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RESPONSES OF SLOWLY ADAPTING TYPE II AFFERENT FIBRES IN CAT HAIRY SKIN TO VIBROTACTILE STIMULI

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SUMMARY

1. Slowly adapting type II (SAII) afferent fibres that supply the forelimb were isolated from the medial cutaneous nerve of anaesthetized cats and examined for their capacity to signal information about vibrotactile events in the hairy skin.

2. The SAII fibres had a single spot-like receptive field focus where they were highly sensitive to steady indentation and vibration applied with probes normal to the skin surface. However, their sensitivity was affected profoundly by the size of the stimulus probe, its position in relation to the receptive field focus and, to a lesser extent, the magnitude of any pre-indentation on which vibration was superimposed. Small stimulus probes (e.g. 250 μm diameter) were much more effective than larger ($\geqslant$ 1–2 mm) ones, and small shifts in the position of the perpendicularly applied probe away from the receptive field focus led to a marked decline in responsiveness.

3. With appropriate choice of stimulus parameters for vibratory stimuli applied at the receptive field focus, the SAII fibres could respond at low threshold ($<$ 100 μm), with a tightly phase-locked, regular 1:1 impulse pattern (one impulse per vibration cycle) that accurately signalled the vibration frequency over a bandwidth that extended to 600 Hz. Furthermore, their responses remained phase-locked up to 1000 Hz. Phase-locking in SAII fibres was marginally tighter than that in SAI fibres and comparable to that of Pacinian corpuscle fibres.

4. The sensitivity of forelimb SAII fibres to tangential skin stretch was directionally selective; stretch across the forelimb was much more effective than along its long axis. Vibration associated with tangential skin stretch led to a marked spatial expansion of the field of vibration sensitivity. SAII fibres could therefore signal information about natural stimuli that contain elements of skin stretch and vibration, as may be encountered when the forelimb brushes against textured surfaces. Should the SAII fibres fail to contribute to the sensory experience of vibrotactile stimuli, the explanation may be related to limitations imposed centrally on the processing of their signals. Nevertheless, the present results demonstrate that, with appropriate stimulus conditions, the SAII afferent fibres have much greater vibrotactile sensitivity than has been suggested by past studies.

INTRODUCTION

Slowly adapting mechanoreceptors in mammalian hairy skin comprise two major classes: the Merkel receptor complex and the Ruffini endings, which are associated respectively with the slowly adapting type I (SAI) and the slowly adapting type II (SAII) classes of cutaneous afferent nerve fibres (Iggo & Muir, 1969; Chambers, Andres, v. Duering & Iggo, 1972). These afferent fibres appear to transmit information about the intensity of a sustained mechanical stimulus (Werner & Mountcastle, 1965; Harrington & Merzenich, 1970) and also, in the case of SAI fibres, information for cutaneous pattern recognition (Johnson & Lamb, 1981; Goodwin & Morley, 1987).

As both the SAI and SAII classes have been reported to respond poorly to vibrotactile stimuli (Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968; Iggo & Ogawa, 1977; Johansson, Landström & Lundström, 1982; Ferrington, 1985), they have generally been excluded from a role in vibrotactile sensibility (Talbot *et al.* 1968; Merzenich & Harrington, 1969; Konietzny & Hensel, 1977; Ochoa & Torebjörk, 1983). However, our recent study of SAI fibres associated with touch domes in the hairy skin of the cat (Vickery, Gynther & Rowe, 1992) has shown that, under appropriate stimulus conditions, the SAI fibres can respond at low thresholds with a precisely phase-locked, one-to-one impulse pattern to a broad bandwidth of vibration frequencies that extends up to 500 Hz. The stimulus parameters that are crucial in determining the effectiveness of vibratory stimuli include the site of the stimulus probe, its position in relation to the touch dome, and the amplitude of any pre-indentation (Vickery *et al.* 1992).

Reports on the sensitivity of SAII fibres to skin vibration and on the potential role of these fibres in vibrotactile sensibility have been widely disparate (Merzenich & Harrington, 1969; Horch & Burgess, 1976; Pertovaara & Hämäläinen, 1981; Johansson *et al.* 1982). For example, Merzenich & Harrington (1969) showed tuning curves from a monkey hairy skin SAII fibre which followed a 1 s train of 300 Hz vibration with a 1:1 response pattern at vibration amplitudes of $< 10\ \mu$m. In contrast, in cat hairy skin, vibration amplitudes of 1 mm have been required to elicit 1:1 following at 40 Hz for a vibration train of only ten cycles (Horch & Burgess, 1976), and an amplitude of approximately 200 μm was required to evoke 1:1 following at 80 Hz for a train that lasted only eight cycles (Pertovaara & Hämäläinen, 1981). The 1:1 vibration thresholds of SAII fibres in cat hairy skin have been reported either to decrease (Pertovaara & Hämäläinen, 1981), or to increase (Horch & Burgess, 1976) as a function of increases in vibration frequency up to 80 Hz. The explanation for the different reports is not known, but may, as with many of the discrepancies in the reports on vibrotactile sensitivity of SAI fibres (Vickery *et al.* 1992), relate to the choice of stimulus parameters.

The aim of the present study was to identify whether, under appropriate stimulus conditions, the Ruffini ending–SAII afferent fibre system is capable of signalling vibrotactile events. The study examined systematically the effects of particular stimulus parameters such as the size of the stimulus probe, its position and orientation, and the amount of pre-indentation or skin stretch, on the vibration sensitivity of the SAII fibres. The results demonstrate first, that with appropriate

stimulus parameters, SAII fibres are capable of high vibrotactile sensitivity; second, that this sensitivity may extend to sites remote from the receptive field focus as a result of skin stretch; and third, that this spatial expansion is dependent on the direction of stretch. A preliminary account of the data has been given in conference proceedings (Gynther, Vickery & Rowe, 1990).

METHODS

Animal preparation

The eleven cats used in this study were anaesthetized initially with an intraperitoneal injection of sodium pentobarbitone (40 mg kg^{-1}), and anaesthesia was maintained by infusion of sodium pentobarbitone (4 mg kg^{-1} h^{-1}, I.V.) in 0·18% saline. Rectal temperature was held at $38 \pm 0{\cdot}5$ °C and blood pressure was monitored at the femoral artery. The forelimb of the animal was fixed in place to prevent movement. The medial cutaneous nerve was exposed in the ventral surface of the forelimb, and fine strands were teased from it and placed over a platinum-wire recording electrode. Skin in the area of the nerve distribution was shaved and then depilated with the use of a commercially available hair remover.

Stimulation and analysis procedures

Stimulation and analysis procedures were essentially similar to those described in a previous paper (Vickery *et al.* 1992), and employed a feedback-controlled mechanical stimulator (Douglas, Ferrington & Rowe, 1978), with a flat-tipped probe (diameter between 0·25 and 2 mm), which was positioned (except in studies on the effect of skin stretch) perpendicular to, and just above the skin surface (≈ 10 μm). The tactile stimuli consisted of a step indentation of the skin up to 1 mm in amplitude, that lasted 1·5 s, and in cases where vibrotactile responsiveness was examined, a 1 s train of sinusoidal vibration was superimposed on the step and commenced 300 ms after its onset. Stimuli were repeated every 10–15 s.

Time interval and cycle histograms were constructed from SAII responses, and for the responses to vibration, a measure of the tightness of phase-locking, the *resultant* (r), which ranges in value from 0 to 1, was calculated from the cycle histograms (see Greenstein, Kavanagh & Rowe, 1987; Vickery *et al.* 1992). The *coefficient of variation*, which is a measure reflecting the regularity of interimpulse intervals, was calculated from time interval histograms, and used as one of the criteria for the identification of SAII fibres. The *coefficient of variation* was taken as the standard deviation (S.D.) of time interval histograms constructed from at least one hundred interimpulse intervals obtained during the static phase (the 1 s segment starting 300 ms after the step onset) of response to the step indentation, divided by the mean interspike interval for the histogram distribution.

RESULTS

Identification of SAII afferent fibres

Slowly adapting afferent fibres in the medial cutaneous nerve were identified by their maintained response to a prolonged skin indentation at the focus of their receptive field. The SAII fibres could be clearly distinguished from the SAI fibres (the subject of a recent investigation, Vickery *et al.* 1992) on several criteria (Burgess, Petit & Warren, 1968; Chambers *et al.* 1972). First, the SAII fibres showed a slowly adapting response (Fig. 1*A*) to sustained indentation of the skin at sites with no visible touch dome, in contrast to the SAI fibres which in hairy skin are invariably associated with touch domes. Second, the SAII fibres had a single spot-like receptive field focus of area ≈ 1 mm^2 (using a 0·2 g von Frey hair), whereas SAI fibres generally innervate 1–3 touch domes (Iggo & Muir, 1969). Third, the SAII fibres displayed a vigorous response to stretching the skin of the receptive field in one direction, and a

lack of effect or a reduction of spontaneous activity when the skin was stretched in the orthogonal direction, whereas SAI afferents are insensitive to skin stretch (Burgess *et al.* 1968). Fourth, the SAII fibres had a low coefficient of variation ($< 0{\cdot}3$, see Methods) for the interimpulse intervals in their responses to a 1·5 s steady

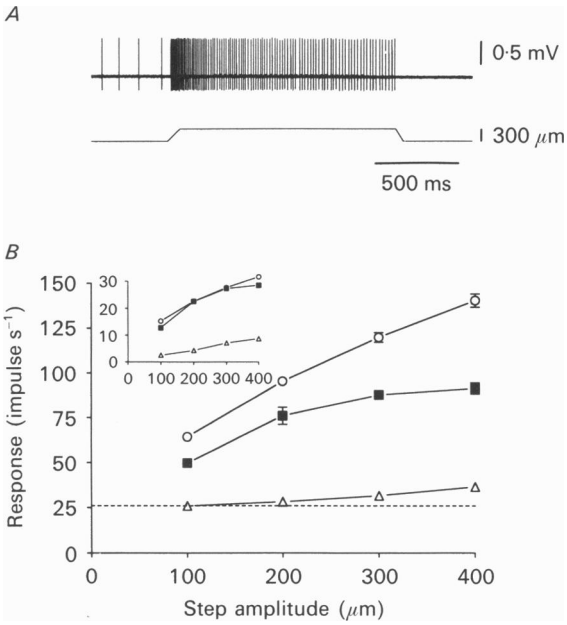

Fig. 1. The effect of probe size and position on SAII responses to skin indentation. *A*, the response (upper trace) to perpendicularly applied skin indentation (lower trace) for a representative SAII afferent fibre. The high rate of response during step onset (dynamic phase) is followed by a slower, but regular, rate of firing in the later (static) phase. The amplitude of skin indentation was 300 μm, applied with a 250 μm probe. *B*, the stimulus–response relations in the main graph plot the number of impulses in the 1 s segment of response that starts 300 ms after step onset, against the amplitude of the skin indentation (○, 250 μm probe; ■, 1 mm probe; both centred on the receptive field focus; △, 250 μm probe positioned 750 μm from receptive field focus). The dashed line at 26 impulses s^{-1} indicates the background activity in the fibre. Error bars are the S.D.s for five responses at each amplitude (where the error bars are not visible the values fall within the data points). The inset stimulus–response relations are based on the number of impulses in the 100 ms dynamic phase of response of the fibre to the step onset.

step indentation of the skin delivered by means of a mechanical stimulator, while SAI fibres have a far more irregular discharge pattern (Chambers *et al.* 1972). In Fig. 1*A*, for example, the SAII fibre had a coefficient of variation of 0·22 for the interspike intervals during the static phase of the response, which is defined as the 1 s period of response that started 300 ms after the onset of the indentation.

Another attribute that assisted with the identification of SAII fibres was the presence of spontaneous activity in many fibres of this class. Of the thirteen fibres that were studied quantitatively seven had spontaneous activity, in marked contrast to its absence, or very low levels in SAI fibres (Iggo & Muir, 1969; Chambers *et al.*

1972). Although the proportion of SAII fibres with spontaneous activity was lower than was observed among SAII fibres of the cat saphenous nerve (forty-one of forty-five fibres; Chambers *et al.* 1972), this may simply reflect differences in the background level of stretch in the two areas of skin studied.

Receptive fields of SAII fibres: responses to steady skin displacement

SAII fibres were highly sensitive to local skin indentation at the focus of their receptive fields (Fig. 1). Indentation applied normal to the skin surface with a small probe (250 μm for Fig. 1*A*) evoked a high rate of response to the onset ramp phase of indentation and a maintained, regular pattern of response to the steady phase of displacement. When spontaneous activity was apparent before the onset of the indentation (see Fig. 1*A*) it was usually absent for a brief period ($\approx$ 2 s) after the end of the stimulus.

In order to assess the capacity of individual SAII fibres to represent in their response the intensity of steady skin indentation, the number of impulses during a 1 s period that commenced 300 ms after the onset of the 1·5 s step indentation was used routinely as a quantitative measure. The mean number of impulses in 5–10 successive responses to a fixed indentation amplitude was used to construct stimulus–response relations (Fig. 1*B*). These relations demonstrated that SAII fibres were much less responsive to stimulation with a 1 mm probe (Fig. 1*B*, ■) than to stimulation with a small 250 μm probe (○), both centred on the most sensitive spot in the receptive field. This provided one indication of the focal nature of the receptive field for SAII fibres, but another indicator was the very sharp spatial profile of the receptive field, as was evident from the weak response to indentation applied normal to the surface with the small probe, 750 μm away from the focus (Fig. 1*B*, △). The punctate nature of the receptive field, when evaluated with small stimulus probes positioned normal to the skin surface, was in contrast to the much broader receptive fields found for SAII fibres when stimuli that generate tangential or more generalized skin stretch were employed (see below, and Looft, 1986). The sharp spatial profile of the receptive field apparent with punctate stimuli was seen not only for the static segment of the response (Fig. 1*B*), but also for the purely dynamic component, assessed as the number of impulses during the 100 ms ramp at the stimulus onset and plotted for different step amplitudes in the inset of Fig. 1*B*. The two different probe sizes generated similar response levels during the dynamic or onset phase of response (Fig. 1*B* inset) in contrast to their different efficacies during the static phase of response, in general agreement with the findings of Vierck (1979).

Responses of SAII fibres to perpendicularly applied skin vibration

Bandwidth of vibrotactile sensitivity in SAII fibres

The range of frequencies over which SAII fibres were sensitive to vibration was characterized quantitatively by determining the tuning point (also referred to as the 1:1 threshold) as a function of vibration frequency. It was obtained for each fibre with the use of the very effective small (250 μm) probe positioned normal to the skin surface at the point of maximum sensitivity, and was defined as the minimum amplitude of vibration required for the discharge of one impulse for each vibration cycle (referred to as 1:1 following) over the entire 1 s train of vibration. Figure 2*A*

illustrates a 50 ms segment of the response of an SAII fibre at its tuning point (30 μm) for vibration at 200 Hz. Tuning curves (plots of tuning point against vibration frequency) for nine SAII fibres plotted in Fig. 2*B* demonstrate their capacity to respond in a 1:1 pattern to vibration frequencies up to 600 Hz when the vibration amplitude was < 100 μm.

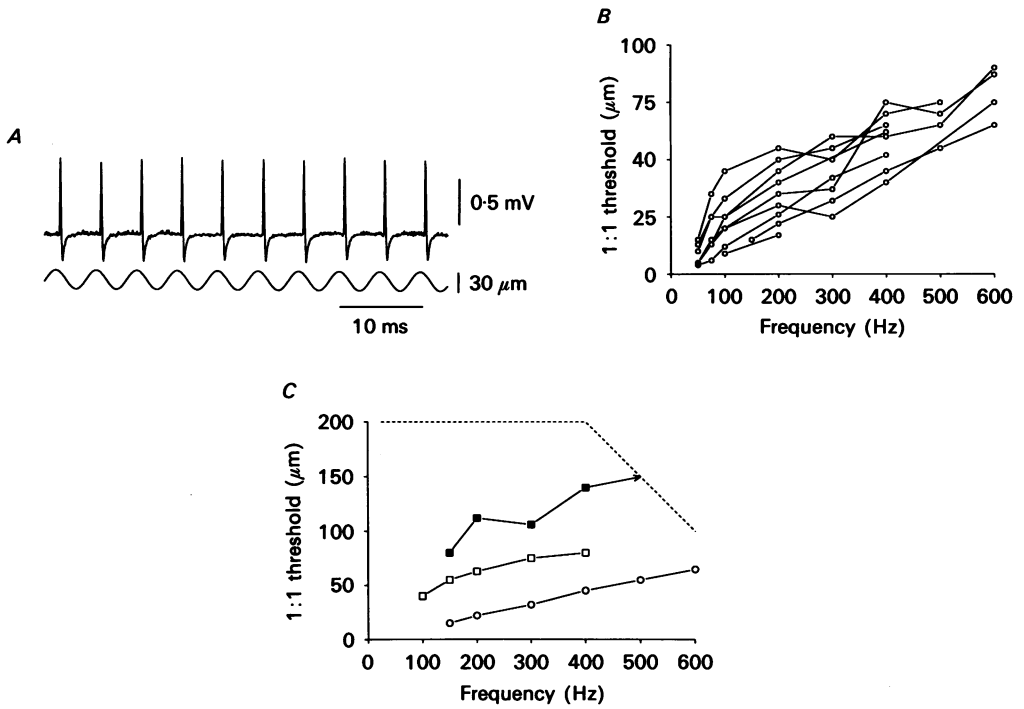

Fig. 2. Vibrotactile thresholds and tuning curves for SAII fibres: effects of probe size and position. *A*, 50 ms segment of response to 200 Hz vibration at an amplitude of 30 μm delivered with a 250 μm probe on a 200 μm pre-indentation. *B*, tuning curves (plots of 1:1 thresholds against vibration frequency) for nine SAII fibres. Vibration was delivered with a 250 μm probe centred on the receptive field focus and with a 200 μm pre-indentation. *C*, tuning curves obtained for a fibre illustrated in *B*, with a 250 μm stimulus probe (○) and a 1 mm probe (■) both centred on the receptive field focus, and with a 1 mm probe with its edge across the receptive field focus (□). The dashed line indicates the maximum vibration amplitude available with the stimulator, and the arrow indicates that at 500 Hz the 1:1 threshold was not reached for this fibre at the stimulator's maximum output (≈ 150 μm). When the 250 μm probe was moved 750 μm away from the focus, 1:1 following could not be obtained for frequencies of 50 Hz and higher, and therefore no tuning curve is plotted for this circumstance.

Effect of probe size and position on vibrotactile tuning curves for SAII fibres

Accurate placement of the probe on the most sensitive point of the receptive field was critical in the determination of the SAII tuning curves, as movement of the probe a short distance away greatly reduced the response of the fibre to vibration. In one instance an SAII fibre responded to 200 Hz (30 μm) vibration at its 'best' point with 180 impulses s^{-1}, but when the probe was moved first, 250 μm, and

second, 500 μm away from this point, the response level was 63 and then 10 impulses s^{-1} respectively. At this last position the response was little different from the background activity associated with the small pre-indentation. The sharply demarcated spatial profile of sensitivity to vibration was similar to that observed in Fig. 1*B* for the SAII responses to step indentations.

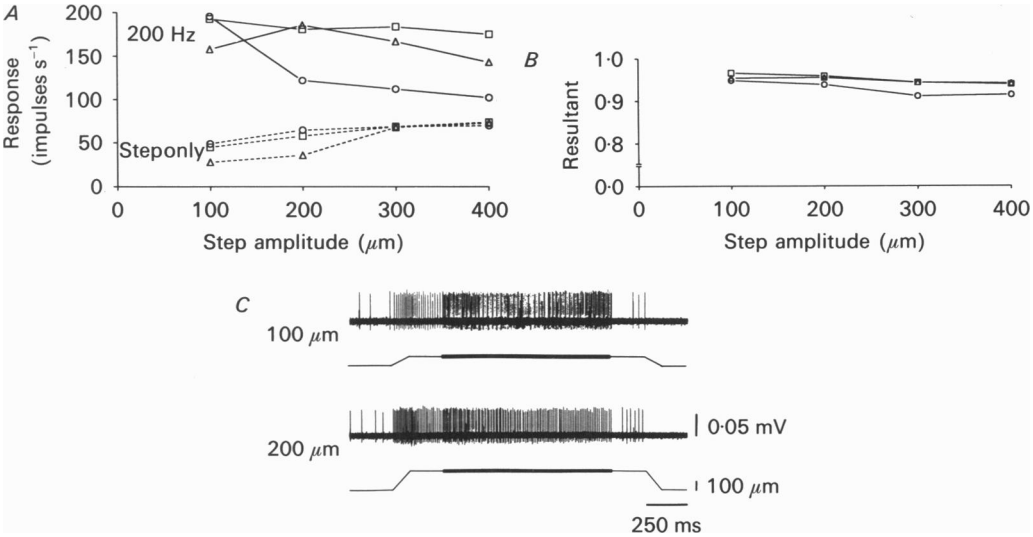

Fig. 3. The effect of pre-indentation on the response of SAII fibres to vibration. *A*, the response (in impulses s^{-1}) of three fibres to a fixed amplitude (see below) of 200 Hz vibration at four different pre-indentation amplitudes (continuous lines); the response of the same three fibres to these pre-indentations alone is shown by the dashed-line relations. The tightness of phase-locking (based on values of the *resultant*, *r*) in the vibration-induced responses with the different pre-indentations is plotted in *B*. *C*, the response traces and stimulus waveforms for the SAII fibre represented by ○ in *A* and *B*, illustrate the attenuation of the vibration-induced response that can take place with increases in the pre-indentation amplitude. Values plotted in *A* represent the mean of five responses and have S.D.s smaller than the symbol size. All results in this figure were obtained with a 250 μm probe centred on the receptive field focus. The amplitude of the 200 Hz vibration was fixed, but slightly different, for each fibre: □, 30 μm; ○, 25 μm; △, 20 μm.

Probe diameter was also a crucial determinant of the response of SAII fibres to vibration. A comparison of tuning curves obtained for one SAII fibre with the 250 μm and the 1 mm diameter probes is shown in Fig. 2*C*. When centred over the most sensitive point in the receptive field, the 1 mm probe (■) was less effective than the 250 μm probe (○) in activating SAII fibres. A greater response could be obtained with the large probe if it was positioned with its edge over the most sensitive point in the receptive field (□).

Effect of pre-indentation on vibration sensitivity of SAII fibres

As SAII fibres were virtually insensitive to vibration applied with a large probe (Fig. 2*C*), the effect of pre-indentation amplitude on the vibration sensitivity was examined with the very effective small (250 μm) probe. When the vibration was

superimposed on different amplitudes of pre-indentation in the range 100–400 μm, the response to the superimposed 200 Hz vibration was lower or unchanged at the higher levels of pre-indentation as shown in Fig. 3*A*, continuous lines, for three representative fibres. This was seen despite the increase in SAII response level that

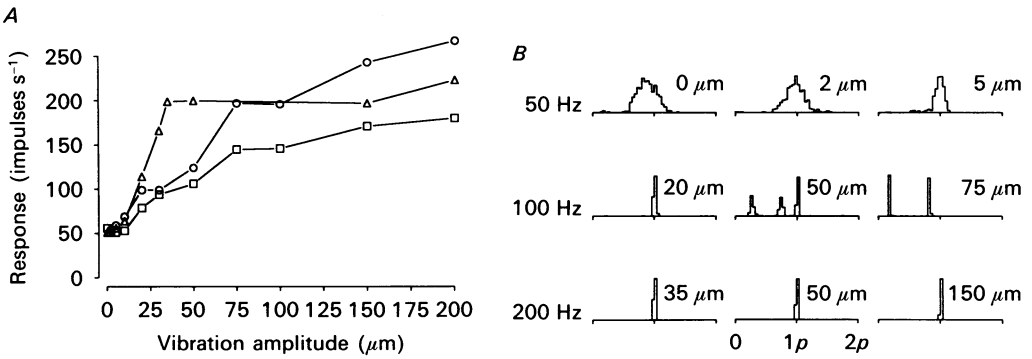

Fig. 4. Stimulus–response relations and impulse patterning in SAII responses to skin vibration. *A*, stimulus–response relations constructed for three frequencies, 50 Hz (□), 100 Hz (○), and 200 Hz (△), over a range of vibration amplitudes from 0 to 200 μm. A broad 1:1 plateau is apparent at 200 Hz, and smaller 1:1 and 2:1 plateaux at 100 Hz. *B*, time interval histograms, derived from the same data as is plotted in *A*, have a duration equal to twice the vibration period, *p* (therefore, 40 ms at 50 Hz, 20 ms at 100 Hz, and 10 ms at 200 Hz). These data were all obtained with a 250 μm probe centred on the receptive field focus, and with the vibration superimposed on a 200 μm pre-indentation.

occurs as a function of increases in the pre-indentation over this same amplitude range (100–400 μm) when the pre-indentation is delivered alone (Fig. 1 and Fig. 3*A*, dashed lines). The impulse traces in Fig. 3*C* for the fibre represented by ○ in Fig. 3*A* and *B*, illustrate the decrease in response to the vibration in association with the increase in pre-indentation from 100 to 200 μm. This result is quite different from that obtained with SAI fibres, where there was a sudden and pronounced, rather than gradual reduction in both the response and the tightness of phase-locking with increases in the pre-indentation amplitude (Vickery *et al.* 1992). As may be seen in Fig. 3*B*, the larger pre-indentations had little or no effect on the tightness of phase-locking in the responses of SAII fibres to vibration.

Effect of vibration amplitude on temporal patterning in responses of SAII fibres

Stimulus–response relations constructed for a representative SAII fibre with 200, 100 and 50 Hz vibration (Fig. 4*A*) demonstrate the interrelation of vibration frequency and amplitude in determining SAII fibre responses to vibration. The relation at 200 Hz shows an abrupt increase in response as a function of vibration amplitude (△ in Fig. 4*A*). The tuning point for 200 Hz, where a 1:1 pattern of response was attained, occurred at an amplitude of 35 μm, and the 1:1 plateau in the response was maintained over an amplitude range from 35 to 150 μm. The 1:1 response plateau over this broad amplitude range means that the impulse pattern in the SAII fibre had the capacity to signal accurately the frequency parameter of the

200 Hz vibrotactile stimulus. This is reflected in the tight grouping of interspike intervals around the 5 ms cycle period (1*p*) in the time interval histograms (TIHs) of Fig. 4*B* at 200 Hz, at each of the three amplitudes, 35, 50 and 150 μm.

At 100 Hz (○ in Fig. 4*A*) there was a narrower 1:1 plateau, and also a 2:1 plateau. The TIHs in *B* for 100 Hz illustrate responses on the 1:1 plateau (20 μm) where all

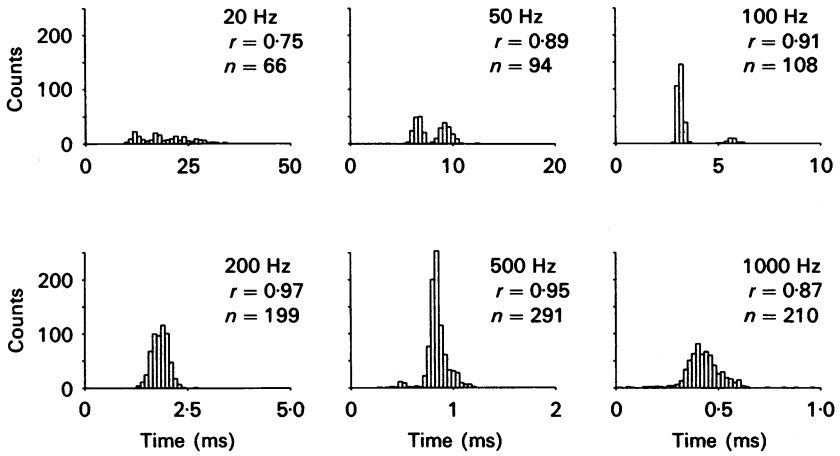

Fig. 5. The preservation of phase-locking in representative SAII responses to vibration over a broad bandwidth of frequencies (20–1000 Hz). The cycle histograms at the six frequencies were constructed from responses to a fixed vibration amplitude of 30 μm. Values of *r* and *n* on each histogram indicate respectively, the values of the *resultant*, and the number of impulses discharged in the 1 s response period, at each frequency. At 100 Hz, the response was close to the 1:1 level ($n = 108$) and at 200 Hz was at the 1:1 level ($n = 199$). At 500 and 1000 Hz the response was below the 1:1 level, but tight phase-locking was retained even at 1000 Hz. The cycle histograms for 20 and 50 Hz have multiple peaks, due to the occurrence of several impulses during each vibration cycle, but some phase-locking was preserved. All the data were obtained with a 200 μm pre-indentation and the 250 μm probe centred on the receptive field focus.

intervals are grouped around the cycle period of 10 ms; on the 2:1 plateau (75 μm) where the pairs of spikes discharged on each cycle lead to an early peak at the short interval of $\approx$ 3 ms and a second peak which occurs at a briefer interval (7–8 ms) than the cycle period; and at an intermediate level (50 μm) where there are groupings of intervals that correspond with all three peaks of the 20 and 75 μm TIHs.

At 50 Hz (□ in Fig. 4*A*) there was virtually no 1:1 plateau as the fibre responded with two or three impulses on individual vibration cycles as vibration amplitude was increased above $\approx$ 10 μm. Furthermore, the behaviour of the fibre at 50 Hz was dominated at low vibration amplitudes by the response (which was above 50 impulses s^{-1}) to the background step or pre-indentation of 200 μm. Although the three smallest vibration amplitudes tested at 50 Hz (2, 5 and 10 μm) led to no increase in response above that generated by the background step, the impulse activity nevertheless became more tightly entrained to the applied vibration. This is shown in the 50 Hz TIHs of Fig. 4*B* by the tighter grouping of interspike intervals around the cycle period at 5 μm, than at 2 μm or 0 μm, and was also reflected in

values of r, the *resultant* (see Methods) derived from cycle histogram distributions at the three amplitudes of 2, 5 and 10 μm, where the r values were 0·32, 0·85 and 0·86 respectively. Therefore, even at very low vibration amplitudes, the SAII response to the background step was modulated by the vibration to generate phase-locked, patterned activity that could effectively encode information about the vibratory stimulus.

Precision of temporal patterning in SAII responses as a function of vibration frequency

Even at response levels where the SAII fibre does not respond 1:1 for every cycle of vibration, the activity may still remain well phase-locked to the vibration waveform as illustrated in the cycle histograms of Fig. 5, constructed from the responses of an SAII fibre to vibration at frequencies of 20, 50, 100, 200, 500 and 1000 Hz, at the fixed amplitude of 30 μm, which was the 1:1 threshold amplitude at 200 Hz. The *resultant* (r), a measure of phase-locking, and the impulse rate (n, in impulses s^{-1}) are shown next to each cycle histogram. The responses at 200 and 500 Hz displayed similar tight levels of phase-locking (r values of 0·97 and 0·95 respectively). However, although the response rate at 500 Hz (291 impulses s^{-1}) was higher than that at 200 Hz (199 impulses s^{-1}) it was below a 1:1 level, and therefore, the impulse patterning could not reflect completely (on a cycle-by-cycle basis), the periodicity of the vibration at 500 Hz. This was also the case at 1000 Hz where one impulse occurred, on average, for every five cycles of vibration, although these impulse occurrences were still tightly phase-locked to the vibration waveform (r = 0·87; Fig. 5). As this SAII fibre responded at rates above a 1:1 level at 50 and 100 Hz, there is evidence of a second peak in these cycle histograms of Fig. 5, in particular at 50 Hz, while the 20 Hz cycle histogram has three or four peaks.

The tightest phase-locking of SAII responses was in the frequency range 100–300 Hz, and, at those and other frequencies, SAII responses were marginally better phase-locked than responses of the SAI fibres ($P < 0·01$, two-factor ANOVA), as judged by their mean *resultants* ($\pm$S.E.M.) at their 1:1 tuning points (Table 1). In the table, SAII values at each frequency are based on five to ten fibres; SAI values are taken from Vickery *et al.* 1992.

Responses of SAII fibres to tangential skin stretch

The SAII fibres studied were activated by static skin stretch and showed striking directional selectivity as reported previously (Chambers *et al.* 1972). However, the orientation of the stretch sensitivity for the forelimb SAII fibres was quite different from that of the hindlimb SAII fibres studied by Chambers *et al.* (1972) and Looft (1986) (see present Discussion). In the present study, eleven out of twelve fibres were activated by static stretch *across* the long axis of the forelimb, whereas stretch *along* the forelimb either reduced the rate of background activity or had no effect. The remaining fibre was most sensitive to oblique stretch at approximately 45 deg from the long axis of the forelimb.

Effect of skin stretch on vibrotactile responsiveness and tuning curves of SAII fibres: directional selectivity depending upon orientation of the stretch

Although the areal extent of vibration sensitivity for SAII fibres was sharply circumscribed when tested with probes positioned normal to the skin surface, it became much more widespread if the skin was vibrated in a tangential direction. This

TABLE 1. Comparison of tightness of phase-locking in SAII and SAI fibres

Frequency (Hz)	SAII (*resultant* ± S.E.M.)	SAI (*resultant* ± S.E.M.)
50	0·92 ± 0·02	0·83 ± 0·07
100	0·96 ± 0·01	0·93 ± 0·01
200	0·97 ± 0·00	0·95 ± 0·01
300	0·97 ± 0·01	0·94 ± 0·01
400	0·93 ± 0·01	0·91 ± 0·01
500	0·87 ± 0·03	0·86 ± 0·02

was achieved by positioning the mechanical stimulator probe at an acute angle of $\approx$ 10–20 deg to the skin surface at distances up to several millimetres from the receptive field's most sensitive point. In this almost tangential position, only the edge of the flat-tipped probe was in contact with the skin. Prior to the onset of the vibration, the skin was stretched approximately 200 μm by a pre-indentation, or step movement of the probe to provide some skin tension to transmit the vibration.

The expansion in the field of vibrotactile sensitivity for SAII fibres in association with tangentially applied vibration was not uniform in all directions (Fig. 6), but displayed the same directional preference that was shown for static stretch. This directional selectivity is apparent first, in the impulse records of Fig. 6*A* and *B* obtained in response to 1 s trains of 200 Hz (35 μm) vibration applied on a 200 μm background stretch in the transverse direction in *A* and in the longitudinal direction in *B*, at a fixed distance in each case (2 mm) from the receptive field focus. This directional preference was confirmed in another SAII fibre (Fig. 6*C* and *D*) for all vibration frequencies tested, by the construction of tuning curves for vibrotactile stretch in the transverse direction (Fig. 6*C*) and the longitudinal direction (Fig. 6*D*). The 1:1 thresholds plotted in Fig. 6*C* as a function of distance in the transverse direction from the receptive field focus, provide a spatial profile of sensitivity to vibrotactile skin stretch. The thresholds were obtained at different vibration frequencies in the range 10–300 Hz, and at each frequency the 1:1 threshold increased as a function of distance from the receptive field focus. However, under these conditions of stretch-enhanced vibration in the transverse direction, the SAII fibre could now be driven in a 1:1 pattern at all frequencies tested at points away from the focus and beyond the receptive field to perpendicularly applied vibration. At 100 Hz, for example, a 1:1 pattern of response was obtained at an amplitude of 17 μm at the receptive field focus, and could still be obtained at distances of 1, 2 and 3 mm away, although with progressively higher thresholds of 77, 92 and 183 μm, respectively.

When the vibration was applied in the presence of skin stretch imposed in the longitudinal direction of the forelimb it was much less effective (Fig. 6*D*). For

example, at four of the vibration frequencies tested, 300, 200, 100 and 75 Hz, the 1:1 thresholds exceeded 200 μm (the maximum vibration amplitude available with the mechanical stimulator, indicated by the dashed horizontal line in *C* and *D*) even at a distance of 1 mm, as indicated by the arrows that project to threshold values in

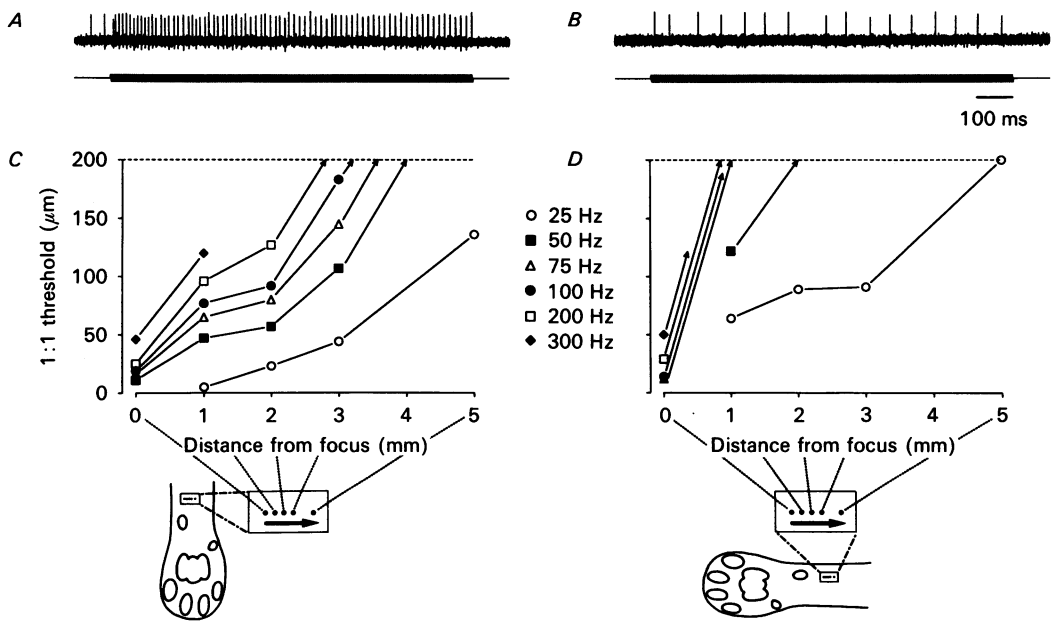

Fig. 6. Directional specificity in the stretch-enhanced responses of SAII fibres to skin vibration. *A* and *B*, impulse traces (1·25 s in length) show responses to vibrotactile stretch of the skin in the transverse (*A*) and longitudinal (*B*) directions (stimulus: 1 s train of 200 Hz, 35 μm vibration superimposed on a background stretch). The probe was 2 mm from the receptive field focus in each case. *C* and *D*, tuning curves for another SAII fibre constructed by plotting 1:1 thresholds for the six indicated frequencies of vibration as a function of distance (up to 5 mm) from the receptive field focus which is indicated as 0 on the *x*-axis. In *C* the transverse vibration was applied at points indicated on the schematic of the paw with accompanying transverse stretch, whereas in *D* the stretch-associated vibration was in the longitudinal axis of the forelimb. The broader curves in *C* for transverse stretch indicate that this orientation of stretch more effectively activated the fibre. The limit on vibration amplitude was 200 μm (dashed line), and arrows pointing to this line indicate that 1:1 following was not attained within these amplitude limits. All data were obtained with the 250 μm probe, with vibration applied on a pre-stretch of approximately 200 μm.

excess of 200 μm for these four frequencies. Only at frequencies of $\leqslant$ 50 Hz could 1:1 thresholds be obtained at distances 1 mm or more away from the receptive field focus under these conditions of longitudinal stretch (Fig. 6*D*). Furthermore, at a 2 mm distance, the 1:1 pattern of response could be obtained only at frequencies of $\leqslant$ 25 Hz.

Although the transverse, stretch-related delivery of the vibration extended the field of sensitivity for the SAII fibre of Fig. 6 to distances up to approximately 5 mm from the receptive field focus (Fig. 6*C*), the fibre had the typical punctate sensitivity

to vibration applied normal to the skin surface. For example, its 1:1 threshold exceeded 200 μm at all frequencies tested, in the range 25–300 Hz, if the vertically oriented probe was moved only 1 mm in either the lateral or proximal direction along the skin from the receptive field focus.

DISCUSSION

Effect of stimulus parameters on bandwidth and sensitivity of SAII responses to vibration

Vibrotactile stimuli delivered with small probes (250 μm diameter) were much more effective than those delivered with large ($\geqslant$ 1 mm) probes for the activation of SAII fibres, as indeed they were for SAI fibre activation (Vickery *et al.* 1992). Once again, the explanation may be related to the capacity of the smaller probe to generate a greater compressive strain at the receptors than the larger probes, for the same degree of skin indentation (Phillips & Johnson, 1981; Vickery *et al.* 1992). Provided that the vibratory stimuli were delivered with the small punctate probe, the SAII fibres responded to vibration amplitudes below 100 μm, with a regular 1:1 impulse pattern over a bandwidth of vibration frequencies that extended to approximately 600 Hz. Lowest thresholds were found at the lower frequencies and increased gradually as a function of increases in vibration frequency (Fig. 2). With large probes ($\geqslant$ 1 mm), the values of the 1:1 thresholds were several times greater and the effective bandwidth of vibration sensitivity was much narrower. This dependence on stimulus probe size and position also applies to SAII fibre sensitivity to simple step indentation stimuli (Fig. 1 and Vierck, 1979).

Small shifts ($<$ 1 mm) of the 250 μm probe position in any direction from the focus of maximum sensitivity in the receptive field of SAII fibres led to a marked drop in sensitivity and responsiveness of the fibres to both vibration (Fig. 2) and step indentations (Fig. 1) applied normal to the skin surface. The difference between this circumstance and that in glabrous skin where this fall-off is not so marked (Johansson, 1978; step indentation only) may be related to the greater stiffness of the glabrous skin. The small receptive field focus found in hairy skin was surprising in view of the large dimensions (up to 2 mm in length) of the Ruffini ending, and may imply that the responses to mechanical stimuli are generated at a small locus within the Ruffini ending. This interpretation would also be consistent with the observation that the edge of the large probe was more effective than the flat face of such a probe (Fig. 2), presumably on account of a greater compressive strain generated within the skin beneath the edge of the probe.

Increases in the amplitude of the pre-indentation on which vibration was superimposed, had little effect or led to some attenuation of vibration-induced responses in SAII fibres over the amplitude range, 100–400 μm. These effects were smaller than those observed in the touch dome-associated SAI fibres (Vickery *et al.* 1992) and the pre-indentation parameter therefore appears to be a less crucial determinant of SAII responsiveness than probe size and position. The present observations show that with appropriate choice of stimulus parameters, the SAII fibres in cat hairy skin have the capacity for high vibrotactile sensitivity over a broad bandwidth of frequencies in contrast to the insensitivity reported in earlier studies

(Horch & Burgess, 1976; Pertovaara & Hämäläinen, 1981; Hämäläinen, Järvilehto & Soininen, 1985). In the latter studies, large (1–2 mm) flat-tipped stimulus probes were used which may account for the discrepancies.

Role of SAII fibres in detection of vibration in hairy skin

Comparison of vibrotactile sensitivity in SAII and SAI fibres

With the use of the effective small probes, the form of the tuning curves, together with 1:1 threshold values and the bandwidth of responsiveness for SAII fibres were all remarkably similar to those of SAI fibres (Vickery *et al.* 1992). This similarity in vibrotactile sensitivity is somewhat surprising as the structures of the respective receptors are quite different (Iggo & Muir, 1969; Chambers *et al.* 1972). The Ruffini endings associated with SAII fibres are large ($\approx$ 1–2 mm long) spindle-shaped structures located within the dermis, without overlying skin landmarks, in contrast to the SAI-associated Merkel receptors which are aggregated at the dermal–epidermal junction, beneath the small ($\approx$ 200 μm) elevated touch domes formed by a raised and thickened portion of epidermis. The SAII afferent terminals contact the collagenous fibres in the inner core of the Ruffini endings which, in turn, are connected to the dermis by collagenous fibres. Despite the substantial differences in size and location of the two receptors, the SAI and SAII fibres share a capacity for responding at low intensities to a broad segment (up to approximately 600 Hz) of the human vibrotactile frequency range of approximately 1000 Hz (Verrillo, 1962). Both classes of fibres display a broad 1:1 plateau in their stimulus–response curves at vibration frequencies of $\geqslant$ 200 Hz (Fig. 4 and Vickery *et al.* 1992). Furthermore, as their responses are tightly phase-locked to the vibration waveform, each class is able to accurately reflect the frequency parameter of the vibration in the precise temporal modulation of its impulse activity. Tightest phase-locking for the SAII fibres (based on values of the *resultant*, r) was seen at 100–600 Hz, but tight phase-locking was retained in the responses to vibration even at frequencies as high as 1000 Hz, although the response level in individual SAII fibres was too low at this frequency to permit a 1:1 impulse pattern that mirrored the periodicity of the vibration (Fig. 5). Over the frequency range 50–500 Hz, the SAII fibres displayed significantly tighter phase-locking than SAI fibres (Table 1) and therefore could convey, in an impulse pattern code, a more reliable signal about the vibration than could SAI fibres.

Comparison of vibrotactile sensitivity in SAII and Pacinian-related fibres

The broad 1:1 response plateau displayed at high vibration frequencies by SAII fibres (for example, at 200 Hz in Fig. 4, it extended over an amplitude range of $\approx$ 150 μm) was similar also to those of Pacinian corpuscle (PC)-related fibres studied in both monkey and cat glabrous skin (Talbot *et al.* 1968; Ferrington & Rowe, 1980; Ferrington, Hora & Rowe, 1984). In addition, the tightness of phase-locking, based on values of r, the *resultant*, obtained from cycle histogram distributions for SAII responses, was similar to that for PC fibres (see Table 1 for SAII values; for PC fibres at 100 Hz, $r = 0{\cdot}92 \pm 0{\cdot}03$, $n = 6$; and at 200 Hz, $r = 0{\cdot}99 \pm 0{\cdot}0$, $n = 3$; R. M. Vickery, S. Ghosh & M. J. Rowe, unpublished observations). Furthermore, as the frequency range over which SAII fibres retained phase-locked responses (to $\approx$ 1000 Hz) is

similar to that of PC fibres, the results of this, and our earlier study (Vickery *et al.* 1992), show that with appropriate stimulus conditions, both SAI and SAII fibres can respond to vibrotactile stimuli with phase-locked responses over a similar frequency bandwidth to that of PC fibres.

Possible role of different fibre classes in vibrotactile detection in hairy skin

Although the thresholds for 1:1 response behaviour are substantially higher for both SAI and SAII fibres than for PC fibres activated from the glabrous skin, PC fibres are absent or rare in nerves that supply hairy skin (Brown & Iggo, 1967; Merzenich & Harrington, 1969; Whitehorn, Howe, Lessler & Burgess, 1974). The PC fibres that can be activated by vibratory stimulation of the hairy skin are presumably at remote locations (Merzenich & Harrington, 1969) that may include the interosseous region, the wrist joint, or even the foot pads. It is not surprising then, that when PC fibres are activated remotely from the hairy skin of the forelimb their thresholds are higher than those measured in glabrous skin; in particular, when the region of hairy skin stimulated is further up the forelimb than the wrist area used for the PC tuning curves constructed by Merzenich & Harrington (1969; see Fig. 10*b* of their paper). Depending on the region of hairy skin stimulated, the PC fibre thresholds (Merzenich & Harrington, 1969) may approximate or even exceed those of both the SAI and SAII fibres (present data, and Vickery *et al.* 1992).

Another set of tactile fibres, the hair follicle afferents in the group II afferent class, do not have especially low thresholds or broad bandwidths of vibration sensitivity and are unlikely to contribute to vibration sensibility at vibration frequencies above approximately 50 Hz (Merzenich & Harrington, 1969; Konietzny & Hensel, 1977). The functional properties of these different classes suggest that SAI and SAII fibres have the potential to contribute to the high-frequency (above 50–100 Hz) segment of vibrotactile sensibility in hairy skin, in contrast to the suggestion of Hämäläinen *et al.* (1985) that this contribution is limited to the very low frequencies ($\leqslant$ 20 Hz). Reports that vibration sensibility in this region of skin has a punctate distribution (Geldard, 1940; Merzenich & Harrington, 1969) would be consistent with the circumscribed, punctate receptive fields of both SAI and SAII fibres to vibratory disturbances applied with perpendicularly oriented probes.

Objections to a role for the SA fibre classes in vibrotactile perception

Arguments that may be raised against a contribution of SA fibres to vibrotactile perception are first, that tuning curves of SAII fibres increase monotonically as vibration frequency increases from 50 to 600 Hz (Fig. 2) whereas subjective detection curves are U-shaped with detection minima at approximately 200 Hz (Merzenich & Harrington, 1969; Konietzny & Hensel, 1977). However, the 1:1 thresholds obtained for SAII fibres at frequencies of $\leqslant$ 100 Hz are less reliable than at higher vibration frequencies, as there is a substantial part of the response related to the pre-indentation component of the stimulus. A second argument against the contribution of SAI or SAII fibres to vibration sensibility is that microstimulation of individual SAI or SAII afferents in glabrous skin produces only a sense of steady pressure in the case of SAI fibres, and no perceptual response in the case of SAII fibres (Ochoa & Torebjörk, 1983; Vallbo, Olsson, Westberg & Clark, 1984; Macefield, Gandevia &

Burke, 1990). However, whether individual SAI and SAII afferents in hairy skin also fail to generate a sense of vibration in association with microstimulation has yet to be determined. If individual SAII fibres fail to do so, it may mean that more than a single fibre of this class needs to be activated to generate a vibrotactile sensation, or perhaps that there is much poorer temporal fidelity in the central transmission of signals from SA fibres than is the case for RA or PC fibres (Ferrington, Rowe & Tarvin, 1986, 1987*a*, *b*).

Another possible reservation about the importance of the SAI and SAII systems for vibration sensibility may be based on the finding that both classes are best activated from circumscribed points of sensitivity distributed rather sparsely in the hairy skin (see Discussion in Vickery *et al.* 1992). For example, the SAII fibres are estimated to have an innervation density of only 1·4–2 fibres cm^{-2} of hairy skin in the cat (Whitehorn *et al.* 1974; Aitken & Lal, 1982). This also represents the density of receptors, as there is a one-to-one relation between Ruffini endings and SAII fibres (Chambers *et al.* 1972). The low density of these and the touch dome-associated SAI endings (see Vickery *et al.* 1992) suggests that the SA endings may be of limited use in the detection of vibrotactile disturbances. However, for both the SAI and SAII fibre systems, there are mechanisms for effectively expanding the spatial receptivity of each as a vibrotactile sensing system. In the case of the SAII fibres, the field of vibration sensitivity may be expanded substantially in the presence of skin stretch (Fig. 6), in comparison with the small punctate zone of sensitivity revealed when vibrating probes are positioned normal to the skin surface. A different strategy may operate in the touch dome–SAI system for expanding the spatial extent of its vibration sensitivity beyond the small fraction of the skin surface (approximately 0·4%; Burgess, Howe, Lessler & Whitehorn, 1974) occupied by the touch domes. This is based on the stiff tylotrich hairs that lie in close association with the touch domes acting as remote sensors of vibratory disturbances impinging on the skin at some distance from the dome (Vickery *et al.* 1992).

Directional selectivity in the stretch-enhanced vibrotactile sensitivity of SAII fibres

The stretch-enhanced expansion of SAII responsiveness to cutaneous vibration was greatest when the stretch was applied across rather than along the skin of the forelimb (Fig. 6). Static stretch sensitivity was also greatest in this direction for the forelimb SAII fibres in contrast to those in the saphenous nerve of the hindlimb which were excited predominantly by longitudinal skin stretch (Chambers *et al.* 1972). This difference may imply a different alignment of the Ruffini endings in these two skin regions. Furthermore the directional specificity suggests that if the forelimb SAII fibres have a role in the tactile sensation of static or vibrotactile-associated skin stretch, the detection thresholds should be lower when the disturbance is imposed across the forelimb rather than along the long axis of the limb.

As the stretch-mediated expansion of the vibrotactile receptive fields and responsiveness in SAII fibres was obtained at relatively low thresholds (for example, < 200 μm at 100 Hz) for distances of 5 mm or more away from the receptive field focus, it appears that vibratory skin stretch applied at any point on the forelimb may activate several SAII fibres. Natural stimuli with elements of both skin stretch and vibration will be encountered when the forelimb is brushed against a rough or textured surface and such stimuli are likely to activate several SAII fibres. The

present results suggest that in these circumstances, the SAII fibres in the forelimb hairy skin have the capacity to signal information about skin stretch and surface texture by virtue of their capacity to respond at low thresholds to a broad bandwidth of vibrotactile disturbances with precisely phase-locked, patterned impulse trains. Should these reliable signals of vibrotactile events in the SAII fibres not be used for the behavioural aspects of vibrotactile sensibility in hairy skin it may mean that the central transmission of their signals is poorer than that for other classes such as the PC fibres. We have shown that the latter group has a remarkable security of transmission that preserves temporal patterning across the synaptic linkage of the dorsal column nuclei (Ferrington *et al.* 1986, 1987*a*, *b*). The issue of central transmission of SAII and SAI signals is currently under investigation in our laboratory.

In summary, the present observations indicate that with appropriate stimulus parameters the SAII fibres have the capacity to signal reliably vibrotactile events in the hairy skin. This adds to their previously suggested roles first, in tactile sensation, for mediating a sense of cutaneous pressure or static skin stretch (Harrington & Merzenich, 1970; Chambers *et al.* 1972), and second for mediating the cutaneous contribution (for review see McCloskey, 1978) to the sense of limb and joint position (Johansson, 1978).

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