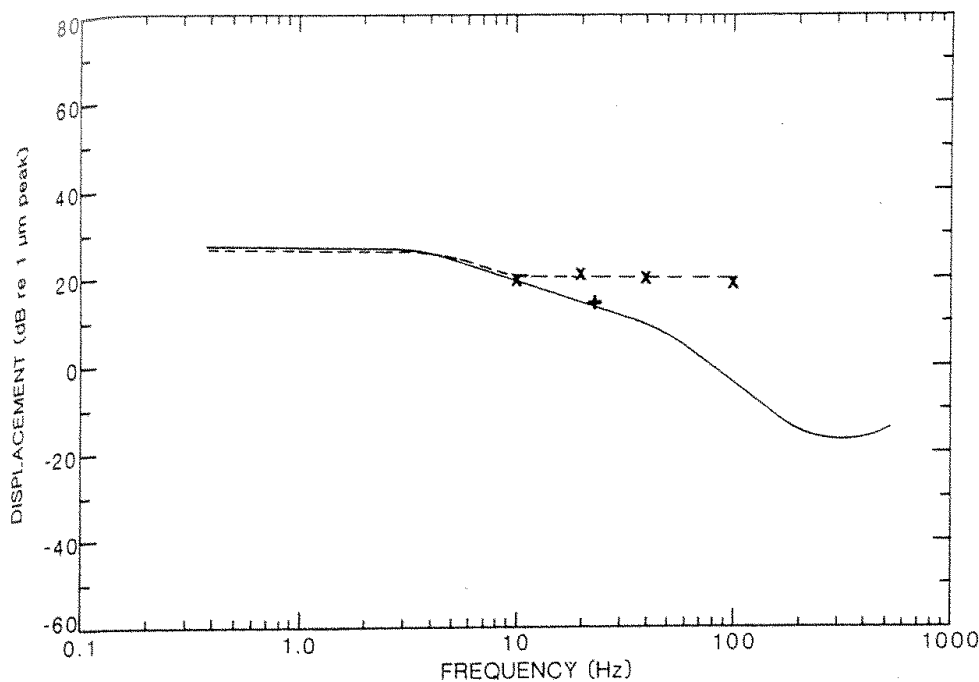
FIG. 4. Threshold-frequency characteristics relating stimulus amplitude to stimulus frequency. The solid curve has been replotted from Fig. 1. The ✕'s are the breakpoints obtained in relation to Figs. 2 (40 Hz) and 3 (10, 20, and 100 Hz). Dashed line has been fitted to the ✕'s and to the flat, low-frequency region of the solid curve lying between 0.4 and 1.0 Hz. The + signifies the lowest breakpoint on the 40-Hz masking stimulus/25-Hz test stimulus masking function of Fig. 5.

with an efficiency of 0.45, the lower portion possessing an efficiency of 0.8, while the upper has an efficiency of 0.31. The masking function is quite unlike that obtained with the 0.7-Hz test stimulus. The lowest point (1 dB SL) of the 25-Hz test stimulus/40-Hz masking function has been plotted in Fig. 4 (+), since it signifies the point at which the channel mediating the 25-Hz test stimulus operates. The breakpoint, as expected, lies almost directly on the overall threshold-frequency characteristic, indicating that both the masking and the test stimuli are being mediated by the same channel (NP I). Since this does not occur when a 0.7-Hz test is used in conjunction with a 40-Hz masking stimulus, a separate channel must be responsible for detecting the 0.7-Hz test. In other words, two independent channels must be determining the psychophysical threshold between 0.4 and 30 Hz: one responsible for signaling detection at 0.7 Hz (and the flat portion of Fig. 1) and the other mediating threshold at 25 Hz (and the − 5.0-dB/oct portions of Fig. 1). The previously known NP I system is responsible for the 25-Hz channel. Following previous nomenclature, we call the newly revealed channel NP III.

C. Effects of skin-surface temperature

It would be possible to define more precisely the frequency at which detection changes from one channel to the other if the two low-frequency channels were differentially affected by changes in skin-surface temperature. Therefore, threshold measurements were made at two additional temperatures, 15 and 40 °C. Other stimulus conditions were identical to those used previously (Fig. 1, 2.9-cm^2 contactor area, 700-ms duration, and 500-ms rise–fall times). The results from the experiments in which the skin-surface temperature was varied are plotted in Fig. 6, along with the results obtained at 30 °C. The lines through the data points have been fitted by eye. Temperature clearly has an effect on the U-shaped portion of all three curves. Increases in tem-

perature increased both the average sensitivity as well as the frequency at which maximum sensitivity occurs, the so-called "best frequency." The high-frequency portion of the three curves is produced by the P channel. The significant effects of temperature on its response profile have already been described (Bolanowski and Verrillo, 1982). The middle- and low-frequency portions of the curves shown in Fig. 1 are produced by the NP I and NP III channels. Exclusive of the P region (40 to 500 Hz), changes in skin-surface temperature have the greatest effect in the region between 1.5 and 4 Hz, that region on all three curves where the sensitivities of NP I and NP III are believed to merge and cross over.

To determine if temperature had a significant effect on thresholds below 40 Hz, a two-way analysis of variance
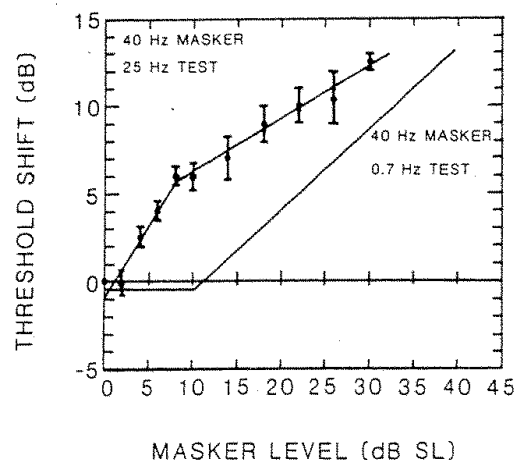

MASKER LEVEL (dB SL)

FIG. 5. The effects of a 40-Hz masking stimulus on the threshold of a 25-Hz test stimulus. The lines through the data points from 0- to 8-dB masker level have been fitted by linear regression ($r = 0.97$, $m = 0.8$) as is the line fitted to the masker levels of 8–30 dB ($r = 0.98$, $m = 0.31$). The masking function shown without data points has been taken from Fig. 2.
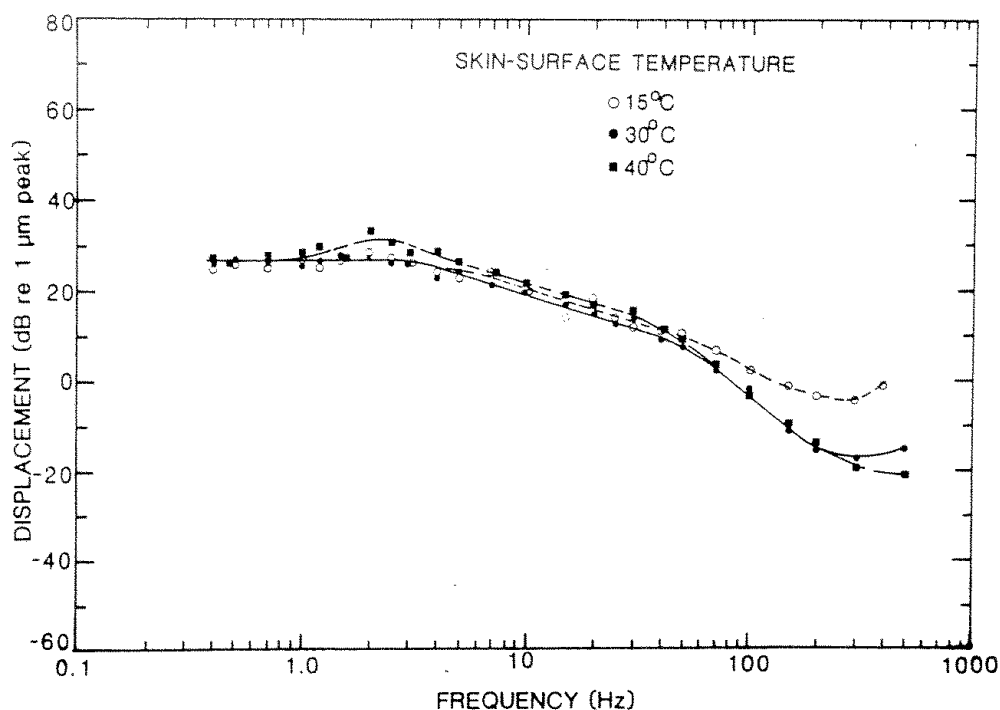
FIG. 6. Threshold-frequency characteristics relating stimulus amplitude to stimulus frequency. Skin surface temperature is the parameter: 15 °C, O; 30 °C, ●; and 40 °C, ■. Error bars are not plotted for clarity although the standard error of the means are identical to those found for Fig. 1 (see Sec. I).

(ANOVA) was performed, using the data obtained for stimulus frequencies from 0.4–40 Hz. The results of the analysis showed that the effect of temperature was highly significant $[F(2,204) = 7.39, p < 0.001]$. Since the masking experiments show that two separate channels appear to be operating over this region, two ANOVAs were performed, one for the frequency range between 2.5 and 40 Hz and the second for the range between 0.4 and 2.0 Hz. In both instances, the effects of varying skin-surface temperature proved to be significant $\{2.5–40$ Hz, $[F(2,120) = 4.08, p < 0.01]$; $0.4–2.0$ Hz, $[F(2,84) = 5.2, p < 0.01]\}$. If the range between 2.5 and 40 Hz is mediated solely by the NP I channel, then it is likely that temperature affects the sensitivity of this channel. Although in previous work from this laboratory (Verrillo and Bolanowski, 1986) NP I appeared insensitive to temperature, this conclusion may have resulted from the fact that the lowest frequency investigated in that study was only 12 Hz. Similarly, since temperature apparently affects sensitivity in the frequency range between 0.4 and 2.0 Hz and, if this region is controlled soley by NP III, then this channel, too, must be temperature sensitive. The ANOVAs performed also showed that the middle-frequency region was strongly affected by vibration frequency $[F(9,120) = 4.08, p < 0.001]$ as the -5.0-dB/oct slope found at a temperature of 30 °C would predict. The low-frequency protions of all three curves are not affected by stimulus frequency $[F(6,84) = 1.6, p > 0.1]$. An ANOVA performed on the data from 0.4 to 40 Hz also showed that frequency has a significant effect on threshold throughout this range $[F(32,204) = 72.98, p < 0.001]$. However, since the interaction between stimulus frequency and temperature on thresholds in all cases was not found to be significant $\{0.4–40$ Hz, $[F(32,204) = 1.36, p > 0.10]$; $0.4–20$ Hz, $[F(12,84) = 1.15, p > 0.25]$ and $2.5–40$ Hz, $[F(18,120) = 1.45, p > 0.10]\}$, it is not possible to determine the exact manner of the effects of temperature on either NP I or NP III.

D. Effects of stimulus size and duration

In order to determine if the NP III channel is affected by stimulus size, thresholds were obtained using a 0.008-cm² contactor area and a skin-surface temperature of 30 °C. Two stimulus frequencies were investigated (0.5 and 1.0 Hz), and the thresholds compared to those obtained with the 2.9-cm² contactor. Spatial summation in NP III would be demonstrated if the smaller stimulus area produced thresholds higher than the larger stimulus area. When the thresholds obtained with the smaller contactor (0.5 Hz, 26.7 dB re: 1-μm peak; 1.0 Hz, 27.6 dB re: 1-μm peak) were compared to those obtained with the large contactor (0.5 Hz, 27.7 dB re: 1-μm peak; 1.0 Hz, 26.4 dB re: 1-μm peak), no differences in threshold were evident or statistically significant $\{0.5$ Hz, $[t(4) = 0.51, p > 0.5]$; 1.0 Hz, $[t(4) = 0.63, p > 0.5]\}$. When the 200-Hz test frequency was used, however, thresholds obtained for a contact surface of 0.008 cm² (11.2 dB re: 1-μm peak) were considerably higher $[t(4) = 8.69, p < 0.001]$ than those obtained with the 2.9-cm² area (-15.4 dB re: 1-μm peak), a result predicted by the presence of spatial summation in the P channel. The results suggest that spatial summation is not found in the NP III channel.

The effects of stimulus duration on the sensitivity of NP III was also investigated. Increases in sensitivity for increases in stimulus duration might suggest some form of temporal integration of the stimulus. This was not found. For example, thresholds obtained at 0.4 Hz (27.6 dB re: 1-μm peak) and 1.0 Hz (26.4 dB re: 1-μm peak) using stimulus duration of 2500 ms with rise–fall times of 500 ms showed no statistically significant difference $\{0.4$ Hz, $[t(4) = 0.86, p > 0.4]$; 1.0 Hz, $[t(4) = 0.15, p > 0.5]\}$ in sensitivity when compared to the thresholds obtained with the 700-ms stimulus (0.4 Hz, 25.6 dB re: 1-μm peak; 1.0 Hz, 28.1-μm peak). This finding also confirms that the thresh-

olds obtained at the shorter burst durations were not confounded by low-frequency energy components in the stimulus (see the Appendix).

III. DISCUSSION

The results presented indicate that vibratory stimuli can be detected at frequencies between 0.4 and > 500 Hz, the threshold-frequency characteristic being U shaped for high frequencies and partially sloping for the lower ones (Figs. 1, 4, and 6). The general shape of the characteristic was first reported by Békésy (1939) and later by Verrillo (1963, 1966a–c), using methods similar to those used here, except that they did not control skin-surface temperature. The major difference between this and the earlier studies, when considered in conjunction with previous experiments from our laboratory (e.g., Capraro et al., 1979; Bolanowski and Verrillo, 1982; Gescheider et al., 1985; Verrillo and Bolanowski, 1986), is that we conclude that there are probably four separate channels mediating the sense of touch. The present study also shows that the previously unknown fourth channel operates at low-stimulus frequencies. Békésy (1939) and Verrillo (1963), on the other hand, postulated a two-channel (duplex) model for vibrotaction based on their early psychophysical results.

The fourth channel, called NP III, appears to operate in the frequency range from 0.4 to > 100 Hz and has an average sensitivity similar to that of the NP I channel (see Fig. 4). As with NP I, NP III does not possess spatial summation. The presence of NP III was determined by masking studies (Figs. 2 and 3) in which masking stimuli were paired with a 0.7-Hz test stimulus. The procedure elevated the thresholds of P, NP I, and NP II for the purpose of defining NP III. When the masking stimuli were intense enough to mask NP III also, a power relationship between masking intensity and threshold shift of the test stimulus was found. The efficiency (i.e., slope; see Gesheider et al., 1983) at which this occurred was approximately 0.44 as determined by least-squares fit to the data. It is important to note that all four masking functions obtained with the 0.7-Hz test stimulus (Figs. 2 and 3) have the same masking efficiencies, providing additional evidence that the same channel (NP III) was mediating detection of the 0.7-Hz test stimulus in each case. In contrast to this, Fig. 5 shows that pairing a masking stimulus of 40 Hz with a test stimulus of 25 Hz produces a very different masking function. This is expected since both the 25-Hz test stimulus and the 40-Hz masking stimulus, even at very low masking levels, are mediated by the same channel. NP I is known to have a masking efficiency of approximately 0.8 (Gescheider et al., 1983). The lower portion of the function obtained with the 40-Hz masker, combined with a 25-Hz test stimulus (Fig. 5) has a slope equal to 0.81, indicating that this portion of the masking function is indeed produced by NP I. The upper portion of the 40-Hz masking-, 25-Hz test-stimulus condition could be due to the 25-Hz test stimulus being detected by either the P, NP II, or NP III channels. The P and NP II channels have masking efficiencies of 0.62 (Gescheider et al., 1983) and 0.9 (Gescheider et al., 1985), respectively. Since the upper portion of the masking function

has a slope of 0.31, it is unlikely that the P or the NP II channels themselves are detecting the test stimulus but that this is being done by NP III. It is also possible, however, that the other channels are sequentially mediating the test stimulus for increases in masker-stimulus intensity. In other words, the 0.31 efficiency calculated may be the result of these other channels contributing to this segment of the masking function in a complicated way.

The experiments in which skin-surface temperature was varied (Fig. 6) indicate that temperature can have a significant effect on threshold sensitivity over most of the frequency range investigated. Exclusive of the P-channel effect already described and discussed by Bolanowski and Verrillo (1982), temperature seems to affect thresholds mediated by both NP I and NP III. The fact that the NP I channel is affected by changes in skin-surface temperature is inconsistent with the report of Verrillo and Bolanowski (1986). However, since they only investigated frequencies above 12 Hz, the effect of temperature in their study could have gone unnoticed.

Since there appear to be four separate channels involved in signaling the sense of touch, previous physiological results suggesting that only three fiber types are involved (e.g., Knibestöl, 1975; Ochoa and Torebjörk, 1983) must be reevaluated. The fact that repetitive, electrical stimulation of SA II fibers apparently does not evoke a sensation (Ochoa and Torebjörk, 1983) suggests that the fibers in their study were not stimulated appropriately. Failure to evoke a sensation could either be a result of an improper impulse pattern or the fact that only a single SA II fiber is activated, perhaps an insufficient number (Ochoa and Torebjörk, 1983). When reevaluating previous physiological results, it would be quite useful, for the purposes of modeling, to correlate each psychophysically defined channel with its underlying physiological substrate. Of primary importance in both instances is the need to select the appropriate neural code used by each fiber group to signal detection of a stimulus (Bolanowski and Verrillo, 1982). The fact that artificial activation of individual fibers may produce a perceptual response (Torebjörk and Ochoa, 1980; Vallbo, 1981; Ochoa and Torebjörk, 1983) may be misleading since it does not prove that the imposed stimulus is the code used by the nervous system. In fact, the sensations evoked by such stimulation have been reported to feel somewhat unnatural (Ochoa and Torebjörk, 1983).

In general, previous reports on the response of peripheral nerve fibers to vibratory stimulation usually present frequency-response curves in which the intensity of the stimulus needed to achieve a predetermined response criterion is plotted as a function of vibration frequency. Only two criteria are usually used: one neural impulse per stimulus cycle (entrainment) or one neural impulse per stimulus burst. They do not describe what happens to the shape of the frequency response as a function of changes in response criteria (e.g., Lindblom and Lund, 1966; Talbot et al., 1968; Merzenich and Harrington, 1969; Tapper et al., 1972; Mountcastle et al., 1972; Pertovaara and Hämäläinen, 1981; Freeman and Johnson, 1982a). In fact, the reason that an entrainment criterion was initially used in the literature on the topic was that it produced frequency-response characteristics of peri-

pheral fibers that qualitatively mimicked threshold-frequency responses obtained from human observers (e.g., Mountcastle *et al.*, 1972). Unfortunately, no reports show intensity characteristics relating afferent neural responses to stimulus intensities at specified frequencies with sufficient sampling points to ascertain the effects of response criterion on the shape of the frequency characteristics (but see Bolanowski and Zwislocki, 1984).

Some of the most carefully conducted research has been on the macaque monkey used as a model for man. However, as Johnson points out (Freeman and Johnson, 1982a,b; Johnson, 1987), the macaque apparently has only three types of response profiles and the SA-unit profile cannot be subdivided. Thus it may not be advantageous to use these data since they may not give a complete description of the mechanisms used by the human somatosensory system. Aside from the fact that there may be a species difference between macaque and man, recent developments in microneurography make it possible to use physiological results obtained from humans as correlates to the psychophysical results presented here. At present, the most complete study assessing single-unit responses to vibratory stimuli in humans is that of Johansson *et al.* (1982a). They reported their results as equiresponse contours in which stimulus intensity was held constant at various levels, stimulus frequency varied, and the number of impulses per cycle recorded. They did this over a stimulus-frequency range of 0.5–400 Hz and for all four fiber types. We replotted their data as intensity characteristics, relating firing rate to stimulus intensity and by interpolating and extrapolating their data when necessary, we were then able to construct isoresponse contours across stimulus frequency. Choosing appropriate response criteria as discussed below, we then fitted the neurophysiological results to a four-channel, psychophysical model. The results of the analysis to be described are given in Fig. 7; the specific neurophysiological-response characteristic correlated with each psychophysically determined channel. Each panel of the figure refers to only one channel [(a), NP I; (b), P; (c), NP III; and (d), NP II].

The RA units, and by inference the NP I channel [see the Introduction; Lindblom, 1965; Talbot *et al.*, 1968 and Fig. 7(a)], are apparently able to signal a threshold event with a single neural impulse on a single fiber (Hensel and Bowman, 1960; Vallbo and Johansson, 1976). This has been supported by experiments using electrical stimulation of RA fibers by Torebjörk and Ochoa (1980), Vallbo (1981), and Ochoa and Torebjörk (1983). Thus the neural code for a threshold event in the NP I channel may, in fact, be a single impulse per stimulus burst. This is consistent with the fact that NP I does not display temporal summation, a phenomenon requiring at least two impulses to demarcate the duration of a stimulus. The upper curve in Fig. 7(a) shows the average ($n = 8$) frequency response of RA fibers as reported by Johansson *et al.* (1982a), but using a criterion of one impulse/stimulus. The data points on the physiological curve in this and the subjacent panels of Fig. 7 are interpolations and/or extrapolations of the data of Johansson *et al.* (1982a). The curved lines have been fitted by eye. Also shown in Fig. 7(a) is the frequency characteristic of the NP I

channel, a portion (12–150 Hz) of which was taken from Verrillo and Bolanowski (1986) with the lower frequency aspect (2.5–12 Hz) based on the results presented above in this study (see Figs. 1 and 4). The shape of the two curves are similar. The average sensitivity of the RA units, however, is 18 dB less sensitive than the psychophysical results. This disparity may be explained by differences in stimulus conditions and the fact that average data were used in constructing the physiological curve. As Mountcastle *et al.* (1972) and Bolanowski and Zwislocki (1984) have shown, the range of sensitivities for mechanoreceptors can be as large as 20 dB. Thus the most sensitive RA fiber, which would be considerably more sensitive than the average, would be mediating threshold. Aside from this consideration, Verrillo (1979) has shown that the presence of an edge either at or near the place of stimulation can significantly (10–15 dB) increase the sensitivity of the NP I channel. The present experiments, as well as most of the previous ones from our laboratory, were performed with the use of a rigid surface that surrounded the stimulus probe. This stimulus configuration introduces two large circular edges, one at the boundary of the surround and the other at the contactor, producing increased sensitivity of NP I. Johansson *et al.* (1982a) did not use a surround in their experiments and, as a consequence, the sensitivities that they measure for the RA population would be expected to be much less than that found psychophysically. Indeed, Johansson *et al.* (1982b) have shown that the presence of an edge in a stimulus produced greater responses in RA fibers than the flat, smooth surface used in their companion study (Johansson *et al.*, 1982a) on which our analyses are based.

Unlike NP I, the P channel [see Fig. 7(b)] is capable of temporal summation. Since increases in stimulus duration can lower detection thresholds, the neural code used by the P channel must incorporate a method by which stimulus duration is signaled. A single impulse-per-stimulus event cannot do this. Therefore, at least two impulses per stimulus must be required on a single Pacinian fiber for a threshold event to be perceived. Furthermore, as Van Doren (1985) has pointed out, a criterion based on entrainment similarly cannot be used by the P channel, again because of the constraint of temporal summation. That is, lengthening the duration of a stimulus that is already producing a threshold event signaled by entrainment will not lower the intensity required for that entrainment. Lastly, Verrillo (1971) has shown that changes in stimulus rise time do not change threshold levels. Since Pacinian fibers are known to discharge at higher instantaneous rates for increases in the onset velocity of ramp-like stimuli (Iggo and Ogawa, 1977), it is unlikely that a firing-rate code is used.

Verrillo (1965) has shown that the P channel can signal detection of a 100-Hz stimulus burst of 20-ms duration. The duration and the rise–fall times that he used allowed for 2 cycles of vibration at 100 Hz with the amount of energy in the stimulus concentrated at 100 Hz. For intense mechanical stimulation, Bolanowski and Zwislocki (1984) have shown that the near-maximal firing rates that can be achieved in isolated Pacinian corpuscles in response to 100-Hz vibrations correspond to 2 spikes/stimulus cycle. Thus a thresh-
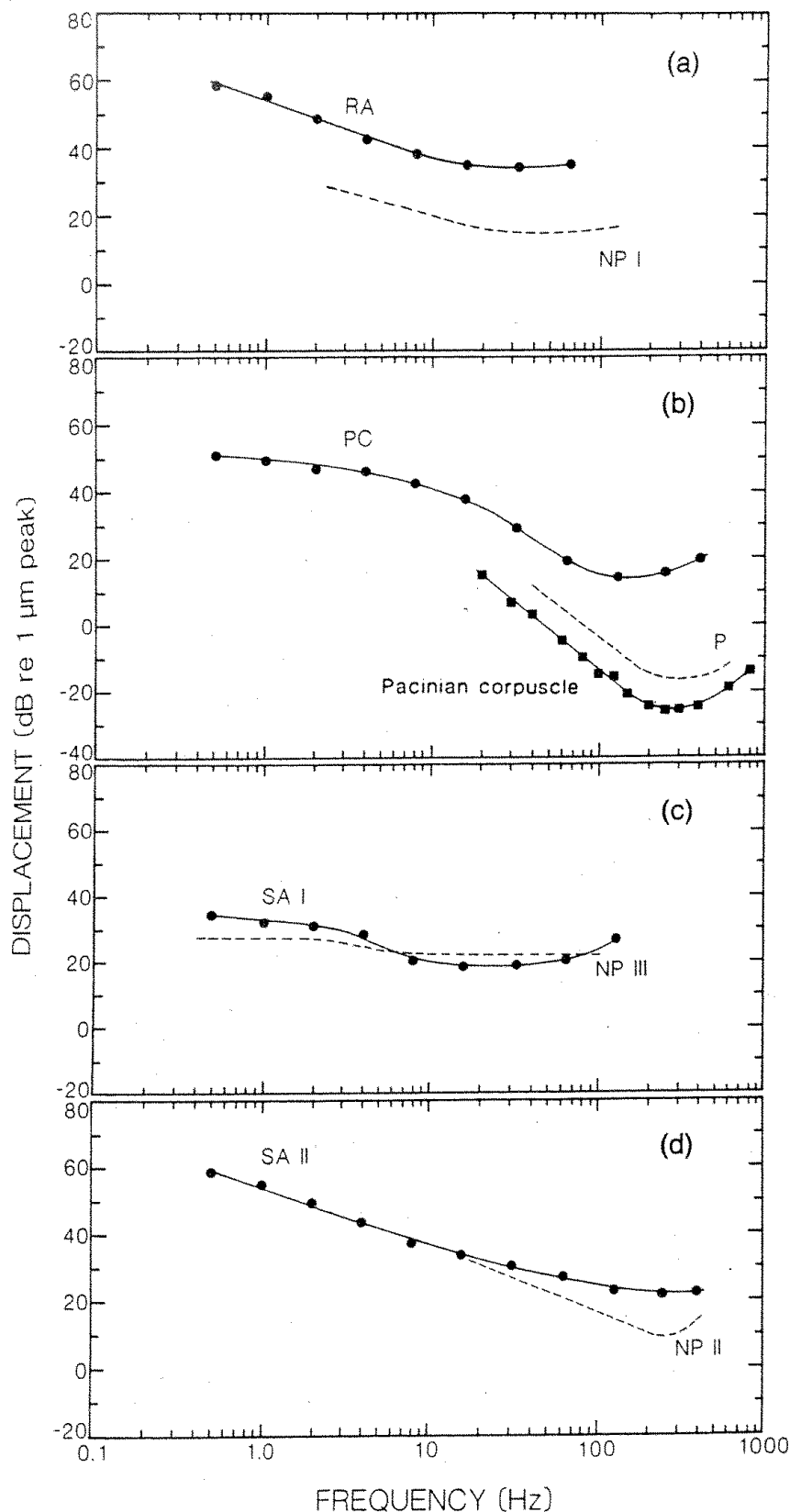
FIG. 7. Relationship between physiologically measured frequency characteristics for different fiber types [(a) RA; (b) PC; (c) SA I; and (d) SA II] and psychophysically obtained thresholds-frequency characteristics [(a) NP I; (b) P; (c) NP III; and (d) NP II]. Neurophysiological data points are interpolations and extrapolations of the average results presented by Johansson *et al.* (1982a) for selected response criteria: (a), 1 impulse/stimulus; (b), 4 impulses/stimulus; (c), 0.8 impulses/s, and (d), 5 spikes/s. For the P channel (b), an additional physiological curve (Pacinian corpuscle) derived from unpublished results of Bolanowski (1981) has been plotted. This curve is the average (*n* = 6) response of excised Pacinian corpuscles maintained at 33 °C and for a response criterion of four impulses occurring during the central 200 ms of a 300-ms stimulus burst.

old event can be signaled by as little as 4 spikes/stimulus. Based on this fact and that at least two impulses/stimulus are required, we suggest that the code used by the P channel for stimulus detection may be between two and four impulses/stimulus. The top curve in Fig. 7(b) is a replot of the results of Johansson *et al.* (1982a) using a four impulse/stimulus for average (*n* = 4) PC responses. The actual shape of the curve is not significantly affected by using a

criterion based on either a lower (2 and 3) or higher (5 and 6) number of impulses/stimulus, although higher numbers (> 7) do change the shape of the curve considerably. Also plotted is the psychophysical result of Bolanowski and Verrillo (1982) showing the frequency response of the P channel measured with a skin-surface temperature of 30 °C and a 2.9-cm^2 contactor surface. Based on previous reports indicating that the P channel is mediated by PC afferents (see the Introduction), it is not surprising that the shape of the physiological and psychophysical curves are similar. However, the best frequency, overall sensitivity, and low-frequency (10–100 Hz) slopes of the two curves are not the same. The third curve in Fig. 7(b) represents results obtained from isolated Pacinian corpuscles, its significance described below.

The difference in the location of the best frequencies and possibly the sensitivity of the PC and P curves of Fig. 7(b) may be due to the fact that Johansson et al. (1982a) did not control the skin-surface temperature that can be as low as 20 °C for relaxed, sedentary human subjects (Bolanowski and Verrillo, 1982; see also Hardy and Bard, 1974). Lower temperatures decrease both the sensitivity and best frequency of the P channel (Bolanowski and Verrillo, 1982). The curve obtained for Pacinian corpuscles and shown in Fig. 7(b) provides an example of this. The curve was generated by averaging the stimulus intensities, at each stimulus frequency, required to produce a fixed-criterion response in six Pacinian corpuscles isolated from cat mesentery and maintained at 33 °C (unpublished results of Bolanowski, 1981, but see Bolanowski and Verrillo, 1982). This temperature was chosen since the actual temperature of Pacinian corpuscles, in situ, probably lies between core temperature (37 °C) and the temperature of the skin surface, in this case, 30 °C. Unlike the PC fiber data, the Pacinian corpuscle experiments monitored activity only during the central 200 ms of a 300-ms burst, that is, in the steady state. The specific criterion that we used to generate the average Pacinian corpuscle curve was four impulses per the 200-ms assessment period. There is fairly good correspondence between the best frequency of the psychophysical and Pacinian corpuscle curves and the sensitivity of the Pacinian corpuscle curve is greater than that found for the PC fibers.

Several other factors can explain the differences in the sensitivity of the psychophysical and PC fiber curves, aside from the fact that corpuscles can vary in their overall sensitivity by 20 dB (Bolanowski and Zwislocki, 1984). One such factor is the presence of spatial summation in the P channel. For example, the psychophysical results were obtained with a contactor surface of 2.9 cm^2, which could substantially increase the sensitivity of this channel over that found in single unit recordings as a result of the central nervous system integrating responses from adjacent Pacinian corpuscles. A second possibility is that Johansson et al. (1982b) may not have stimulated the most sensitive region of an individual unit's large receptive field.

The other apparent discrepancy between the P channel and the PC fiber curves shown in Fig. 7(b) is that there is a difference in the low-frequency (10–100 Hz) slopes of the two curves. It is well known, however, that the P channel

exhibits temporal summation (Verrillo, 1965), a central mediated phenomenon (Zwislocki, 1960). As measured, Verrillo (1965) and Zwislocki (1960), temporal summation will impart a 3-dB/oct increase in sensitivity for increases stimulus frequency. Since the psychophysical results include this centrally mediated effect, this curve should have a low frequency slope that is 3 dB/oct steeper than that found physiologically for peripheral fibers. The slope of the psychophysical curve, as calculated between 20 and 100 Hz — 12 dB/oct. The low-frequency slope of the PC curve measured between 20 and 100 Hz, is — 9 dB/oct. On the other hand, the Pacinian corpuscle data show a — 12-dB oct slope. It is possible that the manner in which these latter data were collected (i.e., in the steady state, see above) artifactually introduced an additional — 3-dB/oct slope. We note that the difference in the low-frequency slopes of physiological and psychophysical data that results from temporal summation requires that the psychophysical channel exhibit temporal summation. Temporal summation not a property of the NP I channel and Fig. 7(a) shows that the psychophysical and physiological curves are fairly parallel. The NP II channel (see below) does exhibit temporal summation, and the physiological and psychophysical curves [see Fig. 7(d)] differ by the expected amount.

The NP III channel [see Fig. 7(c)] is functional down to very low frequencies. Since several investigators (Vallbo 1981; Ochoa and Torebjörk, 1983) have shown that electrical activation of SA I fibers produce "pressure" or a very low-frequency sensation, it is likely that they are the substrate for NP III. Because NP III does not display spatial summation, it is likely that the coding used to signal threshold in this channel occurs on a single fiber. Ochoa and Torebjörk (1983), in fact, have indicated that a sensation can be produced by activating a single SA I fiber. They also found that several impulses were needed for the sensation to occur. We replotted the average (n = 5) results of Johansson et al. (1982a) using several different criterion responses: impulses/cycle, impulses/stimulus, and impulses/s, and compared them to the shape of the NP III channel found in this study [shown as the dashed line in Fig. 7(c)]. The shape of NP III is based on the breakpoints of the masking functions obtained with the 0.7-Hz test stimulus (see Fig. 4) and the flat portion of the overall threshold/frequency characteristic shown in Fig. 1. The best fit to the psychophysical function occurs when an impulse/s code is used, in this case 0.8 impulses/s, although using higher firing rates simply lowers the overall sensitivity of the physiological curve without changing its shape. The other criteria produce frequency characteristics that are U shaped with best frequencies near 0.5 Hz, quite unlike the shape found for the sensitivity of the NP III channel. Thus the response criterion of this system may be an impulse rate at or higher than 0.8 impulses/s.

Since the P, NP I, and NP III channels are probably mediated, respectively, by the PC, RA, and SA I fiber types, by elimination NP II [see Fig. 7(d)] must be mediated by SA II fibers. Since SA II fibers possess spontaneous activity (Knibestöl, 1975; Johansson et al., 1982a), it is unlikely that a low firing rate or a small number of impulses/stimulus burst could act as the neural code for threshold in this chan-

nel. Since Ochoa and Torebjörk (1983) have indicated that SA II fibers cannot produce a sensation even when driven to rather high repetition rates, it is possible that the code requirement is several fibers being activated at one time or a statistical change in the firing rate distribution. In reference to the latter idea, the repetitive pattern of activation used by Ochoa and Torebjörk (1983) may not have had significance for this channel. Since NP II displays temporal summation (Gescheider et al., 1985), a criterion of one impulse/stimulus burst cannot be the appropriate code. At the present time, it is not possible to determine whether several SA II fibers must be activated at the same time for a threshold event to take place, since it is not known whether NP II is capable of spatial summation. Similarly, the results of Johansson et al. (1982a) do not give the temporal pattern of activity produced by the SA II fibers in response to their stimulation. Thus it is impossible to analyze their results using a stochastic process (e.g., variance) as a criterion response. It is clear that, since SA II fibers possess spontaneous activity, a substantial increase in firing above this baseline may be required for a threshold event. As a first approximation in trying to fit the psychophysical results and in order to overcome the effects of spontaneous activity, we selected a firing rate criterion of 5 spikes/s and plot the average ($n = 5$) results in Fig. 7(d). The other curve (---) shows the NP II channel as measured psychophysically by Gescheider et al. (1985; 15–150 Hz) and Verrillo and Bolanowski (1986; 100–500 Hz). The correspondence between the two curves is excellent. Plots of the SA II response profiles for response criteria of impulses/stimulus or even impulses/cycle produce frequency-response characteristics that do not match any of the psychophysically determined channels, including NP III.

The complete psychophysical model is given in Fig. 8 and is a composite of the work presented here, as well as that reported in previous publications from this laboratory (see discussion in relation to Fig. 7). Figure 8 shows four channels with partially overlapping sensitivities that combine to mediate tactile perception. It is important to realize that the absolute sensitivity at a particular frequency as measured psychophysically will normally be determined by the channel having the lowest threshold, this being a function of the stimulus conditions: stimulus size, duration, skin-surface temperature, as well as other factors such as body site and static indentation. This is demonstrated by replotting the data points of Fig. 1 into Fig. 8.

For the stimulus conditions used here, the P channel determines threshold between about 35 and 500 Hz, which is consistent with the findings and predictions of Verrillo (1963, 1966a, 1968). The sensitivity of this channel is U shaped and its low-frequency slope (— 12 dB/oct) ensures that, even if vibrations below 10 Hz are sufficiently intense, the P channel will be activated. A second channel, NP I, has its maximum sensitivity, regardless of stimulus duration or size (see the Introduction), between about 3 and 100 Hz. The low-frequency portion of the NP I characteristic extends to low frequencies with a slope of about — 5.0 dB/oct. Since the NP I channel is much less sensitive at vibratory frequencies greater than 35 Hz than is the P channel, it is ineffective in mediating threshold in this range. NP II, given the stimulus conditions of this study, is not readily apparent. Its operating-frequency range, as ascertained by Gescheider et al. (1985), is similar to the P channel, although its sensitivity is considerably less. Of course, if a small contactor had been used exclusively in this study, the P channel would have been desensitized to such a degree that the overall threshold-
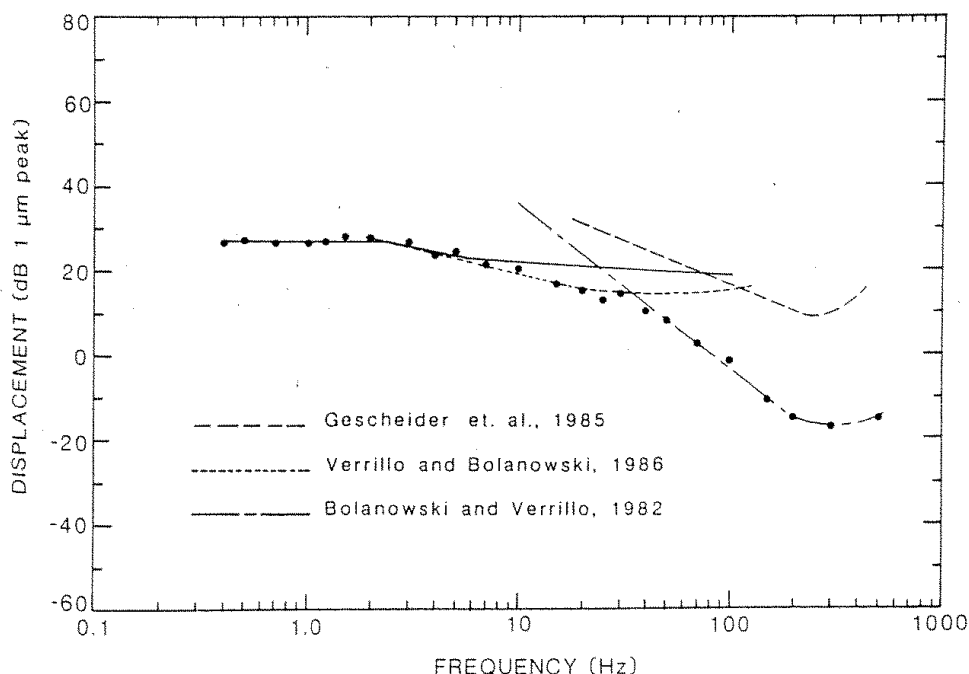

FIG. 8. The four-channel model of vibrotaction showing the threshold-frequency characteristics of the various channels: – – –, PC; - - -, NP I; – – –, NP II; and —, NP III. See text for discussion regarding origin of data. Data points superimposed on the model are replotted from Fig. 1.

frequency characteristic would have extended to higher frequencies along the NP I/NP II curves as shown by Verrillo and Bolanowski (1986). The low-frequency slope of the NP II channel (about − 6 dB/oct) makes it important to note that, like the other channels, NP II can be activated by vibratory stimuli occurring at suprathreshold levels. Lastly, NP III operates from very low frequencies to frequencies greater than 100 Hz. We have not, as yet, determined the full capabilities of NP III, although it is clear that it can be excited by vibratory stimuli over a considerable range of stimulus intensities and frequencies.

The significance of the psychophysical model and its physiological substrate is that a single channel alone may signal the threshold event, depending upon the frequency of stimulation. However, and more importantly, at certain frequencies (e.g., 2.0–4.0 and 35 Hz), more than one channel may be stimulated, even at threshold-level intensities. In fact, probability summation between the channels may be occurring at those frequencies where two or more channels have the same threshold value. There are also regions in the intensity-frequency space of Fig. 8 where multiple channels can be activated with stimuli that are only slightly above the psychophysical threshold. A typical example of this would be a 35-Hz sinusoidal stimulus, or a more complex stimulus with an energy component at 35 Hz, which has an amplitude greater than 40 dB *re*: 1.0-μm peak. Because of the substantial overlapping of sensitivities of the four channels, the model has considerable importance for the understanding of both physiological and psychophysical results obtained with nonsinusoidal stimuli having broad-frequency spectra (e.g., pulse, ramp, noise). These complex stimuli would generally activate several channels at the same time, making it important to take into account each channel's response when attempting to explain perceptual phenomena in terms of physiological mechanisms. Clearly, mechanical stimuli used in physiological experiments where psychophysical responses are not obtained may be activating an ensemble of units, thus preventing the experimenter from truly ascertaining the exact code used at the somatosensory periphery. Discussions of experiments dealing with suprathreshold stimulus conditions must consider the possibility that perceptual qualities with an intensive component (e.g., itch, tickle, texture) may be a result of all four channels being stimulated at the same time and not merely the result of activity in a single channel supposedly encoding intensity (Werner and Mountcastle, 1965; Mountcastle, 1967; Harrington and Merzenich, 1970; Kruger and Kenton, 1973; but see, Knibestöl and Vallbo, 1980; Mei *et al.*, 1983; Johnson, 1983; Poulos *et al.*, 1984).

Lastly, the model suggests that, at suprathreshold levels, the code for perceptual quality may be considerably more sophisticated than had been previously realized, requiring that several channels contribute information for this purpose. In other words, fundamental qualities like "pressure," "flutter," and "vibration" may combine to form the many sensory attributes ascribed to the somatosensory system. One implication of the four-channel model is that, before a true understanding of the manner in which sensory experiences such as "roughness," "softness," or "intensity" (among myriad other attributes) can be achieved, it may be necessary to establish, across all receptor types, the criterion response (psychophysically and physiologically) that signals a sensory event in both single and multiple channels. The development of multichannel stimulation techniques may also be necessary to appropriately engage the requisite channels, especially for the purposes of devising prosthetic devices as surrogate inputs for vision and audition.

APPENDIX

Spectral analysis showed that the energy spectrum of the test-stimulus waveform is approximated by

$$F(n/T) = \{\cos[0.407\pi(n-1)/T]$$
$$- \cos[1.407\pi(n-1)/T]\}/n^2 - 2n + 1$$
$$+ \{\cos[0.407\pi(n+1)/T]$$
$$- \cos[1.407\pi(n+1)/T]\}/n^2 + 2n + 1,$$

where T is the period of the fundamental frequency and $-\infty < n < \infty$. The first, second, third, and fourth harmonic frequency components have amplitudes, respectively, that are: 22.7, 34, 41.8, and 54 dB smaller than that of the fundamental, indicating that the results are not affected by the high-frequency components of the stimulus. For the subharmonics, however, a substantial 0-Hz component can be introduced as the carrier frequency (i.e., test-stimulus frequency) approaches very low frequencies. The spectral analysis indicated that, for the frequencies used in the study, the harmonic components below the fundamental frequency did not have an amplitude component greater than the fundamental. For example, at 0.7 Hz, the largest such component occurred at 0 Hz and was 4 dB lower in amplitude than the fundamental. Thus detection by the observer was to the fundamental frequency and not confounded by subharmonic frequency components spuriously introduced by the stimulus parameters. Additional assurance that stimulus artifact was not responsible for the results was provided by the use of the 2500-ms test stimulus that substantially decreases the 0-Hz component of the spectrum. The results obtained were the same as those found for the 700-ms test stimulus (see Sec. II).

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Békésy, G., von (1939). "Über die Vibrationsempfindung,"Akust. Zeits. 4, 316–334.

Bolanowski, S. J., Jr. (1981). "Intensity and frequency characteristics of Pacinian corpuscles," Ph.D. dissertation and Special Rep., ISR-S-20, Institute for Sensory Research, Syracuse University, Syracuse, NY.

Bolanowski, S. J., Jr., and Verrillo, R. T. (1979). "Effects of response criterion on the frequency characteristics of a mechanoreceptor (Pacinian corpuscle)," J. Acoust. Soc. Am. Suppl. 1 65, S11.

Bolanowski, S. J., Jr., and Verrillo, R. T. (1982). "Temperature and criterion effects in a somatosensory subsystem: A neurophysiological and psychophysical study," J. Neurophysiol. 48, 836–855.

Bolanowski, S. J., Jr., and Zwislocki, J. J. (1984). "Intensity and frequency characteristics of Pacinian corpuscles. I. Action potentials," J. Neurophysiol. 51, 793–811.

Capraro, A. J., Verrillo, R. T., and Zwislocki, J. J. (1979). "Psychophysical evidence for a triplex system of mechanoreception," Sens. Process. 3, 334–352.

Craig, J. C. (1968). "Vibrotactile spatial summation," Percept. Psychophys. 4, 351–354.

Dykes, R. W. (1983). "Parallel processing of somatosensory information: A theory," Brain Res. Rev. 6, 47–115.

Freeman, A. W., and Johnson, K. O. (1982a). "Cutaneous mechanoreceptors in macaque monkey: Temporal discharge patterns evoked by vibration, and a receptor model," J. Physiol. 323, 21–41.

Freeman, A. W., and Johnson, K. O. (1982b). "A model accounting for effects of vibratory amplitude on responses of cutaneous mechanoreceptors in macaque monkey," J. Physiol. 323, 43–64.

Gescheider, G. A. (1976). "Evidence in support of the duplex theory of mechanoreception," Sens. Process. 1, 68–76.

Gescheider, G. A., Frisina, R. D., and Verrillo, R. T. (1979). "Selective adaptation of vibrotactile thresholds," Sen. Process. 3, 37–48.

Gescheider, G. A., O'Malley, M. J., and Verrillo, R. T. (1983). "Vibrotactile forward masking: Evidence for channel independence," J. Acoust. Soc. Am. 74, 474–485.

Gescheider, G. A., Sklar, B. F., Van Doren, C. L., and Verrillo, R. T. (1985). "Vibrotactile forward masking: Psychophysical evidence for a triplex theory of cutaneous mechanoreception," J. Acoust. Soc. Am. 74, 534–543.

Gescheider, G. A., Verrillo, R. T., and Van Doren, C. L. (1982). "Predictions of vibrotactile masking functions," J. Acoust. Soc. Am. 72, 1421–1426.

Hamer, R. D. (1979). "Vibrotactile masking: Evidence for a peripheral energy threshold," Ph.D. dissertation and Special Rep., ISR-S-18, Institute for Sensory Research, Syracuse University, Syracuse, NY.

Hamer, R. D., Verrillo, R. T., and Zwislocki, J. J. (1983). "Vibrotactile masking of Pacinian and non-Pacinian channels," J. Acoust. Soc. Am. 73, 1293–1303.

Hardy, J. D., and Bard, P. (1974). "Body temperature regulation," in Medical Physiology, edited by V. B. Mountcastle (Mosby, St. Louis, MO), pp. 1305–1342.

Harrington, T., and Merzenich, M. M. (1970). "Neural coding in the sense of touch: Human sensations of skin indentation compared with the responses of slowly adapting mechanoreceptive afferents innervating the hairy skin of monkeys," Exp. Brain Res. 10, 251–264.

Hensel, H., and Bowman, K. A. (1960). "Afferent impulses in cutaneous nerves in human subjects," J. Neurophysiol. 23, 564–578.

Iggo, A., and Ogawa, H. (1977). "Correlative physiological and morphological studies of rapidly adapting mechanoreceptors in cat's glabrous skin," J. Physiol. 266, 275–296.

Johansson, R. S. (1976). "Receptive sensitivity profile of mechanosensitive units innervating the glabrous skin of the human hand," Brain Res. 104, 330–334.

Johansson, R. S. (1978). "Tactile sensibility of the human hand: receptive field characteristics of mechanoreceptive units in the glabrous skin," J. Physiol. 281, 101–123.

Johansson, R. S., Landström, U., and Lundström, R. (1982a). "Responses of mechanoreceptive afferent units in the glabrous skin of the human hand to sinusoidal skin displacements," Brain Res. 244, 17–25.

Johansson, R. S., Landstöm, U., and Lundström, R. (1982b). "Sensitivity to edges of mechanoreceptive afferent units innervating the glabrous skin of the human hand," Brain Res. 244, 27–32.

Johansson, R. S., and Vallbo, A. B. (1979). "Tactile sensibility in the human hand: Relative and absolute densities of four types of mechanoreceptive units in glabrous skin," J. Physiol. (London) 286, 283–300.

Johnson, K. O. (1983). "Neural mechanisms of tactual form and texture discrimination," Fed. Proc. 42, 2542–2547.

Johnson, K. O. (1987). Personal communication.

Knibestöl, M. (1975). "Stimulus-response functions of slowly adapting mechanoreceptors in the human glabrous skin area," J. Physiol. (London) 245, 63–80.

Knibestöl, M., and Vallbo, A. B. (1980). "Intensity of sensation related to activity of slowly adapting mechanoreceptive units in the human hand," J. Physiol. (London) 300, 251–267.

Kruger, L., and Kenton, B. (1973). "Quantitative neural and psychophysical data for cutaneous mechanoreceptor function," Brain. Res. 49, 1–24.

Labs, S. M., Gescheider, G. A., Fay, R. R., and Lyons, C. H. (1978). "Psychophysical tuning curves in vibrotaction," Sen. Process. 2, 231–247.

Lindblom, U. (1965). "Properties of touch receptors in distal glabrous skin of the monkey," J. Neurophysiol. 28, 966–985.

Lindblom, U., and Lund, L. (1966). "The discharge from vibration sensitive receptors in the monkey foot," Exp. Neurol. 15, 401–417.

Mei, J., Tuckett, R. P., Poulos, D. A., Horch, K. W., Wei, J. Y., and Burgess, P. R. (1983). "The neural signal for skin indentation depth. II. Steady indentations," J. Neurosci. 3, 2652–2659.

Merzenich, M. M., and Harrington, T. (1969). "The sense of flutter-vibration evoked by stimulation of the hairy skin of primates: Comparisons of human sensory capacity with the responses of mechanoreceptive afferents innervating the hairy skin of monkeys," Exp. Brain Res. 9, 236–260.

Mountcastle, V. B. (1967). "The problem of sensing and the neural coding of sensory events," in The Neurosciences, edited by G. C. Quarton, T. Melnechuck, and F. O. Schmidt (Rockefeller, New York), pp. 393–408.

Mountcastle, V. B., LaMotte, R. H., and Carli, G. (1972). "Detection thresholds for stimuli in humans and monkeys: Comparison with threshold events in mechanoreceptive afferent nerve fibers innervating the monkey hand," J. Neurophysiol. 35, 122–136.

Ochoa, J. L., and Torebjörk, H. E. (1983). "Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand," J. Physiol. 342, 633–653.

Pertovaara, A., and Hämäläinen, H. (1981). "Vibrotactile thresholds in non-Pacinian afferents: the importance of temporal parameters," Acta Physiol. Scand. 113, 519–522.

Poulos, D. A., Mei, J., Horch, K. W., Tuckett, R. P., Wei, J. Y., Cornwall, M. C., and Burgess, P. R. (1984). "The neural signal for the intensity of a tactile stimulus," J. Neurosci. 4, 2016–2024.

Talbot, W. H., Darian-Smith, I., Kornhuber, H. H., and Mountcastle, V. B. (1968). "The sense of flutter-vibration: Comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand," J. Neurophysiol. 31, 301–334.

Tapper, D. N., Galera-Garcia, C., and Brown, P. (1972). "Sinusoidal mechanical stimulation of the tactile pad receptor: tuning curves," Brain Res. 36, 223–227.

Torebjörk, H. E., and Ochoa, J. L. (1980). "Specific sensations evoked by activity in single identified sensory units in man," Acta. Physiol. Scand. 110, 445–447.

Vallbo, A. B. (1981). "Sensations evoked from the glabrous skin of the human hand by electrical stimulation of unitary mechanosensitive afferents," Brain Res. 215, 359–363.

Vallbo, A. B., and Johansson, R. S. (1976). "Skin mechanoreceptors in the human hand: Neural and psychophysical thresholds," in Sensory Functions of the Skin of Primates, with Special Reference to Man, edited by Y. Zotterman (Pergamon, New York), pp. 185–198.

Vallbo, A. B., and Johansson, R. S. (1984). "Properties of cutaneous mechanoreceptors in the human hand related to touch sensation," Human Neurobiol. 3, 3–14.

Van Dorn, C. L. (1985). "Temporal summation by Pacinian corpuscles precludes entrainment at the detection threshold," J. Acoust. Soc. Am. 77, 2188–2189.

Verrillo, R. T. (1962). "Investigation of some parameters of the cutaneous threshold for vibration," J. Acoust Soc. Am. 34, 1768–1773.

Verrillo, R. T. (1963). "Effect of contactor area on the vibrotactile threshold," J. Acoust. Soc. Am. 35, 1962–1966.

Verrillo, R. T. (1965). "Temporal summation in vibrotactile sensitivity," J. Acoust. Soc. Am. 37, 843–846.

Verrillo, R. T. (1966a). "Vibrotactile sensitivity and the frequency response of the Pacinian corpuscle," Psychon. Sci. 4, 135–136.

Verrillo, R. T. (1966b). "Effects of spatial parameters on the vibrotactile threshold," J. Exp. Psychol. 71, 570–574.

Verrillo, R. T. (1966c). "Vibrotactile thresholds for hairy skin," J. Exp. Psychol. 72, 47–50.

Verrillo, R. T. (1968). "A duplex mechanism of mechanoreception," in *The Skin Senses*, edited by D. R. Kenshalo (Thomas, Springfield, IL), pp. 139–159.

Verrillo, R. T. (1971). "The effect of rise time on vibrotactile thresholds," Psychon. Sci. 25, 199–200.

Verrillo, R. T. (1975). "Cutaneous sensation," in *Experimental Sensory Psychology*, edited by B. Scharf (Scott, Foresman, Glenview, IL), pp. 159–184.

Verrillo, R. T. (1979). "The effects of surface gradients on vibrotactile thresholds," Sen. Process. 3, 27–36.

Verrillo, R. T., and Bolanowski, S. J., Jr. (1986). "The effects of skin temperature on the psychophysical responses to vibration on glabrous and hairy skin," J. Acoust. Soc. Am. 80, 528–532.

Verrillo, R. T., and Capraro, A. J. (1974). "Effects of simultaneous auditory stimulation on vibrotactile thresholds," Percept. Psychophys. 16, 597–600.

Verrillo, R. T., and Gescheider, G. A. (1977). "Effects of prior stimulation on vibrotactile thresholds," Sen. Process. 1, 292–300.

Werner, G., and Mountcastle, V. B. (1965). "Neural activity in mechanoreceptive cutaneous afferents: Stimulus response relations, Weber functions, and information transmission," J. Neurophysiol. 28, 359–397.

Zwislocki, J. J. (1960). "Theory of temporal auditory summation," J. Acoust. Soc. Am. 32, 1046–1060.

Zwislocki, J. J., Maire, F., Feldman, A. S., and Rubin, H. J. (1958). "On the effect of practice and motivation on the threshold of audibility," J. Acoust. Soc. Am. 30, 254–262.