

The frequency selectivity of information-processing channels in the tactile sensory system

G. A. GESCHEIDER^{1,3}, S. J. BOLANOWSKI^{2,3} and K. R. HARDICK¹

¹*Hamilton College, Department of Psychology, Clinton, NY 13323, USA;* ²*Department of Bioengineering and Neuroscience, Syracuse University, Syracuse, NY 13244, USA;* ³*Institute for Sensory Research, Syracuse University, Syracuse, NY 13244, USA*

Abstract

The frequency selectivity of the P, NP I, and NP II channels of the four-channel model of mechanoreception for glabrous skin was measured psychophysically by an adaptation tuning curve procedure. The results substantially extend the frequency range over which the frequency selectivity of these channels is known and further confirm the hypothesis that the input stage of each of these channels consists of specific sensory nerve fibers and associated receptors. Specifically, the frequency characteristics of Pacinian nerve fibers, rapidly adapting (RA) nerve fibers, and slowly adapting Type II (SA II) nerve fibers were found to be the peripheral neurophysiological correlates of the P, NP I, and NP II channels, respectively. The finding that the tuning characteristic for a test stimulus of 250 Hz delivered through a small (0.008 cm²) contactor depended dramatically on the duration of the test stimulus whereas the detection threshold did not, provides new evidence in support of the hypothesis that separate NP II and P channels exist.

Key words: *somatosensation, touch, tactile sensitivity, vibrotaction, mechanoreception*

Introduction

The concept of the information-processing channel is fundamental to understanding the properties of sensory systems. A channel is an element that is tuned to a specific region of the energy spectrum to which a system responds. In a multichannel sensory system, different channels, tuned to different regions of the spectrum, provide information about the relative energy levels in various parts of the spectrum representing a particular stimulus. According to this approach, the relative activity levels in each of the several channels determine the qualitative and quantitative dimensions of perceptual experience (see Bolanowski, 1996). There is strong evidence that tuned channels exist in sensory systems, as seen in psychophysical studies of the critical band in hearing (e.g., Fletcher, 1940), color vision (e.g., Wald, 1964), visual contrast sensitivity (e.g., Campbell and Robson, 1968), taste (e.g., Henning, 1916), and touch (e.g., Verrillo and Gescheider, 1975; Bolanowski *et al.*, 1988). If the concept of tuned channels is to be useful, however, then it is essential that the tuning characteristic of each channel be identified over the full range of the energy spectrum to which the sensory system responds. In this way, the relative activity levels of each channel can be determined for any stimulus presented to the sensory system.

What is known about the tuning of tactile channels? The earliest evidence for the existence of tactile

channels was the discovery that, although at low stimulus frequencies detection thresholds are nearly independent of stimulus frequency, they become sharply tuned at higher frequencies with the lowest threshold at 250–300 Hz (Békésy, 1939; Verrillo, 1963; Verrillo *et al.*, 1969; Gescheider, 1976; Bolanowski *et al.*, 1988). The existence of the multi-segmented threshold curve suggests the operation of several independent sensory channels that mediate the detection of vibration. Each segment of the psychophysical function is thought to represent the hypothetical neural threshold for the system, and according to this notion, the psychophysical threshold at a particular frequency is determined by the channel with the lowest threshold.

Verrillo (1966), in comparing his psychophysical threshold data with the neurophysiological frequency characteristics of single Pacinian corpuscles in cat reported by Sato (1961), proposed that the Pacinian corpuscle was the neural entity mediating the U-shaped portion of the psychophysical threshold function. Lindblom (1965) and Mountcastle and co-workers (e.g., Talbot *et al.*, 1968; Mountcastle *et al.*, 1972) identified rapidly adapting (RA) nerve fibers, with associated Meissner-corpuscle receptors, as the neural entity responsible for the detection of mid-frequency vibrations. The low-frequency portion of the threshold curve has been proposed to be mediated by the slowly adapting Type I fibers believed to innervate Merkel-cell neurite complexes (Bolanowski *et al.*, 1988).

The relatively flat frequency characteristics of the non-Pacinian (NP) channels and the highly tuned characteristic of the Pacinian channel (P) have been obtained under and are affected by a wide range of conditions. For example, it was found that the relatively flat segment of the threshold curve is extended to higher frequencies by reducing contactor size (Verrillo, 1963; Gescheider, 1976) or stimulus duration (Gescheider *et al.*, 1977). It is assumed that these results are due to the reduced sensitivity of the spatially and temporally summing Pacinian channel coupled with the fact that the sensitivities of the NP channels are neither affected by changes in contactor size nor stimulus duration.

Although these findings constituted a strong case in support of the hypothesized frequency characteristics of separate tactile channels, further psychophysical measurement of these characteristics over a broader frequency range came with the use of two procedures, each of which was designed to isolate one channel so that its tuning curve could be measured more effectively. In one procedure, selective adaptation was used to elevate the threshold of one channel so that the sensitivity of the other could be measured over a wide range of frequencies (Verrillo and Gescheider, 1977; Capraro *et al.*, 1979; Gescheider and Verrillo, 1979; Hollins *et al.*, 1990). Through the use of this method, the NP channel became divided into two separate channels designated as NP I and NP II (Capraro *et al.*, 1979). Both channels have relatively high thresholds and are broadly tuned with optimal sensitivity of the NP I channel at 30–50 Hz and the optimal sensitivity of the NP II channel at approximately 250 Hz.

In the other procedure, masking was used to isolate channels for the purpose of studying their tuning characteristics (Labs *et al.*, 1978; Gescheider and Verrillo, 1979; Gescheider *et al.*, 1982, 1983, 1985; Hamer *et al.*, 1983; Verrillo *et al.*, 1983; Bolanowski *et al.*, 1988). For example, the existence of the NP II channel was confirmed by using a low-frequency masking stimulus to elevate the thresholds of the NP I channel and by delivering the stimuli through a small contactor to elevate the threshold of the P channel (Gescheider *et al.*, 1985). A fourth channel, NP III, was also discovered through the use of a masking procedure, and as a result, the four-channel model of mechanoreception was proposed (Bolanowski *et al.*, 1988).

Of all of the masking procedures used to isolate and define tactile channels, the procedure analogous to that used in audition to obtain psychoacoustic tuning curves (Vogten, 1974; Zwicker, 1974; Zwicker and Schorn, 1978; Florentine *et al.*, 1980; Bacon and Jesteadt, 1987) provided the most efficient means of determining the tuning of a channel over a wide range of frequencies (Labs *et al.*, 1978). In this method, a test stimulus that activates a single channel is presented at an intensity level slightly above the detection threshold. Then intensities of

masking stimuli presented at various frequencies needed to maintain detectability of the test stimulus at a constant level are measured. The psychophysical tuning curve is a graphic representation of these masking stimulus intensities plotted as a function of their frequency and provides a measure of the frequency characteristic of the channel. A variation of this procedure in which an adapting stimulus is used to elevate the threshold of the test stimulus was used in the present study to measure the tuning of the P, NP I, and NP II channels.

In this procedure, the tuning curve for a channel is obtained by determining the intensities of adapting stimuli of various frequencies needed to maintain a constant level of detectability for a test stimulus presented exclusively within a single channel.

Experiment I

Frequency selectivity of the P channel

The purpose of this experiment was to measure the tuning of the P channel over the frequency range of 2–400 Hz and in so doing to extend the frequency range over which the frequency selectivity of the P channel is known from approximately five to approximately eight octaves. The three additional octaves of the tuning curve measured in this experiment were within the low-frequency range from 2 to 15 Hz. Within this range, electrophysiological recordings from Pacinian nerve fibers in cat suggests that the tuning curve of the P channel may dramatically change at low frequencies becoming nearly independent of frequency (Pawson *et al.*, 1996). Thus, it becomes important to test this hypothesis by psychophysically measuring the frequency selectivity of the P channel over an extended frequency range that includes these low frequencies.

The P channel was isolated by using a 250-Hz test stimulus delivered through a relatively large 1.5-cm² contactor. Because spatial summation, as well as temporal summation, is an exclusive property of this channel, the P channel is exceptionally sensitive when the stimulus is relatively long in duration, e.g., 1 s, and is delivered through a large contactor, e.g., 1.5 cm². Indeed, the detection threshold of the P channel at 250 Hz, under these conditions, is 25–30 dB below that of any other channel (Bolanowski *et al.*, 1988). In this experiment the intensities of adapting stimuli of variable frequency that would raise the threshold of a 250-Hz test stimulus by 10 dB were determined.

The use of the adaptation tuning curve method to measure the tuning of a channel is based upon the assumptions that (1) there is no cross-channel adaptation and (2) adaptation, while elevating thresholds, does so proportionally across frequencies, thus reflecting the tuning of the channel. The results of the present study strongly support the validity of these assumptions.

Method

Observers Three observers, two females and one male, participated in this experiment. The age of the observers ranged from 20 to 22 years and all were healthy with no known neurological disorders. Prior to the experiment, each observer participated in two or three 1-h practice sessions in detecting vibrotactile stimuli in the absence of and in the presence of an adapting stimulus.

Apparatus The observer and stimulus-delivering apparatus were located within a sound and vibration-proofed testing chamber. Vibratory stimuli were produced by a Ling 203-A shaker. Vibratory displacements of the skin were produced relative to a static indentation of the vibrator contactor of 1.0 mm into the skin. This static indentation was sufficient to prevent decoupling of the vibrator contactor from the skin during vibratory stimulation at the high amplitudes used in the present study (see Cohen *et al.*, 1999). Sinusoidal displacements of the skin were measured with a calibrated electromagnetic linear-variable displacement transducer (Schaevitz LVDT) that sensed the displacement of the moving element of the vibrator. All measurements were made with the observer's hand in the test position. The skin was stimulated by a 1.5-cm² circular contactor, contoured to fit the curvature of the skin of the thenar eminence and mounted on the moving element of the vibrator. The edge of the contactor was separated from a rigid surround by a 1.0-mm gap. The rigid surround confines the stimulus to the immediate area of the contactor (Eijkman and Vendrick, 1960) by limiting the spread of surface waves on the skin (Verrillo *et al.*, 1983). Because skin temperature can affect vibrotactile sensitivity (Bolanowski and Verrillo, 1982; Verrillo and Bolanowski, 1986), skin temperature was held constant to within 0.5 °C of 30 °C by a device that circulates water of the appropriate temperature through the hollow chamber of the surround. A Lauda/Brinkman RMG heating and refrigeration unit and pump controlled both the water temperature and the circulation flow rate. Skin temperature was monitored by a thermistor embedded in the surround. Observers wore earphones through which narrow-band noise was delivered to mask the sound of the vibrator. Stimulus waveforms and timing were controlled by a Mac II computer system. The 250-Hz test stimulus was 1.0 s in duration measured at the half-power point and had a rise-fall time of 0.2 s. The adapting stimulus was 15.0 s in duration and had a rise-fall time of 0.5 s.

Procedures The test site was the thenar eminence of the right hand. This site was chosen because the channel organization is better understood on the thenar eminence than elsewhere. Detection thresholds were measured by a two-alternative forced-

choice tracking procedure (Zwislocki *et al.*, 1958) in which the observer is presented with two sequentially presented observation intervals designated by lights, one containing a stimulus and one not. The presentation of the stimulus is distributed randomly between the two observation intervals with a probability of 0.5. The amplitude of the stimulus was decreased by 1.0 dB for every three correct responses (not necessarily consecutive) and was increased by 1.0 dB for every error. This method determines the amplitude of the stimulus resulting in 75% correct responses at the detection threshold. Stimulus amplitude is recorded when performance of the observer is maintained at this criterion and the variability in the tracking record does not exceed 2.0 dB above or below the mean for at least 30 responses. Thresholds were expressed in dB referenced to 1.0 μ m peak displacement amplitude.

When the adaptation tuning curve was measured, the 250-Hz test stimulus was presented at 10 dB above the unadapted detection threshold and the amplitude of the 15-s adapting stimulus necessary to bring the test stimulus to threshold was determined. Again, the two-alternative forced-choice tracking procedure was used, but this time the amplitude of the adapting stimulus was increased by 1.0 dB for every three correct responses (not necessarily consecutive) and decreased by 1.0 dB for every error. Two observation intervals separated by 1.0 s, designated by lights, one containing the test stimulus and one not, were presented 0.2 s after the termination of the adapting stimulus. The observer's task was to push a button to indicate which interval contained the stimulus. The presentation of the test stimulus was randomly presented within the two observation intervals with a probability of 0.5 of it being in one or the other of the intervals. The amplitude of the adapting stimulus was recorded when the observer was able to correctly detect the test stimulus 75% of the time for at least 30 responses with variability in the tracking record not exceeding 2.0 dB above or below the mean. The amplitude of the adapting stimulus required for the observer to maintain this level of performance was expressed in dB referenced to 1.0 μ m peak displacement of the skin. Within each session, the amplitude of the adapting stimulus needed to maintain this test stimulus at threshold was measured for three randomly selected frequencies of the adapting stimulus. Over a series of nine sessions, three tuning curve values were obtained at each of nine frequencies (2, 5, 8, 15, 30, 50, 100, 250, and 400 Hz).

Results and discussion

The mean values of the adapting stimulus for each of the three observers needed to elevate the threshold for detection of the 250-Hz test stimulus by 10 dB are plotted in Figure 1. It should be noted that each value of the adapting stimulus is an amplitude

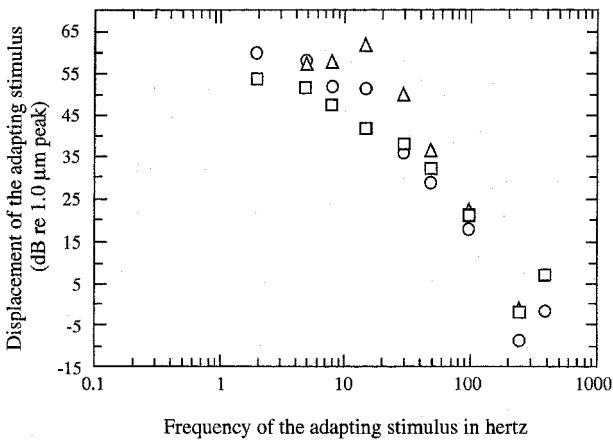


FIGURE 1. Adaptation tuning curves of the P channel for three observers. The intensity of the adapting stimulus in decibels is plotted against its frequency.

expressed in dB relative to 1.0 μ m peak displacement of the skin. The results of the three observers are in close agreement in that they all show U-shaped functions characteristic of the P channel.

The average tuning curve of the three observers is plotted in Figure 2. The solid curve through the data points represents the tuning characteristic for the P channel measured at absolute threshold (from Bolanowski *et al.*, 1988). The vertical position of this function has been adjusted upward by 23 dB along the intensity axis so that it can be directly compared with the results obtained by the adaptation tuning curve method. The exact position of the function was determined by how well the curve appeared to fit the data. It is clear that the tuning of the P channel is essentially the same whether determined by measurement of absolute thresholds or by the adaptation tuning curve. This finding provides strong support for the assumptions that underlie the use of the method, which are that there is no cross-channel adaptation and that the tuning of the P-channel is unaffected by adaptation.

Makous *et al.* (1995) derived P channel tuning curves from masking data that flatten out at low frequencies as do the tuning curves of the present experiment. The flattening of the tuning of the P channel at low frequencies is also seen in the tuning curves of Pacinian corpuscles of the cat when the cat's paw was stimulated at varying frequencies of vibration and action potentials were recorded from single Pacinian nerve fibers (Pawson *et al.*, 1996). As seen in Figure 2, the adaptation tuning curve is compared with the tuning of single Pacinian nerve fibers innervating the monkey palm (Mountcastle *et al.*, 1972) and excised Pacinian corpuscles from cat mesentery (Bolanowski, 1981; also in Bolanowski *et al.*, 1988), although the frequency range is very limited. The neurophysiological results specified as the intensity of vibration required to produce a criterion neural response as a function of frequency are in close agreement with the psychophysical

tuning curve over comparable frequency ranges. Because the tuning of the excised Pacinian corpuscles, intact PC fibers of cat and monkey and the psychophysically measured P channel are essentially the same, it is our conclusion that the activity of Pacinian corpuscles constitutes the neural input to the P channel. It is also apparent from this finding that the mechanics of the skin play no role in determining the frequency selectivity of the P channel. Specifically, the same tuning is observed in intact and excised Pacinian corpuscles. The conclusion that skin mechanics have no effect on the detection of vibration is also supported by the finding that thresholds are unaffected by hydration of the skin (Verrillo *et al.*, 1998) which has an effect on skin mechanics (Blank, 1952; Warner *et al.*, 1988a, b).

The tuning of single Pacinian nerve fibers of humans are also in close agreement with the human frequency selectivity of the P channel when differences in methodology are taken into account. The slope of the tuning curve of the P channel between 15 and 200 Hz has consistently been found to be approximately -12 dB/octave (e.g., Verrillo, 1963; Gescheider, 1976; Verrillo and Gescheider, 1977; Bolanowski *et al.*, 1988; Gescheider *et al.*, 1994) and as seen in Figure 2, this slope also characterizes the tuning curve of single Pacinian nerve fibers in cat and monkey. The tuning curves derived from the data obtained by Johansson *et al.* (1982) on single Pacinian nerve fibers of humans had shallower slopes of approximately -9.0 dB/octave. Checkosky and Bolanowski (1994) accounted for this difference in terms of differences in methodology. The slope of the tuning curve becomes shallower when the number of cycles in a burst of vibration is held constant as frequency is varied, as in Johansson *et al.* (1982), rather than using the more conventional method of holding the duration of the burst constant (Check-

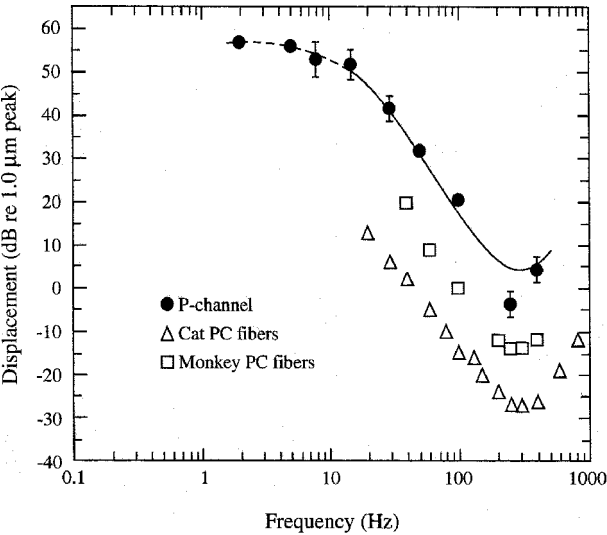


FIGURE 2. Average adaptation tuning curves of the P channel with standard error bars compared with the average neurophysiological tuning curves of PC fibers from monkey (Mountcastle *et al.*, 1972) and cat (Bolanowski, 1981).

osky and Bolanowski, 1994). Psychophysical thresholds within the P channel measured as a function of frequency when the number of cycles in the burst was held constant (Checkosky and Bolanowski, 1994) had a slope of -9.0 dB/octave as did Pacinian nerve fibers of cats measured under comparable conditions. Thus, the psychophysical tuning curves of the P channel are in close agreement with the neurophysiological tuning curves of Pacinian nerve fibers of humans as well as with those of cats and monkeys.

Experiment II

Frequency selectivity of the NP I channel

The purpose of this experiment was to measure the tuning of the NP I channel over a wide range of frequencies. Prior to this experiment, the frequency selectivity of the NP I channel could be specified for stimuli within a frequency range of a little over five octaves (2–100 Hz). The present experiment extends this range, on both low- and high-frequency sides to a little over nine octaves (0.6–500 Hz), and in so doing the results permit a better opportunity for making comparisons of the tuning of the channel with the tuning of RA fibers hypothesized to provide the peripheral neural input and the sole source of frequency selectivity to the NP I channel.

Method

Observers Five observers, three females and two males, participated in this experiment. The age of the observers ranged from 20 to 22 years and none had any known neurological disorders. Prior to the experiment, each observer participated in two or three 1-h practice sessions.

Apparatus The apparatus was identical to that used in Experiment I.

Procedure The procedure was the same as that used in Experiment I. The NP I channel was isolated by using a 22-Hz test stimulus delivered through a 1.5-cm^2 contactor. According to the four-channel model of mechanoreception (Bolanowski *et al.*, 1988), under these conditions, the threshold of the NP I channel is approximately 10 dB below that of the NP III channel, 13 dB below that of the P channel and 20 dB below that of the NP II channel. The frequencies of the adapting stimuli ranged from 0.6 to 400 Hz.

Results and discussion

The mean values of the adapting stimulus, for each of five observers, needed to elevate the threshold for detection of the 22-Hz test stimulus by 10 dB are plotted in Figure 3. The results of the five observers

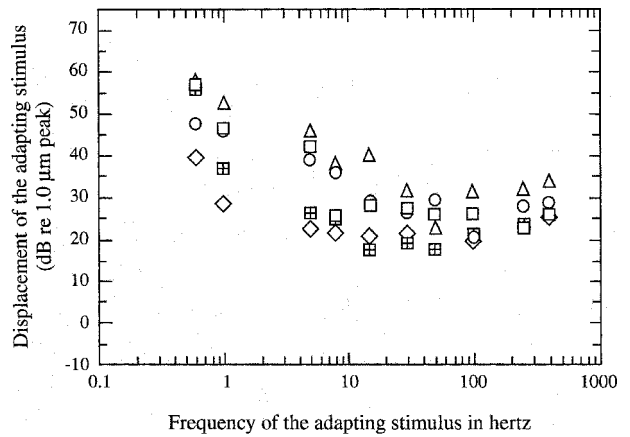


FIGURE 3. Adaptation tuning curves of the NP I channel for five observers. The intensity of the adapting stimulus in decibels is plotted against its frequency.

are in close agreement, all showing functions with gradual slopes characteristic of the NP I channel.

The results averaged over the five subjects are shown in Figure 4. The solid curve represents the absolute threshold function of the NP I channel (from Bolanowski *et al.*, 1988). The vertical position of the absolute threshold function has been adjusted up by 15 dB so that it can be directly compared with the adaptation tuning curve. The exact position was determined by how well the function appeared to fit the data points. The tuning of the NP I channel determined by the adaptation tuning curve procedure is very similar to the tuning characteristic determined by absolute threshold measurements. This finding indicates that there was no cross-channel adaptation and that the tuning of the NP I channel was unaffected by adaptation, thus providing strong support for the use of the adaptation tuning curve procedure to examine the tuning of the NP I channel over a frequency range much wider than that which is possible when measuring absolute thresholds.

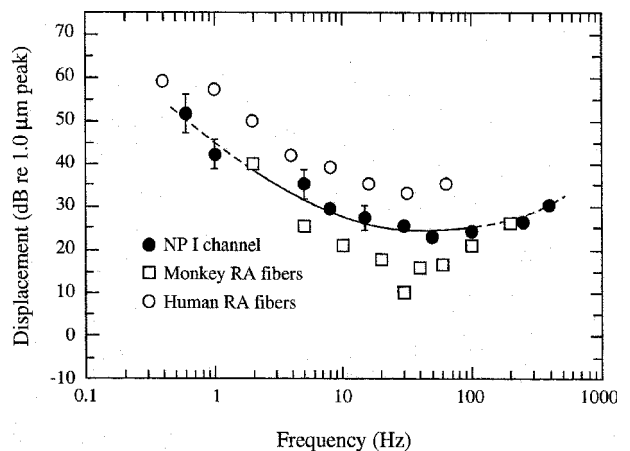


FIGURE 4. Average adaptation tuning curves of the NP I channel with standard error bars compared with the average neurophysiological tuning curves of RA fibers from monkey (Mountcastle *et al.*, 1972) and humans (Johansson *et al.*, 1982).

The dashed portions of the curve in Figure 4 represent the segments of the tuning curve of the NP I channel that were not known prior to this experiment. The entire curve can be described as a U-shaped function having shallow slopes with the best tuning at approximately 30–50 Hz. It is also apparent in Figure 4 that the psychophysical results are in close agreement with the tuning of single RA nerve fibers from humans (Johansson *et al.*, 1982) and monkey (Mountcastle *et al.*, 1972).

The human RA tuning curve of the present study is the same as that seen in Bolanowski *et al.* (1988) and was derived from the data of Johansson *et al.* (1982) assuming a response criterion of a single action potential per burst of vibration. The RA tuning curve for monkey seen in Figure 4 was based on this same response criterion. The forms of the neurophysiological tuning curves for both monkey and humans are in close agreement with the form of the psychophysical tuning curve of the NP I channel, thus supporting the hypothesis that the tuning of this channel is determined by the tuning of the RA fibers and their associated Meissner-corporcle receptors. The data are also consistent with earlier evidence that human observers are capable of detecting the presence, on a single RA nerve fiber, of a single action potential (Hensel and Bowman, 1960; Vallbo and Johansson, 1976; Torebjörk and Ochoa, 1980; Vallbo, 1981; Ochoa and Torebjörk, 1983).

Experiment III

Frequency selectivity of the NP II channel

The NP II channel has been identified in two ways. First, it was discovered that thresholds for detecting high-frequency vibration become independent of stimulus duration indicating the absence of temporal summation, when the stimulus was delivered through a very small ($< 0.02 \text{ cm}^2$) contactor (Verrillo, 1965). When the same stimuli were delivered through larger contactors the P channel, because of its capacity for spatial summation, became exclusively engaged, and temporal summation was exhibited. It was later discovered through adaptation (Capraro *et al.*, 1979) and masking (Gescheider *et al.*, 1985) procedures, that the P and NP II channels could be further distinguished on the bases of their frequency selectivity. The NP II channel was found to be much more broadly tuned than the P channel, although the best frequencies of both channels were found to be 250–300 Hz.

The purpose of the present experiment was to extend the tuning curve of the NP II channel form slightly less than five octaves (15–400 Hz) to slightly more than seven octaves (3–400 Hz). It was hoped that the extended tuning curve would provide a better basis for comparison of the psychophysically measured frequency selectivity of the NP II channel with the tuning of individual SA II afferent fibers

hypothesized to serve as the peripheral input and the sole source of frequency selectivity to the channel.

Method

Observers Three observers, one female and two males, participated in the experiment. The age of the observers ranged from 20 to 22 years and none were known to have any neurological disorders. Prior to the experiment, each observer participated in one or two 1-h practice sessions.

Apparatus The apparatus was identical to that used in the other experiments with the exception that the contactor size was 0.008 cm^2 .

Procedure The procedure for measuring the tuning curves was the same as that used in Experiments I and II. The NP II channel was isolated by using a 50 ms, 250-Hz test stimulus delivered through a 0.008 cm^2 contactor. Preliminary tests revealed that when the test stimulus was presented at an intensity of 10 dB above threshold for a duration of 1.0 s, the tuning curve resembled that of the P channel rather than that of the NP II channel as measured in previous experiments (Capraro *et al.*, 1979; Gescheider *et al.*, 1985). To isolate the NP II channel, it became important to arrange the stimulus conditions so that the test stimulus excited the NP II channel but at an intensity below the threshold of the P channel. Because the P channel, but not the NP II channel, is capable of temporal summation (Gescheider *et al.*, 1999) the threshold of the P channel could be elevated by reducing the duration of the 250-Hz test stimulus from 1.0 s to 50 ms. To further ensure that the test stimulus excited only the NP II channel, its intensity was set at only 6 dB above threshold rather than 10 dB as in the experiments in which the frequency selectivity of the P and NP I channels was measured. After completion of sessions in which the test stimulus had a duration of 50 ms, a series of sessions were conducted in which the test stimulus duration was 1.0 s.

Results and discussion For each of the three observers, the mean values of the adapting stimulus needed to maintain detection of the 250-Hz test stimulus at threshold are plotted in Figure 5. The results of the three observers are in close agreement, each showing the gradually decreasing function to 250 Hz that is characteristic of the NP II channel (see Bolanowski *et al.*, 1988). In Figure 6 it is seen that the average NP II tuning curve is in substantial agreement with the tuning of slowly adapting Type II (SA II) fibers from humans derived from the results of Johansson *et al.* (1982). It is our contention that it is neural activity from SA II fibers that constitutes the input to the NP II channel (Bolanowski *et al.*, 1988).

The tuning curve presented in Figure 6 for the SA II fibers in humans derived from the data of

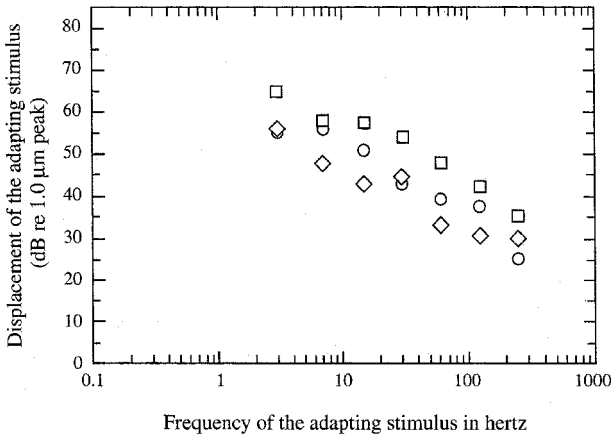


FIGURE 5. Adaptation tuning curves of the NP II channel for three observers. The intensity of the adapting stimulus in decibels is plotted against its frequency.

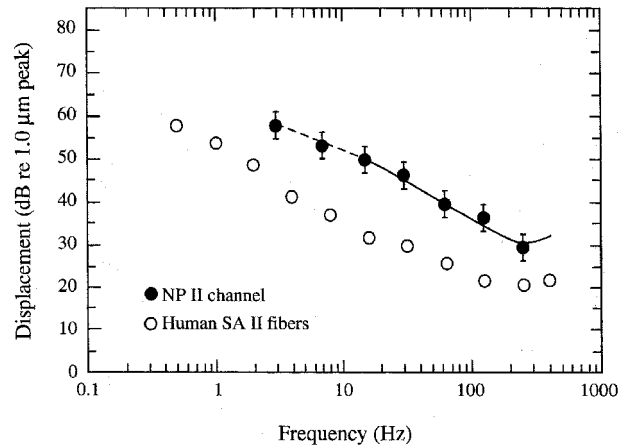


FIGURE 6. Average adaptation tuning curves of the NP II channel with standard error bars compared with average neurophysiological tuning curves of SA II fibers from humans (Johansson *et al.*, 1982).

Johansson *et al.* (1982) is identical to that presented in Bolanowski *et al.* (1988) and identified as the neurophysiological basis for the tuning of the NP II channel. Since SA II fibers exhibit spontaneous activity (Johansson *et al.*, 1982) a relatively high firing rate of 5 spikes/s was chosen as the response criterion for constructing the tuning curve. It should be pointed out that because the production of action potentials through electrical stimulation of single SA II fibers in humans failed to elicit reports of sensation by observers (Ochoa and Torebjörk, 1983) the neural code at the detection threshold may require activation of more than one fiber.

The tuning curve of the NP II channel measured psychophysically in the present study is also very similar in form to those measured earlier over a narrower frequency range by forward masking (Gescheider *et al.*, 1985) and adaptation (Capraro *et al.*, 1979). The solid curve through the data points represents the NP II tuning curve obtained earlier by forward masking (Gescheider *et al.*, 1985). The exact position of the forward-masking tuning curve was determined by how well the curve appeared to fit the data points. The dashed curve is the extension of this tuning curve obtained in the present experiment.

Shown in Figure 7 are the psychophysical results seen in Figure 6 and also four data points on a tuning curve that were obtained when the duration of the stimulus was extended to 1.0 s. The use of a 1.0 s test stimulus failed to capture the tuning characteristic of the NP II channel with its typical slope of -5.0 to -6.0 dB per doubling of frequency between 15 and 250 Hz (Capraro *et al.*, 1979; Gescheider *et al.*, 1985; Bolanowski *et al.*, 1988). Instead, the tuning curve obtained under this condition has the much steeper slope of approximately -12 /octave characteristic of the high-frequency portion of the tuning curve of the P channel seen in Figure 2. The P channel tuning curve obtained in Experiment I, when adjusted along the intensity axis, fits the data points well and strongly suggests the involvement of

the P channel when the duration of the test stimulus was 1.0 s. Only when the duration of the test stimulus was shortened to 50 ms did the tuning of the NP II channel become apparent.

Why does the form of the tuning curve obtained when a 250-Hz stimulus is delivered to the skin through a very small contactor depend so dramatically on stimulus duration? The answer resides in the fact that the P channel is known to be capable of temporal summation in the detection of stimuli while the NP II is not (Verrillo, 1965; Gescheider, 1976; Gescheider *et al.*, 1999). The inability of the NP II channel to become more sensitive to a stimulus as its duration is increased was also demonstrated in the present study in which the average threshold for detecting the 250-Hz, 50-ms test stimulus (9.13 dB) did not differ significantly from the average threshold for detecting this stimulus when presented for 1.0 s (9.60 dB). Had the same stimuli been delivered through a larger contactor that would engage the P channel, the detection threshold would have been approximately 6.0 dB lower when the stimulus was

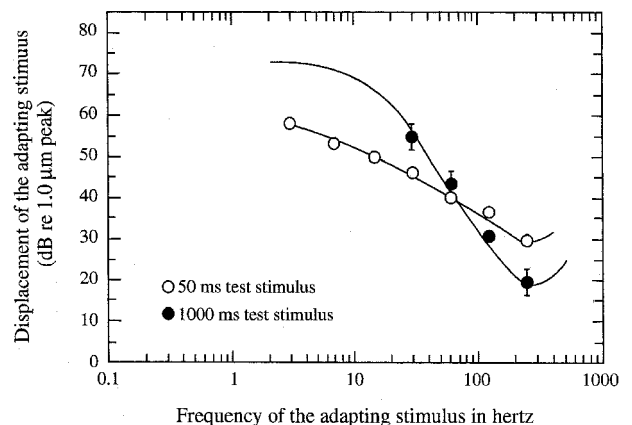


FIGURE 7. Average adaptation tuning curve obtained when the 250-Hz test stimulus was applied through a 0.008 cm^2 contactor for 1.0 s or for 50 ms at an intensity of 6.0 dB above the unadapted threshold.

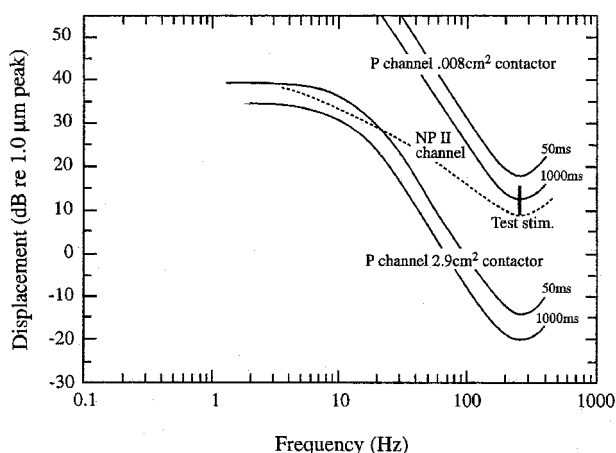


FIGURE 8. Theoretical tuning curves for the P and NP II channels when 50 ms and 1.0 s stimuli are delivered through a large 2.9 cm² or a small 0.008 cm² contactor.

1.0 s in duration than when its duration was 50 ms (Verrillo, 1965; Gescheider, 1976). This difference in the capacities of the P and NP II channels for temporal summation, as it applies to the problem of understanding the effects of stimulus duration on the psychophysical tuning curve, is illustrated in Figure 8. Because of temporal summation, the threshold of the P channel is lowered by approximately 6 dB when the duration of the stimulus is increased from 50 ms to 1.0 s. Furthermore, because of the unique ability of the P channel to exhibit spatial summation, the thresholds of this channel are approximately 30.0 dB lower when the large (2.9 cm²) rather than the small (0.008 cm²) contactor is used. As illustrated in Figure 8, it is our contention that the threshold of the P channel for responding to a 250-Hz stimulus of relatively long duration (e.g., 1.0 s) delivered through a small 0.008 cm² contactor is only a few decibels (less than 6 dB) above that of the NP II channel. Consequently, both the P channel and the NP II channel are excited by the 1.0-s test stimulus presented 6 dB above the unadapted detection threshold, and as a result, the adaptation tuning curve procedure revealed the segment of the P channel tuning curve seen in Figure 7. This is because, at any frequency, the adapting stimulus must be intense enough to adapt both the P and NP II channels sufficiently to elevate the threshold for detecting the test stimulus by 6.0 dB. In contrast, when the 250-Hz test stimulus is presented for only 50 ms, the threshold of the temporally summing P channel is elevated by approximately 6.0 dB relative to that for detecting a 1.0 s stimulus (Verrillo, 1965; Gescheider, 1976; Checkosky and Bolanowski, 1992; Gescheider *et al.*, 1999). From the change, as seen in Figure 7, in the shape of the tuning curve resulting from a reduction in the duration of the test stimulus to 50 ms, it appears that the threshold of the P channel has become sufficiently high that the 6.0 dB SL test stimulus excites only the non-summing NP II channel. The adaptation tuning

curve, determined under these conditions, reveals the tuning of the NP II channel uncontaminated by any influence of the P channel.

Thus, the results of Experiment III provide additional evidence in support of the hypothesis that separate P and the NP II channels exist, with both optimally tuned to 250 Hz but with the NP II channel more broadly tuned than the P channel. But it could be the case that in Experiment III not two but only one channel was involved, the P channel, which changes its tuning when the duration of the stimulus is changed. This explanation of the results fails to be supported by an earlier finding that the tuning of the P channel determined by detection threshold measurements using a large 3.0 cm² contactor to isolate the channel is unaffected by changes in stimulus duration (Gescheider *et al.*, 1977). Thus, the present results are best explained in terms of separate P and NP II channels with the P channel being more narrowly tuned and exclusively capable of temporal summation.

General discussion

Through the use of an adaptation tuning curve method, knowledge of the frequency selectivity of the P, NP I, and NP II channels of the tactile sensory system has been expanded beyond that presented in our original four-channel model (Bolanowski *et al.*, 1988). In Figure 9 the revised four-channel model of mechanoreception is presented with extended frequency ranges of the tuning curves for the P, NP I, and NP II (data from Gescheider *et al.*, 1994a). According to the model, the detection threshold at a particular frequency is determined by the channel with the lowest threshold at that frequency. Thus, because of the considerable overlap between the tuning curves of each of the four channels, the psychophysical threshold functions reflect a series, from low to high frequency, of limited segments of the tuning curves of the individual channels. Specifically, from 0.3 to 2 Hz, thresholds measured with either the large or small contactor are determined by the NP III channel. When the large 2.9 cm² contactor is used, thresholds are determined by the NP I channel over the frequency range of 2–40 Hz and above 40 Hz threshold is determined by the P channel. When the small 0.008 cm² contactor is used, thresholds are determined by the NP I channel over the frequency range of a 2–100 Hz and above 100 Hz threshold is determined by the NP II channel. The P and NP I channels are thought to be mediated by Pacinian and RA nerve fibers, respectively. The fiber types that are thought to mediate the NP III and NP II channels are SA I and SA II fibers, respectively (Bolanowski *et al.*, 1988).

Each of the tuning curves presented in Figure 9 is presumed to represent the frequency characteristic at the level of the absolute thresholds of the channel. Because these estimated threshold tuning curves

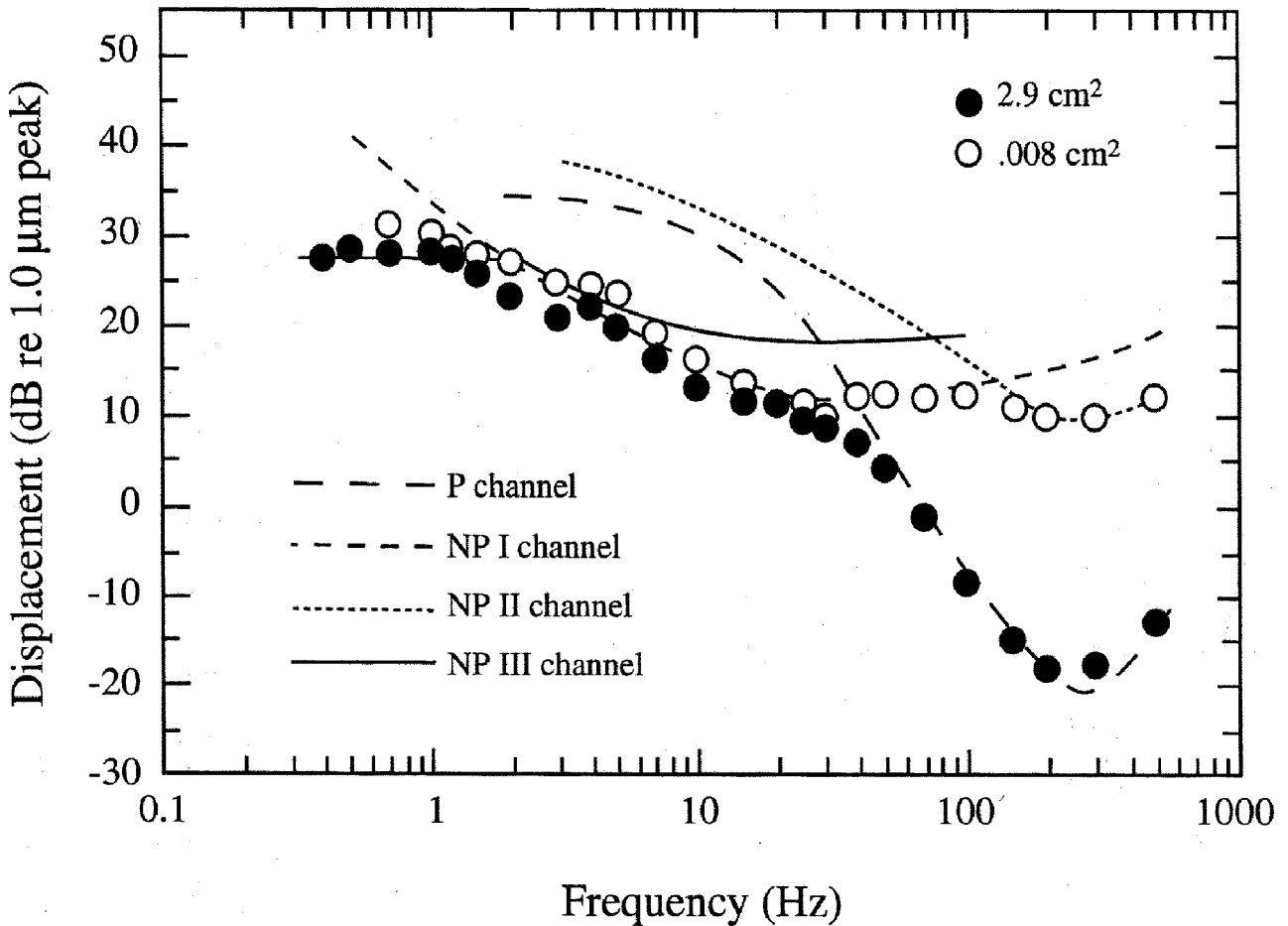


FIGURE 9. Four-channel model of mechanoreception with extended frequency ranges of the tuning curves of the P, NP I, and NP II channels. Data are detection threshold measurements from young adult observers (Gescheider *et al.*, 1994a). The tuning curve for the NP III channel was determined by Bolanowski *et al.* (1988). The tuning curves of the NP I, NP II, and P channels were determined in the present study.

were based on the tuning curves obtained at higher intensity levels when the channel was in a state of adaptation, the adaptation tuning curve had to be shifted down on the intensity axis to fit the absolute threshold data. The assumptions that adaptation does not affect the tuning of the channel and that there is no cross-channel adaptation are supported by the fact that, for each channel, there is a close correspondence between the adaptation tuning curves, when adjusted downward on the intensity axis, and the absolute threshold measurements obtained over a comparable frequency range. Thus, the use of the adaptation tuning curve method to determine the frequency characteristics at threshold for the P, NP I, and NP II channels is justified.

The neurophysiological tuning curves presented in this paper are in excellent agreement with our psychophysical tuning curves. Indeed, it has been the observation of this close correspondence between the responses of single nerve fibers innervating specific mechanoreceptors that has provided a basis for identifying the physiological mechanism responsible for the frequency selectivity of each psychophysical channel (Bolanowski, 1996; Bolanowski *et al.*,

1988). It appears that the frequency selectivity of a psychophysical channel is determined exclusively by the tuning of specific mechanoreceptors and associated nerve fibers that constitute the input stage to the channel. It is important to point out, however, that the form of a neurophysiological tuning curve, in which the intensity of a stimulus needed to produce a criterion neural response is plotted as a function of frequency, is highly dependent on which criterion neural response is chosen by the investigator. For example, if action potentials are recorded, and the response criterion is expressed in terms of spikes per second, the shape of the tuning curve will change as the specified criterion firing rate changes. Likewise, if one specifies the criterion as a certain number of spikes occurring in a burst of stimulation, the tuning curve's shape depends on how many spikes in the burst are taken as the response criterion (Bolanowski, 1996). Thus, in making comparisons between psychophysical and neurophysiological tuning, one must, in constructing the neurophysiological tuning curve, have a well developed rationale for the choice of a neural response criterion. In the present study and in the original formulation of our

four-channel model (Bolanowski *et al.*, 1988) these choices were guided by the formulation of hypotheses about the nature of the neural codes for the detection of a stimulus by the channels.

The choice of one spike per stimulus burst as the neural code for the NP I channel was based on substantial evidence that observers are capable of detecting a single action potential on a RA fiber (e.g., Vallbo and Johansson, 1976). The choice of four spikes per stimulus burst as an estimation of the neural code for the P channel was based on the fact that temporal summation, as a process of neural integration (Gescheider *et al.*, 1999), requires more than a single spike per burst but less than the number required to entrain spikes to the sinusoidal stimulus (Van Doren, 1985) and as demonstrated by Checkosky and Bolanowski (1992), more than a single corpuscle must be involved. Although the exact code for the P channel cannot be specified at this time, it is clear from examination of the tuning curves constructed from different neural response criteria (Bolanowski, 1996) that the peripheral input to the P channel is the activity of PC fibers. The neural code of five spikes per second chosen for the NP II channel is sufficiently high to overcome the spontaneous activity that is inherent in SA II fibers. The exact spike rate that constitutes the neural code is uncertain but the similarity between the tuning of the NP II channel and the tuning curves of SA II fibers constructed from a wide range of spike rates chosen as response criteria (Bolanowski, 1996) is consistent with the hypothesis that the input to the NP II channel consists of neural activity in SA II fibers. It appears to be the case that, to be detected, neural activity on several SA II fibers must occur because spikes on a single fiber elicit no reports of conscious awareness from observers (Ochoa and Torebjörk, 1983).

Although it is possible to identify the specific peripheral mechanoreceptive nerve fibers that constitute the input stage to each of the four psychophysical channels, it is only the NP I channel for which we can specify with confidence the exact neural code at the periphery for detection of a stimulus. Although we have some understanding of the conditions that limit possible neural codes for the other channels, further research will be necessary to permit exact specification of these codes.

Perhaps the most important feature of the present study is that it provides a more complete description of the frequency selectivity of each of the four channels of the glabrous skin of the hand. This new information will permit testing of hypotheses concerning the nature of the interaction among channels at suprathreshold levels of stimulation. According to our four-channel model, the perception of suprathreshold tactile stimuli of all types involves contributions from each of the four channels with their overlapping frequency characteristics. That channels interact at suprathreshold levels is supported by the

finding that channels summate in the perceived magnitudes of stimuli presented to separate channels (Verrillo and Gescheider, 1975; Marks, 1979). But these experiments were limited by the fact that interactions between only two channels, P and NP I, could be investigated. Knowing the tuning characteristics for each of the four channels will permit the investigation of interactions among all of the channels over the entire frequency range thereby enhancing our understanding of the perception of complex tactile stimuli. Finally, the additional information provided by this study on the frequency selectivity of the psychophysical channels should provide greater opportunities to make accurate comparisons with the tuning curves of both peripheral and central tactile neurons and in so doing, the search for the neural codes that underlie tactile perception should be facilitated.

Acknowledgements

This work was supported in part by the National Institutes of Health, DC00380 and DC38661.

References

- BACON, S.P., and W. JESTEADT (1987) Effects of pure-tone forward masker duration on psychophysical measures of frequency selectivity. *J Acoust Soc Am* **82**: 1925–1932.
- BÉKÉSY, G. VON (1939) Über die Vibrationsempfindung. *Akustische Zeitschrift* **4**: 316–334.
- BLANK, I.H. (1952) Factors which influence the water content of the stratum corneum. *J Invest Dermatol* **18**: 432–440.
- 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. (1996) Information processing channels in the sense of touch. In *Somesthesia and the Neurobiology of the Somatosensory Cortex*, O. FRANZEN, R. JOHANSSON, and L. TERENIUS, eds., pp. 103–108, Birkhäuser Verlag, Basel, Switzerland.
- BOLANOWSKI, S.J., G.A. GESCHEIDER, R.T. VERRILLO, and C.M. CHECKOSKY (1988) Four channels mediate the mechanical aspects of touch. *J Acoust Soc Am* **84**: 1680–1694.
- BOLANOWSKI, S.J., and R.T. VERRILLO (1982) Temperature and criterion effects in a somatosensory subsystem: a neurophysiological and psychophysical study. *J Neurophysiol* **48**: 836–855.
- CAMPBELL, F.W., and J.G. ROBSON (1968) Application of Fourier analysis to the visibility of gratings. *J Physiol* **197**: 551–566.
- CAPRARO, A.J., R.T. VERRILLO, and J.J. ZWISLOCKI (1979) Psychophysical evidence for a triplex system of mechanoreception. *Sens Process* **3**: 334–352.
- CHECKOSKY, C.M., and S.J. BOLANOWSKI (1992) The effects of stimulus duration on the response properties of Pacinian corpuscles: implications for the neural code. *J Acoust Soc Am* **91**: 3372–3380.
- CHECKOSKY, C.M., and S.J. BOLANOWSKI (1994) The effects of stimulus duration on frequency-response functions in the Pacinian (P) channel. *Somatosens Mot Res* **11**: 47–56.
- COHEN, J.C., J.C. MAKOUS, and S.J. BOLANOWSKI (1999) Under which conditions do the skin and probe decouple during sinusoidal vibrations? *Exp Brain Res* **129**: 211–217.
- EIJKMAN, E., and A.J.H. VENDRIK (1960) Dynamics of the vibration sense at low frequency. *J Acoust Soc Am* **32**: 1134–1139.
- FLETCHER, H. (1940) Auditory patterns. *Rev Mod Phys* **12**: 47–65.
- FLORENTINE, M., S. BUUS, B. SCHARF, and E. ZWICKER (1980) Frequency selectivity in normally-hearing and hearing-impaired observers. *J Speech Hear Res* **23**: 646–669.

- GESCHEIDER, G.A. (1976) Evidence in support of the duplex theory of mechanoreception. *Sens Process* 1: 68–76.
- GESCHEIDER, G.A., M.E. BERRYHILL, R.T. VERRILLO, and S.J. BOLANOWSKI (1999) Vibrotactile temporal summation: probability summation or neural integration? *Somatosens Mot Res* 16: 229–242.
- GESCHEIDER, G.A., S.J. BOLANOWSKI, R.T. VERRILLO, K.L. HALL, and K.E. HOFFMAN (1994a) The effects of aging on information-processing channels in the sense of touch: I. Absolute sensitivity. *Somatosens Mot Res* 11: 279–290.
- GESCHEIDER, G.A., K.E. HOFFMAN, M.A. HARRISON, M.L. TRAVIS, and S.J. BOLANOWSKI (1994b) The effects of masking on vibrotactile temporal summation in the detection of sinusoidal and noise stimuli. *J Acoust Soc Am* 95: 1006–1016.
- GESCHEIDER, G.A., M.J. O'MALLEY, and R.T. VERRILLO (1983) Vibrotactile forward masking: evidence for channel independence. *J Acoust Soc Am* 74: 474–485.
- GESCHEIDER, G.A., B.F. SKLAR, C.L. VAN DOREN, and R.T. VERRILLO (1985) Vibrotactile forward masking: psychophysical evidence for a triplex theory of cutaneous mechanoreception. *J Acoust Soc Am* 78: 534–543.
- GESCHEIDER, G.A., and R.T. VERRILLO (1979) Vibrotactile frequency characteristics determined by adaptation and masking procedures. In *Sensory Functions of the Skin of Humans*, D.R. KENSHALO, ed., pp. 183–205, Plenum, New York.
- GESCHEIDER, G.A., R.T. VERRILLO, A.J. CAPRARO, and R.D. HAMER (1977) Enhancement of vibrotactile sensation magnitude and predictions from the duplex model of mechanoreception. *Sens Process* 1: 187–203.
- GESCHEIDER, G.A., R.T. VERRILLO, and C.L. VAN DOREN (1982) Prediction of vibrotactile masking functions. *J Acoust Soc Am* 72: 1421–1426.
- HAMER, R.D., R.T. VERRILLO, and J.J. ZWISLOCKI (1983) Vibrotactile masking of Pacinian and non-Pacinian channels. *J Acoust Soc Am* 73: 1293–1303.
- HENNING, H. (1916) Die Qualitätenreihe des Geschmacks. *Z Psychol* 73: 203–219.
- HENSEL, H., and K.A. BOWMAN (1960) Afferent impulses in cutaneous nerves in human subjects. *J Neurophysiol* 23: 564–578.
- HOLLINS, M., A.K. GOBLE, B.L. WHITSEL, and M. TOMMERDAHL (1990) Time course and actions spectrum of vibrotactile adaptation. *Somatosens Mot Res* 7: 205–221.
- JOHANSSON, R.S., U. LANDSTRÖM, and R. LUNDSTRÖM (1982) Responses of mechanoreceptive afferent units in glabrous skin of the human hand to sinusoidal skin displacements. *Brain Res* 244: 17–25.
- LABS, S.M., G.A. GESCHEIDER, R.R. FAY, and C.H. LYONS (1978) Psychophysical tuning curves in vibrotactile. *Sens Process* 2: 231–247.
- LINDBLOM, U. (1965) Properties of touch receptors in distal glabrous skin of the monkey. *J Neurophysiol* 28: 966–985.
- MAKOUS, J.C., R.M. FRIEDMAN, and C.J. VIERCK JR. (1995) A critical band filter in touch. *J Neurosci* 15: 2808–2818.
- MARKS, L.E. (1979) Summation of vibrotactile intensity: an analog to auditory critical bands. *Sens Process* 3: 188–203.
- MOUNTCASTLE, V.B., R.H. LAMOTTE, and G. CARLI (1972) Detection thresholds for stimuli in humans and monkeys: comparison with threshold events in mechanoreceptive afferent fibers innervating the monkey hand. *J Neurophysiol* 35: 122–136.
- OCHOA, J.L., and H.E. TOREBJÖRK (1983) Sensations evoked by intraneural microstimulation of single mechanoreceptor units innervating the human hand. *J Physiol* 342: 633–653.
- PAWSON, L., S.J. BOLANOWSKI, C.M. CHECKOSKY, and J.C. MAKOUS (1996) Mesenteric and tactile pacinian corpuscles (PC) are physiologically comparable. *Soc Neurosci Abstr* 22: 1807.
- SATO, M. (1961) Response of Pacinian corpuscles to sinusoidal vibration. *J Physiol* 159: 391–409.
- TALBOT, W.H., I. DARIEN-SMITH, H.H. KORNHUBER, and V.B. MOUNTCASTLE (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.
- TOREBJÖRK, H.E., and J.L. OCHOA (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 mechanoreceptive afferents. *Brain Res* 215: 359–363.
- VALLBO, A.B., and R.S. JOHANSSON (1976) Skin mechanoreceptors in the human hand: neural and psychophysical thresholds. In *Sensory Functions of the Skin of Primates, with Special Reference to Man*, Y. ZOTTERMAN, ed., pp. 185–198, Pergamon, New York.
- VANDORN, C.L. (1985) Temporal summation by Pacinian corpuscles precludes entrainment at the detection threshold. *J Acoust Soc Am* 77: 2188–2189.
- VERRILLO, R.T. (1963) Effect of contactor area on 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. (1966) Vibrotactile sensitivity and the frequency response of Pacinian corpuscles. *Psychonom Sci* 4: 135–136.
- VERRILLO, R.T., and S.J. BOLANOWSKI 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., S.J. BOLANOWSKI, C.M. CHECKOSKY, and F.P. MCGLONE (1998) Effects of hydration on tactile sensation. *Somatosens Mot Res* 15: 93–108.
- VERRILLO, R.T., A.J. FRAIOLI, and R.L. SMITH (1969) Sensory magnitude of vibrotactile stimuli. *Percept Psychophys* 6: 366–372.
- VERRILLO, R.T., and G.A. GESCHEIDER (1975) Enhancement and summation in the perception of two successive vibrotactile stimuli. *Percept Psychophys* 18: 128–136.
- VERRILLO, R.T., and G.A. GESCHEIDER (1977) Effect of prior stimulation on vibrotactile thresholds. *Sens Process* 1: 292–300.
- VERRILLO, R.T., G.A. GESCHEIDER, B.G. CALMAN, and C.L. VAN DOREN (1983) Vibrotactile masking: effects of one and two-site stimulation. *Percept Psychophys* 33: 379–387.
- VOGTEN, L.L.M. (1974) Pure tone masking: a new result from a new method. In *Facts and Models in Hearing*, E. ZWICKER and E. TERHARDT, eds., Springer-Verlag, Berlin.
- WALD, G. (1964) The receptors of human color vision. *Science* 145: 1007–1017.
- WARNER, R.R., M.C. MYERS, and D.A. TAYLOR (1988a) Electron probe analysis of human skin: element concentration profiles. *J Invest Dermatol* 90: 78–85.
- WARNER, R.R., M.C. MYERS, and D.A. TAYLOR (1988b) Electron probe analysis of human skin: determination of the water concentration profile. *J Invest Dermatol* 90: 218–224.
- ZWICKER, E. (1974) On a psychoacoustical equivalent of tuning curves. In *Facts and Models in Hearing*, E. ZWICKER and E. TERHARDT, eds., pp. 132–139, Springer-Verlag, Berlin.
- ZWICKER, E., and K. SCHORN (1978) Psychoacoustical tuning curves in audiology. *Audiology* 17: 120–140.
- ZWISLOCKI, J.J., F. MAIRE, A.S. FELDMAN, and H. RUBIN (1958) On some poststimulatory effects at the threshold of audibility. *J Acoust Soc Am* 30: 254–262.

Copyright of Somatosensory & Motor Research is the property of Carfax Publishing Company and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.

Copyright of Somatosensory & Motor Research is the property of Taylor & Francis Ltd and its content may not be copied or emailed to multiple sites or posted to a listserv without the copyright holder's express written permission. However, users may print, download, or email articles for individual use.