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A four-channel analysis of the tactile sensitivity of the fingertip: frequency selectivity, spatial summation, and temporal summation

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Abstract

Thresholds were measured for the detection of vibratory stimuli of variable frequency and duration applied to the index fingertip and thenar eminence through contactors of different sizes. The effects of stimulus frequency could be accounted for by the frequency characteristics of the Pacinian (P), non-Pacinian (NP) I, and NP III channels previously determined for the thenar eminence (Bolanowski *et al.*, *J Acoust Soc Am* 84: 1680–1694, 1988; Gescheider *et al.*, *Somatosens Mot Res* 18: 191–201, 2001). The effect of changing stimulus duration was also essentially identical for both sites, demonstrating the same amount of temporal summation in the P channel. Although the effect of changing stimulus frequency and changing stimulus duration did not differ for the two sites, the effect of varying the size of the stimulus was significantly greater for the thenar eminence than for the fingertip. The attenuated amount of spatial summation on the fingertip was interpreted as an indication that the mechanism of spatial summation consists of the operations of both neural integration and probability summation.

Key words: somatosensation, tactile sensitivity, tactile channels, mechanoreception

Introduction

Information processing channels in sensory systems are elements that are tuned to specific regions of the energy spectrum to which the system responds. The relative activity levels in each of several channels determines the qualitative and quantitative dimensions of perceptual experience (see Bolanowski, 1996). The characteristics of channels have been determined psychophysically, as seen in 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).

The earliest evidence for the existence of channels in the tactile sensory system was the discovery that detection thresholds are sharply tuned at high frequencies with the lowest thresholds at 250–300 Hz, but at low frequencies of vibratory stimulation, thresholds are nearly independent of frequency (Békésy, 1939; Verrillo, 1963; Talbot *et al.*, 1968; Verrillo *et al.*, 1969; Gescheider, 1976). The multi-segmented curve obtained experimentally when the detection threshold is plotted as a function of frequency suggests the operation of several independent sensory channels that mediate the detection of vibration (Bolanowski *et al.*, 1988). Each segment of the curve is thought to represent the hypothetical

neural threshold for the channel, and according to this notion, the psychophysical threshold at a particular frequency is determined by the channel with the lowest threshold (Bolanowski *et al.*, 1988). The highly tuned U-shaped portion of the threshold function is known to be mediated by the neural activity of Pacinian corpuscles (Verrillo, 1966) while the mid-frequency portion is mediated by rapidly adapting (RA) nerve fibers, with associated Meissner corpuscle receptors (e.g., Lindblom, 1965; Talbot *et al.*, 1968; Mountcastle *et al.*, 1972).

Although it was clear from Verrillo's early experiments on the effects of contactor size (Verrillo, 1963) and stimulus duration (Verrillo, 1965) on threshold that there were separate Pacinian (P) and non-Pacinian (NP) channels that mediated the detection of vibration, it was not until much later that it was discovered, through the use of adaptation (Capraro *et al.*, 1979) and masking (Gescheider *et al.*, 1985), that there were two separate NP channels. The NP I channel mediates detection thresholds in the mid-range of vibration frequency and is optimally tuned at 30–50 Hz, and the NP II channel, observed only with small vibrator contactors ($< 0.02 \text{ cm}^2$), determines thresholds at higher frequencies and is optimally tuned at 250–300 Hz. A third NP channel, NP III, was subsequently discovered using a forward-masking procedure (Bolanowski *et al.*, 1988). The neural input to the P and NP I channels are thought

to be Pacinian and RA fibers, respectively, while the fiber types that are thought to provide the input to the NP III and NP II channels are SA I and SA II fibers, respectively (Bolanowski *et al.*, 1988). The four psychophysical channels and their neurophysiological substrates are referred to as the four-channel model of mechanoreception (Bolanowski *et al.*, 1988).

Although extensive research has been conducted on the characteristics of the four channels (e.g., see Gescheider *et al.*, 1994a on the effects of aging; Bolanowski *et al.*, 2000 on touch–pain interactions), our understanding of the channels has been limited by the fact that almost all the work on channels has been on the glabrous skin of the thenar eminence or the hairy skin of the volar forearm (Bolanowski *et al.*, 1994). There has been extensive research conducted on spatial perception when stimuli are applied to the fingertip (see Craig and Rollman, 1999). However, little is known about the organization of tactile channels at this site (Verrillo, 1971; Bernstein *et al.*, 1986; Goble *et al.*, 1996).

The goal of the present study was to examine the applicability of the four-channel model of mechanoreception to the detection of vibratory stimuli applied to the index fingertip. To this end, the effects of stimulus frequency were examined, and the results were compared with those obtained from testing on the thenar eminence. Given that the frequency selectivity of the tactile system is assumed to be established at the periphery (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001) and because the same four kinds of mechanoreceptors are found in the fingertip as in the thenar eminence, it was predicted that the effects of frequency on the detection threshold should be the same at both the thenar eminence and the fingertip. Confirmation of this prediction would strongly suggest that the premises of the four-channel model can be generalized from the thenar eminence to the fingertip. Experiments were also conducted to test the hypothesis that spatial and temporal summation operate in the same ways on the fingertip and the thenar eminence.

Experiment I. Frequency selectivity of tactile information processing channels of the fingertip

In this experiment, thresholds for detecting vibratory stimuli applied to the index fingertip were measured over a wide range of frequencies, ranging from 0.4 to 500 Hz. One of the objectives was to determine whether the tuning curves for each of the four information processing channels (P, NP I, NP II, NP III) established for the thenar eminence of the hand (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001) could account for the changes in threshold as the frequency of the stimulus applied to the fingertip is changed. To this end, a second series of experimental sessions was conducted in which a forward-masking

procedure was used to test the hypothesis that two separate channels, the NP I and NP III, mediate the detection of low frequency stimuli applied to the fingertip.

Method

Observers

Five volunteer observers, three females and two males, participated in the experiment. The observers ranged in age from 19 to 22 years and all were healthy with no indications of neurological disorders. Prior to the experiment, each observer participated in two or three 1-h practice sessions in detecting vibratory stimuli.

Apparatus

The observer and stimulus-delivering apparatus were located within a sound and vibration-proofed testing chamber. Vibratory stimuli were produced by a Goodmans 390 A shaker. Vibratory displacements of the skin were produced relative to a static indentation of the vibrator contactor of 0.5 mm into the skin. This static indentation was sufficient to prevent decoupling of the vibrator contactor from the skin during vibratory stimulation at the 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 0.72 cm² circular contactor 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 $\pm 0.5^\circ\text{C}$ of 30°C by a device that circulates water of the appropriate temperature through the hollow chamber of the surround. A Lauda/Brinkman RM-6 heating and refrigeration unit with 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 temporal envelopes of stimuli were synthesized by the computer and modulated an electrical sine wave of variable frequency that was applied to the vibrator after amplification.

Procedures

The test site was the index fingertip of the right hand. 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 the other 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. 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 μm peak displacement amplitude.

The duration of the test stimulus was 700 ms and its rise–fall time was 500 ms. Under these conditions harmonics of the fundamental frequency of vibration were well below the detection threshold even at the lowest frequencies (Bolanowski *et al.*, 1988). Thresholds were measured at 24 stimulus frequencies, ranging from 0.4 to 500 Hz.

During each session, the detection thresholds of an observer were measured at each of six of the 24 frequencies used in the experiment. Thus, over 12 sessions, 3 thresholds were measured at each of 24 frequencies.

In a second set of experimental sessions, only a 700-ms test stimulus with a frequency of 0.7 Hz was used, but a conditioning stimulus that produced forward masking (Gescheider *et al.*, 1985, 1989) of the detectability of the test stimulus was presented for 4 s with a rise–fall time of 50 ms and was followed by a period of 25 ms after which the test stimulus was presented. No stimulation was presented during the 25-ms temporal gap between the masking stimulus and the test stimulus. Masking occurs only when the masking and test stimuli excite the same channel (Labs *et al.*, 1978; Gescheider *et al.*, 1982, 1985, 2001; Hamer *et al.*, 1983). Thus, it is possible, depending upon the masking- and test-stimulus frequencies, to differentiate between two channels by masking one without affecting the other. For example, if the frequency and intensity of the masking stimulus is such that the stimulus activates the same channel that the test stimulus activates, detection of the test stimulus will be impaired. The amount of masking increases with increases in the intensity of the masking stimulus (Gescheider *et al.*, 1982; Bolanowski *et al.*, 1988). If, on the other hand, the masking and test stimuli activate different channels, then no masking will occur.

In our experiment, the intensities of the masking stimuli were expressed relative to the threshold for detecting the masking stimulus, i.e., sensation level (SL), and are given in db above the masking stimulus threshold (dB SL). In each experimental session, the detection threshold of the masking stimulus was determined, and the intensity of the masking stimulus was set in db relative to this value. Thresholds were then measured for detecting the test stimulus in the presence of the masking stimulus set at various SLs (intensity levels above the detection threshold). Finally, after determining the test-stimulus threshold at each sensation level of the masking stimulus, the threshold for detecting the test stimulus presented alone was again measured. The amount of masking was expressed as the shift in threshold calculated by subtracting the average threshold for the test stimulus presented alone from the threshold of the test stimulus in the presence of the masking stimulus.

During an experimental session, one threshold was measured at each SL of the masking stimulus, which had a frequency of either 20 or 40 Hz. Three sessions were conducted, yielding three thresholds at each sensation level of the masking stimulus for each of the two frequencies. The objective of the forward-masking sessions was to determine whether detection of very low frequency stimuli below 1.5 Hz (e.g., 0.7 Hz) is mediated by the same or by a different channel than the channel that detects stimuli in the mid-frequency range, e.g., 20 or 40 Hz. When stimulating the thenar eminence, the NP I channel mediates detection of stimuli in the mid-range of 2–40 Hz, but detection of very low frequencies (< 2 Hz) is mediated by the NP III channel (Bolanowski *et al.*, 1988). If this is also true for stimulation of the fingertip, then no masking should occur for the detection of a 0.7 Hz test stimulus in the presence of a 20 or 40 Hz masking stimulus until the masker is sufficiently intense to stimulate the NP III channel as well as the NP I channel.

Results and discussion

Average thresholds for detecting vibration on the fingertip (open diamonds) are plotted as a function of frequency in Figure 1. Also seen in the figure are the tuning curves for each of the four information processing channels measured for the thenar eminence (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001). Because the sensitivities of the various channels on the fingertip are somewhat different than those on the thenar eminence (perhaps due to receptor-density differences, see Johansson, 1979 and Greenspan and Bolanowski, 1996, for review), the vertical positions of the P, NP I, and NP III curves have independently been adjusted to best fit the threshold measurements of the frequency range within which the channel mediates stimulus detection. The NP II frequency response curve, which is

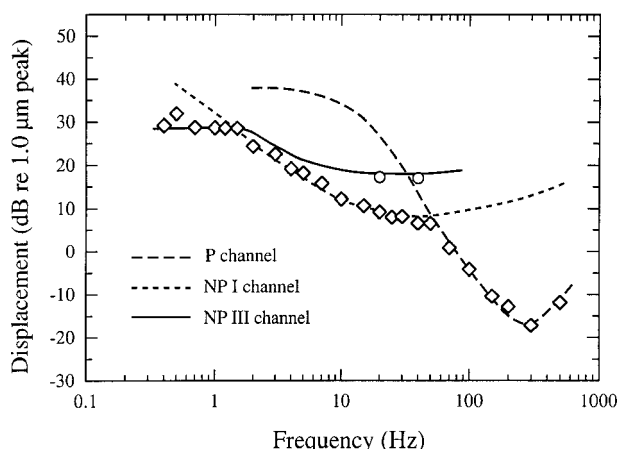


FIGURE 1. Average threshold as a function of stimulus frequency for stimulation of the index fingertip. Tuning curves of the P, NP I, and NP III channels determined for the thenar eminence (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001) were adjusted vertically by eye to fit the data points.

absent, can only be determined through the use of a small contactor in which case, the threshold of the NP II channel is lower than that of the spatially summing P channel, rendering it measurable. Unfortunately, it is not possible to examine the tuning of this channel for fingertip stimulation because the P channel is exceptionally sensitive to small contactor stimulation of this site (Verrillo, 1971).

Consistent with our expectations, the tuning curves derived from psychophysical measurement of the tactile sensitivity of the thenar eminence provide excellent fits to the threshold measurements of the fingertip obtained in the present experiment. The -12 dB/octave slope of the frequency response between 15 and 200 Hz characteristic of the P channel (Verrillo, 1963; Gescheider, 1976; Verrillo and Gescheider, 1977; Bolanowski *et al.*, 1988; Gescheider *et al.*, 1994a, 2001) is clearly evident in the present study when the stimuli applied to the fingertip were within the frequency range of 50 and 200 Hz. However, below 50 Hz, threshold is determined by other channels. At very low frequencies, between 0.4 and 1.5 Hz, threshold becomes independent of stimulus frequency and is determined by the NP III channel. At intermediate frequencies between 1.5 and 50 Hz, the NP I channel determines threshold.

The results of the forward-masking experiment are seen in Figure 2. The average threshold shift is plotted as a function of the sensation level (decibels above the detection threshold) of the masking stimulus when the masking stimulus was either 40 or 20 Hz. The line through the data points for the 40 Hz masking stimulus on the rising segment of the function was fitted by a least-squares analysis. Below a masking intensity of 10.0 db SL, the masking stimuli did not change threshold, indicating that the masking stimulus did not affect the

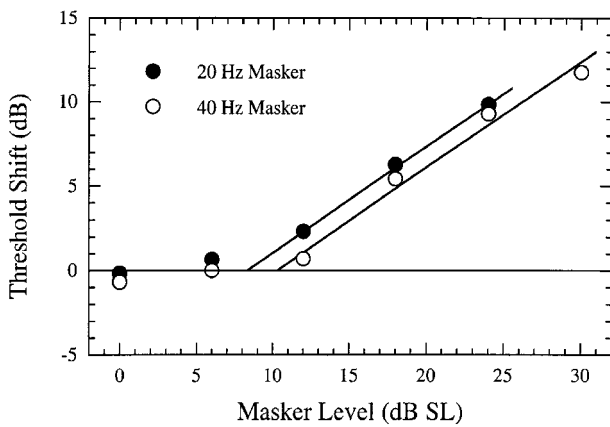


FIGURE 2. Average amount of masking in the detection of a 0.7 Hz stimulus expressed as a threshold shift in dB relative to the unmasked threshold as a function of the intensity level of a 20 Hz and a 40 Hz masking stimulus, expressed in dB above threshold.

channel mediating the 0.7 Hz test. Masking stimuli greater than 10.0 db SL, however, produced threshold elevations above the unmasked threshold of the test stimulus. The observation that masking occurred above 10.0 db SL indicates that the channel mediating the detection of the 0.7 Hz test stimulus was being affected by the masking stimulus at these intensity levels. Thus, the value of 10.0 db at the breakpoint of the masking function provides an estimate of the threshold at 40 Hz of the NP III channel mediating the detection of the 0.7 Hz test stimulus. Specifically, the channel mediating detection at 0.7 Hz has a threshold at 40 Hz that is 10.0 db above the unmasked threshold of 7 db *re* 1.0 μ m peak displacement at 40 Hz seen in Figure 1. This value of 17.00 db is plotted as an open circle in Figure 1.

A similar approach was taken in interpreting the results obtained in sessions in which the frequency of the masking stimulus and the test stimulus was 20 and 0.7 Hz, respectively. In this case, the least-squares analysis indicated that the breakpoint occurred at 8.2 db SL of the masking stimulus. Therefore, it was estimated that the threshold of the channel mediating detection of the test stimulus was 8.2 db above the unmasked threshold of 9 db *re* 1.0 μ m peak displacement seen in Figure 1 for detecting the 20 Hz stimulus. This value of 17.2 db is plotted as an open circle in Figure 1.

The open circle points in Figure 1 at 20 and 40 Hz representing the estimated values of the thresholds at these frequencies of the NP III channel are almost exactly the same as corresponding values on the NP III tuning curve derived by these same procedures for the thenar eminence (Bolanowski *et al.*, 1988). This result indicates that separate channels mediate the detection of very low frequency stimuli (e.g., 0.7 Hz) and moderately low frequency stimuli (e.g., 20 and 40 Hz) at both the fingertip and thenar eminence. Thus, as with the thenar eminence, the

NP III channel mediates detection of very low frequency stimuli between 0.4 and 1.5 Hz applied to the fingertip whereas the NP I channel mediates detection of moderately low frequency stimuli between 1.5 and 40 Hz.

Experiment II. A comparison of the sensitivities of the thenar eminence and fingertip

The purpose of this experiment was to compare sensitivity of the fingertip and thenar eminence within the frequency ranges of the P, NP I, and NP III channels. There is a substantial difference in receptor density within these two sites as estimated by microneurographic studies of humans (Johansson, 1979). Indeed, the density of receptors is approximately 4.2 times greater at the fingertip than at the palm. If receptor density plays a role in sensitivity to vibratory stimulation, then one would expect to find the sensitivity of the fingertip to be superior to that of the thenar eminence.

The ratio of receptor densities at the fingertip to that at the palm, however, is not constant across receptor types. The estimates are 5.7:1, 8.8:1, 2.3:1, and 1:1.7 for RA, SA I, PC, and SA II receptors, respectively (Johansson, 1979). Thus, if receptor density is positively correlated with sensitivity, then detection thresholds of the NP I channel with its RA fibers and detection thresholds of the NP III channel with its SA I fibers should be substantially lower on the fingertip where receptor density is much higher than it is at the thenar eminence. Thresholds in the P channel would also be expected to be lower on the fingertip with more than double the receptor density than on the thenar eminence, but by only about 3.6 dB, assuming an inverse linear relation between receptor density and stimulus energy needed for threshold. For the NP I and NP III channels, the predicted difference in the detection threshold in favor of the fingertip would be 7.6 and 9.4 dB, respectively.

Method

Observers

Five volunteer observers, three female and two males, participated in the experiment. As in Experiment I, observers ranged in age from 19 to 22 years and all were healthy with no indication of neurological disorders. Prior to the experiment, each observer participated in two or three 1-h practice sessions in which they detected vibratory stimuli applied to the thenar eminence and index fingertip.

Apparatus

The apparatus was the same as that used in Experiment I.

Procedure

Thresholds were measured for the detection of vibratory stimuli applied to either the thenar eminence or the fingertip through the

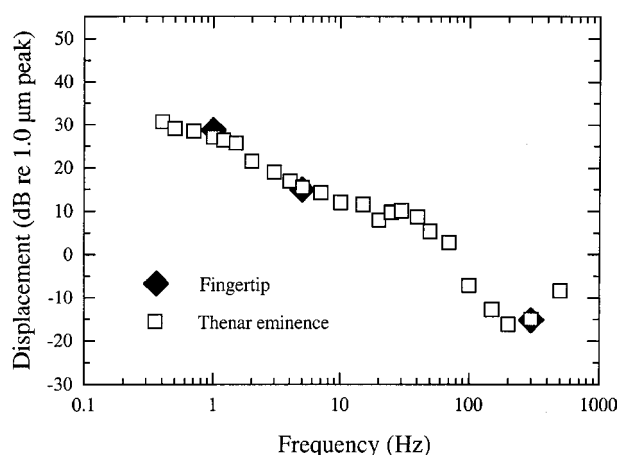


FIGURE 3. Average thresholds as a function of stimulus frequency for stimulation of the thenar eminence and stimulation of the index fingertip.

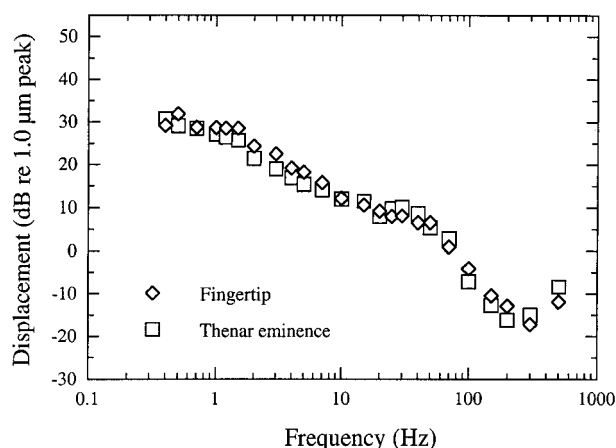


FIGURE 4. Average thresholds for detection of stimulation of the fingertip determined in Experiment I and average thresholds for detection of stimulation of the thenar eminence plotted as a function of stimulus frequency.

same 0.72 cm^2 contactor used in Experiment I. The thresholds at the thenar eminence were measured at 24 frequencies, ranging from 0.4 to 500 Hz and at the fingertip, thresholds were measured at 1.0, 5, and 300 Hz to assess the sensitivities of the NP III, NP I, and P channels of the fingertip, respectively. For each observer, three thresholds were measured at each of the 24 stimulus frequencies used to determine the sensitivity of the thenar eminence. Three thresholds were also measured at each of the three frequencies used to measure the fingertip's sensitivity. All other conditions of threshold measurement were essentially the same as those used in Experiment I, making it possible to compare directly the results obtained for the fingertip in Experiment I for one group of five subjects with those of a group of five subjects, comparable in age and medical status, who were tested on the thenar eminence as well as the fingertip.

Results and discussion

In Figure 3 are the average thresholds measured for stimulation of the thenar eminence and the fingertip plotted as a function of frequency. For this relatively large contactor of 0.72 cm^2 that covers most of the fingertip, thresholds on the fingertip and thenar eminence are essentially the same at each of the three frequencies at which thresholds were measured. Despite substantial differences in receptor density, the sensitivities to vibration within the NP III, NP I, and P channels do not differ at the two sites. In Figure 4, a comparison is made of the average thresholds measured for thenar eminence stimulation with the average thresholds for fingertip stimulation measured in Experiment I. Again, thresholds measured on the thenar eminence did not differ significantly from those measured on the fingertip.

It was not entirely surprising that thresholds of the NP III channel (frequencies between 0.4 and 1.5 Hz) and of the NP I channel (frequencies between 1.5 and 50 Hz) did not differ, even though the receptor densities were much higher on the fingertip (8.8 times higher at the fingertip for the SA I fibers of the NP III channel and 5.7 times higher on the fingertip for the RA fiber of

the NP I channel). These channels have been found to have little, if any, capacity for spatial summation (Bolanowski *et al.*, 1988; Gescheider *et al.*, 1994a). Therefore, their sensitivities do not improve as the number of receptors activated increases as the size of the stimulus applied to the skin is increased. Thus, it can be argued that if sensitivity is not improved in these channels by increasing the number of activated receptors resulting from increasing the size of the stimulus, then neither should the difference in the number of activated receptors resulting from stimulating sites of different receptor density affect detection thresholds.

More surprising, however, is the finding that receptor density had no effect on the sensitivity of the P channel, the sole channel known to be capable of spatial summation (Verrillo, 1963; Craig, 1976; Gescheider, 1976). A possible mechanism of spatial summation in the P channel is the integration of neural activity from an increasing number of active neurons as the size of the contactor delivering the stimulus is increased, resulting in a decline in the detection threshold. If such a mechanism operates in the spatially summing P channel, then the threshold for detecting high frequency vibration applied to various skin areas through a contactor of a particular size should be inversely related to the density of Pacinian corpuscles. Indeed, the reduced sensitivity of the P channel as a result of aging has been explained in this way (Verrillo, 1979; Gescheider *et al.*, 1994a; Goble *et al.*, 1996). Specifically, the reduced density of mechanoreceptors associated with aging (Cauna, 1965) is correlated with substantial elevations in the detection threshold. This is particularly pronounced in the P channel where it is thought that the capacity for neural integration over the neural activity generated from many receptors is critical to the channel's exquisite sensitivity (Gescheider *et al.*, 1994a).

Why then are high frequency thresholds the same on the thenar eminence and fingertip? A simple model in which the receptor populations on the thenar and fingertip are identical in every way, with the exception of their spatial density, would lead one to expect that the fingertip thresholds should be approximately 3.6 db lower than thresholds measured for detection of the same high frequency stimuli delivered through the same size contactor to the thenar eminence. But, aspects of the two populations of Pacinian corpuscles may differ in a number of other ways that could counteract the effects of differences in receptor density. For example, differences in the sensitivities of individual receptors (Bolanowski, 1981; Bolanowski and Zwislocki, 1984) could result in one site having receptors with an average sensitivity level that differed from the other. Furthermore, the variability in sensitivities of individual receptors could differ among sites resulting in a greater likelihood at one site than another that one or more exceptionally sensitive receptors would be activated by the vibratory stimulus. These factors alone could be enough to offset the small 3.6 db difference in thresholds predicted on the basis of receptor densities at the fingertip and thenar eminence.

Experiment III. Spatial summation in the P channel for fingertip and thenar eminence stimulation

In this experiment, we measured thresholds for detecting a 300-Hz stimulus applied through contactors of various sizes to the fingertip and to the thenar eminence. The objective was to determine whether our finding in Experiment II that thresholds at the two sites did not differ would also be evident when the experiment was repeated with smaller contactors. It was hypothesized that the difference in receptor density at the two sites would become an important factor in determining the sensitivity of the P channel when stimuli are delivered to a very small skin area through a small contactor. Given the known variability in the sensitivity of Pacinian corpuscles (Bolanowski, 1981; Bolanowski and Zwislocki, 1984), the probability of this small stimulus being delivered near one or more highly sensitive receptors within the receptor population should be higher at the fingertip where receptors are more densely populated than at the thenar eminence. This difference in the probability of exciting the most sensitive units should decline as the contactor is made large enough to encompass a sufficiently large proportion of the receptor population including the more sensitive units at either site. Thus, when the contactor is small, thresholds should be lower at the fingertip than at the thenar eminence, but the difference in threshold between the two sites should progressively decrease as the size of the contactor increases.

Method

Observers

Five observers, three females and two males, ranging in age from 18 to 21 years, participated in the experiment. All were in good health and were free from any known neurological disorder. Prior to the experiment, each observer participated in two or three practice sessions.

Apparatus

The apparatus was essentially the same as that used in the previous experiments.

Procedures

The procedures for measuring threshold were the same as used in the first two experiments. Thresholds were measured for the detection of a 300-Hz stimulus with a duration of 1,000 ms and a rise-fall time of 50 ms applied through contactors of variable size. Within each session, thresholds were measured with contactors that were 0.025, 0.10, 0.38, and 0.75 cm² in size that were applied to either the fingertip or the thenar eminence. Over a series of six experimental sessions, three thresholds were determined with each contactor size at each of the two test sites.

Results and discussion

Thresholds at the two test sites as a function of contactor size are plotted in Figure 5. At both sites, thresholds declined as the size of the contactor was increased, but the effect was greater at the thenar eminence than at the fingertip as revealed by the significant interaction of contactor size with site of stimulation, which was evident in an ANOVA, $F(3,12) = 5.05$, $p = 0.017$. A straight line with a slope of -3.0 dB/doubling of contactor size, representing perfect energy summation over the area of stimulation, was fitted to the data points obtained for the thenar eminence. Every 3.0 db drop in threshold represents a decrease of one half of the energy in the stimulus. Thus, doubling the contactor size drops the energy requirement for threshold by one half. This relationship between threshold and contactor size has been reported consistently for stimulation of the thenar eminence (Verrillo, 1963; Gescheider, 1976; Goble *et al.*, 1996) and has been interpreted as an indication that the P channel is capable of integrating neural activity over the stimulated area. As expected from the difference in receptor density at the fingertip and thenar eminence, thresholds were lower at the fingertip when contactors up to 0.1 cm² were used, and as seen in Figure 5, the slope of the spatial summation function of -3 dB/doubling of contactor size was evident at both sites. When larger contactors were used, however, the thresholds at the two sites were nearly the same with the slope of the spatial summation function at the thenar eminence remaining unchanged and with the function becoming nearly flat at the fingertip.

The results obtained at the fingertip cast doubt on the theory that spatial summation results solely from neural integration and support an alternative explanation in which the improvement in the detection threshold as the area of stimulation increases results from a process of probability summation as

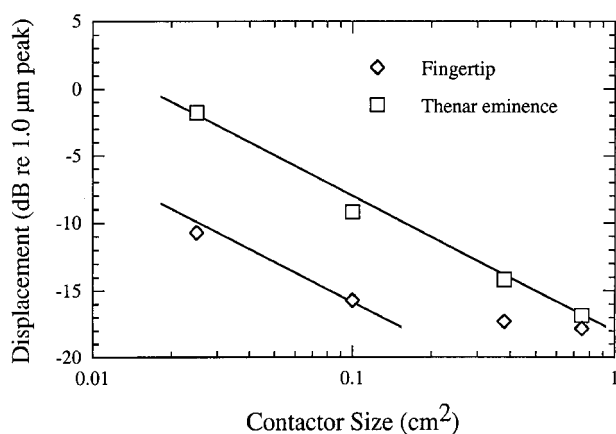


FIGURE 5. Average threshold for the detection of a 300 Hz stimulus applied to either the fingertip or to the thenar eminence as a function of the size of the contactor through which the stimulus was delivered.

well as neural integration. In contrast to neural integration, what is added up in probability summation as the size of the stimulus increases is not neural activity but instead is the probability that the neural threshold of the sensory system will be exceeded. This kind of model of spatial summation is based on the assumption that the sensitivity of the sensory system is variable over the area containing sensory receptors. Accordingly, the likelihood that as the size of the stimulus increases, the most sensitive receptors will be excited will increase as the stimulus is applied to an increasingly larger number of receptors.

In the P channel of the tactile sensory system, the sensitivities of Pacinian receptors in cat are known to differ by as much as 20 db (Bolanowski, 1981; Bolanowski and Zwislocki, 1984). Thus, it must be the case that the probability of exciting the most sensitive units requiring the lowest levels of stimulus intensity increases as the contactor size increases. If the neural code for detecting the stimulus is the activation of n Pacinian nerve fibers (see Checkosky and Bolanowski, 1992), then this is achieved by either applying a weak stimulus over a large area that would activate n of the most sensitive units or by applying a stronger stimulus over a smaller area that would activate n of the units with sensitivities more toward the mean of the distributions of receptor thresholds. In this model, receptor density should play a role in determining the effects of changing the size of the contactor. If receptors are densely packed, then the probability of exciting the most sensitive receptors will be high with either a small or a large stimulus, and consequently, variation of contactor size should have little effect on the detection threshold. In both cases, the threshold should be relatively low. When receptor density is very low, thresholds may be high for both small and large contactors because the probability of exciting the most sensi-

tive receptor is low in both cases. It is only when receptor density is moderate that the effects of variation in contactor size would result in substantial spatial summation with the detection threshold decreasing as contactor size increases. At moderate receptor densities, the probability that the stimulus will include excitation of the most sensitive receptors within the population should increase as the contactor size increases. The finding of the present experiment that the amount of spatial summation measured with contactors larger than 0.1 cm² is greater on the thenar eminence where the relative density of receptors is moderate relative to that of the fingertip, is consistent with the probability summation hypothesis. However, without knowing the distributions of thresholds at the fingertip and thenar eminence of humans, it is impossible to predict the forms of the spatial summation functions at the two sites.

As in Experiment II, the results of Experiment III indicate that when the size of the contactor is large and covers most of the fingertip, sensitivities of the fingertip and the thenar eminence are equivalent. Only when contactors smaller than 0.75 cm² are used does the fingertip become more sensitive than the thenar eminence. In terms of the probability-summation hypothesis, it is when the area of stimulation is relatively small that the probability of activating highly sensitive receptors is greater at a site of high than at a site of low receptor density. When a large contactor is used, a sufficiently large sample of the receptor population is included under the contactor to ensure that the most sensitive receptors will be stimulated at both sites.

Although the results of the present experiment are consistent with a probability summation model of spatial summation, they do not rule out the possibility that neural integration plays some role in the process. Checkosky and Bolanowski (1992) have shown that temporal summation, defined as the decrease in the detection threshold that results from an increase in stimulus duration, can be modeled within the P channel only if a temporal integrator receives input from more than one PC fiber. This result suggests that the process of temporal summation involves neural integration over both time and space. Therefore, it is a reasonable hypothesis that at least some degree of neural integration is also involved in spatial summation.

In conclusion, the results of the present psychophysical experiments show that for contactors greater than 0.1 cm² the fingertip exhibits less spatial summation than the thenar eminence and that thresholds measured with small but not large contactors are lower for the fingertip than for the thenar eminence. These findings, in conjunction with the finding that the sensitivities of individual receptors differ substantially, strongly suggest that probability summation is at least a component of spatial summation. Knowledge of the details of

how probability summation and neural integration are related in spatial summation will require further research.

Experiment IV. Temporal summation in the detection of stimuli applied to the fingertip and thenar eminence

The process of temporal summation in sensory systems is exemplified by the well-documented phenomenon of a progressive decrease in the detection threshold as signal duration is increased. This phenomenon has been extensively studied in touch (Verrillo, 1965; Gescheider, 1976; Green, 1976; Frisina and Gescheider, 1977; Gescheider and Joelson, 1983; Van Doren, 1985; Checkosky and Bolanowski, 1992; Gescheider *et al.*, 1994b, 1999, 2001) as well as in other modalities. The temporal-summation effect in the detection of vibrotactile stimuli follows a negative exponential function with a time constant of 200 ms describing how the detection threshold decreases as stimulus duration increases, with the effect complete at stimulus durations longer than 1,000 ms. Beyond 1,000 ms, threshold does not improve with further increases in stimulus duration. Such changes in threshold have been found at stimulus frequencies that preferentially activate the P channel, but not for lower frequencies (Gescheider, 1976) in which case, the NP I channel detects the stimulus. The effect is also absent at high frequencies when a very small contactor is used (Verrillo, 1965; Gescheider *et al.*, 1999), resulting in the stimulus being detected by the NP II channel.

Temporal summation in the P channel has been found to operate by a process of neural integration in which persisting neural responses to the stimulus are integrated over the duration of stimulus exposure (Gescheider *et al.*, 1999). This process is modeled well by Zwislowski's (1960) theory of temporal summation originally formulated to account for temporal summation in hearing (Verrillo, 1965; Gescheider, 1976; Gescheider *et al.*, 1994b). The purpose of the present experiment was to compare the operation of temporal summation at the fingertip and the thenar eminence. To this end, detection thresholds at the fingertip and thenar eminence were measured as a function of stimulus duration.

Method

Observers

The same observers who participated in Experiment III also participated in this experiment. Prior to the experiment, each observer participated in two or three practice sessions.

Apparatus

The apparatus was essentially the same as used in the other experiments.

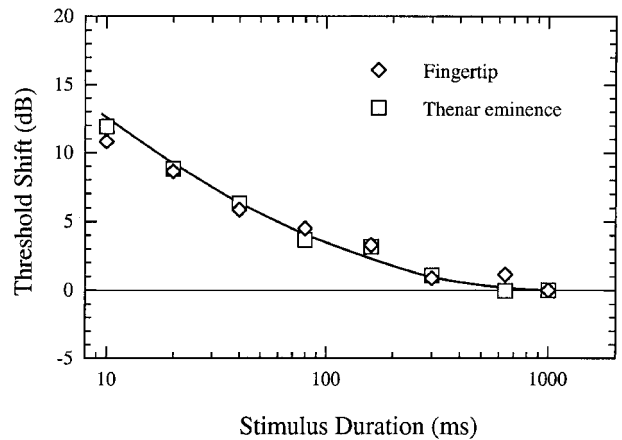


FIGURE 6. Average threshold shift in dB relative to the threshold for the detection of a 300 Hz stimulus delivered to either the fingertip or the thenar eminence for 1,000 ms.

Procedures

The frequency of stimulus was 300 Hz and its duration was either 10, 20, 40, 80, 160, 300, 640, or 1,000 ms. The rise-fall time of the stimulus was 5 ms. At the start and at the end of each session a threshold was measured for detection of the 1,000 ms stimulus and between these two measurements, thresholds were measured at each of the other durations. Threshold shifts attributable to changes in the duration of the stimulus were computed as the difference between the threshold measured at a particular stimulus duration and the average threshold measured at a stimulus duration of 1,000 ms. Within a session, thresholds were measured for detecting stimuli applied either to the fingertip or to the thenar eminence. Over six sessions, three threshold shifts were determined at each stimulus duration for the fingertip and for the thenar eminence.

Results and discussion

The average threshold shifts at the two sites plotted as a function of stimulus duration seen in Figure 6 did not significantly differ according to the results of an ANOVA, which revealed no significant main effect of testing site or significant interaction of testing site with stimulus duration. The solid function is predicted from Zwislowski's (1960) model of temporal summation in which neural activity is integrated over time to exceed a neural threshold at some specific level (also see Gescheider *et al.*, 1999). Because more time is available for neural integration at long durations of the stimuli, weaker stimuli are required to exceed the neural threshold at such durations. The psychophysical threshold rises as the duration of the stimulus becomes progressively shorter because more intense stimuli are required when less time is available for neural integration (see Gescheider *et al.*, 1999). Thus, because the temporal-summation functions of Figure 6 are essentially the same at the fingertip and thenar eminence and conform to the predictions of Zwislowski's model, it is reasonable to conclude that the mechanism of temporal summation is neural integration for stimulation at the fingertip as well as at thenar eminence.

Conclusion

Our results clearly demonstrate that the tuning characteristics of the P, NP I, and NP III information-processing channels previously determined for the thenar eminence (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001) account well for changes in vibratory thresholds on the fingertip that occur as a function of stimulus frequency. Each of these channels has been associated with a specific type of mechanoreceptor and the nerve fiber that innervates it. The evidence that Pacinian corpuscles exclusively provide the neural input to the P channel is strong. Of the mechanoreceptive nerve fibers, of which there are four types, in glabrous skin (PC, RA, SA I, and SA II), it is only the PC nerve fiber where the frequency tuning characteristic of the fiber matches that of the psychophysically measured frequency selectivity of the P channel (Verrillo, 1966; Talbot *et al.*, 1968; Mountcastle *et al.*, 1972; Bolanowski and Verrillo, 1982; Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001). The close correspondence between the tuning of PC fibers and the P channel indicates that the frequency selectivity of this channel is determined entirely at the level of the sensory receptor. It also appears to be the case that close matches exist between the tuning of RA, SA II, and SA I nerve fibers and the tuning of NP I, NP II, and NP III channels, respectively (Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001).

Receptor types with their associated nerve fibers utilized for the detection of mechanical displacements of the skin are the same in the glabrous skin of the fingertip and thenar eminence (Johansson *et al.*, 1982). It is reasonable, therefore, to conclude that, as in the thenar eminence, the neural inputs to the P, NP I, and NP III channels of the fingertip are Pacinian corpuscles with their PC fibers, Meissner corpuscles, with their rapidly adapting (RA) nerve fibers, and Merkel-cell neurite complexes with slowly adapting (SA) type I nerve fibers, respectively.

The results of the present study indicate that although the frequency characteristics of the psychophysical channels are essentially identical for the fingertip and thenar eminence, and the associated receptor-nerve fiber type mediating the frequency selectivity of a particular channel is the same at the two sites, the characteristics of spatial summation in the P channel are different. This result cannot be explained by a simple model of neural integration in which, somewhere in the central nervous system, the neural responses generated from individual receptors with approximately the same neural thresholds are added together to either exceed or fail to exceed a detection threshold of the observer. If this model were valid, then the threshold would decrease in proportion to the number of activated receptors, which is a joint function of the size of the stimulus and the

density of activated receptors. Since the density of Pacinian receptors is approximately twice as great on the fingertip than on the thenar eminence, thresholds for detecting the stimulus delivered through any contactor of a particular size should be approximately 3.0 dB lower on the fingertip than on the thenar eminence. The value of -3.0 dB, representing a halving of the energy of the stimulation needed for detection, should also occur when the size of the contactor is doubled, which in turn, doubles the number of activated receptors. The fact that these predictions were not confirmed for contactors greater than 0.1 cm² indicates the importance, in understanding spatial summation, of taking into account the difference in the thresholds of individual receptors and the process of probability summation that follows from this fact. At any intensity level of the stimulus, it is the case that as the size of the stimulus delivered to the skin increases, not only does the number of activated receptors increase, but the probability of activating the most sensitive receptors with the lowest threshold also increases. Thus, it is possible that threshold could be achieved through spatial summation when a certain number of receptors are activated, but at a lower stimulus intensity when a large contactor is used, increasing the probability through probability summation that the activated receptors will be ones with relatively low neural thresholds. Green and Zaharchuk (2001) have come to essentially the same conclusion regarding spatial summation in cutaneous temperature sensitivity. They found that the effects of increasing the size of a thermal stimulus on the skin on the threshold for detecting warm and cold sensations and on the perceived magnitude of warm and cold sensations are substantially influenced by variability in temperature sensitivity over the surface of the skin. As is true in our study of spatial summation in the sense of touch, spatial summation in temperature sensitivity as pointed out by Green and Zaharchuk cannot be meaningfully interpreted unless, as originally observed by Hardy and Oppel (1937), local variations in sensitivity are taken into account.

Temporal summation in the P channel, a process known to be based on neural integration over time in most circumstances rather than probability summation, was the same for stimulation of the fingertip and the thenar eminence. It appears that receptor density and the variability of individual receptor thresholds play a large role in spatial summation through the process of probability summation, but are unimportant in temporal summation. Instead, what appears to be important in temporal summation is the integration of neural activity over time within the central nervous system which originates from the activation of more than one Pacinian corpuscle (Checkosky and Bolanowski, 1992; Gescheider *et al.*, 1999).

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