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Research report

Some characteristics of tactile channels☆

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Abstract

The four information-processing channels of glabrous skin have distinct tuning characteristics which appear to be determined in the periphery at the level of sensory receptors and their afferent nerve fibers. The four-channel model [J Acoust Soc Am 84 (1988) 1680] has been updated to include measurement over a wider frequency range of tuning of the P and NP I channels, psychophysically determined by forward-masking and adaptation tuning curve methods. In addition to differences in their tuning, the P and NP channels differ in the following ways: (1) the P channel, but not NP channels, has been found to be capable of temporal summation, which operates by neural integration; (2) the capacity for spatial summation is also an exclusive property of the P channel; (3) sensitivity declines with age at a greater rate in the P channel than in the NP channels; (4) the masking or adaptation of a channel has no effect on the sensitivity of the other channels, although the channels interact in the summation of the perceived magnitudes of stimuli presented to separate channels.

Keywords: Tactile sensitivity; Tactile channels; Temporal summation; Aging; Tactile receptors

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1. Introduction

Fundamental to understanding the properties of sensory systems is the concept of the information-processing channel. A channel is an element that is tuned to a specific region of the energy spectrum to which the system responds. Channels have been discovered in the sense of touch as well as in other modalities [25]. 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, qualitative and quantitative dimensions of perceptual experience are determined by the relative activity levels in each of several channels (see [2]).

2. The tuning of tactile channels

When all but the smallest contactors are used to stimulate glabrous [21] or hairy (e.g. [23]) skin, vibrotactile thresholds are a U-shaped function of stimulus frequency with the lowest values at approximately 250–300 Hz. In addition, it has been demonstrated that this threshold function becomes relatively flat at low frequencies. The change in the slope of the function at low frequencies was interpreted by Békésy [1] as evidence that separate mechanisms mediate the detection of low and high frequency vibration. This principle was elaborated upon by Verrillo [21] who examined the effects of contactor size and stimulus frequency on the threshold for detecting vibratory stimulation of the thenar eminence. The system mediating thresholds along the U-shaped portion of the threshold curve exhibited spatial summation indicated by a decline, within this frequency range, of the psychophysical threshold as the size of the contactor was increased. At lower frequencies, thresholds were relatively independent of frequency and contactor size. Therefore, it was concluded that spatial summation was absent in the system mediating thresholds along the flat portion of the curve.

The duplex theory of mechanoreception was supported by neurophysiological data obtained by recording from cutaneous nerve fibers. Verrillo [24], in comparing his psychophysical threshold data with the neurophysiological tuning curves of Sato [19] for single Pacinian corpuscles in cat, discovered that it was this receptor that was the neural element mediating the U-shaped portion of the psychophysical threshold function. The neural element mediating

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detection of vibration at lower frequencies was subsequently identified as rapidly adapting nerve fibers associated with Meissner corpuscles [15,20].

The tuning characteristics of these separate neural systems have been studied by adaptation (e.g. [12,28]) and masking (e.g. [3,10,11,14]). The most important findings were that (a) masking and adaptation occur within a system but not across systems and (b) in glabrous skin there are four systems that mediate the detection of vibrotactile stimuli. Because the sensitivity of each of these four systems is not affected by adaptation or masking within another system, we have chosen to refer to these systems as information-processing channels.

Of all of the masking procedures used to isolate and define the frequency characteristics of tactile channels, the procedure analogous to that used in audition to obtain psychoacoustic tuning curves (e.g. [29]) provides the most efficient means of determining the tuning of a channel over a wide range of frequencies [14]. In this method, a test stimulus that activates a single channel is presented at a level slightly above the observer's unmasked detection threshold. Then the intensities of masking stimuli presented at various frequencies needed to render the detectability of the test stimulus at a masked threshold level are determined. The psychophysical tuning curve in which these masking intensities are plotted as a function of their frequency provides a measure of the tuning of the channel. In Fig. 1, the P channel tuning curves of three observers are illustrated. In the experiment, a forward masking procedure was used in which a 250-Hz test stimulus with a duration of 50 ms was presented 25 ms after the termination of a 750 ms masking stimulus. The intensities of the masking stimuli at various frequencies needed to cause a 10 dB elevation in the threshold of the test stimulus were determined. For frequencies above 20 Hz, the results are in close agreement with the tuning curve of the P channel postulated in the four-channel model of mechanoreception [3]. Specifically, thresholds decrease at a rate of approximately −12 dB per octave until the optimal frequency of 250 Hz is reached, whereupon thresholds begin to increase with further increase in frequency. The new information derived from these forward masking tuning curves is that at lower frequencies the sensitivity of the P channel becomes much less affected by changes in frequency. Makous, Friedman and Vierck [16] also derived tuning curves for the P channel that flatten out at low frequencies.

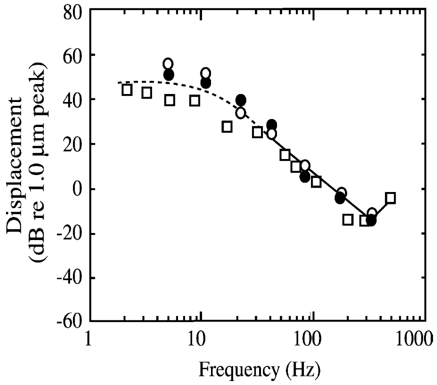

Fig. 1. Forward-masking tuning curves of the P channel for three observers.

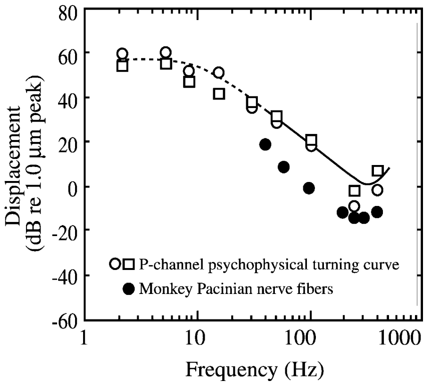

Fig. 2. Adaptation-tuning curves of the P channel for two observers compared with average neurophysiological tuning curve for Pacinian nerve fibers adapted from Mountcastle, LaMotte, and Carli [18].

Recently, we have also employed an adaptation-tuning curve method to measure the tuning characteristics of channels. In these experiments, a 15 s adapting stimulus was presented followed immediately by two observation intervals—one containing the test stimulus and the other interval without the stimulus. Immediately after the observer indicated which interval contained the test stimulus, the adapting stimulus was presented again, followed by the two observation intervals to which the observer again responded. This was repeated until stable performance was achieved. The intensity of the test stimulus was held constant at 10 dB above the unadapted threshold. The tuning curve consisted of the intensities of adapting stimuli of various frequencies needed to shift the observer's threshold for detecting the test stimulus by 10 dB.

Illustrated in Fig. 2 are the tuning curves of the P channel for two observers measured with a 250-Hz test stimulus. The overall form of the tuning curve with its U-shaped segment and its relatively flat segment at low frequencies is consistent with the forward masking tuning curves seen in Fig. 1. Furthermore, the results are also in close agreement with the tuning curves of single Pacinian nerve fibers in monkey [18].

The tuning of the NP I channel was also examined by using the adaptation tuning curve procedure. In this case, the intensity of a 22-Hz test stimulus was held constant at 10 dB above the unadapted threshold. Under these conditions, the test stimulus should be exclusively processed by the NP I channel. Plotted in Fig. 3 are the values for two subjects of the adapting stimulus needed to shift the threshold by 10 dB. The entire NP I tuning 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 Fig. 3 that the psychophysical results are in close agreement

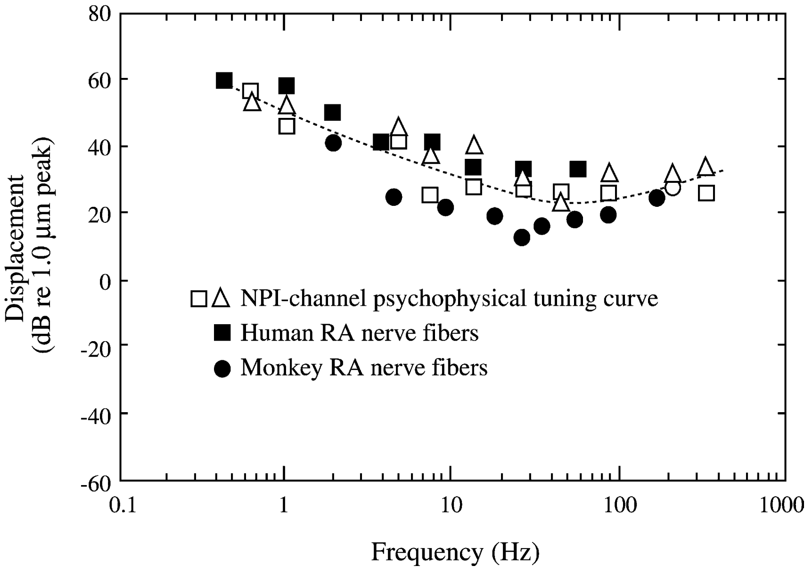

Fig. 3. Adaptation-tuning curves of the NP I channel for two observers compared with the average neurophysiological tuning curves of RA fibers from humans adapted from Johansson, Landström, and Lundström [13] and monkey adapted from Mountcastle, LaMotte, and Carli [18].

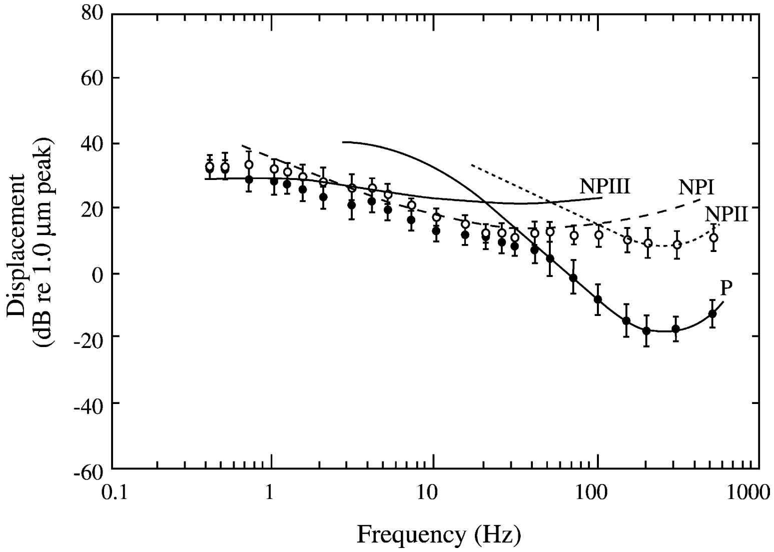

Fig. 4. Four-channel model of mechanoreception with extended frequency ranges of the tuning curves of the P and NP I channels measured by the adaptation-tuning curve procedure. The data points (filled, large contactor; unfilled, small contactor) are from Gescheider, Bolanowski, Verrillo, Hall, and Hoffman [8].

with the tuning of single RA nerve fibers from humans [13] and monkey [18].

In Fig. 4, the four-channel model of mechanoreception [3] is presented with extended frequency ranges of the tuning curves for the P and NP I channels determined in the experiments described above. The data points are from a study by Gescheider, Bolanowski, Verrillo, Hall, and Hoffman [8]. From 0.4 to 2 Hz, thresholds are determined by the NP III channel when measured with either the large or the small contactor. When the large contactor was used, thresholds were determined by the NP I channel over the frequency range of 2–40 Hz and above 40 Hz thresholds were determined by the P channel. When the small contactor was used, thresholds were determined by the NP I channel over the frequency range of 2–100 Hz and above 100 Hz thresholds were determined by the NP II channel. As stated previously, the P and NP I channels are thought to be mediated by Pacinian and RA nerve fibers, respectively. The fiber types thought to mediate the NP III and NP II channels are SA I and SA II fibers, respectively [3].

3. Temporal and spatial summation

Verrillo [22] found that when a 250-Hz stimulus delivered through a large 2.9 cm^2 contactor to the thenar eminence

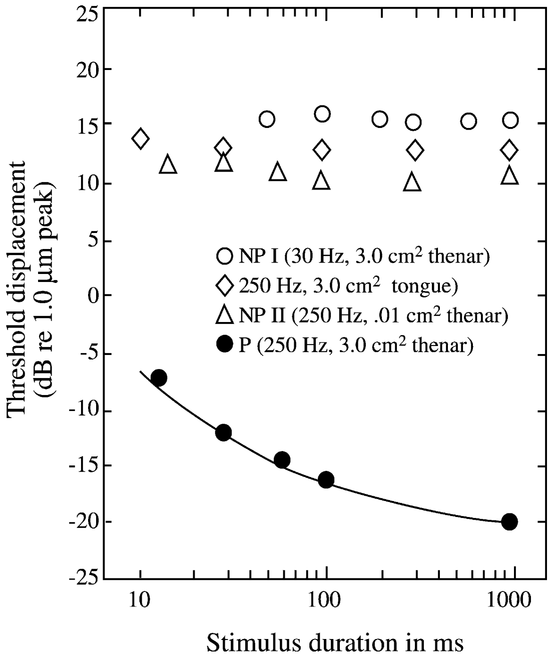

Fig. 5. Vibrotactile thresholds plotted as a function of stimulus duration when stimuli are presented to the P channel (250 Hz, 3.0 cm^2 contactor), adapted from Gescheider, Hoffman, Harrison, Travis, and Bolanowski [9], the NP channel (30 Hz, 3.0 cm^2 contactor), adapted from Gescheider [7], and the NP II channel (250 Hz, 0.01 cm^2 contactor), adapted from Gescheider, Hoffman, Harrison, Travis, and Bolanowski [9], of the glabrous skin of the thenar eminence. Results are also presented for the dorsal surface of the tongue, an area lacking Pacinian corpuscles (adapted from Verrillo [25]).

excites Pacinian corpuscles, the detection threshold decreases as stimulus duration increases up to a duration of about 1.0 s. However, when the same stimuli are applied through a small 0.01 cm^2 contactor, incapable of exciting the P channel but capable of exciting the NP II channel, the detection threshold is independent of stimulus duration. These results indicate that the P channel is capable of temporal summation but that the NP II channel is not. Gescheider [7] later found that temporal summation is also absent at low stimulus frequencies that only excite the non-Pacinian receptors of the NP I channel. These results are summarized in Fig. 5. Also, seen in the figure are results obtained by Verrillo [25] in which no temporal summation was observed when this same stimulus was presented to the dorsal surface of the tongue—an area known to be lacking in Pacinian corpuscles.

The solid curve for the P channel in Fig. 5 is the predicted results from Zwislocki's [30] theory of temporal neural integration. In this model, the magnitude of the neural response increases over time of stimulation and when it exceeds threshold level, a detection response is made by the observer. Because this threshold is reached sooner with more intense stimuli, the inverse relationship found experimentally between the intensity of the stimulus at the psychophysical threshold and stimulus duration is explained. We have recently demonstrated that this process of neural integration can account for temporal summation over stimulus exposure times as long as 800 ms. At longer exposure times, probability summation can enhance stimulus detectability [6].

Large amounts of spatial summation are found for the P channel but not for any of the NP channels. In Fig. 4 it is apparent that the size of the contactor substantially affects tactile sensitivity only within the frequency range where thresholds are determined by the P channel. Similarly to temporal summation, the two main competing explanations of spatial summation are neural integration and probability summation. In both explanations, the observer's detection threshold decreases as the number of receptors activated increases with increasing stimulus size. According to the neural-integration model, the increased neural activity generated by activating additional receptors as the size of the stimulus is increased, is integrated at some point within the central nervous system and as a result, the psychophysical threshold is lowered. Lower thresholds are also predicted from the probability summation model as the size of the stimulus increases. The mechanism of probability summation is dependent on the fact that individual receptors differ in their sensitivities [4]. The larger the area of stimulation, the greater the probability that the most sensitive receptors will be activated and consequently, the psychophysical threshold is predicted to decrease as the size of the contactor is increased.

Unfortunately, at the present time, a definitive experiment, analogous to that reported above for temporal summation [6] to determine whether either probability summation or neural integration can account for the phenomenon of spatial summation, has yet to be done.

4. The effects of aging in the sensitivity of tactile channels

The most interesting aspect of the finding that the sense of touch, like other sensory systems, suffers from the deleterious effects of aging is that the rate at which tactile sensitivity declines with age is not the same in each of the tactile channels. This is clearly seen in the results presented in Fig. 6 in which the average detection threshold on the thenar eminence is plotted as a function of the average age of eight groups of observers. The sensitivities of the P, NP I, and NP III channels were assessed by measuring thresholds for detecting 250-, 10-, and 1-Hz stimuli, respectively, all delivered through a 2.9 cm^2 contactor. The thresholds of the NP II channel were measured by presenting the 250-Hz stimuli through a 0.008 cm^2 contactor. The effects of aging were substantially greater for the P channel than for the three NP channels which all showed upward shifts in threshold of 10–12 dB over approximately eight decades. A much larger shift of 24 dB was seen in the P channel. Why should aging effects be greater in the P than in the NP channels? Part of the answer may be found in the fact that the P channel, but not the NP channels, is capable of significant amounts of

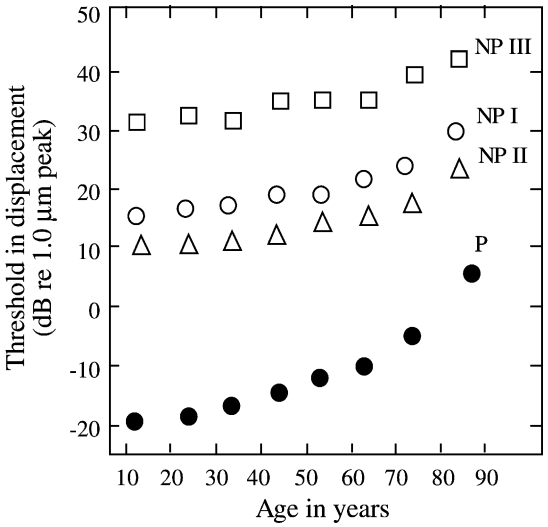

Fig. 6. Vibrotactile thresholds as a function of age for the P channel (250 Hz stimulus delivered through a 2.9 cm^2 contractor), NP I channel (10 Hz delivered through a 2.9 cm^2 contractor), NP II channel (250 Hz stimulus delivered through a 0.008 cm^2 contractor), and the NP III channel (1 Hz stimulus delivered through a 2.9 cm^2 contactor). Adapted from Gescheider, Bolanowski, Verrillo, Hall, and Hoffman [8].

spatial summation. As seen in Fig. 4, stimulating more tactile receptors by increasing the size of the contactor greatly lowers the detection threshold only in the P channel. The progressive loss of receptors with age [5] should greatly reduce the sensitivity of the spatially-summating P channel because the sensitivity of this channel depends largely on the number of activated receptors. Much smaller effects of aging are expected for the NP channels because their sensitivities are nearly independent of the number of activated receptors.

5. Channel interactions

Clearly, the results of psychophysical and neurophysiological studies have determined that separate information-processing channels, each with its own physiological mechanism, the origin of which lies in specific receptors and peripheral nerve fibers, exist for the perception of tactile stimuli. However, fundamental questions remain concerning the nature of how these channels, with their individual properties, operate together in the perception of tactile stimuli encountered in the natural environment. We hypothesize that suprathreshold stimulation of a sufficiently high intensity level to activate all of the channels is associated with tactile perceptions that result from an integration in the central nervous system of the activities of the separate channels. The initial support for this hypothesis came from the results of a study in which the perceived intensity of two brief stimuli presented in rapid succession was found to be equal to the sum of the perceived intensity of each stimulus presented alone, provided that they activated separate channels [27]. In contrast, when the two stimuli activated the same channel, the perceived intensity of the pair was determined, not by the sum of individual perceived intensities, but by the total energy of the two stimuli (also see [17]). In our experiment, the sensation magnitude of a pair of 20 ms stimuli was measured by requiring the observer to match the sensation magnitude of a matching stimulus, presented after the pair, to the total sensation magnitude of the pair. In Fig. 7 the difference in decibels between matches to the pair and matches to one member of the pair are plotted as a function of the time interval between the first and second stimulus of the pair. When the stimuli were in separate channels, 300 Hz for the P channel and 25 Hz for the NP I channel, at short time intervals between stimuli,

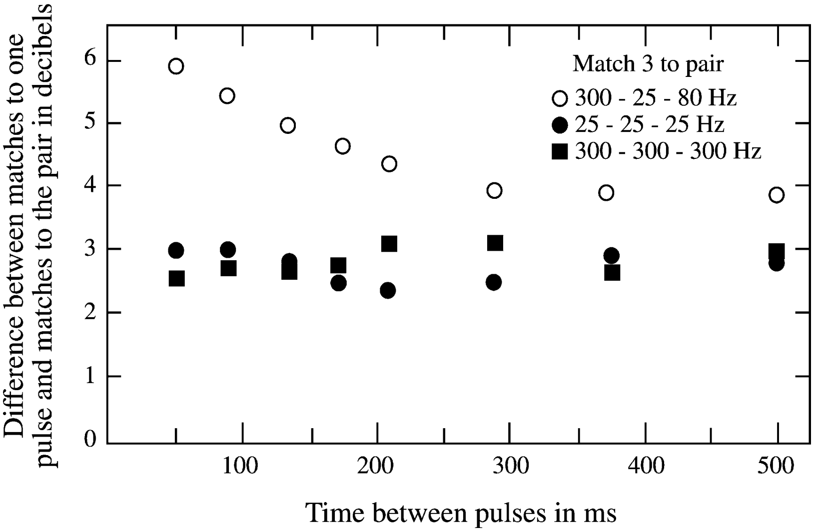

Fig. 7. Difference in decibels between the intensity level of a matching stimulus needed to equate its sensation magnitude to that of a single stimulus and the intensity level needed to match the sensation magnitude of the pair of stimuli. Data are plotted as a function of the time interval between the stimuli of the pair. Adapted from Verrillo and Gescheider [27].

the observer set the matching stimulus 6.0 dB higher when matching to the sensation magnitude of the pair than when matching to individual stimuli in the pair. This 6.0 dB difference corresponds to a doubling of sensation magnitude as measured in magnitude estimation [26]. When the two stimuli in the pair were 25 Hz (both within the NP I channel) and when they were both 300 Hz (both within the P channel) the observer adjusted the matching stimulus to be 3.0 dB higher when matching to the pair than when matching to the individual stimuli. This 3.0 dB difference corresponds to a doubling of stimulus energy. These findings indicate that while perceptual interactions within a channel occur at the level of the stimuli in the form of the summation of their energies, interactions between channels occur at a later stage of processing after stimulus energies have been transformed into perceptual magnitudes.

An adequate test of the hypothesis that the perception of any complex tactile stimulus involves the interaction of channels requires that we fully understand the characteristics of each channel and determine the rules by which channels interact. The discovery of linear summation of perceived magnitudes from different channels provides partial confirmation of the hypothesis. There are, however, many other possible ways in which channels interact that must be investigated before the hypothesis becomes a general principle of tactile information processing.

Acknowledgements

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References

[1] Béskésy G von. Über die Vibrationsempfindung. Akust Z 1939;4:316–34.

[2] Bolanowski SJ. Tactile channels and their interactions. In: Franzén O, Johansson R, Terenius L, editors. Somesthesis and the neurobiology of the somatosensory cortex. Basel: Birkhäuser Verlag; 1996. p. 103–8.

[3] Bolanowski SJ, Gescheider GA, Verrillo RT, Checkosky CM. Four channels mediate the mechanical aspects of touch. J Acoust Soc Am 1988;84:1680–94.

[4] Bolanowski Jr SJ, Zwislocki JJ. Intensity and frequency characteristics of Pacinian corpuscles. I. Action potentials. J Neurophysiol 1984;51:793–811.

[5] Cauna N. The effects of aging on the receptor organs of the human dermis. In: Montagna W, editor. Advances in biology of skin: aging, vol. VI. New York: Pergamon; 1965. p. 63–96.

[6] Gescheider GA, Berryhill ME, Verrillo RT, Bolanowski SJ. Vibrotactile temporal summation: probability summation or neural integration? Somatosens Mot Res 1999;16:229–42.

[7] Gescheider GA. Evidence in support of the duplex theory of mechanoreception. Sens Process 1976;1:68–76.

[8] Gescheider GA, Bolanowski SJ, Verrillo RT, Hall KL, Hoffman KE. The effects of aging on information-processing channels in the sense of touch: I. Absolute sensitivity. Somatosens Mot Res 1994;11:279–90.

[9] Gescheider GA, Hoffman KE, Harrison MA, Travis ML, Bolanowski SJ. The effects of masking on vibrotactile temporal summation in the detection of sinusoidal and noise stimuli. J Acoust Soc Am 1994;95:1006–16.

[10] Gescheider GA, Sklar BF, Van Doren CL, Verrillo RT. Vibrotactile forward masking: psychophysical evidence for a triplex theory of cutaneous mechanoreception. J Acoust Soc Am 1985;78:534–43.

[11] Gescheider GA, Verrillo RT, Van Doren CL. Prediction of vibrotactile masking functions. J Acoust Soc Am 1982;72:1421–6.

[12] Hollins M, Goble AK, Whitsel BL, Tommerdahl M. Time course and actions spectrum of vibrotactile adaptation. Somatosens Mot Res 1990;7:205–21.

[13] Johansson RS, Landström U, Lundström R. Responses of mechnoreceptive afferent units in glabrous skin of the human hand to sinusoidal skin displacements. Brain Res 1982;244:17–25.

[14] Labs SM, Gescheider GA, Fay RR, Lyons CH. Psychophysical tuning curves in vibrotaction. Sens Process 1978;2:231–47.

[15] Lindblom U. Properties of touch receptors in distal glabrous skin of the monkey. J Neurophysiol 1965;28:966–85.

[16] Makous JC, Friedman RM, Vierck Jr CJ. A critical band filter in touch. J Neurosci 1995;15:2808–18.

[17] Marks LE. Summation of vibrotactile intensity: an analog to auditory critical bands. Sens Process 1979;3:188–203.

[18] Mountcastle VB, LaMotte RH, Carli G. Detection thresholds for stimuli in humans and monkeys: comparison with threshold events in mechanoreceptive afferent fibers innervating the monkey hand. J Neurophysiol 1972;35:122–36.

[19] Sato M. Response of Pacinian corpuscles to sinusoidal vibration. J Physiol 1961;159:391–409.

[20] Talbot WH, Darien-Smith I, Kornhuber HH, Mountcastle VB. The sense of flutter vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. J Neurophysiol 1968;31:301–34.

[21] Verrillo RT. Effect of contactor area on vibrotactile threshold. J Acoust Soc Am 1963;35:1962–6.

[22] Verrillo RT. Temporal summation in vibrotactile sensitivity. J Acoust Soc Am 1965;37:843–6.

[23] Verrillo RT. Vibrotactile thresholds for hairy skin. J Exp Psychol 1966a;72:47–50.

[24] Verrillo RT. Vibrotactile sensitivity and the frequency response of Pacinian corpuscles. Psychonom Sci 1966b;4:135–6.

[25] Verrillo RT. A duplex mechanism of mechanoreception. In: Kenshalo DR, editor. The skin senses. Springfield, IL: Thomas; 1968. p. 135–59.

[26] Verrillo RT, Fraioli AJ, Smith RL. Sensory magnitude of vibrotactile stimuli. Percept Psychophys 1969;6:366–72.

[27] Verrillo RT, Gescheider GA. Enhancement and summation in the perception of two successive vibrotactile stimuli. Percept Psychophys 1975;18:128–36.

[28] Verrillo RT, Gescheider GA. Effect of prior stimulation on vibrotactile thresholds. Sens Process 1977;1:292–300.

[29] Zwicker E. On a psychoacoustical equivalent of tuning curves. In: Zwicker E, Terhardt E, editors. Facts and models in hearing. New York: Springer-Verlag; 1974. p. 132–9.

[30] Zwislocki JJ. Theory of temporal auditory summation. J Acoust Soc Am 1960;32:1046–60.