

Tactile sensory coding in the glabrous skin of the human hand

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The human hand and the brain are close partners in two important and closely interconnected functions, i.e. to explore the physical world and to reshape selected segments of it according to man's intentions. Both these functions are highly dependent on accurate descriptions of mechanical events when objects are brought in contact with the hand. A key role in providing such information is played by the population of mechanoreceptive afferent units innervating the hairless skin of the volar aspect of the hand, i.e. the glabrous skin. Recently it became possible to explore the characteristics of these units in man and to elucidate their role in perception as well as in motor functions.

The neuronal data to be reviewed here were gathered mainly from studies on young adult volunteers, using the microneurographic technique introduced by Vallbo and Hagbarth²⁵. This method of recording impulses from single nerve fibres in awake human subjects, is based on percutaneously inserted tungsten microelectrodes impaling

the peripheral nerve. With this technique it became possible to analyse tactile neural mechanisms in man with a precision and a resolution previously available only in experiments on anaesthetized animals while at the same time, the subject's experience of the stimuli may be explored with psychophysical methods. Moreover, the sensation induced by activity in single afferents whose properties have been assessed may be studied by using the microelectrode for electrical stimulation^{23,24}. The first more systematic analysis of the functional properties of the mechanoreceptive

units in the glabrous skin of the human hand was made in 1970¹⁵. Since then, the amount of data has grown very quickly²⁶.

The analysis of tactile mechanisms of the human hand is heavily based upon physiological information previously extracted from studies of mechanoreceptive units in other species, but also from histological studies on man^{2,5}. However, in many respects the studies in man have taken a different route, focusing on functional aspects of the tactile system that were not explored in other species.

For afferent units innervating the glabrous skin of the primate hand there is a quite simple relation between the function of units and the thickness of the afferent nerve fibre. The fast-conducting, large-diameter myelinated fibres (A α) belong to mechanoreceptive units (cf. Fig. 1), whereas the slower-conducting, small-diameter myelinated fibres (A δ) and the unmyelinated fibres (C) belong to nociceptive and thermosensitive units.

Types of mechanoreceptive units

There are about 17 000 mechanoreceptive units innervating the glabrous skin of the human hand⁸. In accordance with studies on animals, they have been classified into two major categories by the nature of their response to a sustained step indentation of the skin (Fig. 2). About half of the units (44%) are slowly adapting, i.e. they respond with a sustained discharge.

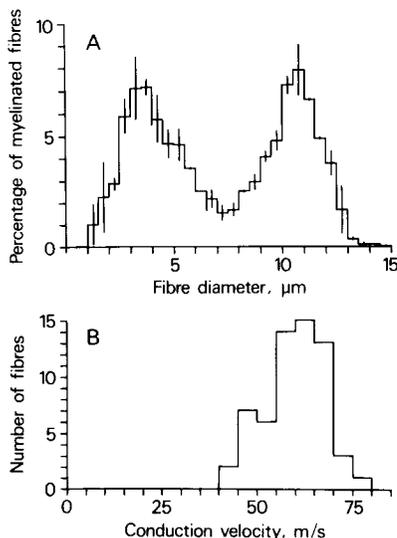


Fig. 1. (A) Diameter distribution of myelinated nerve fibres in the median nerve at the wrist, based on nerve specimens from two neurologically healthy individuals (23 years and 45 years). It has been estimated that about 90% of the fibres larger than 7 μm (A α) belong to mechanoreceptive units of the glabrous skin⁸.

(B) Conduction velocities of 61 mechanoreceptive units with receptive fields in the glabrous skin area of the human hand. The units were electrically stimulated at the receptive field and single-unit nerve impulses were recorded from the median nerve about 10 cm proximal to the elbow. Conduction velocities were normalized for a temperature of 36°C at the level of the wrist, using $2 \text{ m}^\circ\text{C}^{-1}\text{sec}^{-1}$ as correction factor.

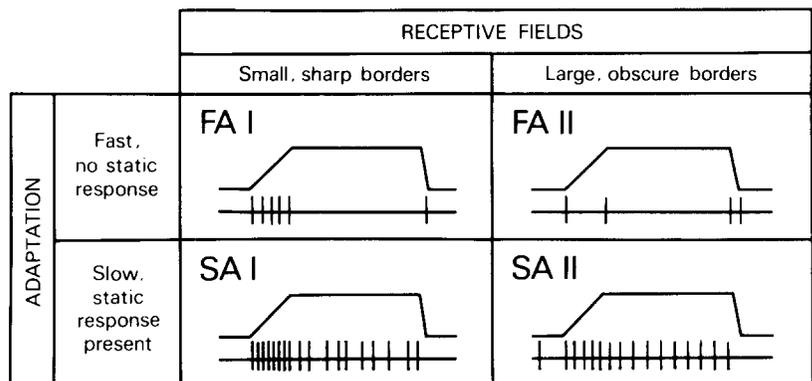


Fig. 2. Types of mechanoreceptive afferent units in the glabrous skin of the human hand, classified on the basis of adaptation and receptive-field properties^{13,14,15}. Graphs show the impulse discharge (lower trace) to perpendicular ramp indentation of the skin (upper trace) for each unit type. The FA I units are preferentially sensitive to the rate of skin indentation, whereas the FA II units are highly sensitive to acceleration and higher derivatives. The fast-adapting units, particularly the FA II, respond not only when the indentation is increasing, but also when the stimulus is retracted. The slow-adapting units exhibit a sustained discharge during constant skin indentation in addition to their discharge during increasing skin indentation. The SA I units have a high dynamic sensitivity and often a rather irregular sustained discharge. The SA II units, on the other hand, have a less pronounced dynamic sensitivity and a very regular sustained discharge. Often they show a spontaneous discharge in the absence of tactile stimulation.

Since these four unit types are similar to four types that have been identified in other species with regard to functional properties, the terminology introduced for subhuman species has frequently been used. Thus, the FA I units have been denoted RA (rapidly adapting) or QA (quickly adapting). However, these terms are unfortunate as the FA I units constitute but one group of the fast-adapting units. Moreover, the FA II units have been denoted PC which is a term based on the assumed structure of the end-organ (Pacinian corpuscles) and not on functional properties (cf. Fig. 4).

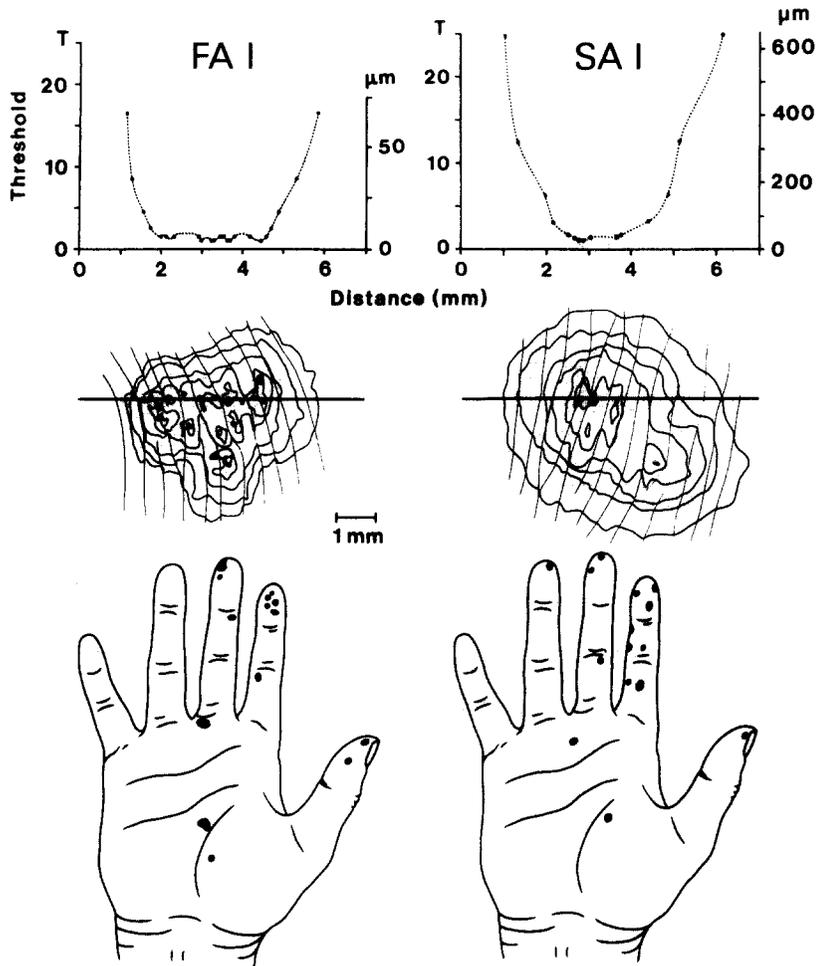


Fig. 3. Receptive fields of FA I and SA I units. The black patches of the drawing of the hands indicate receptive fields of 15 FA I and 15 SA I units as measured with von Frey hairs providing a force of four to five times the threshold force of the individual unit. The fields of these units are small with distinctive borders, and have in most cases an approximately circular or oval shape. Most of the FA I and SA I fields range between 3 mm^2 and 50 mm^2 , which correspond to circular areas of 2–8 mm diameter¹⁰.

In the middle of the figure are shown sensitivity maps of receptive fields of a single FA I and SA I unit¹⁴. The thin lines mark the grooves between the papillary ridges, whereas the closed lines are isosensitivity lines enclosing skin areas where the unit responds at given skin displacements. Thus, the sensitivity of the units is indicated in a way similar to how the height profile of a mountain is indicated on a map. The sensitivity profile was constructed by mapping the field with a small pointed probe (0.4 mm diameter with a hemispherical tip) moved in triangular ramp indentations at a constant velocity (4 mm sec^{-1}).

Above, a section of the field is illustrated with regard to threshold variations along the straight line shown in the map in the middle. The ordinates give the indentation amplitude divided into multiples of the lowest threshold (T) as well as into actual amplitudes (μm). The abscissa is a distance scale with arbitrary origin. Thus, the fields are composed of multiple points of high sensitivity ($n = 12\text{--}17$ for the FA I, and $n = 4\text{--}7$ for the SA I units). It can be seen that, in the central area of the field, the sensitivity is almost uniform, whereas it decreases very steeply towards the periphery.

The remaining units (56%) are fast adapting and respond with a burst of impulses only at the onset and removal of the stimulus, i.e. when the stimulus is moving. Within each of these two categories, two different types of units can be distinguished on the basis of the properties of their receptive fields: the fast-adapting type I (FA I) units and the slow-adapting type I (SA I) units have small and well defined fields, whereas the fast-adapting type II (FA II) units and the slow-adapting type II (SA II)

units have wider fields with obscure borders (Fig. 2). However, there are a number of additional distinguishing parameters which will be considered below.

Units with small and well-defined receptive fields

A fundamental task of the tactile apparatus of the hand is to extract information about spatial details of skin deformations during manual manipulation and exploration. The FA I and SA I units have

receptive fields which make them suitable for this task (Fig. 3). Their fields are made up of an approximately circular or oval area of high and relatively uniform sensitivity, typically covering 4–10 papillary ridges and their sensitivity diminishes steeply with increasing distance from this area. Within the area of high sensitivity there are several zones of maximal sensitivity. These zones most likely correspond to the location of end-organs belonging to the afferent fibre. Thus, the single sensory unit has a number of endings of approximately uniform sensitivity, which are located close enough to

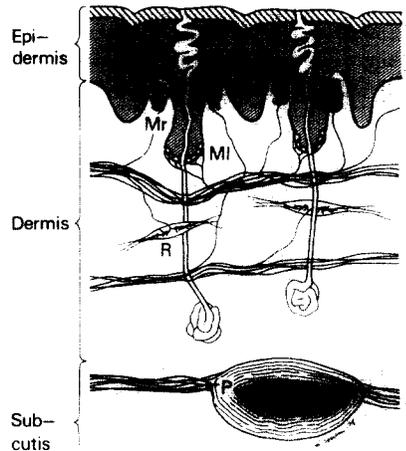


Fig. 4. Vertical section through the glabrous skin of the human hand schematically demonstrating the locations of the four types of organized nerve terminals which most likely constitute the end-organs of the four types of mechanoreceptive afferent units innervating this skin area. The Meissner corpuscles (Mr) are probably the end-organs of the FA I units. They are located in the papillary ridges of the dermis and have a capsule enclosing the nerve terminals, which are flattened sheets of nervous tissue interleaved with flattened lamina cells. The Merkel cell neurite complexes (MI) are located at the tip of the intermediate epidermal ridges. They consist of Merkel cells which enclose expanded endings of branches of myelinated axons of the SA I units. The Ruffini endings (R) are probably the end-organ of the SA II units. They are located in the dermis and have a thin and spindle-shaped capsule. The nerve terminals are intermingled with collagen fibrils longitudinally passing through the corpuscle and anchoring the corpuscle in the dermal collagen at its poles, thus providing the mechanical linkage to the fibrous tissues of the dermis. The Pacinian corpuscle (P), the end-organ of the FA II unit, is found in the deeper layers of the skin as well as in the subcutaneous tissues. The nerve terminal is surrounded by layers of concentric lamellae which filter mechanical deformations so that only high-frequency components reach the nerve terminal. Smaller and simpler lamellated endings (Golgi-Mazzoni bodies) probably belong to the same type of unit.

The indicated correlation between the structure of the end-organ and the type of unit has been proposed on the basis of indirect evidence from separate morphological and physiological studies in man, as well as combined studies of structure and function in other species^{5,6}.

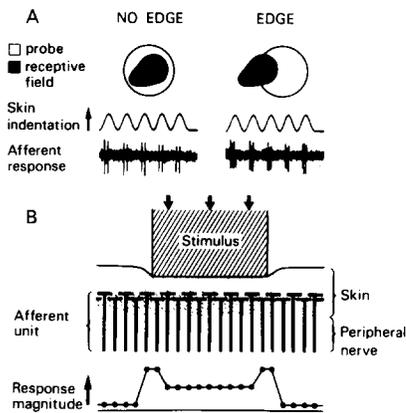


Fig. 5. Edge sensitivity of SA I units.

(A) Responses of a SA I unit to perpendicular skin displacements delivered with a cylindrical probe with a flat contactor surface (diameter = 6 mm). The afferent responses are shown for two different conditions: (1) the probe covers the complete receptive field (no edge condition); and (2) the probe covers only part of the field (edge condition). Note the stronger response when the edge cuts through the field. Skin displacements were mechanical sinusoids (16 Hz, 0.2 mm amplitude) superimposed on a static preindentation (0.5 mm).

(B) Schematic illustration of the spatial profile of total response from a group of SA I units when the skin is stimulated by a block indentation. The response profile would show a marked edge enhancement.

provide a practically uniform sensitivity within a sharply demarcated area. The end-organs of the FA I and SA I units are most likely the Meissner corpuscles and the Merkel cell-neurite complexes, respectively (Fig. 4).

An important feature of these unit types, particularly the SA I units, is their exquisite sensitivity to edge contours of objects indenting the skin. This has been demonstrated in man as well as in the monkey^{12,21}. Thus, the response is strong when the edge of an object cuts through the receptive field, while it is weaker when the whole field is depressed (Fig. 5A). This indicates that the afferent signal from the population of SA I and FA I units appropriately describes the location of edge contours of objects in contact with the skin (Fig. 5B). Hence, mechanisms accounting for enhancement of spatial contrast and our awareness of edges of objects seem to occur not only in the central nervous system due to lateral inhibitory mechanisms as earlier proposed¹, but also at the level of the tactile afferent units.

Spatial discrimination

The spatial acuity of tactile sensibility in the hand, as determined with psychophysical methods, is characterized by a pronounced regional variation. It is maximal at the finger tips, which are the preferred site

for tactual exploration, and it decreases towards the wrist (Fig. 6A). An important question is whether this gradient is accounted for by the signal processing in the central nervous system, or by peripheral limitations. Since there are no drastic differences in receptive-field properties between units in the various regions of the glabrous skin, a critical factor for the resolving power might be the density of afferent units. A comparison between the density of FA I and SA I units and the spatial discriminative capacity shows that these two measures go reasonably in parallel (Fig. 6B). Thus, the density is highest in the finger tip, distal to the whorl of the papillary ridges and decreases towards the wrist. However, there is not a smooth and continuous change but a striking decrease from the distal to the proximal half of the terminal phalanx. There is also a density step, although smaller, between the palm and the bases of the fingers. In the very finger tip, the density of FA I units and SA I units is about 140 units cm⁻² and 70 units cm⁻². If the centres of the fields were evenly spaced over the skin, the centre-to-centre distances would be 0.9 mm and 1.3 mm, respectively. The corresponding values for the palm are 2.2 mm and 3.8 mm. That the finger tips have an outstanding capacity in spatial discrimination is strikingly illustrated with optacon reading. Optacon is a tactile reading aid for the blind. The reading rate is high when the finger tip is used, but is drastically slower when the proximal half of the distal phalanx is used⁹.

By combining the density data and the field-size data, it is possible to produce a description of the spatial organization of the population of the mechanoreceptive units¹⁰. For instance, the mean overlap of the receptive fields (highly sensitive areas, see Fig. 3) of the FA I units is about 20 in the finger tip, and 9 in the main part of the finger and in the palm, whereas the corresponding values for the SA I units are 16, 6 and 2, respectively. A model based on a reconstruction of the distribution of receptive fields on the skin surface suggests that man's spatial discrimination of pointed stimuli in the psychophysical test is virtually at the limit imposed by the peripheral mechanisms¹⁰. In contrast, the psychophysical capacity of point localization is less accurate than the capacity of the peripheral organization as predicted by the model. It may be relevant that point localization engages memory to an extent that is not the case in, for instance, two-point discrimination.

Units with large receptive fields with obscure boundaries

The FA II and SA II units have receptive

fields of completely different characteristics compared to the FA I and SA I units. It is a single zone of maximal sensitivity and wide surrounding area where the sensitivity gently falls off (Fig. 7). These units constitute only about 30% of the total number of tactile afferents in the glabrous skin of the hand. Their low density, which is also relatively uniform from the wrist to the finger tip (Fig. 6B), as well as the indistinct receptive fields indicate that they are not primarily involved in detailed spatial discrimination. In contrast to the type I units, the end-organs of the type II units – the Pacinian corpuscles and smaller paciniform endings, and the Ruffini endings, respectively – are located deep in the dermis and in the subcutaneous tissues (Fig. 4).

The FA II units are extremely sensitive to remote mechanical transients. Typically, their receptive fields cover a whole finger or a great part of the palm when defined by taps with a finger or a pencil (Fig. 7). The

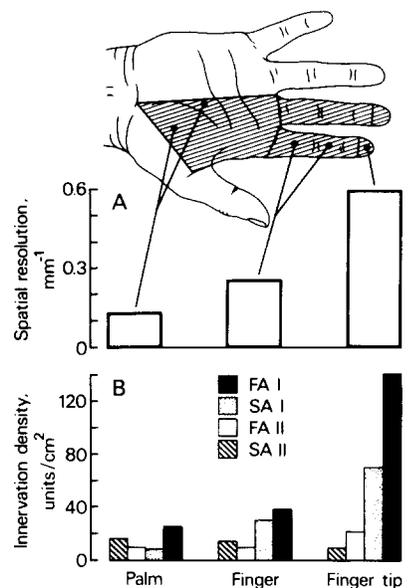


Fig. 6. (A) Spatial resolution in a psychophysical test of two-point discrimination. The height of the columns give the inverse of the two-point threshold in units of mm⁻¹ (Ref. 28).

(B) Histogram showing the density of innervation of the four types of mechanoreceptive units in different regions of the glabrous skin area of the human hand: the tip of the finger, the rest of the finger, and the palm. The relative densities in these three regions are 4.2, 1.6 and 1.0, respectively. It can be seen that these differences are mainly accounted for by the FA I and SA I units, whereas the densities of the FA II and SA II units are more uniform. Note that the spatial resolution increases roughly in parallel with the increase in density of the FA I and SA I units. The estimates of unit density were based on morphological data and on microneurographic data from the central part of the innervation territory of the median nerve as indicated on the drawing of the hand⁹.

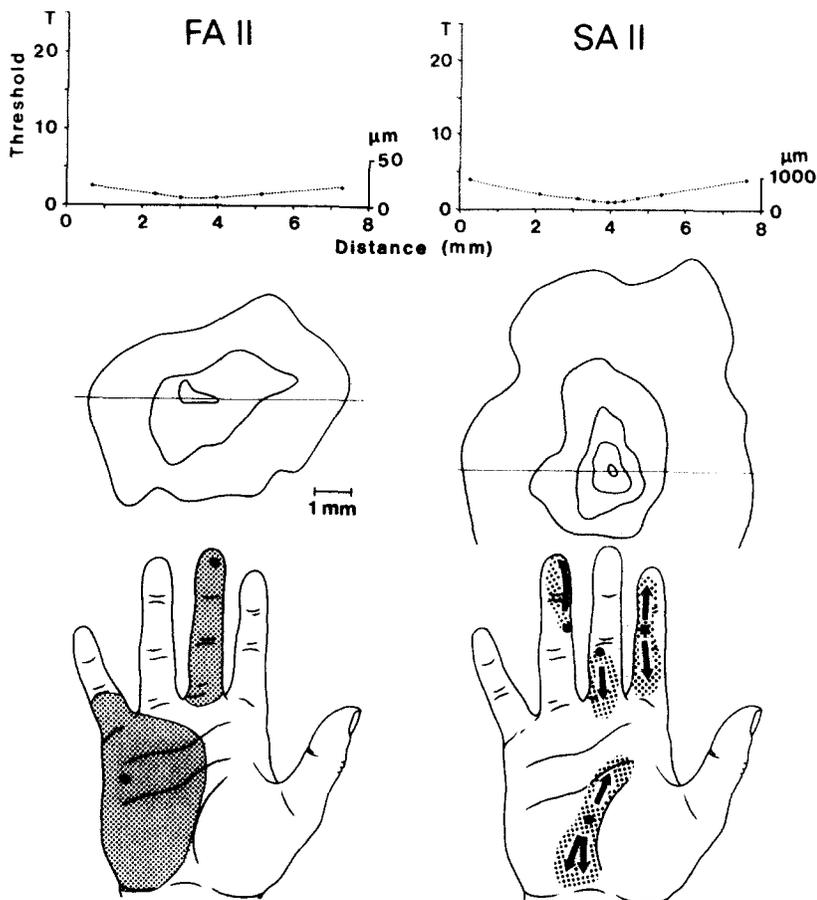


Fig. 7. Receptive fields of FA II and SA II units. The dashed areas in the drawings of the hand illustrate the receptive fields of two FA II units and four SA II units as determined by manually delivered stimuli, i.e. taps with a small glass rod and skin stretch, respectively. The location of the zone of maximal sensitivity to local deformation is indicated by dots. As to the SA II units, the arrows indicate directions of skin stretch which gave rise to an increase of the discharge. The sensitivity to skin stretch varies from one SA II unit to the other. Some units are excited when the skin is stretched in two opposite directions. When the skin is stretched at right angles to these directions any ongoing discharge decreases. Other SA II units are only excited by stretch in one direction and inhibited by stretch in the opposite direction. These two patterns may be explained by differences in the fixation of the spindle-shaped end-organ (Ruffini, Fig. 4) to the surrounding tissues⁶.

In the middle are shown sensitivity maps of a FA II and a SA II receptive field. They were constructed as described in Fig. 3. Thus, the closed lines are isosensitivity lines corresponding to the threshold amplitudes as given in the sections of the fields shown in the top diagrams.

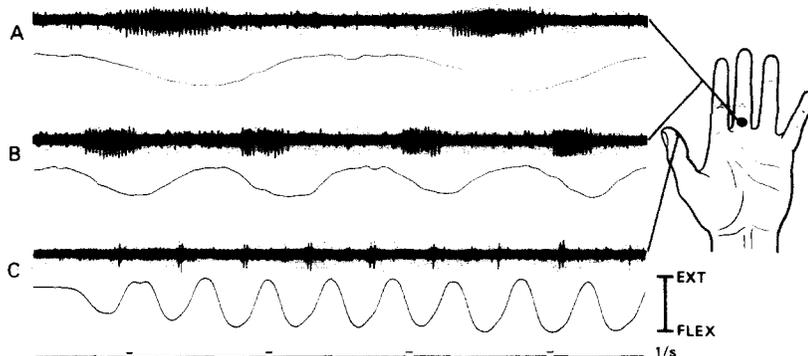


Fig. 8. The responses of skin afferents to joint movement. In (A) and (B), the responses of a SA II unit to oscillatory movements of the finger are illustrated. In (C), the responses of a FA I unit to movements of the thumb are shown. The receptive fields to skin indentations of the two units are indicated on the drawing of the hand. Upper trace - nerve signal. Lower trace - finger movements. (From Hulliger *et al.*⁴, reproduced with permission.)

FA II units are most easily excited by mechanical oscillations of the skin of frequencies ranging between 100 Hz and 300 Hz. At these frequencies a movement of only $1\mu\text{m}$ may be enough to elicit a nerve impulse on each stimulus cycle¹¹.

The sense of vibration

The detection of vibrations elicited by mechanical sinusoids of frequencies above *c.* 40 Hz is dependent on activity in these units, whereas the detection of 'flutter' elicited by frequencies between *c.* 5 Hz and 40 Hz is mediated by activity in the FA I units^{11,22}. At lower sinusoidal frequencies, primarily felt as slow movements of the skin, the slow-adapting unit types may convey the decisive information. Thus, there are several peripheral mechanisms for encoding temporally ordered indentations of the skin. However, the selective frequency sensitivity described above appears only at low stimulus intensities. At higher intensities, there is a considerable overlap between the different types of units¹¹.

Skin stretch sensitivity

Characteristic features of the SA II units are the occurrence of an ongoing discharge in the absence of externally produced skin deformation, which is present in some units, and an exquisite sensitivity to lateral skin stretch. The stretch sensitivity appears when stimuli are applied far away from the zone of maximal sensitivity. The direction of skin stretch is critical: pulling in certain directions may give rise to an increase of the afferent discharge whereas pulling in other directions may decrease ongoing activity (Fig. 7). The primary function of the SA II units may be to provide detailed information on the direction and magnitude of the lateral tension within the skin, as well as between the skin and deeper structures of the hand⁶. Such information should be of significance for the evaluation of shearing forces between the skin and hand-held objects, and may be important for the control of, for instance, the grip forces.

Sensitivity to joint movements

The mechanoreceptive afferents of the glabrous skin are classified as exteroceptors because a prominent function is to extract information about the external world. However, a large group of these afferents also respond to movements of the hand and finger joints when direct touch is not involved (Fig. 8)⁴. The SA II units are particularly responsive, probably due to their high sensitivity to the changing patterns of tension within the skin which occur with joint movements. Nearly all the SA II units (94%) respond to movements and many of

them exhibit a static discharge related to joint position. Movements also excite all the FA II units, and even a majority of the FA I and SA I units (57% and 66%, respectively) give some response. It seems reasonable to conclude that the cutaneous mechanoreceptors, and particularly the SA II and FA II units, may provide not only exteroceptive but also proprioceptive information. The fact that units with functional and structural properties similar to the FA II and SA II units of the skin are widely distributed in deeper fibrous tissues, e.g. joint capsulae, interosseous membranes and tendon sheets, fits with this view.

The functional role of cutaneous mechanoreceptors in motor control, kinaesthesia and position sense is not at all clear. There is evidence that they may contribute to position sense and kinaesthesia in the absence of afferent input from joint and muscle tendon receptors¹⁹. Moreover, information in afferents from the fingers accounts for a general facilitatory effect on motor commands to the hand and finger muscles^{18,19}. However, recent findings indicate a more specific role of these units in the motor control. When handling objects in the precision grip between the tips of the fingers and the thumb, the human subject automatically balances the grip forces to prevent the object from slipping or cracking. This very accurate force control requires information from tactile units about the frictional conditions between the skin and the object (G. Westling and R. S. Johansson, unpublished observations). Of interest in this context is that the primate motor cortex, which is known to play a key role in the control of fine finger movements, receives detailed information over very rapid pathways from the mechanoreceptive units of the glabrous skin¹⁷.

Correlation between neuronal and psychophysical events

The ultimate aim of analyses of correlations between activity in afferent units, on the one hand, and psychophysical phenomena, on the other, is to bridge the gap between biophysical events in the nervous system and mental events in the mind. Thus, we want to gain insight in the basic rules that the brain is bound to follow when its purpose is to produce a sensation from the afferent message in the peripheral nerves.

Detection

The concept of a sensory threshold has been much discussed and it has been debated whether central or peripheral

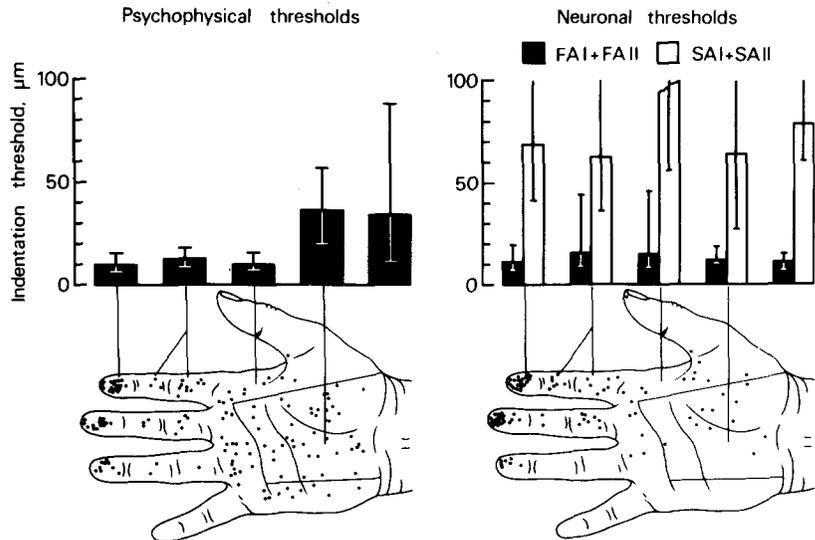


Fig. 9. Relations between psychophysical detection threshold and absolute thresholds of the FA and SA mechanoreceptive units. The left diagram shows psychophysical thresholds in various regions of the glabrous skin area to triangular skin indentations of the same kind as described in the legend of Fig. 3. From left to right, the columns give data from the terminal phalanx, the rest of the finger, the peripheral part of the palm, the central part of the palm, and to the extreme right; data from the lateral aspects of the fingers and the regions of the creases are taken together. The test points are indicated in the drawing of the hand. The diagram to the right shows thresholds for evoking a single nerve impulse in mechanoreceptive units supplying the same skin regions. Dots on the drawing of the hand indicate the location of the receptive fields of units tested. The FA I and FA II are pooled since they have about the same threshold distribution for this type of stimulus. Also, the slow-adapting units, which have much higher thresholds are pooled. Column heights give medians, and bars give 25th and 75th percentiles. Note that the psychophysical thresholds were similar to the neural thresholds for fast-adapting units in certain skin regions and considerably higher in other regions. In several instances, when recording from highly sensitive FA I units, the neural and the psychophysical thresholds perfectly coincided²⁷. (From Johansson and Vallbo², with permission.)

mechanisms set the limit of detection. When minute touch stimuli were applied to the glabrous skin while impulses from single nerve fibres were recorded, it was found that the threshold of FA I and FA II units matched the psychophysical thresholds whereas the thresholds of the SA units were considerably higher. However, the FA I and FA II units were not equally potent in eliciting a psychophysical response in a detection task. A single impulse in a single FA I unit could often reach the mind, as was shown with mechanical stimulation as well as electrical microstimulation. For a FA II unit, on the other hand, a series of impulses seems to be required. Thus, the findings indicate that the psychophysical threshold is set by peripheral mechanisms, i.e. the sensitivity of the FA I units. Any signal, however small, from these units may reach the mind. However, this was true only for skin areas with the most important role in tactile mechanisms, e.g. the finger tips, whereas the threshold, for instance, in the centre of the palm seems to be set by central mechanisms (Fig. 9).

Magnitude scaling

It has been suggested on the basis of

neurophysiological experiments on the monkey and psychophysical experiments on man that a subject's experience of stimulus intensity is linearly related to the amount of activity in single slow-adapting units²⁰. The direct recording of afferent impulses in man failed to support this hypothesis because it was found that the sensation grows faster with the stimulus intensity than does the activity in single units¹⁶. It seems that peripheral factors, e.g. the recruitment of units with increasing stimulus intensity⁷, as well as central processing may account for this mismatch. That central mechanisms may play a decisive role is suggested by the large inter-subject variation in psychophysical performance, in spite of the afferent units having uniform response characteristics for different subjects.

Microstimulation

Any touch stimulus that we normally pay attention to excites a large number of afferent units of several types. However, when trying to understand how the brain works to produce a sensation we often need to break down the complex neural message and try to produce an afferent signal that is more simple and uniform. One approach which

has been attempted lately is to electrically stimulate a single afferent nerve fibre in conscious human subjects and analyse the sensation that might result^{23,24}. In these studies, impulses from a single tactile unit is first recorded and the functional properties of the unit are assessed. The electrode is then reconnected to a stimulator and a train of weak pulses (0.2–2.0 μ A) is delivered. It has been found that a sensation of light mechanical deformation is often experienced within the receptive field of the particular afferent unit that was recorded immediately before. The extent over the skin surface where this sensation is experienced is usually in the same order of magnitude as the extent of the receptive field. When stimulus intensity was successively raised, one or two additional sensations of similar type appeared usually well separated and often at a considerable distance on the skin surface from the primary sensation, suggesting that other units were stimulated. At still higher intensities, the subjects usually reported either a localized painful sensation or a paraesthetic sensation over a larger area. Differential attributes of the sensations were usually reported when the electrode saw a SA I unit and a FA I unit. For instance, with a SA I unit a light and uniform pressure may be felt, similar to the pressure of a soft water-colour brush steadily held against the skin. With a FA I unit, a buzzing, wobbling or fluttery sensation may appear. The findings obtained so far suggest that studies with this method may shed light on a set of fundamental problems in the border-line between neurophysiology and psychophysics.

This contribution has briefly been concerned with some recent findings regarding the tactile sensory mechanisms of the human hand. As to the future, we believe that these results may serve as a basis for further studies of the interactions between the hand and the brain during integrative hand functions. Such studies will most certainly yield progress when carried out on conscious human subjects, able to participate in sophisticated and co-operative experimental tests.

Acknowledgements

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Position and proximity in the development of maps and stripes

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Recent evidence indicates that neural-map formation is a multiphase process in which presynaptic proximity-dependent sorting of terminals is superimposed on relatively weaker interactions that match neuronal processes by virtue of their positions in the pre- and post-synaptic populations. This biphasic mechanism will produce highly ordered contacts with little 'pre-specified' cell surface information. Exactly the same process will produce periodic patterns of segregated afferents when two different afferent populations map within a single target zone.

In recent years considerable interest has been generated by the widespread occurrence of periodic subdivisions within many terminal zones of the vertebrate brain. These regular patterns can take the form of either patches or alternating source-specific stripes. They have been observed in pathways as diverse as the pyramidal tract input to the dorsal-column nuclei, inputs to the cerebellum, to the neocortex and several of the different projections which converge upon the mammalian superior colliculus. Thus, this afferent ordering is likely to reflect principles of fundamental importance to brain organization, but even in the best-studied instances, such as the ocular dominance columns of the cat and primate

cortex, the reason for such terminal segregation is not at all clear.

Some insight into the determinants of periodic input patterning was unexpectedly obtained in my laboratory several years ago as a result of work on the retinotectal pathway of the common leopard frog *Rana pipiens*. In the frog, axons from only one retina normally form a continuous map within the superficial neuropil of the contralateral optic tectum. However, we forced two retinas to co-innervate one tectal lobe, either by implanting a third eye primordium into a young embryo^{6,21} or by removing one optic tectum in a late tadpole or a young post-metamorphic frog²⁰. We invariably obtained the same end result. Axon termi-