# THE RESPONSES OF AFFERENT FIBRES FROM THE GLABROUS SKIN OF THE HAND DURING VOLUNTARY FINGER MOVEMENTS IN MAN

By M. HULLIGER\*, E. NORDH, A.-E. THELIN AND Å. B. VALLBO

*From the Department of Physiology, University of Umeå,
S-901 87 UMEÅ, Sweden*

## SUMMARY

1. Afferent activity of 111 single units from the glabrous skin area was recorded percutaneously in the median nerve of human subjects, using tungsten electrodes.

2. The majority of the units (103) were classified as low-threshold mechanosensitive units belonging to one of the four categories previously described: rapidly adapting with small receptive fields (RA), rapidly adapting with large receptive fields (PC, presumed Pacinian corpuscle units), slowly adapting with small fields (SA I), and slowly adapting with large fields (SA II). The size of the responses (in number of impulses) to indentation and stretching of the skin was compared with that of the responses elicited during voluntary isotonic finger movements, which avoided trivial excitation of the units by direct touch.

3. All four types of units, and 77% of the single units, were activated by isotonic movements. The decreasing order of responsiveness was PC, SA II, SA I, RA.

4. Almost all responsive units were excited during the dynamic phase of ramp and smooth oscillatory movements. Static responses, on the other hand, occurred only with 50% of the slowly adapting units, corresponding to a third of the total sample (SA II, 81%; SA I, 17%).

5. For all four types of units the dynamic responses to movements were of similar size as the responses to localized skin indentation with a von Frey hair at five times threshold.

6. The results are discussed with regard to the possible implications for kinaesthesia and motor control.

## INTRODUCTION

It has been established that four different types of low-threshold mechanosensitive units can be found in the nerve fascicles innervating the glabrous skin of the human hand (Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975; Johansson, 1976, 1978). They have been characterized by their responses to indentation and stretching of the skin, in accordance with the earlier studies in the cat and primates. Two types of rapidly adapting units have been described: RA units and presumed Pacinian corpuscle (PC) units (Lindblom, 1965; Lindblom & Lund, 1966; Talbot, Darian-

---

\* Present address: Brain Research Institute, University of Zürich, August-Forel-Strasse 1, CH-8029 Zürich, Switzerland.

Smith, Kornhuber & Mountcastle, 1968; Jänig, Schmidt & Zimmermann, 1968; Lynn, 1969; Iggo & Ogawa, 1977), and two types of slowly adapting units have been described: SA I (Iggo & Muir, 1969) and SA II units (Chambers, Andres, Duering & Iggo, 1972). Of the rapidly adapting afferents, RA units have small and well defined receptive fields, whereas PC units have large and poorly defined fields, which make them susceptible to remote mechanical stimulation. For the two types of slowly adapting afferents, the SA I units exhibit small and well defined fields and, in addition, a rather high dynamic sensitivity. The SA II units, on the other hand, are characterized by larger fields and an appreciable sensitivity to stretching of the skin.

In contrast to the well documented responsiveness to passive deformation of the skin, little is known about the responses of these afferents during active movements apart from a few casual observations and inferences on SA II units (Hagbarth, Hongell, Hallin & Torebjörk, 1970; Knibestöl & Vallbo, 1970; Knibestöl, 1975). This question seemed, however, of considerable interest with regard to the possible contribution of cutaneous afferent signals to kinaesthesia and to motor control at subconscious levels. The present study showed that all four types of afferent units in the glabrous skin area are readily activated by voluntary finger movements that avoided incidental excitation by direct touch. The PC and SA II units showed the greatest responsiveness. The discharge of the total sample elicited during the dynamic phases of movements was appreciable, whereas the maintained responses during the static phases were rather small.

## METHODS

*General procedure.* The experiments were conducted on thirty-nine healthy human volunteers (20–37 years old). The activity of single afferent units was recorded from the left median nerve using the microneurographic method of Vallbo & Hagbarth (1968) (for details see Vallbo, 1972). Briefly, tungsten electrodes (with an impedance of 100–300 kΩ at 1 kHz, and with a tip diameter around 10 μm) were inserted percutaneously above the elbow. After the penetration of the nerve sheath, cutaneous afferents were usually first seen in multi-unit recordings during systematic exploration of the hand. Single units were then isolated by manually adjusting the position of the electrode in minute steps while touch and light taps were continually applied to the skin. It should be stressed that the fingers *were not* moved routinely during the searching procedures. Rather, the mechanical stimuli were applied simultaneously to the dorsal and ventral aspects of the hand, so that the fingers were held in an intermediate position. The subject was also asked to relax the muscles of the forearm and not to move hand and fingers of his own volition. However, in the initial experiments attention was focused on units with a maintained discharge or a static response to joint angle within the range of active finger movements. This might have led to an over-representation of SA II units (cf. Johansson & Vallbo, 1979). Possible effects of such sample bias were calculated, but found to be negligible, and they are therefore not further elaborated.

When the quality of the nerve impulses permitted unambiguous discrimination with conventional trigger circuits, the afferent responses to the standard tests were recorded on magnetic tape, together with the signals from a strain gauge and a distance transducer monitoring finger movements (cf. below). When the signal to noise ratio was less favourable, it was nevertheless often feasible to pick out the spikes of an individual afferent, relying on visual and acoustical clues from the appropriately filtered signal. Thus the responses to skin indentations and movements could still be assessed qualitatively. The responses of sixty out of the 111 units of the present report were recorded on tape and were available for off-line analysis.

Stimulation with graded forces within the receptive field was performed with von Frey hairs. For the recording of the time course of finger movements an ultrasonic distance transducer, which provided an analogue measure of the distance between an emitter and a small receiver of

ultrasonic waves (38 kHz), was employed. The receiver (diameter 1 cm) was mounted on a suitable part of the finger moved during the tests, often on the dorsum of the proximal phalanx, always avoiding too close proximity to the receptive field of the unit. The signals obtained from this device, although not linearly related to joint angle, provided satisfactory indication of the timing of movements. The ultrasonic signal was not used to measure the amplitude of the movements, because this would have required time consuming calibrations for every individual arrangement. Instead, any maintained finger position was characterized by the joint angles, which were estimated with a protractor. Such estimates of the joint angles will always be given in the order metacarpo-phalangeal, proximal and distal inter-phalangeal joint.

*Classification.* Mechanosensitive afferents from the skin and underlying non-muscular structures were classified according to the criteria described previously (Knibestöl & Vallbo, 1970; Knibestöl, 1973, 1975). Units were classified as originating from deep structures if they failed to respond to stretching and pinching of the skin with a pair of forceps. Among the mechanosensitive units from the glabrous skin two kinds of slowly adapting and one kind of rapidly adapting units were distinguished. Together with the PC units, whose end organs were probably located in deep structures, they are henceforth referred to as 'mechanosensitive units from the skin area'. Rapidly adapting cutaneous units were classified as RA units if they had small and well defined receptive fields, and thus a poor responsiveness to remote stimulation. This classification was further supported if properties of the receptive field could be demonstrated which were compatible with a profile exhibiting several maxima of sensitivity (Johansson, 1976, 1978). In contrast, rapidly adapting receptors were taken as Pacinian units (PC), if they had large receptive fields with poorly defined boundaries and if they responded readily to taps on remote parts of the hand.

Slowly adapting receptors responded with a maintained discharge to steady displacement with von Frey hairs of glass rods. Some of them were spontaneously active. Units were classified as type I receptors (SA I) if they exhibited at least three of the following features: a small and sharply delimited receptive field at five times threshold, a poor responsiveness to stretching of the skin outside the receptive field, a high dynamic sensitivity, a profile of sensitivity within the field with apparently several maxima and a high variability of inter-spike intervals during maintained discharge. In contrast, slowly adapting units were allocated to the type II category (SA II) if they met three out of the following conditions: responses to stretching of the skin which were comparable with the firing elicited by direct stimulation within the receptive field using von Frey hairs at five times threshold, a larger receptive field with less precisely defined boundaries, apparently only a single zone of maximum sensitivity, a comparatively low dynamic sensitivity and a low variability of inter-spike intervals.

With all four receptor types the distinctness of the field boundaries was assessed by stimulating the skin with glass rods and von Frey hairs at five, twenty-five or fifty times threshold. The boundaries of the fields were marked on the skin and the fields were drawn in normalized diagrams of the human hand. When the responsiveness to skin stretching was determined, care was taken to apply the stretch to remote regions, in order to minimize indentation of the skin within the receptive field. Usually this precaution was effective, since there were no responses to vigorous indentation of the area to which the stretch was applied. The comparison of the responses to stretching and to indentation within the field (at five times threshold) was in most cases only qualitative. Because of the often appreciable dynamic sensitivity of the SA I receptors it was still desirable to compare the static and dynamic components of the responses separately. The responsiveness to stretching was considered low or high when the stretch-evoked responses were clearly lower or higher than those provoked by indentation.

*Test programme.* As soon as a unit had been classified a series of standardized tests was performed as follows:

*Test 1.* Using von Frey hairs at five times threshold, the approximate centre of the receptive field was stimulated both with brief dynamic taps and static indentations maintained for about 1 sec. The purpose of this test was to collect data permitting a qualitative comparison of the sensitivity to movement and indentation.

For the following tests the subjects were then asked to perform various isotonic finger movements. Usually the finger on which the receptive field of the unit was situated, or the one nearest to the receptive field, was moved. Occasionally several fingers were engaged simultaneously. In most cases flexion and extension movements were studied; occasionally abduction and ad-

duction were tested as well. With afferents which were affected by movements of the thumb, opposition and reposition were sometimes also included in the test programme. At the beginning of an experiment the desired movements were demonstrated when the experimenter performed them with his own fingers and gave verbal instructions. The subject was then asked to practise the movements. Thus there was no display of a command signal, but the subjects were free to watch their fingers during the performance of the tasks, and most of them indeed made spontaneous use of such direct visual feed-back.

*Test 2.* The subject was instructed to perform sequences of ramp and hold movements at a repeat frequency of about 0·1 Hz. These started with either flexion or extension movements from an intermediate resting position (with joint angles of approximately 150°, 150° and 165° in proximo-distal order). They terminated with a ramp movement back to the intermediate position. The hold phases were, ideally, either in full extension (180°, 180°, 180°) or in a position of finger flexion just short of direct contact between finger tips and palm (about 90°, 90°, 140°). As regards the terminology adopted in the present paper, the ranges on either side of the intermediate position are referred to as the flexion and the extension range. The ramp movements are described as flexion and extension movements, no matter whether they were performed in the flexion or extension range or at the beginning or the end of the ramp sequence. The actual performance of these movements did not always meet the requirements and there were considerable variations with respect to amplitude and velocity of the movements. However, it was at least ensured that the movements engaged both the metacarpo-phalangeal and the interphalangeal joints.

*Test 3.* If the unit under examination had a steady discharge in any of the maintained positions of test 2, more detailed tests of the static responsiveness to angular position were carried out. To this end the subjects were asked to perform staircase movements with a step size of up to 10°. Individual static phases of the staircase movement lasted 5–10 sec. In contrast to the ramp and hold movements of test 2, the staircase movements were confined, within practical limits, to the particular joint which activated the receptor most effectively.

*Test 4.* The subject carried out oscillatory movements around the intermediate resting position at the maximum frequency which could be comfortably sustained. Neither the amplitude nor the exact time course of the movements were specified. But it was required that all joints of a finger should participate.

*Test 5.* If the afferent responded to the movements of test 4, a more systematic examination of the sensitivity to oscillatory movements was undertaken. The subject was then instructed to perform quasi-sinusoidal movements, following an auditory command signal. This consisted of clicks from a loudspeaker occurring at a steady frequency.

*Quantitative analysis.* All responses recorded on tape were played back and filmed. The quantitative measures were taken from these records.

The dynamic component of the afferent responses during ramp and hold movements was determined by first counting the number of spikes ($N$) during the dynamic phase of the movement. For the units with no maintained discharge in the steady positions this was taken as a measure of the dynamic response ($N_D$). For the units with a steady discharge in one or both of the maintained positions the number of impulses attributable simply to a static position response ($N_{ST}$) was calculated as:

$$N_{ST} = \tfrac{1}{2}(f_H + f_L) \cdot \Delta t,$$

with $f_H$ and $f_L$ denoting the rates of firing at the higher and lower plateaux, and $\Delta t$ the duration of the dynamic phase. $N_{ST}$ was then subtracted from the total number of impulses ($N$) giving the dynamic component of the response ($N_D$, in number of impulses):

$$N_D = N - N_{ST}.$$

For individual responses $N_D$ is proportional to the mean difference between the actual rate of firing and the rate of discharge attributable to a pure static position response. Because of the complexity of the present finger movements, no attempt was made continuously to monitor the time course of individual joint angles. The $N_D$ values could not therefore be normalized with respect to the amplitude and velocity of the movements (cf. test 2).

RESULTS

Fig. 1*A* shows multi-unit responses to voluntary isotonic ramp movements of the thumb and index finger of the left hand. This activity originated from the skin of the hand, since no responses could be evoked by firm localized pressure on the muscles of the forearm. Responses similar to those of Fig. 1*A* could, however, be elicited by light localized pressure to the skin of the thumb, index finger and adjacent area of the palm (cf. Fig. 1*B* and the inset with the drawing of the hand). Such
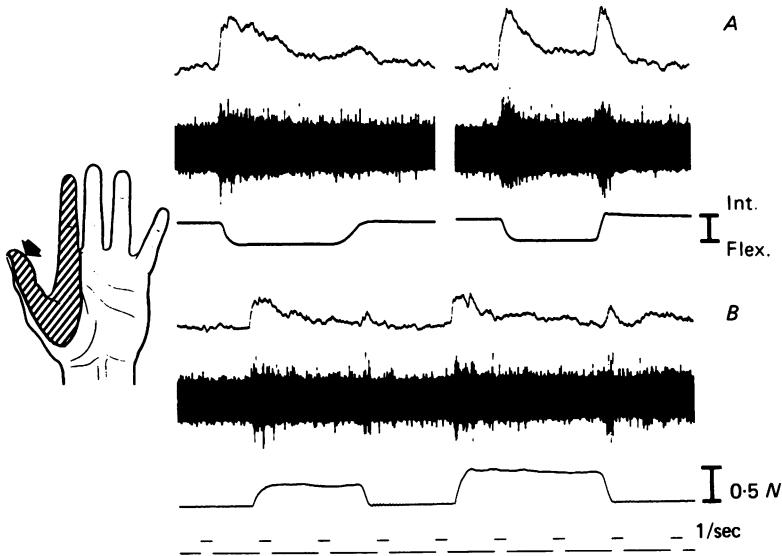


Fig. 1. Multi-unit responses to isotonic movements (*A*) and to local pressure (*B*). In *A*, flexion (Flex.) movements of the thumb and index finger were performed, starting from an intermediate (Int.) position. In *B*, pressure was applied to the distal phalanx of the thumb with a strain-gauge mounted probe with a padded contact area of about 1 cm². The receptive area of the multi-unit recording site was determined by monitoring the responses to such local pressure. It covered the palmar aspects of the thumb and index finger and the adjacent parts of the thenar and palm, as indicated in the drawing on the left. It was not altered substantially during the finger movements, indicating that the electrode had remained within the same fascicle of the median nerve. Middle trace, nerve activity. Upper trace integrated neurogram (time constant 100 msec). Lower trace, in *A*, movement of the thumb monitored by an ultra-sonic device (see Methods) which was mounted on the dorsal aspects of the thumb outside the receptive area. In *B*, force of local indentation.

selectiveness for either cutaneous (as in Fig. 1) or muscular activity was a common finding, indicating that the electrode was lying in a fascicle of the nerve which was dominated by one or the other (cf. Vallbo & Hagbarth, 1968). Two features are particularly notable in Fig. 1. First, it is evident that the dynamic response (during the transient phase of the ramp movement) was much more pronounced than the static response. Secondly, both the static and dynamic responses to movement were comparable in size to the responses provoked by localized light pressure applied within the receptive area.

For a detailed analysis of the receptor types and properties responsible for mass responses as in Fig. 1, a single unit analysis was carried out. One-hundred and eleven single afferent units from the hand were classified and studied during voluntary finger movements. One-hundred and three units were allocated to one of the four principal types of mechanosensitive units of the skin area described. The remaining eight units belonged to receptor types less frequently encountered in the skin fascicles of the median nerve. This group is dealt with separately at the end of the Results. The frequency of occurrence of the four main categories was 12·6% for PC units, 27·2% for RA units, 28·2% for SA I units and 32% for SA II units. Thirty-six per cent of the SA II afferents originated from the area of the finger nails (Knibestöl, 1975; Johansson, 1978). Using the set of criteria described in Methods the classification was considered to be unambiguous in eighty cases, reasonably certain in nineteen of the remaining cases, and uncertain, but nevertheless used, in four cases.
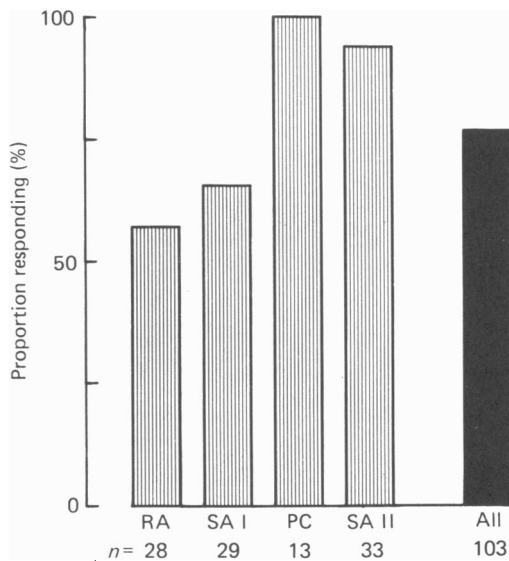


Fig. 2. The responsiveness of low-threshold mechanosensitive units to isotonic movements, expressed as the proportion of afferents responding with either an occurrence of afferent firing or a modulation of spontaneous activity. The height of the columns indicates the over-all responsiveness, which is based on the occurrence of responses to ramp or smooth oscillatory movements or both. The four columns to the left (hatched) show the responsiveness of the four main types of units, the fifth column (dark) illustrates the responsiveness of the total sample.

On successful isolation and classification of a single unit the test programme described in the Methods was followed as long as stable recording conditions prevailed. The movements were usually confined to a single finger, occasionally to a pair of adjacent fingers. Single cutaneous afferents responded unambiguously to isotonic movements, either of the receptor-bearing finger, or, in the case of afferents from the palm, of one or two of the fingers closest to their receptive fields. Figs. 2, 3 and 7 summarize the main qualitative findings by displaying the proportion of units responding to the types and parameters of the movements tested. The responsiveness
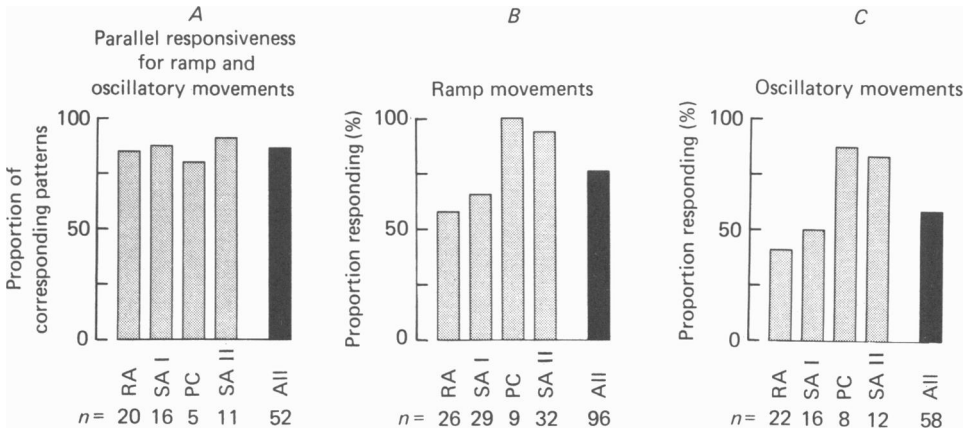
Fig. 3. The responsiveness of the four receptor types to ramp and smooth oscillatory movements. In *A*, the parallel responsiveness is illustrated by displaying the proportion of units which behaved in the same way during ramp and oscillatory movements by either responding or not responding. In *B*, the responsiveness to ramp movements alone and in *C*, the responsiveness to smooth oscillatory movements alone is shown. Method of illustration as in Fig. 2.
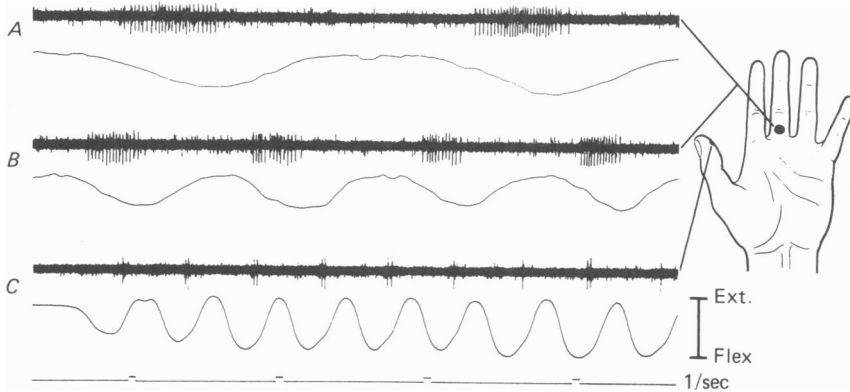


Fig. 4. The responses of skin afferents to smooth oscillatory finger movements. In *A* and *B*, the responses of a SA II unit to oscillatory movements of the middle finger are illustrated. In *C*, the responses of a RA unit to movements of the thumb are shown. The receptive fields of the units were located on the fingers which were moved, as indicated on the drawing of the hand. The command signals given to the subjects were clicks from a loudspeaker, occurring at 0·5 Hz (*A*), 1 Hz (*B*), and 2·5 Hz (*C*). Upper trace, nerve signal. Lower trace, finger movement recorded with an ultrasonic device.

was assessed qualitatively by simply determining whether the rate of afferent firing was increased consistently during the test.

The majority of the units (77%) responded to at least one of the two types of movements tested. This over-all responsiveness was particularly pronounced for PC and SA II units (100 and 94%) and it was still appreciable for RA and SA I units (57 and 66%; cf. Fig. 2). When the responsiveness to the two kinds of movement was analysed separately it emerged that the responsiveness to ramp movements was as

high as the over-all responsiveness (Figs. 2 and 3*B*), but slightly lower absolute values of responsiveness were found for smooth oscillatory movements (Fig. 3*C* compared with Fig. 2 and 3*B*). Finally, the direct correlation of the two types of movements showed that the majority of units behaved in the same way during either kind of movement, by either responding or not responding. The frequency of such parallel responsiveness is illustrated in Fig. 3*A*. As will be shown, separate analysis of the dynamic and static component of the responses showed that the former was largely responsible for the high values for responsiveness.

*Dynamic responses*

*Smooth repetitive movements.* The subjects were asked to perform regular oscillatory movements at the highest frequency that could be sustained for a few seconds. If the afferent response was modulated in phase with the movement, additional tests were performed with repetitive movements of controlled frequency. The subject was then instructed to perform smooth oscillatory movements at the frequency defined by regular clicks from a loudspeaker. Examples of such repetitive movements and of the responses elicited from single afferents are given in Fig. 4. Both the SA II unit of Fig. 4*A* and *B* and the RA unit of Fig. 4*C* responded consistently with bursts of impulses during certain phases of the movement cycle. No attempt was made to vary the amplitude of movement systematically, and the subjects were in fact asked to perform movements of approximately constant amplitude. Usually they succeeded reasonably well, as is illustrated in the lower traces of Fig. 4. The majority of units discharged an individual impulse or single bursts of impulses during certain segments of the movement cycle, as in Fig. 4. A small number of units responded with two bursts per cycle. For stimulation with von Frey hairs, the same units usually gave both on- and off-responses to indentation. Finally, one unit with spontaneous activity in the resting position responded with a continuous modulation of the rate of firing without any periods of silence. Of the fifty-eight units investigated with smooth oscillatory movements, thirty-four gave positive responses at one or several frequencies. A quantitative analysis was carried out with those units which were tested at two or more frequencies and which gave a positive response at least at one frequency (nineteen out of thirty-four). Fig. 5 shows the mean dynamic discharge of this sample over the range of frequencies tested. The positive responses were measured by counting the number of impulses per cycle, or if the unit was continuously active, the number of impulses per cycle minus the number of impulses corresponding to a continuous discharge at the lowest level of firing of the modulated response. Both positive values and zeros (for frequencies at which the unit did not respond) were included in the material. The data were then divided into five segments according to the frequency of movement, and means and standard deviations were calculated. As seen in Fig. 5 the response per cycle for the four main types of afferents taken together decreases as the frequency increases. This may be attributed to the SA I and SA II receptors whose response decreases monotonically as opposed to the response of the RA and PC receptors which shows a relative maximum around 2 Hz. In contrast, the response expressed as impulses per second increased with increasing frequency, as may be readily deduced from Fig. 5. For each unit the frequency above which it responded was also determined. Fourteen out of thirty-four units had a threshold which was equal to or less than 0·75 Hz.
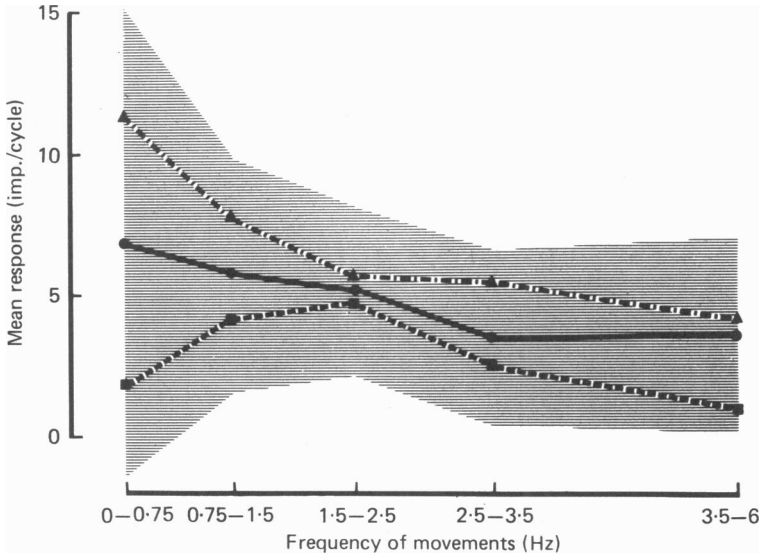
Fig. 5. The response *per cycle* during smooth oscillatory movements for the range of frequencies studied. For each frequency the *mean number of impulses per cycle* was calculated for nineteen responsive units. The number of impulses within the five segments of frequency chosen was then averaged and is shown separately for the slowly adapting units (SA I, SA II, ▲ ·--· ▲, nine units), for the rapidly adapting units (RA, PC, ■--■, ten units) and for the total sample (mean: ●—●, s.D.: hatched area). The number of observations in each frequency class were, from the low frequencies upwards, 9, 8, 7, 2, 5 for SA I and SA II, and 8, 10, 8, 4, 1, for the RA and PC units.
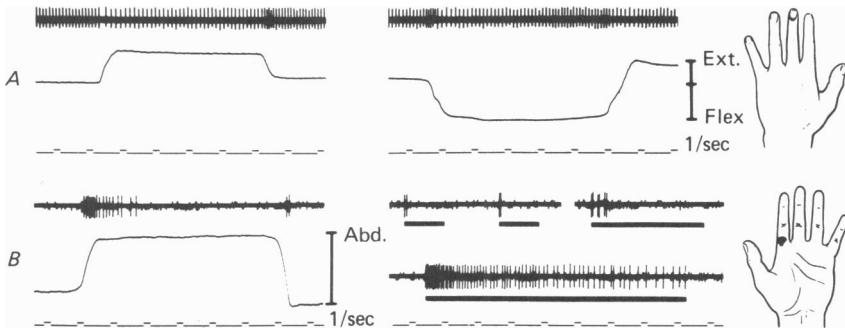


Fig. 6. The responses of cutaneous afferents to active ramp and hold movements and to passive indentation within the receptive field. In *A*, the discharge of a SA II unit is shown during isotonic extension (Ext.; left) and flexion (Flex.; right) movements of the long finger. In *B*, a separate SA II unit is illustrated during voluntary abduction (Abd.) of the index (left) and, for comparison, during passive stimulation (right), with von Frey hairs at five times threshold (5 g, upper row, first two responses) and at twenty-five times threshold (25 g, upper row, last response), and during indentations of the receptive field with a glass rod (lower row). Upper trace, nerve signal. Lower trace, finger movement with extension (*A*) and abduction (*B*) upwards. In *B*, the horizontal bars indicate the duration of stimulation with von Frey hairs and glass rod. The locations of the receptive fields are indicated as in Fig. 3.

*Ramp and hold movements.* Dynamic responses were also encountered when the subject performed isotonic ramp and hold movements. This is illustrated with the two examples of Fig. 6. The SA II unit of Fig. 6*A* showed a combined static and dynamic response. It exhibited a steady discharge at all maintained angular positions, a dynamic burst during the flexion phase, and a decrease below the lowest static response during the extension. The SA II unit of Fig. 6*B* gave mainly dynamic responses, with bursts of firing during both abduction and adduction of the index. Seventy per cent of the total population gave similar dynamic responses during one
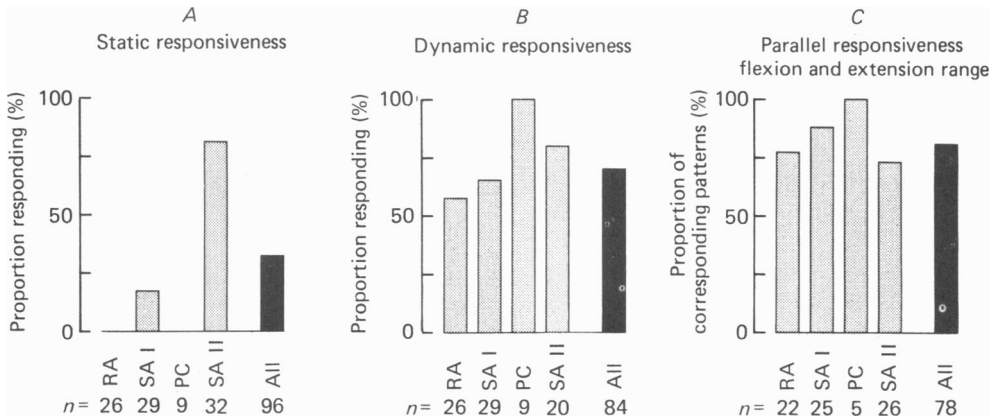


Fig. 7. The responsiveness to ramp and hold movements of mechanosensitive units from the skin area, expressed as the proportion of afferents responding. In *A*, the static responsiveness is illustrated. This was assessed by determining the occurrence of alterations of the static firing on changing from one position to the other. In *B*, the dynamic responsiveness is shown, based on the occurrence of responses during the dynamic phase of the movement which exceeded any static position response. In *C*, the parallel responsiveness for ramp movements in the flexion and extension range is displayed. This gives the proportion of units behaving in the same way in the flexion and extension range, by either responding or not responding to ramp movements.

or both of the transient phases of the ramp movement. For the units which under no condition had a maintained discharge the response manifested itself with isolated bursts of firing during the dynamic phases (as in Fig. 6*B*). For the units with a steady discharge in one or both of the maintained angular positions, as in Fig. 6*A*, a dynamic response manifested itself by a deviation from a purely static pattern of firing, that is a discharge solely related to the angular position. In these cases the qualitative assessment, concerning the mere occurrence of a dynamic response, was always based on a quantitative analysis of the discharge patterns (as detailed below). As regards the relative responsiveness of the four receptor types the same ranking was found for dynamic ramp responsiveness, responsiveness to oscillatory movements, the total ramp responsiveness, and the over-all movement responsiveness (PC, SA II, SA I, RA). This is illustrated in Figs. 2, 3*B* and *C*, and 7*B*. This order, concerning the proportion of units responding is not necessarily the same as for the magnitude of the afferent responses. Indeed, a different order was found for the size of the dynamic response of ramp movements (PC, SA I, SA II, RA).

For sixty-three units data were available which allowed a qualitative analysis of the dependence of responsiveness on the direction of movement. It was found that only a minority of RA and PC units (13 %) responded to either flexion alone or extension alone. In contrast about 50 % of the SA units exhibited such direction-specific behaviour.

The question arose whether there were any systematic differences between the responsiveness to ramp sequences in the flexion and in the extension range, with either type starting from the intermediate resting position. Fig. 7$C$ shows that this was not the case when the occurrence of any response was considered (both static and dynamic, and regardless of the beginning or end of the movement). Nor was there any difference between the flexion and extension range, when only the incidence of dynamic responses (both at the beginning and end of the movement) was taken into account (not illustrated).

The dynamic component of the ramp response was assessed by determining the number of impulses, $N_D$ attributable to the movement *per se*. For individual units a mean $N_D$ was determined separately for the initial and terminal ramps of the sequences in both the flexion and extension range. No appreciable difference was found when the flexion and extension *range* was compared, with the values from the initial and terminal ramps pooled. Nor was there any obvious difference between flexion and extension when the values for the same *direction* (either flexion or extension *movement*) were pooled. For individual units an averaged $N_D$ value was therefore computed by pooling the $N_D$ values from all ramp movements. No striking differences between the four categories of units were encountered, and the mean size of their responses was between 3 and 6 impulses. A number of receptors were studied both with ramp movements and dynamic stimulation with von Frey hairs (at five times threshold), applied to the zones of highest sensitivity. The quantitative comparison of the responses showed that, for PC and RA, the dynamic response to ramp movements was about twice as large as for the mechanical indentation at five times von Frey threshold. For SA I the ratio is about one, and for SA II about 1·5.

*Static responses*

As pointed out above, it was a common feature of multi-unit recordings that little afferent activity was maintained when the hand was held in a steady position. The single unit analysis confirmed this impression. First it was noted that only a few of the slowly adapting units exhibited spontaneous activity in the resting position (ten out of sixty-two), and that it was exclusively SA II units which exhibited this feature. Thus, 30% of the SA II units were spontaneously active. Likewise, about a third of the total sample (32%, cf. Fig. 7$A$) exhibited a static responsiveness to angular position, seen as changes of the steady rate of firing as a function of angular position. As regards individual receptor types it emerged, that such static responsiveness was typical mainly for the SA II units, since it was encountered with 81% of the SA II and with only 17% of the SA I units (cf. Fig. 7$A$). Thus, apart from the SA II units, the low values of static responsiveness are in clear contrast to the high values of dynamic and over-all responsiveness. This is illustrated in Figs. 7$A$, $B$ and 2.

Units with a static responsiveness were investigated in more detail to check whether there was any general relationship between angular position and their rate of discharge. To this end three separate angular ranges were defined which, for each joint, were centred around the positions usually found in a hand with all fingers either flexed, in intermediate position, or extended (corresponding to the three positions of the hand described in the Methods, test 2). Averaged responses of the individual units were then allocated to one of the three ranges. Thirty-two out of the investigated sixty-two slowly adapting units showed a steady rate of discharge in at least one of the angular ranges. Fig. 8$A$ shows the mean responses for the activated SA I and SA II units. The rate of firing rarely exceeded 15 impulses/sec. When the

mean response for the total sample of SA I and SA II units was calculated (including the afferents which never gave a maintained response), it is even more manifest that the total static response was rather moderate. In order to examine to what extent the SA units showed any systematic relationship between afferent firing and joint angles, units which were activated in at least one of the angular ranges were investigated. It was found that out of twenty-one afferents twelve exhibited an increasing and three a decreasing response with increasing joint angle, as is illustrated in Fig. 8*B*. Notably, major changes of the rate of discharge occurred only in extreme angular positions. The remaining six units were spontaneously active and did not respond to joint angle at all.
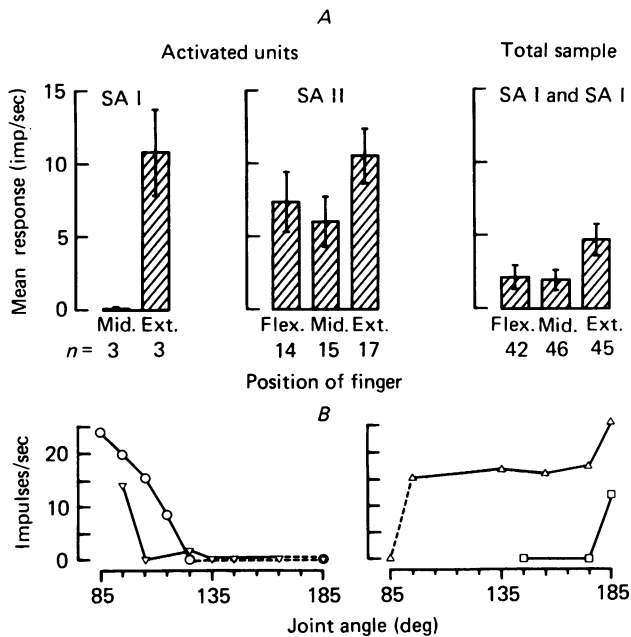


Fig. 8. The static position sensitivity of SA I and SA II units. In *A*, the mean rate of discharge in the three ranges of finger position described in the text is shown separately for the responsive SA I and SA II units in the left-hand diagrams. On the right the dependence of the mean rate of steady firing on the finger position is shown for the total sample of slowly adapting units, including both responsive and non-responsive units which were studied in at least two positions. The vertical bars give the standard error. In *B*, the dependence of the rate of steady discharge on the angle of the moved joint is shown for four separate SA II units, with decreasing relationships on the left, and increasing relationships on the right. Continuous lines connect data points from the responses to staircase movements. The remaining points connected by interrupted lines were supplemented from responses to ramp movements.

### Movement responsiveness related to unit properties

In an attempt to elucidate the mechanisms responsible for the results described above, the responsiveness to isotonic movements was correlated with four functional properties of the units: size and location of the receptive field, and sensitivity to indentation and to stretching of the skin. It emerged that no individual parameter

could easily be singled out which by itself could account for the present data. The comparisons were largely restricted to the RA and SA I units, since they together comprised most of the non-responsive units. For any meaningful correlation of properties it was of course necessary to use a sample with comparable proportions of responsive and non-responsive units. Those RA and SA I units which had low thresholds for stimulation with von Frey hairs also tended to respond more readily to isotonic movements. However, some of the afferents with very low von Frey thresholds failed to respond, and likewise some units with high thresholds responded readily. Moreover, SA II units showed a greater movement responsiveness than SA I units, in spite of their higher von Frey thresholds (the median was 16 mN as opposed to 4 mN for the SA I units).

The size of the receptive field might conceivably influence the movement responsiveness of a unit. This aspect was again analysed with the RA and SA I categories. The results showed that the frequency distributions of responding and non-responding units exhibited an almost complete overlap.

During movements of the human hand local deformations of the skin are presumably most pronounced in the immediate vicinity of the flexion lines of the palm and the fingers. A close spatial relationship between receptive field and flexion lines might therefore favour movement responsiveness. However, only 26% of the responsive RA and SA I units had flexion lines passing through their receptive fields. Moreover, 14% of the non-responsive afferents of these two categories had flexion lines within their fields.

Finally, the sensitivity to skin stretching, which is such a typical feature of the SA II units, might be responsible for the appreciable movement responsiveness of these afferents. It might also account for the behaviour of the SA I units, since it was noted that these units too tended to show some, albeit weaker, sensitivity to skin stretching. Stretch sensitivity was indeed quite likely as a contributing factor, since an appreciable agreement was found between the responsiveness to stretch and to movement, both for the static components alone and for the combined static and dynamic components.

*Other unit types*

Eight units did not belong to any of the four main types of mechanosensitive units from the skin area: two units were classified as joint receptors, four as slowly adapting units in deep structures but of otherwise unknown nature, one was a hair receptor and one a high-threshold mechanoreceptor. The two joint receptors were associated with inter-phalangeal joints. They were slowly adapting and discharged continuously only near one of the extreme joint angles. The eight units, treated as a residual group, did not differ significantly from the main sample as regards their movement responsiveness and the findings are not further elaborated. It is, however, of considerable interest that so few joint receptors were encountered in the median nerve with the joints of the hand in an intermediate position and the muscles of the forearm relaxed.

## DISCUSSION

The present report is concerned with the low-threshold mechanosensitive units in the glabrous skin area of the human hand. These units are generally assumed to subserve an exteroceptive function. The main finding of the investigation is that they responded to isotonic movements when incidental excitation by direct touch

was avoided. This result did not depend on the particular kind of movement studied, and it was obtained with both ramp and hold and oscillatory movements. These statements hold for each of the four main receptor types, in spite of some quantitative differences between them. The over-all movement responsiveness was more pronounced for the PC and SA II units than for the SA I and RA units. It was also a very distinct finding that dynamic responses were more frequent than static responses.

It should be emphasized that the assessment of the movement responsiveness was largely qualitative. This was mainly because the voluntary movements could be standardarized only to a limited degree, although they were generally of fairly large amplitude. However, the movements were undoubtedly natural and occurred within the physiological range. As regards sampling bias, it should be noted that during the search for single units the subject's hand was not moved in a way that would favour the discovery of units responding to finger movements, since the joints of the hand were kept in a constant intermediate position. The subjects were also asked to relax the muscles of the forearm and not to move their fingers. Otherwise, the presence of any ongoing passive or voluntary movements could easily have led to overestimates of the dynamic movement responsiveness.

It is noteworthy that very few afferents from joint receptors were encountered in the median nerve. This seems to indicate that in man joint afferents do not normally exhibit spontaneous activity, with the finger joints at intermediate angles and the muscles relaxed. This interpretation would agree with a number of studies on joint afferents in the cat and monkey (Burgess & Clark, 1969; Clark & Burgess, 1975; Grigg & Greenspan, 1977). Joint receptors might have been under-represented because of the size of their axon diameters, since the present recording technique is likely to give a sampling bias in favour of large fibres. However, in the cat, joint afferents conduct at a wide range of speeds including the highest (Burgess & Clark, 1969).

The movement responsiveness of the mechanosensitive afferents from the skin may be related to their properties established in earlier investigations using mainly indentation and stretching of the skin. But no single factor could be defined which was exclusively responsible for the movement responsiveness. Rather, this property appears to be determined by a number of mechanisms, whose contributions may vary from one type of unit to another. Qualitatively the prevalence of movement responsiveness among the PC and SA II units fits in with the fact that their receptive fields are large. In contrast, the less responsive SA I and RA units exhibit smaller and better delimited receptive fields; however, for responsive and non-responsive units of the latter types, the separate analysis of the size distribution of the receptive fields failed to reveal a clear cut relation between the field size and the movement responsiveness. The higher responsiveness of SA II and PC units could be due to the location of their end organs in deeper layers, where they might be exposed to larger deformations. The sensitivity to indentation of the skin is likely to be a contributory factor, and for the slowly adapting units also the sensitivity to skin stretching appeared to be rather influential. The occurrence of creases within the receptive field may similarly contribute to the manifestation of movement responsiveness.

The predominance of the dynamic movement responsiveness agrees qualitatively with the prevalence of the dynamic sensitivity to skin indentation, which is so pronounced with the RA, PC and SA I units. It should be noted, however, that the

SA II units, which represent the dynamically least sensitive group, showed a higher dynamic responsiveness to movement than the RA and SA I units.

Are the responses provoked by isotonic movement large enough to be important functionally? We think that the answer should be 'yes'. It was shown that the dynamic responses to isotonic ramp movements were of the same order of magnitude as the responses to skin indentation at five times von Frey threshold. Moreover, it has been demonstrated that the threshold for psychophysical detection of a direct skin indentation may correspond to the occurrence of a single impulse in rather few mechanosensitive units (Vallbo & Johansson, 1976). Since the movement responsiveness of the mechanosensitive units is so pronounced, a movement to full extension of the fingers may be expected to excite a sizeable fraction of the 17,000 low-threshold units, which have been estimated to be present in the glabrous skin area of the human hand (Johansson & Vallbo, 1979). Whatever the precise number, it is bound to be a huge number in comparison with the rather limited number of afferents which are likely to be excited by just detectable indentations applied with small probes. Furthermore, since the movement responses of individual units would be three to six times larger than with the indentation at psychophysical threshold, the total afferent response to movement should therefore be massive in relation to the total response to just detectable indentation of the skin.

What then is the functional significance of the responses to isotonic movements? The dynamic responses of the afferents could provide information on the occurrence, direction or velocity of movement. The present study indicates beyond doubt that the low threshold mechanoreceptors provided information from which at least the occurrence of movements could be deduced. In addition, the findings suggest that a certain amount of information on the direction and speed of the movements might be deduced. With respect to the static responsiveness to joint angle, it is notable that only a few units were encountered which exhibited this property. In addition, their responses were weak and occurred largely at the extremes of the physiological range of joint angles. It is quite unlikely that the responsive units were under-represented since, if anything, the total sample was biased in their favour (p. 234).

Given these patterns of afferent response it seems unlikely that the low threshold mechanoreceptors of the glabrous skin area contribute directly to position sense. In particular they largely failed to supply static information in the intermediate range of joint angles. Thus they do not provide much supplementary information on angular position in a range where joint afferents too hardly responded (cf. Clark & Burgess, 1975; Grigg & Greenspan, 1977). These findings agree with those of Horch, Burgess & Clark (1975) which implied that static discharge from cutaneous afferents is unlikely to be essential for limb position sense, since sensations associated with maintained indentations of the skin completely faded within a couple of minutes. However, Gandevia & McCloskey (1976) considered specific contributions to position sense from cutaneous afferents, since a sense of static joint position was preserved when both joint and muscle afferents were unlikely to be excited. However, such contributions need not depend on the occurrence of static discharge of cutaneous afferents. Rather, the information on position could be derived from transient responses, appropriately integrated and remembered by higher centres, as was discussed by Horch *et al.* (1975).

Several studies in other species have indicated that cutaneous afferent signals,

elicited by direct touch or electrical stimulation, have the potential of affecting the motor performance (Mori, Reynolds & Brookhart, 1970; Marsden, Merton & Morton, 1977; Forssberg, Grillner & Rossignol, 1977; Duysens, 1977). In relation to the present findings it seems relevant to consider the kinds of natural stimuli which might exert an influence on the motor output by exciting low threshold skin afferents. There seem to be two basic alternatives. Motor effects could be induced either by direct skin contact with an external object, or by movements *per se* without such contacts. In the latter case information on the mere occurrence of movements might be useful for any gating or gain control of motor reflexes. It is also conceiveable that the skin afferent activity contributes to some feed-back control of the ongoing movement as long as an adequate description of the movement is provided. The present study suggests that any description furnished by the skin afferents in the glabrous skin area of the hand is rather crude. However, more detailed information on joint movements may be provided from other areas, where the skin is less tightly fixed to deep structures, and therefore perhaps more readily deformed by joint movements. When direct contact is made with an external object the activity in skin afferents may play a more specific role by directing further movements and adjusting muscular force. Such a role seems particularly adequate in the primate hand (Rosén & Asanuma, 1972).

It seems only reasonable that any effects elicited in motor centres by cutaneous inputs should be different for movements *per se* and for movements accompanied by direct skin contacts. The fact that the information from the skin area is carried in the same afferent channels should not invalidate this possibility since a differentiation between the two kinds of stimuli should be possible at the subconscious level as readily as at the perceptive level. As to the latter, it is a common experience that the percept from the skin elicited by the slightest contact with an external object is drastically different from the percept of movements although, as is shown in the present study, the same types of units are excited to a similar degree in the two situations. Moreover, it is very likely that the spatial and temporal patterns of afferent activity differ significantly, and that during voluntary movements motor commands participate in the evaluation of the afferent sensory discharge (MacKay, 1973). Either factor might indeed play an important role in the generation of the perceptive experience.

## REFERENCES

BURGESS, P. R. & CLARK, F. J. (1969). Characteristics of knee joint receptors in the cat. *J. Physiol.* **203**, 317–335.

CHAMBERS, M. R., ANDRES, K. H., VON DUERING, M. & IGGO, A. (1972). The structure and function of the slowly adapting type II mechanoreceptor in hairy skin. *Q. Jl exp. Physiol.* **57**, 417–445.

CLARK, F. J. & BURGESS, P. R. (1975). Slowly adapting receptors in cat knee joint: Can they signal joint angle? *J. Neurophysiol.* **38**, 1448–1463.

DUYSENS, J. (1977). Reflex control of locomotion as revealed by stimulation of cutaneous afferents in spontaneously walking premamillary cats. *J. Neurophysiol.* **40**, 737–751.

FORSSBERG, H., GRILLNER, S. & ROSSIGNOL, S. (1977). Phasic gain control of reflexes from the dorsum of the paw during spinal locomotion. *Brain Res.* **132**, 121–139.

GANDEVIA, S. C. & McCLOSKEY, D. I. (1976). Joint sense, muscle sense and their combination as position sense, measured at the distal interphalangeal joint of the middle finger. *J. Physiol.* **260**, 387–407.

GRIGG, P. & GREENSPAN, B. J. (1977). Response of primate joint afferent neurons to mechanical stimulation of knee joint. *J. Neurophysiol.* **40**, 1–8.

HAGBARTH, K.-E., HONGELL, A., HALLIN, R. G. & TOREBJÖRK, H. E. (1970). Afferent impulses in median nerve fascicles evoked by tactile stimuli of the human hand. *Brain Res.* **24**, 423–442.

HORCH, K. W., CLARK, F. J. & BURGESS, P. R. (1975). Awareness of knee joint angle under static conditions. *J. Neurophysiol.* **38**, 1436–1447.

IGGO, A. & MUIR, A. R. (1969). The structure and function of a slowly adapting touch corpuscle in hairy skin. *J. Physiol.* **200**, 763–796.

IGGO, A. & OGAWA, H. (1977). Correlative physiological and morphological studies of rapidly adapting units in the cat's glabrous skin. *J. Physiol.* **266**, 275–296.

JÄNIG, W., SCHMIDT, R. F. & ZIMMERMANN, M. (1968). Single unit responses and the total afferent outflow from the cat's food pad upon mechanical stimulation. *Expl Brain Res.* **6**, 100–115.

JOHANSSON, R. S. (1976). Receptive field sensitivity profile of mechanosensitive units innervating the glabrous skin of the human hand. *Brain Res.* **104**, 330–334.

JOHANSSON, R. S. (1978). Tactile sensibility in the human hand: receptive field characteristics of mechanoreceptor units in the glabrous skin. *J. Physiol.* **281**, 101–123.

JOHANSSON, R. S. & VALLBO, Å. B. (1979). Tactile sensibility in the human hand: relative and absolute densities of four types of mechanoreceptive units in the glabrous skin area. *J. Physiol.* **286**, 283–300.

KNIBESTÖL, M. (1973). Stimulus–response functions of rapidly adapting mechanoreceptors in the human glabrous skin area. *J. Physiol.* **232**, 427–452.

KNIBESTÖL, M. (1975). Stimulus response functions of slowly adapting mechanoreceptors in the human glabrous skin area. *J. Physiol.* **245**, 63–80.

KNIBESTÖL, M. & VALLBO, Å. B. (1970). Single unit analysis of mechanoreceptor activity from the human glabrous skin. *Acta physiol. scand.* **80**, 178–195.

LINDBLOM, U. (1965). Properties of touch receptors in distal glabrous skin of the monkey. *J. Neurophysiol.* **28**, 966–985.

LINDBLOM, U. & LUND, L. (1966). The discharge from vibration-sensitive receptors in the monkey foot. *Expl Neurol.* **15**, 401–417.

LYNN, B. (1969). The nature and location of certain phasic mechanoreceptors in the cat's foot. *J. Physiol.* **201**, 765–773.

MacKAY, D. M. (1973). Visual stability and voluntary eye movements. *Handbook of Sensory Physiology.* 8/3, *Central Visual Information A*, ed. JUNG, R., pp. 307–331. Berlin: Springer-Verlag.

MARSDEN, C. D., MERTON, P. A. & MORTON, H. B. (1977). The sensory mechanism of servo action in human muscle. *J. Physiol.* **265**, 521–535.

MORI, S., REYNOLDS, P. J. & BROOKHART, J. M. (1970). Contribution of pedal afferents to postural control in the dog. *Am. J. Physiol.* **218**, 726–734.

ROSÉN, I. & ASANUMA, H. (1972). Peripheral afferent inputs to the forelimb area of the monkey cortex: input–output relations. *Brain Res.* **14**, 257–273.

TALBOT, W. H., DARIAN-SMITH, I., KORNHUBER, H. H. & MOUNTCASTLE, V. B. (1968). The sense of flutter-vibration: comparison of the human capacity with response patterns of mechanoreceptive afferents from the monkey hand. *J. Neurophysiol.* **31**, 301–334.

VALLBO, Å. B. (1972). Single unit recording from human peripheral nerves: muscle receptor discharge in resting muscles and during voluntary contractions. In *Neurophysiology Studied in Man*, ed. SOMJEN, G. G., pp. 283–297. Amsterdam: Excerpta Medica.

VALLBO, Å. B. & HAGBARTH, K.-E. (1968). Activity from skin mechanoreceptors recorded percutaneously in awake human subjects. *Expl Neurol.* **21**, 270–289.

VALLBO, Å. B. & JOHANSSON, R. S. (1976). Skin mechanoreceptors in the human hand: Neural and psychophysical thresholds. In *Sensory Functions of the Skin in Primates*, ed. ZOTTERMAN, Y., pp. 185–199. Oxford: Pergamon Press.