TITLE PAGE

Independent Responses of Pacinian and non-Pacinian Systems with Hand-transmitted Vibration Detected from Masked Thresholds

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Masked thresholds for hand-transmitted vibration

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Abstract

This study was designed to identify psychophysical channels responsible for the detection of hand-transmitted vibration. Perception thresholds for vibration (16, 31.5, 63 and 125 Hz sinusoidal for 600 ms) at the distal phalanx of the middle finger and the whole hand were determined with and without simultaneous masking stimuli (1/3 octave bandwidth Gaussian random vibration centered on either 16 Hz or 125 Hz for 3000 ms, varying in magnitude 0 to 30 dB above threshold). At all frequencies from 16 and 125 Hz, absolute thresholds for the hand were significantly lower than those for the finger. Changes in threshold as a function of masker level were used to estimate the thresholds of three psychophysical channels (i.e. P, NP I, and NP II channels). Increased vibrotactile sensitivity of the hand compared to the finger seems to be not entirely due to increased spatial summation via the Pacinian sytem (P channel); non-Pacinian system (NP I and NP II channels) also contributed to perception. Differing transmission of vibration between the hand and the finger may have also influenced the thresholds.

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TEXT

Introduction

Vibration at the hand (hand-transmitted vibration) can provide useful tactile feedback of tasks, but it can also cause discomfort and interfere with activities (Griffin, 1990). Excessive exposure to hand-transmitted vibration can present a risk of injury, with vascular and neurological disorders including loss of tactile sensation (Bovenzi, 1990). Acute impairment of tactile sensitivity due to exposure to hand-transmitted vibration, is described as a temporary threshold shift, TTS (Nishiyama and Watanabe, 1981; Harada and Griffin 1990), and according to Lundström and Johansson (1986), can be explained by a depression of the excitability of the mechanoreceptive nerve fibers.

Four classes of mechanoreceptive nerve fibers innervating the glabrous skin of the hand are thought to mediate the perception of vibrotactile stimuli applied to the hand. Neurophysiologically, they have been identified as two fast adapting fibers (FA I and FA II) and two slowly adapting fibers (SA I and SA II) (Johansson and Vallbo, 1979a, b). It is widely assumed that the threshold curves of the four types of nerve fibers have overlapping frequency ranges; vibrotactile thresholds are thought to be determined by the nerve fibers that have the highest probability of detection for the applied stimulus. Güçlü and Bolanoswki (2004) have investigated how the probability of stimulus detection is related to the number active fibers contributing to the detection of a stimulus.

Psychophysical studies of vibrotactile thresholds initially elicited responses from two types of independent sensory systems, often distinguished as Pacinian and non-Pacinian systems (see summary by Gescheider and Verrillo, 1979). The Pacinian system has distinctive characteristics: spatial and temporal summation and a dependence on skin temperature (Gescheider *et al*., 1978), and is associated with Pacinian corpuscles (FA II) (Bolanowski and Verrillo, 1982; Mountcastle *et al.,* 1972; Verrillo, 1966). The non-Pacinian system, later discriminated as NP I, NP II, and NP III channels (i.e. FA I, SA II and SA I, respectively), some of which seem incapable of temporal or spatial summation and whose responses depend on stimulus gradients (i.e. the configuration of the limiting edge on the surface of the skin produced by the presence of a rigid border or surround; Gescheider, 1976; Verrillo, 1985).

The characteristics of the psychophysical channels in the non-Pacinian system have been investigated using two different techniques designed to eliminate responses of one channel so that the threshold curve of another channel can be determined over a range of frequencies: (i) by using adaptation stimuli (Verrillo and Gescheider, 1977; Capraro *et al*., 1979; Gescheider and Verrillo, 1979; Gescheider, *et al*., 2001); or (ii) by using masking stimuli (Bolanowski *et al*., 1988; Gescheider *et al*., 1982; Gescheider and O'Malley, 1983; Gescheider *et al*. 1985; Hamer *et al*., 1983; Labs *et al*., 1978; Verrillo and Bolanowski, 1986). Masking (impaired detection of a test stimulus caused by a masking stimulus) occurs only when the masker and the test stimulus excite the same channel, which is referred as in-channel masking (Gescheider *et al*., 1982; Hamer, 1979; Hamer *et al*., 1983). If the masker and the test stimulus stimulate different channels, no masking occurs, which is referred as cross-channel masking. By varying the intensity and the frequency of the masking stimulus and the frequency of the test stimulus, it is possible to determine threshold curves for each channel. A small vibrating contactor has often been used with these techniques so as to reduce responses from the Pacinian channel - leading to the establishment of the triplex model (Gescheider *et al*., 1985) and a four-channel model of vibrotactile perception (Bolanowski *et al*., 1988; Gescheider *et al*., 2001).

These models identify characteristics of psychophysical channels in the glabrous skin responsible for perception thresholds at each frequency.

There are many situations in which vibration enters the hand by touching or grasping a vibrating tool, or other vibrating object, and it is desired to reduce the perceptibility of vibration in the hand. Absolute perception thresholds have been determined for hand-transmitted vibration in several studies (Miwa, 1967; Reynolds *et al*. 1977; Morioka and Griffin 1999; Brisben *et al*., 1999) and the threshold contours are in good agreement, showing U-shaped curves with minimum displacement required for perception between 150 and 200 Hz. However, it is not known which psychophysical channels are involved in the detection of vibration by the whole hand, or which channels are responsible for the sensations (e.g. discomfort) at magnitudes greater than perception thresholds, or which channels are damaged by vibration, or what affect this damage has on the sense of touch.

The location of contact influences sensitivity to hand-transmitted vibration: increasing the area of contact from the distal phalanx of a finger to the whole area of the glabrous skin of the hand decreases absolute perception thresholds at frequencies between 16 and 125 Hz (Morioka and Griffin, 1999) and also increases sensation magnitudes for supra-threshold stimuli (Morioka and Griffin, 2001). If thresholds were mediated by NP I channel at both the fingertip and the whole hand, it might be expected that thresholds would be the same for excitation of the finger and the hand, since the NP I channel does not exhibit spatial summation. The previous results allow several alternative explanations. The greater sensitivity with the larger area of the hand may be due to spatial summation, implying that over the frequency range 16 to 125 Hz thresholds for the perception of vibration of the hand are mediated entirely by the Pacinian system (FA II). Alternatively, psychophysical channels that mediate thresholds of the hand may be different from those mediating thresholds of the finger at the same stimulus frequency. It is not possible to decide which mechanisms are responsible for the difference without knowledge of which psychophysical chennels mediate thresholds for hand-transmitted vibration.

This study was designed to determine the supra-threshold sensitivity of psychophysical channels responsible for the detection of vibration applied to the distal finger and to the palmar surface of the hand. It was specifically intended to assist the interpretation of threshold for the fingers and hand obtained by Morioka and Griffin (1999). Two alternative hypotheses were investigated: (i) the lower thresholds for the glabrous area of the palmar hand than the distal finger are entirely due to spatial summation in the Pacinian system, or (ii) other channels (within the non-Pacinian system) are involved in mediating thresholds for hand-transmitted vibration. The hypotheses were tested by deriving threshold curves for the psychophysical channels mediating perception of vibration applied to the finger and the hand. Masked thresholds were determined in the presence of 16 and 125 Hz masking stimuli (1/3 octave bandwidth random vibration centered on 16 or 125 Hz), allowing the isolation of responses mediated by both the Pacinian and the non-Pacinian systems.

Method

Subjects

Six healthy paid volunteers (five males and one female), aged between 18 and 27 years (mean 23.2 years, standard deviation, SD = 2.94), took part in the study. The average stature and average weight of the six subjects were 176.7 cm (SD = 7.6) and 72.8 kg (SD = 12.8), respectively. They were all non-smokers, right handed and had no history of occupational exposure to hand-transmitted vibration. Their hand and finger dimensions (i.e. hand length, hand breadth, hand depth, finger length, finger length, and finger breadth) were measured to determine whether there were any correlations with the measured thresholds. The study was approved by the Human Experimentation Safety and Ethics Committee of the ISVR, University of Southampton. Informed consent to participate in the experiment was given by all subjects.

Apparatus

Vertical vibration was delivered by an electromagnetic vibrator (Derritron VP30) powered by a 300-watt amplifier (Derritron TA300) with a cooling fan (model 9MS8). A force cell (DS Europe, type LT-05A5) was mounted on the vibrator table, with the output indicated on a force meter so that the subjects could monitor their applied forces. A rigid flat wooden plate (220 mm by 150 mm) was secured to the force cell. A piezoelectric accelerometer (DJ Birchall, type A/20T) was attached near the middle of the lower surface of the wooden plate and the signal amplified by a charge amplifier (Brüel and Kjær, type 2635).

Vibration signals were generated and acquired using *HVLab* Data Acquisition and Analysis Software (version 3.81) via a personal computer fitted with anti-aliasing filters (TechFilter) and an analogue-to-digital and digital-to-analogue converter (PCL-818). The signals were generated at 5000 samples per second and passed through 400 Hz low-pass filters. The stimulus parameters and the psychophysical measurement procedures were controlled by the computer.

During the tests, the subjects were exposed to white noise at 70 dB(A) via a pair of headphones to: i) prevent them from hearing the vibration, and ii) assist their concentration on the vibration by masking any distracting sounds. The acoustic noise generated by the vibration was inaudible without the masking noise.

Skin-stimulus Coupling Conditions

Vibration stimuli were delivered either to the distal phalanx of the middle finger (i.e., FINGER) or to the whole hand (i.e., HAND), with fixed postures as shown in Figure 1. For the FINGER condition, the subjects placed their fingers over a nylon contactor probe (cylindrical shape, 30 mm diameter) attached to the wooden plate: the glabrous part of the whole distal phalanx of the finger was in contact with the probe. For the HAND condition, the subjects rested the whole of their right hand over the wooden flat plate (220 mm by 150 mm). A height-adjustable armrest was provided to maintain a fixed hand posture for the subjects (the hand and arm horizontal and level with the vibrating surface) during the measurements. The downward contact forces applied by the finger and hand were 1 N and 5 N, respectively.

FIGURE 1 ABOUT HERE

The skin temperature of the fingertip was measured at the beginning of every session using a thermocouple. Measurements proceeded if the skin temperature was greater than 29° Celsius, otherwise the subjects were asked to warm their hands until reaching this temperature.

Stimulus Parameters

Sinusoidal vibratory stimuli, 600 ms in duration, with rise and fall times of 100 ms were created with cosine-tapered ends. Four test stimuli, with frequencies at 16, 31.5, 63, and 125 Hz, were prepared. A Gaussian random masking stimulus, 3000 ms in duration, was created with a 1/3-octave bandwidth centered on either 16 Hz (filter pass-band range 14.1 to 17.8 Hz) or 125 Hz (filter pass-band range 112 to 140 Hz). The magnitudes of the masking stimuli varied according to each subject’s perception threshold for the masker measured at the beginning of each session, and were presented at 11 levels from threshold up to 30 dB SL (i.e. 30 dB above the threshold level of the subject) in 3 dB steps. The stimulus parameters, including the combination of test and masker stimulus, are shown in Table 1.

TABLE 1 ABOUT HERE

The experiment included the determination of in-channel masking functions to confirm that a slope of unity (i.e. threshold increasing in proportion to masker level) was obtained when using stimuli with similar frequency (i.e. 16 Hz test and 16 Hz masker; 125 Hz test and 125 Hz masker). It was expected that for both frequencies the masking stimuli would stimulate the same channel as the test stimuli, producing in-channel masking functions (i.e. a slope of 1.0). In-channel masking functions were tested with only five magnitudes of masking stimulus (i.e. 0, 3, 12, 21 and 30 dB SL), so as to reduce the testing time. One of the six subjects completed the masked threshold tests with 3 dB steps of masker intensity in order to confirm that the expected slope of the in-channel masking function.

Procedure

Unmasked thresholds (i.e. the absolute threshold of a test stimulus without a masking stimulus) and masker thresholds (i.e. absolute threshold of the masking stimulus) were determined at the beginning of every session in which masked thresholds were determined with a combination of test stimuli and a masker.

A two-interval two-alternative forced-choice (2IFC) tracking method (Zwislocki *et al.*, 1958) in conjunction with the up-down transformed response (UDTR) procedure with three-down one-up rule described by Wetherill and Levitt (1965) was employed for vibrotactile threshold measurements. For the unmasked thresholds (including the thresholds for the masker stimulus), subjects were presented with pairs of stimuli, each 600 ms in duration, separated by a 600 ms pause. The two observation periods were designated to the subjects by cue lights. For the masked thresholds, a 600 ms test stimulus was presented followed by a 600 ms pause followed by a 3000 ms masker stimulus; the masker stimulus contained a set of two observation periods, each 600 ms in duration, placed in the middle of the masker stimulus. The sequence of stimuli in a trial is illustrated in Figure 2. The duration of 600 ms was chosen for the observation, the pause, and masking duration (both before and after the onset of a test signal), because it appears that temporal summation of the Pacinian system affects thresholds below about 500 ms (Gescheider *et al*., 1978). The 600 ms of pause between the test stimulus and the masker is thought to have eliminated forward-masking, according to Gescheider *et al.* (1989) who found that the forward masking effect was virtually eliminated after about 600 ms. For the masked threshold condition, different cue lights were presented so as to distinguish the period of a test stimulus from the observation periods; the light blinked during the period of a test stimulus, and the light appeared continuously during the two observation periods. For unmasked and masker threshold tests, the subjects' task was to judge whether the first or the second observation period contained a vibration stimulus. In the case of masked threshold tests, the subjects were asked to judge whether the first or the second observation period contained the test stimulus presented at the beginning of each trial. The subjects responded saying, "first" or "second". The magnitude of the vibration stimulus was increased by 2.0 dB (25.8% increment) after a negative (incorrect) response and decreased by 2.0 dB after three consecutive positive (correct) responses. This procedure provides thresholds corresponding to 79.4% correct responses. The measurement was terminated after six reversals: a point where the stimulus level reversed direction (i.e. at either a peak or a trough). The threshold was calculated from the mean of the last two peaks and the last two troughs, omitting the first two reversals, as suggested by Levitt (1971).

FIGURE 2 ABOUT HERE

A single session consisted of three tests: an unmasked threshold test and a masker threshold test followed by a masked threshold test using one of the four test stimuli (i.e. 16, 31.5, 63 or 125 Hz) with 11 sensation levels of masker (0 to 30 dB SL) with either 16 or 125 Hz 1/3 octave bandwidth random vibration. The masking stimuli at 11 different intensities were presented in a random order with the restriction that the masked threshold test started with low-intensity maskers (i.e. 0-15 dB SL) and ended with high-intensity maskers (i.e. 15-30 dB SL). This procedure was adopted so as to minimize any cumulative effects of adaptation (Gescheider and O'Malley, 1983).

The orders of applying the two contact conditions (i.e. FINGER or HAND) and the two masking stimuli (i.e. 16 and 125 Hz 1/3 octave bandwidth random vibration) were balanced between the subjects. The order of presenting the four test stimuli (i.e. 16, 31.5, 63 and 125 Hz) was randomized between the sessions.

Analysis

All thresholds were measured in acceleration (ms^{-2} r.m.s.) and converted into peak displacement using the equation:

$$\text{Displacement (in meters, peak)} = \frac{a_f}{(2\pi f)^2} \cdot \sqrt{2} \qquad (1)$$

where a_f is the acceleration (ms^{-2} r.m.s.) measured at the stimulus frequency, f.

The amount of masking is presented in decibels, taking the unmasked threshold of each subject as a reference:

$$\text{Threshold shift (dB)} = 20 \cdot \log_{10}\left(\frac{A_f}{B_f}\right) \qquad (2)$$

where A_f is the acceleration of the masked threshold, B_f is the acceleration of the unmasked threshold at the stimulus frequency, f.

A masked threshold was determined by measuring the acceleration of the sinusoidal vibration test stimulus presented at the beginning of each trial (see Figure 2). Statistical analysis was performed using non-parametric tests: Friedman two-way analysis of variance for k-sample case and Wilcoxon signed ranks test for two-sample case.

Estimation of Threshold Curves

The estimation of threshold curves for each psychophysical channel was based on the assumptions of Gescheider *et al*. (1982): (i) two or more channels with different frequency characteristics mediate the detection of vibrotactile stimuli; (ii) at any particular frequency of the test stimulus the psychophysical threshold is determined by the channel with the lowest threshold; (iii) neural activity in one channel cannot mask neural activity in another channel. Duplex and triplex models have been proposed (Verrillo, 1968; Gescheider, 1976; Gescheider *et al*., 1985) and are based on thresholds determined using a small contactor (e.g. 0.01 cm^2) chosen to elevate thresholds of the Pacinian channel. With the contact conditions of the current study, it was expected that the Pacinian threshold curve would be lower (due to increased spatial summation) while the NP I threshold curve was expected to be higher (due to reduced pressure gradients) than those in the triplex model of perception for a smaller contact area. It is not known whether the third channel (SA II) has spatial summation (Bolanowski *et al*., 1988): the sensitivity of the third receptor might increase when the area of excitation is increased from the fingertip to the whole hand.

Figure 3 illustrates a theoretical example of the method of estimating threshold curves from the masking function for the test frequency of 63 Hz with the 125 Hz masker. With increasing masker level, the threshold of the test stimulus is initially increased, with slope of 1.0, by a level 'a' due to in-channel masking, possibly within the Pacinian channel (assuming the 125 Hz masker is mediated by the Pacinian corpuscle). With increases in the masker intensity up to the end of a level of 'A', there is no elevation of thresholds (seen as 'α' in Figure 3), indicating that the test stimulus was mediated by a different channel (e.g. NP II). With further increases in the masker level, the threshold of the test stimulus is elevated by a further amount 'b', until the test stimulus reaches the threshold of another channel (e.g. NP I), because above 'a', the masker has reached the threshold of NP II. The horizontal line 'β' is seen because the test stimulus is mediated by NP I while the masker is still mediated by NP II over the range 'B'. When the masker reaches the threshold of NP I, in-channel masking starts, marked as 'c' and 'C' in Figure 3. According to this rationale, it is possible to estimate thresholds for each receptor at each frequency, and so determine threshold curves for each of the psychophysical channels.

The two alternative triplex models illustrated in Figure 4 were developed to predict threshold curves for the individual channels from the current results, adopting the slopes provided by Gescheider *et al*. (1985) (i.e. 0 dB/octave for NP I, -12 dB/octave for P and -4.5 dB/octave for NP II). The two alternatives arise from shifting the NP II threshold curve up (Triplex model 1) or down (Triplex model 2). Schematic predictions of masking functions corresponding to each of the two alternative triplex models are illustrated in Figure 4. The Pacinian channel has the lowest thresholds at 125 Hz in both models, whereas at 31.5 Hz either the Pacinian or the NP II thresholds were the lowest. The masking functions are therefore not identical for the two alternative triplex models: there is a change in the intersections between the threshold curves of the three channels due to an alteration in sensitivity of the NP II thresholds.

FIGURES 3 AND 4 ABOUT HERE

Results

Unmasked Thresholds

Throughout all sessions, the unmasked thresholds of vibration perception (i.e. the absolute thresholds of the test stimuli with no masking stimuli) for each test frequency were measured twice per subject. The unmasked thresholds were dependent on stimulus frequency and contact area (Wilcoxon, $p < .01$), with no effect of repeated measurement (Wilcoxon, $p > .1$). Unmasked thresholds were averaged over the two measurements for each subject. The median thresholds for the two contact conditions expressed in terms of both the r.m.s. acceleration and the peak displacement are shown in Figure 5. The HAND condition gave significantly lower thresholds compared with the FINGER condition at all frequencies (Wilcoxon, $p < .01$), by 8.8, 17.4, 8.6 and 9.0 dB at 16, 31.5, 63 and 125 Hz, respectively.

FIGURE 5 ABOUT HERE

Absolute thresholds of vibration perception for the masker stimuli (1/3 octave bandwidth Gaussian random vibration centered on either 16 Hz or 125 Hz) were also measured so as to examine whether the amplitude required to detect the masker is the same as that required for the test stimulus. No significant difference in threshold was found between the two vibration waveforms for the two (Wilcoxon, $p > .1$).

Masked Thresholds

The first approach to analyze the masked thresholds was to observe the overall patterns of all of the masking functions within each of the six subjects. Threshold shifts (in dB) were calculated from the measured masked thresholds and unmasked thresholds (Equation 2).

In-channel masking

Figure 6 shows threshold shifts (in dB) versus the sensation level of the masker (in dB SL), presented for in-channel masking functions (i.e. 125 Hz centered masker with 125 Hz test stimulus, 16 Hz centered masker with 16 Hz test stimulus). The masked thresholds increased linearly, with a slope of approximately 1.0 (mean 0.99, SD = 0.099) and mean R^2 of 0.986 (SD = 0.011); thresholds shifted upwards by the amount of the increment in the masker. It is evident that the 1/3-octave random vibration stimuli masked the detection of the sinusoidal stimuli, indicating that both stimuli were mediated by the same channel.

FIGURE 6 ABOUT HERE

Cross-channel masking

The other masking conditions are all considered as cross-channel masking functions, containing both horizontal lines and slopes of 1.0. Cross-channel masking is often based on the assumption that Pacinian and non-Pacinian systems are independent in response: a masker stimulating one system should not alter the detectability of a signal in the other system (Labs *et al*., 1978; Hamer, 1979; Hamer *et al*., 1983; Gescheider *et al*., 1982; Verrillo *et al*., 1983). A horizontal line in a masking function implies independence in the detection response, as indicated by Hamer *et al*. (1983): for example, a Pacinian system masker should not affect signal detectability within the non-Pacinian system, or vice-versa.

Figure 7 presents cross-channel masking functions from selected stimulus conditions (i.e. 16 Hz centered masker with FINGER condition, 125 Hz centred masker with HAND condition). On close inspection of Figure 5 it can be seen that some individual data contain more than one horizontal line. This indicates that more than two independent channels were involved in the detection of the vibration stimuli, with the threshold of each channel reflected in the masking functions. It is expected that the sensitivities of channels vary between subjects, as apparent in the unmasked thresholds (Figure 5); some subjects may be sensitive to stimuli exciting particular receptors while others are insensitive. Analysis undertaken to determine threshold curves was therefore performed on data from each subject rather than median data.

FIGURE 7 ABOUT HERE

The masking functions determined for the subjects were mostly consistent with the Triplex model 1 (Figure 4). Threshold curves of psychophysical channels were derived from masking functions determined with each test frequency. Figure 8 illustrates the determination of receptor thresholds for the HAND condition from empirical masked thresholds of one subject (i.e. Subject 6), following the masking theory shown in Figure 3. All the thresholds were determined in terms of acceleration then converted to peak displacement. Threshold curves for three psychophysical channels (expressed in peak displacement) determined from the masking functions of the six subjects are shown in Figure 9. At some frequencies the threshold curves in Figure 9 consist of less than six data points from the six subjects, particularly for NP I with the HAND condition. It was thought that thresholds of the NP I channel may lie 30 dB above the threshold of the Pacinian channel for some subjects. Missing thresholds of NP I channel occurred where an individual NP I threshold curve was higher (by more than 30 dB) than the most sensitive threshold curve (i.e. P thresholds) for a subject, so that the masker could not mask the NP I channel within the 30 dB range of the masker. With incomplete data, either a median or a mean of the threshold curves of each receptor channel may underestimate the threshold curve. The procedure for determining median values taking into account the missing values was as follows:

(i) Take the median value if six values were available.

(ii) Take the mean of the second and third highest measured value if five measured values were available.

(iii) Take the mean of the highest and second highest measured value if four measured values were available.

(iv) Take the highest measured value if less than four measured values were available.

FIGURES 8 AND 9 ABOUT HERE

Effect of frequency

The median estimated threshold curves for the psychophysical channels, expressed in displacement, are shown in Figure 10. Within the NP II channel, the displacement thresholds depended on stimulus frequency for both the FINGER and HAND condition (Friedman $p < .05$). The NP I displacement threshold curve for the HAND was independent of frequency (Friedman $p = .145$), but the NP I threshold curve for the FINGER depended on frequency (Friedman $p = .039$), although with no significant frequency dependence from 31.5 Hz to 125 Hz. The NP II displacement threshold curve was significantly dependent on frequency at the FINGER (Friedman $p = .006$) and at the HAND (Friedman $p = .05$). The frequency-dependence of the threshold curves for the P, NP I and NP II channels showed no statistically significant quadratic trends ($p > .1$), but significant power trends ($p < .05$). It was therefore assumed that the thresholds of the Pacinian, NPI and NP II channels could be expressed by linear slopes on log-log coordinates.

FIGURE 10 ABOUT HERE

Effect of contact size

Generally, the HAND showed lower thresholds than the FINGER within each receptor channel. For the Pacinian channel, the shapes of the threshold curves for the FINGER and the HAND are similar, with a significant lowering of the threshold for the HAND compared to the FINGER at all frequencies (Wilcoxon, $p < .028$). This is consistent with spatial summation via Pacinian channel. The NP I thresholds at the FINGER and the HAND did not differ at 63 or 125 Hz (Wilcoxon, $p > .5$), but there was a significant reduction in NP I thresholds for the HAND at 16 and 31.5 Hz (Wilcoxon, $p = .028$). For the NP II channel, thresholds at the HAND were lower than at the FINGER at both 31.5 and 63 Hz (Wilcoxon, $p = .028$).

DISCUSSION

As expected, in-channel masking was observed when using test and masking stimuli at the same frequency (i.e. 16 Hz or 125 Hz). Masked thresholds increased in proportion to masker level with a slope of 1.0 and were virtually identical with both low frequency and high frequency maskers. In-channel masking functions have been examined in several studies with vibrotactile stimuli (e.g. Verrillo and Capraro, 1975; Hamer *et al*., 1983) and with auditory stimuli within a critical band (e.g., Hawkins and Stevens, 1950). These studies also found masking functions with a slope of 1.0 above about 10 dB SL, while displaying negative masking at low masker levels (below about 10 dB SL). In the present study, the negative masking phenomenon was not clearly displayed, this may be partly due to the small number of data points obtained in the in-channel masking tests (only examined with 0, 3, 15 and 30 dB SL for five subjects) and partly due to the use of a random masking stimulus. Hamer *et al*. (1983) found that the negative masking effect was more extensive when using a sinusoidal masker than when using a random noise masker. Green (1960) investigated signal detectability using auditory stimuli and reported that the detection of sinusoidal signals in noise was improved when the signal was presented as an in-phase addition to a background sinusoid of the same frequency.

The masking functions determined in the present study indicate that there were more than two independent response channels within the range of magnitudes of the masking stimuli employed in the study, so threshold curves for three-individual psychophysical channels (referred to as P, NP I and NP II) could be estimated for both the FINGER and HAND contact conditions. The median threshold curves of the three channels and the median unmasked thresholds for each contact condition are presented in Figure 11. Over the frequency range, the lowest thresholds of the three channels trace the absolute threshold contours: the channel with the lowest threshold is responsible for the absolute threshold. It is evident that the threshold curves for the three channels intersect over the frequency range 16 to 125 Hz, for both the FINGER and the HAND contact conditions. Accordingly, the initial hypothesis in which Pacinian channel is entirely responsible for absolute thresholds in both contact conditions (suggesting thresholds decrease with increasing contact area due to spatial summation exhibited by Pacinian system) must be withdrawn. An alternative hypothesis, in which two or more channels are responsible for absolute thresholds, is required to explain why absolute thresholds for the HAND are lower at all frequencies than those for the FINGER.

FIGURE 11 ABOUT HERE

The threshold curves of the Pacinian channel determined in this study are in good agreement with threshold curves of the same receptors demonstrated in previous studies. The slope of the threshold curve of the Pacinian channel between

15 and 200 Hz has been suggested to be approximately -12 dB/octave when expressed in displacement (e.g., Verrillo, 1963; Gescheider, 1976; Verrillo and Gescheider, 1977; Bolanowski *et al*., 1988; Gescheider *et al*., 2001), as observed here in the threshold curve of the Pacinian channel for both the HAND and the FINGER. As expected from the results of previous studies, the Pacinian threshold curve for the HAND was lower than that for the FINGER, consistent with spatial summation. Although spatial summation may be present, the reduction in threshold is smaller than that found by Verrillo (1963): a 3 dB decrease per doubling of contact area over a range of contact areas from 0.005 to 5.1 cm^2 (with a constant 1.0 mm gap between probe and surround applied at the thenar eminence). In the present study, the threshold decreased by approximately 11 dB while the contact area increased from approximately 2.07 cm^2 (FINGER) to 42.44 cm^2 (HAND), nearly a 20-fold increase in contact area. An increase of 3dB per doubling of contact area would have resulted in the HAND threshold being about 13 dB lower than the FINGER threshold. The somewhat less than expected spatial summation may be partially explained by a difference in contact pressure applied at the FINGER and at the HAND: estimated pressures at 0.48 N/cm^2 and 0.12 N/cm^2, respectively. It has been found that a decrease in contact pressure results in reduced sensitivity of Pacinian channel (Craig and Sherrick, 1969; Lamoré and Keemink, 1988; Harada and Griffin, 1991).

It may be intuitively recognized that when the contact area is increased from the FINGER to the HAND, there is an increase in the number of activated nerve fibers as well as an increased probability of exciting the most sensitive nerve fibers, and this may also offer an explanation for the somewhat lower than expected threshold at the HAND. Spatial summation via the Pacinian channel has been explained by Gescheider *et al.* (2001) in terms of neural integration and probability summation.

The term ‘neural integration’ implies an increasing number of active nerve fibers with increasing contact area, resulting in a decrease in the threshold. The term ‘probability summation’ implies that the probability of exciting the most sensitive fibers increases with increasing contact area, also resulting in a decrease in the threshold. Both terms, neural integration and probability summation, indicate an importance of the number of active fibers rather than the contact area. Mecanoreceptive nerve fibers are innervated more densely on the fingertip than on the hand: by a ratio of about 2:1 for Pacinian corpuscles between the fingers and the palm (Johansson and Vallbo, 1979a). It is therefore not reasonable to expect that a difference in threshold can be predicted solely from the difference in contact area between the HAND and the FINGER. Further, as there was no surround around the contactor at either the FINGER or the HAND, Pacinian corpuscles located over an area larger than the contact surface, such as other areas of the finger, may have been activated due to the propagation of vibration stimuli as suggested by Brisben *et al*. (1999).

There are some discrepancies between the triplex model and the estimated thresholds. For the NP I channel, the threshold curve might be expected to be a flat horizontal line (0 dB/octave, i.e., constant displacement), as demonstrated in the triplex model (Gescheider *et al*., 1985). The threshold curves for the NP I channel predicted from the present study appear to show contours with unique shapes. For the HAND, the NP I threshold curve has a slope of about -5.0 dB/octave between 16 and 31.5 Hz, although no statistically significant difference was found between the frequencies. For the FINGER, the threshold curve showed the inverse trend: no difference in threshold between 16 and 31.5 Hz then a significant decrease in threshold with increasing frequency. These findings show some agreement and some disagreement with the results of previous studies. Bolanowski *et al*. (1988) proposed a four-channel model that has the NP I characteristic with a slope of about

-5.0 dB/octave between approximately 3 and 35 Hz. Gescheider *et al.* (2001) presented a threshold curve for the NP I channel over a wide range of frequencies (0.6 – 500 Hz) with a U-shaped function having the most sensitive frequency at approximately 30 to 50 Hz. In the present study, an apparent reduction in the threshold of the NP I channel was observed below 63 Hz when changing the contact area from the FINGER to the HAND, even though the NP I channel is known to have little capability of spatial summation (Bolanowski *et al.*, 1988). Studies to elicit a response from the NP I channel (i.e. Bolanowski *et al.*, 1988; Gescheider *et al.*, 2001) have employed a surround around the contactor with a gap of 1.0 mm, which is expected to reduce NP I thresholds since sensitivity of the non-Pacinian system is increased by gradient stimuli, such as the presence of an edge (Verrillo, 1979). Johansson, Landström, and Lundström (1982b) measured afferent discharge of the FA I nerve fibers at 2, 20 and 200 Hz, both with and without an edge around a 6 mm diameter contactor (with 1 mm gap) over the glabrous skin of the hand. It was found that sensitivity was increased with the edge, with a greater increase at lower frequencies (2 and 20 Hz) than at 200 Hz. The absence of gradient stimuli with the FINGER and the HAND contact in the present experiment may have resulted in a differently shaped threshold curve for the NP I channel. There are currently no known comparable psychophysical studies of threshold curves for the NP I channel without a surround or with large contact areas (more than 2.9 cm^2). Additionally, different contact forces (i.e. static pressures) applied by the FINGER and the HAND may have contributed to the different thresholds. Lamoré and Keemink (1988) investigated the effect of static force (from 0.1 to 4.5 N) on absolute thresholds for the distal finger, the thenar eminence, and inner forearm using a 1.5 cm^2 contactor with and without a surround (1 mm gap between the contactor and the surround). It was found that an increase in static force decreased perception thresholds at frequencies above 30 Hz, while an increase in static force increased perception thresholds at frequencies below 30 Hz; it was suggested that the former phenomenon was due to the response of Pacinian channel and the latter was due to the response of the other channels.

Threshold curves for the NP II channel estimated in the current study appear to agree with the findings of some previous studies. The slopes of the NP II threshold curves for both the FINGER and the HAND were about half the slopes of the Pacinian threshold curves, which seems to be a typical characteristic of the SA II receptor: a 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). There was a reduction in the NP II threshold for the HAND compared to the FINGER at 31.5 Hz and 63 Hz, by approximately 17 and 3 dB, respectively (see Figure 9). The characteristics of the NP II channel have been identified in several studies: they are innervated in the same skin area as Pacinian corpuscles (FA II) and capable of temporal summation (Bolanowski *et al*., 1988; Gescheider *et al*., 1985), although some studies have found no temporal summation (Gescheider, 1976; Gescheider *et al*., 2001). It is not currently known if the NP II channel displays spatial summation (Bolanowski *et al*., 1988). Previous psychophysical studies have employed a small contactor with a surround in order to elicit NP II responses and minimize Pacinian responses: a 0.01 cm^2 contactor (Gescheider *et al*., 1985); and a 0.008 cm^2 contactor (Bolanowski *et al*., 1988; Gescheider *et al*., 2001).

Any spatial summation within the NP II channel could be explained by probability summation or by neural integration. Neurophysiological studies have reported that the SA II fibers have a low density over the hand, but some clustering around nails and joints (Johansson and Vallbo, 1979b; Ochoa and Torebjörk, 1983). The SA II fibers are characterized as having large receptive fields and obscure boundaries and are sensitive to tactile stimuli, particularly directional skin stretch (Johansson *et al.*, 1982a). According to a review by Pasterkamp (1999), SA II and FA II fibers are sensitive to joint movements and also have a functional role in motor control, kinesthesia and position sense. Since the HAND condition would have transmitted vibration to other areas of the hand and arm to a greater extent than the FINGER condition, there was a greater probability of activating a larger area and finding the more sensitive SA II fibers (probability summation), as well as activating a greater number of active fibers (neural integration), with the HAND condition.

In the present results, the absolute thresholds (i.e. unmasked thresholds) at the HAND were lower than the absolute thresholds at the FINGER at all frequencies: by 8.8, 17.4, 8.6 and 9.0 dB at 16, 31.5, 63 and 125 Hz, respectively (see Figure 3). The threshold contours are in good agreement with thresholds determined in previous studies with the same contact conditions and measurement methods (Morioka and Griffin, 1999; 2000). Lower thresholds with the larger contact area of the HAND than with the smaller area of the FINGER were also displayed within each of the psychophysical channels (P, NP I and NP II) at many frequencies. Such a difference is consistent with spatial summation, but not necessarily caused by spatial summation. With all three receptor channels, the difference in threshold between the FINGER and the HAND was statistically significant at 31.5 Hz, reflecting the more substantial 17.4 dB difference in absolute thresholds (i.e. unmasked thresholds) at this frequency between the FINGER AND THE HAND conditions. The increased difference between the thresholds for the HAND and FINGER in all three channels at 31.5 Hz might be a reflection of different dynamic responses in the hand-arm system and the finger-hand-arm system. These two systems will have mechanical responses that are dependent on various contact conditions, including contact force, but a resonance of the hand-arm-system in the region of 30 Hz seems possible for the contact conditions employed (Reynolds and Jokel, 1974; Reynolds and Angevine, 1977; Mishoe and Suggs; 1977; Sörensson and Burström, 1997). Possibly, vibration at 31.5 Hz was amplified by a resonance of the hand and arm in the HAND contact condition, resulting in a lowering of all thresholds at this frequency. A very different dynamic response to would be expected for the FINGER condition with, perhaps, reduced thresholds relative to HAND condition due to joint movement at the lowest frequencies (see Figure 5).

Psychophysical channels responsible for absolute thresholds at the FINGER and the HAND can be identified from the present results (see Figure 11). At 125 Hz, the Pacinian thresholds were the lowest for both the FINGER and the HAND, whereas thresholds for the NP II and NP I thresholds were about 10 and 30 dB, respectively, above the thresholds of the Pacinian channel. At 63 Hz, thresholds appear to be mediated by either the Pacinian or the NP II channel in the FINGER and the HAND conditions, depending on the sensitivity of psychophysical channel of the individual person, as can be seen in Figure 9. At 31.5 Hz, the thresholds for all three receptor channels were close together, with no significant difference in thresholds at 31.5 Hz in either contact condition (Friedman, $p > .3$). At this frequency any of the three channels could mediate absolute thresholds in both the FINGER and the HAND conditions, depending on the relative sensitivity of the three receptors in an individual subject. At 16 Hz, the NP I appeared mostly responsible for absolute thresholds with both FINGER and HAND contact conditions; the other two receptors were relatively insensitive to vibration at 16 Hz, having thresholds about 15 to 20 dB higher than the NP I thresholds.

CONCLUSIONS

Over the frequency range 16 to 125 Hz, unmasked thresholds (i.e. absolute thresholds) for the whole hand (i.e. HAND) are appreciably lower than thresholds for the distal phalanx of middle finger (i.e. FINGER).

Threshold curves for three types of psychophysical channels were estimated from masking functions of the FINGER and the HAND. The threshold curves for the Pacinian, NP I and NP II channels seem to lie within a range about 30 dB above the absolute thresholds of unmasked stimuli, and are assumed to associate with Pacinian corpuscles, Ruffini endings and Meissner corpuscles, respectively. Lower thresholds were found for the larger HAND contact than the smaller FINGER contact within the Pacinian channel for all frequencies, and also within the NP I and NP II channels at some frequencies, which may be explained by some combination of probability summation, neural integration, and biodynamic responses.

The greater sensitivity with vibration of the whole hand than vibration of the finger cannot be explained solely in terms of spatial summation of the Pacinian system (i.e. Pacinian channel). It seems that the non-Pacinian system (i.e. NP I and NP II channels) also contributed to the lower absolute thresholds on the hand.

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Table 1. *Stimulus parameters of the test and the masker*

Test	Masker	
	Frequency	Intensity
16 Hz sinusoidal	16 Hz centered 1/3 octave bandwidth vibration	0, 3, 12, 21 and 30 dBSL
31.5 Hz sinusoidal		0, 3, 6, 9, 12, 15, 18, 21, 24, 27, and 30 dBSL
63 Hz sinusoidal		
125 Hz sinusoidal		
16 Hz sinusoidal	125 Hz centered 1/3 octave bandwidth vibration	
31.5 Hz sinusoidal		
63 Hz sinusoidal		
125 Hz sinusoidal		0, 3, 12, 21 and 30 dBSL

Note. dBSL = decibels in intensity of vibration subtracted by absolute threshold of masker.

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Figure Captions

Figure 1. Two contact conditions, FINGER (distal phalanx of middle finger) and HAND (whole hand), employed in the study.

Figure 2. Stimulus timing of a 2IFC (two-interval forced-choice) trial for unmasked and the masked thresholds. The figure illustrates a test stimulus of 16 Hz with a masking stimulus of 125 Hz in which the stimulus occurred during the second stimulus observation.

Figure 3. Illustration of how the masking function for the 63 Hz test stimulus with the 125 Hz centered masker was predicted.

Figure 4. Estimation of threshold curves from masking functions.

Figure 5. Median absolute thresholds (unmasked thresholds) at the FINGER and the HAND contact conditions. Data expressed in acceleration (left graph) and displacement (right graph). Error bars represent range of thresholds from the six subjects.

Figure 6. In-channel masking function for the FINGER and the HAND conditions. Threshold shifts (in dB) are shown as a function of the masker intensity relative to perception threshold level (in dB SL) determined by 125 Hz centered masker with 125 Hz test stimulus, 16 Hz centered masker with 16 Hz test stimulus. One subject (S6) completed with 3 dB steps of masker levels.

Figure 7. Cross-channel masking function for HAND and FINGER conditions. Threshold shifts (in dB) are shown as a function of the masker intensity relative to perception threshold level (in dB SL) with selected combination of stimuli (i.e. 16 Hz centered masker with FINGER condition, 125 Hz centred masker with HAND condition). The subject legend is the same as in Figure 6.

Figure 8. Masked thresholds determined with the HAND condition for Subject 6: fitted slopes (strictly formed from either horizontal lines or a slope with gradient of

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1.0) represent masking functions to determine thresholds of Pacinian (P) and two non-Pacinian (NP I and NP II) channels. Threshold: ▲ NP I, △ NP I (estimated), ◆ P, ● NP II.

Figure 9. Threshold curves of three individual channels (P, NP II, and NP I) from six subjects determined with the FINGER and the HAND conditions.

Figure 10. Comparison of median threshold curves determined by FINGER and HAND conditions.

Figure 11. Summary of median absolute threshold curves and median threshold curves of psychophysical channels for the FINGER and the HAND conditions.

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Figure 1.

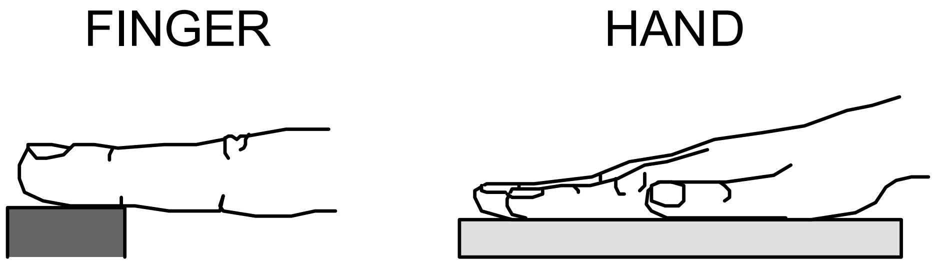

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Figure 2.

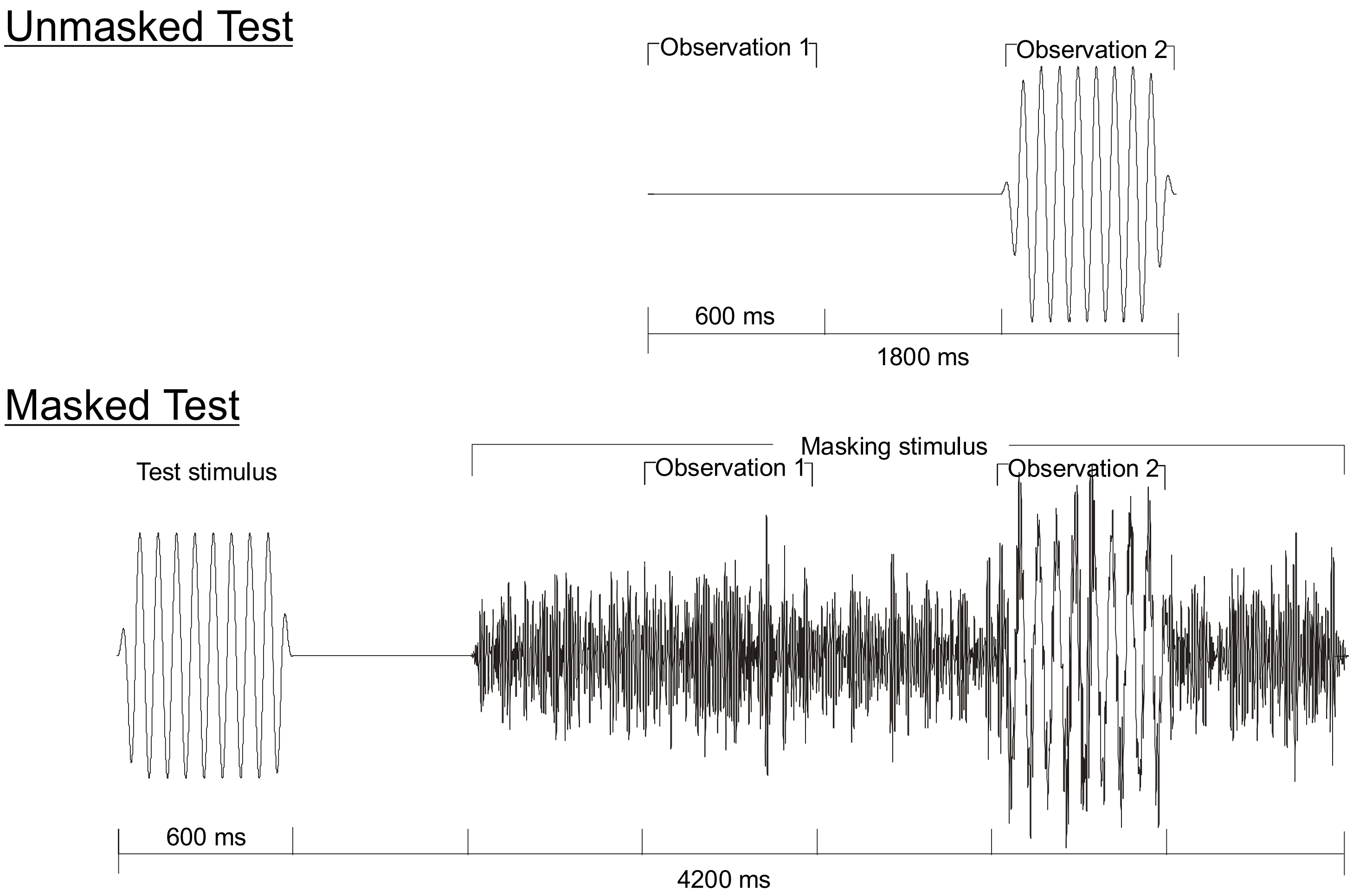
Unmasked Test
Observation 1
Observation 2
600 ms
1800 ms
Masked Test
Masking stimulus
Test stimulus
Observation 1
Observation 2
600 ms
4200 ms

Figure 3.

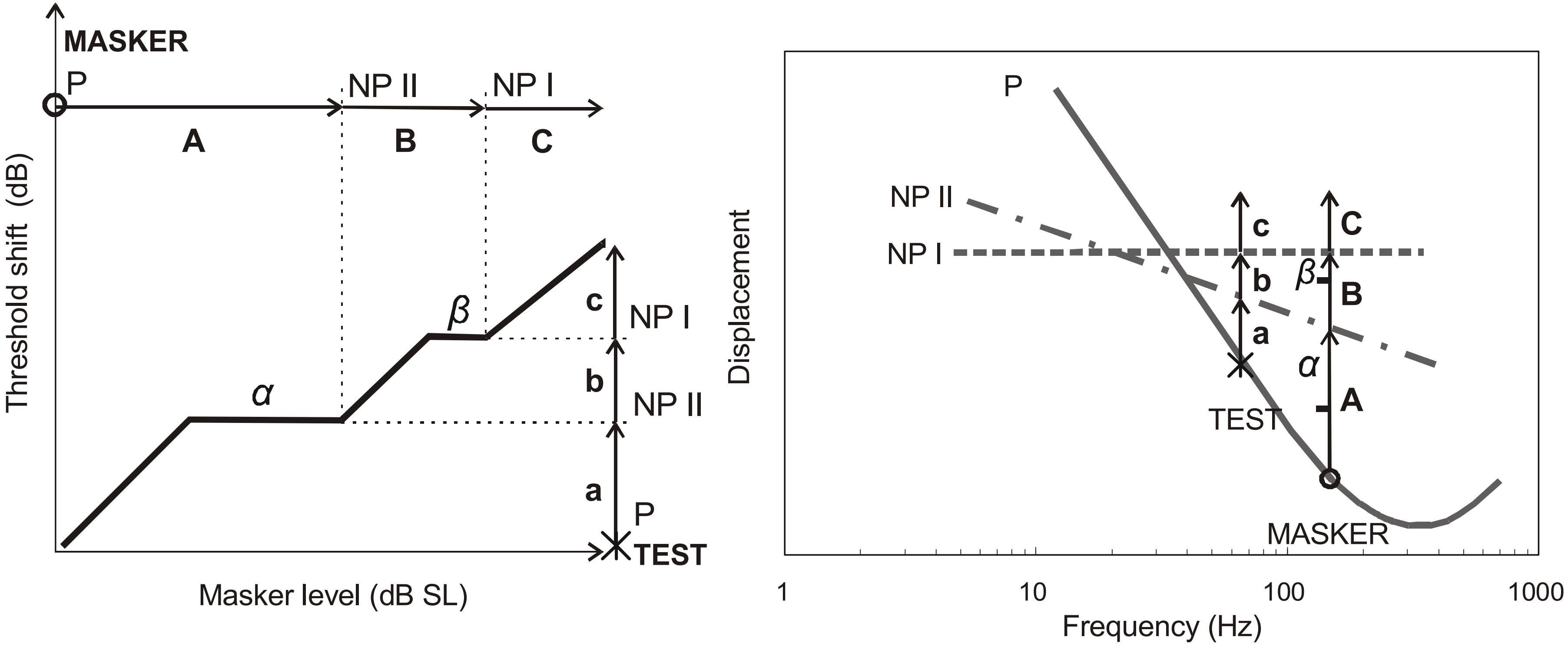
MASKER
P
NP II
NP I
A
B
C
Threshold shift (dB)
α
β
c
NP I
b
NP II
a
P
TEST
Masker level (dB SL)
P
NP II
NP I
c
C
b
β
B
a
α
A
TEST
MASKER
Displacement
1
10
100
1000
Frequency (Hz)

Figure 4.

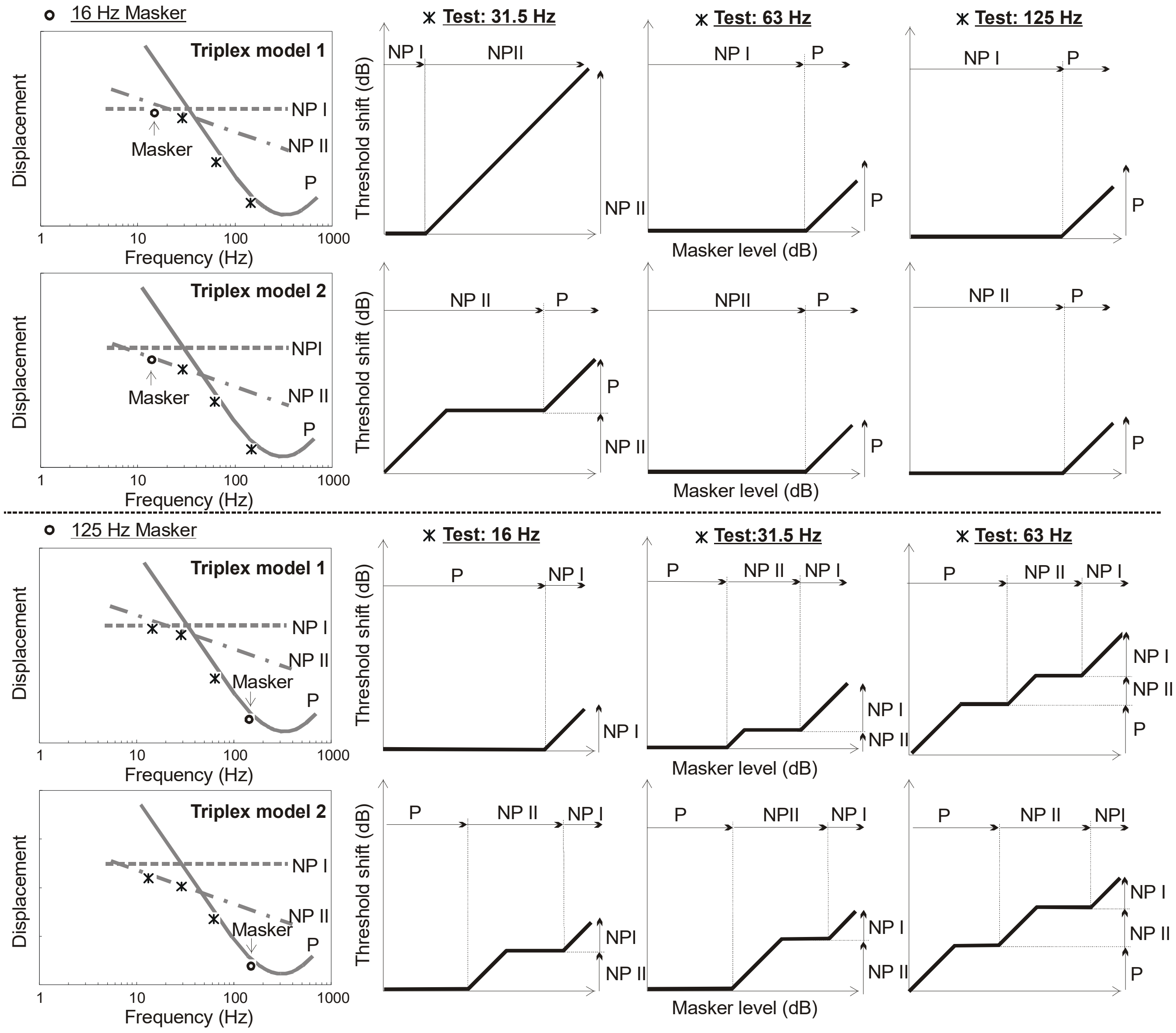

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Figure 5.

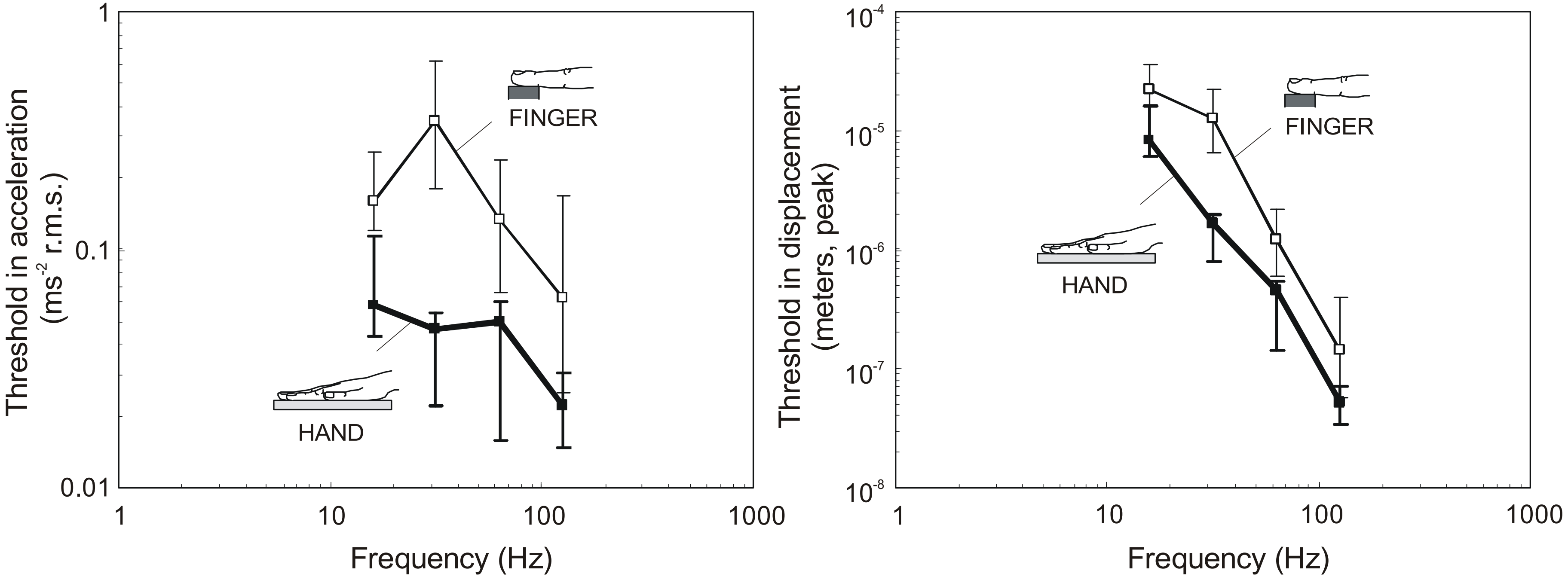

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Figure 6.

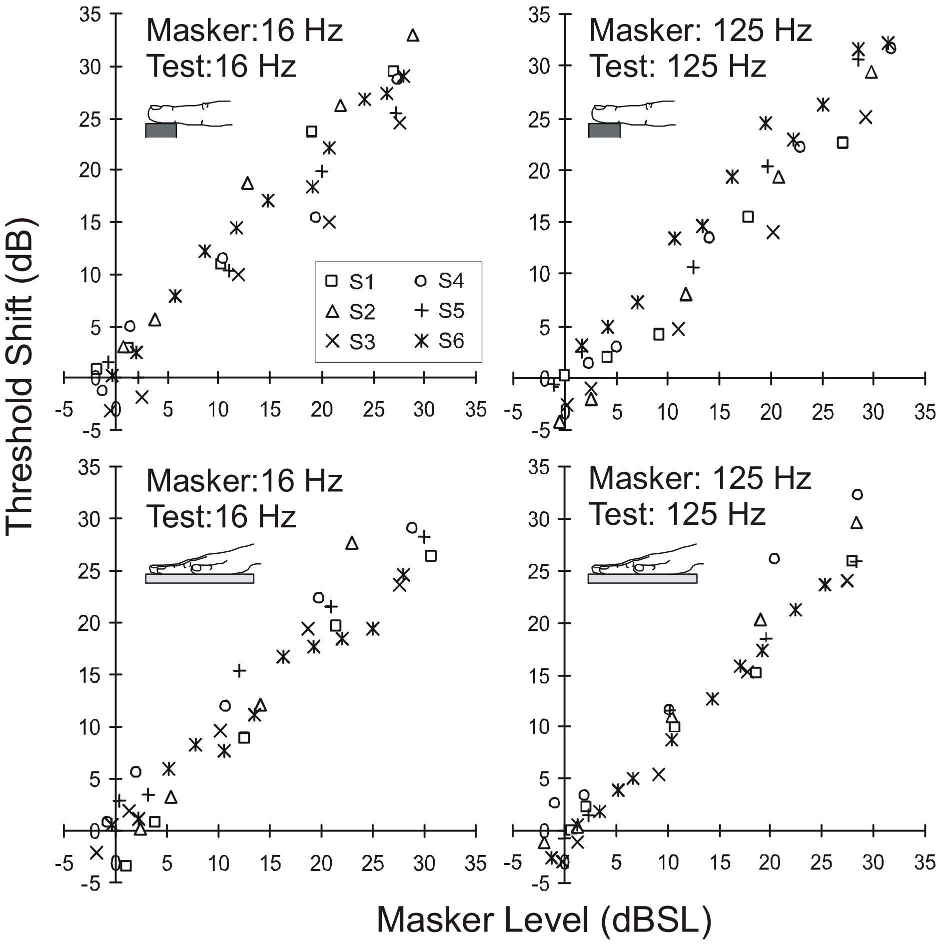
Masker:16 Hz
Test:16 Hz
Masker: 125 Hz
Test: 125 Hz
Masker:16 Hz
Test:16 Hz
Masker: 125 Hz
Test: 125 Hz
□ S1
○ S4
△ S2
+ S5
× S3
⋇ S6
Threshold Shift (dB)
Masker Level (dBSL)
-5
0
5
10
15
20
25
30
35

Figure 7.

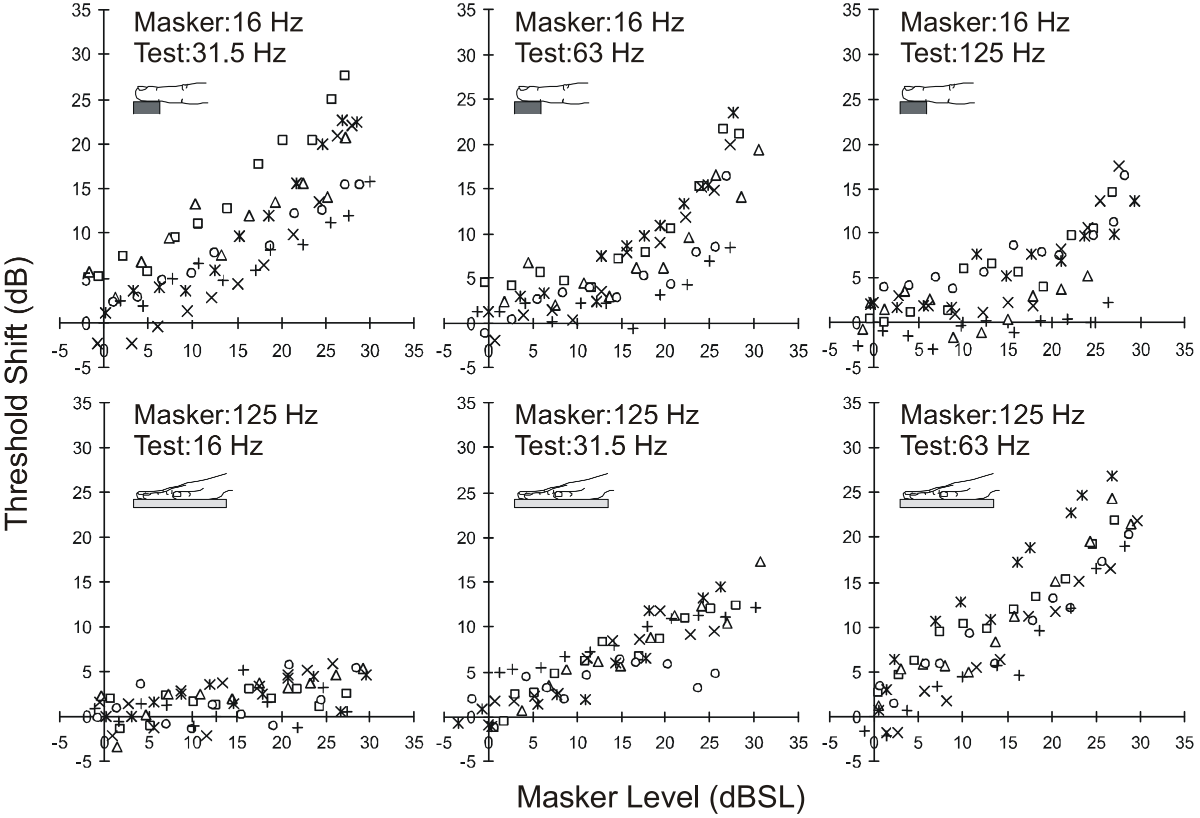
Masker:16 Hz
Test:31.5 Hz
Masker:16 Hz
Test:63 Hz
Masker:16 Hz
Test:125 Hz
Masker:125 Hz
Test:16 Hz
Masker:125 Hz
Test:31.5 Hz
Masker:125 Hz
Test:63 Hz
Threshold Shift (dB)
Masker Level (dBSL)
-5
0
5
10
15
20
25
30
35

Figure 8.

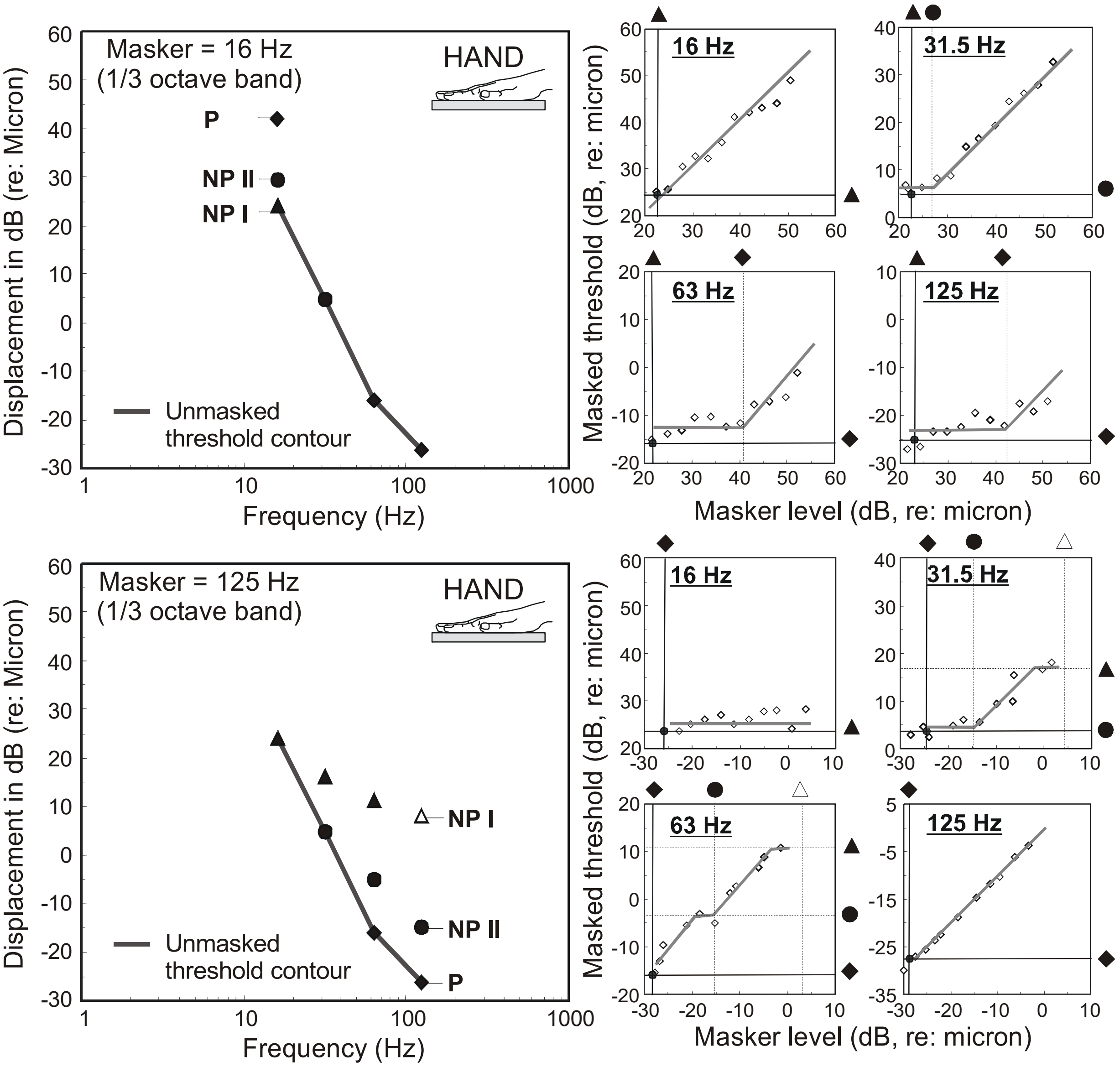

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Figure 9.

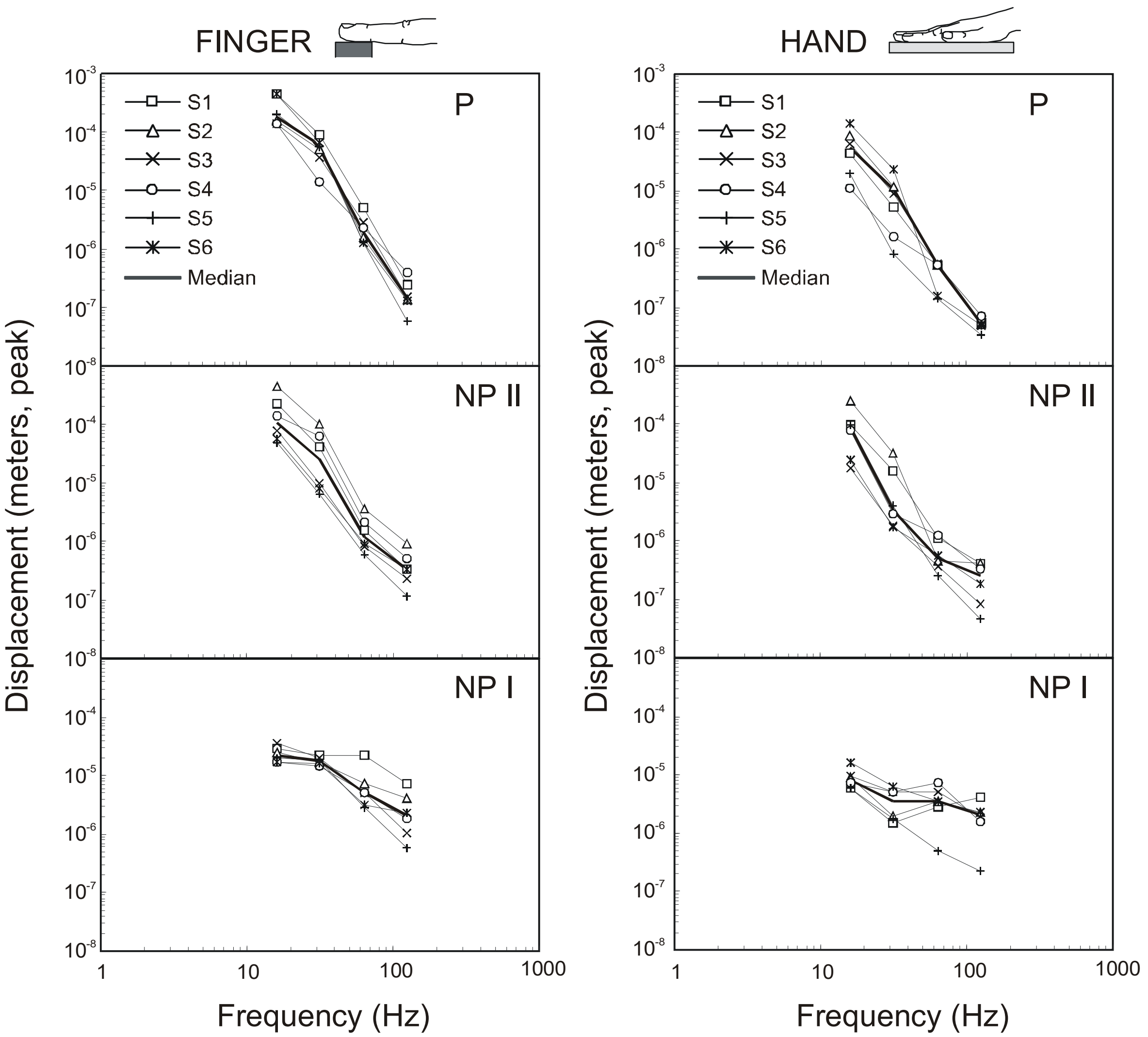

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Figure 10.

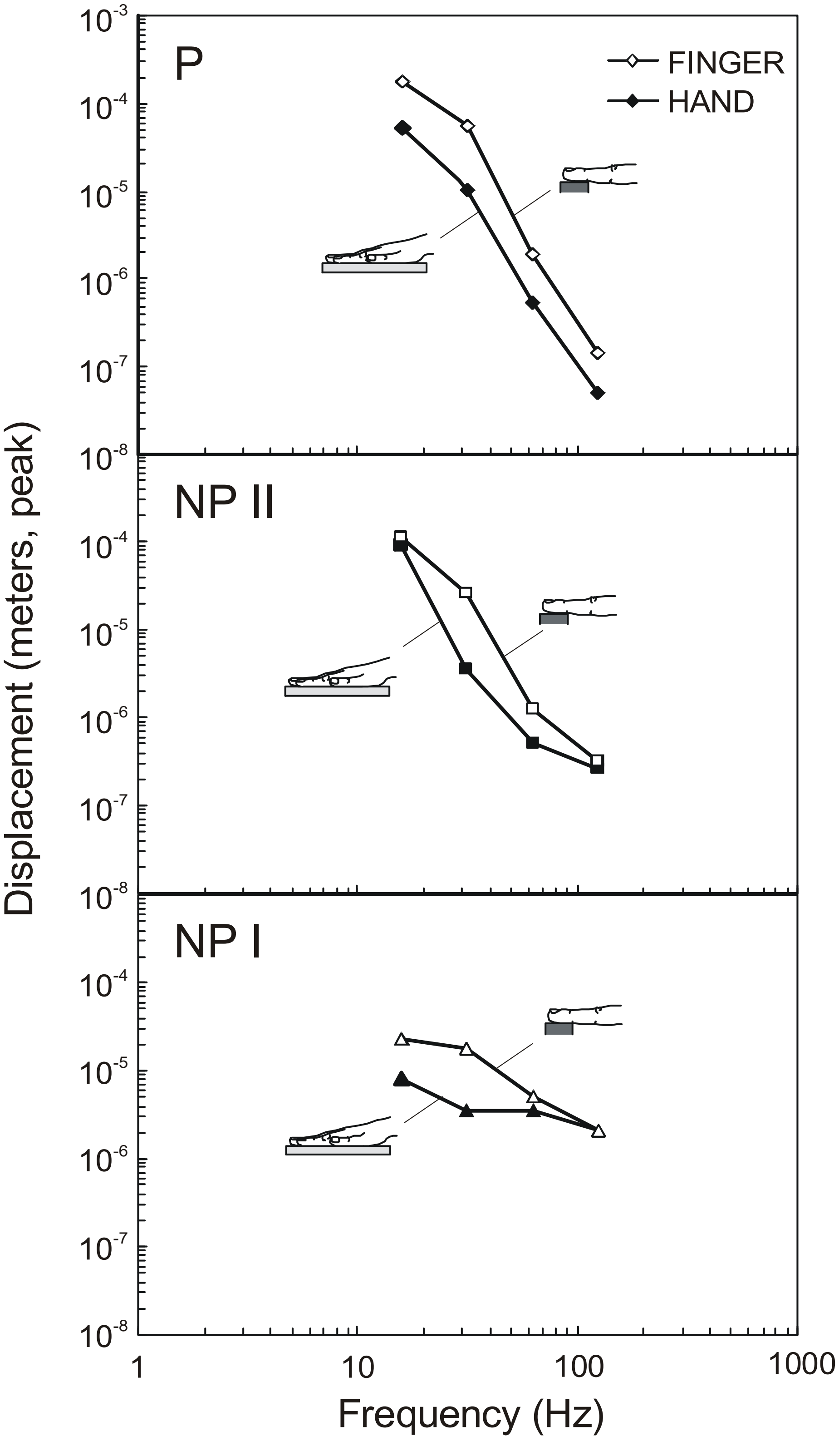
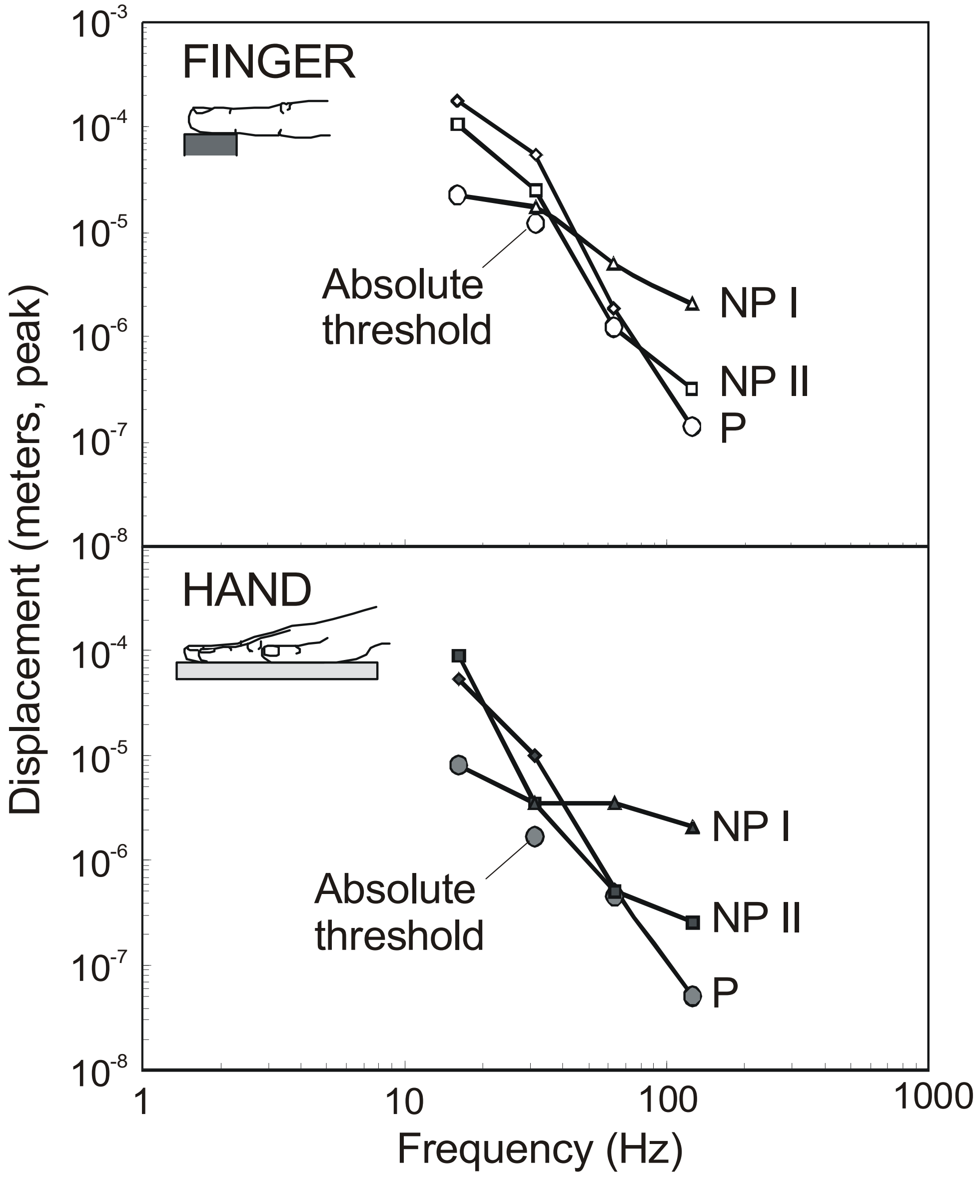

P
FINGER
HAND
NP II
NP I
Displacement (meters, peak)
10^-3
10^-4
10^-5
10^-6
10^-7
10^-8
1
10
100
1000
Frequency (Hz)

Figure 11.



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