Vibrotactile Frequency Discrimination in Human Hairy Skin

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Mahns, D. A., N. M. Perkins, V. Sahai, L. Robinson, and M. J. Rowe. Vibrotactile frequency discrimination in human hairy skin. *J Neurophysiol* 95: 1442–1450, 2006. First published November 30, 2005; doi:10.1152/jn.00483.2005. The human capacity for vibrotactile frequency discrimination has been compared directly for glabrous and hairy skin regions by means of a two-alternative, forced-choice psychophysical procedure in five subjects. Sinusoidal vibratory stimuli, delivered by means of a 4-mm-diam probe, were first used to obtain detection threshold values for the two skin sites, the finger tip and the dorsal forearm, at four standard frequencies, 20, 50, 100, and 200 Hz. Values confirmed previous results showing detection thresholds were markedly higher on hairy skin than on glabrous skin. For the discrimination task, each standard frequency, at an amplitude four times detection threshold, was paired with a series of comparison frequencies, and discrimination capacity then was quantified by deriving from psychometric function curves, measures of the discriminable frequency increment (Δf) and the Weber Fraction ($\Delta f/f$), which, when plotted as a function of the four standard frequencies, revealed similar capacities for frequency discrimination at the two skin sites at the standard frequencies of 20, 100, and 200 Hz but an equivocal difference at 50 Hz. Cutaneous local anesthesia produced a marked impairment in vibrotactile detection and discrimination at the low standard frequencies of 20 and 50 Hz but little effect at higher frequencies. In summary, the results reveal, first, a striking similarity in vibrotactile discriminative performance in hairy and glabrous skin despite marked differences in detection thresholds for the two sites, and, second, the results confirm that vibrotactile detection and discrimination in hairy skin depend on superficial receptors at low frequencies but depend on deep, probably Pacinian corpuscle, receptors for high frequencies.

INTRODUCTION

Vibrotactile detection thresholds on the hairy skin of human subjects are known to be approximately an order of magnitude higher than those for the glabrous skin of the fingertips (Merzenich and Harrington 1969; Talbot et al. 1968; Wilska 1954). These differences have, in part, been attributed to differences in the sensory receptors and afferent fiber classes supplying these different skin areas. In particular, at low vibrotactile frequencies (less than ~80 Hz), the detection of vibrotactile inputs from the hairy skin appears to depend on sensory fibers associated with hair follicles, the *hair follicle afferent* (HFA) fibers, whereas the glabrous skin input arises from the *rapidly adapting* (RA) class of fibers associated with encapsulated intradermal receptors, known as Meissner corpuscles in primates. At higher frequencies (more than ~80 Hz), within the human vibrotactile range of ~5–1,000 Hz, the Pacinian Corpuscle (PC) receptors are responsible for vibrotactile sensibility in the glabrous skin (LaMotte and Mountcastle 1975; Mountcastle et al. 1972; Talbot et al. 1968). Although PC

receptors are not present in the superficial subcutaneous regions of hairy skin (Brown and Iggo 1967; Burgess et al. 1968; Tuckett et al. 1978), they are present in the deeper underlying tissue surrounding joints and bone (Calne and Pallis 1966). As HFA fibers in hairy skin are limited in their capacity to respond to vibratory stimuli above ~80 Hz (Merzenich and Harrington 1969; Zachariah et al. 2001), subjective vibrotactile sensibility within the hairy skin at the higher frequencies (approximately >80 Hz) may depend on the deeply located PC receptors.

Although human subjects are poorer in their subjective capacity for vibrotactile *detection* in the hairy skin than in glabrous skin (Merzenich and Harrington 1969; Talbot et al. 1968), it is unclear whether the subjective capacity for vibrotactile frequency *discrimination* is also poorer in hairy skin. No individual psychophysical study has directly compared the subjective capacity for vibrotactile frequency discrimination between hairy and glabrous skin sites based on the use of sinusoidal stimuli. The various studies that have been conducted for either glabrous (Franzen and Nordmark 1975; Goble and Hollins 1994; Goff 1967; LaMotte and Mountcastle 1975; Mountcastle et al. 1969, 1990; Mowbray and Gebhard 1957) or for hairy skin (Rothenberg et al. 1977) vary in the waveform or type of the vibratory stimulus used, the psychophysical testing paradigm, and the skin sites that have been chosen, making comparisons between studies difficult to assess. It therefore remains unclear whether the capacity for frequency discrimination of sinusoidal vibrotactile stimuli is poorer in the hairy skin than the glabrous skin, as is the case for the detection of such stimuli.

The present study sought first to compare the human subjective capacity for vibrotactile frequency discrimination between hairy and glabrous skin and second to establish, for the hairy skin, the relative contribution to vibrotactile detection and discrimination of the more superficial receptors believed to be associated with HFA sensory fibers, and the deeply located PC receptors.

METHODS

The subjective capacities to detect vibration and to discriminate between frequencies in the hairy skin of the forearm were compared with these capacities in the glabrous skin of the fingertip in five human subjects (2 males and 3 females). A two-alternative, forced-choice psychophysical procedure was used for the frequency discrimination task (McNicol 1972; Morley and Rowe 1990). Subjects, all of whom were naive about the objectives of the experiment, were tested at both skin sites with the order of testing differing among subjects. White noise was delivered through headphones to eliminate any auditory cues associated with the mechanical stimulator used to deliver the vibration to the fingertip or forearm.

Vibrotactile stimuli

Vibration was applied to the skin by means of a circular Perspex probe (4 mm diam) driven by a feedback-controlled mechanical stimulator similar to those used in our earlier studies (e.g., Coleman et al. 2003; Ferrington and Rowe 1980a; Morley and Rowe 1990; Zachariah et al. 2001). For fingertip testing, the subjects sat with their writing hand resting palm upwards on a bench top. The index finger was secured with plasticine in a Perspex chamber to stabilize the finger against movement. The stimulator was mounted above the hand and positioned such that the Perspex probe just contacted the glabrous skin of the distal finger pad. For forearm testing, the subject sat with the right arm secured and stabilized comfortably in a full-length fiberglass cast that was rigidly affixed to the bench top. A window was cut in the cast to expose the dorsal forearm hairy skin immediately overlying the brachioradialis muscle and the Perspex stimulator probe positioned, from above and normal to the skin surface ~5 cm distal to the elbow.

Stimulation procedure

Detection thresholds at each of the four chosen standard frequencies (20, 50, 100, and 200 Hz) were determined for each subject using the method of limits and based on an average of three ascending/descending trials at each frequency. Individual trials consisted of a 1-s vibration train superimposed on a 1-mm step, repeated once every 5 s.

For the frequency-discrimination task, the stimulator was driven by a control unit with seven output channels, each of which allowed a preset frequency/amplitude combination to be selected. The first channel had the standard vibration frequency (20, 50, 100, or 200 Hz) with a peak-to-peak amplitude set at four times the particular subject's detection threshold. These suprathreshold stimuli were chosen to ensure that stimuli were easily and unequivocally detectable and that there was a stable and effective coupling between the stimulus probe and the skin site. The remaining six channels were preset for comparison vibration trains at a series of frequencies at, or higher than, the standard. However, settings on individual channels were adjusted during some trials to extend the number of different comparison frequencies to as many as ten (see Fig. 4).

The standard and comparison trains of vibration, each lasting 1 s, were delivered in sequence and were superimposed on a 3.5-s background step indentation of 1 mm (Fig. 1). Prior to the test session the subjects were given practice sessions to become familiar with the stimulus protocol and were presented with vibration stimuli at different frequencies to ensure they understood what was meant by changes in pitch (frequency). Prior to assessing the discriminative capacity of individual subjects, the perceived intensity of the standard and comparison stimuli were matched by instructing the subjects, as far as possible, to disregard the pitch difference and report *only* on the perceived amplitude of the comparison as it was systematically varied in amplitude from trial to trial. This procedure was repeated until the subject consistently reported that standard and comparison stimuli were of equal subjective intensity and was done to ensure that
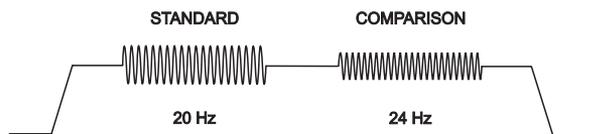
amplitude could not provide a discriminable cue during the frequency discrimination trials (Goff 1967; LaMotte and Mountcastle 1975).

For the two-alternative forced-choice procedure, subjects were instructed that the task was to determine whether the pitch (frequency) of the comparison stimulus was higher than or the same as that of the standard. In each test session, the comparison stimuli (1 of which was the same frequency as the standard to test for false positives) were each presented 10 times in a pseudorandom order. As may be seen in Fig. 4, for each standard frequency there were at least 6, but ≤10, different comparison frequencies presented. After each delivery of the paired vibration trains, the response, *higher* or *same*, was indicated verbally by the subject with the outcome being recorded by the experimenter in a laboratory computer. A rest period of ~10 s was permitted after each pair of stimuli to allow the subject to make a decision and also to minimize the extent of adaptation that might take place in the subject's sensitivity to the vibrotactile stimuli (O'Mara et al. 1988).

Psychometric function curves were constructed by plotting the percentage of responses called "higher" by the subject against the frequency increment between the standard and the comparison frequencies. The discriminable increment (Δf) was measured from these curves using the criterion described by LaMotte and Mountcastle (1975), namely, half the sum of the frequency increment at which a subject calls the comparison frequency "higher" 75% of the time and the frequency increment called "higher" 25% of the time; that is

$$\Delta f = \left[\frac{\Delta f_{(75\%)} + \Delta f_{(25\%)}}{2} \right]$$

The Weber fraction ($\Delta f/f$) was also calculated as the discriminable increment (Δf) divided by the standard frequency (f) for that trial. The discriminable increment (Δf) and the Weber fraction ($\Delta f/f$) were then each plotted as a function of frequency (f) for the standard vibration stimulus.

Determination of the relative contribution of PC receptors and HFA receptors to vibration sensibility in the dorsal forearm hairy skin

To examine whether there is a differential contribution to vibrotactile sensibility in the forearm hairy skin made by the deeply located PC receptors and the cutaneous HFA fibers, a second series of experiments was performed. In this case, six subjects were tested for detection threshold values, four of whom were also tested for their capacity for frequency discrimination at 20, 50, and 200 Hz before and after an intradermal injection of local anesthetic (1 ml, 2% lidocaine). This subcutaneous injection of local anesthetic agent will inactivate the cutaneous receptors but leave intact the forearm PC receptors because of their deep location in the vicinity of the joints and interosseous membrane. Thus any difference in the relative contribution of PC and HFA receptors to vibration sensibility in the dorsal forearm at low and high vibration frequencies could be determined. The effectiveness of the cutaneous anesthesia was verified prior to psychophysical testing, by establishing that subjects were insensitive to light mechanical stimulation of the hairs or skin, or pin-prick stimuli, in an area of 2–3 cm in radius around the stimulus probe.

RESULTS

Detection thresholds: comparison of hairy and glabrous skin

Detection threshold values for sinusoidal vibration on the hairy skin of the forearm were consistently higher than those for the glabrous fingertip (Fig. 2), being as much as 10-fold higher at 20 Hz, consistent with previous findings (Merzenich and Harrington 1969; Talbot et al. 1968). Values obtained for

FIG. 1. Representation of the stimulus sequence, consisting of 2 1-s trains of vibration superimposed on a 3.-s step indentation of 1-mm amplitude. The frequency of the 1st (standard) train of vibration was 20, 50, 100, or 200 Hz, and its amplitude was set at 4 times each subject's detection threshold at that frequency. The 2nd train of vibration (the comparison) had a frequency either at or above that of the standard, and its amplitude preset by each subject to a level subjectively equivalent to that of the standard. For the 20-Hz standard frequency, for example, the comparison frequencies used were 20, 24, 28, 32, 36, and 40 Hz as may be seen in Fig. 4.
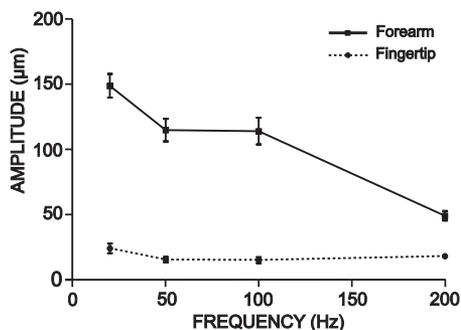
FIG. 2. Mean vibrotactile detection thresholds for the forearm (hairy skin; $n = 8$) compared with the fingertip (glabrous skin; $n = 5$) at frequencies of 20, 50, 100, and 200 Hz. Error bars represent SE but for the fingertip are small and fall largely within the bounds of the symbols for the mean threshold values.
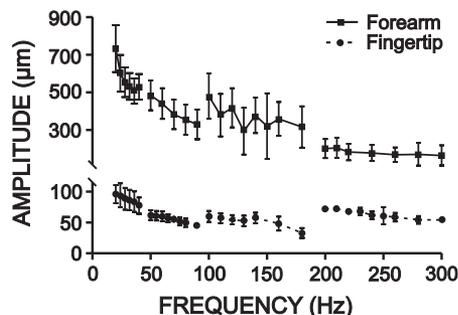

FIG. 3. Mean values of vibration amplitude to achieve an equal subjective intensity rating for comparison frequencies with the standard vibration frequencies of 20, 50, 100, and 200 Hz for the forearm (hairy skin) and for the fingertip (glabrous skin; $n = 5$; error bars = SE).

the hairy skin of the dorsal forearm were ~150 μm at 20 Hz and fell as a function of increases in vibration frequency over the range 20–200 Hz (Fig. 2 and Table 1). This is also consistent with previous results for the hairy skin of the ventral forearm (Merzenich and Harrington 1969).

Amplitude changes to achieve equal subjective intensity at different vibration frequencies

To ensure that intensity differences between standard and comparison stimulus could not provide a discriminable cue during frequency discrimination trials, subjects were required to adjust the intensities of the comparison vibratory stimuli to be subjectively equal to the intensity of the standard frequency (set at 4 times the threshold value obtained as in Fig. 2 but for individual subjects). For each of the higher frequency comparison stimuli, the mean amplitude ($\pm$SE, $n = 5$) judged to be equivalent in intensity to the standard is plotted in Fig. 3 and tended to decrease as a function of increases in frequencies at each of the four standard frequencies, 20, 50, 100, and 200 Hz.

Comparison of vibrotactile frequency discrimination in hairy and glabrous skin

Vibrotactile frequency discrimination at the two skin sites was quantified in Fig. 4 by plotting, on the ordinate, the proportion of comparison stimuli that were called higher—as a function of the increment in vibration frequency between standard and comparison stimuli (abscissa). The psychometric function curves constructed for the four standard frequencies of 20, 50, 100, and 200 Hz in Fig. 4 allow direct comparison of discriminative capacities between the hairy skin of the dorsal forearm (continuous line) and the glabrous skin of the finger tip (broken line). In both skin regions, there was a similarly graded

relation, in particular for the 20, 100, and 200 Hz standard frequencies. Furthermore, at each of these frequencies, there was no significant difference ($P > 0.05$) between the relations for the two skin sites based on a two-way, repeated-measures ANOVA. However, at 50 Hz, there was a little more separation of the relations with the forearm values over the lower part of the curve (with frequency increments of 10 and 20 Hz) falling below those of the finger tip. These two relations were significantly different ($P < 0.0001$), based on the ANOVA, with the difference being attributable to the differences observed at the lower frequency increments where paired t-test with the Bonferroni correction demonstrated a significant difference at increments of 10 Hz ($P < 0.05$) and 20 Hz ($P < 0.05$) but not at higher frequency increments ($P > 0.05$). Nevertheless, despite these differences at 50 Hz, when one considers the data for all four relations in Fig. 4, the striking overall finding is the similarity of discriminative performance in the two skin areas.

Quantification of vibrotactile frequency discrimination in hairy and glabrous skin

The discriminative increment (Δf) or *just noticeable difference* (jnd) was calculated at each standard frequency as described in METHODS. This value was plotted in hertz (ordinate) for the two skin sites for each of the five subjects as a function of the four standard frequencies (abscissa) in Fig. 5A. Considerable subject-to-subject variation is apparent in the Δf values at each of the standard frequencies. However, when the mean values were plotted (Fig. 5B and Table 1), there was a graded increase, at both skin sites, in the discriminative increment, Δf, as a function of increases in the standard frequency, reflecting the larger absolute increase in frequency needed for subjective discrimination, the higher the standard frequency. When the Weber Fraction ($\Delta f/f$) was plotted as a function of f, the

TABLE 1. *Mean vibrotactile detection thresholds, and discriminable increments (Δf) and Weber Fractions ($\Delta f/f$) for frequency discrimination, on the forearm and fingertip at the standard frequencies of 20, 50, 100, and 200 Hz*

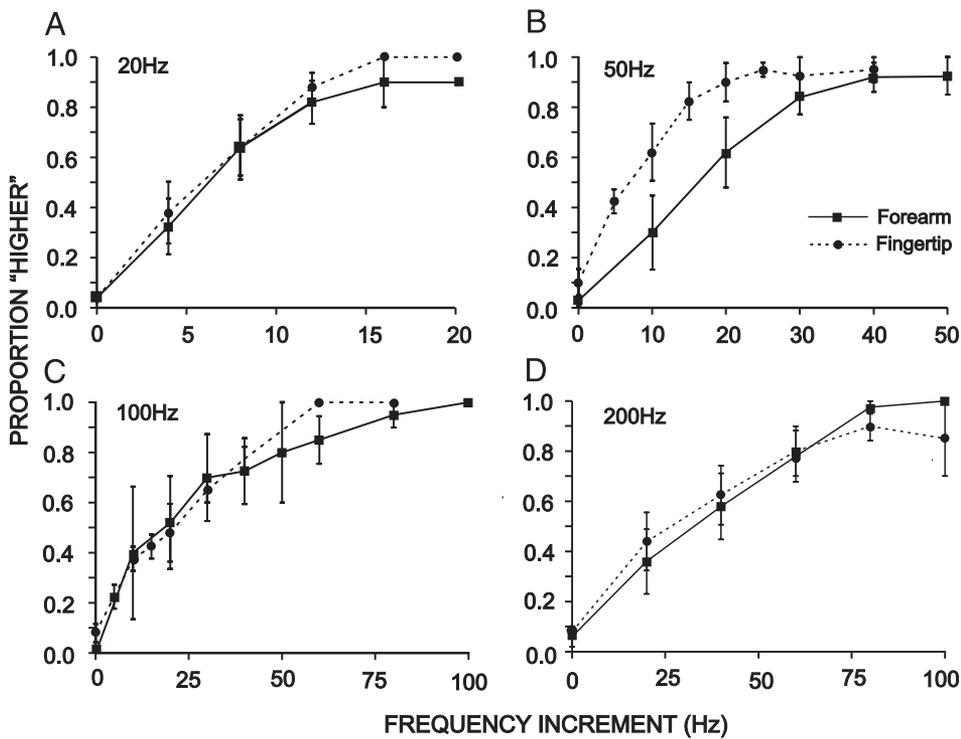|		20 Hz	50 Hz	100 Hz	200 Hz
Vibrotactile detection thresholds (μm)	Fingertip	24 ± 3.7	15.4 ± 2.0	15.0 ± 2.2	18.0 ± 1.2
	Forearm	149 ± 9.0	114.9 ± 8.7	114.1 ± 10.2	49.2 ± 3.7
Vibrotactile discrimination (Δf)	Fingertip	6.6 ± 1.4	9.7 ± 2.9	21.4 ± 3.4	27.2 ± 7.6
	Forearm	7.6 ± 1.1	18.0 ± 5.1	27.2 ± 8.5	33.9 ± 7.3
Vibrotactile discrimination ($\Delta f/f$)	Fingertip	0.32 ± 0.07	0.19 ± 0.07	0.21 ± 0.03	0.14 ± 0.04
	Forearm	0.36 ± 0.07	0.38 ± 0.10	0.27 ± 0.09	0.17 ± 0.04

Values are means ± SE.

FIG. 4. Mean psychometric function curves for vibrotactile frequency discrimination at standard frequencies of 20, 50, 100, and 200 Hz for the forearm and fingertip sites. The proportion of responses called "higher" by subjects is plotted against the frequency increment for the comparison relative to the standard frequency ($n = 5$; error bars = SE).

relations for the five subjects (Fig. 5C) and for those based on the mean values (Fig. 5D and Table 1) were relatively flat or even showed a slight decline. If one performs a two-way, repeated-measures ANOVA (Graph Pad Prism, Version 3) on these relations in Fig. 5, B and D, there was a small but significant difference ($P < 0.05$), suggesting that vibrotactile frequency discrimination may be marginally poorer on the forearm. However, paired t-test with the Bonferroni correction revealed no significant difference ($P > 0.05$) between the two skin sites at the individual frequencies of 20, 100, and 200 Hz. At 50 Hz, the result was equivocal as there was no significant

difference for the Δf values ($P > 0.05$), but a difference arose ($P < 0.05$) when the data were normalized by conversion to the Weber Fraction ($\Delta f/f$).

Discriminative performance evaluated in terms of absolute temporal changes

Although the discriminable increment in frequency (Δf) at both skin sites rises as a function of frequency from a mean of $\sim$6–7 Hz at a standard frequency of 20 Hz to a mean of $\sim$25 Hz at 200 Hz (Fig. 5B), the subjective performance, in terms of
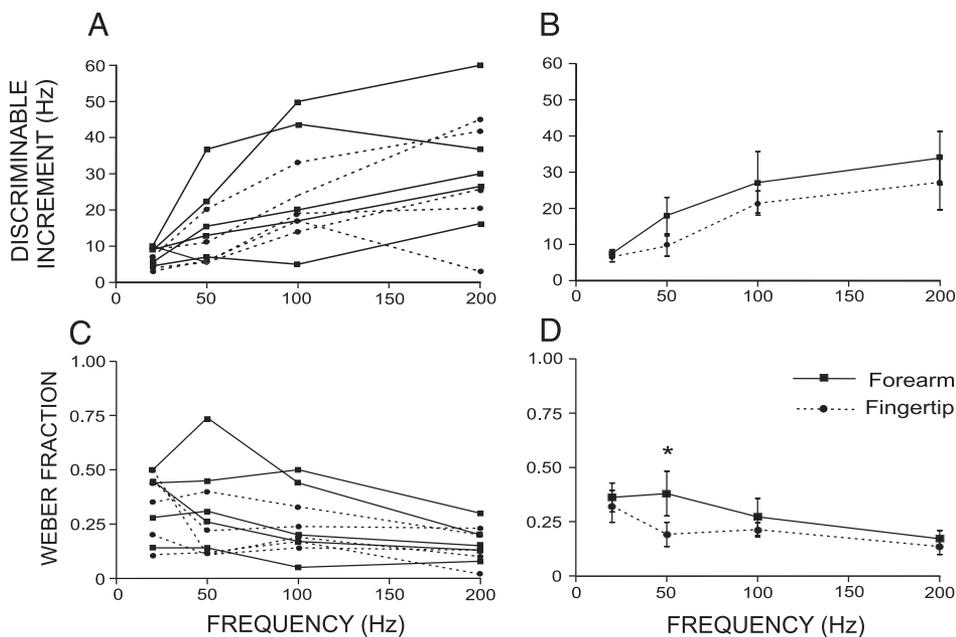

FIG. 5. Discriminable frequency increments (Δf) and Weber Fractions ($\Delta f/f$) for vibration on the forearm hairy skin and fingertip skin. A: the value for f, in Hz, is plotted for each of the 5 subjects as a function of the 4 standard frequencies, 20, 50, 100, and 200 Hz, for the 2 skin sites. B: means ± SE for the 5 subjects. C: the Weber fraction ($\Delta f/f$) is plotted for each of the 5 subjects with means ± SE plotted in D.
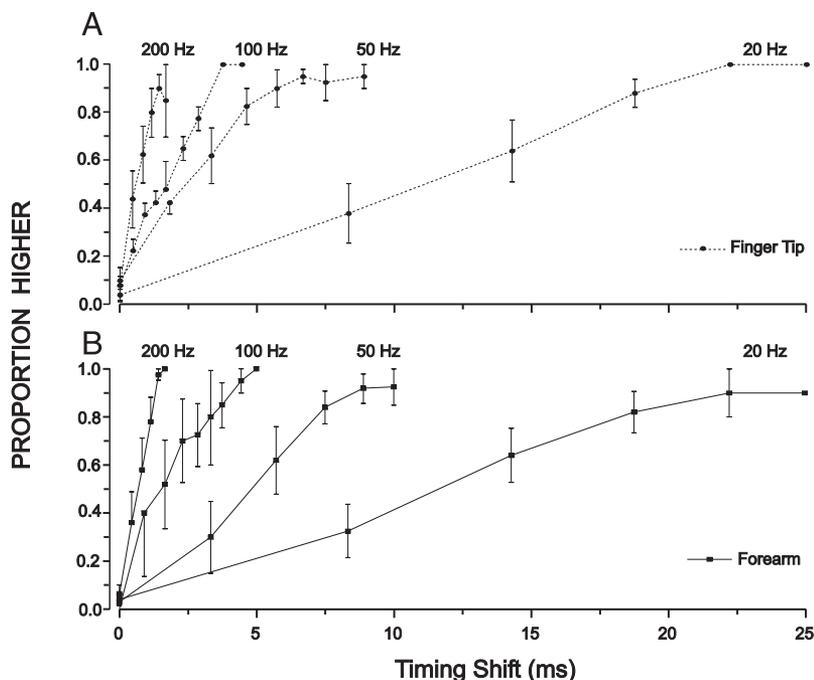
FIG. 6. Psychometric function curves for vibrotactile frequency discrimination in forearm hairy and fingertip glabrous skin plotted from Fig. 4 data for the 5 subjects, but in terms of absolute temporal changes in cycle period (abscissa) needed for discrimination at each of the four standard frequencies, 20, 50, 100, and 200 Hz (error bars = SE).

judging absolute shifts in the cycle length of the vibrotactile stimulus, increases in acuity the higher the standard frequency. This may be seen in Fig. 6 if one replots the psychometric function curves of Fig. 4 with the abscissa scaled in terms of the absolute change (timing shift in ms) in the length of the cycle period of the comparison vibration frequency compared with the standard frequency. This has been done with the pooled data for the five subjects for the fingertip glabrous skin in Fig. 6A and for the forearm hairy skin in Fig. 6B at the four standard frequencies of 20, 50, 100, and 200 Hz. The graphs show that at both skin sites, the subjective discrimination of changes in vibrotactile frequency requires much greater absolute time shifts at the low frequencies (20 and 50 Hz) compared with the high standard frequencies (100 and 200 Hz). Furthermore, they emphasize once again, the similarity of subjective discriminative performance at the two skin sites, in contrast to the marked differences in *detection* performance. For these data in Fig. 6, statistical testing (ANOVA) confirmed again that there was no significant difference between the two skin sites in frequency discrimination at 20, 100, and 200 Hz ($P > 0.05$ in each case), although at 50 Hz, as found in Fig. 4, there was again a difference ($P < 0.01$) for the 10- and 20-Hz increments (where the absolute time shifts in the vibratory cycle length are 3.3 ms, going from 50 to 60 Hz, and 5.7 ms, going from 50 to 70 Hz).

Differential contributions of superficial and deep receptors to vibrotactile sensibility in the hairy skin of the forearm

To examine the relative contributions of superficial and deep receptors to vibrotactile frequency discrimination, we employed cutaneous local anesthesia (see METHODS) to selectively block the contributions from superficial tactile receptors (putative HFA-related endings) and therefore isolate any contribution from deep receptors. When this procedure was carried out in six subjects, the detection thresholds were first measured and found to be elevated in association with skin blockade at

frequencies below ~100 Hz, in agreement with the observations of Merzenich and Harrington (1969). The impact was most marked at the lowest frequency tested, 20 Hz (Fig. 7), where detection thresholds increased by a factor of two to three times, and declined progressively going from 20 to 200 Hz (Fig. 7). Paired t-test with Bonferroni corrections established that the threshold changes were significant at 20 Hz ($P < 0.001$) and 50 Hz ($P < 0.05$), but that at 100 Hz ($P > 0.05$) and 200 Hz ($P > 0.05$) they were not.

Frequency discrimination at the standard frequency of 20 Hz was effectively abolished (Fig. 8A), as subjects could not feel the 20-Hz standard vibration and were only effectively aware of the comparison train of vibration when the comparison frequency reached ~40 Hz (i.e., a ≥20-Hz increment). As the vibration train was 500 μm in amplitude at this comparison frequency, it may have spread sufficiently to activate some deeply located Pacinian corpuscles. At 50 Hz, subjective discriminative performance was also markedly impaired by superficial anesthesia (Fig. 8B), the two curves being signifi-
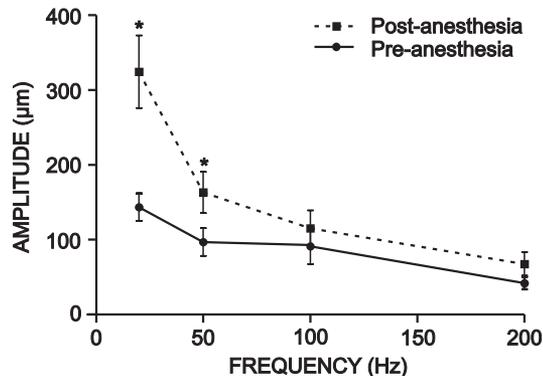

FIG. 7. Mean vibrotactile detection thresholds ($n = 8$) for the forearm hairy skin prior to, and after, superficial cutaneous anesthesia ($n = 6$; error bars = SE).
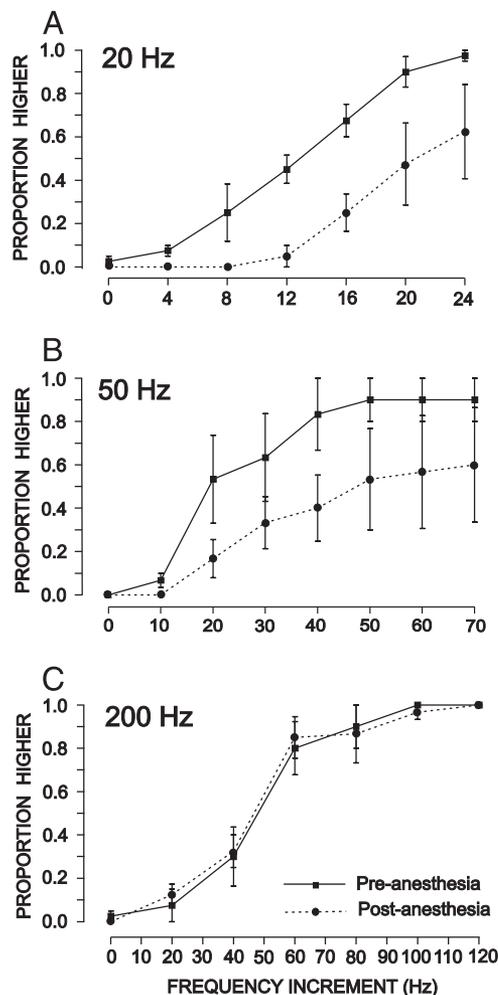
FIG. 8. Psychometric function curves for vibrotactile frequency discrimination on the forearm prior to and after, superficial cutaneous anesthesia. Psychometric function curves are shown for stimulus amplitudes of 2 times (*A*) and 4 times (*B*) threshold at frequencies of 20, 50, and 200 Hz (*n* = 4; error bars = SE).

cantly different ($P < 0.001$; based on ANOVA). At 200 Hz (Fig. 8*C*), there was no effect of the anesthesia ($P = 0.85$).

DISCUSSION

The finger tips and hand represent a source of high acuity tactile information that is reminiscent of the foveal input in vision. Receptor and afferent fiber density is far greater than in more proximal regions of the limbs and the trunk, conferring high accuracy of localization and spatial resolution, reflected, for example, in the two-point discriminative capacities in this skin area (Weinstein 1968). Furthermore, detection thresholds within the glabrous skin of the finger tips and palms are almost an order of magnitude better than those in the hairy skin (Merzenich and Harrington 1969; Talbot et al. 1968; Verrillo 1966) as a consequence of the different nature of the receptors (see Introduction) and, perhaps, differences in skin mechanics in the two skin regions.

Vibrotactile detection in hairy and glabrous skin

The present study has confirmed these marked differences in subjective vibrotactile detection thresholds (Fig. 2), which are consistent with the detection task over the low-frequency segment of the vibrotactile range being dependent on the HFA fiber class in hairy skin and the RA class in glabrous skin. Observations on the sensitivity of HFA fibers in the cat (Tuckett et al. 1978) and in the macaque monkey (Merzenich and Harrington 1969) show that their thresholds for activation by vibration match subjective detection values over the low-frequency segment (~5–80 Hz) of the human vibrotactile frequency range. The much lower subjective detection values in the glabrous skin over this low-frequency range are matched by the thresholds for the RA class of fibers associated with the Meissner corpuscles (Talbot et al. 1968).

In the upper frequency segment (80->500 Hz) of the vibrotactile range, subjective thresholds are also higher in hairy skin than in glabrous skin, with values of, for example, ~100 μm at 100 Hz and ~50 μm at 250 Hz in hairy skin (Fig. 2) compared with <10 μm and <4 μm for these frequencies in glabrous skin (Talbot et al. 1968). However, it is unlikely that these differences can be attributed to different receptor types in the two locations as PC receptors and afferent fibers probably account for subjective detection over the high-frequency range in both locations (see following text). Instead, the threshold differences may be explained by the differential proximity of the PC receptors in the two locations. Those associated with the glabrous skin lie in an immediate subcutaneous location, whereas PC receptors are absent within the hairy skin (Brown and Iggo 1967; Burgess et al. 1968; Tuckett et al. 1978) and lie remote and deep to the hairy skin of the forearm in locations such as the interosseous membrane, and in the regions of the wrist or elbow joint. Considerable stimulus spread is therefore required from the stimulus site on the dorsal surface of the forearm, with inevitable attenuation of the vibrotactile disturbance over these substantial distances. Nevertheless, high-frequency vibratory disturbances are known to be well transmitted through cutaneous and subcutaneous tissues from analysis of the visco-elastic properties of these tissues (Moore 1970) and also from the common observation in electrophysiological experiments that PC fibers can be activated by transient mechanical disturbances, often quite remote from the receptor location.

Vibrotactile frequency discrimination in hairy and glabrous skin

In contrast to the detection task, for which there are marked differences between the two skin sites, discriminative performance was remarkably similar probably because of a common coding mechanism for vibrotactile frequency information at the two skin sites. Much evidence points to the frequency parameter for vibration being encoded in an impulse pattern code in which the interspike intervals in the neural responses approximate the cycle period of the vibration. This arises because the impulse activity, elicited in RA, HFA, and PC fibers by vibratory stimuli, becomes tightly phase locked to the vibration waveform, generating a pattern of activity that accurately reflects the periodicity of the vibration stimulus (Ferrington and Rowe 1980b; Ferrington et al. 1984; Merzenich and Harrington 1969; Talbot et al. 1968; Zachariah et al. 2001). The explanation for the retention of impulse patterning at higher vibration frequencies, such as 200 Hz, is that the more abrupt temporal changes in the waveform of the 200-Hz

sinusoid are better able to synchronize or phase lock the impulse activity than the more gradual slow changes in the waveform of a 20- or 50-Hz sinusoid.

Although the precision of the impulse patterning in response to vibration is most striking at the level of the primary afferent fibers, it is retained, with some progressive degradation, in the responses of central neurons, going from the level of the dorsal column nuclei (Connor et al. 1984; Douglas et al. 1978; Ferrington et al. 1987a–c; Rowe 2002) to the thalamus (Ghosh et al. 1992, 1994) and to the primary and secondary somatosensory areas (SI and SII) of the cerebral cortex (Bennett et al. 1980; Ferrington and Rowe 1980a; Mountcastle et al. 1969, 1990; Rowe et al. 1985; Turman et al. 1992; Zhang et al. 1996). This deterioration in the precision of impulse patterning is due to a decline in both the tightness of phase locking and in the capacity to sustain high rates of discharge in the responses of individual neurons at higher levels of the central pathway (see also DISCUSSION in our companion paper, Sahai et al. 2006).

An alternative hypothesis has been enunciated by Romo and colleagues for coding the frequency parameter of vibrotactile stimuli (Hernandez et al. 2000; Romo and Salinas 2001; Salinas et al. 2000). They propose a code based on impulse rate or cumulative impulse counts rather than one based on phase locking and temporal patterning. At the primary fiber level this hypothesis is plausible perhaps for the PC fiber contribution as impulse rate in these fibers increases systematically with increases in vibration frequency.

However, within the central tactile pathways, and, in particular, at the level of the somatosensory cortex, the concept of a rate code is much less tenable. The reason for this is that cortical neurons show no systematic change in impulse rate with quite marked changes in vibration frequency. Instead, response levels in individual cortical neurons saturate and reach a plateau at relatively low impulse rates. This may be seen strikingly in the data of Mountcastle et al. (1969) for quickly adapting SI cortical neurons, in particular, in their Fig. 5 and their comments that, for these neurons, "on the basis of discharge rate there is no signal which might allow discrimination between any two frequencies lying between 30 and 200 Hz. " Although Romo's group found that 38% of SI neurons displayed an apparent rate code at vibration frequencies up to ~30 Hz (Hernandez et al. 2000), it must be emphasized that the impulse rate of cortical RA neurons peaks at vibration frequencies around 30 Hz and then reaches a plateau or declines as frequency is extended to 50 or 100 Hz (e.g., see Fig. 4 in Bennett et al. 1980 and Fig. 5 in Mountcastle et al. 1969). When this happens, there is no longer a monotonic increase in impulse rate as a function of frequency and potential ambiguity arises in the rate signal. Furthermore, ~75% of the neurons in the Romo group's studies displayed an impulse periodicity (or pattern code) that could account for pitch discrimination. Finally, they note that "although periodic firing can in principle provide a better code for stimulus frequency, firing rate cannot be dismissed" (Salinas et al. 2000).

In the case of the afferent fiber classes that respond to low-frequency vibrotactile stimuli, there appears to be little difference between the RA fibers in glabrous skin and the HFA fibers of hairy skin in the tightness of phase locking to the vibration (Ferrington and Rowe 1980b; Ferrington et al. 1984; Merzenich and Harrington 1969; Talbot et al. 1968; Zachariah et al. 2001). Furthermore, there is no evidence for any differ-

ential degradation of this frequency signal from these two sources in the responses of their corresponding target neurons of the cuneate nucleus. Those cuneate neurons linked to HFA inputs show tightly phase-locked responses to skin vibration, based on studies that include paired simultaneous recording from single HFA fibers and their target cuneate neurons (Sahai et al. 2006; Zachariah et al. 2001), as do cuneate neurons receiving RA fiber input (Bystrzycka et al. 1977; Connor et al. 1984; Douglas et al. 1978). Thus provided the intensity of the vibrotactile stimulus is high enough to activate the HFA endings in the hairy skin, these input fibers and their central target neurons are similar to their glabrous skin counterparts in their capacity to signal the frequency parameter of cutaneous vibratory disturbances.

Although the overall performance for vibrotactile frequency discrimination was similar for these hairy and glabrous skin sites, a possible exception to this exists at ~50 Hz (Figs. 4–6) where performance in the forearm hairy skin was poorer. This part of the vibrotactile frequency range falls in the transition zone from a dependency on intra-cutaneous afferents to the PC afferent fibers, and also marks the change-over in the subjective description of the sensation from one of flutter to one of vibration (Douglas et al. 1978; Merzenich and Harrington 1969; Talbot et al. 1968). It is possible that both the RA and PC classes contribute to subjective vibrotactile performance at these frequencies in the glabrous skin. However, in the hairy skin, the subjective performance may have to depend largely on HFA afferents as the PC afferent fibers may be too remote from the stimulus site to be effectively engaged by these vibrotactile frequencies except at very high amplitudes. Furthermore, in the circumstance where the PC fibers are recruited along with HFA fibers at these frequencies, the two subsets may be spatially separate enough to introduce some temporal discrepancies in the impulse patterning of the overall afferent input. This may lead to a degradation of the vibrotactile frequency signal compared with the information contained in the impulse patterns of each fiber subset.

Some evidence for the switch-over from intra-cutaneous receptors to PC receptors and afferent fibers at frequencies around the 50- to 60-Hz region comes from reports that local anesthesia of the superficial glabrous or hairy skin preferentially disrupts low-frequency vibrotactile detection leaving high-frequency detection intact (Merzenich and Harrington 1969; Talbot et al. 1968). In the present experiments, we have observed this differential impairment of vibratory detection with local anesthesia of the hairy skin in the dorsal forearm. However, consistent with this, we also observed that frequency discrimination in the low-frequency range (20 and 50 Hz; Fig. 8) was abolished or greatly impaired, whereas there was no effect at 200 Hz (Fig. 8). The residual impaired discriminative performance at 20 and 50 Hz may be attributable to a weak engagement of remote PC afferents by spread of the high-amplitude comparison vibration, which, at the 50% level on the psychometric function curve, was achieved only by an approximate doubling of frequency and at high-intensity for both the 20- and 50-Hz standard frequencies (Fig. 8).

The absence of any effect of local anesthesia on frequency discrimination at 200 Hz (Fig. 8) is consistent with the deeply located PC receptors being responsible for detection and discrimination at this frequency. Further evidence for this conclusion comes from our recent electrophysiological study in the

cat (Sahai et al. 2006) that showed that some cuneate neurons activated from the dorsal surface of the forearm had vibrotactile bandwidths extending to 300 Hz or beyond that is consistent with their input coming from remotely located deep PC receptors of the forearm as HFA fibers have bandwidths that rarely exceed 80 Hz (Merzenich and Harrington 1969; Zachariah et al. 2001).

Are there contributions to vibrotactile sensibility from other receptor classes?

Although slowly adapting (SA) afferent fibers in both glabrous (Talbot et al. 1968) and hairy skin (Gynther et al. 1992; Merzenich and Harrington 1969; Vickery et al. 1992) are highly sensitive to skin vibration, in particular, at low vibration frequencies, it is felt that they do not contribute to the vibrotactile sense (Merzenich and Harrington 1969; Talbot et al. 1968). This is because of a mismatch between subjective thresholds for vibration detection and the thresholds for entrainment of the SA responses to the vibration stimulus. At low vibration frequencies, the SA fiber can be entrained by vibratory stimuli at intensities well below subjective detection thresholds but at high frequencies, require intensities well above the subjective thresholds. Furthermore, correlative neural and psychophysical studies by Bolanowski et al. (1988, 1994) indicate that at the vibration frequencies >20 Hz examined in the present study, the SA fibers are less sensitive than other classes and are unlikely to contribute to vibrotactile sensibility. Further evidence that SA afferent fibers are unable to contribute to vibrotactile sensibility comes from microneurography experiments in conscious human subjects in which single SA fibers have been selectively activated by intraneural microstimulation. When this was done, with trains of electrical stimuli at frequencies of 20–100 Hz, the percept described, in the case of SAI fibers, is one of steady pressure or deformation in the region of the fiber's receptive field, in contrast to the vibrotactile percept generated by the same train of stimuli delivered to individual RA or PC fibers (Macefield et al. 1990; Ochoa and Torebjörk 1983; Vallbo et al. 1984). With the activation of single SAII afferent fibers, it was found by Ochoa and Torebjörk (1983) that *no* perceptual response was generated.

Human capacity for vibrotactile frequency discrimination

The increase in absolute magnitude of the jnd, or Δf, for frequency discrimination from ~5 Hz at a standard frequency of 20 Hz to values of ~25 Hz at 200 Hz (Fig. 5B) suggests that there is a deterioration in discriminative performance as a function of increases in frequency. However, when expressed as a ratio of the standard frequency, that is, as the Weber Fraction, $\Delta f/f$, this ratio is independent of, or even falls slightly, as a function of increases in the standard frequency, at least ≤200 Hz (Fig. 5C). Furthermore, as Fig. 6 emphasizes, the absolute temporal shift in cycle length with a Δf of 5 Hz for the standard frequency of 20 Hz is 10 ms, whereas the 25-Hz increment at 200 Hz represents an absolute change in cycle length of ~0.5 ms. Thus despite the absolute frequency shift (Δf) for discrimination being coarser at 200 than at 20 Hz, the absolute temporal shift that has been discriminated at 200 Hz is ~1/20 of that at 20 Hz. The explanation for this is presum-

ably linked to the fact that the more abrupt transitions in the rise and fall of the vibration waveform at high frequencies, such as 200 Hz, compared with those that occur at 20 Hz, serve to entrain the impulse activity more tightly in an absolute temporal sense at the high frequencies. This is borne out by comparison of the cycle histogram distributions of the probability of impulse occurrences at different frequencies. Those at 200 Hz in the primary afferent fibers tend to be confined within ~10% of the cycle period; that is, within ~0.5 ms, whereas the impulse occurrences at 20 Hz are spread across ~20% of the cycle period or 10 ms (Ferrington and Rowe 1980b; Ferrington et al. 1984, 1987a,b; Rowe 2002; Talbot et al. 1968).

The values for the Weber Fraction of ~0.25–0.35 in Fig. 5C are similar to those reported by Goff (1967) for the finger tip and Rothenberg et al. (1977) for the sparsely haired skin of the volar forearm when using sinusoidal vibration. Our finding that the Weber Fraction was independent of changes in the standard frequency or showed a small decline as a function of frequency (Fig. 5C), at least up to standard frequencies of 200 Hz, differed slightly from Goff's (1967) finding of a tendency for the Weber Fraction to increase over this same range. As Rothenberg et al. (1977) also found when using sinusoidal stimuli that the Weber Fraction for frequency discrimination showed no real trend as a function of frequency, it appears, at least over this segment of the vibrotactile range, that there is little departure from Weber's Law that $\Delta s/s$ is a constant.

Certain other studies have reported remarkably low values of the Weber Fraction (~0.03) even at frequencies >200 Hz (Franzen and Nordmark 1975; Mowbray and Gebhard 1957). However, these were obtained with various methodological differences (see Rothenberg et al. 1977), among them the use of trains of brief mechanical pulses rather than sinusoidal vibration. Such stimuli, with more abrupt dynamic components, may entrain the neural activity much more tightly than does sinusoidal vibration and may have contributed to the reported discriminable increments being as low as ~3%.

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