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Receptive field characteristics of tactile units with myelinated afferents in hairy skin of human subjects

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1. Impulses in single nerve fibres from the lateral antebrachial cutaneous nerve were recorded using the microneurography technique in human subjects.
2. In a sample of fifty-five mechanoreceptive units with fast-conducting nerve fibres, five types were identified, i.e. SAI (slowly adapting type I, Merkel), SAII (slowly adapting type II, Ruffini), hair units, field units and Pacinian-type units. The latter three unit types were all rapidly adapting.
3. The detailed structure of thirty-five receptive fields of SAI, SAII, hair and field units was explored with a method which was objective and independent of the experimenter's skill and experience. A lightweight probe was used to scan the receptive field area in a series of tracks 0·23 mm apart while single-unit activity was recorded.
4. SAI fields were small and composed of two to four well-separated high-sensitivity spots and often, in addition, one minor spot of lower sensitivity. SAII units typically fired spontaneously at a low and regular rate. Most fields consisted of one single spot of high sensitivity with diffuse borders. The hair units innervated ten to thirty-three (or more) hairs, which were evenly distributed over a large area. The field units were characterized by a number of small and closely packed high-sensitivity spots with diffuse borders. A conservative estimate indicated eleven spots per unit.
5. The findings indicate that the sheet of mechanoreceptors on the skin of the forearm is distinctly different from that on the dorsum of the hand and in the face. It seems reasonable to assume that the former is more representative for the hairy skin covering the main parts of the body.

Tactile afferents in glabrous skin of the human hand have been analysed extensively (Johansson & Vallbo, 1983; Vallbo & Johansson, 1984), and the geography of the receptive fields has been described in detail (Johansson, 1978). In contrast, our knowledge of mechanoreceptors in hairy skin is less detailed, particularly regarding the characteristics of their receptive fields, although a number of studies have been published on the innervation of the hand dorsum (Järvilehto, Hämäläinen & Kekoni, 1976*a*; Järvilehto, Hämäläinen & Laurinen, 1976*b*; Konietzny & Hensel, 1977; Järvilehto, Hämäläinen & Soininen, 1981; Edin & Abbs, 1991; Edin, 1992) and the face (Johansson, Trulsson, Olsson & Westberg, 1988; Nordin & Hagbarth, 1989). Moreover, there are reasons to suspect that these areas are not representative of hairy skin covering the trunk and the main parts of the extremities. For instance, hairs are particularly scant on the dorsum of the hand, and the facial skin may be uniquely innervated by the trigeminal nerve.

In mammals, five main types of mechanoreceptors with large myelinated afferents have been identified in hairy skin, i.e. slowly adapting type I (SAI) and II (SAII), hair units, field units and Pacinian units (Burgess, Petit & Warren, 1968; Iggo, 1974). In addition, sensitive mechano-receptive units with unmyelinated afferents are abundant, at least in cat, rat and rabbit (Douglas & Ritchie, 1957; Lynn & Carpenter, 1982; Shea & Perl, 1985).

In the present study, the geography of single-unit receptive fields was analysed in hairy skin of the human forearm using a scanning procedure. A preliminary report has been published (Wessberg, Olausson & Vallbo, 1992). The study was limited to myelinated afferents; tactile units with unmyelinated afferents have been described separately (Vallbo, Olausson, Wessberg & Norrsell, 1993).

METHODS

Mechanoreceptive units, with fast-conducting afferents and receptive fields, in hairy skin were studied in twenty-seven experiments on twenty-one young healthy subjects: nine females and twelve males, 21–31 years old. Most subjects were students at the local medical or odontological faculty.

The informed consent of the subjects was obtained according to the Declaration of Helsinki. The study was approved by the Ethical Committee of the Medical Faculty, Göteborg University.

Microneurography

The lateral antebrachial cutaneous nerve was explored at the level of the elbow, either slightly above or below (1–2 cm) the cubital fold. According to textbooks this nerve innervates the radial aspects of the forearm, but we encountered a few fields on the dorsum of the hand as well. This nerve was hard to find with the electrode and seemed to consist of very thin fascicles which were difficult to hit and penetrate, and the electrode slipped out easily. Therefore the search procedure was particularly dependent on the subjects' perceived response to electrical stimulation, rather than background neural activity.

Unit identification

Afferents were readily separated into rapidly and slowly adapting units by sustained skin indentation. Three groups of rapidly adapting units and two groups of slowly adapting units were identified.

Hair units were identified by their brisk response to movements of individual hairs and light air puffs onto the receptive field area. The latter stimulus was not absolutely selective, however, since some other units responded to the puffs with a few impulses. Rapidly adapting units with multiple high-sensitivity spots that were not particularly sensitive to hair movements, and that lacked a response to remote taps, were classified as field units (Burgess *et al.* 1968).

Pacinian (PC) units were identified on the basis of the combination of the receptive field having a single spot of maximal sensitivity and a vigorous response to remote taps on large areas of the forearm.

The slowly adapting type SAI and SAII units were differentiated on the basis of several features, i.e. spontaneous firing, dynamic response, stretch sensitivity, and interspike interval histograms (Chambers, Andres, von Duering & Iggo, 1972). In the subsample of units analysed in detail, eight of ten SAII units fired spontaneously, whereas none of the SAI units did. The interspike interval histogram was skewed and broad for SAI units, whereas it was symmetrical and narrow for SAII units. Coefficients of variation of interspike intervals were 0·63 (0·38–1·05, median and range, $n = 12$) for the SAI units and 0·19 (0·04–0·31, $n = 11$) for the SAII units. Hence, there was no overlap between the two types.

Impulse trains were analysed for uniformity of spike shape and size on an expanded time scale, using the microcomputer-based Zoom system designed by Anders Bäckström (Umeå, Sweden).

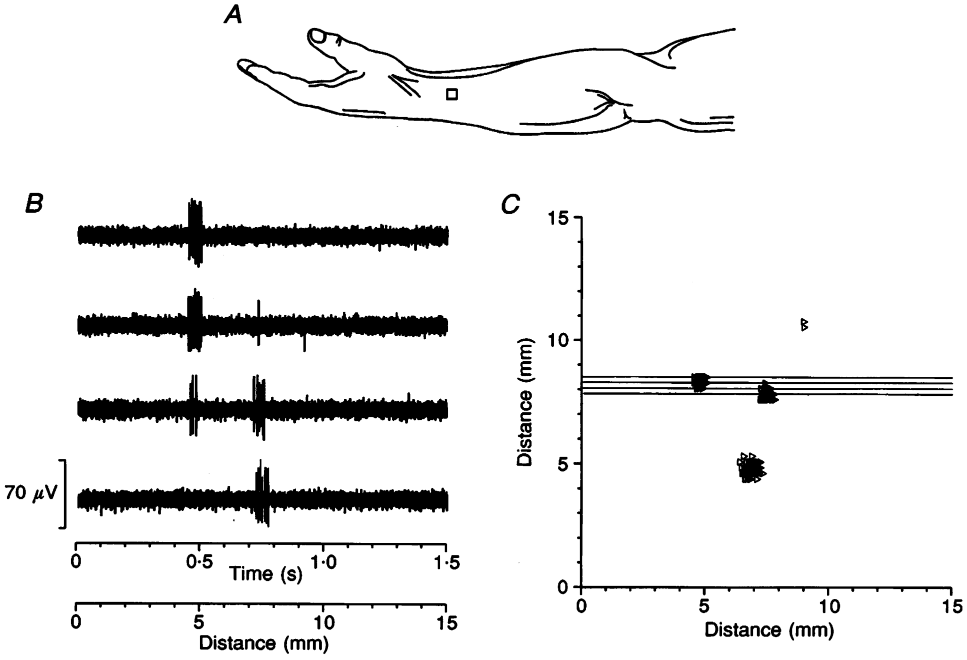

Figure 1. Method of exploring receptive fields of tactile units

Data from a SAI unit. *A*, location of the area explored (15 × 15 mm; □) with a small probe moving along the skin surface in 65 tracks 0·23 mm apart and in the proximodistal direction. *B*, nerve impulse responses along adjacent tracks. *C*, receptive field map representing the cutaneous area explored showing the 4 tracks from *B* (lines) with the afferent response (arrowheads), as well as the complete response of the unit to other tracks. In this and all other figures, the origin of the co-ordinates corresponds to the laterodistal corner of the explored area, while the *x*-axis represents the proximodistal dimension. Arrowheads pointing right indicate scanning probe movements in the proximal direction along the arm.

Each spike was judged individually before it was accepted as belonging to the afferent unit.

Mechanical stimulation

The general properties of the afferents were explored with various hand-held instruments, including a strain-gauge device and a series of calibrated von Frey hairs (available forces; 0·1, 0·3, 0·6, 1·3, 2·5, 5·0, 10, 20, 40 and 80 mN).

Scanning method for exploring the receptive field

The size and geography of thirty-five receptive fields were assessed using a scanning method. After shaving the skin, a small probe was moved over the skin surface by means of a modified $X-Y$ plotter controlled by a microcomputer. The stimulus probe consisted of a metal tube with a half-sphere at the end in contact with the skin. It was held approximately perpendicular to the skin surface by plastic bushes that allowed vertical movement with minimal friction. Hence, the indentation force remained approximately equal to the gravitational force on the tube. The housing of the stimulus probe and its bushes were rigidly fixed to an adjustable metal arm extending from the moving head of the $X-Y$ plotter.

The probe was made to scan a rectangular skin area covering the receptive field of the unit with a series of parallel tracks 0·23 mm apart (Fig. 1*C*). Each track was traversed twice, first proximal to distal and then distal to proximal. The tracks were always aligned in a strictly proximodistal direction along the forearm.

In the standard experiment, the probe had a diameter of 1 mm, a weight of 0·22 or 0·25 g, and travelled at a speed of 10 mm s^{-1}. For eight units higher probe speeds were used (18, 30 or 33 mm s^{-1}). Entrainment of spike discharge by the plotter steps (0·032 mm) was not seen in the subsample of units explored in detail.

Construction of receptive field maps

Figure 1*B* shows nerve impulse responses of a SAI unit to unidirectional movements in four adjacent tracks. Timing signals for start and stop of probe movements, along with nerve recordings, provided the database for computer construction of unit response in relation to probe position. Figure 1*C* shows the four tracks illustrated in *B*, as well as the complete response of this unit, in terms of a receptive field map. Each impulse in Fig. 1*B* is represented in *C* by an arrowhead riding on a track. Distal or proximal directions of probe movement are indicated

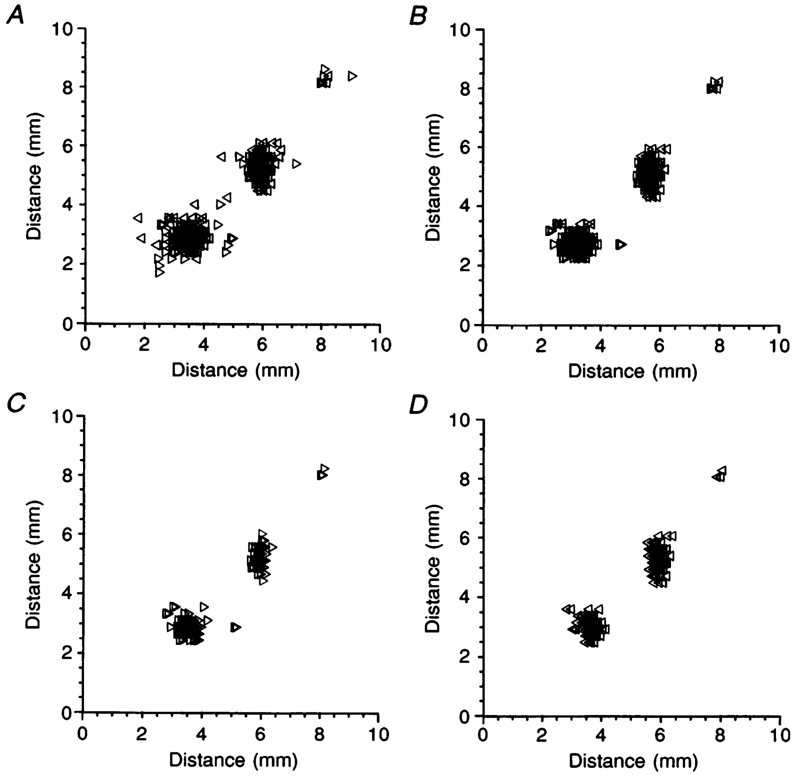

Figure 2. Receptive field maps of a single SAI unit

A, bidirectional map including all impulses. *B*, bidirectional map of the same unit after removal of erratic impulses, defined as those that lacked a neighbour within 0·23 mm. *C*, unidirectional map for probe movements in the distoproximal direction after removal of erratic spikes. *D*, same as in *C* but for proximodistal probe movements. Arrowheads pointing left or right indicate scanning probe movements in the distal or the proximal directions along the arm. Origin of co-ordinates as in Fig.1. The same unit as shown in Fig. 4*A*.

by arrowheads pointing left or right in the receptive field maps. When such maps were constructed conduction time in the nerve fibre was not accounted for, because the delay seemed negligible, corresponding to a probe movement of not more than 0·05 mm (plotter speed 10 mm s^{-1}).

Before the measurement of receptive field sizes, erratic impulses were discarded; these were defined as spikes that lacked a neighbour within 0·23 mm on bidirectional maps. Control tests, in which a few tracks were explored repeatedly, demonstrated that such impulses did not appear consistently.

Figure 2*A* and *B* shows the effect of this filtering on the bidirectional map of one SAI unit. The receptive field maps in Figs 4, 7 and 8 are based on similarly filtered unidirectional maps. For receptive field maps, as well as for measurements of sizes of receptive fields, the unidirectional map that had the most intense response was used (Fig. 2*D*).

The receptive field size of spontaneously active SAII units ($n = 8$) was measured after spikes with an instantaneous rate below three times the spontaneous rate had been removed. Control tests, when the same unit was explored several times, showed that such filtering gave the largest receptive field maps that appeared consistently. For the SAII units which lacked spontaneous activity ($n = 2$), the receptive field size was measured after removal of erratic spikes (see above).

Three-dimensional plots of the receptive fields were derived from the raw spatial event plots by placing a 40 × 40 cell grid over the plot yielding 1681 nodes with 0·25 or 0·5 mm internode distances depending on field type. The weight of each node was then calculated in terms of spatial spike density (spikes mm^{-2}) on the basis of nerve impulses within a radius of 1 mm. The weight of the individual impulse was graded according to its distance from the node. A $\cos^2$ weighting function was employed, with a weight of 1 at 0 mm and 0 at or beyond 1 mm:

$$\text{weight} = \cos^2(\text{distance} \times \pi/2), \qquad (1)$$

where angles are measured in radians. For instance, the weight of a spike 0·2 mm from the node was 0·90, and the weight of a spike 0·5 mm from the node was 0·5. The numerical value allocated to the individual node, i.e. the spatial spike density value (spikes mm^{-2}), is the sum of weighted spikes within 1 mm radius divided by a constant corresponding to the area weighted, again using the $\cos^2$ function. The spatial spike densities are indicated by a colour code in Fig. 5 from white for 0 density through blue to red for the highest density.

Measurement of field size

The sizes of receptive fields were measured with a digitizer from prints of the kind illustrated in Figs 4, 7 and 8. Charts based on optimal direction of probe movement were employed after removal of erratic spikes or, in the case of eight SAII units, after removal of the spontaneous activity as described above.

Statistics

Sample descriptions are given as median values and ranges because the samples were too small to judge whether or not they were normally distributed.

RESULTS

Altogether fifty-five low-threshold mechanoreceptive units with receptive fields in the hairy skin of the forearm or the proximal part of the hand were studied. The

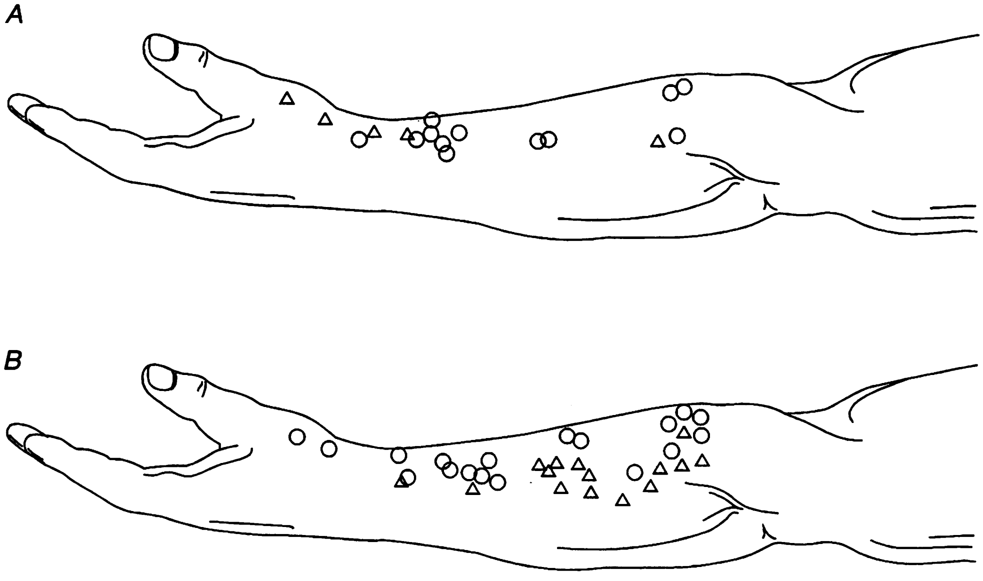

Figure 3. Locations of receptive fields explored in detail

A, rapidly adapting hair (○) and field (△) units. *B*, slowly adapting SAI (○) and SAII (△) units.

locations of fifty-two fields are shown in Fig. 3, but information on three SAI units was lacking in the experimental protocols. Basic data of the sample are presented in Table 1.

The units were readily separated into five types on the basis of the criteria described in Methods, i.e. (i) slowly adapting type I (SAI, Merkel), (ii) slowly adapting type II (SAII, Ruffini), (iii) hair units, rapidly adapting, (iv) field units, rapidly adapting, and (v) Pacinian-type (PC), rapidly adapting.

The second column of Table 1 shows the number and the third column shows the proportion of units of the five types. SAII units may be overrepresented since many of them were spontaneously firing and, therefore, immediately noticed by the experimenter. The fourth column gives the von Frey thresholds of a subset of units. The field units were extremely sensitive with a median threshold of only 0·1 mN. The SAI threshold was about five times higher and the SAII threshold about three times higher than the SAI threshold. No attempt was made to measure the threshold of the hair units.

Receptive field analysis

Of the total sample, thirty-five units were analysed in detail with regard to their receptive field structure (Table 1). No PC field was explored.

SAI (Merkel) receptive fields

Figure 4 shows representative fields of four SAI units, based on responses to unidirectional probe movements as described in Methods. It can be seen that the fields consisted of multiple spots which produced intensive firing in response to light indentations. It seems likely

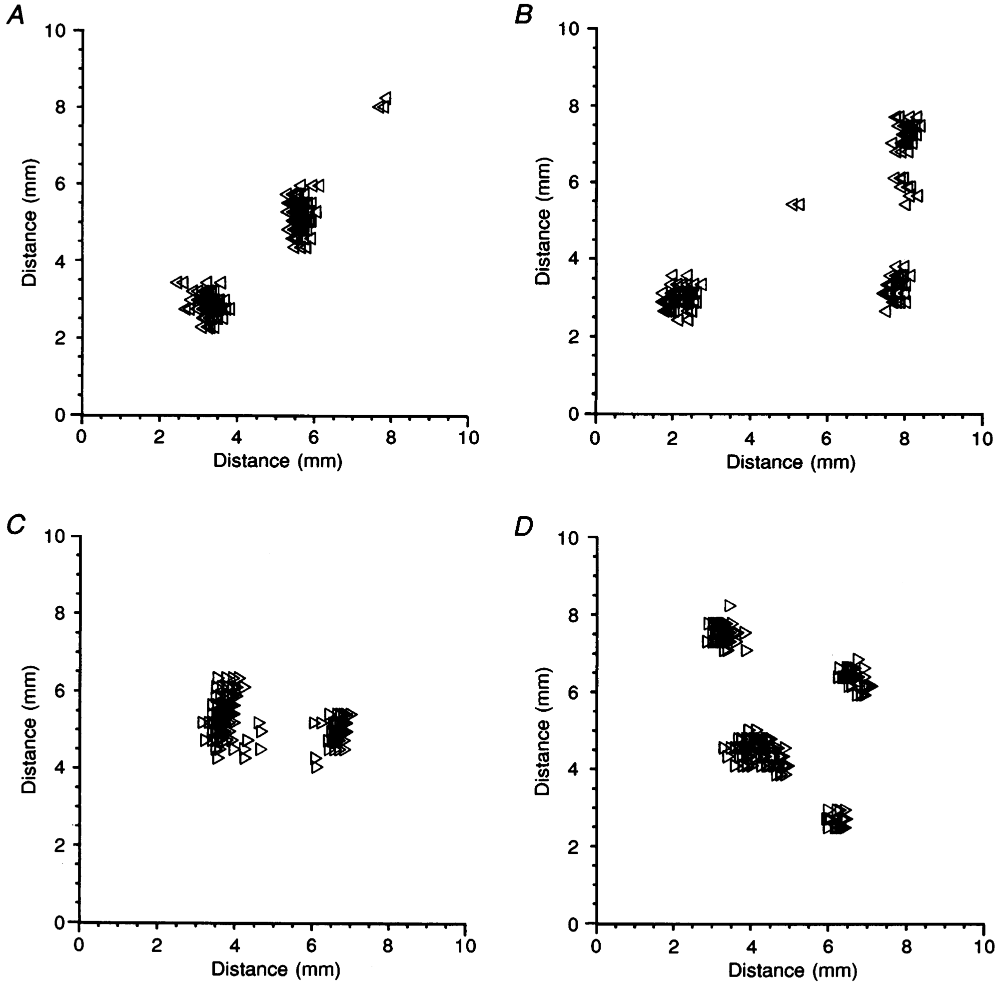

Figure 4. Receptive field maps of four SAI units

Unidirectional, filtered maps. The origin of the co-ordinates corresponds to the laterodistal corner of the explored area. Directions of probe movements as in Fig. 2.

Table 1. Properties of unit samples

Type	No.	Per cent of total	Median threshold (mN)	n	Area (mm^2) Median	Area (mm^2) Range	n
SAI	21	38	0·45	10	11	3·7–21	11
SAII	15	27	1·3	7	1·4	0·5–14	10
Hair	12	22	—	—	113	44–21	10
Field	5	9	0·10	3	78	42–115	4
PC	2	4	—	—	—	—	—
Total	55	100	—	20	—	—	35

that these spots correspond to the touch spots and domes covering clusters of Merkel cells as previously described in other mammals (Pinkus, 1904; Iggo & Muir, 1969). None of the eleven SAI units was spontaneously firing.

The spots were very distinct and well separated by silent areas. In addition to the regular spots, a responsive spot of much smaller size was present in five fields (i.e. Figs 1*C*, 4*A* and *B*) and in one field two such dwarf spots were identified.

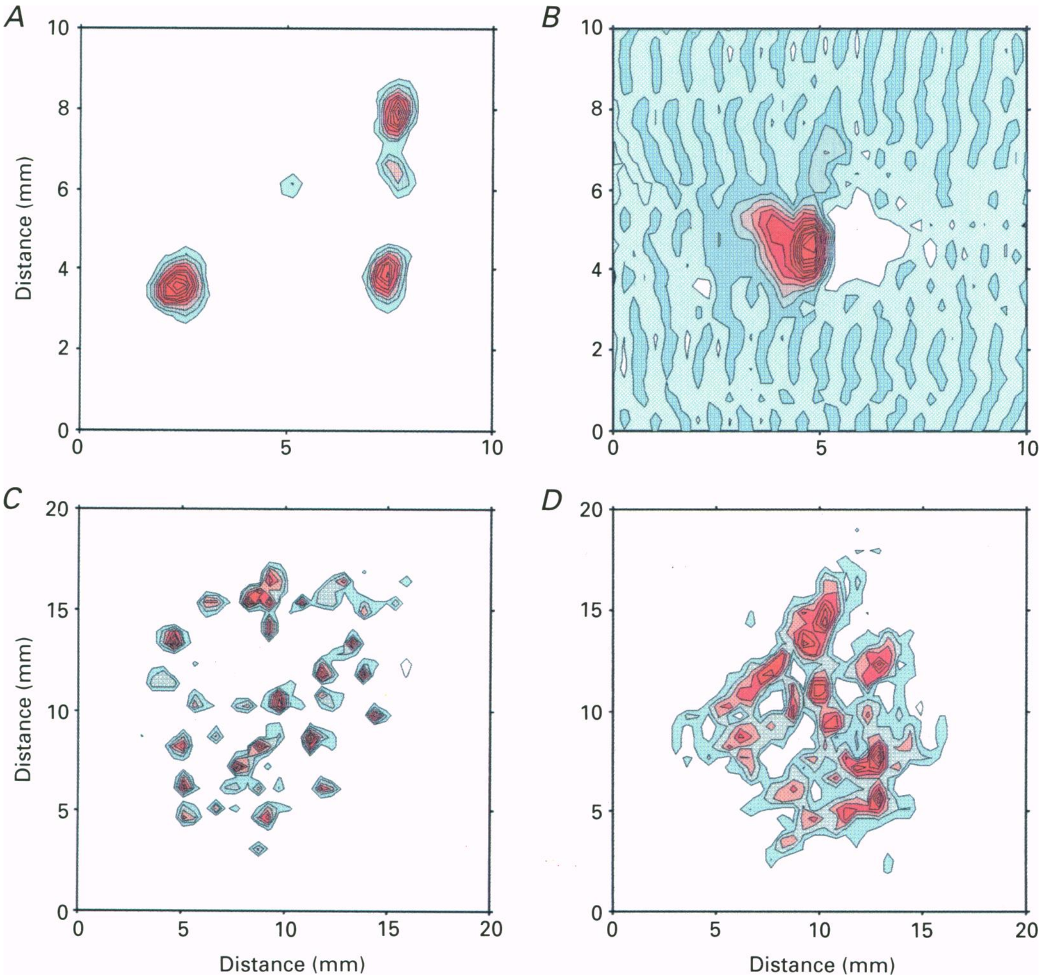

Figure 5. Colour-coded plots of four kinds of mechanoreceptive field

The plots are based on unidirectional, unfiltered maps. *A*, a SAI field, same unit as shown in Fig. 4*B*. *B*, a SAII field, same unit as shown in Fig. 6*B*. *C*, a hair field, same unit as shown in Fig. 7*C*. *D*, a field unit, same unit as shown in Fig. 8*A*.

Each field consisted of two to four regular spots. When more than two spots were present, they were often arranged in a triangle ($n = 6$). Other formations were a quadrangle ($n = 1$) or along a nearly straight line ($n = 2$). There was no preference in orientation of the receptive field in relation to the arm. Values for the area of the envelope housing the regular spots are given in Table 1. The individual regular spots had a median size of 0·8 mm^2 (0·2–2·2 mm^2, $n = 21$). There was a considerable variation between sizes of regular spots of a single field, the ratio between largest and smallest spot ranging from 1·3 to 4·8 in different units. All the figures showing spot size are based on a subsample of SAI units ($n = 7$) that was studied with a probe speed of 10 mm s^{-1}, the rationale being that higher speeds seemed to result in slightly smaller spot size.

The dwarf spots were all much smaller than the regular touch spots, i.e. median 0·02 mm^2. Since there was no overlap in any data between regular and dwarf spots, it seems reasonable to suggest that they are of a different nature. The dwarf spot was never located distal to the main set of spots but was either proximal, distal, medial or within the main set.

The median centre-to-centre distance between the regular spots was 3·0 mm, which was calculated from the minimal number of lines connecting all the spots in an open chain of minimal length. The median distance between the peripheries of the two most separated spots was 6·4 mm.

In the receptive field maps of Fig. 4 the intensity of firing as a function of location does not stand out very clearly. In order to highlight this third dimension, colour-coded

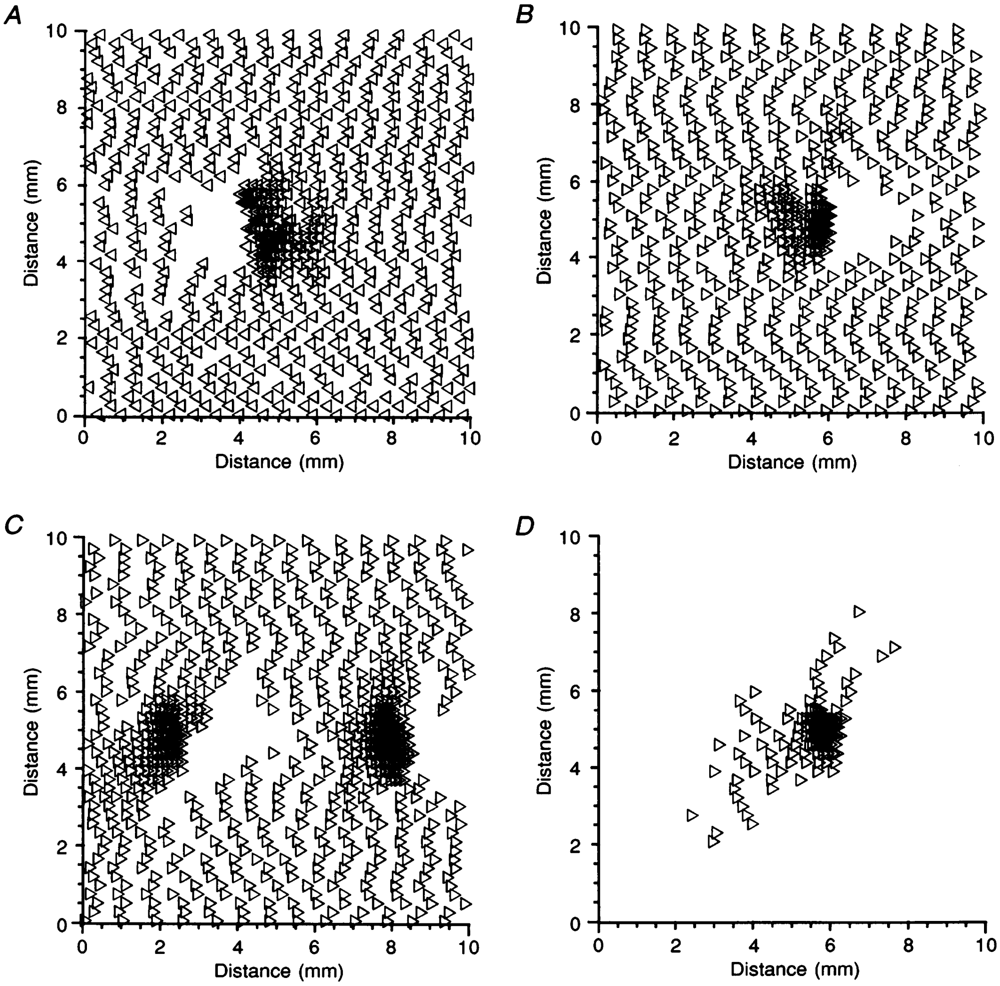

Figure 6. Receptive field maps of four SAII units

The maps were not filtered in order to include the spontaneous activity. Directions of probe movements indicated as in Fig. 2. Origin of co-ordinates as in Fig. 1.

contour plots were constructed as described in Methods. A SAI unit is illustrated in Fig. 5*A*, demonstrating the intense and distinct firing at the regular touch spots and the modest response at the dwarf spot.

SAII (Ruffini) receptive fields

Nine of ten SAII fields had a single responsive area and were, therefore, clearly different to SAI fields. Figure 6 shows maps of four SAII fields. Only one of ten SAII units had two high-sensitivity spots (Fig. 6*C*). Eight of the ten SAII units were continuously firing at a low and regular rate; this appears as a regular pattern in the receptive field maps of Fig. 6.

The plots in Fig. 6 demonstrate that the high-sensitivity spot was not as distinct as in the SAI units but the firing gradually increased as the probe approached the spot with the most intense firing. These phenomena were interpreted as the results of skin deformation which increased the strain on the ending. It was a regular finding that the spontaneous discharge stopped for a few tenths of a second when the probe had passed the high-sensitivity spot. Similar pauses in the spontaneous discharge were also seen after removal of a long-lasting indentation with a von Frey hair, suggesting that this might well be a fatigue phenomenon rather than an effect of specific skin deformation.

The median size of the receptive fields was 1·4 mm^2 (Table 1), defined as the area where the rate was above three times the mean spontaneous rate or, in the case of no spontaneous discharge, the area that remained after

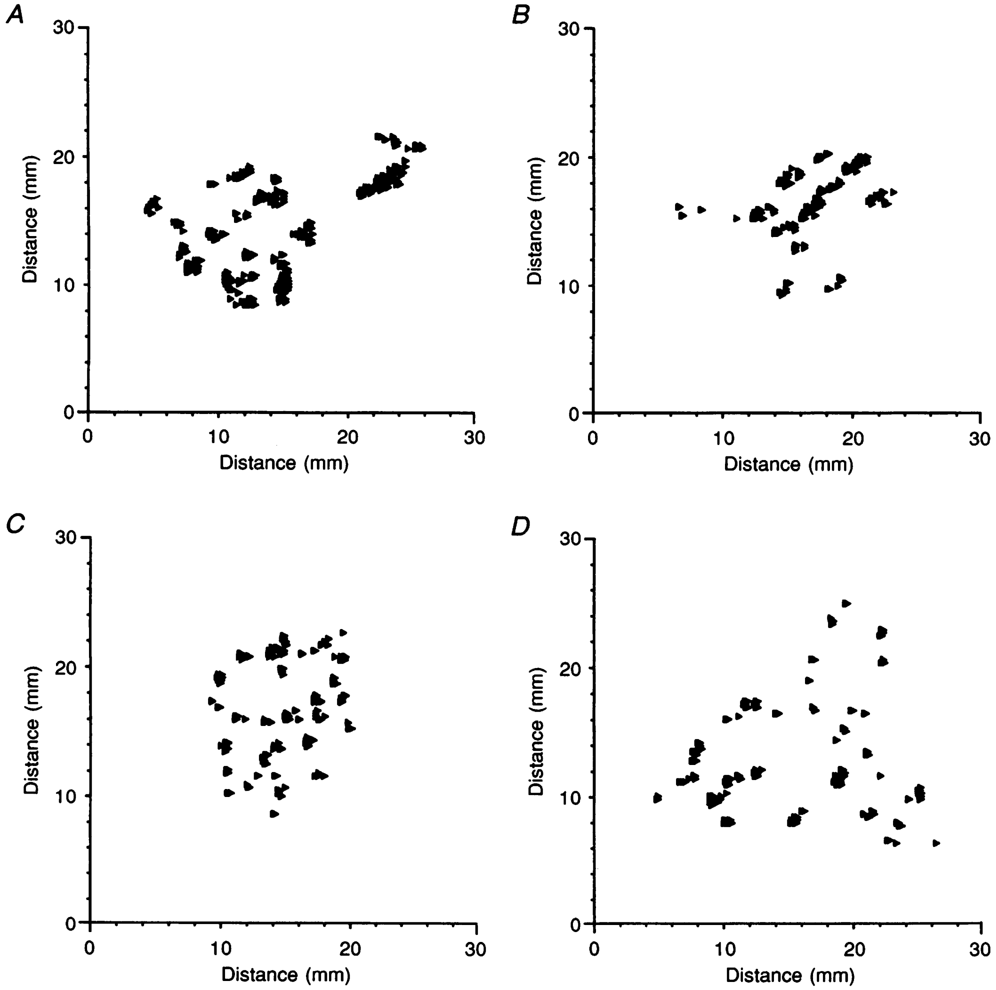

Figure 7. Receptive field maps of four hair units

Erratic spikes removed. Note that the scales are different from those in Figs 4 and 6. The symbols are scaled accordingly. Direction of probe movements indicated as in Fig. 2. Origins of co-ordinates as in Fig. 1.

removal of erratic spikes (see Methods). The exceptional unit with two high-sensitivity spots had a field of 14 mm^2, defined as the envelope housing the two spots. Figure 5*B* shows a colour-coded plot of a SAII unit.

Hair unit receptive fields

Figure 7 illustrates that the hair fields were much different in size and structure compared with the SAI and SAII fields described above. Note that the scales in Fig. 7 are different from those in Figs 4 and 6. The size of the symbols has been decreased to show the detailed geography of the fields.

The size of the hair fields was an order of magnitude larger than the SAI fields (Table 1). They were oval or irregular in shape, with no preference regarding orientation. The median lengths of the long and short axes were 16 and 11 mm, respectively.

Movements of the scanning probe in the proximal direction were regularly more effective than in the distal direction. It seems likely that this was related to the fact that probe movements against the hair direction were more effective than movements in the hair direction, in spite of the fact that the hairs had been cut short by shaving. With the other unit types there was no consistent difference with regard to intensity of response for the two directions of probe movement.

The receptive field maps of the hair units indicate that the individual afferent was connected to a large number of sensory endings which were fairly evenly but thinly distributed over the whole field.

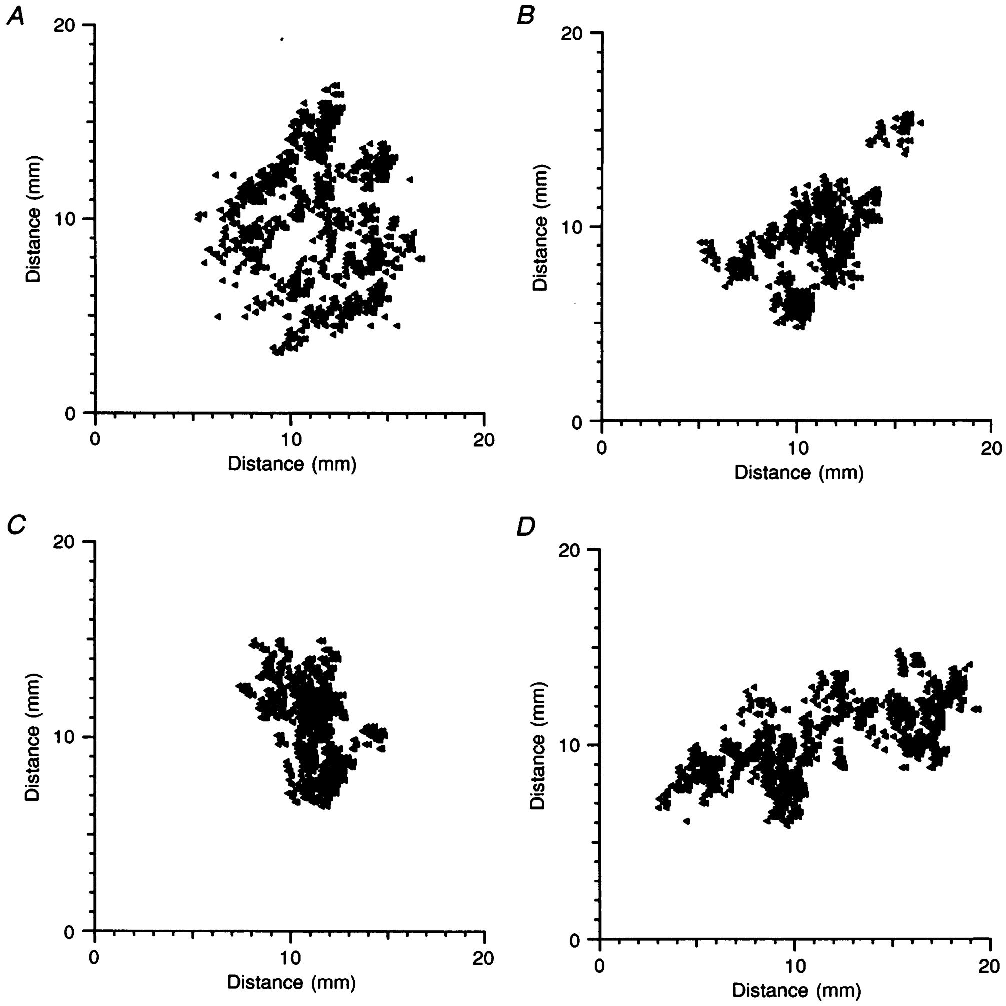

Figure 8. Receptive field maps of four field units

Erratic spikes removed. Note that the scales are different from those in Figs 4, 6 and 7. Direction of probe movements indicated as in Fig. 2. Origin of co-ordinates as in Fig. 1.

The individual high-sensitivity spots were often close together and not easy to separate from the neighbours on these plots. The exact number of high-sensitivity spots was sometimes difficult to determine but a conservative estimate indicated that at least twenty hairs were connected to the individual afferent (10–33, $n = 10$).

A colour-coded contour map (Fig. 5*C*) emphasizes that there were considerable differences in neural response from the separate sensory endings, suggesting a substantial variation in sensitivity. It cannot be excluded, however, that varying mechanical conditions contribute to the variation in response between endings. There was no significant difference in field size between units located in the proximal and the distal halves of the arm, a finding that was true for the other unit types as well.

Field units

The receptive fields of the field units showed some resemblance to the hair fields in that they were made up of numerous high-sensitivity spots distributed over a fairly large area (Fig. 8). The field sizes were large compared with the SAI and SAII fields and in the same range as the hair fields (Table 1). Also, these fields were oval or irregular in shape with no preference regarding orientation. The median lengths of the long and short axes were 13 and 7·0 mm, respectively.

Compared with the hair units, the individual high-sensitivity spots of the field units were larger, more closely packed and had more diffuse borders. The difference in structure stands out more clearly in the colour-coded contour plots where the field unit stands out as a single confluent area (Fig. 5*D*) against the archipelago structure of the hair unit (Fig. 5*C*).

Since the individual spots were not clearly separated from each other, it was difficult to define the exact number of high-sensitivity spots with the field units, but a conservative estimate gave a median value of eleven spots per unit (10–12, $n = 4$).

DISCUSSION

The primary aim of the present investigation was to assess the detailed structure of tactile receptive fields in human hairy skin. It should be emphasized, however, that the receptive field of an afferent unit is not an invariant entity. Its exact size, shape and geography are dependent on the characteristics of the stimulus employed to activate the unit (Johansson, 1978).

Method of stimulation

A very light and spatially focused skin indentation was made to scan the relevant skin area in a series of closely adjacent tracks. This approach to assess the receptive field geography was selected because it is objective and independent of the experimenter's skill and experience. It provides a comprehensive exploration of the field as it unravels all sensitive regions of the afferent. It provides an account of the point-to-point variation in sensitivity. A moving stimulus is highly relevant from a physiological point of view because most stimuli that attract our attention involve movements over the skin surface. It has also been shown that spatial acuity is better for moving compared with static stimuli (Norrsell & Olausson, 1994). From a clinical point of view, the response to a moving stimulus is of particular interest because an important test of cutaneous sensibility is based on patients' ability to judge the direction of a moving tactile stimulus (i.e. Wall & Noordenbos, 1977; Bender, Stacy & Cohen, 1982; Hankey & Edis, 1989). On the other hand, a scanning probe produces a stimulus that is highly complex from a biophysical point of view.

A different scanning method, based on a rotating wheel with embossed dots, was described some years ago and has been used with great success to explore tactile mechanisms of glabrous skin in the monkey (Johnson & Phillips, 1988). In addition, this method has recently been applied to the human hand and used to investigate the field geography of single units in glabrous skin (Phillips, Johansson & Johnson, 1990). However, the spatial resolution was not adequate to reveal the fine details of receptive field structures previously demonstrated with high precision punctate indentations (Westling, Johansson & Vallbo, 1976; Johansson, 1978). The present findings indicate that the scanning approach is better suited to mapping the detailed geography of afferents in hairy skin where the fields are larger than in glabrous skin.

It was important to use a light indentation force to reveal the sensitivity profiles of the receptive fields in detail. Control experiments indicated that stronger indentations generally resulted in more blurred representations of the field structures. Moreover, the impulse rates of the SAII units, as well as the sizes of their fields, increased considerably with indentation force, whereas SAI units were much less sensitive in these respects. In the present study a uniform indentation force was used throughout, implying that the force, in relation to their thresholds, was particularly small for the SAII units and high for the field units. Hence, the response of the former in terms of impulse rates was often small, while the maps of the field units were probably more blurred than was ideal.

Plotter speed had some effects on the firing rate and the size of the individual high-sensitivity spot, whereas other characteristics of the fields were not influenced much.

Unit types in the hairy skin of the forearm

The present sample of units naturally split into distinct groups on the basis of receptive field characteristics alone. Moreover, additional data were collected that matched these groups, e.g. adaptation, indentation threshold, interspike interval distributions, and responses to hair movements (not shown). Taken together, these findings demonstrated that the hairy skin of the human forearm is equipped with five different types of mechanoreceptive unit with fast-conducting nerve fibres, i.e. slowly adapting type I (SAI, Merkel), slowly adapting type II (SAII, Ruffini), and three types of rapidly adapting units, i.e. hair, field and Pacinian units. The same five types have previously been identified in other mammals (Iggo, 1974) although several kinds of field unit seem to be present in the cat (Burgess *et al.* 1968). However, the present findings do not refute the possibility that subtypes are present among the human field and hair units; it may be possible to identify these with other experimental approaches (Brown & Iggo, 1967).

Moreover, it has recently been shown that the hairy skin of the forearm is equipped with an additional tactile system, i.e. unmyelinated mechanoreceptive afferents that respond intensely to light tactile stimuli (Vallbo *et al.* 1993), and have similar functional properties to those previously demonstrated in other mammals (Douglas & Ritchie, 1957; Iggo, 1960; Bessou, Burgess, Perl & Taylor, 1971; Kumazawa & Perl, 1977).

SAI units and touch spots

It has been shown in animal experiments that SAI afferents supply clusters of Merkel cells that are located closely together below small spots of specialized epidermal structures forming touch spots in the hairy skin (Iggo & Muir, 1969). The structure of our SAI fields conforms very well to this pattern, assuming that each high-sensitivity spot corresponds to a single dome or touch spot, as originally described by Pinkus (1904).

An additional detail, not previously described, was that many SAI fields had a very small spot in addition to the two to four regular touch spots. This suggests either that there are smaller or less sensitive groups of Merkel cells in the vicinity of the main domes or that other structures of the units have mechanoreceptive properties.

The present data on SAI units may be used to estimate a lower limit for the density of touch spots in the skin. Since interdome distance for single units was 3·0 mm, the average number of domes cm^{-2} would be about 12, on the assumption that SAI fields are arranged in a mosaic pattern with equal distances between spots. This implies, in turn, that the average number of SAI units cm^{-2} would be 4, since the average number of domes per afferent is three. Obviously, these figures represent a lower limit, based on the assumption that the SAI fields do not overlap. However, it would be feasible to check this aspect with morphological methods.

Hair *versus* field units

The hair and field units had several features in common, i.e. they were both rapidly adapting and had large fields with a large number of high-sensitivity spots. It may be reasonable to raise the question of whether the two types are homologous, the essential difference being whether or not the endings are connected to hair follicles. The present data indicate a clear difference because the high-sensitivity spots of the hair units were more widely scattered and isolated by silent areas, whereas the maps of the field units were more confluent and compact. The data also suggest that the hair units had larger fields and a larger number of high-sensitivity spots than the field units, although these differences failed to reach statistical significance. The histological structure of the end organs of the field receptors remains an open question.

Regional differences in tactile sensory sheet

A comparison between the present findings and published data suggests that there are definite differences between the sensory sheet of the forearm skin on the one hand, and the innervation of the face and the dorsum of the hand on the other (Järvilehto *et al.* 1976*a*, *b*, 1981; Konietzny & Hensel, 1977; Johansson *et al.* 1988; Nordin & Hagbarth, 1989; Edin & Abbs, 1991).

In our study, the two main types of rapidly adapting units, i.e. hair and field units, were characterized by fairly large receptive fields. We found no rapidly adapting units with small fields; these seem to be common on the face and on the dorsum of the hand (Johansson *et al.* 1988; Nordin & Hagbarth, 1989; Edin & Abbs, 1991). Quantitative data on this point are available from a few studies that used weak and reasonably well-controlled stimuli (Johansson & Vallbo, 1980; Johansson *et al.* 1988; Edin & Abbs, 1991), whereas most studies either offer only qualitative information or are based on dissimilar stimulation techniques. However, a comparison of quantitative data leaves no doubt that the two main groups of rapidly adapting units on the forearm, i.e. field and hair units, had considerably larger receptive fields (78 and 113 mm^2, respectively) than the rapidly adapting units on the dorsum of the hand (24 mm^2; Edin & Abbs, 1991), in the face (17 mm^2; Johansson *et al.* 1988), and the FAI units of the glabrous skin (13 mm^2; Johansson & Vallbo, 1980).

The SAI fields, however, were remarkably similar in size in glabrous skin on the hand (11 mm^2; Johansson & Vallbo, 1980), on the face (7 mm^2; Johansson *et al.* 1988), on the dorsum of the hand (16 mm^2; Edin & Abbs, 1991), and on the forearm (11 mm^2). All these numbers refer to median values.

The SAI fields on the forearm were all composed of several distinct and well-separated touch spots, as previously demonstrated in the hairy skin of other mammals (Iggo & Muir, 1969). In contrast, the vast majority of the SAI fields on the dorsum of the hand and in facial skin have a single sensitive area with no distinct organization (Järvilehto *et al.* 1981; Johansson *et al.* 1988; Nordin & Hagbarth, 1989; Edin & Abbs, 1991).

In addition to these regional differences in myelinated afferents, a system of unmyelinated tactile afferents is present on the forearm (Vallbo *et al.* 1993) and on the face (Johansson *et al.* 1988; Nordin, 1990), but this has not been found on the hand, neither in hairy skin on the dorsum, nor in the glabrous skin on the palm.

Hence, the mechanoreceptive innervation of the human forearm skin has several similarities with the innervation of the hairy skin of other mammals, whereas differences have been identified in man between forearm skin, and the skin of the face and hand.

It seems reasonable to assume that the innervation of the forearm skin is more representative of the hairy skin covering the main part of the extremities and the trunk, whereas the face and the hands may be regarded as specialized sensory regions which, therefore, may have some unique innervation features.

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