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VIBROTACTILE SENSITIVITY OF SLOWLY ADAPTING TYPE I SENSORY FIBRES ASSOCIATED WITH TOUCH DOMES IN CAT HAIRY SKIN

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SUMMARY

1. Recordings were made from single slowly adapting type I (SAI) afferent fibres associated with touch domes in the cat hairy skin. Controlled vibratory stimuli were used first, to characterize the precision with which these SAI afferents reflect the temporal aspects of vibrotactile stimuli, and second, to determine whether earlier disparate reports of SAI responsiveness to vibration may be attributable to highly specific stimulus requirements.

2. Eighteen SAI fibres from femoral cutaneous nerve branches were examined; each was associated with one to three touch domes. SAI responses to both steps and sinusoidal vibration (1–1·5 s in duration) were affected profoundly by both probe size and position. Punctate stimulus probes (250 μm) produced much higher response levels and steeper stimulus–response relations than those elicited with large (2 mm) probes, probably on account of focal distortion created within the dome by the smaller probes. SAI sensitivity to vibration was also affected markedly by the amplitude of any pre-indentation on which the vibration was superimposed; sensitivity was much lower when the pre-indentation exceeded 100 μm, in particular with larger stimulus probes.

3. Measures of both vibration sensitivity and the precision of impulse patterning demonstrated that, if appropriate stimulus parameters are chosen, the SAI fibres can respond to 1 s trains of vibration (amplitude $\leqslant$ 100 μm) in a tightly phase-locked, 1 : 1 manner for frequencies up to 500 Hz. At frequencies from $\sim$ 100–500 Hz the SAI fibres displayed broad 1 : 1 plateaus, where their response rate remained constant over a range of amplitudes, and phased-locking was tightest. Responses remained phase-locked up to 1000 Hz, but could not follow the vibration with a 1 : 1 pattern above 500 Hz.

4. The results demonstrate that with appropriate stimulus parameters, touch dome-associated SAI fibres are capable of signalling vibrotactile information over a similar bandwidth of frequencies as do Pacinian sensory fibres. The variability in past reports of SAI vibration sensitivity may relate principally to differences in stimulus conditions. However, in view of the SAI capacity for responding to vibration with temporally precise, patterned activity, it appears that their reported

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failure to contribute to vibrotactile sensibility must be attributed to limitations imposed in the central processing of SAI signals.

INTRODUCTION

One of the first correlations between morphologically identified receptors and physiologically identified tactile afferent fibre types was for the receptors found in the touch dome or Haarscheibe (Iggo, 1961). Haarscheiben are found in the hairy skin of mammals, and were first described by Pinkus (1904) in man, while the first physiological recording from the sensory nerves that supply the receptors beneath the touch dome, was in the rabbit (Frankenhaeuser, 1949). Touch domes are visible as small protuberances, 100 to 400 μm in diameter, in the hairy skin. A single touch dome may contain up to fifty Merkel cells associated with axonal endplates, which derive, in almost every case, from a single large myelinated fibre (Smith, 1967; Iggo & Muir, 1969). In the cat, between one and five touch domes are innervated by a single afferent fibre, which has a slowly adapting response to a static skin indentation, but also displays a marked dynamic sensitivity (Iggo & Muir, 1969). These fibres are designated slowly adapting type I (SAI) to distinguish them from the other class of slowly adapting tactile afferent (SAII), which is associated with Ruffini endings (Chambers, Andres, v. Duering & Iggo, 1972). Tapper (1965), and Werner & Mountcastle (1965) among others, examined in detail the responses of touch dome SAI afferent fibres to step indentations in cats and monkeys, although both of these papers probably also included responses from SAII fibres in the sample, as the two slowly adapting types were only distinguished clearly in 1967 (Chambers & Iggo). The receptors beneath touch domes resemble the Merkel receptor complex found in glabrous skin (Jänig, 1971), and a slowly adapting Merkel cell-associated receptor is also found in sinus hair follicles (Gottschaldt, Iggo & Young, 1973).

The distinctive sensitivity of touch dome-associated SAI fibres to maintained skin displacement, and the results of psychophysical studies, have led to the view that these fibres subserve a sense of pressure and play no role in the detection and discrimination of vibration (Merzenich & Harrington, 1969). Reports on the vibration sensitivity of these SAI afferents have varied considerably. Observations within one species, the cat, have led to reports that SAI fibres rarely follow frequencies above 200 Hz (Horch & Burgess, 1976) or, alternatively, are most sensitive at $\sim$ 400 Hz (Tapper, Galera-García & Brown, 1972). In contrast, the SA fibres (presumed SAI) associated with the sinus hair follicles in the cat, are reported to show 1:1 responses up to 1200 Hz (Gottschaldt & Vahle-Hinz, 1981). Merzenich & Harrington's (1969) observations on SA fibres of primate hairy skin suggest that 1:1 thresholds are lowest below 100 Hz, but are very sensitive to the on-going rate of discharge in the afferent. The SAI afferents that supply human hairy skin do not show 1:1 following even at 200 Hz (Järvilehto, Hämäläinen & Laurinen, 1976).

The aim of the present study was first, to characterize the precision with which SAI fibres associated with touch domes can reflect the temporal aspects of a vibrotactile stimulus, and second, to determine whether the disparate accounts of SAI responsiveness to vibration are related to these fibres having highly specific requirements for the stimulus parameters employed. A preliminary account of the data has been given in conference proceedings (Vickery, Gynther & Rowe, 1990).

METHODS

Animal preparation

Eight adult cats were used. Anaesthesia was induced by intraperitoneal injection of sodium pentobarbitone (40 mg kg^{-1}), and maintained by infusion of sodium pentobarbitone (4 mg kg^{-1} h^{-1}) in 0·18% saline delivered by the cephalic vein. Rectal temperature was held at $38 \pm 0{\cdot}5$ °C and blood pressure monitored at the carotid artery. The hips and hindpaw of the animal were fixed in place to prevent movement of the limb. An incision was made in the dorsal surface of the proximal portion of the hindlimb, and the posterior femoral cutaneous nerve or other cutaneous branches of the femoral nerve were exposed. A paraffin pool was formed by stitching the skin flaps to a brass ring. The nerve was cut and fine strands teased and placed over a platinum wire recording electrode. Skin in the area of the nerve distribution was shaved and, in five out of the eight cats, was then depilated, using a commercially available hair remover. No differences were apparent in results depending on whether the skin was depilated or merely shaved.

Identification and mechanical stimulation of touch domes

The region of distribution for the nerve strand was examined with hand-held probes, and areas from which slowly adapting neural responses could be obtained were examined under a dissecting microscope with a von Frey hair in order to identify touch domes. Touch domes and their SAI afferent fibres could be identified unequivocally by their slowly adapting responses with irregular interspike intervals (see Fig. 1*A*), their insensitivity to skin stretch at a distance, and the localization of the area of tactile sensitivity to raised domes on the skin surface (Chambers *et al.* 1972). After the number of touch domes associated with the SAI fibre under study was identified, a mechanical stimulator (Douglas, Ferrington & Rowe, 1978), with a flat-tipped probe (diameter between 0·25 to 2 mm), was positioned perpendicular to the skin, lowered until just touching the surface of the dome, and then raised fractionally ($\sim 10\ \mu$m). This stimulator was capable of delivering precisely controlled static and sinusoidal displacements. Stimuli consisted of step indentations up to 1 mm in amplitude, that lasted 1·5 s and, for vibration studies, had a superimposed 1 s train of vibration commencing 300 ms after the onset of the step. Stimuli were repeated every 10–15 s.

Analysis of the SAI response data

Analysis of the SAI fibre responses to vibration involved construction of cycle histograms, which have a duration equal to the period of the applied sinusoidal vibration. The phase of the vibration cycle at which each impulse occurred determined the histogram column to be incremented. However, because of the conduction time from the receptor to the recording electrode, this did not represent the absolute phase at which the response occurred. A tightly phase-locked response was apparent as a single narrow peak in the cycle histogram. The *resultant* (r) is a measure of the concentration of a circular distribution, such as a cycle histogram where it indicates the tightness of phase-locking in the response to vibration. The *resultant* is the length of the mean vector of the distribution, and its calculation depends on the phase angle at which each impulse occurs (x_i), and the total number of impulses (n). It is calculated from the formula:

$$r = \frac{\sqrt{\left\{\left[\sum_{i}^{n} \cos(x_i)\right]^2 + \left[\sum_{i}^{n} \sin(x_i)\right]^2\right\}}}{n},$$

and has a value from 0 to 1, where 0 indicates no phase-locking, and 1 indicates perfect phase-locking. A value of r less than 0·17 indicates no significant phase preference in the response ($P >$ 0·05 for $n = 100$), while a value of r greater than 0·3 indicates a highly significant phase preference in the response ($P < 0{\cdot}0001$ for $n = 100$; Durand & Greenwood, 1958). Values of r greater than 0·7 are common in phase-responsive biological systems, such as the auditory system (Lavine, 1971), and the somatosensory system (Greenstein, Kavanagh & Rowe, 1987).

RESULTS

Touch domes were readily identified in depilated or shaved skin in the cat hindlimb, as smooth, domed elevations of the epidermis, 100 to 400 μm in diameter

(Smith, 1967; Iggo & Muir, 1969), whose shape varied from small sessile domes, to large slightly pedunculated structures. The touch domes were often associated with tylotrich hairs – a single hair lying across and indenting the surface of a touch dome. Movement of the hair often resulted in compression of the touch dome.

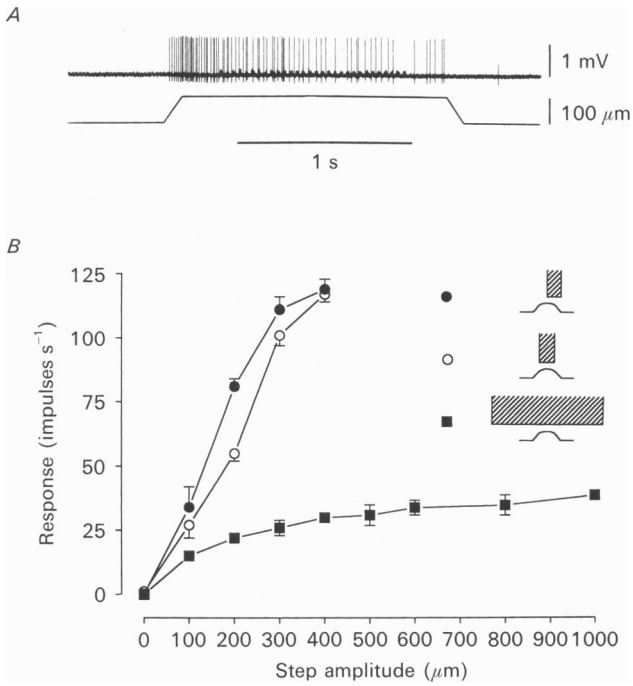

Fig. 1. Effect of probe size and position on SAI responses to step indentations of the associated touch dome. *A*, SAI response to a 1·5 s duration, 100 μm step indentation (rise time 100 ms). The number of impulses in the 1 s segment commencing 300 ms after the onset of the step (indicated by the bar beneath the stimulus waveform) was used as a quantitative measure of response. This measure was plotted in *B* for one SAI fibre, and illustrates the effect of different probe sizes and positions (see inset in *B*) on the responses to step indentations. Responses in *B* are the means of five values and error bars are one standard deviation (note some S.D.s are smaller than the symbol). ■, 2 mm probe centred on touch dome; ○, 250 μm probe centred on touch dome; ●, 250 μm probe edge across touch dome.

General response properties to step indentations

From one to three touch domes were associated with each of the eighteen SAI fibres studied, with two being most frequent. SAI fibres were identified by their slowly adapting response to step indentation of a touch dome, and the absence of a response when the skin immediately adjacent to the touch dome was stimulated. Figure 1*A* illustrates the response of an SAI fibre to a 100 μm vertical step indentation of a touch dome, delivered by means of a 250 μm diameter probe. The fibre responded with an instantaneous frequency up to 200 impulses s^{-1} to the onset of the step, which had a velocity of 1 mm s^{-1}. This initial dynamic response was

followed by a maintained but lower level of response for the duration of the step. No off-response was observed at the termination of the step. SAI fibres rarely showed any spontaneous activity in the absence of mechanical stimulation of touch domes.

Effects of stimulus parameters on SAI responses

Responses to step indentations

The effect of stimulus probe size and position on SAI responses to step indentations was assessed by constructing stimulus–response relations based on the response rate during the static phase of indentation as a function of the indentation amplitude (Fig. 1*B*). The small probe (250 μm diameter) positioned directly over the touch dome (○), or with its edge across the centre of the dome (●), produced a greater response at all step amplitudes tested than did the large (2 mm) probe centred over the dome (■, Fig. 1*B*). Step amplitudes above 400 μm were not tested with the small probe so as to avoid damaging the touch dome. The steeper stimulus–response relations obtained with the small probe indicate that the SAI fibre can convey a more reliable and graded signal of indentation amplitude in the range up to ~ 0·5 mm when the stimulus source is a small punctate one than when a large contact surface is employed. At higher amplitudes the stimulus–response relation obtained with the punctate stimulus probe appeared to approach a plateau at a response rate of 120 impulses s^{-1} (Fig. 1*B*, ○ and ●). However, the response to the large probe also reached a plateau at step indentations of ~ 0·5 mm, even though the response rate of the afferent was only 30 impulses s^{-1} (Fig. 1*B*, ■). The indenting stimulus with the small probe was more effective when the 250 μm probe edge was placed across the touch dome, as this produced the steepest stimulus–response relation shown in Fig. 1*B* (●).

Vibration sensitivity assessed with tuning curves: effect of probe size and position

The main aims of these experiments were to identify the factors that affect the response of touch dome-associated SAI fibres to cutaneous vibration and to explain the quite different claims made about vibrotactile sensitivity of SAI fibres. The usual stimulus consisted of a 1·5 s step indentation of the skin, which ensured good contact between the probe and the skin during the 1 s of vibration which commenced 300 ms after the onset of the step. The 1:1 threshold of the SAI fibre at each vibration frequency was defined as the minimum amplitude of probe vibration required for the discharge of one impulse for each vibration cycle over the entire 1 s of vibration (1:1 following). Figure 2*A* shows the response of an SAI fibre at its 1:1 threshold for vibration at 200 Hz, in this instance, at a peak-to-peak vibration amplitude of 32 μm. Tuning curves (plots of 1:1 threshold against frequency) for six SAI fibres, obtained using a small probe (250 μm) centred over the touch dome, are shown in Fig. 2*B*. These fibres followed vibration frequencies up to ~ 500 Hz at amplitudes below 100 μm. It was usually not possible to obtain meaningful 1:1 thresholds at frequencies below 100 Hz, as the slowly adapting response evoked by the step indentation alone was often 50 to 100 impulses s^{-1}, with the applied vibration only modulating the temporal pattern of the afferent response.

Vibration delivered with the 250 μm diameter probe was a far more effective stimulus for SAI fibres (Fig. 2*C*; ● and ○) than that delivered with the 2 mm

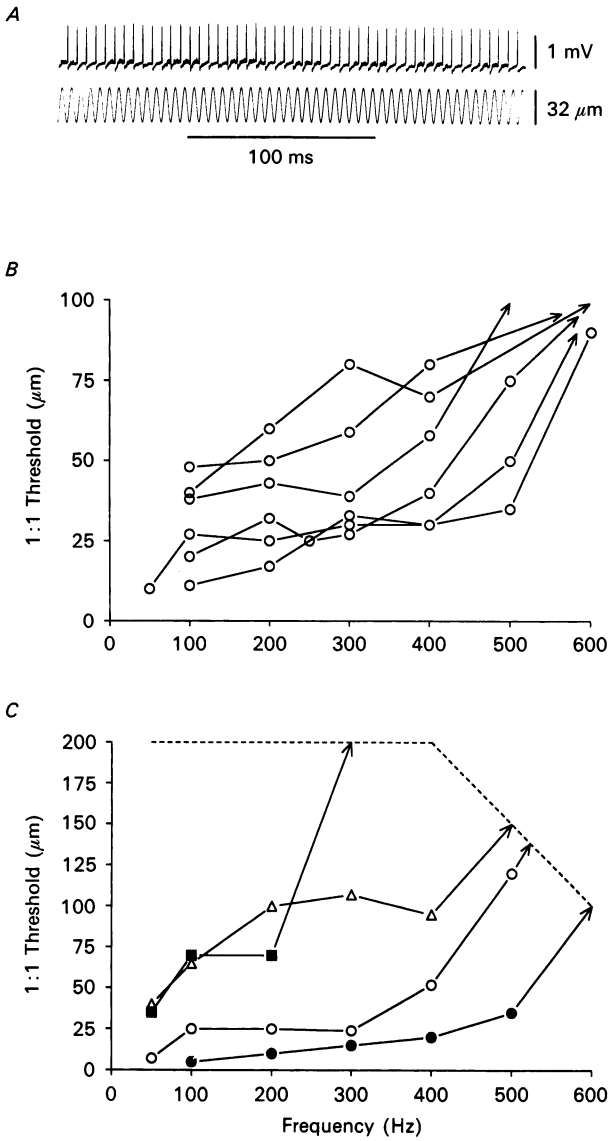

Fig. 2. Vibration sensitivity of SAI fibres. *A*, a 250 ms segment showing the 1:1 pattern of response of an SAI fibre to 200 Hz vibration (superimposed on a 100 μm step indentation). The illustrated segment commenced 200 ms after the onset of the 1 s train of vibration. *B*, tuning curves for six SAI fibres, based on 1:1 thresholds as a function of vibration frequency, and obtained with a 250 μm probe centred over the touch dome (vibration superimposed on a 100 μm step indentation). Arrows extending towards 100 μm indicate that 1:1 following was not achieved at that frequency at the 100 μm amplitude. *C*, tuning curves illustrate the effects of probe size and position on vibration sensitivity in a further SAI fibre (not shown in *B*). The dashed line indicates the maximum output amplitude of the mechanical stimulator. ■, 2 mm probe centred on touch dome; ○, 250 μm probe centred on touch dome; ●, 250 μm probe edge across touch dome; △, 250 μm probe applied to the tylotrich hair associated with the touch dome, at a distance of 600 μm from the base of the hair.

diameter probe, which rarely elicited 1:1 following at frequencies above 200 Hz for amplitudes below 200 μm (Fig. 2*C*, ■). However, the 1:1 threshold at any vibration frequency, determined with the 250 μm probe, was very sensitive to the probe position as may be seen in Fig. 2*C* where the 1:1 thresholds fell by roughly half when the 250 μm probe was moved from a position centred over the dome (○) to one in which the edge of the probe crossed the centre of the dome (●, Fig. 2*C*; also see inset diagram in Fig. 1*B*).

The SAI fibres were essentially unresponsive when the 250 μm probe was moved 1 mm onto the skin immediately adjacent to the touch dome. The only effective form of remote vibrotactile stimulation was through the tylotrich hairs that lay across the touch domes. Figure 2*C* (△) shows that the SAI fibre followed vibration at frequencies up to 400 Hz when the probe contacted the tylotrich hair at a distance of 600 μm from the touch dome. Although the fibre was more sensitive to vibration when the small probe was applied directly to the touch dome (Fig. 2*C*, ○ and ●), the transmission of vibratory disturbances to touch domes by means of the tylotrich hairs may act to increase the receptive field size of SAI fibres. The response of SAI fibres to vibration of the associated tylotrich hair diminished as the probe was moved along the hair away from the touch dome. At 200 Hz for example, the 1:1 thresholds for the fibre illustrated in Fig. 2*C* were 18, 100, and 162 μm when the probe was positioned at distances of 300, 600 and 900 μm respectively along the tylotrich hair from the touch dome.

Effectiveness of stimulation is determined by probe size and dome shape

Large probes (2 mm) were less effective for vibrotactile stimulation of the SAI fibres than the small, 250 μm probes, but their effectiveness varied greatly depending upon the shape of the stimulated touch dome. For example, when applied to large protuberant domes, the 2 mm probe did not contact the surrounding skin during a 100 μm pre-indentation, and in such cases, the SAI fibre was quite sensitive to vibration. In contrast, when applied to sessile domes the large probe would compress the surrounding skin during a 100 μm pre-indentation, and the SAI fibre generally responded poorly to vibration.

The response to step indentations without vibration was also sensitive to the combination of probe size and dome shape. Large domes (> 250–300 μm in diameter and 100 μm in height) had ratios of response rates during step indentation by the small probe, to those elicited by the large probe, that ranged from 1:1 to approximately 2·5:1 ($n = 6$), while small domes had ratios of 4:1 to 9:1 ($n = 3$). The response of SAI fibres associated with the small sessile domes was thus much more dependent upon the precise nature of the stimulus, than was that of SAIs associated with larger domes.

Effects of the pre-indentation amplitude on vibration-induced responses of SAI fibres

Individual SAI fibres showed marked differences in vibration sensitivity when different levels of pre-indentation were applied, in particular with the large (2 mm) probe. This is illustrated by the three stimulus–response relations of Fig. 3*A*, which plot the responses of an individual SAI fibre to 200 Hz vibration, when three

different pre-indentation amplitudes were used. Vibration superimposed upon a 100 μm pre-indentation (□) was dramatically more effective than when superimposed upon a 300 μm (○) or 500 μm (△) step. These larger pre-indentations caused the probe to compress *both* the touch dome and the surrounding skin.

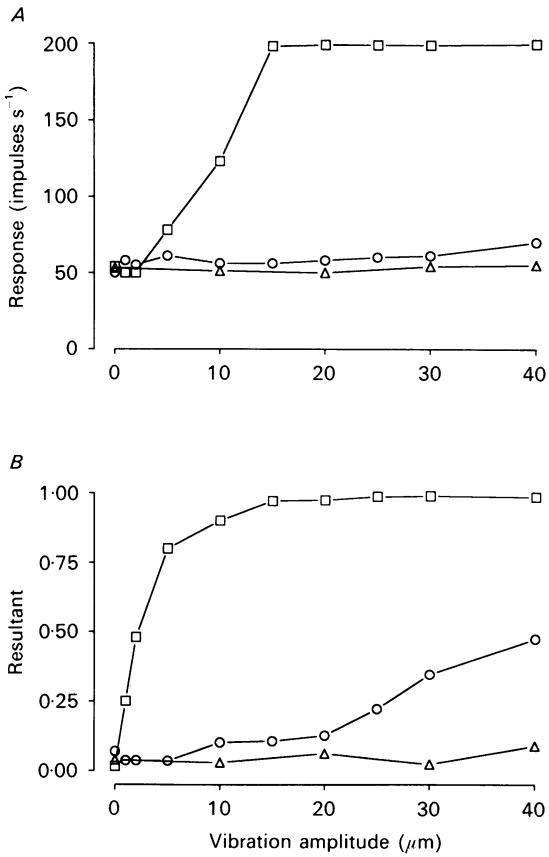

Fig. 3. Effects of amplitude of a pre-indentation step on vibration sensitivity of an SAI afferent. The 2 mm diameter probe was used to deliver vibration with different pre-indentations to a large dome; in *A* and *B*: △, 500 μm step; ○, 300 μm step; □, 100 μm step. *A*, stimulus–response curves constructed at 200 Hz for the three pre-indentations. Each value is the mean of five responses; the standard deviations of these values were not plotted as they were in general smaller than the size of the symbols. The one exception was the value at 10 μm on the graph for the 100 μm step (mean response of 123 ± 10 impulses s^{-1}). *B*, the relation between phase-locking (as measured by the resultant, see Methods) and vibration amplitude at 200 Hz, is plotted for the three different pre-indentations from the data used in *A*. With the larger step indentations (300 and 500 μm) there is virtually no response to the vibration, and therefore no phase-locking. For the small step (100 μm), the onset of 1:1 following in *A* at 15 μm vibration amplitude coincides with the appearance of extremely tight phase-locking (resultant > 0·95) in *B*.

The tightness of phase-locking in the SAI responses to vibration was also critically dependent upon stimulus parameters, including the size of any pre-indentation. The marked reduction in response level with large pre-indentations (Fig. 3*A*) was

paralleled by the decline in the resultant, plotted in Fig. 3*B* as a measure of phase-locking (see Methods), for the same responses used for Fig. 3*A*. With a 100 μm pre-indentation (□, Fig. 3*B*), the resultant approached its maximum value of 1 at the 1 : 1 threshold of the fibre (15 μm). Some phase-locking occurred at higher amplitudes

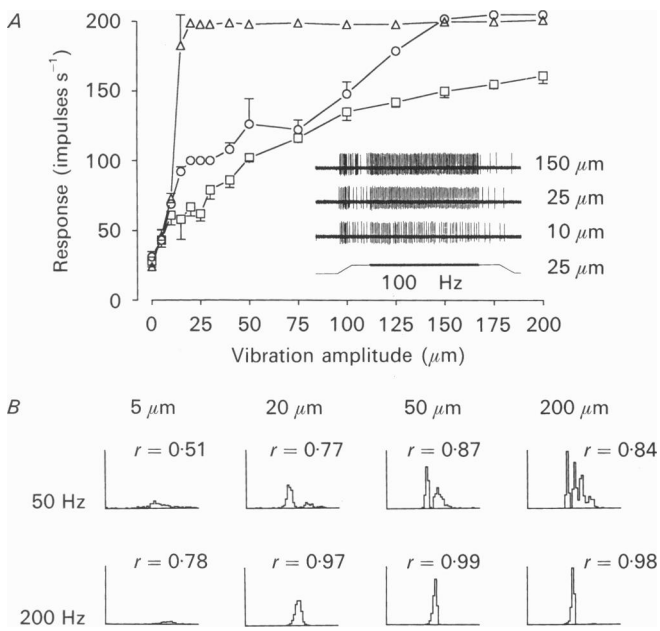

Fig. 4. Effect of amplitude and frequency of vibration on the responses of a representative SAI fibre. *A*, each point in the three stimulus–response relations (at 50, 100 and 200 Hz) is the mean of at least five responses, and the errors bars are standard deviations. The relation at 200 Hz (△) has a prominent 1 : 1 plateau, while that at 100 Hz (○) has a briefer plateau at both a 1 : 1 and a 2 : 1 response level. The relation at 50 Hz (□) has no plateau as the response of the afferent increased gradually with increasing vibration amplitude. The 250 μm diameter probe was used with a step indentation of 100 μm. The data traces in the inset in *A* last 1·9 s and are from the 100 Hz series. They show the impulse patterning, in particular, the regular 1 : 1 pattern of response to a 1 s train of vibration at 100 Hz (25 μ). *B*, the cycle histograms (see Methods) at 50 and 200 Hz show the extent of phase-locking (indicated by the values of *r*, the resultant) as a function of vibration amplitude. The 50 Hz histograms have a duration (horizontal axis) of 20 ms, and the 200 Hz histograms, 5 ms. They were all constructed from responses to three 1 s vibration trains. The vertical axis at 50 Hz indicates 100 counts, and at 200 Hz indicates 310 counts.

of vibration with a 300 μm step (○, Fig. 3*B*), but with a 500 μm pre-indentation (△, Fig. 3*B*), the SAI fibre was virtually insensitive to vibration as shown by the low, and amplitude invariant, value of both the response rate (Fig. 3*A*) and the resultant (Fig. 3*B*).

The 250 μm probe was smaller in diameter than most touch domes, and therefore did not contact the surrounding skin during a step indentation. It was probably on account of this circumstance that no consistent relation was observed between pre-

indentation amplitude and the response of SAI fibres to vibration delivered with the 250 μm probe.

Precision of SAI responses to sinusoidal vibration

Effect of vibration amplitude

The range of vibration amplitudes over which an afferent fibre exhibits 1:1 following is known as the 1:1 plateau or tuning plateau (Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968). The 1:1 threshold delimits the lower end of the plateau, while the upper end is marked by the initial appearance of two impulses in an individual vibration cycle. At the 1:1 plateau, responses are characterized by intervals between successive impulses that equal the period of the vibration, and this is thought to be the basis for the neural coding of vibration frequency (Talbot *et al.* 1968; Douglas *et al.* 1978). Vibration at 200 Hz produced a clear 1:1 plateau in the responses of SAI fibres, as may be seen in Fig. 4*A* (△), which plots the response level of an SAI fibre over a range of amplitudes at three different vibration frequencies. With 100 Hz vibration (Fig. 4*A*, ○) the fibre showed both a 1:1 and 2:1 (two impulses per cycle) plateau; while with 50 Hz (□) the response was relatively graded throughout the range of vibration amplitudes examined, with no clear 1:1 plateau.

The inset in Fig. 4*A* shows impulse traces in response to 100 Hz vibration at three amplitude levels: below the 1:1 plateau (10 μm), on the 1:1 plateau (25 μm), and on the 2:1 plateau (150 μm). The regularity of the interimpulse interval on the 1:1 plateau is apparent in the response trace at 25 μm. Furthermore, the cycle histograms for 200 Hz in Fig. 4*B* show that on the 1:1 plateau the impulses occur within a very narrow segment of the cycle period and are therefore tightly phase-locked as reflected in the high values of the resultant (r).

Phase-locking in SAI responses at different vibration frequencies

The impulse activity of the SAI fibres remained phase-locked to the vibration even at response levels that were above or below the 1:1 response level. This is evident from the cycle histograms in Fig. 5 constructed from responses of an SAI fibre to different vibration frequencies at a fixed vibration amplitude of 15 μm (the 1:1 threshold at 200 Hz). The 15 μm amplitude was below the 1:1 plateau for 400, 700 and 1000 Hz, and above the 1:1 plateau for 10, 40 and 100 Hz, as indicated in each histogram by the value of n, the mean number of impulses evoked by a 1 s train of vibration (Fig. 5). At 100, 400 and 700 Hz, the fibre showed tight phase-locking to the applied vibration (resultant $r > 0{\cdot}7$, see Methods), and although at the higher frequencies the response to vibration (n) diminished, significant phase-locking was still present even at 1000 Hz (Fig. 5). The cycle histograms constructed from responses at levels above the 1:1 plateau (especially 10 and 40 Hz) show multiple peaks, as the fibre often responded with two or more impulses within each cycle of vibration; for example, the cycle histogram for 40 Hz shows two peaks as the fibre was almost at the 2:1 plateau (Fig. 5).

The quality of phase-locking varied with the frequency of the applied vibration, even with responses that were standardized at a 1:1 level at each frequency. Figure 6*A* plots the mean value of the resultants of ten fibres tested at their 1:1 thresholds

for several frequencies. This was not the maximum value of the resultant at each vibration frequency, as this occurs at higher amplitudes on the 1:1 plateau (Figs 3 and 4), but the 1:1 threshold provides a functional standard for comparisons across the population of fibres (see also Talbot *et al.* 1968; Ferrington & Rowe, 1980). The

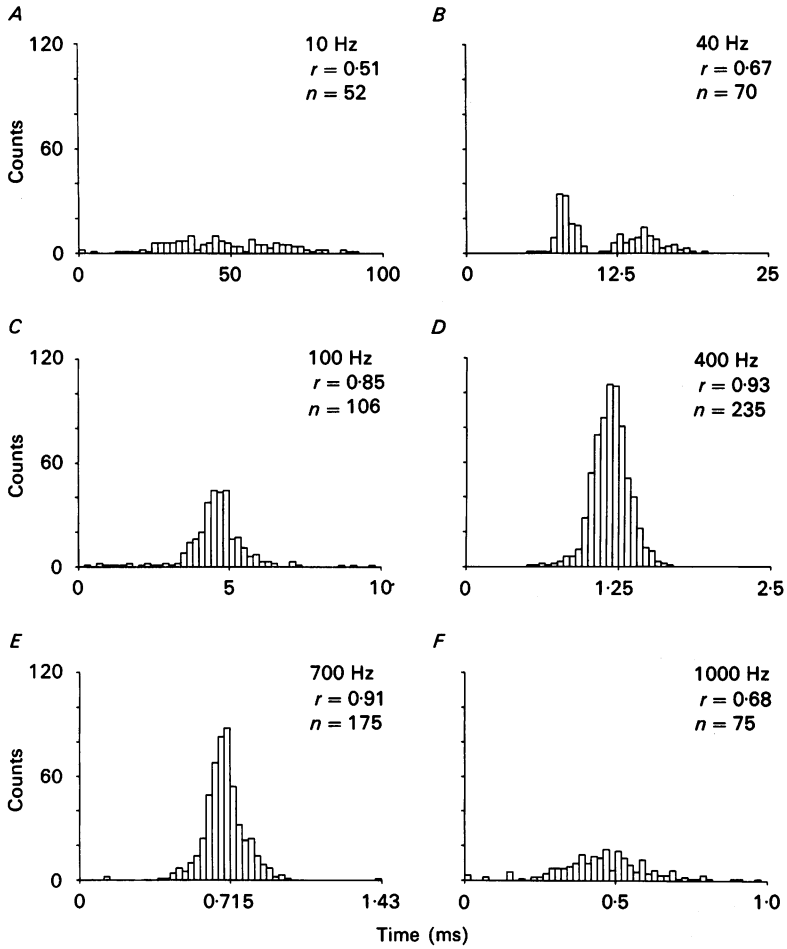

Fig. 5. Cycle histograms constructed from the response of an SAI fibre to 15 μm vibration at six different frequencies. The analysis time, represented by the horizontal axis in each CH, equals the *period* of the vibration and is divided into fifty addresses. Each histogram was built up from the accumulated responses to five 1 s trains of vibration on a 100 μm pre-indentation, delivered with the 250 μm probe. The extent of phase-locking is indicated by the spread of the distributions and by the resultant value (r). n denotes the mean response rate (impulses s^{-1}). The multiple peaks in the histogram at 10 and 40 Hz contribute to poorer measures of phase-locking, while at 700 and 1000 Hz the response level was lower (n well below the applied frequency, and less than the response obtained at 400 Hz), but there was still relatively good phase-locking, in particular at 700 Hz.

phase-locking was best at 200 Hz, although for individual fibres the best frequency varied from 100 to 400 Hz. The quality of the phase-locking falls off sharply at and below 50 Hz, and at 500 Hz and above. There was little variation between fibres

except at 50 Hz, as the small standard error bars show. The cycle histograms in Fig. 6*B* are from a representative SAI fibre and indicate the extent of phase-locking at the 1:1 response level for each vibration frequency.

DISCUSSION

Responses of SAI fibres to step indentations of touch domes

Since the original electrophysiological experiments on single cutaneous afferent fibres (Adrian & Zotterman, 1926), it has been recognized that the frequency of

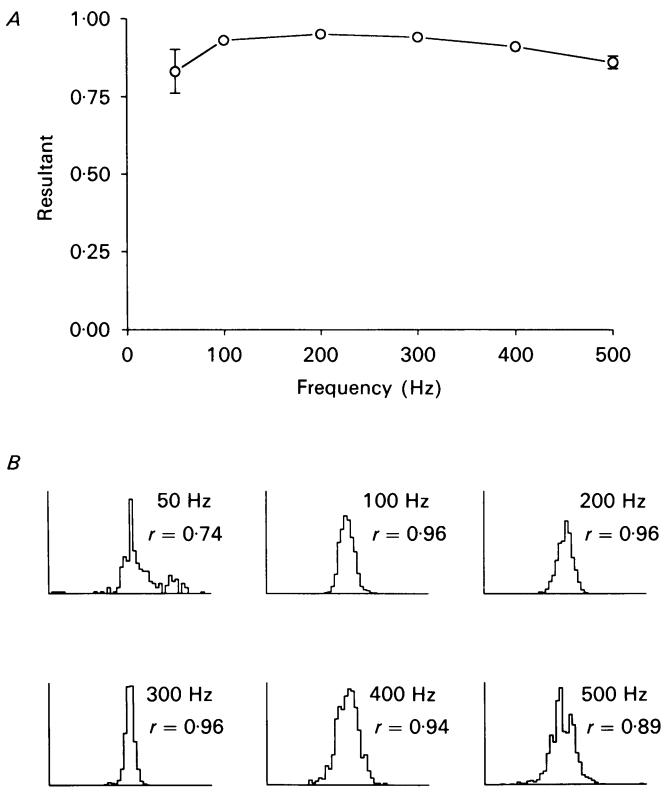

Fig. 6. Effect of vibration frequency on the tightness of phase-locking at the 1:1 threshold. *A*, the mean resultant (r) is plotted as a function of vibration frequency for ten SAI fibres responding at their 1:1 thresholds. Error bars are standard errors of the mean. Values in *A* for the mean resultant at each frequency ($\pm$S.E.M.) are: 50 Hz: $r = 0{\cdot}83 \pm 0{\cdot}07$ ($n = 4$); 100 Hz: $r = 0{\cdot}93 \pm 0{\cdot}01$ ($n = 10$); 200 Hz: $r = 0{\cdot}95 \pm 0{\cdot}01$ ($n = 10$); 300 Hz: $r = 0{\cdot}94 \pm 0{\cdot}01$ ($n = 9$); 400 Hz: $r = 0{\cdot}91 \pm 0{\cdot}01$ ($n = 10$); 500 Hz: $r = 0{\cdot}86 \pm 0{\cdot}02$ ($n = 4$). *B*, the cycle histograms are from responses of a representative SAI fibre and illustrate the phase-locking in the response at the 1:1 level for six vibration frequencies, and the broad range of frequencies for which there is tight phase-locking at the 1:1 threshold.

impulse generation in an afferent fibre is an essential component of the neural code for the intensity of stimulation. Experiments based on electrical stimulation of single SAI afferent fibres in the glabrous skin of man (Torebjörk & Ochoa, 1980), have provided further support for this idea. In the present study, the number of impulses

over a 1 s stimulus segment commencing 300 ms after the onset of the step indentation, was chosen as the measure of impulse frequency, elicited in SAI fibres by static skin indentation. This analysis segment was chosen so as to avoid both the dynamic response and most of the 'transient' rapidly adapting component of the static response (Tapper, 1965). When this response measure for the SAI fibre is plotted against stimulus intensity, a stimulus–response curve with a monotonically positive slope is obtained that reflects the static displacement sensitivity of the fibre. No attempt was made to determine whether these stimulus–response relations were best characterized by linear or power law functions, as the validity of such attempts has been seriously questioned (Kruger & Kenton, 1973).

Susceptibility of SAI responsiveness to stimulus parameters

Many factors affect the responsiveness of touch dome-associated SAI fibres to stimuli delivered by perpendicularly oriented probes. Some, such as temperature and velocity of indentation have been well studied (Tapper, 1965; Iggo & Muir, 1969). For the present study, the onset time for the step indentation was in general 100 ms, and although the temperature of the leg was not monitored, it was not subject to transient changes known to affect SAI responses (Tapper, 1965).

Probe size played a major role in determining the response of the SAI fibres to static indentations (Fig. 1*B*). The more effective smaller probe presumably generates a greater compressive strain at the receptors beneath the touch dome, than does the larger one for the same degree of indentation, and this has been shown to be the local stimulus for glabrous SAI units (Phillips & Johnson, 1981). Our observations (for *both* step and vibration stimuli) are in agreement with earlier findings that step stimuli were more effective when applied to touch domes as a punctate stimulus than as a distributed one in the form of a 5 mm diameter disc (Vierck, 1979).

Effect of stimulus parameters on vibrotactile responses of SAI fibres

Probe size also exerted a profound effect on the responses of SAI fibres to vibration (Fig. 2*C*). However, this effect was influenced by whether the pre-indentation was large enough (typically $> 100\ \mu$m) to cause the probe to contact the skin surrounding the touch dome (Fig. 3). We believe that this is due to the distribution of the force of the vibration to the surrounding skin at the larger step amplitudes, resulting in little effective strain across the touch dome, which seems to be the requirement for activation of the afferent. These observations are not in conflict with Horch & Burgess' report (1975) that the presence of an offset (or pre-indentation) enhanced SAI sensitivity to *single* sine cycles (in particular, at very low frequencies, 1–10 Hz), as the offsets used for their study of SAI fibres were $< 100\ \mu$m. Furthermore, they did not specify the size of the probe used; nor did they examine the vibratory following capacity of the fibres.

As SAI fibres are most effectively activated by punctate stimuli that generate localized distortion within the touch dome, it would appear that a tactile sensing system based on a sparsely distributed system of sensitive points in the hairy skin (less than 0·4 % of the skin surface; Burgess, Howe, Lessler & Whitehorn, 1974) may be of little use for the moment-to-moment detection and recognition of cutaneous

disturbances. However, the presence of the large, stiff tylotrich hairs in close association with individual domes provides a remote sensing mechanism for the dome and allows a localized strain to be generated within the dome by stimuli that need not make direct contact with the dome itself (see Fig. 2). This provision effectively expands the spatial receptivity of the touch dome–SAI system; nevertheless, the system would still require that stimuli (whether remote, or imposed directly on the dome) generate a focal distortion, or intra-dome strain in order to activate effectively the SAI fibres.

Resolution of disparate reports of the vibration sensitivity in touch dome-associated SAI fibres

We believe the sensitive dependence on the stimulus parameters of the SAI fibre response to vibration, accounts to a large degree for the widely varying reports of the vibration sensitivity of this class of afferent. Lindblom & Tapper (1967) observed 1:1 following for at least sixty-four sine cycles at 400 Hz (the highest value tested) with less than 30 μm vibration amplitude in the hairy skin of both cats and monkeys when they employed a 300 μm flat-tipped probe to deliver vibration. Tapper *et al.* (1972) extended these results to higher frequencies, and were able to produce 1:1 following in SAI afferents at up to 600 Hz with less than 100 μm of vibration. Their results were obtained with a 300 μm rounded-tip probe and without background skin displacement – conditions which our study shows optimize the SAI response to vibration. Much lower sensitivity and responsiveness have been described in other studies. For example, even though Horch & Burgess (1976) used only very brief trains (ten stimulus cycles) in studies of cat SAI fibres they rarely observed 1:1 following at 250 Hz, and furthermore the 1:1 thresholds were high (e.g. 200–300 μm at $\sim$ 200 Hz). They employed 1–2 mm flat-tipped probes, and background indentations larger than 100 μm. In human hairy skin, SAI afferents have not been found to follow 1:1 at vibration frequencies above 200 Hz (Järvilehto *et al.* 1976; Vedel & Roll, 1982). Both these studies employed large probes (1·5 mm and 5 mm respectively), and although neither study specifies the level of pre-indentation, it was sufficient to cause a static response. The evidence of the present study indicates that the low vibration sensitivity reported for these human SAI afferents may well be attributable to the nature of the stimulus parameters, rather than to species differences. In another study of primate sensory fibres, in monkey hairy skin, Merzenich & Harrington (1969) argued against a role for SAI fibres in vibrotactile sensibility, but their observations were confined, for the most part, to the purely dynamically sensitive afferent fibres. Although they refer to additional observations in which punctate 100 Hz stimulation of human touch domes elicited no sensation of vibration, they provided no details of stimulus parameters or results.

Comparison with SAI afferents in other skin locations

As there is no protuberant structure overlying SAI endings in the glabrous skin, the stimulation of SAI fibres in this location may resemble the circumstance in which a large probe and large step indentation are used on touch domes in hairy skin. The distribution of the load over the surrounding skin, together with the greater stiffness of glabrous skin will reduce the effective strain across the receptors, and may

account for the low responsiveness of glabrous SAI fibres to vibration: for example, in the cat glabrous skin they are unable to follow vibration frequencies above about 10–20 Hz (Iggo & Ogawa, 1977; Ferrington, 1985). In contrast, the very different, and strikingly high response rates (up to 1200 impulses s^{-1} over 500 ms stimulus segments) induced by vibration in SAI fibres associated with sinus hairs (Gottschaldt & Vahle-Hinz, 1981), may be related to high levels of shearing strain generated by their method of direct attachment of the probe to the associated vibrissa. It is unclear whether the high impulse rates in these SAI fibres ($\sim$ twice those observed in the present study) reflect specific properties of the vibrissal-associated Merkel receptors, or especially high levels of strain achieved by virtue of the vibrissal-mediated stimulus procedure.

Quality of temporal patterning in vibrotactile-induced responses of SAI fibres

The quality of impulse patterning in the responses of touch dome-associated SAI fibres to vibration, was studied in detail in order to compare their capacity for encoding information about the frequency parameter of vibrotactile stimuli, with that of purely dynamically sensitive fibres (e.g. those associated with Pacinian corpuscles, the PC fibres) that are implicated in vibrotactile sensibility (Talbot *et al.* 1968; LaMotte & Mountcastle, 1975). The regularity or precision of the impulse pattern, and therefore its capacity to reflect accurately the frequency of the applied vibration, depends upon two conditions; first, the tightness of phase-locking in the response, and second, whether the impulse rate is high enough for the mean interspike interval to approximate the cycle period of the vibration. Both conditions are affected profoundly in the SAI fibres by the stimulus parameters (Figs 2*C*, 3*A* and *B*), and both are usually best met when the sensory fibre responds on the 1:1 plateau of its stimulus–response relation (see Fig. 4, and Talbot *et al.* 1968; Ferrington & Rowe, 1980). Therefore, the wider this plateau, the greater the range of amplitudes over which the fibre can provide an unambiguous signal of the vibration frequency. This 1:1 plateau for the touch dome SAI afferents was wider at higher stimulus frequencies (> 100 Hz; see Fig. 4), as is the case for PC sensory fibres, and was very similar in width to those of PC fibres in both monkey and cat glabrous skin (Talbot *et al.* 1968; Ferrington & Rowe, 1980). The quality of phase-locking as measured by the resultant (Fig. 6*A*), was also similar for the SAI and PC afferent fibre classes. SAI afferent fibres had responses that were as tightly phase-locked as those of PC fibres at 50 and 100 Hz. For example, the mean value for the resultant r for SAI responses at 100 Hz was $0{\cdot}93 \pm 0{\cdot}01$ S.E.M. ($n = 10$), compared with $r = 0{\cdot}92 \pm 0{\cdot}03$ ($n = 6$) for PC fibres (R. M. Vickery, S. Ghosh & M. J. Rowe, unpublished observations). Even at frequencies of 200–500 Hz the precision of phase-locking in SAI responses was only marginally poorer than in the PC fibres; for example, at 200 Hz, where phase-locking was tightest for both classes of fibres, the values for SAI fibres were $r = 0{\cdot}95 \pm 0{\cdot}01$ ($n = 10$) and PC fibres: $r = 0{\cdot}99 \pm 0{\cdot}00$ ($n = 3$); (R. M. Vickery, S. Ghosh & M. J. Rowe, unpublished observations). Furthermore, as the SAI fibres retained tight phase-locking up to at least 1000 Hz (see Fig. 5) it is clear that their capacity for phase-locked responses extends over a similar bandwidth to the PC fibres, although thresholds for the onset of 1:1 patterned responses are lower for the PC fibres (Ferrington & Rowe, 1980).

Is there a role for SAI fibres in cutaneous vibration sensibility?

Our data suggest that, in some of the earlier studies, the stimulus parameters (in particular, probe size and position) may not have been optimal for the generation of phase-locked, patterned activity in the SAI responses to vibration, and therefore may have contributed to the reported failure of SAI afferents to give rise to a sense of vibration. However, the importance of appropriate stimulus parameters cannot explain why individual SAI fibres associated with glabrous skin fail to generate a sense of flutter or vibration when activated by trains of electrical stimuli in intraneural microstimulation experiments (Ochoa & Torebjörk, 1983; Vallbo, Olsson, Westberg & Clark, 1984; Macefield, Gandevia & Burke 1990). Whether individual SAI afferents from the hairy skin can generate a sense of flutter vibration in association with intraneural microstimulation remains to be determined. However, the sense of steady skin pressure reported in association with this form of stimulation in glabrous skin SAI fibres, in contrast to the perception of flutter vibration which accompanies the equivalent stimulation of *individual* rapidly adapting fibres (called RA fibres) or PC fibres, may mean that there is much less temporal fidelity in the central transmission of signals from SAI fibres than there is for RA and PC fibres. In the case of PC fibres, earlier studies from our laboratory have shown that individual fibres have very secure transmission across the dorsal column nuclei, which preserves, in the postsynaptic neurones, much of the temporal patterning in the vibrotactile-induced responses of the incoming PC fibres (Ferrington, Rowe & Tarvin, 1987*a*, *b*). Perhaps the transmission characteristics for SAI inputs do not permit the retention of comparable fidelity in the impulse patterns of the SAI target neurones. These central transmission characteristics for SAI fibres are the subject of our current investigations.

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