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A QUANTITATIVE STUDY OF SENSITIVE CUTANEOUS THERMORECEPTORS WITH C AFFERENT FIBRES

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It has been demonstrated that heating or cooling the cat's skin can elicit a discharge of impulses in slowly-conducting (C) afferent fibres (Iggo, 1958*b*, 1959*a*, *b*; Douglas, Ritchie & Straub, 1959; Douglas & Ritchie, 1959). However, it was not clear whether the C group contained fibres from 'specific' thermoreceptors comparable in sensitivity with those in the cat's tongue (Hensel & Zotterman, 1951*a*; Dodt & Zotterman, 1952). Most of the C fibre thermoreceptors hitherto found responded only to rather extreme heating or cooling (Iggo, 1959*a*, *b*) and therefore were possibly concerned with pain. They were relatively insensitive to mechanical stimulation. There are also numerous C fibres which respond both to mild mechanical stimulation and to sudden cooling of the skin (Douglas *et al.* 1959; Iggo, 1959*a*). They have been classified as mechanoreceptors by Iggo (1960).

In the present investigation sensitive specific cold and warm receptors with afferent C fibres have been found and their behaviour has been studied quantitatively. The opportunity has also been taken to examine quantitatively the responses of C heat receptors (Iggo, 1959*b*) and of a few C mechanoreceptors to thermal stimulation. A preliminary account of these results has been published (Hensel, Iggo & Witt, 1959).

METHODS

The cats used were anaesthetized with chloralose (60 mg/kg intramuscular) and urethane (250 mg/kg intramuscular). After depilation the leg was fixed by drill pins inserted through each end of the tibia. The skin over the saphenous nerve was incised, the nerve was ligated proximally and dissected free from connective tissue. The cut edges of the skin were tied to a metal ring and the trough formed was filled with liquid paraffin B.P. Fine strands of the nerve were dissected on a black Perspex plate and laid on silver electrodes. A pair of stimulating electrodes was placed under the nerve about 3 cm distal to the recording electrodes and an earthed plate was placed between the two pairs of electrodes. The amplified impulses in the fine nerve strand were recorded by means of two separate systems, each consisting of a cathode-ray oscilloscope and a recording camera. The first system recorded the impulses in the usual way with a stationary cathode-ray beam and moving bromide paper (Fig. 1*A*). The expanded sweep of the second oscilloscope was triggered by the square-wave pulse

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generator used for electrical stimulation of the nerve, and allowed an exact measurement of conduction velocity. Photographic records of the moving beam were taken on slowly moving bromide paper (Fig. 1*B*). In order to test mechanical sensitivity, the skin was stroked or pressed with a wooden pin or touched with cotton wool. Calibrated hairs of various stiffness were used for more quantitative stimulation.

Quantitative thermal stimulation was accomplished by a water-circulated thermode of 2 cm diam., which was placed on the receptive field of the afferent fibre. The water was supplied by 4 ultra-thermostats set at various constant temperatures (± 0·02° C). By means of a special switch each thermostat could be connected with the thermode, and constant temperatures or rapid thermal changes could thus be applied to the skin. The thermode allowed thermal changes to be imposed without any alteration in the mechanical stimulus. A fine thermocouple was placed on the receptive field and the temperature was recorded synchronously with the deflexions of the first oscilloscope with a special recording camera (Hensel, 1953). In some experiments thermal radiation was also used for heating the skin.

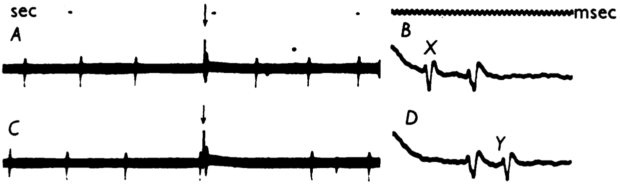

Fig. 1. The identification of the active cold fibre in a multi-fibre strand of the saphenous nerve.

A, Spontaneous discharge of a single C cold fibre and effect of electrical stimulation of the saphenous nerve (fibre No. 1). Arrows mark stimulus artifacts in *A* and *C*. *B*, Record with expanded sweep corresponding to that part of *A* marked by arrow. The first impulse (marked *X*) is the spontaneous cold fibre discharge, the second is from another C fibre excited by electrical stimulation. *C*, The same discharge as in *A*, but with stronger electrical stimulation. There is now a gap in the series of impulses. *D*, Expanded sweep. Both impulses were caused by electrical stimulation, the first is identical with the second in the upper record, the second is in the cold fibre. The conduction velocity was 1·1 m/sec. (See text for further explanation.)

RESULTS

Identification of single C fibres

This was based on the 'collision' technique (Iggo, 1958*a*), which makes it possible to measure conduction velocity in the one active fibre of a strand containing other fibres capable of conducting but not active. Figure 1 shows a record, taken with two oscilloscopes, of the impulses in a thin strand of the saphenous nerve. The steady discharge of a single cold fibre (fibre No. 1) in Fig. 1*A* and *C* was caused by a constant skin temperature of 25° C. During the natural discharge two electric shocks were sent into the saphenous nerve. The upper pair of tracings (Fig. 1*A* and *B*) shows a failure of the electrically produced impulse to interfere with the train of impulses from the receptor; the expanded sweep, Fig. 1*B*, shows one of the ascending impulses first (marked *X* in the figure) followed by an impulse in a different fibre caused by the shock to the nerve.

The lower pair of tracings shows in Fig. 1*C* a gap in the train of impulses. This appears immediately after the shock artifact and was caused by collision of the electrically produced antidromic impulse, corresponding to *Y*, with the natural impulse from the receptor. The expanded sweep, Fig. 1*D*, shows two impulses; the first is identical with the second impulse in the upper record and the second, *Y*, is an impulse in the cold fibre caused by the shock to the saphenous nerve. The similarity of this impulse to the first impulse in the upper tracing is further evidence that the second impulse in the lower tracing is in the cold fibre. The time between electrical stimulus and recorded impulse was 28 msec and the conduction distance was 31 mm, so that the conduction velocity turned out to be 1·1 m/sec.

In some experiments the slowly conducting fibres were identified only by the shape and duration of the C impulse and the typical sound in the loudspeaker.

Receptors excited by cooling the skin

Several C fibres responded to moderate cooling of the skin with an increase in frequency, and to heating with a decrease or complete inhibition, of the discharge. Within a certain range of constant temperatures a steady discharge was observed. These cold fibres were not excited by the mechanical stimuli used. In some examples the size of the receptive field was assessed by stimulation with small thermodes. The receptive fields were not larger than a few square millimetres.

The impulses in a single C fibre when the skin was cooled are shown in Fig. 2. A steady discharge can be seen at the constant initial temperatures (Fig. 2*C*, *D*, *E*). During cooling the impulse frequency rose rapidly, reached a maximum within the first second and then declined gradually. In the records *B–E* a slight transient temperature rise of about 1° C just before cooling led to a complete inhibition of the steady discharge.

The discharge frequency of another single C fibre (fibre No. 3) on cooling and rewarming the skin is shown in Fig. 3. The initial temperatures between 31 and 33·5° C corresponded to an indifferent temperature sensation in man. Even very slight cooling from 33 to 32·3° C increased the frequency from 1 to 22 impulses/sec, whereas warming by about a tenth of a degree caused the discharge to stop immediately. The 'dynamic' sensitivity of this cold receptor was 30 impulses/sec. ° C. This means that sudden cooling of 1° C would raise the impulse frequency by 30 impulses/sec. At indifferent temperatures a discharge was elicited by cooling of only 0·2° C. This was the final value of the external temperature change; the actual cooling when the first impulse was recorded was smaller than 0·1° C.

At constant temperatures the cold receptors exhibited a steady discharge, the frequency being a function of absolute temperature. The steady

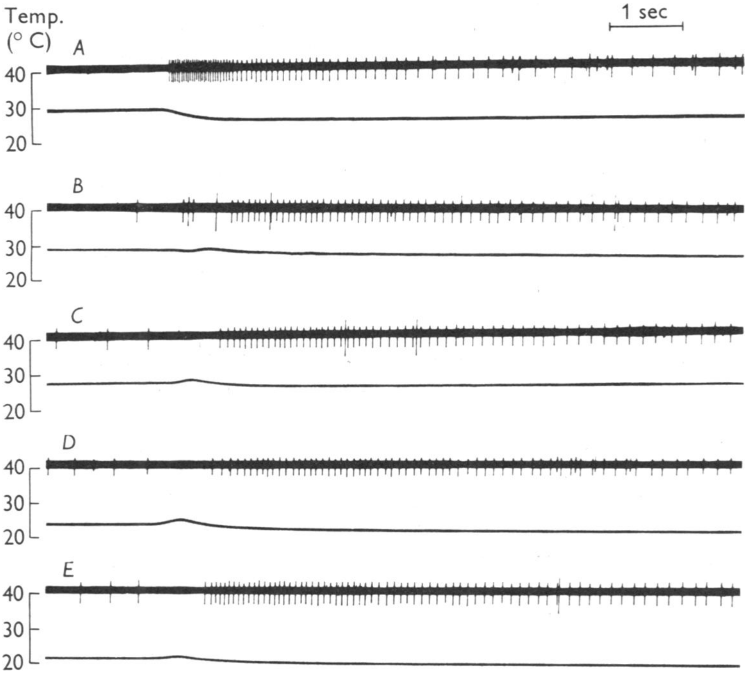

Fig. 2. Afferent impulses of a single C fibre and skin temperature when cooling the skin (fibre No. 1). Conduction velocity 1·1 m/sec. *A*, Cooling from 29 to 25·5° C; *B*, 29·3–28° C; *C*, 28·0–26·5° C; *D*, 24·5–22·5° C; *E*, 22–20·5° C.

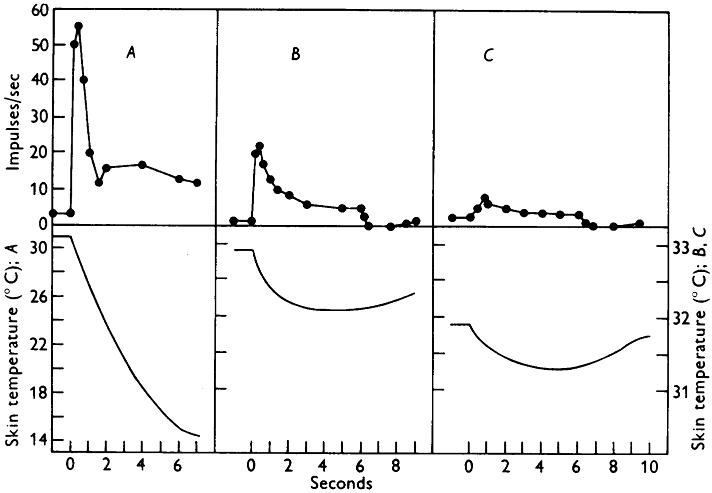

Fig. 3. Impulse frequency of a single cold fibre when cooling and warming the skin (fibre No. 3). The conduction velocity of the fibre was 1·5 m/sec. The left-hand temperature scale refers to *A*, and the right-hand scale to *B* and *C*.

discharge of the cold fibre No. 3 at constant temperatures between 28·8 and 14·2° C is shown in Fig. 4, and the steady discharge frequency is plotted against temperature in Fig. 5. Curve 1 was obtained by lowering the constant temperature stepwise from 37 to 14° C, keeping the temperature constant for 3 min after each step. Curve 2 was the result of the reverse procedure, starting at the lowest temperature. As the two curves are not identical it is probable that the adaptation time of 3 min was not quite sufficient to reach the final value of the steady discharge. The maximum frequency was reached at temperatures of 16·5 and 19·5° C, respectively. The width of the maximum varies considerably for different fibres (Fig. 6). Whereas fibre No. 3 has a well defined maximum, the cold fibre No. 1 exhibits practically the same impulse frequency over a temperature range of more than 10° C.

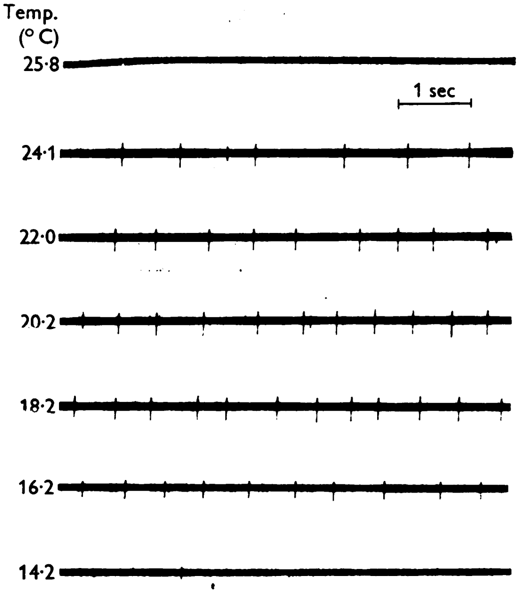

Fig. 4. Steady discharge of impulses in the single *C* fibre shown in Fig. 3 (fibre No. 3) at various constant temperatures of the skin.

Receptors excited by heating the skin

C fibres have been found which could be excited by an external warming of only 0·3° C. This was the final value of temperature rise, the actual value at the first impulse being less than 0·1° C (Fig. 7*A*). Cooling by the same amount (Fig. 7*B*) inhibited the discharge completely. Most of these warm fibres were not excited by the mechanical stimuli used; one fibre had a mechanical threshold of 2 g when touching the receptive field with a von Frey hair. There was no reaction of the warm fibres on sudden cooling from 30–33° C to low temperatures (10° C).

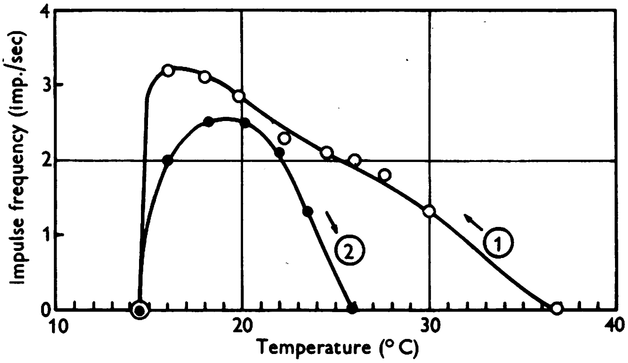

Fig. 5. Steady discharge frequency of a single C fibre (fibre No. 3), excited by cooling, at various constant temperatures. 1, Starting from high temperatures; 2, starting from low temperatures.

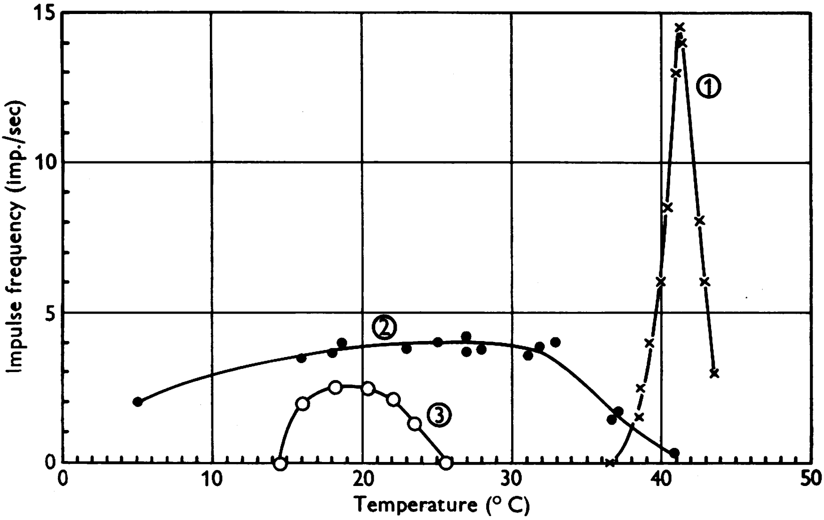

Fig. 6. Steady discharge frequency of three different single C fibres as a function of constant skin temperature. 1, Fibre excited by warming, fibre No. 8; 2, fibre excited by cooling, fibre No. 1; 3, fibre excited by cooling, fibre No. 3.

The frequency of discharge in a single warm fibre during various temperature changes, starting from indifferent initial temperatures between 31 and 33·5° C, is shown in Fig. 8. At a constant temperature of 40° C (last curve) a steady discharge is seen. Slight cooling of a few tenths of a degree stopped the discharge; slight warming by the same amount made the discharge reappear. The dynamic sensitivity of this warm receptor was +33 impulses/sec. ° C, which is of the same order as that of the C cold receptor. The maximum frequency of discharge and the time course of adaptation was also similar to that of the cold fibres (cf. Fig. 3).

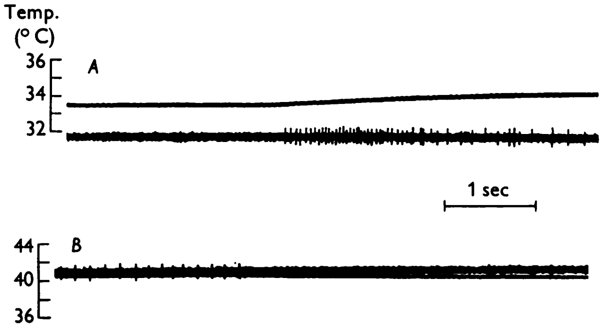

Fig. 7. Afferent impulses recorded in a single warm fibre (fibre No. 7) and the skin temperature, during slight warming and cooling of the skin.

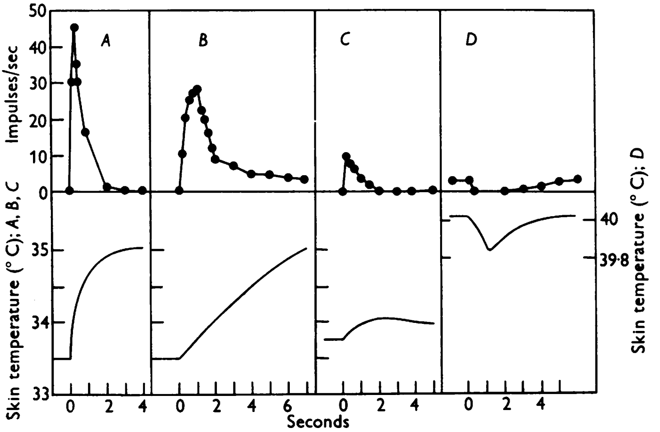

Fig. 8. Frequency of the discharge of impulses in a single C fibre (fibre No. 7), from a warm receptor, during cutaneous temperature changes. The left-hand temperature scale applies to *A*, *B* and *C* and the right-hand scale to *D*.

The warm fibre with the highest sensitivity exhibited a steady discharge at constant temperatures between 38·5 and 43° C. It fired a regular sequence of impulses, and showed a very sharp maximum at 41·2° C (Fig. 6, curve 1).

A number of non-myelinated fibres were found which could only be excited by heating the skin from indifferent temperatures (30–33° C) to more than 37° C. These probably correspond to the C heat receptors described by Iggo (1959*b*). In some cases, only a slow phasic discharge occurred during the temperature rise; other fibres also fired at high constant temperatures, some with periodical bursts of impulses. One fibre with a high maximum frequency of 80 impulses/sec was silent at temperatures above 58° C; the inhibition was reversible. No other fibres were tested at these high cutaneous temperatures.

In order to prevent damage of the skin by the high temperatures, the thermal stimuli were maintained for not longer than about 30 sec. Under these conditions the threshold temperatures for a steady discharge of at least 30 sec duration varied from 38·5 to above 48° C in various fibres. Since the constant temperatures were maintained only for a short period of time, the values obtained may possibly not represent the true thresholds for the steady discharge.

Two of these less sensitive warm fibres were excited by the mechanical stimuli used. One fibre reacted to pressing the finger against the skin with a maximum discharge of 35 impulses/sec; on heating, the same fibre reached a maximum frequency of 44 impulses/sec.

Some features of 18 non-myelinated cold and heat fibres are summarized in Table 1. The temperature ranges for the steady discharge of the warm fibres 8 to 18 may not be correct, because the adaptation time was only 30 sec.

Receptors excited by mechanical stimulation

Cutaneous mechanoreceptors with afferent C fibres are more easily found than thermoreceptors, since the number of mechanosensitive nerve endings seems to exceed that of thermoreceptors. The sensitivity of these C mechanoreceptors varies within a wide range (Iggo, 1960). The threshold of the most sensitive units (hair 20 mg) was similar to that of the most sensitive A mechanoreceptors in the cat's skin (Witt & Hensel, 1959). A typical feature of the C mechanoreceptors was a marked after-discharge, as described first by Zotterman (1939). This phenomenon was never observed in the A fibres.

In the present investigation impulses of mechanosensitive C fibres have not been studied systematically. We have confirmed previous findings (Iggo, 1959*a*, *b*, 1960), that C mechanoreceptors were excited by cooling the skin. In our occasional observations the maximum frequencies of three different C fibres amounted to only 17, 11 and 5 impulses/sec on sudden severe cooling from 32 to 8° C, whereas mechanical stimulation caused a discharge frequency as high as 100 impulses/sec. The lowest threshold for a phasic discharge of a C mechanoreceptor was cooling by 2° C. The discharge of two C fibres is shown in Fig. 9; one was excited by heating the skin (a warm fibre) and the other (spikes downward) reacting to light mechanical vibration of the thermode due to turbulence caused by switching on the hot and cold water supply. The latter fibre was excited briefly during cooling of the skin, whereas the warm fibre was not.

TABLE 1. Responses of single thermosensitive C fibres

Fibre no.	Conduction velocity (m/sec)	Response to thermal stimulation†		Max. frequency (imp./sec)	Threshold temp. change (° C) (initial temp. ca. 32° C)	Temp. for steady discharge (° C)		Response to mechanical stimulation‡
		Cooling	Warming			Lowest	Highest	
1	1·1	+	–	38	< –1 (*x*)	14	26 (> 30)	0
2	*C**	+	–	45	< –4	.	< 28	0
3	1·5	+	–	55	–0·2	< 6·5	41	0
4	.	+	–	.	.	.	*ca.* 32	0
5	0·6	+	–	40	.	5	32	0
6	*C*	–	+	55	+0·3	> 36	.	Threshold 2 g
7	.	–	+	65	+0·3	38·5	43	0
8	.	.	+	.	39 (*xx*)	> 48	.	0
9	.	.	+	.	42	45	.	0
10	*C*	–	+	80§	41	41	57	0
11	.	.	+	60	.	*ca.* 40	.	0
12	.	.	+	44	44	46	.	Firm pressure
13	.	.	+	.	41	.	.	0
14	.	–	+	50§	37	38·5	.	0
15	0·85	.	+	.	43	.	.	High threshold
16	.	.	+	.	< 47	> 48	.	0
17	*C*	–	+	38§	38	42	.	0
18	.	–	+	.	38·5	.	.	0

(*x*) The final values of the external temperature change are given.

(*xx*) For fibres 8–18 the absolute values of the final temperature are given.

* *C* indicates that the conduction velocity was less than 2 m/sec, but was not measured accurately.

† +, Excitation; –, inhibition. The effect depended on the initial temperature; when this was in the range where the fibre was excited then the activity was inhibited, otherwise there was no response. ‡ 0 = no response. § Bursts.

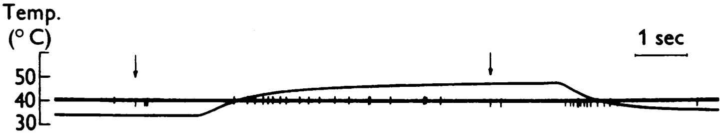

Fig. 9. Afferent impulses of two C fibres and the skin temperature when heating and cooling the skin. Arrows mark the slight mechanical vibration of the thermode caused by changing the water flow. There are two active fibres in this strand. The diphasic impulses are from a unit excited by heating the skin. This unit was not excited by the light mechanical stimuli which excited the other fibre. This latter fibre was excited by suddenly cooling the skin.

DISCUSSION

The old and controversial problem of 'specificity' of cutaneous sensory mechanisms has been carried to a new stage by recent electrophysiological and histological investigations. It should be kept in mind that the concept of 'specific' sensory fibres or receptors has two quite different aspects: (1) the specific *sensation* aroused by stimulation of a receptor ('specific energy' in the sense of Müller (1844) and (2) the response of a *receptor* to a specific stimulus. Of course, only the second problem can be adequately solved by animal experiments, and even then it remains uncertain whether the results can be properly applied to man. Since certain cutaneous and other receptors in the cat respond to both mechanical and thermal stimulation (Hensel & Zotterman, 1951*b*; Hensel, 1952; Witt & Hensel, 1959; Iggo, 1959*a*, *b*, 1960; Douglas & Ritchie, 1959; Lele & Weddell, 1959), the classification of cutaneous receptors as 'mechanoreceptors' or 'thermoreceptors' may seem to be arbitrary. However, *quantitative* measurements of the sensitivity of some individual receptors to both kinds of stimuli have revealed systematic differences. *Qualitative* experiments alone are not sufficient and may sometimes be misleading. Until the properties of an individual unit have been examined quantitatively it would perhaps be better not to use the terms 'specific' and 'non-specific' and it would certainly be premature to argue about peripheral 'specificity'. At the least it is necessary to define exactly the properties of the 'specific' receptor being dealt with. For the cold (warm) receptors the following definition is proposed with respect to the discharge in the afferent fibre: (1) Frequency rise (fall) on sudden cooling, (2) no response on sudden warming (cooling), if the fibre is silent, or an inhibition of a resting discharge, (3) a steady discharge dependent on temperature, (4) no response to non-painful mechanical stimulation (or at least a considerably higher threshold than the most sensitive mechanoreceptors, cf. Fig. 7, Iggo, 1960), (5) thermal sensitivity comparable with temperature sense in man.

The results described in this paper demonstrate clearly the existence of cutaneous sensory C fibres whose endings are sensitive either to warming or to cooling, whereas they are not excited by mild or non-painful mechanical stimulation. Unlike the heat and cold fibres described by Iggo (1959*b*), which may be concerned with pain, several C fibres found in the present investigation were stimulated by temperatures which in man cause no pain at all. The thresholds of these cold and warm receptors, amounting to only a few tenths of a degree from an indifferent temperature (30–33° C), correspond well with the thresholds of cutaneous cold and warm sensation in man (Hensel, 1952). On our proposed definition they are thermoreceptors.

The general behaviour of the cutaneous C thermoreceptors is comparable with that of the thermoreceptors in the cat's tongue. The values for the dynamic and static responses of the non-myelinated cold and warm fibres (Table 2) are of the same order as those found for the specific cold receptors in the tongue (Hensel & Zotterman, 1951*a*). However, there are some differences between the C thermoreceptors in the skin and the thermoreceptors in the tongue. The lingual nerve of the cat apparently contains no C fibres sensitive to mild thermal stimuli (Zotterman, personal communication); in this nerve there are A fibres sensitive to gentle warming or cooling. The cutaneous warm receptors with C fibres are more sensitive than the lingual warm fibres and show no paradoxical discharge (Dodt & Zotterman, 1952) during cooling. Further, the C cold fibres from the skin seem to be active at lower constant temperatures and to have a maximum discharge at a lower temperature than the cold fibres in the tongue.

TABLE 2. Maximum sensitivity (impulses/sec.° C) of single temperature fibres in the cat

		Cutaneous warm receptor with C fibre	Cutaneous cold receptor with C fibre	Lingual cold receptor with A fibre*
Dynamic sensitivity		+33	−30	−30
Static sensitivity	Positive range	+ 8	+ 3	+ 1
	Negative range	− 5	− 0·7	− 2·5

* From Hensel & Zotterman (1951*a*).

A number of A fibres which responded to thermal as well as light mechanical stimulation were found by Witt & Hensel (1959) in the saphenous nerve of the cat. No fibres were detected in the A group which were stimulated by temperature alone. These findings support the view that cutaneous temperature impulses in the cat may be carried mainly in non-myelinated fibres. We do not know the cat's temperature sensation, but the existence of thermal receptors is indicated by vasomotor reflexes in the ear to moderate heating or cooling of the legs in the unanaesthetized cat. These reactions were not caused by changes in blood temperature, which were actually the reverse of those necessary to give the observed changes in ear blood flow. The recorded hypothalamic and rectal temperatures rose during cooling and fell during heating of the extremities (Kundt, Brück & Hensel, 1957).

There are several reports dealing with the excitation of cutaneous fibres by both mild mechanical stimuli and cooling. Some cutaneous A fibres (Witt & Hensel, 1959) and C fibres (Douglas *et al.* 1959; Iggo, 1959*a*, 1960; this paper) in the cat are excited by non-injurious pressure and by cooling. The A fibres sometimes gave a steady discharge with constant temperatures whereas the C fibres were excited only when the cutaneous temperature was falling. The results have been interpreted in different ways. Iggo (1960) has suggested that the C fibres innervate mechanoreceptors which, in common with other mechanoreceptors, are excited by cooling. Douglas *et al.* (1959) consider that the response may indicate dual specificity of the endings. The present results, which show clearly that there are cutaneous C thermoreceptors which are much more sensitive to thermal changes than the C mechanoreceptors, provide a more convincing explanation for cutaneous thermosensitive mechanisms. If the A and C fibres described do indeed innervate mechanoreceptors, the results may account for the old observation (Weber's illusion, 1846) that weights feel heavier when they are cold (Hensel & Zotterman, 1951*b*; Douglas *et al.* 1959; Witt & Hensel, 1959).

In the last few years, in what has aptly been referred to as 'the tide of recent work', the classical doctrine of specific cutaneous receptors has been severely attacked on the basis of new histological findings and physiological investigations (Hagen, Knoche, Sinclair & Weddell, 1953; Weddell, Palmer & Pallie, 1955; Sinclair, 1955; Lele & Weddell, 1956, 1959; Oppenheimer, Palmer & Weddell, 1958; Weddell, Palmer & Taylor, 1959). Weddell *et al.* (1955) confirmed the original observation of Adrian (1931) that touching hairs sets up impulses in rapidly-conducting cutaneous fibres. Thermal stimuli failed to do so. Since the hair follicles have a distinctive innervation by large nerve fibres, Weddell (1960) now considers that their nerve endings may be specifically excited by light mechanical stimuli. To this extent he thus revives von Frey's (1895) suggestion that different qualities of cutaneous sensation are served by distinct histological structures. The other major type of afferent innervation of hairy skin is the diffuse arborization of 'free' nerve endings (Weddell *et al.* 1959). These presumably serve the other modalities (Weddell, 1960) even though there are apparently no histological differences to be seen among them. However, as Sinclair (1955) admits, it remains possible that specialized endings exist, but that the differences are too subtle to be revealed by present histological methods. This latter view is supported by the present work on C fibres innervating receptors in hairy skin and by recent investigations on the neurohistology of the cat's tongue, where Kantner (1957) has found only a network of 'free' nerve endings, although specific mechanoreceptors and thermoreceptors are present in the area. On the other hand there are reports of cutaneous nerve endings which, it is claimed, are not highly specific. In some regions, such as the cornea (Lele & Weddell, 1959) the non-specific fibres are thought to predominate. These conclusions rely on experiments with multi-fibre techniques for recording from the cutaneous nerves. Such techniques give results which are notoriously difficult to interpret. In addition, an important assumption in Lele & Weddell's argument appears to be that specific thermoreceptors are absent from the cornea. The present work makes this assumption less convincing. Lele & Weddell may have missed the thermoreceptors because the afferent fibres were non-myelinated. They recorded impulses in the myelinated fibres only.

SUMMARY

1. Impulses in slowly-conducting (C) afferent fibres were recorded in fine strands dissected from the saphenous nerves of cats anaesthetized with chloralose. The conduction velocities in some of the fibres ranged from 0·6 to 1·5 m/sec.

2. In response to well defined thermal stimuli the fibres responded either to warming or to cooling of the skin. The thresholds for mechanical stimulation were high.

3. Changes in skin temperature of 0·2° C or less were sufficient to excite the most sensitive cold and warm fibres.

4. The dynamic sensitivity of some fibres was 30 impulses/sec. ° C, which is as great as both the sensitivity of the most sensitive cold fibres in the cat's tongue and the temperature sense in man.

5. Constant temperatures led to a steady discharge of impulses, with a maximum between 16 and 27° C for the cold fibres and above 41° C for the warm fibres.

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Note added in proof

I. Iriuchijima & Y. Zotterman (*Acta physiol. scand.*, in the Press) have also recorded from cutaneous thermal fibres similar to those described in this paper.