

PROPERTIES OF CUTANEOUS TOUCH RECEPTORS IN CAT

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In their analysis of discharge patterns in cutaneous afferent fibres in cat, Maruhashi, Mizuguchi & Tasaki (1952) noted some fibres which showed discharge to mechanical stimulation of small receptive fields, often with spots of high sensitivity. The receptors adapted rapidly. Recently Witt & Hensel (1959) described responses in cutaneous fibres of cat with receptors sensitive to both mechanical and thermal stimuli. The receptors of such fibres often displayed localized areas of mechanical sensitivity. They also showed many of the characteristics of cold receptors previously described in the tongue (Hensel & Zotterman, 1951*a*), responding particularly to phasic cooling.

In the course of a study of fibre diameter and receptor function in isolated fibres of sural nerve, described in the paper which follows (Hunt & McIntyre, 1960), it was found that a type of receptor could be categorized which possessed features some of which were noted by Maruhashi *et al.* (1952) and by Witt & Hensel (1959). These receptors, which, together with their fibres, have been called touch units, have highly localized regions of mechanical sensitivity and many show responses to thermal as well as tactile stimuli. This paper is concerned with a detailed description of touch receptors in the skin of cat innervated by the sural nerve. The data are derived from study of 114 isolated touch units.

METHODS

Adult cats anaesthetized with pentobarbital sodium (Nembutal; Abbott Laboratories) were used. After laminectomy in the lumbosacral region, the exposed spinal cord and roots were covered with paraffin oil equilibrated with 95% O₂ and 5% CO₂. Dorsal and ventral roots from L6 to S2 were divided near the cord. By an incision over the popliteal fossa the sural nerve was exposed and placed intact on stimulating electrodes in a pool of paraffin oil. Other nerves in the hind limb and hip were cut. Single afferent fibres were isolated in filaments of dorsal root.

Skin temperature was measured by a small bead thermistor introduced subcutaneously at some distance from the receptor under study and then passed under the skin until it rested a few millimetres from the receptor, pointing outwards against the skin. In this position it responded within a few seconds to changes in skin temperature produced by

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cooling with ice or ether or by warming by infra-red radiation. While the thermistor temperature cannot be taken as indicating directly the temperature of the receptor, it served as a reasonable approximation to the latter. The thermistor was connected to a bridge circuit, the output of which could be read on a calibrated meter or displayed on one beam of the cathode-ray oscilloscope. A switching arrangement permitted resistance equal to the thermistor resistance at known temperatures to be connected to the bridge in place of the thermistor, thus providing reference calibration during the course of the experiment.

Mechanical stimulation of the skin was produced by pressure against the skin by a blunt stylus attached to the piston of a syringe. Air pressure was applied to the syringe through a variable-demand valve regulator, the duration of the constant pressure being controlled by a transistor-regulated relay.

RESULTS

Responses to mechanical stimuli

Touch receptors could usually be readily distinguished from other types of receptors in the skin that were sensitive to mechanical stimulation. The latter, which are more fully described in the paper which follows, include hair receptors, pressure receptors, and probable nociceptive units. Hair receptors responded to movement of hairs without otherwise deforming the skin and usually displacement of any of a considerable number of hairs sufficed to evoke discharge. Touch receptors, on the other hand, usually discharged only when the skin was actually touched and careful mapping indicated that the receptive area was limited to one or more very discrete spots. Further, hair receptors were invariably rapidly-adapting, while touch receptors were generally slowly-adapting. Occasionally very sensitive touch receptors discharged to movement of hairs, but they could be distinguished from hair receptors by other aspects of their behaviour. Pressure receptors were of much higher threshold and had no sharply localized receptive spots.

Touching the skin with a large blunt object evoked discharge in fibres or touch receptors which was usually sustained for the duration of the stimulus. In response to this type of stimulus the discharge was of moderate frequency (up to about 100/sec) and was graded by the degree of pressure employed. Generally only light touch was required to initiate discharge. Often traction on the skin at some distance from the receptive area would evoke a low-frequency discharge from touch receptors, but they were always much less responsive to such remote stimulation than highly sensitive hair receptors (Hunt & McIntyre, 1960).

More detailed examination of the mechanical responses of touch receptors was carried out with a fine probe such as a cat's vibrissa. To such a mechanical stimulus the receptive region was found to be limited to very discrete spots, numbering one to five in a given touch unit. In units showing multiple receptive spots these were usually arranged in a cluster, the individual spots being 1-5 mm apart. Some of the arrangements

observed are shown in Fig. 1. The number of receptive spots per unit observed in 77 touch fibres was as follows: 1 spot—30 fibres, 2 spots—34 fibres, 3 spots—8 fibres, 4 spots—2 fibres and 5 spots—3 fibres. Light touch to regions between sensitive spots usually caused no discharge, although sufficient pressure to such regions could do so, presumably by the deformation transmitted to a receptive spot. Only a few units were found in which the spots were not highly localized. In these, light touch to an area of some 30–60 mm² was capable of producing response, but even in such units several spots of heightened sensitivity were noted.

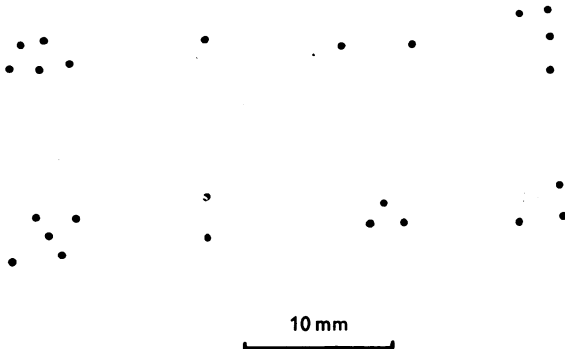


Fig. 1. Examples of the distribution of receptive spots taken from eight touch units.

The discharge evoked by mechanical stimulation of a discrete receptive spot could be graded in frequency by intensity of stimulation but could be of much higher frequency than that evoked by more diffuse pressure. Indeed, touch of a discrete receptive spot by localized pressure of moderate intensity characteristically produced a high-frequency train of impulses (up to about 400/sec) which tended to fall in frequency with maintained stimulation, although discharge usually continued until stimulation ceased (Figs. 2, 7). In contrast, the discharge to more diffuse pressure, while showing a lower initial frequency, tended to fall off less in frequency with maintained stimulation.

Repeated probing of a receptive spot sometimes led to unresponsiveness, although if a fibre had multiple receptive spots the remaining spots continued to respond to mechanical stimuli. The onset of block was associated with a diminution in number and frequency of impulses evoked by a tactile stimulus of a given duration and intensity to the receptive spot (Fig. 2). Together with this reduction in response there occurred an increase in rate of adaptation, so that impulses were evoked only at the onset of the tactile stimulus. Finally, there was absence of discharge to the mechanical stimulus even if this were made several times more intense than that

which originally evoked a high-frequency discharge. Following a period of rest of 5–15 min some blocked receptive spots recovered their responsiveness. Heavy pressure or pinching the skin, as was sometimes employed in seeking responses of possible nociceptive units, seemed to predispose toward block of touch-receptive spots.

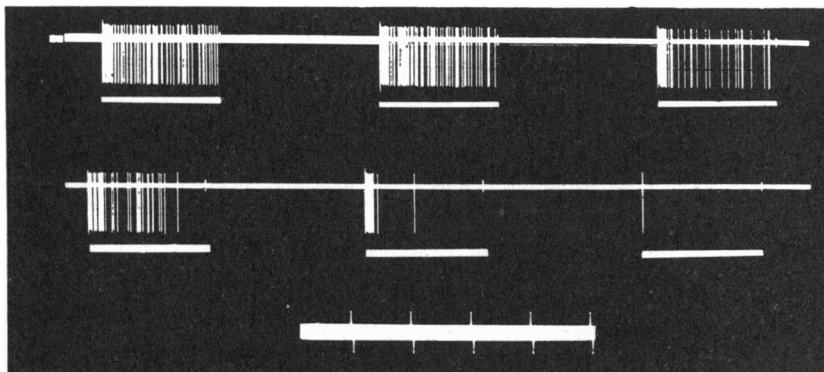


Fig. 2. Responses elicited from a touch unit by successive stimuli to a receptive spot, showing the development of block. Thermistor temperature 35°C . Horizontal bars indicate approximate duration of mechanical stimulus. Time marker, 1 sec.

Responses to temperature

A large number of the touch units examined displayed background discharge at the usual resting levels of skin temperature ($32\text{--}35^{\circ}\text{C}$). At a constant temperature the discharge was often aperiodic, particularly when the average frequency was low. Changing the skin temperature to a new steady level usually altered the average discharge frequency, as is shown by the example in Fig. 3. This fibre showed discharge to tactile stimulation of discrete receptive spots, was slowly-adapting and displayed the usual characteristics of touch units. The background discharge in the absence of tactile stimulation is shown at three fairly constant levels of skin temperature (Fig. 3). This discharge had its highest average frequency at a thermistor temperature of 30°C ; when the temperature was raised to 34.5 or lowered to 25.6°C the average frequency fell. When warmed or cooled sufficiently the discharge ceased. Figure 4 illustrates four examples of the relation between average discharge frequency and static temperature level as recorded by the thermistor. Units varied considerably as to the temperature at which peak frequency of discharge occurred, as well as to the range of temperature associated with discharge. In general the temperature range associated with discharge was approximately $22\text{--}42^{\circ}\text{C}$, although in many units the range was more narrow. The curves of Fig. 4

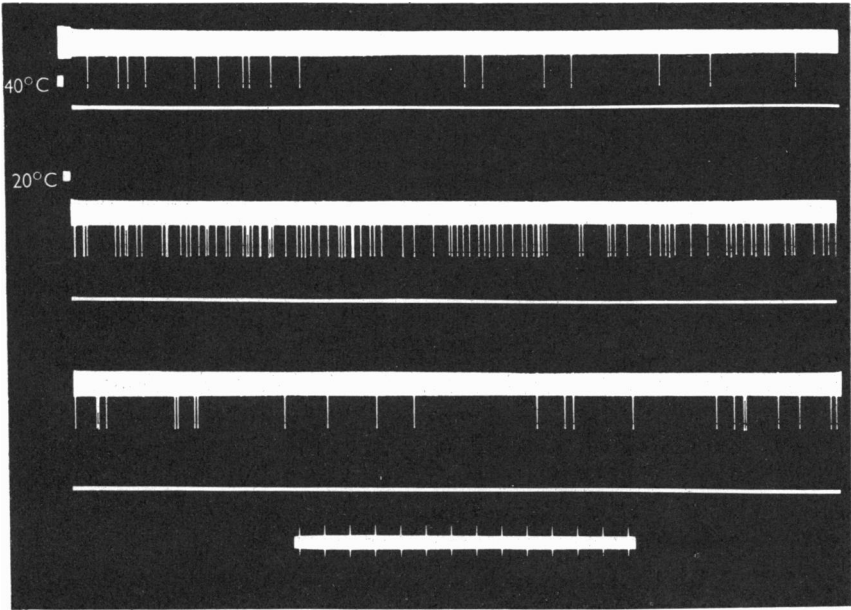


Fig. 3. Base-line discharge in a touch unit at three different skin temperatures. Thermistor temperature at onset of upper record 34.5, middle record 30, lower record 25.6° C. Time marker, 1 sec.

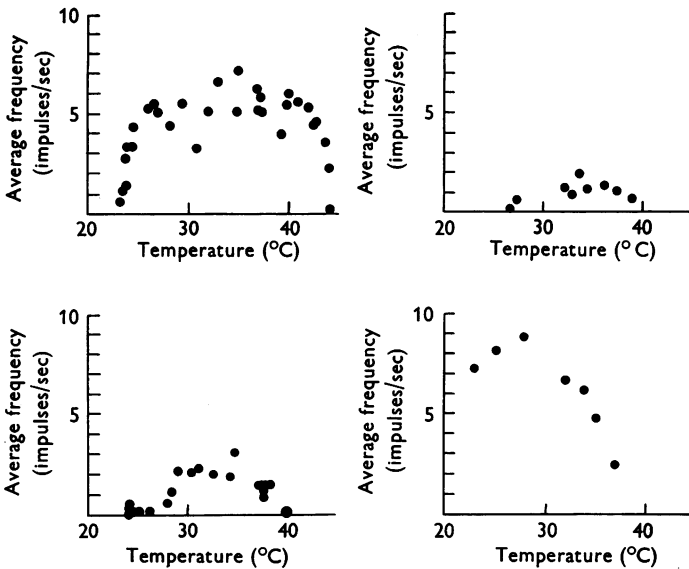


Fig. 4. Relation between base-line discharge frequency and skin temperature in four touch units. Ordinate, average frequency (impulses/sec). Abscissa—thermistor temperature.

are selected from units showing the most reproducible frequency changes at various temperature levels. In this selected group considerable variability of mean frequency is evident at the various temperature levels. In many other units such variation was more evident and it was difficult to obtain reproducible curves relating average frequency to temperature (cf. Witt & Hensel, 1959).

In addition to units which showed discharge with a frequency maximum in the 28–38° C range, others were found which showed no discharge until the temperature as recorded reached 40–42° C, whereupon repetitive discharge began and as the temperature was further raised the discharge frequency increased until it abruptly ceased. The upper limit of temperature studied was limited to about 45° C, in order to avoid tissue damage. On removal of the heat source, rapid cooling from the temperature maximum was generally accompanied by a discharge at considerably higher

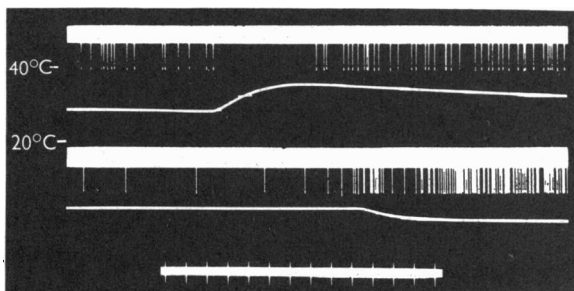


Fig. 5. Effect of warming and cooling on base-line discharge of a touch unit. Upper record, application of warm water raised temperature from 29 to 36° C. Lower record, application of cold water lowered temperature from 36 to 32.5° C. Time marker, 1 sec.

frequency than during warming. Indeed, a number of units were observed which showed no discharge to warming and discharged only after the heat source was removed.

An example of a unit which exhibited responses similar to cold receptor units (Hensel & Zotterman, 1951*a*; Witt & Hensel, 1959) is shown in Fig. 5. Allowing cold water to flow over the receptive area caused a marked increase in discharge. In contrast, similar application of warm water produced an inhibition of the base-line discharge during the period of phasic warming. There seemed to be no apparent mechanical stimulation associated with the latter. Direction and rate of temperature change are important determinants of responses of touch units to thermal stimuli. The most effective stimulus was usually rapid cooling and some touch units responded only during sudden phasic lowering of temperature.

Not all units behaved in a manner analogous to the responses of cold

receptors. The unit of Fig. 6 is an example of such an exception. As temperature was raised no discharge occurred until the thermistor temperature was above 41.2°C . With further temperature increase the discharge continued until it stopped abruptly at about 43.5°C . Removal of the infra-red heat source was followed by a fall in temperature at a rate equivalent to that which occurred during warming, but no discharge was evoked. At least over the temperature range shown, this unit was more responsive to warming than cooling. However, rapid cooling was quite effective in evoking discharge, as can be seen in the lower record of Fig. 6, which illustrates the response to application of ether to the skin.

The findings described above suggest that many touch receptors have some properties of cold receptors. Witt & Hensel (1959) have previously noted receptors of cat skin which behaved in several respects like cold receptors and which also responded to mechanical stimuli (see Discussion).

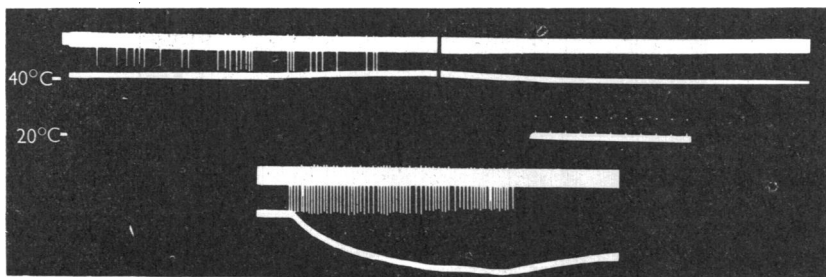


Fig. 6. Effect of slow warming and cooling and of rapid cooling on a touch unit. Upper record shows gradual warming from 41.2 to 43.6°C and subsequent cooling when infra-red heat was removed, the temperature fall being from 43.6 to 41°C . Lower record shows discharge evoked by rapid cooling from 40.6 to 20°C .

Effects of temperature on responses to tactile stimulation

With a constant-pressure stimulus which could be delivered for a pre-determined duration (see Methods), the responses of touch units to mechanical stimulation were studied at varying skin temperatures. It was found that responses to constant tactile stimuli varied as a function of temperature. At the extremes of the temperature range studied touch receptors often completely failed to respond to the mechanical stimulus. This failure of response commonly occurred below 22 and above 42°C . In the range between these extremes the discharge to a constant mechanical stimulus was significantly altered by skin temperature. The unit of Fig. 7 displays some of the effects of cooling. The uppermost record (A) shows a base-line discharge and the increase in discharge which accompanied cooling. Following this, two applications of a constant-pressure stimulus (2 sec duration) to a receptive spot caused a sustained discharge during

the period of stimulation. The second record (*B*) shows a period of further cooling which was accompanied by discharge and the responses to subsequent mechanical stimulation. Although the temperature had fallen from about 32–24·7° C, the responses to mechanical stimuli were approximately similar. The third (*C*) and fourth (*D*) records show the effects of still further cooling: during the cooling discharge again occurred. At a temperature of 20° C two applications of the pressure stimulus of 2 sec duration resulted only in 3 or 4 impulses at the onset of the stimulus. A similar effect occurred at the upper temperature extreme studied (about 43° C.)

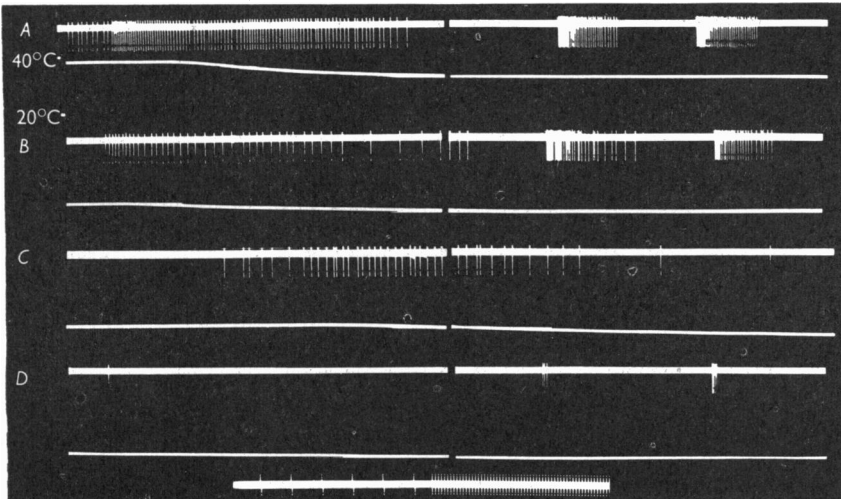


Fig. 7. Effect of cooling on responses of a touch receptor to mechanical stimulation. Upper record (*A*) shows cooling from initial temperature of 38·2 to 32·4° C; at right responses to two pressure pulses (2 sec duration) applied to receptive spot (at average temperature of 31·8° C). Second record (*B*) shows further cooling from 28·8 to 24·7° C; at right responses to mechanical stimulation at temperature 24·7° C. Third (*C*) and fourth (*D*) records show still further cooling from 24·7 to 20° C; at right of lowest record are responses to two pressure pulses at temperature 20° C. Note brief responses although duration of pulse was similar to that in right upper record. Time marker, 1 sec and 0·1 sec.

If the intensity of mechanical stimulus in Fig. 7 had been constant for its duration, the brief discharge at 20° C would indicate that the receptor adapted more rapidly at this temperature than at 31·8 and 24·7° C. Another possible explanation of these results would be that the mechanical deformation was greater at the onset of the pressure pulse and that the change in discharge following cooling resulted from an increased threshold of the receptor. However, strong pressure by a finger to the receptive field, which at normal temperatures evoked sustained discharge, elicited only

a brief discharge on application when the skin was cooled or warmed. These findings indicate that although touch receptors generally adapt slowly over a considerable temperature range, they can adapt rapidly when the skin is sufficiently warmed or cooled.

Certain effects of tactile stimulation on the base-line discharge of touch units may also be seen in Fig. 8. The base-line discharge was interrupted following the application of a mechanical stimulus, the response to the pressure pulse being followed by a period of silence. In some circumstances the base-line discharge reappeared after a short interval, but repetition of the response to mechanical stimulation led to a longer silence of the base-line discharge. A similar period of cessation of background discharge was seen after high frequency tetanic stimulation of the sural nerve.

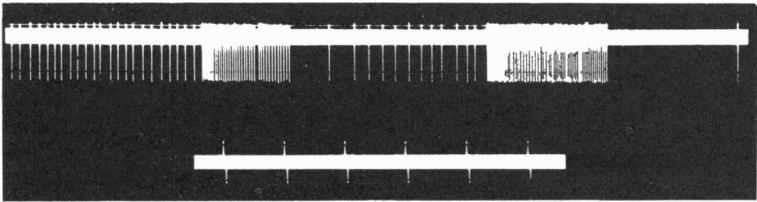


Fig. 8. Response of touch unit showing base-line discharge and responses to two pressure pulses. Note brief pause in base-line discharge after first mechanical stimulus and the more prolonged pause after the second. Thermistor temperature 35.6°C . Time marker, 1 and 0.1 sec.

DISCUSSION

Touch receptors have been shown to signal tactile stimulation of the skin by a discharge which is graded in frequency according to the degree of mechanical deformation. In general this discharge is slowly-adapting and can provide sensory information concerning maintained tactile stimulation. This is in contrast to hair receptors which signal principally rate of change of hair movement. Touch receptors of cat skin have discrete receptive spots which may bear similarity to the well known touch spots of human skin. Many touch units in the cat have multiple receptive spots, often located several millimetres apart. The morphology of such receptive spots in the skin of cat is not yet known. However, the discreteness of the touch receptive spots suggests that a given point on the skin could possibly be subserved by only one touch receptor fibre.

Of considerable interest is the fact that many touch units show discharge not only in response to mechanical stimulation but also to thermal stimuli. Although the responses to tactile stimuli are fairly consistent among touch units, the responses to thermal stimuli vary considerably among different units and even in a given unit may show considerable variability.

The majority of the touch units show considerable aperiodicity of discharge at a given skin temperature. Many show a more consistent behaviour to phasic changes than to static levels of skin temperature. As noted by Witt & Hensel (1959) the majority of the thermosensitive touch units have some of the properties of cold receptors as described in the lingual nerve (Hensel & Zotterman, 1951*a*). However, the highly reproducible responses to tactile stimuli, in contrast to the rather variable responses to thermal stimuli, suggest that touch units should be considered primarily as mechanoreceptors with a possible secondary function as thermoreceptors. Other examples of receptors responsive to both mechanical and thermal stimulation are known. Thus the pit receptors of *Crotalidae* are responsive to both infra-red radiation and to mechanical stimuli (Bullock & Diecke, 1956). Also, certain receptors of the tongue which are responsive to pressure also show discharge to rapid cooling (Hensel & Zotterman, 1951*b*).

The mechanism by which touch receptors are sensitive to both mechanical and thermal stimuli is not known. However, such dual sensitivity does occur and it seems clear that receptor specificity is less strict than has been generally assumed (cf. Sinclair, Weddell & Zander, 1952). Nevertheless some degree of specificity is indicated by the fact that hair receptors generally fail to respond to changes in skin temperature whereas most touch receptors do (Hunt & McIntyre, 1960).

It is possible that sensory information relating to both touch and temperature may be conveyed by the same fibres. At the present time the means whereby these two types of information might be decoded by the central nervous system can only be surmised. One factor that could be of importance is the fact that the frequencies of discharge associated with rather slow changes in skin temperature are generally considerably lower than those resulting from tactile stimulation. It is conceivable that collaterals of touch unit fibres could establish synaptic connexions with two types of second-order neurones. In one type of relay characteristics of synaptic transmission could limit response of the second-order neurone to the lower range of frequencies that are generally involved in responses of touch units to thermal stimuli. The other type of relay could transmit the higher frequencies generally associated with responses to mechanical stimuli and would be responsive predominantly to phasic changes in discharge. Such a scheme would not provide for complete differentiation of the two types of information.

At the present time the possibility that some small myelinated fibres convey temperature information exclusively cannot be excluded (see Maruhashi *et al.* 1952; Hunt & McIntyre, 1960). Also, the role of non-myelinated fibres in signalling temperature (Douglas, Ritchie & Straub, 1959; Iggo, 1959) must be considered in interpreting cutaneous temperature sensibility.

SUMMARY

By recording from single afferent fibres from the sural nerve of cat, the following characteristics of cutaneous touch receptors have been found:

1. Touch units display 1-5 discrete receptive spots and show a slowly-adapting discharge to mechanical displacement of such spots. Touch receptive spots may become blocked by repeated mechanical stimulation.
2. Many touch units show a base-line discharge, in the absence of mechanical stimulation, which is dependent in average frequency on skin temperature.
3. The responses of touch units to mechanical stimuli can be influenced by sufficient warming or cooling of the skin. In these circumstances the receptor becomes rapidly-adapting and fewer discharges are evoked by a constant mechanical stimulus.
4. The relation of these findings to the problem of specificity of receptors to thermal and mechanical stimuli is considered.

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