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AN ANALYSIS OF FIBRE DIAMETER AND RECEPTOR CHARACTERISTICS OF MYELINATED CUTANEOUS AFFERENT FIBRES IN CAT

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The preceding paper considered the characteristics of touch receptors in the skin of cat, the analysis being made on certain of the fibres that were isolated in the course of the study now to be described. The present report is concerned with the relation between fibre diameter and receptor characteristics, as determined in 421 individual myelinated afferent fibres from the sural nerve of cat.

Several considerations caused us to undertake this problem. Although there have been many studies on perception of cutaneous sensation in man, comparatively few investigations have been concerned with the receptor characteristics of individual myelinated cutaneous afferent fibres in mammals (see Discussion). Another factor was that recent anatomical studies (Sinclair, Weddell & Zander, 1952) have suggested re-evaluation of the generally held 'doctrine of specific nerve energies', i.e. the specificity of a given receptor for a particular type of stimulus. Although it has long been recognized that the specificity of receptors for particular types of stimulus was not absolute, the concept that sensory information for a particular type of natural stimulus is transmitted exclusively in certain afferent fibres has been widely accepted.

The use of volleys in cutaneous nerves, graded in size by stimulus strength, for the study of spinal reflexes and of sensory systems has also posed a need for more information on the relation between receptor characteristics and fibre diameters. Similarly, the detailed information now available on responses to natural stimuli of cortical neurones of the primary sensory receiving area (Mountcastle, 1957) requires, for its fuller interpretation, more information as to receptive fields and response characteristics as recorded in primary afferent fibres.

It will be shown that several distinct categories of receptors may be recognized by their responses to adequate or natural stimulation, and the relation of fibre diameter to these categories has been defined. Also, receptor characteristics have been more fully described and receptive fields of various types of receptors have been mapped.

METHODS

Adult cats anaesthetized with sodium pentobarbital (Nembutal; Abbott Laboratories) were used. Laminectomy was performed, the appropriate dorsal roots (and associated ventral roots) were cut near the spinal cord, and nerves in the hind limb other than the sural were also cut. In most preparations single afferent fibres were isolated in dorsal root filaments. The presence of a fibre from the sural nerve was detected by an impulse evoked by stimulation of the latter. Conduction times were determined from stimulus–response intervals. The latter were measured by a Berkeley 1 MC counter (see Hunt & McIntyre, 1960*a*). The beginning of the counted interval was signalled by the stimulus, the end by the onset of the impulse. In all cases the stimulus–impulse interval was observed on one beam of a dual-beam Tektronix oscilloscope (model 502) and the gated interval simultaneously on the other beam. On completion of each experiment the conducting pathway between stimulating cathode and proximal recording electrode was excised and measured. From the conduction time, 0·1 msec was deducted for utilization time, and conduction velocity then calculated (Hunt, 1954). In measuring conduction time stimulus strength was made approximately twice threshold strength.

Exposed tissues were covered with paraffin oil initially equilibrated with 5% CO_2 and 95% O_2. Body temperature was kept between 37 and 39° C. The region of the skin innervated by the sural nerve was carefully clipped so that the hairs protruded about 1 mm from the skin. The limb was held by a pin inserted into the medial malleolus, so that the sural area was suspended in air.

RESULTS

Of the total of 421 single myelinated afferent fibres studied from sural nerve, the great majority exhibited discharge in response to some form of natural or adequate stimulation. Most afferent fibres and their receptors (units) studied fell into one of several distinct categories with respect to the type of stimulus most effective in eliciting discharge. The most commonly encountered fibres had receptors in which activity was evoked primarily by displacement of hairs, and have been designated 'hair units'. Another major category consisted of 'touch units', as described in the preceding paper (Hunt & McIntyre, 1960*b*). Fibres showing discharge in response to other types of stimulation included those responding to heavy pressure, to brief tap on the skin, to pinch or pin prick, as well as others in which discharge was evoked by stimulation of subcutaneous or joint structures. The response characteristics of the various types of units will be considered separately.

Since myelinated cutaneous fibres have a wide and characteristic distribution of fibre diameters, it was of interest to compare the distribution of calculated fibre diameters with the histological spectrum in order to assess the adequacy of sampling. For conversion of conduction velocity to diameter, direct proportionality by a factor of 6 has been used (Hursh, 1939). The calculated diameter distribution of the 421 fibres sampled is shown in Fig. 1. According to the conversion used, the largest fibres would be in the 16–17 μ band, the peak of the α group at 10–12 μ, and the peak of the δ group at 3–4 μ. In general this distribution is similar to the histological spectrum shown in Fig. 8 of Gasser & Grundfest's (1939) paper. The peak of the δ group in the calculated fibre diameter spectrum is probably at too small a diameter; from histological spectra this would be expected to occur at slightly larger diameter. While it seems likely that conduction velocity (m/sec) is related to diameter (μ) by a factor of 6 in the largest fibres, the factor of conversion may deviate more widely among δ fibres. This could explain a difference in peak distribution of δ fibre diameters between the isolated fibre and histological spectra. In spite of this uncertainty, the calculated diameter distribution indicates that fibres throughout the myelinated range were sampled. Probably because of the greater ease of isolating larger fibres, the sample of α fibres may be disproportionately large. However, the sample may be considered representative of the spectrum of fibre diameters with the possible exception of the smallest δ fibres. The conduction velocities also suggest that the largest α fibres are considerably faster than Group II fibres of muscle nerves (Lloyd & Chang, 1948; Hunt, 1954). Also, the minimum in the distribution separating the α from the δ modes occurs at a larger diameter than that separating Groups II and III in muscle nerves. In the

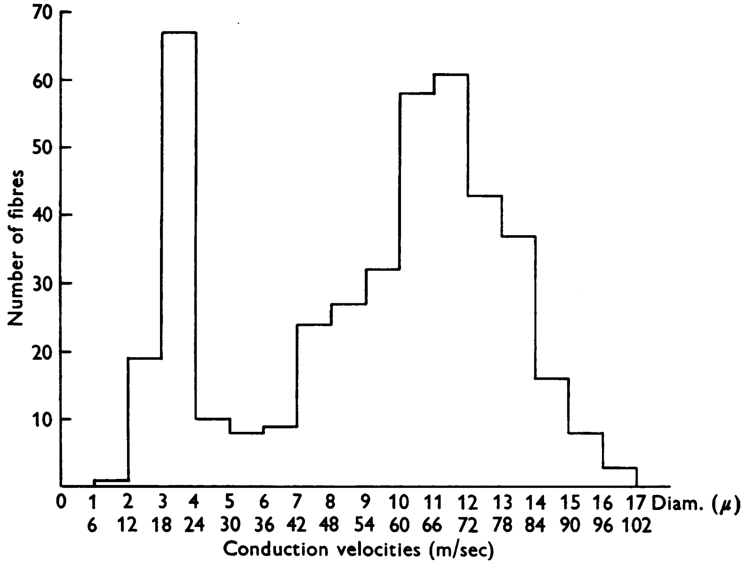

Fig. 1. Distribution of fibres according to conduction velocities and calculated diameters, total sample of 421 sural fibres.

present study fibres with calculated diameters between 6 and 17 μ will be called α, those between 1 and 6 μ δ (see Gasser, 1960).

Hair receptors

Units responding principally to hair movement numbered 263 of the total sample, = 62 %. Movement of hairs was the most effective means of eliciting discharge. Hair movement was produced by brushing the hairs, which had been clipped short, with a fine hairbrush, with a cat's vibrissa, or by displacing hairs with fine watch-maker's forceps. Movement of hair without otherwise deforming the skin served to evoke discharge, in contrast to the touch units considered below. A typical response of a hair unit is shown in Fig. 2.

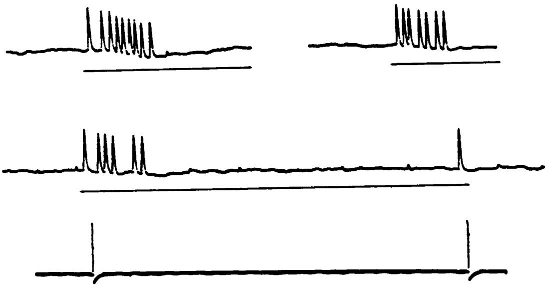

Fig. 2. Discharge in a hair receptor fibre to bending of hairs. Bar gives estimate of duration of bending. Time marker, 100 msec, lowest trace.

Hair units were always rapidly-adapting and ceased discharging when hairs were maintained in the bent position. However, some were so sensitive that slight movement of hairs while in the bent position would result in discharge. Although all were rapidly-adapting, differences in the rate of adaptation were evident among the various hair units. Thus the most rapidly-adapting responded only when the hair movement was rapid and not to slow bending of hairs. Others discharged even when hairs were moved slowly.

The calculated diameter distribution of fibres of hair units is shown in Fig. 3. The distribution is clearly bimodal, with peaks in the α and δ ranges. Comparison with Fig. 1 reveals that hair units accounted for the bulk of the δ group and a very substantial fraction of the α group. Also, the largest fibres in the α range were from hair receptors. Hair units appear to occur over the entire myelinated fibre range, from small δ to largest α, and there seems to be no band of fibre diameters free of fibres from hair receptors.

The receptive fields of hair units are shown in the charts of Fig. 4. A total of 152 units are shown on six projections of the region of skin innervated by the sural nerve. This number of hair units was contained in a sample of about 300 sural fibres. Assuming the sural nerve to have about 1200 fibres (an unpublished count (Gasser, personal communication) of the myelinated fibres in sural nerve totalled 1073), one may

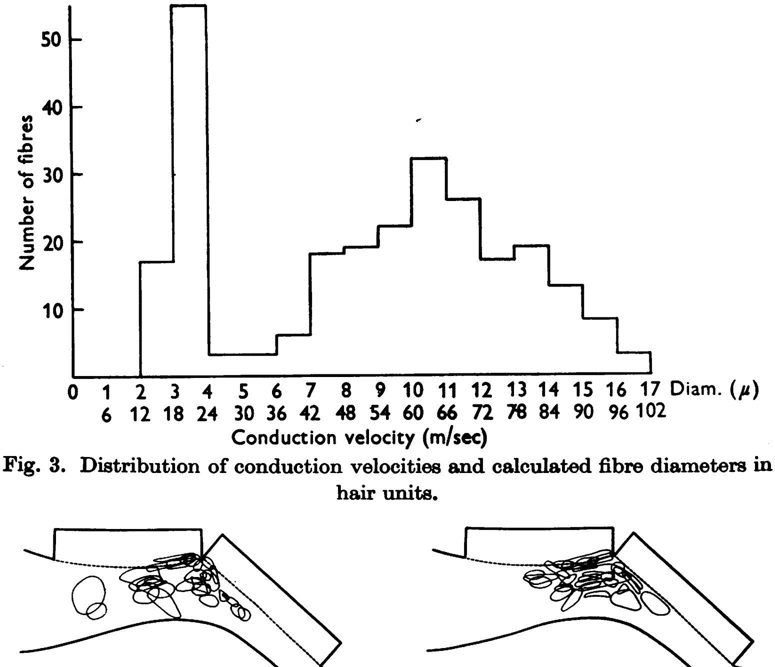

Fig. 3. Distribution of conduction velocities and calculated fibre diameters in hair units.

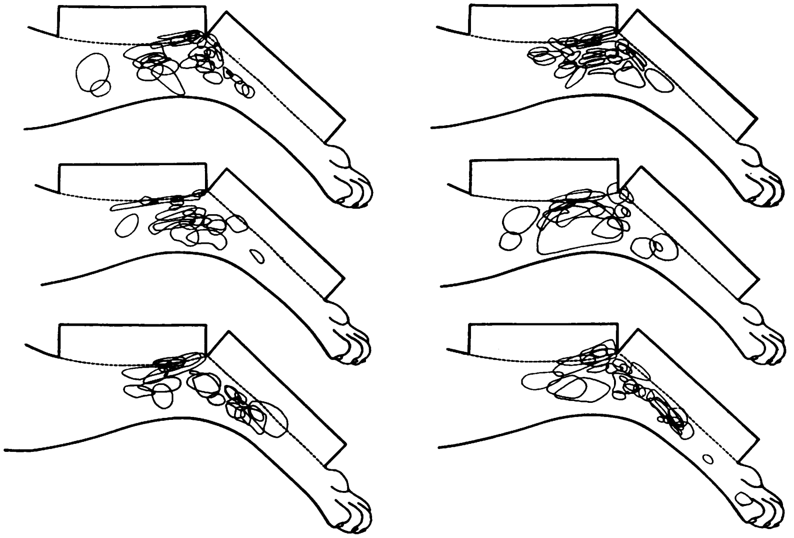

Fig. 4. Receptive fields of 152 hair units. Lateral view of cat hind limb and foot shown, with flaps indicating skin medial to mid line (indicated by dotted line).

obtain a rough estimate of the density and degree of overlap of hair-receptive fields in the sural region of a cat by combining the projections of Fig. 4 and multiplying by a factor of approximately 4. In this manner it would be possible to estimate the approximate number of hair units excited by movement of hairs in a given area. Actually the density of innervation of hair units would be slightly greater than this estimate, since the data have been derived from a number of animals in which the region supplied by the sural nerve is not exactly the same.

The areas of receptive fields of individual hair units were estimated by drawing to scale on graph paper the outline of each unit's field. The individual fields were then cut out and weighed and their areas estimated by comparison with the weights of standard areas. The receptive-field areas showed wide variations, the smallest being about 3 mm^2 and the largest 828 mm^2. The latter was quite exceptional, and all but two units had field areas between 3 and 185 mm^2. A plot of receptive-field areas of 156 hair units is shown as a function of calculated fibre diameter in Fig. 5. Although there is wide scatter, two features are clear: there was a greater incidence of large receptive fields among smaller fibres, and the smallest

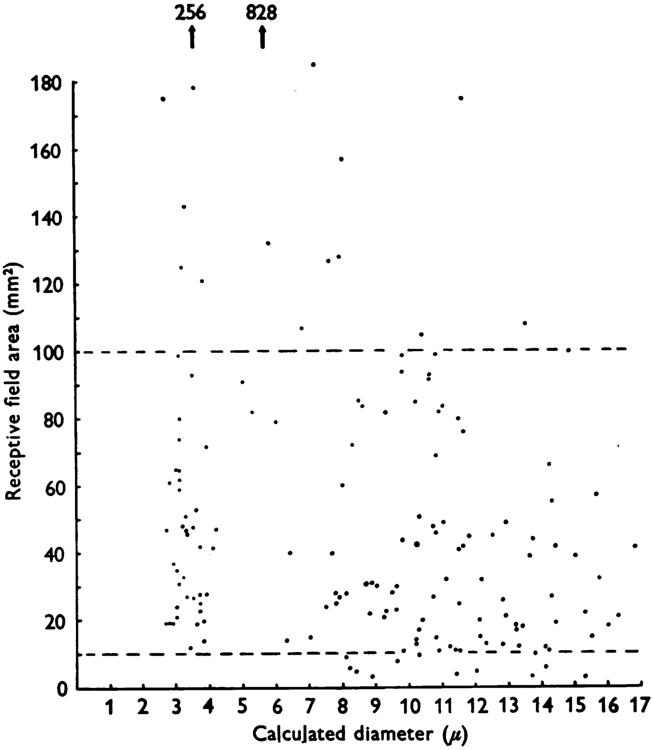

Fig. 5. Relation between receptive-field area and diameter of afferent fibre of the same hair units shown in Fig. 4. Interrupted horizontal lines at receptive-field areas of 10 and 100 mm^2.

receptive fields (less than 10 mm^2) were found only in fibres of α diameter. However, except for these features there was little correlation between receptive-field area and fibre diameter.

The sensitivity of hair receptors varied considerably. Some were so sensitive that very slight movement of the skin transmitted from a considerable distance would evoke discharge. For example, a number of units were found, with receptive fields central to the lateral malleolus, which responded when the foot was moved a small distance. Such units showed discharge to gentle blowing on the skin. Great care was necessary to define the limits of distribution of the hair receptors of such units. At the other extreme were units which responded only when the hairs were briskly moved, for example, by rapid stroking with a brush. Between these extremes there were many units with intermediate sensitivities. In general, if a unit showed great sensitivity the entire receptive field exhibited this characteristic and, conversely, in a less sensitive unit movement of various hairs within the receptive field indicated the same order of sensitivity. However, some differences in sensitivity within the field of a given unit could sometimes be detected, particularly in units of intermediate sensitivity.

In a number of hair units an estimate was made of the receptor sensitivity, grading on a basis of from 1 to 4 plus. While such estimates are only approximate, the range of sensitivity was sufficiently broad to give it significance. A significant correlation was found between sensitivity and fibre diameter, indicating that the fibres of slower conduction velocity and smaller diameter tend to have the more sensitive receptors. In this regard it may be recalled that Zotterman (1939) noted that very light stroking of the skin elicited discharge confined to fibres considered to be in the δ range.

Spontaneous discharge was rarely found in hair units. A few were noted which gave an impulse associated with each heart beat. In some cases this occurred only when the responsive hairs were bent to a certain position. No background discharge of the kind found in touch units (see below) was noted in hair units. Also, hair receptors were usually unresponsive to temperature changes of the skin although on rare occasions hair units showed a few discharges when the skin temperature was raised above 41–42° C. In contrast to touch units (Hunt & McIntyre, 1960*b*), hair receptors did not develop non-responsiveness after repeated mechanical stimulation of the skin.

Touch receptors

Units showing discharge to light touch of the skin numbered 114 or 27 % of the total sample. Their responses to both mechanical and thermal stimulation have been described in the previous paper (Hunt & McIntyre, 1960*b*). As was there noted, they could usually be readily differentiated from hair receptors and other mechanoreceptors.

The calculated diameter distribution of touch units is shown in Fig. 6. In contrast to that of hair units, touch receptor fibres have a unimodal distribution which is essentially confined to the α group. In the α range the distributions of hair and touch receptor fibres overlap considerably, although the largest touch units are appreciably smaller than the largest hair fibres.

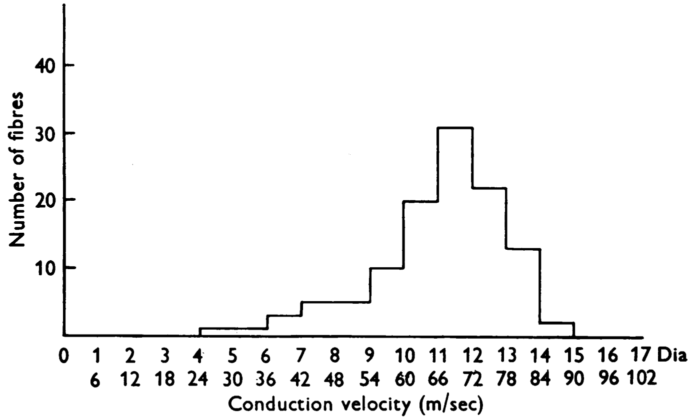

Fig. 6. Conduction velocity and calculated diameter distribution of 114 touch unit fibres.

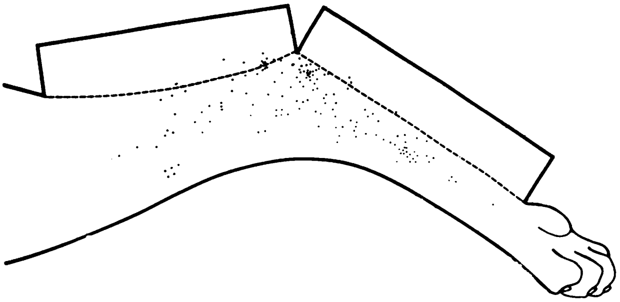

Fig. 7. Distribution of receptive spots of 77 touch units. Projection similar to those of Fig. 4.

The distribution of receptive spots of 77 touch units is shown in Fig. 7. Multiplication of the number of receptive spots shown by about 4 (see above) would indicate the approximate density of innervation by this type receptor. It is clear that the density of touch receptor spots is high. However, the spots are so discrete that a given point on the skin may well be served by only one receptor.

Pressure receptors

A total of 21 units were isolated which showed discharge on pressure to the skin of considerably greater intensity than that required to evoke impulses from the touch receptors noted above. However, the degree of pressure necessary to cause discharge in pressure units was judged less than that which would be noxious. The discharge was sustained when pressure was maintained. Hence these receptors may be considered slowly-adapting. While it was not possible to define precisely the limits of a receptive field, pressure was effective only when applied to a fairly limited area. In most cases the receptive area shifted with movement of the skin, but in occasional units the receptors did not appear to follow skin movement and were judged to be subcutaneous. However, even units which appeared to shift their receptive areas with skin movement might have been located deep to the skin itself.

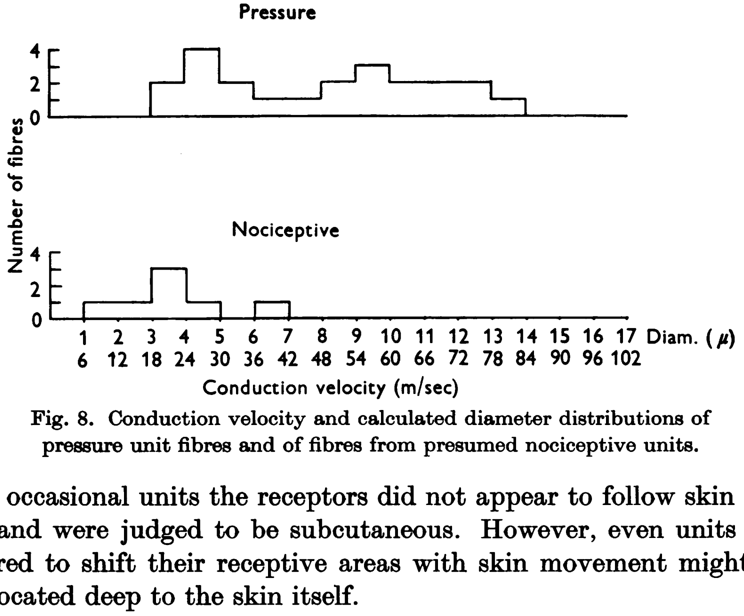

Fig. 8. Conduction velocity and calculated diameter distributions of pressure unit fibres and of fibres from presumed nociceptive units.

The diameters of pressure receptor fibres were scattered from 3 to 14μ with no distinct mode (Fig. 8). They thus occur in both the α and δ fibre groups. Unlike the touch receptors, pressure receptors did not show spontaneous or background discharge and did not respond to thermal stimuli.

Probable nociceptive receptors

A total of seven fibres were isolated which showed discharge only to heavy pinching of the skin or pin-prick, stimuli judged to be noxious in character. Those responding to pinching of the skin were often slowly-adapting, discharge being maintained for the duration of the stimulus. Units responding to pin-prick frequently gave only a few impulses on pricking the skin or scratching the skin surface with a pin. No after-discharge was seen, in contrast to that found in nociceptive non-myelinated units (Zotterman, 1939).

The presumed nociceptive units were essentially confined to the δ range of fibre diameters (Fig. 8). The relatively small number of such units may be accounted for, in part, by the fact that severe handling of the skin was minimized because it led to block of touch receptors. However, even if the six δ units which were unidentified as to receptor function were considered as possibly 'nociceptive', the total number of nociceptive units would be small relative to the number of δ hair units.

Other receptors

A few units with receptor characteristics different from the above were encountered. These included five units which responded only to a brisk tap on the skin, usually with only one or two impulses. These units had fibres between 8 and 14μ and may possibly have been nearly blocked touch receptors. Another category consisted of two units responding to mechanical stimulation of the ankle joint or associated ligamentous structures. One of these was in the δ range (4·1μ), the other in the α band (10·5μ). One unit (calculated diameter 11·7) had its receptor in the fascia of the gastrocnemius muscle. It gave a sustained discharge to pulling on the fascia.

Of the total sample of fibres eight were isolated which showed no response to mechanical stimulation; the three of these that were examined also failed to respond to warming or cooling of the skin. As was noted above, six of the unidentified units were in the δ range and could possibly be nociceptive. The remaining two unidentified units were of the α band and might have been blocked touch receptors.

DISCUSSION

The present study indicates that the most common receptor type among myelinated fibres in the sural nerve of cat is activated primarily by movement of hairs. Responses to this type of stimulation have been noted previously by Adrian (1930) and by Zotterman (1939), both of whom described impulses of both large and small size when recording from a cutaneous nerve and lightly stroking the skin. Zotterman (1939) utilized relative spike potential amplitude as an index of fibre diameter and concluded that receptors of smaller fibres (judged to be δ) were activated by lighter touch than that required to initiate discharge in larger fibres. While he did not relate such stimulation specifically to hair receptors, his findings are supported by the present results, which indicate that the lowest threshold hair receptors tend to have fibres of small diameter. Maruhashi, Mizaguchi & Tasaki (1952) also reported responses in fibres of saphenous nerve of cat related to hair movement. The relative number of hair receptors found was considerably less than in the present study, and the range of diameters was from 6 to 12 μ. The smaller fibres which they designated as 'wide receptive field', ranging in size from 2 to 5 μ, are probably the same as those here reported as δ hair units.

Receptors responding to touch of one or two spots on the skin were noted by Maruhashi *et al.* (1952) and found to be associated with fibres between 8 and 14 μ in diameter. The previous paper (Hunt & McIntyre, 1960*b*) provided a more detailed description of their behaviour and indicated that these receptors are generally slowly-adapting. The finding that the same fibres may show discharge to mechanical stimulation of the skin and changes in frequency on variation of skin temperature has recently been reported by Witt & Hensel (1959). While the latter authors stated that some such units showed localized areas of mechanical sensitivity, the mechanoreceptive characteristics of these fibres were not described in detail. The experiments reported here show that touch units alone, among the mechanoreceptors of skin innervated by myelinated fibres, exhibit modulation of background discharge by variations in skin temperature.

Two aspects of the distribution of receptor types in the present sample of myelinated fibres are surprising. One is the relative paucity of units responding to nociceptive stimulation. As noted in Results (p. 107), the unidentified units in the δ range could possibly have been nociceptive. Even including these the relative number would be small. Another potential deficit in sampling may be that relatively few of the smallest δ fibres might have been isolated and these could have been nociceptive in function. One problem in assessing the adequacy of the sample in the 1–3 μ range is the uncertainty of the factor converting conduction velocity to diameter in this range. There are still other difficulties in evaluating what is a nociceptive stimulus. The mechanical stimuli employed may be so intense as to be capable of initiating impulses in nerve fibres themselves. While the present sample shows nociceptive units confined to the δ diameter range, it might be possible to stimulate directly the fibres of blocked touch units and so erroneously to conclude they were nociceptive. In spite of the reservations expressed above, it seems clear that the bulk of the δ fibres are from hair receptors and that nociceptive units must constitute only a small fraction of the δ group of fibres.

The reservation expressed as to adequacy of sampling of the smallest δ fibres may also be applicable to the apparent lack of fibres concerned solely with thermoreception. Maruhashi *et al.* (1952) reported the isolation of a number of fibres in cat cutaneous nerve with directly measured diameters of 1·5–3 μ which showed discharge to cooling the skin but not to mechanical stimulation. Such fibres might not have been detected in the present study. From the present results the possibility cannot be excluded that myelinated fibres other than those of touch units may convey information concerning skin temperature. In addition to the myelinated fibres, non-myelinated fibres have thermosensitive receptors (Iggo, 1958, 1959; Douglas, Ritchie & Straub, 1959).

The diameter distributions of cutaneous myelinated afferent fibres of different receptor types are of importance in evaluating the central effects of graded afferent volleys in cutaneous nerves. Hair receptor fibres are distributed throughout the α and δ fibre diameter ranges. Hence volleys of increasing size, from those including only a few of the largest to those in which the entire population of myelinated fibres is activated, will involve increasing numbers of hair units. In contrast, once a volley occupies all of the α fibres a further increase in stimulus strength to include δ fibres would be expected to recruit activity in very few additional fibres from touch receptors. The considerable overlap in diameters of fibres from receptors of various types would make it very difficult to relate reflex actions evoked by volleys of graded size to specific receptors.

One factor of importance in interpreting the effects of natural stimulation of the skin is the large overlap of receptive fields of hair units. Movement of hairs in a restricted area of the cat's skin is certain to activate hair receptors of a number of hair units. In contrast, the touch units may show little overlap because of the discreteness of their receptive spots. With regard to the touch receptor, information as to tactile stimulation must often be derived by the central nervous system from an increment in discharge superimposed upon a temperature-dependent background discharge. This background discharge must also be considered in experiments in which cutaneous nerves are left intact, for in such circumstances there is an appreciable input into the spinal cord from this source.

While doubt has been expressed as to the specificity of receptors based on the lack of morphological differentiation seen in nerve endings in certain areas of skin (Sinclair *et al.* 1952), it seems clear from the present results as well as those of previous studies (Zotterman, 1939; Maruhashi *et al.* 1952) that some degree of receptor specialization exists. Thus, cutaneous afferent fibres can be isolated which show responses only to particular kinds of mechanical stimulation. The fact that touch receptor units display a discharge which is dependent on skin temperature as well as showing responses to tactile stimulation (Witt & Hensel, 1959; Hunt & McIntyre, 1960*b*) suggests that the specificity is not as absolute as was generally considered. However, the lack of such temperature responses in hair units indicates a degree of functional differentiation between hair and touch receptors. A reasonable view in the light of available evidence would appear to be that some degree of receptor specificity exists but that possibly in some fibres information relating to more than one type of cutaneous sensation may be transmitted.

Evidence as to cutaneous receptors in cat skin must be interpreted with caution in relation to the problem of sensory modalities in man. It is quite possible that the relative proportions of various receptor types may differ considerably between cat and man. In particular, the greater amount of hair in an animal such as cat might be associated with a greater density of hair receptors. The large amount of overlap in receptive fields of hair units in the cat suggests that localization of a stimulus which activates only this type of receptor would require a central mechanism that could decipher this information from relative frequencies of discharge in a number of fibres. On the other hand, from the standpoint of peripheral organization alone, touch units could signal spatial discrimination in a simpler fashion. In view of the recent evidence that receptors of non-myelinated fibres also signal touch (Douglas & Ritchie, 1957; Iggo, 1958; see also Zotterman, 1939), activity from such receptors must also be considered in evaluating peripheral mechanisms of cutaneous tactile sensibility.

SUMMARY

A study of conduction velocity and discharge pattern of 421 isolated myelinated afferent fibres in the sural nerve of cat indicates the following:

1. Hair receptor fibres were the most numerous, accounting for the bulk of the δ fibres and a large proportion of α fibres. They accounted for the largest fibres in the sural nerve.
2. Receptive fields of hair units have been determined and show a large amount of overlap. Receptive field areas varied widely and there was some tendency for the smaller fibres to have larger receptive fields.
3. Hair receptors were invariably rapidly-adapting and varied in sensitivity to natural stimulation, the smaller fibres tending to have the more sensitive receptors.
4. Touch receptor fibres (Hunt & McIntyre, 1960*b*) were essentially confined to the α diameter band, the largest being less in diameter than the hair receptor fibres of greatest diameter.
5. Units responding to pressure greater than that required to activate touch receptors were distributed widely in diameter. Such units showed slow adaptation. Some appeared to be located in the skin, others subcutaneously.
6. A variety of other receptor types were noted. These included seven which were presumably nociceptive, five responding to brief tap of the skin, two joint units, and eight in which discharge could not be elicited by the stimuli employed.

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