

# Detection of Vibration Transmitted Through an Object Grasped in the Hand

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**Brisben, A. J., S. S. Hsiao, and K. O. Johnson.** Detection of vibration transmitted through an object grasped in the hand. *J. Neurophysiol.* 81: 1548–1558, 1999. A tool or probe often functions as an extension of the hand, transmitting vibrations to the hand to produce a percept of the object contacting the tool or probe. This paper reports the psychophysical results of a combined psychophysical and neurophysiological study of the perception of vibration transmitted through a cylinder grasped in the hand. In the first part of the psychophysical study, 19 subjects grasped a cylinder, 32 mm diam, with an embedded motor that caused vibration parallel to the axis of the cylinder. The relationship between threshold and frequency was the traditional U-shaped function with a minimum between 150 and 200 Hz. Except a study by Békésy in which subjects grasped a rod that vibrated parallel to the skin surface, thresholds above 20 Hz were lower and the slopes were steeper than any reported previously. Thresholds were  $<0.01 \mu\text{m}$  in some subjects. Data from both the psychophysical and the neurophysiological studies suggest that detection performance at frequencies  $>20$  Hz was based on activity in Pacinian afferents. The extreme sensitivity compared with previous reports may have resulted from differences in contact area, direction of vibration, contact force, and the shape of the stimulus probe. The effects of each of these variables were studied. At 40 and 300 Hz (frequencies near the lower and upper end of the Pacinian range) thresholds were 9.8 and 18.5 dB (68 and 88%) lower, respectively, when subjects grasped the cylinder than when a 1-mm-diam probe vibrated perpendicular to the skin. These differences were accounted for as follows: 1) thresholds at a single fingerpad obtained with the large cylindrical surface were, on average, 20 and 60% lower, respectively, than thresholds with the punctate probe; 2) thresholds at the palm were, on average, 15 and 40% lower, respectively, than at the fingerpads; 3) thresholds obtained when the subjects grasped the cylinder averaged 40 and 20% less, respectively, than when the cylinder contacted only the palm; 4) thresholds with the cylinder contacting two fingers were 10 and 30% lower, respectively, than thresholds with the cylinder contacting a single finger; and 5) thresholds with vibration parallel to the skin surface were, on average, 10 and 30% lower, respectively, than thresholds with vibration perpendicular to the skin. Contact force, which was varied from 0.05 to 1.0 N, had no effect.

## INTRODUCTION

When we have become skilled in the use of a tool or a probe, we often perceive the events at the working surface of the tool or probe as effectively as if our fingers were at that surface. Katz (1925) demonstrated this when he showed that we can discriminate some textures as effectively with a probe as with direct contact with the fingers. Further, he showed that this

capacity is based on transmitted vibrations; subjects' judgments were impaired when the transmitted vibrations were dampened. The Pacinian corpuscle is strongly implicated as the mechanoreceptor primarily responsible for the perception of transmitted vibration. This was shown initially by Hunt (1961), who used an accelerometer to show that the spontaneous discharge of a Pacinian afferent fiber was synchronized with ambient vibrations in the building where he was conducting his experiments. Indeed, a standard diagnostic procedure for identifying Pacinian responses is to tap lightly on the table holding the neurophysiological preparation. Subsequent studies linking psychophysical and neurophysiological data showed that the limits of vibratory detection at high frequencies depend on activity in Pacinian afferents (Lindblom and Lund 1966; Mountcastle et al. 1972; Verrillo 1963).

Although tactile vibratory perception has been studied extensively (Békésy 1939; Bernstein et al. 1986; Bolanowski et al. 1988; Craig 1968; Goble et al. 1996; Lamore and Keemink 1988; Lofvenberg and Johansson 1984; Mountcastle et al. 1972, 1990; Rabinowitz et al. 1987; Verrillo 1968), no previous study has addressed the perception of transmitted vibrations through an object held in the hand. Predicting the human ability to detect and discriminate transmitted vibrations with any certainty is still not possible. When we grasp an object, it contacts multiple skin sites simultaneously, vibrations may occur in any direction, the grip force is usually determined by demands of the motor task rather than the need to optimize one's sensory capacity, and there is typically no constraining surround as in many studies of vibratory detection. One of these variables, the direction of vibration relative to the skin, has not been studied at all. Thus we have undertaken combined psychophysical and neurophysiological experiments in which a manual probe, a cylinder 32 mm diam, transmits vibrations induced by a motor embedded within the cylinder.

The first experiment shows that at frequencies  $>20$  Hz thresholds are lower and the threshold-versus-frequency curves are steeper than any reported previously except those by Békésy (1939), whose stimulus procedures were similar to those used in this study. The results of the first experiment suggest that the detection performance at frequencies exceeding 20–25 Hz is based on neural activity in Pacinian afferent fibers. This interpretation is supported directly by a companion neurophysiological study in monkeys using the same stimulus procedures, which showed that only Pacinian responses could account for the detection performance at 40 Hz (unpublished observations). These data suggest that the detection of transmitted vibration over almost the entire frequency range rele-

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vant for the perception of transmitted vibration is based on activity in Pacinian afferent fibers. Four more experiments were performed to determine how contact area, contact force, direction of vibration, and the shape of the contactor affect this performance at low (40 Hz) and high (300 Hz) frequencies within the range served by Pacinian mechanisms. Except contact force, each of these factors affected detection performance.

## METHODS

Subjects were seated comfortably in front of a computer terminal. Their right arm and hand rested on a foam support mounted on the vibration isolation table (Technical Manufacturing, model 63-17595) that held the vibratory stimulator. A screen blocked the subjects' view of the apparatus and their hand. Although there was no audible signal associated with the vibratory stimuli near threshold, subjects wore headphones delivering pseudo-white masking noise (bandwidth 100 Hz to 15 kHz) to obscure any possible sounds related to the vibratory stimuli. When subjects actively grasped the stimulus (*experiments 1 and 2*), the arm and hand were unrestrained. Otherwise, the subject's right hand was restrained in a mold made of thermoplastic (North Coast Medical), which was covered with moleskin; the fingers were embedded in plasticine, and the thumb was suspended with a sling made of moleskin to keep it away from the stimulators. Skin temperature was monitored throughout the experiments and never fell below 30°C. After each stimulus trial the computer prompted the subject for a response. Subjects signaled readiness for the next trial by hitting a

key. The subjects received no feedback during any of the experiments in this study. Each experimental session consisted of two to four tasks and lasted for  $\leq 1$  h. Occasionally, subjects participated in two sessions in a single day, but in this case the sessions were separated by  $\geq 3$  h.

## Stimulators

The stimulators were mounted on the vibration isolation table. Vibratory stimuli were delivered parallel or perpendicular to the skin surface (see methods specific to each experiment). Vibratory stimuli perpendicular to the skin surface were delivered with a servo-controlled linear motor (Chubbuck 1966). Except *experiment 1*, vibratory stimuli parallel to the skin surface were delivered by the stimulator shown in Fig. 1, which consisted of an acrylic cylinder, 32 mm diam and 160 mm long, driven by a linear motor (Schneider 1988) mounted within the cylinder. The linear motor functioned as a shaker, delivering a force to the cylinder that was equal and opposite to the force required to accelerate the shaft of the linear motor. The cylinder was mounted with monofilaments, as illustrated in Fig. 1, to allow movement in the axial direction while constraining movement in the off-axial directions. This assembly was mounted on a counter-balanced pivot arm with an adjustable counterweight that allowed the contact force to be adjusted. In *experiment 1*, the cylinder was driven by the Chubbuck linear motor (Chubbuck 1966) mounted externally.

No matter which stimulator was used, the motion of the object in contact with the skin was monitored continuously by a triaxial accel-

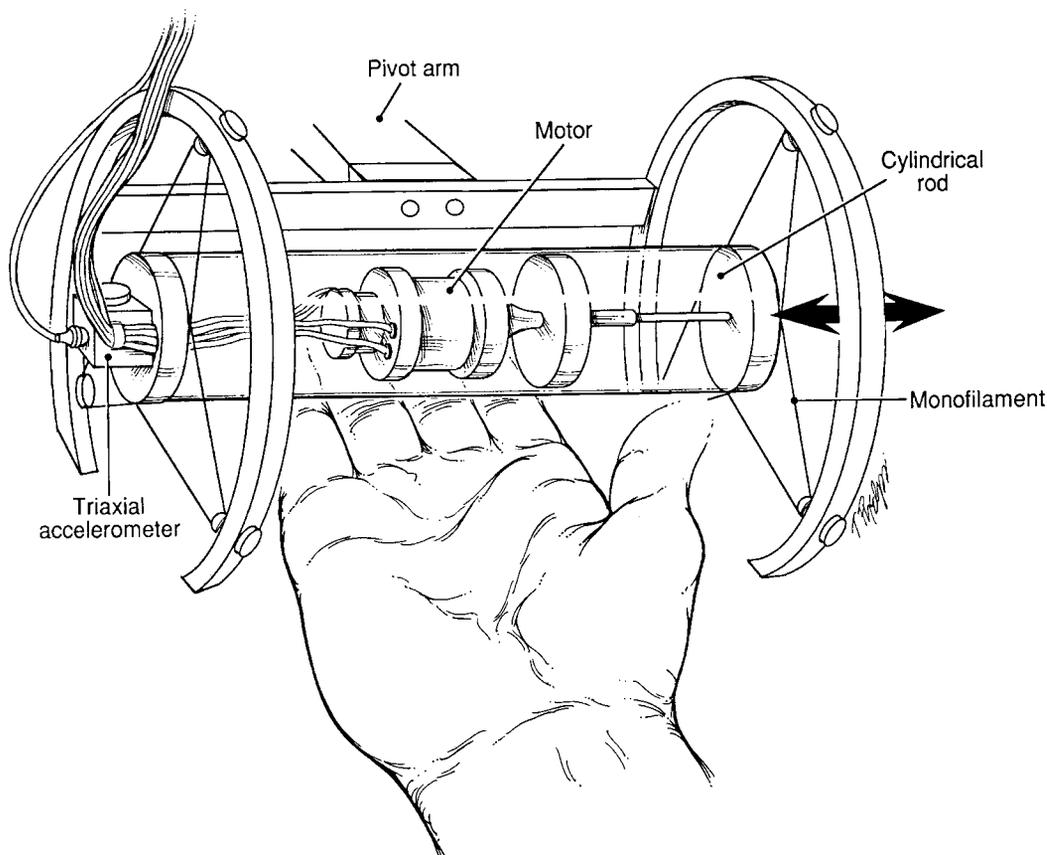


FIG. 1. Cylinder stimulator. The vibratory stimulator illustrated here consisted of an acrylic plastic cylinder (32 mm diam, 160 mm long) mounted within an open frame fixed to a counterbalanced pivot arm. The cylinder was fixed within the frame by 6 monofilament lines at each end, which allowed the cylinder to move axially over several mm but held it rigidly in all directions perpendicular to its axis. The cylinder was driven axially by the reactive force produced by a linear motor (Schneider 1988) mounted within the cylinder. The sinusoidal reactive force driving the cylinder was equal and opposite to the sinusoidal force required to drive the motor's shaft. Weights (not illustrated) attached to the pivot arm were adjusted to set the contact force on the hand. Motion in 3 dimensions was monitored by a triaxial accelerometer mounted on one end of the cylinder.

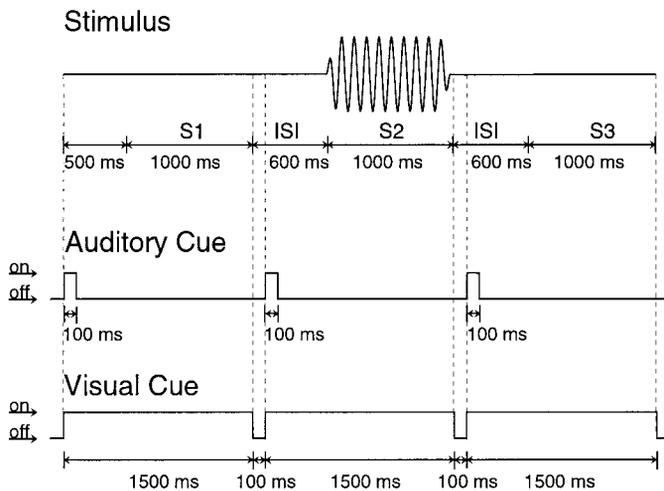


FIG. 2. Stimulus sequence within a 3-interval, forced-choice (3 IFC) trial. Shortly after hitting a key to initiate a trial, auditory (100 Hz tone for 100 ms) and visual (light-emitting diode on for 1.5 s) cues indicated the beginning of the 1st interval in which a stimulus might occur. If a vibratory stimulus occurred, it began 500 ms after the onset of the auditory and visual cues and persisted for 1 s. After 1.5 s the visual cue went off to signal the end of the period in which a vibratory stimulus might occur. After a brief pause (100 ms) the cues were repeated. After 2 (in *experiment 1*) or 3 (all other experiments) cued intervals, the subject was required to identify the interval in which the stimulus occurred by striking the number 1, 2, or 3 on a numeric keypad. The figure illustrates a 3 IFC trial in which the stimulus occurred in the 2nd stimulus interval.

erometer (Kistler, M8692B5,  $\pm 50 \text{ m} \cdot \text{s}^{-2}$  range,  $0.005 \text{ m} \cdot \text{s}^{-2}$  sensitivity, which corresponds to 80- and 1.4-nm peak displacements at 40 and 300 Hz, respectively) mounted so that one of its axes was collinear with the direction of vibration. In all experiments in which the Chubbuck linear motor was used, the accelerometer was mounted in series between the motor and the stimulus surface contacting the skin. In all experiments in which the stimulator pictured in Fig. 1 was used, the accelerometer was mounted on the end of the cylinder. Vibratory amplitudes in the off-axial directions were  $<10\%$  of the axial amplitudes in all experiments. Although both linear motors (Chubbuck 1966; Schneider 1988) had their own displacement transducers, the vibratory amplitudes reported here were derived from the accelerometer because of its greater sensitivity. When the vibratory amplitudes were large enough to register clearly on the motors' displacement transducers (amplitudes  $>1 \mu\text{m}$ ), the measurements from the accelerometer and the motors agreed.

Sinusoidal, vibratory waveforms were created with an array processor card (AP2, Tucker-Davis Technologies, TDT) and stored with a temporal resolution of 5,000 samples per second. The driving voltages for the servomotors were produced with a 16-bit D/A converter (DA3-4, TDT), a low-pass anti-aliasing filter with a 1-kHz cutoff frequency (FT5, TDT), and a programmable attenuator (PA4, TDT, 0–99.9 dB, 0.1-dB resolution).

### Psychophysical methods

Trials were initiated by the subject hitting a key. Trials consisted of two (*experiment 1*) or three (all other experiments) intervals, each 1 s long, in which the vibratory stimulus might appear. After each trial, the subject was required to choose the interval in which the stimulus occurred. A three interval forced choice (3 IFC) trial, the stimulus, and the timing of cues are illustrated in Fig. 2.

Detection thresholds were determined with adaptive tracking procedures. During each task the stimulus frequency was fixed and the amplitude varied from trial to trial based on the tracking rules. The initial stimulus amplitude was always higher than the subject's threshold. In *experiment 1*, a one-up, two-down adaptive tracking procedure

was used in which the stimulus was increased after each incorrect response and decreased after each pair of successive correct responses. In the remaining experiments, which employed a 3 IFC design, a one-up, three-down tracking rule was used because it has been shown to obtain thresholds more efficiently (Green 1990; Green et al. 1989; Kollmeier et al. 1988; Shelton and Scarrow 1984). In this method, the stimulus amplitude is increased after each incorrect response and decreased after three successive correct responses. In both methods, amplitudes were changed initially by 4 dB and then by 1 dB after three reversals. Each task continued until 12 reversals were obtained at the 1-dB step size. The threshold was estimated as the average of those last 12 reversal amplitudes. Detection thresholds obtained in this way correspond, on average, to 70.1% correct responses for the one-up, two-down procedure and 79.4% for the one-up, three-down procedure (Levitt 1970).

The 12 reversal amplitudes were also used to obtain the standard error of the estimate of the threshold. The 12 reversals provide, in pairs, 6 estimates of the threshold, the mean threshold, and the standard error of the mean. More specifically, the six pair-wise estimates of threshold were used as repeated measures in analyses of variance. All analysis was done with SPSS for Windows Version 7.0 (SPSS, Chicago, IL).

### Methods specific to each experiment

**EXPERIMENT 1: ACTIVELY GRIPPING THE CYLINDER.** In this experiment the subject was instructed to grasp a cylinder with whatever force felt most comfortable. The forces actually used were not measured, but subjects reported using a light-to-moderate force. The cylinder was suspended by filaments as in Fig. 1 but was driven axially by the Chubbuck linear motor, which was attached at one end. Most of the glabrous skin of the hand was in contact with the cylinder during this experiment. The experimental design, described above, was a 2 IFC design, and a one-up, two-down adaptive tracking rule was used to find the threshold.

**EXPERIMENT 2: EFFECT OF STIMULUS LOCATION WITH THE CYLINDRICAL STIMULATOR.** This experiment employed the stimulator illustrated in Fig. 1 and had two parts. In the first part, subjects grasped the cylinder actively as in *experiment 1*, the purpose being to repeat and verify the results of *experiment 1* with the newer stimulator and the 3 IFC psychophysical design. In the second part, subjects' hands were restrained (see general methods above) in an open, palm-up position, while the cylinder rested on the skin with a 0.5-N contact force; that is, vibratory stimuli are delivered under passive conditions.

The contact area associated with each of the different stimulus placements was measured by coating a subject's hand with blotting ink and lowering the cylinder onto the skin, which transferred the ink to the surface of the cylinder. The cylinder was raised, and a piece of paper was wrapped around it to obtain an impression of the contact area. The cylinder was then cleaned with isopropyl alcohol, and the procedure was repeated for each stimulus condition presented in this experiment. The resulting ink blots were placed on a digitizing sketch pad (Summa Sketch, Summagraphics) and digitized with a software graphics program (AutoCAD, Autodesk), which calculated the contact areas.

**EXPERIMENT 3: EFFECT OF CONTACT FORCE.** *Experiment 3* was conducted with the cylinder illustrated in Fig. 1, and the hand was restrained as in *experiment 2*. Vibratory detection thresholds were obtained for five contact forces: 0.05, 0.1, 0.2, 0.5, and 1.0 N. At 1.0 N the force is light but firm. Contact force was set by adjusting a counterweight at the opposite end of the pivot arm on which the cylinder was mounted. The force applied by the cylinder was measured with a digital force gauge (Omega Engineering).

**EXPERIMENT 4: EFFECT OF STIMULUS LOCATION WITH THE PUNCTATE PROBE.** The purpose of *experiment 4* was to compare thresholds obtained with the cylinder in *experiment 2* with thresholds

obtained with a punctate probe at the same stimulus sites. The subjects, the hand restraint, and the procedures were the same as in *experiment 2*. The punctate probe was made of Delrin (Dupont), was 1 mm diam at the tip, and was mounted on the Chubbuck linear motor (Chubbuck 1966). The tip of the punctate probe was glued to the skin surface (Freeman and Johnson 1982), and the indentation depth was adjusted until there was no reaction force (so the skin vibrated around its resting position without harmonic distortion).

**EXPERIMENT 5: EFFECTS OF STIMULUS DIRECTION AND CONTACT AREA.** Two probes, a cylindrical surface and a punctate probe, 1 mm diam, were used in *experiment 5*. The cylindrical surface was constructed from the same stock used to make the cylinder in *experiment 2* (acrylic plastic, 32 mm diam) and was mounted on the shaft of the Chubbuck motor. The axis of the cylinder was perpendicular to the motor shaft so the surface of the cylinder contacting the skin vibrated in a direction perpendicular to the skin surface. Indentation depth was set to produce a reaction force of 0.2 N. The punctate probe was identical to the probe used in *experiment 4* (a Delrin shaft machined to a tip, 1 mm diam) and was clamped to the cylinder illustrated in Fig. 1 with a Delrin collar. The punctate probe's shaft was mounted perpendicular to the axis of the cylinder and oriented so that it was perpendicular to the skin. As in *experiment 4*, the punctate probe was glued to the skin, and the pivot arm was balanced to produce no net force on the skin. Activation of the motor within the cylinder produced motion parallel to the skin surface.

*Gluing the probe to the skin.* The purpose of gluing the probe to the skin was to ensure that the differences in threshold between the cylinder and the punctate probe (*experiment 4*) and between vibration perpendicular and parallel to the surface of the skin (*experiment 5*) did not arise because the skin did not follow the sinusoidal motion of the probe when vibrated perpendicular to the skin surface. When the cylinder and punctate probe vibrate parallel to the skin surface, they remain in constant contact with the skin; consequently, the stimulus energy is confined to the fundamental frequency being tested. When a probe vibrates perpendicular to the skin surface, it may or may not remain in contact with the skin throughout each sinusoidal cycle (Goodwin et al. 1989). If it does, there is no problem, and the presence or absence of the glue is irrelevant. If it does not, the skin displacement profile is not sinusoidal, the displacement amplitude at the fundamental frequency is decreased, and harmonic frequencies are introduced. The first effect (diminished displacement amplitude at the fundamental) will raise the threshold. The second effect (the introduction of stimulus energy at multiple of the fundamental frequency) may decrease the threshold when the higher harmonics fall at more

sensitive frequencies. Gluing the skin to the probe ensured that the motion was sinusoidal under all conditions. Note that this causes the probe to pull the skin upward *only if* the probe would otherwise have lifted off the skin. The vibratory amplitude was very small at threshold, so partial skin following may not have been a problem even if we had not glued the skin. In that case the glue had no effect. However, having glued the skin to the probe, we can be assured that the effects observed in *experiments 4* and *5* are not due to a simple biomechanical factor like the introduction of harmonic distortion because of failure to follow the probe.

## RESULTS

The experimental designs are summarized in Table 1. In the first experiment, vibratory thresholds were determined for 19 subjects who actively grasped a cylinder vibrated in a direction parallel to the skin. The thresholds were lower than those obtained previously with probes vibrated perpendicular to the skin surface (e.g., Bernstein et al. 1986; Gescheider et al. 1994; Lamore and Keemink 1988; Mountcastle et al. 1972; Rabinowitz et al. 1987; Verrillo 1968). Factors that may have resulted in the lower thresholds are studied in *experiments 2–5*. The effect of stimulus location is studied in *experiments 2* and *4*. The effect of stimulus type (cylinder or punctate probe) is studied in *experiments 4* and *5*; the effect of task mode (active or passive), contact area, and stimulus location are studied in *experiment 2*; the effect of contact force is studied in *experiment 3*; and the effect of stimulus direction is studied in *experiment 5*. The same four subjects participated in *experiments 2–5* to make within-subject comparisons possible.

### *Experiment 1: actively gripping the cylinder*

The purpose of this experiment was to determine the human capacity to detect transmitted vibration when grasping a cylinder whose size and shape (32 mm diam, 160 mm long) were much like the handle of a common tool (e.g., a screwdriver) or probe (e.g., a cane). A relatively large number of subjects were studied to obtain a representative sample of this human capacity; 19 subjects (11 male, 8 female, ages 21–45) participated in this experiment. Figure 3 illustrates the average thresholds at

TABLE 1. *Experimental designs*

Experiment	Description	Number of Subjects	Method	Frequencies	Contact Force	Active/Passive	Probe	Direction of Vibration	Placement
1	Active grip	19	2IFC	10, 20, 30, 40, 60, 100, 150, 200, 300 Hz	N/A	Active	Cylinder	Parallel	Grip (entire hand)
2	Skin locus	4	3IFC	40, 300 Hz	Active, N/A; passive, 0.5 N	Active and passive	Cylinder	Parallel	D3d, D3m, D3p, D34d, D34m, D34p, palm-d, palm-p, grip (entire hand)
3	Contact force	4	3IFC	40, 300 Hz	0.05, 0.1, 0.2, 0.5, 1.0 N	Passive	Cylinder	Parallel	D3d, palm-d
4	Skin locus	4	3IFC	40, 300 Hz	0 N	Passive	Punctate	Perpendicular	D3d, D3m, D3p, palm-d, palm-pl, palm-pm
5	Direction of vibration	4	3IFC	40, 300 Hz	Punctate, 0 N; cylinder, 0.2 N	Passive	Cylinder and punctate	Punctate, parallel; cylinder, perpendicular	D3d

2IFC, two-interval forced choice response; 3IFC, three-interval forced choice response; D3, digit 3; D34, digits 3 and 4; d, m, and p, distal, middle, and proximal, respectively.

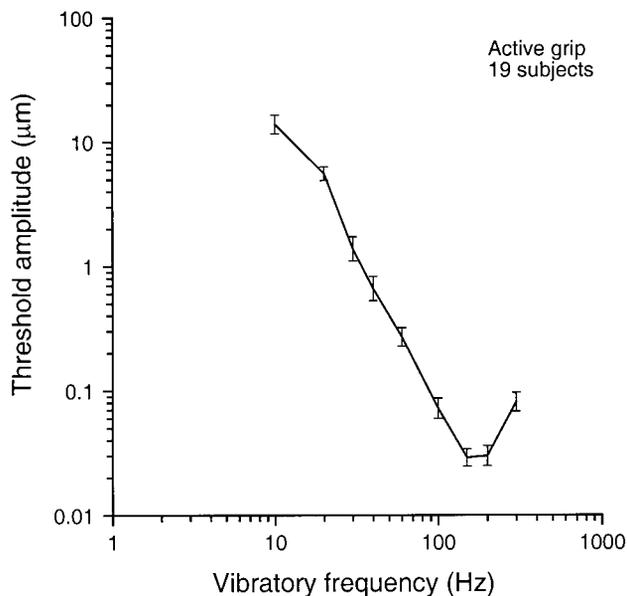


FIG. 3. Active grip: detection threshold vs. vibratory frequency. Nineteen subjects lightly gripped a cylinder similar to the one shown in Fig. 1. The ordinate displays the mean threshold (half the peak-to-peak excursion). The error bars represent standard errors of the means.

frequencies ranging from 10 to 300 Hz. The threshold was 14  $\mu\text{m}$  at 10 Hz, declined to 5.6  $\mu\text{m}$  at 20 Hz, and then reached a minimum of 0.03  $\mu\text{m}$  at 150 and 200 Hz. The decline in threshold was 85% per frequency doubling ( $-15.7$  dB per octave) between 20 and 150 Hz. The slope and magnitudes of the thresholds illustrated in Fig. 3 are nearly identical with those reported by Békésy in experiments where subjects grasped a rod vibrating parallel to the skin surface (Békésy 1939) ( $-15.4$  dB per octave slope and 0.03  $\mu\text{m}$  threshold at 200 Hz). Apart from Békésy's results, the slope is steeper and the minimum threshold is lower than any in the literature. We surmised that this may be attributed to differences in contact mode (active vs. passive), stimulus location on the hand, contact area, the direction of vibration, or the force of application. We explored each of these potential factors in *experiments 2–5*.

#### *Experiment 2: effect of stimulus location with the cylindrical stimulator*

Four subjects (2 male, ages 19 and 26, and 2 female, ages 27 and 34) participated in this and the remaining experiments (*experiments 2–5*). In this experiment and the remaining experiments, the data are displayed on logarithmic coordinates, means are geometric means, and the analyses were done on the logarithms of the thresholds. Every analysis includes a factor for individual subjects so that differences between subjects are not counted as random variation; this makes each analysis more sensitive to the stimulus parameter being varied. Differences between subjects were statistically significant in all tests ( $P < 0.01$ ).

*Experiment 2* employed the stimulator shown in Fig. 1. Stimuli were applied under passive conditions (0.5 N force, see METHODS) to eight different sites: three on the middle finger (distal: D3d; middle: D3m; and proximal phalanx: D3p), three on the middle and ring fingers combined (distal: D34d; middle: D34m; and proximal phalanges: D34p), and two on the palm

(Palm-d and Palm-p, see Fig. 4). Subjects also grasped the cylinder actively, as in *experiment 1*, so the data from the four subjects in *experiments 2–5* could be compared with the larger group that participated in *experiment 1*. The mean contact areas at each site are listed in Fig. 4.

The average thresholds are shown in Fig. 4. All the analyses of statistical significance were based on ANOVA. At 40 Hz, the threshold at the middle phalanx was significantly greater than the rest, and the threshold resulting from the active grip was less than the rest ( $P < 0.05$ ). Apart from that, the differences between conditions shown in Fig. 4 failed to reach significance ( $P > 0.05$ ). At 300 Hz, the threshold was lowest when the subjects grasped the cylinder, next lowest when the cylinder contacted the palm, and then rose as the cylinder moved away from the palm on the fingers. All these differences were highly significant ( $P < 0.01$ ).

When two phalanges were stimulated, the thresholds were, on average, lower than when only a single phalanx was stimulated (see Fig. 4). Because the force rather than the pressure was held constant, the areal increase averaged 44% rather than 100%. This resulted in an average drop in threshold of 1.55 dB ( $-0.7$  dB at 40 Hz;  $-2.4$  dB at 300 Hz), which is equivalent to 2.95 dB drop per doubling in contact area.

#### *Experiment 3: effect of contact force*

The effects of contact force (see Fig. 5) were evaluated at the distal phalanx of the middle finger (D3d in Fig. 4) and the distal part of the palm (Palm-d in Fig. 4). Contact force was varied in five steps from 0.05 to 1.0 N. Overall, contact force had no significant effect. The regression slope of the logarithm of threshold on the logarithm of force yielded positive coefficients in two of the four conditions and negative coefficients in the other two conditions. In one case (300 Hz, Palm-d) the slope was statistically significant ( $-0.8$  dB per doubling of contact force,  $P < 0.05$ , *t*-test), but when corrected for multiple comparisons it was not significant. These results suggest that contact force played little, if any, role in the detection performance measured in *experiment 1*.

#### *Experiment 4: effect of stimulus location with the punctate probe*

The aim of *experiment 4* was to compare thresholds obtained with the cylinder in *experiment 2* with thresholds obtained with a punctate probe at the same stimulus sites. Figure 6, *A* and *B*, show the results of *experiment 4*. On average, the punctate thresholds on the fingers were lower at 40 Hz and higher at 300 Hz than the thresholds on the palm, but the difference was only significant at 300 Hz (ANOVA,  $P = 0.002$ ). The more interesting comparison, however, is the comparison between thresholds with the two kinds of probes, which is illustrated in Fig. 6, *C* and *D*. The punctate thresholds were significantly greater than the thresholds with the cylinders at both the fingers and the palm ( $P < 0.001$ , *t*-test). At 40 Hz, the difference was significantly greater on the palm (9.0 dB on average) than on the fingers (3.1 dB on average; ANOVA,  $P = 0.014$ ). At 300 Hz, the difference, which averaged 9.2 dB, did not depend on location in any significant way.

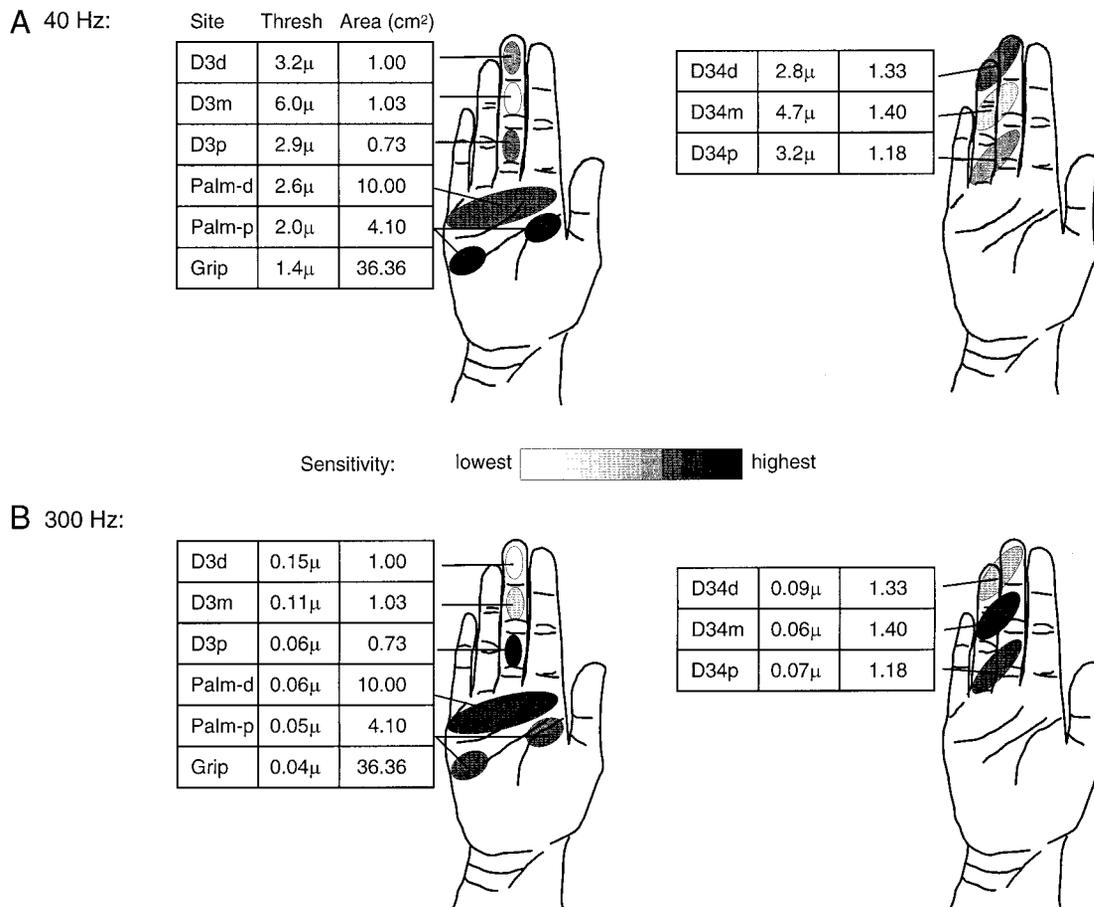


FIG. 4. Vibratory threshold vs. contact location and area. The cylinder displayed in Fig. 1 was either gripped or placed against the passive hand in 1 of 8 locations (D3 = digit 3; D34 = digits 3 and 4; d, m, and p = distal, middle, and proximal, respectively). Thresholds in the A and B represent thresholds at 40 and 300 Hz, respectively. The 1st column in each table represents the stimulus location; the 2nd column lists the geometric mean threshold (4 subjects); the 3rd column lists the contact areas.

#### Experiment 5: effects of vibratory direction and contact area

The cylinder was vibrated parallel to the skin surface in *experiment 3*; the punctate probe was vibrated perpendicular to the skin surface in *experiment 4*. The other two conditions required of a balanced  $2 \times 2$  factorial experiment designed to determine the effects of contact area and vibratory direction (cylinder vibrated perpendicular to the skin surface and punctate probe vibrated parallel to the skin surface) are investigated in *experiment 5*. One of these conditions was effected by mounting a cylinder segment (same diameter as the cylinder illustrated in Fig. 1) on the shaft of a linear motor and by vibrating it perpendicular to the skin. The other condition (punctate probe vibrated parallel to the skin surface) was effected by attaching a punctate probe with the same dimensions as the probe used in *experiment 4* to the cylinder (Fig. 1) and vibrating it parallel to the skin surface. The probe was glued to the skin to ensure skin movement comparable with that in *experiment 4*. *Experiment 5* was performed on D3d at 40 and 300 Hz.

The data are displayed in Fig. 7. Thresholds obtained with the cylinder at 40 Hz were, on average, 23% (2.3 dB) lower than the punctate thresholds; thresholds obtained with vibration parallel to the skin surface were, on average, 14% (1.3 dB) lower than the thresholds obtained with perpendicular vibration. At 300 Hz, the effects of probe type and vibratory

direction were similar but larger, being 61% (8.2 dB) and 32% (3.3 dB), respectively. Only the relationship between probe type and thresholds was statistically significant at 300 Hz ( $P = 0.04$ , 2-way ANOVA of threshold vs. direction and stimulus type). Thus we infer that stimulus direction has a small effect at both low and high frequencies and that the differences between thresholds obtained in *experiments 3* and *4* are primarily attributable to differences in contact area.

#### DISCUSSION

The first experiment in this study was aimed at determining the human capacity to detect transmitted vibration when grasping a cylinder whose size and shape were much like the handle of a common tool (e.g., a screwdriver) or probe (e.g., a cane). The result was that the detection thresholds were lower than any reported previously except those by Békésy (1939), who also had subjects grip a probe actively between the fingertips. As in Békésy's experiment, the cylinder vibrated parallel to the skin surface, and the subjects were free to adopt a grip force that seemed most comfortable. The mean thresholds at 10 and 20 Hz were comparable with thresholds observed in previous studies in which a probe contacted the skin without a constraining surround (Békésy 1939; Mountcastle et al. 1972; Van Doren 1990) and were higher than those observed in some studies in which an annulus surrounded the vibrating probe

(Bernstein et al. 1986; Lamore and Keemink 1988). At frequencies above 30 Hz, however, the mean thresholds in *experiment 1* (e.g., 0.66  $\mu\text{m}$  at 40 Hz and 0.03  $\mu\text{m}$  at 200 Hz) are as low or lower than any reported previously. The difference is most pronounced at 40 Hz where the thresholds were 6–18 dB lower than any reported previously (Békésy 1939; Bernstein et al. 1986; Lamore et al. 1986; Mountcastle et al. 1972; Rabinowitz et al. 1987; Verrillo et al. 1983). Between 20 and 150 Hz, the thresholds in *experiment 1* dropped at 15.7 dB per octave; in Békésy's (1939) experiments, thresholds dropped at 15.4 dB per octave over the same range. The average peak sensitivity reported here, 0.03  $\mu\text{m}$  (0.02  $\mu\text{m}$  root-mean-square) detection threshold at 200 Hz, is the same as that reported by Békésy and is lower than that reported in other studies (e.g., Bernstein et al. 1986; Gescheider et al. 1994; Lamore and Keemink 1988; Mountcastle et al. 1972; Rabinowitz et al. 1987; Verrillo 1968). The minimum threshold for some subjects was  $<0.01 \mu\text{m}$ , which represents a vibratory excursion at the skin surface not much greater than the thickness of a cell membrane.

*Experiments 2–5* were designed to examine the factors yielding this sensitivity. In these experiments we varied contact area, stimulus location, contact force, probe shape, and stimulus direction. The results are summarized in Fig. 8, where the stimulus conditions A–H are arranged in order of decreasing thresholds at both 40 and 300 Hz. Between the condition with the highest threshold (vibration perpendicular to the skin of the pad of the 3rd digit with a 1-mm-diam probe) and the lowest threshold (subjects actively gripping a 32-mm-diam cylinder

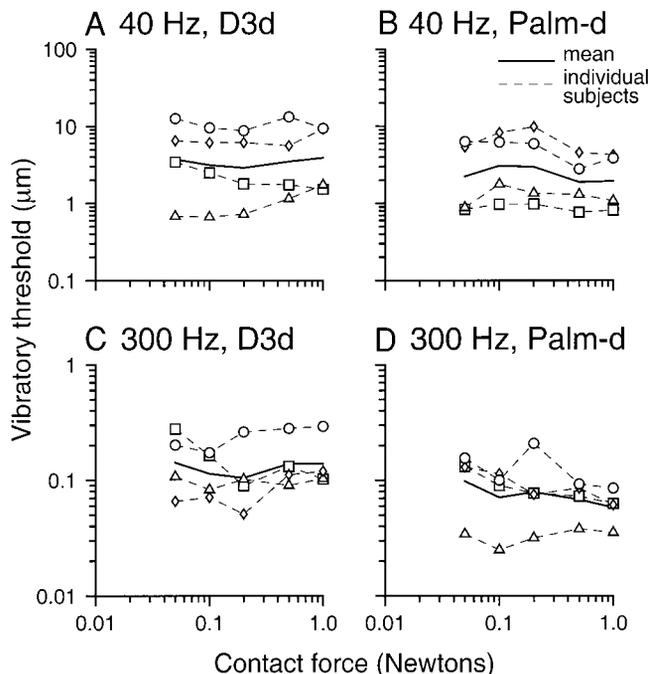


FIG. 5. Effect of contact force on detection thresholds at 40 and 300 Hz. Ordinates represent vibratory thresholds ( $\mu\text{m}$  zero-to-peak). The abscissas represent contact forces (Newtons). A and C: results from stimulus application at the distal phalanx of the 3rd digit (D3d). B and D: results from stimulus application at the the distal part of the palm (Palm-d; see Fig. 4). A and B: results from experiments with 40-Hz stimuli. C and D: 300-Hz stimuli. In this and all other figures in which data from individual subjects are shown, dashed lines represent thresholds from individual subjects ( $\square$ , AJB;  $\triangle$ , CMJ;  $\diamond$ , DCE;  $\circ$ , DTB), and the solid lines represent the geometric mean thresholds across subjects.

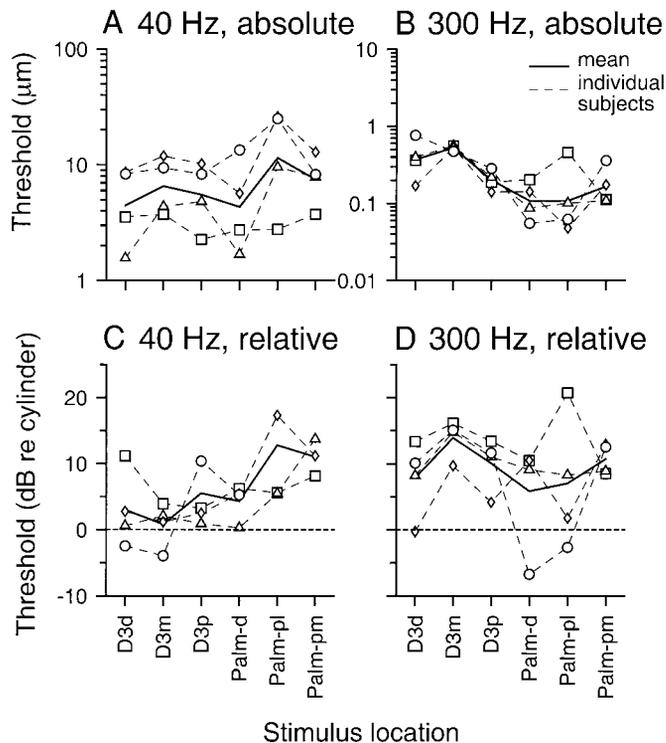


FIG. 6. Punctate thresholds. The abscissas of all graphs represent stimulus location (see Fig. 4). Palm-pm and palm-pl represent the medial and lateral palm-p regions illustrated in Fig. 4. The ordinates of A and B represent vibratory thresholds ( $\mu\text{m}$  zero-to-peak) obtained with a punctate probe vibrating in a direction perpendicular to the skin surface. The ordinates of C and D represent the differences between the thresholds obtained with the punctate probe and the cylinder (Fig. 4). Symbols represent the same subjects as in Fig. 5.

vibrating parallel to the skin surface), the thresholds at 40 and 300 Hz dropped by 9.8 and 18.5 dB, respectively. The factors that were examined contributed in varying degree to the gradual decline in threshold across the various stimulus conditions represented in Fig. 8. Contact force had no effect over the range tested. Direction of vibration had a small effect: vibration parallel to the skin surface produced thresholds at 40 and 300 Hz that were 1.3 and 3.3 dB lower, respectively, than with vibration perpendicular to the skin surface. Contact area, probe type, and stimulus location had the major effects.

#### Neural mechanisms

Vibratory detection has been studied extensively. The large number of studies of vibratory detection results from the large number of variables that can affect vibratory perception: vibratory frequency, duration, direction, contact geometry, contact area, contact force, state of adaptation, context (e.g., masking), mode (active vs. passive), skin site, skin temperature, age, and pathology. The results of these many studies are accounted for well by the hypothesis that vibratory detection depends on some critical level of activity in Pacinian afferents at high frequencies (Lindblom and Lund 1966; Talbot et al. 1968; Verrillo 1963) and in a separate set of afferents at low frequencies (Verrillo 1963), which have been identified as Meissner afferents (Mountcastle et al. 1972).

The result of this dual mechanism is a curve of threshold-versus-frequency with two limbs (Békésy 1939; Talbot et al.

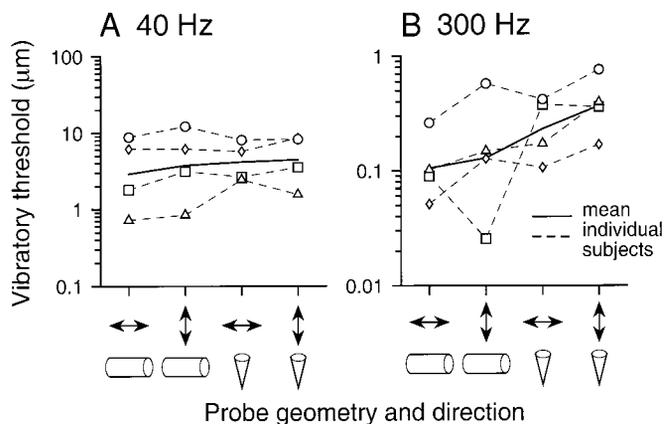


FIG. 7. Effects of probe geometry and vibration direction. The data represent thresholds obtained in a 3-way design involving all 8 combinations of 2 contactor types (punctate probe and 32 mm diam cylinder), 2 vibratory directions (parallel and perpendicular to the skin), and 2 vibratory frequencies (40 and 300 Hz). *A*: 40-Hz thresholds. *B*: 300-Hz thresholds. In *A* and *B* the ordinate represents the vibratory threshold ( $\mu\text{m}$ , zero-to-peak). The abscissas represent the stimulus conditions; from left to right they are 1) a cylinder vibrated in a direction parallel to the skin surface (Fig. 1), 2) a cylinder vibrated in a direction perpendicular to the skin surface, 3) a 1-mm-diam punctate probe oriented perpendicular to the skin but vibrated in a direction parallel to the skin surface, and 4) the same punctate probe vibrated in a direction perpendicular to the skin surface. Symbols represent the same subjects as in Fig. 5.

1968; Verrillo 1968) whose intersection defines the transition frequency between the regions dominated by Meissner and Pacinian afferents. The high-frequency limb is steeper than the low-frequency limb; therefore changes in the stimulus that modify Meissner or Pacinian engagement (e.g., contactor area) have a predictable effect on the transition frequency (Gescheider et al. 1978; Goble et al. 1996; Lamore and Keemink 1988; Talbot et al. 1968; Verrillo 1963). Most important in relation to the present study is the demonstration by Verrillo (1963) that increasing vibratory contact area produces increasing vibratory sensitivity in the high-frequency region, which drives the transition point between the Meissner and Pacinian domains to lower frequencies.

We believe that the transition frequency between the Meissner and Pacinian domains in *experiment 1* was 20–25 Hz. Threshold slope changes by 2:1 at 20 Hz (see Fig. 3); the

slopes below and above 20 Hz were 7.9 and 15.7 dB per octave, respectively, and the change in slope is highly significant (paired sample *t*-test,  $P < 0.001$ ). Békésy's results (Békésy 1939), which are similar to our own, extend down to 0.3 Hz. In those experiments, the transition point between the low- and high-frequency domains occurred at 20–25 Hz. Between 0.3 and 20 Hz, the threshold declined at 2 dB per octave; between 20 and 200 Hz, the decline was 15.4 dB per octave. Our inference that detection performance above 20–25 Hz was based on activity in Pacinian afferents is supported by neurophysiological studies in our laboratory in which the stimulus methods were the same as in *experiment 2*. Recordings from primary afferents in the rhesus monkey showed that only Pacinian thresholds are low enough at 40 Hz to account for the psychophysical thresholds (unpublished observations). In the remainder of this section, we discuss studies of the Pacinian corpuscle and then speculate on the specific mechanisms underlying the results of *experiments 2–5*.

#### Pacinian response properties

The first neurophysiological study of the Pacinian corpuscle was an inadvertent demonstration of its extreme sensitivity to transmitted vibration. Adrian and Umrath (1929) indented an exposed Pacinian with a punctate probe and observed a sustained discharge that increased monotonically with increasing force. Because of this observation, the Pacinian corpuscle was thought to be a pressure receptor. The Pacinian's insensitivity to sustained deformation, its selective sensitivity to transient deformation, and its extreme sensitivity to vibration were discovered subsequently (Gray and Malcolm 1950; Sato 1961; Scott 1951), but the reason for Adrian and Umrath's observation was not discovered until Hunt (1961) showed that a sensitive Pacinian responds to the ambient vibrations transmitted through a building. Adrian and Umrath were evidently coupling ambient vibration to their Pacinian more effectively as they drove their probes into the Pacinian lamellae.

The most remarkable feature of the Pacinian corpuscle is its large size and its multilayered, lamellar structure surrounded by a continuous capsule (Pease and Quilliam 1957; Zelena 1994). The principal function of these lamellae, we believe, is to protect the extremely sensitive receptor ending from the high

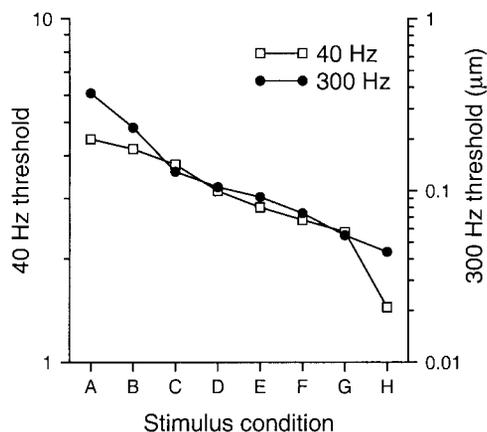


FIG. 8. Summary diagram of vibratory thresholds for 8 stimulus conditions. The left ordinate of the graph represents vibratory thresholds ( $\mu\text{m}$ , zero-to-peak) at 40 Hz, the right ordinate at 300 Hz. The abscissa, which is arranged in order of declining thresholds at both 40 and 300 Hz, represents the stimulus conditions specified in the accompanying table. The individual points represent geometric mean thresholds over all subjects at the specified stimulus conditions.

	Probe	Direction	Location	Area ( $\text{cm}^2$ )	Mode
A	punctate	perpendicular	D3d	0.01	passive
B	punctate	parallel	D3d	0.01	passive
C	cylinder	perpendicular	D3d	1.00	passive
D	cylinder	parallel	D3d	1.00	passive
E	cylinder	parallel	D34d	1.33	passive
F	cylinder	parallel	Palm-d	10.00	passive
G	cylinder	parallel	Palm-p	4.10	passive
H	cylinder	parallel	grip	36.40	active

static and low-frequency forces that occur in many motor acts, thereby leaving the ending sensitive to transmitted vibrations with amplitudes as small as 10 nm. The capsule is continuous and can retain fluid under slight pressure (Gray and Sato 1955; Pease and Quilliam 1957). Slow mechanical distortion causes a simple redistribution of the fluid in the outer lamellae, leaving the inner lamellae and the unmyelinated ending undisturbed, whereas rapid mechanical events are transmitted to the core through the viscous shear forces in the fluid as it is redistributed within the lamellae (Hubbard 1958; Lowenstein and Skalak 1966). The critical feature of the Pacinian corpuscle (and other corpuscular receptors like the Meissner corpuscle) is that it bathes its extremely sensitive receptor within an aqueous medium that is completely incompressible at all physiologically relevant loads. This provides a partial explanation for the complete insensitivity to force that we observed between 0.05 and 1.0 N.

#### *Effects of stimulus location*

The effect of stimulus location could depend on variation in the density of Pacinian receptors, variation in receptor sensitivity between locations, and on biomechanical factors such as proximity to a large mass of Pacinian corpuscles or proximity to a structure, such as bone, that transmits vibrations for great distances. There is no physiological evidence for variation in Pacinian sensitivity between locations in the hand (Mountcastle et al. 1972; Talbot et al. 1968). Direct anatomic methods (Bushong 1963; Cauna and Mannan 1958, 1959) and indirect methods based on fiber counts in the median nerve at the wrist (Johansson and Vallbo 1979) provide consistent estimates of the number and distribution of Pacinian corpuscles in the human hand. Serial reconstructions of a fetal finger by Cauna and Mannan (1958, 1959) yielded counts of 62, 55, and 61 Pacinian's in the radial half of the distal, middle, and proximal phalanges. Bushong (1963) found 176 Pacinian corpuscles in half a fetal thumb. These studies suggest that there are ~350 Pacinian corpuscles per finger. Attributing half that number to the fifth finger yields an estimate of ~1,600 Pacinian corpuscles in the fingers. Bushong (1963) also reconstructed approximately half the palm of a fetus and found 428 Pacinian corpuscles, which yields a rough estimate of 800 Pacinian corpuscles for the entire palm and 2,400 Pacinian corpuscles for the entire hand. This ratio of 2:1 for the distribution of Pacinian corpuscles between the fingers and the palm corresponds almost exactly to the ratio found by Johansson and Vallbo (1979); in a sample of 374 mechanoreceptive afferents recorded from the median nerve they found 28 Pacinian corpuscles in the fingers and 15 in the palm. Thus Pacinian corpuscle density appears to be higher in the fingers than in the palm. However, the total number of Pacinian corpuscles near a stimulus applied to the palm is much larger than the number near a stimulus applied to any single finger. For example, suppose that near threshold the stimulus engages the most sensitive Pacinian corpuscles at distances up to 25 mm from the probe. In this case, the stimulus labeled palm-d in Fig. 4 will affect a population of 6–700 Pacinian corpuscles (2–300 in the palm and ~100 in the proximal phalanges of the four fingers, D2–D5). The stimulus applied to D3d will, in contrast, affect only ~1–200 Pacinian corpuscles.

The two factors with the greatest effect, contact area and

stimulus location, are accounted for by assuming that vibratory detection depends on a threshold level of activation in the Pacinian population, which might be specified as the activation of a specified minimum number of Pacinian afferents or the production of a specified minimum population impulse rate. When the receptor thresholds vary widely, as they do in Pacinian afferents (Freeman and Johnson 1982; Mountcastle et al. 1972), increasing vibratory amplitude increases the total population response by increasing the total tissue volume in which the vibratory field exceeds the threshold of the most sensitive afferents, by recruiting less sensitive afferents to the active population, and by increasing the discharge rate in those already recruited to activity (Johnson 1974). When the contact region is small (e.g., the punctate probe in *experiment 4*) and is applied to a region in which relatively few Pacinian corpuscles are close to the probe (e.g., a fingerpad), a greater vibratory amplitude is required to produce the minimum Pacinian engagement required for threshold. When the contact region is large and the probe is applied to a location where there are many Pacinian corpuscles nearby (e.g., the palm-d placement in *experiment 2*) the vibratory amplitude required to produce a fixed level of activity will be lower.

#### *Effects of contact force*

Our report that a 20-fold change in contact force from 0.05 to 1 N had no detectable effect on threshold is at odds with previous reports of the effect of force over the same force range (Craig and Sherrick 1969; Lamore and Keemink 1988; Verrillo 1962). The study with stimulus conditions most like the conditions in this study is by Lamore and Keemink (1988), who reported almost a 30-db decline in threshold between 0.05 and 0.5 N at 210 Hz when applying a 14-mm-diam probe with no surround to the distal pad of the third finger and to the thenar eminence; between 0.5 and 2.0 N their threshold was essentially constant (at 0.05  $\mu\text{m}$  at the thenar eminence). An explanation for the difference between our study and previous studies can be found in a study by Goodwin et al. (1989) on the skin's failure to follow vertical, sinusoidal skin indentation; under some stimulus conditions (e.g., high-frequency and low indentation depth before vibration) the peak-to-peak skin excursion is a small fraction of the peak-to-peak probe excursion. The reason relates to the forces producing skin contact during withdrawal. During withdrawal, the only forces driving the skin are its own viscoelastic restoring forces. If the probe withdraws more rapidly than the skin's natural recovery rate, it leaves the skin. Reduced skin-following at higher frequencies is explained by higher probe withdrawal velocities. Increased skin-following with increased mean indentation depth is explained by Newton's second law: increased mean force produces increased depth until the restoring (reaction) force equals the indentation force. This, in turn, produces increased recovery velocity, better skin-following, and increased peak-to-peak skin excursion. This accounts for the substantial reduction in threshold reported by Lamore and Keemink (1988) with increasing force. In our experiments in which the probe vibrated parallel to the skin surface, the probe was always in contact with the skin; therefore the skin movement produced by the probe was independent of the mean force.

Because the forces that we and others (Lamore and Keemink 1988; Verrillo 1962) have used in psychophysical experiments

are two to three orders of magnitude lower than forces that may occur in manual tasks, extending these investigations to higher forces is important. Nevertheless, common experience suggests that we are sensitive to minute transmitted vibrations even when gripping an object with high force. The preservation of this sensitivity in the presence of high static forces likely results from the corpuscular structure of the Pacinian corpuscle as discussed above. Predicting the outcome of a psychophysical experiment with contact forces  $>1-2$  N is difficult. Increasing force beyond  $1-2$  N could lower thresholds by coupling transmitted vibrations to bones and tendons that might transmit the vibrations more effectively to distant Pacinian corpuscles. Conversely, the engagement of other mechanoreceptors by higher forces might mask the effects of small, transmitted vibrations.

### Effects of stimulus direction

Thresholds were lower on average when the probe vibrated parallel to the skin surface than when it vibrated perpendicular to the skin surface. The effect was relatively small (15% at 40 Hz and 30% at 300 Hz), but it was consistent at all four combinations of stimulus type (cylindrical surface and the punctate probe) and frequency. No previous studies of which we are aware directly compare the effects of stimulus direction on vibratory detection. The reasons that vibration parallel to the skin surface is more effective than vibration perpendicular to the skin surface is not clear. The ultimate stimulus is dynamic strain (Hubbard 1956; Lowenstein and Skalak 1966). The explanation may be that horizontal skin vibration produces shear strain in the subcutaneous tissues (Pereira et al. 1991) more effectively than does perpendicular vibration when tissue motion is constrained by hard tissues 3–4 mm below the surface of the skin.

### Active versus passive touch

The idea that active and passive touch are different in some fundamental way (Gibson 1962) has a long history (reviewed in Vega-Bermudez et al. 1991). To determine whether there is a difference between perceptual capacity in active and passive touch, the stimulus conditions must be identical in the two conditions. Under these circumstances, the result has been either that the perceptual capacity is the same in the two circumstances (Vega-Bermudez et al. 1991) or that it is superior in the passive condition (Magee and Kennedy 1980). The explanation advanced for the latter finding is that active touch requires division of attention between the sensory and motor tasks (Magee and Kennedy 1980).

In the experiments reported here, active touch produced the lowest thresholds. However, the difference between the thresholds during active gripping ( $H$  in Fig. 8) and the lowest threshold during passive presentation ( $G$  in Fig. 8, Palm-P in Fig. 4), which amounted to 4 dB at 40 Hz and 2 dB at 300 Hz, is not large enough to demonstrate some special advantage for active touch. The difference is no greater than would be predicted from the larger total contact area ( $36.4$  vs.  $10$  cm<sup>2</sup>) and therefore the larger number of Pacinian corpuscles engaged by the stimulus in the active grip condition. Another possibility that we cannot exclude is that the muscle contraction that accompanies active grasping may have made muscle spindles

more sensitive to high-frequency vibration, but the thresholds reported in *experiment 1* are, as far as we know, much lower than any reported for the activation of muscle spindle afferents (Brown et al. 1967; Gregory and Proske 1988).

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### REFERENCES

- ADRIAN, E. D. AND UMRATH, K. The impulse discharge from the Pacinian corpuscle. *J. Physiol. (Lond.)* 68: 139–154, 1929.
- BÉKÉSY, G. Über die Vibrationsempfindung. *Aleustische Zeitschrift* 4: 315–334, 1939.
- BERNSTEIN, L. E., SCHECHTER, M. B., AND GOLDSTEIN, M. H., JR. Child and adult vibrotactile thresholds for sinusoidal and pulsatile stimuli. *J. Acoust. Soc. Am.* 80: 118–123, 1986.
- BOLANOWSKI, S. J., GESCHIEDER, G. A., VERRILLO, R. T., AND CHECKOSKY, C. M. Four channels mediate the mechanical aspects of touch. *J. Acoust. Soc. Am.* 84: 1680–1694, 1988.
- BROWN, M. C., ENGBERG, I., AND MATTHEWS, P.B.C. The relative sensitivity to vibration of muscle receptors of the cat. *J. Physiol. (Lond.)* 192: 773–800, 1967.
- BUSHONG, J. *A Report of the Frequency and Distribution of the Pacinian Corpuscle in a Palm of a Seven Month Human Fetus* (Master's thesis). Baltimore, MD: Johns Hopkins University, 1963.
- CAUNA, N. AND MANNAN, G. The structure of human digital Pacinian corpuscles (corpuscula lamellosa) and its functional significance. *J. Anat.* 92: 1–20, 1958.
- CAUNA, N. AND MANNAN, G. Development and postnatal changes of digital Pacinian corpuscles (corpuscula lamellosa) in the human hand. *J. Anat.* 93: 271–286, 1959.
- CHUBBUCK, J. G. Small motion biological stimulator. *Johns Hopkins APL Tech. Digest* May–June: 18–23, 1966.
- CRAIG, J. C. Vibrotactile spatial summation. *Percept. Psychophys.* 4: 351–354, 1968.
- CRAIG, J. C. AND SHERRICK, C. E. The role of skin coupling in the determination of vibrotactile spatial summation. *Percept. Psychophys.* 6: 97–101, 1969.
- FREEMAN, A. W. AND JOHNSON, K. O. A model accounting for effects of vibratory amplitude on responses of cutaneous mechanoreceptors in macaque monkey. *J. Physiol. (Lond.)* 323: 43–64, 1982.
- GESCHIEDER, G. A., BOLANOWSKI, S. J., HALL, K. L., HOFFMAN, K. E., AND VERRILLO, R. T. The effects of aging on information processing channels in the sense of touch. I. Absolute sensitivity. *Somatosens. Mot. Res.* 11: 345–357, 1994.
- GESCHIEDER, G. A., CAPRARO, A. J., FRISINA, R. D., HAMER, R. D., AND VERRILLO, R. T. The effects of a surround on vibrotactile thresholds. *Sens. Processes* 2: 99–115, 1978.
- GIBSON, J. J. Observations on active touch. *Psychol. Rev.* 69: 477–491, 1962.
- GOBLE, A. K., COLLINS, A. A., AND CHOLEWIAK, R. W. Vibrotactile threshold in young and old observers: the effects of spatial summation and the presence of a rigid surround. *J. Acoust. Soc. Am.* 99: 2256–2269, 1996.
- GOODWIN, A. W., JOHN, K. T., AND DARIAN-SMITH, I. Skin profiles during sinusoidal vibration of the fingerpad. *Exp. Brain Res.* 77: 79–86, 1989.
- GRAY, J.A.B. AND MALCOLM, J. L. The initiation of nerve impulses by mesenteric Pacinian corpuscles. *Proc. R. Soc. Lond. B. Biol. Sci.* 137: 96–114, 1950.
- GRAY, J.A.B. AND SATO, M. The movement of sodium and other ions in Pacinian corpuscles. *J. Physiol. (Lond.)* 129: 594–607, 1955.
- GREEN, D. M. Stimulus selection in adaptive psychophysical procedures. *J. Acoust. Soc. Am.* 87: 2662–2674, 1990.

- GREEN, D. M., RICHARDS, V. M., AND FORREST, T. G. Stimulus step size and heterogeneous stimulus conditions in adaptive psychophysics. *J. Acoust. Soc. Am.* 86: 629–636, 1989.
- GREGORY, J. E. AND PROSKE, U. The responses of muscle spindles in the kitten to stretch and vibration. *Exp. Brain Res.* 73: 606–614, 1988.
- HUBBARD, S. J. The mechanical properties of Pacinian corpuscles. *J. Physiol. (Lond.)* 132: 23, 1956.
- HUBBARD, S. J. A study of rapid mechanical events in a mechanoreceptor. *J. Physiol. (Lond.)* 141: 198–218, 1958.
- HUNT, C. C. On the nature of vibration receptors in the hind limb of the cat. *J. Physiol. (Lond.)* 155: 175–186, 1961.
- JOHANSSON, R. S. AND VALLBO, Å. B. Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in glabrous skin. *J. Physiol. (Lond.)* 286: 283–300, 1979.
- JOHNSON, K. O. Reconstruction of population response to a vibratory stimulus in quickly adapting mechanoreceptive afferent fiber population innervating glabrous skin of the monkey. *J. Neurophysiol.* 37: 48–72, 1974.
- KATZ, D. *The World of Touch*. Hillsdale, NJ: Erlbaum (translated by L. E. Krueger; published originally in 1925), 1989.
- KOLLMEIER, B., GILKEY, R. H., AND SIEBEN, U. K. Adaptive staircase techniques in psychoacoustics: a comparison of human data and a mathematical model. *J. Acoust. Soc. Am.* 83: 1852–1862, 1988.
- LAMORE, P. J. AND KEEMINK, C. J. Evidence for different types of mechanoreceptors from measurements of the psychophysical threshold for vibrations under different stimulation conditions. *J. Acoust. Soc. Am.* 83: 2339–2351, 1988.
- LAMORE, P. J., MUIJSER, H., AND KEEMINK, C. J. Envelope detection of amplitude-modulated high-frequency sinusoidal signals by skin mechanoreceptors. *J. Acoust. Soc. Am.* 79: 1082–1085, 1986.
- LEVITT, H. Transformed up-down methods in psychoacoustics. *J. Acoust. Soc. Am.* 49: 467–477, 1970.
- LINDBLOM, U. AND LUND, L. The discharge from vibration-sensitive receptors in the monkey foot. *Exp. Neurol.* 15: 401–417, 1966.
- LOFVENBERG, J. AND JOHANSSON, R. S. Regional differences and interindividual variability in sensitivity to vibration in the glabrous skin of the human hand. *Brain Res.* 301: 65–72, 1984.
- LOWENSTEIN, W. R. AND SKALAK, R. Mechanical transmission in a Pacinian corpuscle. An analysis and a theory. *J. Physiol. (Lond.)* 182: 346–378, 1966.
- MAGEE, L. E. AND KENNEDY, J. M. Exploring pictures tactually. *Nature* 283: 287–288, 1980.
- MOUNTCASTLE, V. B., LAMOTTE, R. H., AND CARLI, G. Detection thresholds for stimuli in humans and monkeys: comparison with threshold events in mechanoreceptive afferent nerve fibers innervating the monkey hand. *J. Neurophysiol.* 35: 122–136, 1972.
- MOUNTCASTLE, V. B., STEINMETZ, M. A., AND ROMO, R. Frequency discrimination in the sense of flutter: psychophysical measurements correlated with postcentral events in behaving monkeys. *J. Neurosci.* 10: 3032–3044, 1990.
- PEASE, T. C. AND QUILLIAM, T. A. Electron microscopy of the Pacinian corpuscle. *J. Biophys. Biochem. Cytol.* 3: 331–342, 1957.
- PEREIRA, J. M., MANSOUR, J. M., AND DAVIS, B. R. The effects of layer properties on shear disturbance propagation in skin. *J. Biomech. Eng.* 113: 30–35, 1991.
- RABINOWITZ, W. M., HOUTSMA, A.J.M., DURLACH, N. I., AND DELHORNE, L. A. Multidimensional tactile displays: identification of vibratory intensity, frequency, and contactor area. *J. Acoust. Soc. Am.* 82: 1243–1252, 1987.
- SATO, M. Response of Pacinian corpuscles to sinusoidal vibration. *J. Physiol. (Lond.)* 159: 391–409, 1961.
- SCHNEIDER, W. The tactile array stimulator. *Johns Hopkins APL Tech. Digest* 9: 39–43, 1988.
- SCOTT, D. Response of the Pacinian corpuscle to oscillatory stimulation. *Federation Proc.* 10: 123, 1951.
- SHELTON, B. R. AND SCARROW, I. Two-alternative versus three-alternative procedures for threshold estimation. *Percept. Psychophys.* 35: 385–392, 1984.
- TALBOT, W. H., DARIAN-SMITH, I., KORNHUBER, H. H., AND MOUNTCASTLE, V. B. The sense of flutter-vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. *J. Neurophysiol.* 31: 301–334, 1968.
- VAN DOREN, C. L. The effects of a surround on vibrotactile thresholds: evidence for spatial and temporal independence in the non-Pacinian I (NPI) channel. *J. Acoust. Soc. Am.* 87: 2655–2661, 1990.
- VEGA-BERMEDEZ, F., JOHNSON, K. O., AND HSIAO, S. S. Human tactile pattern recognition: active versus passive touch, velocity effects, and patterns of confusion. *J. Neurophysiol.* 65: 531–546, 1991.
- VERRILLO, R. T. Investigation of some parameters of the cutaneous threshold for vibration. *J. Acoust. Soc. Am.* 34: 1768–1773, 1962.
- VERRILLO, R. T. Effect of contactor area on the vibrotactile threshold. *J. Acoust. Soc. Am.* 35: 1962–1966, 1963.
- VERRILLO, R. T. A duplex mechanism of mechanoreception. In: *The Skin Senses*, edited by D. R. Kenshalo. Springfield, IL: Charles C. Thomas, 1968, p. 139–159.
- VERRILLO, R. T., GESCHIEDER, G. A., CALMAN, B. S., AND VAN DOREN, C. L. Vibrotactile masking: effects of one- and two-site stimulation. *Percept. Psychophys.* 33: 379–387, 1983.
- ZELENA, J. *Nerves and Mechanoreceptors*. London: Chapman Hall, 1994.