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TACTILE SENSIBILITY IN THE HUMAN HAND: RELATIVE AND ABSOLUTE DENSITIES OF FOUR TYPES OF MECHANORECEPTIVE UNITS IN GLABROUS SKIN

BY R. S. JOHANSSON AND Å. B. VALLBO
From the Department of Physiology, University of Umeå, S-901 87 Umeå, Sweden

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SUMMARY

1. Single unit impulses were recorded with percutaneously inserted tungsten needle electrodes from the median nerve in conscious human subjects.

2. A sample of 334 low threshold mechanoreceptive units innervating the glabrous skin area of the hand were studied. In accordance with earlier investigations, the units were separated into four groups on the basis of their adaptation and receptive field properties: RA, PC, SA I and SA II units.

3. The locations of the receptive fields of individual units were determined and the relative unit densities within various skin regions were calculated. The over-all density was found to increase in the proximo-distal direction. There was a slight increase from the palm to the main part of the finger and an abrupt increase from the main part of the finger to the finger tip. The relative densities in these three regions were 1, 1·6, 4·2.

4. The differences in over-all density were essentially accounted for by the two types of units characterized by small and well defined receptive fields, the RA and SA I units, whereas the PC and SA II units were almost evenly distributed over the whole glabrous skin area.

5. The spatial distribution of densities supports the idea that the RA and SA I units account for spatial acuity in psychophysical tests. This capacity is known to increase in distal direction along the hand.

6. On the basis of histological data regarding the number of myelinated fibres in the median nerve, a model of the absolute unit density was proposed. It was estimated that the density of low threshold mechanoreceptive units at the finger tip is as high as 241 u./cm^2, whereas in the palm it is only 58 u./cm^2.

INTRODUCTION

The human hand is an organ of remarkable capacity and versatility in motor and sensory tasks as well as in combinations of the two. Its complex functions are undoubtedly dependent upon a number of neural factors, peripheral as well as central. A basic factor is the peripheral equipment serving the tactile skin sensibility, i.e. the population of low threshold mechanoreceptive units responding to skin deformation.

It has been shown in earlier studies that there are four different types of highly sensitive mechanoreceptive units in the glabrous skin area of the human hand (Knibestöl & Vallbo, 1970). Their basic physiological properties are similar to those of four types of units which have been described in other species (Lindblom, 1965; Lindblom & Lund, 1966; Jänig, Schmidt & Zimmermann, 1968; Talbot, Darian-Smith, Kornhuber & Mountcastle, 1968; Iggo & Muir, 1969; Lynn, 1969; Chambers, Andres, Duering & Iggo, 1972). The human glabrous skin units have accordingly been denoted RA, PC, SA I, and SA II units. Their functional properties have been studied in some detail with special emphasis on the quantitative relation between the stimulus intensity and the neural discharge (Knibestöl, 1973, 1975). Other reports have been focused on the sensitivity profile of their cutaneous receptive fields (Johansson, 1976*a*, *b*, 1978).

The findings agree with the notion that the end-organs of the RA, PC, SA I and SA II units are Meissner corpuscles, Pacinian corpuscles or paciniform end-organs, Merkel cell neurite complexes, and Ruffini end-organs (Iggo & Muir, 1969; Munger, 1971; Chambers *et al.* 1972; Lynn, 1969; Iggo & Ogawa, 1977; Johansson, 1978). It is known that these four types of end-organs are present in the glabrous skin area of the human hand (Miller, Ralston & Kasahara, 1958).

An important population parameter is the density of sensory units innervating a skin area. It is generally believed that the density of cutaneous innervation in man varies considerably from one region to the other (e.g. Mountcastle, 1974). For instance, the peripheral parts of the extremities are held to be much more densely innervated than the proximal parts and the trunk. It seems that this view is based upon three types of investigations: (i) measurements of the sizes of nerves and spinal roots distributed to different skin regions (Ingbert, 1903; Sunderland, 1968), (ii) psychophysical studies on cutaneous sensibility (Weber, 1835; Weinstein, 1968), (iii) measurements of the relative sizes of the primary projection areas from different skin regions in the somatosensory cortex (Penfield & Boldrey, 1937; von Békésy, 1955). However, the last two types of studies are very indirect and the first type provides only a rather schematic view of the density of cutaneous innervation. It is, for instance, not possible to evaluate the density of units subserving a particular submodality of skin sensibility.

The present study was undertaken in order to elucidate the distribution of tactile cutaneous units in the glabrous skin area of the human hand. The analysis is based on a sample of units collected using micro-electrode recordings from the median nerve. It is shown that the unit density increased in distal direction from the palm to the finger tips. The rise was not smooth but there seemed to be two rather abrupt increases. This is accounted for mainly by the RA and SA I units. The PC and the SA II units, on the other hand, were approximately evenly distributed over the skin area. The absolute densities were calculated on the basis of an estimate of the total number of myelinated nerve fibres in the median nerve at the wrist. The results have, in part, been presented in preliminary reports (Johansson & Vallbo, 1976*a*, *b*; Vallbo & Johansson, 1978).

METHODS

Neurophysiological experiments. Fifty-two experiments were performed on forty healthy adults. The subjects were between 18 and 28 yr old except two who were 16 and 42 yr old. The subjects were females in twenty-four experiments and males in twenty-eight experiments. Nerve impulses from single units were recorded with tungsten needle electrodes, using the method described earlier (Vallbo & Hagbarth, 1968). The electrodes were percutaneously inserted into the median nerve on the upper arm about 10 cm proximal to the elbow. When multi-unit activity was encountered indicating that a fascicle had been impaled, the electrode was moved on in very small steps. After each step the skin territory innervated by the median nerve was carefully explored to assess whether a single unit responding to slight deformation of the skin was discriminable against the background activity. The approximate location of the centre of the unit's receptive field was then determined by probing with a small blunt glass rod.

In accordance with earlier studies the units were classified on the basis of their adaptation and receptive field properties (Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975; Johansson, 1976*a*, *b*, 1978). It was assessed whether the receptive field was sharply delimited or if the unit responded readily to remote taps or skin stretch. Additional clues for the differentiation were obtained by mapping the receptive field with a set of nylon thread von Frey hairs. These data will be presented in a separate report. Further, the degree of regularity of interspike interval during long lasting indentation was also used to differentiate between SA I and SA II units (Chambers *et al.* 1972). These properties aiding unit classification were merely estimated. Occasionally units which apparently had their endings in deep structures were encountered. They often had higher thresholds and it was usually not possible to define a receptive field with a point of maximal sensitivity or a sharply delimited area on the skin. Deep indentations were required to evoke a response whereas forceful mechanical stimulation of the skin such as pinching a skin fold was ineffective. A large proportion of them were spontaneously active. Many units from the thumb were deliberately excluded as a large area of the glabrous skin on the volar and ulnar side of the thumb was not easily accessible for mechanical stimulation in the experimental set-up. Otherwise, care was taken to avoid sampling bias.

Measurement of the size of glabrous skin areas. In order to measure the size of various skin areas, transparent tape sheets were stuck over the whole glabrous skin. All the folds of the tape were carefully squeezed together and all surplus tape was cut away with a pair of scissors. The boundary of the glabrous skin and the flexure lines were marked with a pen on the tape. The tape was then removed from the hand and stuck onto a flat surface and the sizes of the various regions were measured using a planimeter. Data from six subjects were collected, four females and two males.

Histology. A section of a median nerve from the wrist level was obtained, for histological investigation, from a 23-year-old woman who had been killed in a car accident. The specimen was taken 10 hr after death. It was fixed in buffered glutaraldehyde, post-fixed in osmium tetroxide, dehydrated and embedded in Epon as described by Behse, Buchthal, Carlsen & Knappeis (1974). The cross-section of the nerve was photographed at 100 and 1000 magnifications. The total endoneurial area was measured. The average density of myelinated nerve fibres was estimated from a count of the number of fibres within 28% of the endoneurial cross-sectional area (7644 fibres). The total number of myelinated fibres was estimated on the basis of fibre density and endoneurial area. A calibre spectrum of the myelinated fibres was constructed on the basis of measurements of the diameters of 1000 fibres taken from four different areas of the cross-section. (The histological analysis of the median nerve was kindly carried out by Drs Buchthal and Behse in Copenhagen.)

Statistics. The binomial test (e.g. Siegel, 1956) was employed to assess the statistical significance of any differences in the unit density between two skin regions. The hypothesis tested is given by the equation:

$$P_A = \frac{a}{a+b}, \tag{1}$$

where a and b are the sizes of the two skin regions A and B and P_A is the proportion of units sampled from region A of the total number of units sampled from A and B. The test of this hypothesis can readily be shown to be equivalent to a test of the hypothesis that the unit densities in skin regions *A* and *B* are equal. When the probability was greater than 0·05 to obtain the observed sample proportion or a more extreme proportion in a two-tailed test, the hypothesis of equal density was accepted.

RESULTS

Size of the glabrous skin area. The total glabrous skin area varied in size from 150·0 cm^2 to 237·1 cm^2 in the six subjects whose hands were examined. The data are presented in Fig. 1*A* where the size of the glabrous skin area was plotted against the product of length and width of the hand. These two distances were measured,

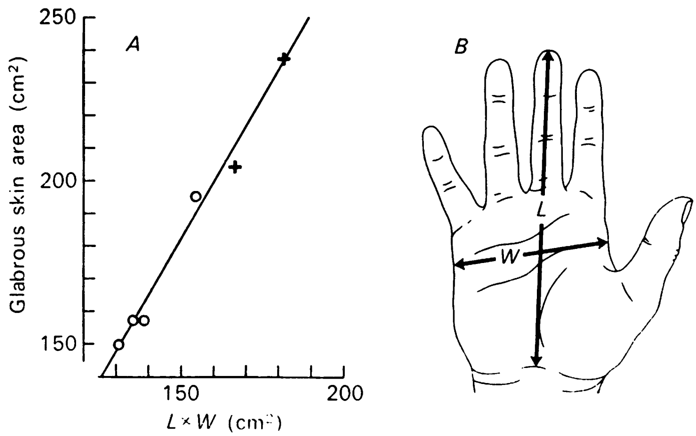

Fig. 1. *A*, relation between the size of the total glabrous skin area and the product of the length and width of the human hand as defined in *B*. The regression line represents the equation

$$Y = 1{\cdot}7 \times (L \times W) - 76,$$

where *Y* is the size of the glabrous skin area and *L* and *W* are the length and width of the hand as given in *B*. The correlation coefficient (r) was 0·992. *B*, definition of length and width of the human hand.

as indicated in Fig. 1*B*, from the contours of the hand. The length was measured from the tip of the long finger to the distal flexure line of the wrist at the point of intersection with the groove between the two superficial tendons. The width was measured as the distance between the points where the two transverse flexure lines of the palm reach the edges of the hand. In Fig. 1*A* the crosses and the circles represent data from male and female subjects. The value of the correlation coefficient (r = 0·992) indicates that the glabrous skin size may be estimated with reasonable accuracy from two simple measurements using the equation given in the legend. For the following calculations the mean value, which was 184 cm^2 is used. The total glabrous skin area was primarily separated into eighteen regions largely defined by the natural flexure lines as is schematically indicated in Fig. 2*A*. The four regions of the palm were bordered by the three main flexure lines and their extensions and, in addition by a line drawn in proximo-distal direction between the two transverse creases as an extension of the second interdigital space. In the schematic drawing of Fig. 2*A*, the size of the individual blocks is proportional to the size of the corresponding glabrous skin areas, whereas the numerals within the individual blocks give the percentage of the total glabrous skin area. The fact that the glabrous skin extends over the finger tips obviously accounts for the larger sizes of the terminal phalanges compared to the middle and the base phalanges.

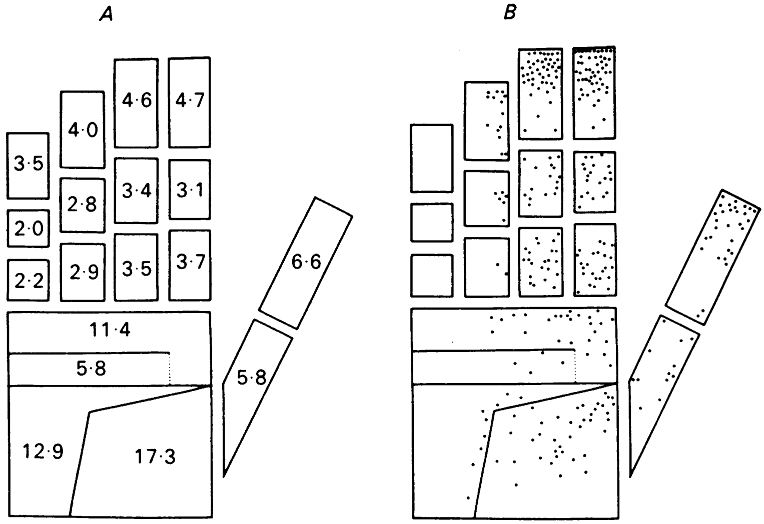

Fig. 2. *A*, relative sizes of the glabrous skin regions. The individual blocks are proportional in size to the corresponding glabrous skin areas. Numerals give the percentage of the total glabrous skin area. *B*, locations of receptive field centres of 334 glabrous skin mechanoreceptive units.

TABLE 1. Sampled number of glabrous skin units

Unit type	Sampled number of units	%
RA	143	42·8
PC	43	12·9
SA I	84	25·1
SA II Nail units	14	4·2
Other	50	15·0
Total	64	19·2
Total	334	100·0

Unit sample. Three hundred and seventy-four mechanoreceptive units were studied. Twenty afferents came from deep structures according to the definition given in methods. For another twenty units, or 5·6 %, of the skin mechanoreceptive units the receptive fields were located within the non-glabrous skin area on the dorsal aspect of the fingers. The remaining 334 units constitute the basis of the present account. They were classified as RA, PC, SA I and SA II units. The classification was unequivocal for all units with regard to the adaptation properties. However, for a small minority (less than 5 %) it was difficult to achieve the additional subdivisions within the adaptation categories, largely due to scanty information. Table 1 shows the numbers and the proportions of the four types of units. It can be seen that the rapidly adapting units, i.e. RA and PC units, constituted a little more than half of the units. By far the most common unit type were the RA units, followed by SA I units whereas the PC units constituted the smallest group. Moreover, it can be seen that the two types of units which are characterized by sharply defined receptive fields, i.e. the RA and SA I units, clearly outnumber the other two types.

The locations of the receptive fields of all the 334 units are schematically indicated in Fig. 2*B*. A schematic drawing was used to provide an adequate visual representation of the sampled unit densities within the various regions. The individual symbols represent the approximate centres of the fields. All fields but one were located within the classical innervation area of the median nerve. This area comprises

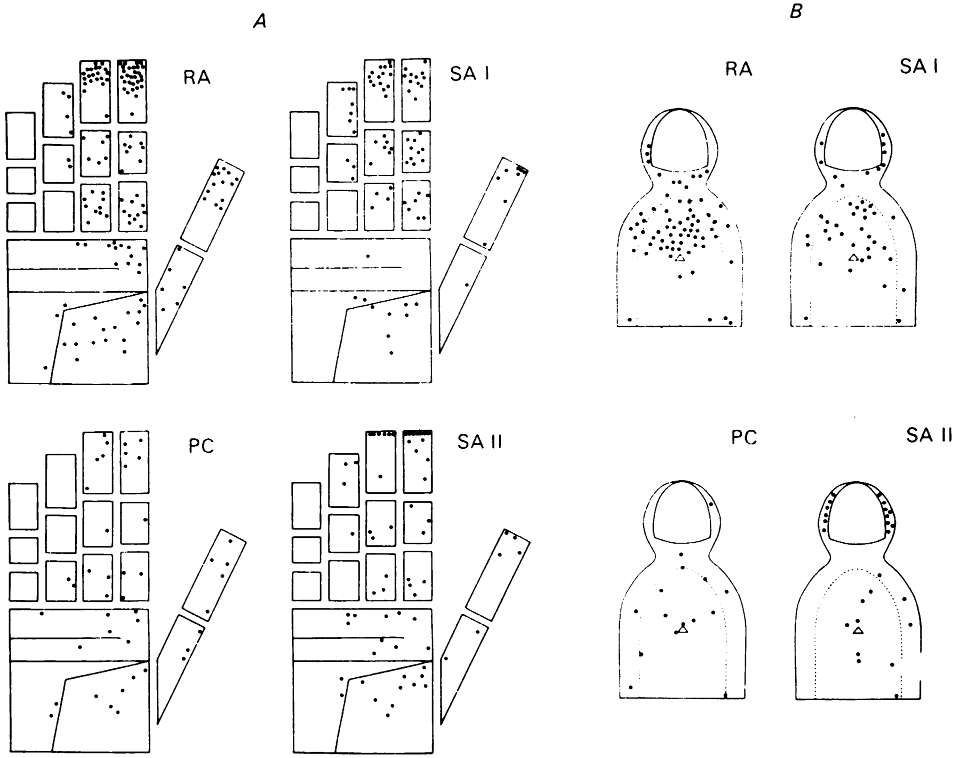

Fig. 3. Locations of the receptive field centres of 334 glabrous skin mechanoreceptive units separated according to unit type. *A*, total glabrous skin area. *B*, terminal phalanges and the nail projected on to a two-dimensional surface. Interrupted lines indicate the contours of the fingers as seen from the volar side while the triangles indicate the vortices of the skin ridges.

the glabrous skin of the three radial fingers, the radial half of the fourth finger, and the corresponding area of the palm with the exception of a radial band over the first metacarpus. It is evident that there were drastic differences between various regions. Most striking is the pronounced accumulation of units in the distal parts of the terminal phalanges. Moreover, the unit density seems slightly lower in the palm than on the proximal parts of the fingers. Thus, the findings suggest that the unit density does not increase smoothly in the proximo-distal direction but rather abruptly at two levels of the hand. In Fig. 3 it is illustrated to what extent the regional variations can be accounted for by the separate unit types. The locations of the receptive fields are indicated separately for the four different unit types. It is obvious that for RA and SA I units the density profile was basically similar to that of the total sample, whereas the PC units were practically evenly distributed over the whole glabrous skin area innervated by the median nerve. Also, the SA II units had a distribution similar to that of the PC units, with the exception of the SA II units related to the nails (Knibestöl, 1975; Johansson, 1976*b*, 1978). These nail units are indicated as a row of points along the distal ends of the blocks, representing the terminal phalanges. The SA II nail units were characterized by two features. First, they responded vigorously to forces applied to the nail. Secondly, the cutaneous receptive fields as defined with von Frey hairs were bordered by the nail. These units are functionally related to the nails rather than the skin itself and their endings are probably located underneath the nail (Johansson, 1976*b*, 1978).

To further illustrate the proximo-distal gradient in unit density on the terminal phalanges, more detailed maps of this region were constructed (Fig. 3*B*). The schematic drawings represent the glabrous skin area of the terminal phalanges and the nail projected onto a two-dimensional surface. The interrupted lines indicate the contours of the finger as seen from the volar side while the triangles represent the vortices of the skin ridges. On these maps all the units collected from the index and the long finger are indicated, but not those from the thumb and ring finger (see below). Again, it is obvious from Fig. 3*B* that the concentration of RA and SA I units was much higher in the distal part of the phalanx than in the proximal part, whereas the PC and SA II units were more evenly distributed, with the exception of a relatively large number of SA II nail units which are indicated by points along the border of the nail.

As may be seen from Figs. 2*B* and 3*A*, there was no indication that the sampled unit density was generally higher on the volar aspects of the fingers than on the lateral aspects covered by glabrous skin.

In addition to the proximo-distal gradient of sampled unit density there was a density gradient in the transverse direction as well. The concentration of units was higher on the index and the long finger than on the thumb and the radial half of the ring finger. It seemed reasonable to ascribe this to two factors. First, the sampling was deliberately biased towards an under-representation of units from the thumb as pointed out in Methods. Secondly, it is known that there are anatomical variations with regard to the extent of the area innervated by the median nerve. This is mostly seen as a radial displacement of the border between the areas of the median and the ulnar nerve (Sunderland, 1968). This factor might account for an under-representation of the number of units sampled from the strip of the median nerve region bordering the ulnar nerve region. Regardless of whether these factors provide a full explanation, it seems pertinent to define an area within the territory innervated by the median nerve where these effects should be minimal. An area was therefore selected which comprises the glabrous skin of the index and long finger as well as an area of the palm, defined by the extension of the third inter-digital space, the flexure line at the base of the thumb, and a line which bisects the latter and meets the former at the distal flexure line of the wrist. This area is referred to as the central median area, and it is shown in light grey in Fig. 4. In the following, exclusively data from this area will be considered for quantitative analysis.

Relative unit density. The sampled unit densities were calculated for separate regions within the central median area on the basis of the average sizes of the regions. Table 2 shows the densities within the palm, the base and the middle phalanges taken together, the finger tip and the terminal phalanx as a whole. The

TABLE 2. Number of units sampled per cm² glabrous skin area from four regions: the palm, the base and the middle phalanges taken together, the finger tip and the whole terminal phalanx

Unit type	Palm	Base and middle phalanges	Finger tip	Terminal phalanx
RA	0·93 n.s.	1·40	5·30***	2·92
PC	0·35 n.s.	0·36	0·81 n.s.	0·58
SA I	0·30***	1·12	2·65**	1·57
SA II excl. nail units	0·59 n.s.	0·52	0·35 n.s.	0·29
SA II total			1·84	1·05
Total excl. nail units	2·17**	3·40	9·11***	5·36
Total			10·60	6·12

The figures are based upon data from the central median area as defined in the text and shown in grey in Fig. 4*A*. The symbols in the first and the third columns indicate the significance levels of the differences with regard to unit density in relation to the densities in the base and middle phalanges given in the second column.

* Significant at 0·05 level; ** Significant at 0·01 level; *** Significant at 0·001 level. n.s. not significant.

Tests of significance were made using the binomial method applied to the total numbers in each category as described in Methods. Therefore the significance values of the differences apply exclusively to the pooled sample whereas variability from subject to subject has not been taken into account.

densities within the former three regions will be compared in some detail. The finger tip was delimited by a transverse line through the vortex of the skin ridges which divided the glabrous skin area of the terminal phalanx in two halves. The data from the separate regions of the index and the long finger were pooled as no statistically significant difference was found between corresponding regions of these two fingers.

It may be seen that the over-all unit density increased in the distal direction from the palm. The relative densities were 1·0, 1·6 and 4·9 for the palm, the base and the middle phalanges taken together and the finger tip. However, as indicated above there is some justification for excluding the SA II nail units when considering the innervation of the glabrous skin. If the SA II nail units are not included the ratio of unit density between the palm and the finger tip is 1/4·2. Also for the RA and SA I units there was a considerable increase in unit density in the distal direction. As indicated in Table 2 the differences were statistically significant between the three skin regions for the over-all unit density, for the density of the RA and SA I units but not for the density of the PC and SA II units. An exception was that the difference in the density of RA units between the palm and the main part of the finger was not significantly different.

On the other hand, no significant differences were found between the middle and the base phalanges, nor between the proximal and distal halves of the palm with regard to over-all unit density or the density of the four unit types separately. Hence the analysis supported the impression that the rise in over-all unit density in the proximo-distal direction was not smooth and continuous but largely occurred at two levels: between the palm and the finger and between the proximal and distal part of the terminal phalanx. The analysis also supported the impression that the rise in over-all unit density was accounted for by the RA and SA I units.

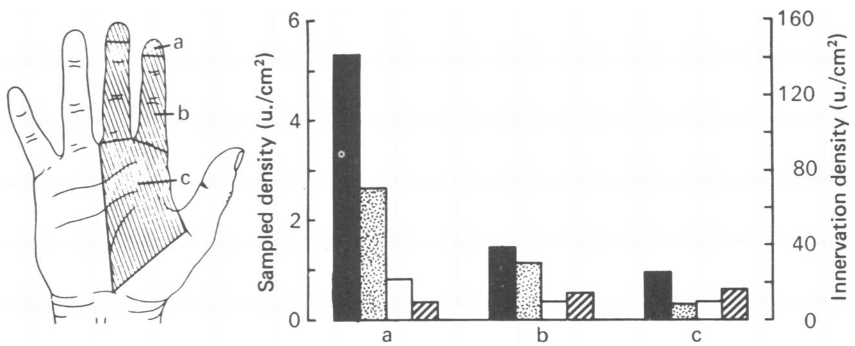

Fig. 4. Diagram to demonstrate the densities of the four types of mechanoreceptive units in three different regions of the glabrous skin: the finger tip (a), the remaining part of the finger (b) and the palm (c). Filled, stippled, hollow and hatched blocks refer to RA, SA I, PC and SA II units respectively. Left ordinate indicates the number of units sampled per cm^2. The right ordinate represents an estimate of the absolute number of units per cm^2. The data refer to the central part of the skin area innervated by the median nerve as indicated by the hatched zone in the drawing of the hand. Those SA II units which were related to the nail rather than to the glabrous skin were excluded in the diagram.

The unit densities in the three-skin regions of the four unit types are shown graphically in Fig. 4. The diagrams illustrate rather strikingly the dominance of RA and SA I units with regard to the relative number of units. Moreover that they account for the differences in over-all unit density between the three skin areas. The middle columns refer to data from the base and middle phalanges only but the difference would be negligible if the data from the proximal half of the terminal phalanx were included.

From Fig. 2*B* it may be seen that the unit density within the proximal half of the terminal phalanx was low compared to the more proximal finger skin areas. However, a quantitative analysis was not carried out since the small number of units sampled implies a high degree of uncertainty.

In order to illustrate the relative number of input channels to the central nervous system from the different regions, a schematic drawing of the hand (Fig. 5) was constructed. The areas of the blocks are proportional to the number of units innervating the various regions and were calculated on the basis of the unit densities within the central nerve area. The terminal phalanges were separated into two parts representing the skin distal and proximal to the vortex. A striking feature of this drawing is the disproportionally large area of the finger tip in relation to the other areas.

Absolute unit density. An inference of absolute unit density was made on the basis of (i) the relative unit densities presented in the previous section, (ii) an estimate of the number of large myelinated fibres in the median nerve innervating the glabrous skin. This estimate was based upon the histological analysis described in Methods. The total number of myelinated fibres in the median nerve at the wrist was 27,300. The fibre diameter spectrum of the nerve showed a pronounced trough at 7 μm which may be assumed to represent the dividing line between Aα and Aδ fibres (cf. Fig. 9 in Vallbo & Johansson, 1978). 50·1 % of the fibres had diameters above 7 μm. To arrive at an estimate of the number of Aα fibres innervating the glabrous skin the total number of fibres should be reduced by the fibres innervating (i) the small hand muscles, (ii) the non-muscular deep structures and (iii) the non-glabrousskin on the dorsal aspect of the fingers.

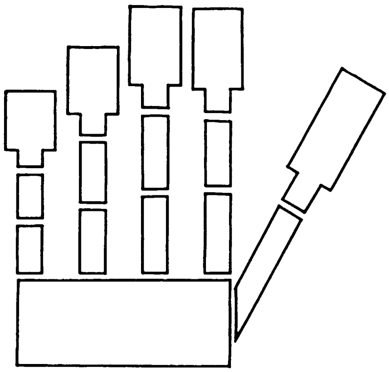

Fig. 5. Schematic drawing to visualize the relative number of tactile sensory units innervating the various regions of the glabrous skin. The blocks are proportional in size to the number of high sensitivity mechanoreceptive units innervating the regions represented by the blocks.

From measurements of the fascicular cross-sectional areas in the median nerve (Sunderland & Bedbrook, 1949) it may be inferred that the recurrent branch of the median nerve which constitutes the main muscular branch in the hand accounts for 5·6 % of the total nerve cross-sectional area at the wrist. Lee, Asby, White & Aguayo (1975) have counted the number of myelinated fibres in this branch. They obtained an average number (1562) corresponding to 5·7 % of the total number of myelinated fibres in the median nerve as stated above. The agreement between these two figures is remarkable. The comparison between the proportion of cross-sectional area and the proportion of number of fibres seems reasonable as the fibre diameter spectrum of the recurrent branch (Lee *et al.* 1975) is reasonably similar to that of the total median nerve. No estimate of the number of fibres innervating other deep structures has been found in the literature, but it is known from morphological studies (e.g. Stilwell, 1957) that there is an abundance of highly organized sensory end organs connected to large diameter nerve fibres within the deep structures. On the basis of the proportion of deep units found in the present sample it was assumed that 5 % of the remaining large fibres innervate the deep structures not supplied by the recurrent branch. This assumption is clearly arbitrary but, as long as this figure is low its precise value should not have major effects on the accuracy of our calculations. The assumptions imply that, in all, 10·4 % of the large myelinated fibres at the wrist are distributed to deep structures in the hand. As reported above, 5·6 % of the skin mechanoreceptive units sampled innervated the non-glabrous skin on the dorsal aspect of the fingers. It was assumed that this figure was representative for the population. These considerations lead to the estimate that 11,564 large myelinated fibres in the median nerve supply the glabrous skin area. As there is evidence that all the large fibres from the glabrous skin belong to high sensitivity mechanoreceptive units (see Discussion), it was concluded that the above figure gives the absolute number of such units innervating the glabrous skin supplied by the median nerve.

On the basis of the figures arrived at in earlier sections for the sizes of the glabrous skin areas, the sampled unit densities, and the number of sensory units in the median nerve, a scaling factor was derived for the estimate of the absolute unit densities. To this end, the total area innervated by the median nerve was taken as 118·0 cm^2. It comprised 44·1 cm^2 of skin in the palm, 40·9 cm^2 of skin on the base and the middle phalanges and 33·0 cm^2 of skin on the terminal phalanges. In Table 2 the sampled unit densities within these three skin areas are given. The respective skin areas and unit densities were multiplied and the products were summed up to obtain the total number of units which would have been sampled if no regional selection bias had been present. The result was 436·6 units. Dividing 11,564 by this figure gives a scaling factor of 26·5.

A multiplication of the experimental unit densities of Table 2 by this factor gives an estimate of the absolute unit densities. A graphical presentation is shown in Fig. 4 where the right hand ordinate represents the estimated absolute densities of the four unit types separately. It may be noted, for instance, that the density of RA units at the finger tip is as high as 141 units/cm^2 whereas in the palm it is only 25 units/cm^2. The total number of tactile units innervating the tip of the index, i.e. the area of glabrous skin distal to the vortex of the skin ridges, excluding SA II nail units, would be one thousand (1038), whereas the whole remaining glabrous skin area of this finger would be innervated by not more than one thousand five hundred units (1514). The whole palm area, on the other hand, would be innervated by five thousand units (5014), assuming similar density within ulnar and median nerve regions. The total number of tactile sensory units innervating the whole glabrous skin area of the human hand would be seventeen thousand (17,023), again assuming similar densities within the ulnar and the median nerve territories.

DISCUSSION

A number of studies have been published in recent years on the high sensitivity mechanoreceptive units in the glabrous skin area of the primate hand, including man (e.g. Lindblom, 1965; Lindblom & Lund, 1966; Mountcastle, Talbot & Kornhuber, 1966; Talbot *et al.* 1968; Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975; Johansson, 1976*a*, *b*, 1978; for further references see Burgess & Perl, 1973). However, very little information is available on the relative and absolute frequencies of the four types of units and their density distribution over the glabrous skin area. A reasonably clear picture of these basic population properties is obviously desirable for psychological analyses of the tactile capabilities of the hand as well as for physiological and clinical studies of tactile sensory mechanisms.

Single unit sample

The method of single unit recording used in the present study probably entails a preferential selection of Aα fibres over Aδ and C fibres. Studies on primates, including man, indicate that there are no high sensitivity mechanoreceptive units with unmyelinated fibres present in the distal parts of the limbs (van Hees & Gybels, 1972; Torebjörk, 1974; Torebjörk & Hallin, 1974; Georgopoulos, 1976; Kumazawa & Perl, 1977). Other studies of myelinated nerve fibres innervating the glabrous skin in subhuman primates have shown that the high sensitivity mechanoreceptive units are connected to large diameter nerve fibres (Aα), whereas the small diameter myelinated nerve fibre units (Aδ) have other functional properties (Darian-Smith, Johnson & Dykes, 1973; Georgopoulos, 1976). Therefore it seems that an analysis of large diameter afferents would essentially cover the peripheral equipment relevant to cutaneous tactile sensibility in the glabrous skin of the human hand. As to terminology, the units studied have mostly been denoted, high sensitivity mechanoreceptive units. It seems that tactile units is also a reasonable term, although other unit types may play a role in tactile sensibility.

Possible sample bias. A bias in the sampling procedure would probably be introduced if there were marked differences in nerve fibre diameter between the different types of units. However, there is no indication in the literature of any major differences, neither between the four types of glabrous skin units, nor between similar unit types in hairy skin. Small differences have been reported in some studies suggesting that the SA II and the PC units conduct at a slightly lower velocity than the two other types (Iggo, 1963; Brown & Iggo, 1967; Burgess, Petit & Warren, 1968; Perl, 1968; Jänig *et al.* 1968; Talbot *et al.* 1968; Merzenich & Harrington, 1969; Brown & Hayden, 1971; Knibestöl, 1973, 1975; Whitehorn, Howe, Lessler & Burgess, 1974; Pubols & Pubols, 1976; Iggo & Ogawa, 1977). However, the difference in conduction velocity would correspond to a mean difference in nerve fibre diameter of only 1–2 μm. It seems unlikely that such a small difference would introduce any major bias in the selection of units (Burgess *et al.* 1968; Whitehorn *et al.* 1974).

Another type of bias related to the functional properties of the endings may be relevant. It seems reasonable to assume that PC and SA II units are more easily detected than the RA and SA I units because the PC units have very wide receptive fields and many of the SA II units were spontaneously active. These facts may contribute to some over-representation of these two unit types. Any difference in nerve fibre diameters, as considered above, would work in the opposite direction and the two effects might partly cancel each other.

Relative number of slowly and rapidly adapting units. A little more than 50% of the units sampled were rapidly adapting. Earlier investigations on man suggest that the slowly adapting units outnumber the rapidly adapting ones (Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975). In restrospect, it seems possible that these earlier experiments were biased by an interest in collecting responses of slowly adapting units to long lasting skin indentations, as psychophysical magnitude estimation of such stimuli was a topic of interest in these experiments. Moreover, findings from other species too fail to agree on this point. There are investigations which indicate that the rapidly adapting units outnumber the slowly adapting ones (Lindblom, 1965; Talbot *et al.* 1968) as well as vice versa (Georgopoulos, 1976; Perl, 1969; Pubols & Pubols, 1976). Although there is some variation, most of the studies available indicate that roughly half of the high sensitivity mechanoreceptive units in the glabrous skin area are rapidly adapting both in monkey and in man.

Spatial distribution of units. Three sets of morphological observations in the literature are qualitatively in agreement with the present findings concerning the spatial distribution of units over the glabrous skin area. The density of Meissner corpuscles is considerably higher at the finger tip than in the palm (Bolton, Winkelmann & Dyck, 1966; Sinclair, 1967), the ratio (4·4) being similar to the ratio of RA units as found in the present study (5·7) (Table 2). On the other hand, Cauna & Mannan (1958) have found that the Pacinian corpuscles are approximately evenly distributed along the finger, as were the PC units of the present sample. On the basis of dissection of nerve fascicles, Sunderland (1945) concluded that the cross-sectional area of the median nerve occupied by fibres distributed to the palm is much smaller than the area occupied by fibres connected to the digits.

A striking result of the present study was the detection of a pronounced rise in unit density in the proximo-distal direction. The findings indicate that there was not a smooth gradient in unit density but a slight increase from the palm to the main parts of the fingers and an abrupt increase from the main part of the finger to the finger tip. A second striking result was the fact that the difference in unit density was mainly accounted for by two types of units, the RA and the SA I units, which are both characterized by small and well defined receptive fields. The other two types of units, the PC and the SA II units, were practically evenly distributed over the total skin area providing that the SA II units of the nails were excluded.

The high density of units in the distal half of the terminal phalanx seems to match the function of this skin area as an outstanding sensory region. When the human hand is used to explore a surface structure or the details of an object with fine manipulatory movements, it is the distal parts of the terminal phalanges which make contact with the surface of the object. Results of psychophysical tests on the capacity of spatial analysis, e.g. two-point discrimination and localization tests, also indicate that this capacity rises in the distal direction along the arm and that it is particularly high at the finger tip (e.g. Weber, 1834, 1835; Kottenkampf & Ullrich, 1870; Henri, 1898; Boring, 1942; Weinstein, 1968). A preliminary investigation indicates indeed that the decrease in two-point discrimination capacity from the finger tip to the main part of the finger and to the palm corresponds reasonably well to the decrease in density of RA and SA I units found in the present study (Johansson & Vallbo, 1976; Vallbo & Johansson, 1978). Thus, it seems that the spatial distribution of the RA and SA I units as well as their receptive field properties make these two systems of mechanoreceptive units particularly suitable for tactile spatial analysis.

The findings that the PC and SA II units are evenly distributed over the glabrous skin area corroborates the tentative conclusion that their main role in tactile sensibility does not lie in spatial discrimination. It seems possible that the SA II units have a role in kinesthesia as was pointed out in previous studies (Vallbo & Knibestöl, 1970; Knibestöl, 1975). In addition they may play a specific role in the glabrous skin region of the hand providing information on the shearing forces between the skin surface and any object held in the hand. Information of this type might be highly significant for the adjustment of the muscular activity in order to avoid slipping of a hand-held object.

Absolute density of innervation

A model of the absolute density of innervation was made principally on the basis of two types of information: (i) the relative density of high sensitivity mechanoreceptive units within the glabrous skin area innervated by the median nerve, (ii) an estimate of the number of myelinated fibres in the median nerve innervating such units. The validity of the model is clearly dependent upon the reliability of these data. The first set of data was discussed above and the second set will be considered below.

Estimate of a scaling factor. A scaling factor was derived which allowed the calculation of the absolute unit density from the sampled density on the basis of an estimate of the number of myelinated fibres in the median nerve at the wrist. Some data are available in the literature which allow similar but cruder estimates of absolute unit densities in rather limited respects. Bolton *et al.* (1966) counted the number of Meissner corpuscles at the finger tip and in the thenar eminence. They found a density of 24·0 and 5·4 corpuscles per mm^2. Johansson (1978) estimated the average number of endings per RA unit to a minimum of 14·4, whereas 20 was considered to be a more likely figure. An estimate was made of the RA unit density on the basis of these figures, assuming that the Meissner corpuscles are the endings of the RA units. It was found that the RA unit density per cm^2 would be 120 and 27 at the finger tip and in the palm. There is a reasonable agreement between these figures and the values (141 and 25) derived in the Results section. An assumption in this reasoning is that the individual Meissner corpuscle is innervated by only one afferent stem fibre. Morphological findings indicate that several myelinated fibres may enter a single Meissner corpuscle (Cauna, 1956). However, it is not known whether these fibres are branches from the same stem fibre or not (Iggo, 1974). The above reasoning suggests that multiple innervation of Meissner corpuscles, if present, is not very prominent.

Furthermore, a scaling factor may be derived using the findings of Buchthal & Rosenfalck (1966) who counted the number of myelinated fibres in the digital nerve at the level of the second phalanx. They found, on average, 1200 fibres, 62 % (744) of which were large fibres. It is not stated in their report exactly where the section was taken, nor how large a part of the finger would be innervated by the fibres counted. A reasonable assumption is that this nerve supplied half the middle phalanx and the whole distal phalanx. This area would thus be innervated by 1488 large myelinated fibres. In the present study the number of tactile sensory units sampled from this skin area were 68 units, including units with receptive fields on the dorsal aspect of the finger (average of index and middle finger). Therefore the present sampled unit densities should be scaled up by a factor of 22 in order to give the absolute unit densities. This figure agrees satisfactorily with the figure (26·5) calculated in the Results section. However, the former figure was estimated on the basis of two additional approximations. Innervation of the deep structures was not taken into account, nor was allowance made for the reduction of the number of nerve elements with age (Corbin & Gardner, 1937; Gardner, 1940; Swallow, 1966; O'Sullivan & Swallow, 1968). Buchthal & Rosenfalck's preparations were taken from older subjects (49 and 62 yr) than those in the present study. Reasonable corrections for these two points would rather bring the two scaling factors closer together. Thus, three different approaches to the estimate of unit density give reasonably uniform results. However, there is one set of data in the literature which gives result substantially different when employed for the calculation of unit density. Buchthal & Rosenfalck (1966) estimated the total number of myelinated fibres in the median nerve, at the wrist, to only 6500, i.e. about 24% of the number given in the Results section of the present report. It has not been possible to clarify the basis of this discrepancy but it seems obvious that the lower figure implies a serious underestimate of the number of fibres in the normal median nerve of young adults (F. Buchthal & A. Rosenfalck, personal communication). The scaling factor arrived at in the present study is somewhat higher than that given in a preliminary report (Johansson & Vallbo, 1976*a*).

Validity and relevance of the model of the absolute innervation density. It should be stressed that the aim of the present study was to provide a model describing the main features of the tactile cutaneous innervation, whereas absolute accuracy is not claimed. Several considerations support this statement. The study is based upon an estimate of the number of myelinated fibres in the median nerve in a single preparation. It was assumed that this particular nerve supplied the classical innervation area of the median nerve as defined in Results, and that the specimen was taken from a hand of average size. It is well known that there are inter-individual variations both with regard to the shape of the median nerve area and the size of the glabrous skin area (see Results). As regards the number of myelinated fibres in the median nerve, studies in the monkey suggest that the variation in this number is small (Matsumoto & Mori, 1975). In addition, a number of approximations are included in the calculations. Alternative assumptions in these cases would, however, not greatly affect the end result, but they would certainly alter the exact figures to some extent. For instance, the proportion of large myelinated fibres distributed to deep structures, besides those running in the recurrent branch, was assumed to be 5%. If this proportion was twice or three times larger, the densities of cutaneous innervation should be reduced by 5 or 11%. Other population properties based upon this model will be presented in a subsequent paper.

Practically all data were collected from subjects in the age group 18–28 yr and thus the model should be valid primarily for this group. According to the study by Gardner (1940) the number of myelinated fibres present in the second and the third decade of life is reduced by about 5% per decade. This implies, for instance, that in the eighth decade the number of myelinated fibres innervating the total glabrous skin area of a human hand would have been reduced from 17,000 to 13,000.

Note added in proof. Since this manuscript was submitted another median nerve specimen has been histologically analysed as described in Methods. The specimen was taken from a 45 yr old man. The composition of this nerve was essentially similar to the one described in Results. It is contained 31,000 myelinated fibres, 53% of which were larger than 7 μm.

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