J. Physiol. (1972), **224**, *pp.* 647–664
With 1 plate and 9 text-figures
Printed in Great Britain

THE TEMPERATURE SENSITIVITY OF THE TYPE I SLOWLY ADAPTING MECHANORECEPTORS IN CATS AND MONKEYS

BY ROLAND DUCLAUX* AND DAN R. KENSHALO

From the Department of Psychology, Florida State University, Tallahassee, Florida 32306, U.S.A.

(*Received 21 February 1972*)

SUMMARY

1. The sensitivity of Type I slowly adapting mechanoreceptors in cat and monkey skin to temperature and changes in temperature was investigated.

2. Multiple receptors innervated by a single axon appeared to be more frequent in the monkey than in the cat skin.

3. The responses of these receptors to thermal stimulation at static skin temperatures from 27 to 40° C were similar in cats and monkeys. At 43° C the monkey receptors showed a higher steady-state activity than the cat receptors.

4. A maximum steady-state frequency of 5·5 impulses/sec occurred in both the cat and monkey receptors at a static skin temperature of 37° C.

5. The maximum dynamic response to cooling occurred at a skin temperature of 40° C. The response was near its maximum at 2° C cooling and increased but little with further increases in the intensity of cooling.

6. Dynamic responses to cooling disappeared after the skin had been heated to 51° C for 35 sec and to mechanical stimulation after heating to 53° C for 35 sec. Excitation by either mechanical or thermal stimulation did not reappear within 1–2 hr.

7. The response characteristics of the Type I slowly adapting mechanoreceptors to temperature and temperature changes differ from those of specific cold receptors.

INTRODUCTION

The mechanical sensitivity of a distinctive type of cutaneous receptor in the hairy skin of cats and monkeys has been the subject of research by many investigators. These structures, variously referred to as touch

* Present address: Université Claude Bernard, Laboratoire de Physiologie, U.E.R. Medicale Lyon Sud Ouest, BP 12, 69 Oullins, France.

receptors, touch corpuscles and tactile pad receptors, are identical with the Haarscheibe described by Pinkus in 1902 (Catton, 1970). In this paper the terminology of Brown & Iggo (1967) will be adopted and these receptors will be referred to as Type I slowly adapting mechanoreceptors (SAI).

The SAI receptor is not a specific mechanoreceptor in the sense that it responds exclusively to mechanical skin deformation and no other energy form. Its neural response to mechanical stimuli is modulated by skin temperature and changes in skin temperature produce phasic changes in its neural activity. Even though it shows an apparently bimodal sensitivity its predominant response occurs to mechanical stimulation. Its peak frequency of discharge during skin indentation is as high as 1500 impulses/sec, whereas rapid skin cooling produce maximum peak discharge frequencies of only 80 impulses/sec (Iggo & Muir, 1969).

The distinctive response characteristics of SAI receptors to mechanical stimulation alone have been carefully investigated in cats (Iggo & Muir, 1969; Kenton & Kruger, 1971; Werner & Mountcastle, 1965) and in monkeys (Werner & Mountcastle, 1965). Changes in the mechanical response produced by changes in skin temperature have been systematically investigated by Casey & Hahn (1970) and Tapper (1965). Few reports exist, however, on the changes in activity of SAI receptors produced by thermal stimuli and none are known that involve a systematic investigation of the conditions of thermal stimulation on more than three or four of these units. While it appears probable that their function is exclusively in the tactile domain they may contribute to temperature sensitivity or to thermal sensations. In order to establish their role (or the lack of it) in the temperature sense, detailed information of their responses to various conditions of thermal stimulation is necessary.

Described here are the changes in response of SAI receptors to static skin temperature and to changes in skin temperature during constant mechanical pressure applied to the receptor. Several anatomical characteristics of these receptors in cats and monkeys are also described.

METHODS

Animals and apparatus. The results are drawn from twenty-five cats (*Felix domesticus*) and five rhesus monkeys (*Macaca mulatta*). The cats were anaesthetized with sodium pentobarbitone 35 mg/kg I.P. (Diabutal, Diamond Laboratories). Additional anaesthetic was given during the experiment to maintain an areflexic condition. The monkeys were first given phencyclidine hydrochloride 0·05 mg/kg (Sernylan, Parke Davis Laboratories), a primate tranquillizer. Sodium pentobarbitone was then injected I.V. to maintain an areflexic condition. The animals were placed on a heating pad controlled to maintain a 37° C rectal temperature. The

neural signals were amplified by a preamplifier, and displayed on one channel of a dual beam oscilloscope, as well as being monitored aurally.

Thermal stimuli were delivered by means of a Peltier device (Kenshalo, 1963). This stimulator (thermode) was composed of junctions of copper and *p* or *n* bismuth telluride. The amount and direction of current flow through the junctions determined the amount and direction of the resultant temperature change. The thermode covered a 4·82 cm^2 area. A thermistor, attached to the bottom surface of the thermode and insulated from it by a thin layer of epoxy, registered the temperature at the thermode-skin interface. The thermistor temperature was displayed on the second beam of the oscilloscope. Information was recorded photographically and on magnetic tape. The latter was used for off-line analysis by a PDP-12 digital computer of the temporal relations between the stimuli and responses.

No provision was made to monitor the skin temperature of the limb used in the preparation. The thermistor on the thermode provided feed-back to the electronic control circuit of the thermode. In this way, the thermode-skin interface was maintained at one of the several adapting temperatures used in the thermal stimuli series throughout the entire observation period.

Procedure

The skin on the hind leg of the anaesthetized cats or monkeys was shaved and depilated, and the saphenous nerve was exposed in the thigh. The edge of the skin wound was sutured to a metal ring and the resulting cavity was filled with liquid paraffin. The nerve bundle, placed on a Lucite dissection platform, was stripped of its outer sheaths and cut centrally. Small twigs were dissected free of the main bundle with sharp needles and forceps, and these strands were draped across a platinum wire electrode and examined for single units innervating the SA I receptor. In the monkey an additional preparation was made from the femoral nerve and two were made from the musculocutaneous nerve in the upper arm. The procedure was the same in these preparations. The single SA I unit was identified by the following criteria: (*a*) the presence of the distinctive cutaneous dome structure in cat's skin (at times this was difficult to distinguish in monkeys' skin so greater reliance was placed on the remaining criteria; see Pl. 1, figs. 1 and 2); (*b*) punctate mechanical stimulation of the dome gave a high frequency burst of activity; (*c*) the frequency of discharge decreased to a low, irregular rate of discharge to maintained pressure (see Text-fig. 2); (*d*) there was no neural activity in the absence of intentional mechanical stimulation; and (*e*) punctate mechanical stimulation or mild stretching of immediately adjacent skin areas failed to excite neural activity.

Receptors found near the wound edges were discarded. When it had been determined that a single fibre innervated an SA I receptor the adjacent skin area was searched for additional SA I receptors innervated by the same fibre. The Peltier stimulator was then placed in contact with the skin so that all of the receptors innervated by the fibre were located as close to the centre of the stimulator as possible.

The receptors were adapted for 10–15 min to the pressure and a temperature of 27 or 37° C of the thermode before the two-hour thermal stimulation session began. The adapting temperatures used in the series were 27, 30, 33, 37, 40 and 43° C. The adapting temperature series began either at 27° C and increased to 43° C or began at 37° C, decreased to 27° C, then was followed by the 40 and 43° C adapting temperatures. The 40 and 43° C adapting temperatures were always used last because of the potential danger of these high temperatures to the receptors.

Temperature change series were superimposed on the adapting temperature series. The cool stimuli series consisted of 0·5, 1·0, 2 and 5° C cooling from each adapting temperature at rates of 0·4, 0·6, 1·0 and 1·3° C/sec, respectively. The warm stimuli

series consisted of 0·7, 1·2, 2·5 and 6·0° C warming from an adapting temperature of 30° C at rates of 0·6, 1·0, 1·2, and 1·5° C/sec, respectively. Each temperature change was maintained for 35 sec with 60 sec intervals at the adapting temperature between the temperature changes. The skin had been adapted to the adapting temperature for at least 5 min before the thermal stimuli series commenced.

At the end of the thermal stimulation session most of the units were tested for their resistance to heat. The receptors were warmed, from a 43° C adapting temperature, by 5, 6, 7°, etc., until they failed to respond to cooling and to mechanical stimulation. Each of these stimuli lasted for 35 sec with 60 sec at 43° C between each stimulus.

An attempt was made to initiate activity in a number of the SAI units by radiant heating and cooling. Radiant heat stimulation was produced by an electric heating coil that warmed the skin at the rate of about 2° C/sec. Radiant cold was supplied by a small block of solid CO_2 (dry ice) held within 1 mm but not touching the receptor surface.

The magnetic taped responses to each condition of stimulation were analysed, off-line, with a PDP-12 computer. The programme counted the action potentials during successive 100 msec intervals and computed the frequency to provide graphs in the form of post-stimulus time histograms. A programme option averaged the frequency of activity during three consecutive 100 msec intervals to provide a 'running average' for the mid-interval of the three. In spite of this, the histograms of the neural activity of the SAI receptors appeared irregular even during the dynamic phase of thermal stimulation. A second programme option averaged the responses of all units to each common stimulating condition to provide cumulative post-stimulus time histograms.

RESULTS

Anatomy

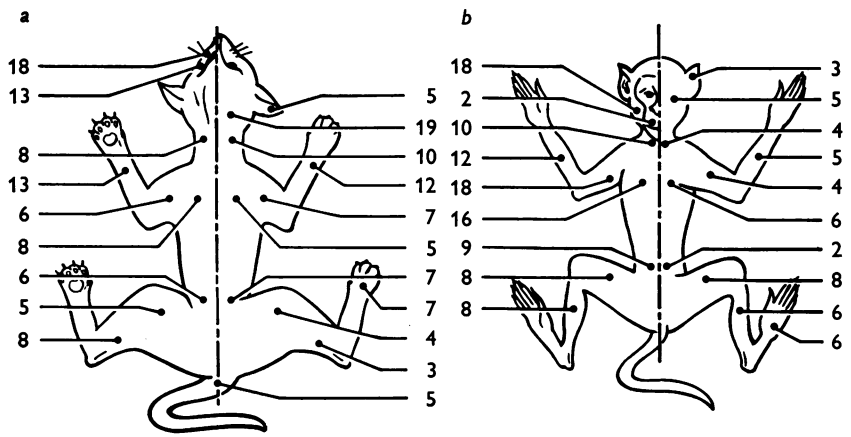
The SAI receptors can be readily identified in the depilated cat skin under low power magnification ($\times 10$ to $\times 20$) as smooth dome-like elevations of the skin of 0·1–0·4 mm diameter. We observed, as did Iggo & Muir (1969), that they frequently exist apart from tylotrich hair-follicles although we made no count. The lack of a regular and close association between the dome and the tylotrich follicle in cat skin suggests that the two are independent entities and not a single complex receptive structure as suggested by Straile (1969) for the rabbit, mouse, and sheep.

Pl. 1, figs. 1 and 2 show scanning electron micrographs of SAI receptors as seen in cat and monkey skin, respectively. In cats, the skin area identified by electrophysiological response criteria as containing an SAI receptor always contained the readily identifiable dome structure. In monkeys, however, while the SAI receptor is clearly discernible in Pl. fig. 2, there were instances when its identification by strictly anatomical characteristics would have been questionable. In these instances the dome was almost lacking and the edges of the receptor were delimited only by skin furrows. A similar description of Haarscheiben in human skin has been given by Straile (1969).

Another anatomical characteristic of the cat SAI receptor is a reddish

spot in the core of the dome. Light and electron micrographs have shown that this spot is due to a dense vascular plexus in the dermal layer within the dome itself (Iggo & Muir, 1969; Straile, 1969). The vascular plexus in one of the cat SA I receptors is made visible in its entirety in Pl. 1, fig. 3. The vascular plexus in the monkey SA I receptors does not appear to be a common feature (see Pl. 1, fig. 4). We were unable to demonstrate it in any instant by the methods that were successful in the cat.

We have seen no data on the density of SA I receptor distribution in the hairy skin of either the cat, except the inner thigh (Iggo & Muir, 1969), or the monkey. Text-fig. 1 shows the mean SA I receptors/cm^2 found visually



Text-fig. 1. The distribution of the mean number of Type 1 slowly adapting mechanoreceptors/cm^2 in selected sites on the dorsal (left) and ventral (right) skin of three cats (*a*) and three monkeys (*b*). The density of the SA I receptors in monkey's skin is probably underestimated because of difficulty in visual identification of the receptor site.

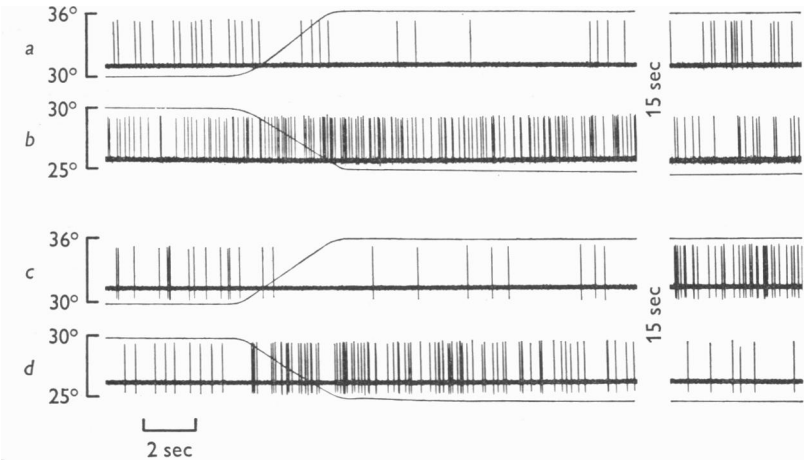
on various dorsal and ventral skin sites of three cats and three monkeys. In both species there appeared to be increasing caudo-rostral and dorso-ventral density gradients. However, there was a considerable variability between animals in both the numbers and the distribution of these receptors.

Electrophysiology

In both the cat and the monkey from 1 to 6 individual SA I receptors were innervated by single axons. A mean of 2·3 receptors/axon in the cats and 2·8 receptors/axon in the monkeys were found. Even though these means are not statistically different there appeared to be a greater tendency for multiple receptors innervated by single axons in the monkeys than in the cats, as is shown by the distributions. In 19 units from the cat, single SA I receptors/axon were found 9 times, 2/axon 3 times, 3, 4, and 5/axon twice, each, and 6/axon once. In 14 units from the monkey single

SA I receptors/axon were found only 3 times, 2/axon 4 times, 3/axon 3 times, 4/axon twice, and 5 and 6/axon once, each.

When more than one receptor/axon was found the thermode was positioned over all receptors. The static and dynamic responses of these multiple receptor units to temperature changes did not differ in any detectable way from those of the single receptor units, e.g. higher fre-



Text-fig. 2. The neural activity in a single Type 1 slowly adapting mechanoreceptor unit from cat's skin (*a* and *b*) and from monkey's skin (*c* and *d*). The steady-state discharge was irregular and warming the skin from 30° C to 36° C (*a* and *c*) markedly reduced, or even stopped activity during warming. The activity slowly returned and after 15 sec the steady-state frequency was higher than before warming. Cooling the unit from 30 to 25° C (*b* and *d*) produced a phasic increase in activity but 15 sec later a new steady-state frequency was established that was lower than the pre-stimulus frequency. The change in pre- and post-stimulus steady-state frequencies is consistent with the fact that the steady-state frequency increased as adapting temperature increased up to 37 or 43° C, as shown in Text-fig. 5.

quency of discharge or distinctive temporal pattern of discharge. Apparently, impulses that arise from thermal stimulation originate from only one receptor at a time, as with mechanical stimulation (Lindblom & Tapper, 1966). The responses of all units within a species to temperature stimuli were, therefore, combined.

In all, sixty-three single units innervating SA I receptors were identified, forty-eight in the cats and fifteen in the monkeys. Complete sets of responses to all of the thermal stimuli were obtained from thirteen cat units and thirteen monkey units.

General response characteristics to thermal stimuli. Text-fig. 2 shows the changes in neural activity to thermal stimulation of SA I units from cat

and monkey. The skin containing the units had been adapted to 30° C. During the time of static thermode temperature there was an irregular steady-state discharge which is one characteristic of the SA I type of receptor. Upon cooling the skin from 30 to 25° C there was a phasic increase in the discharge frequency and the rapid establishment of a new, slower steady-state level of activity. The peak frequency of discharge during cooling was 16 and 20 impulses/sec for the cat and monkey SA I receptors, respectively. We define peak frequency as the highest rate of discharge sustained for a 300 msec interval. Not shown here, but a regular observation in all of these preparations, was the suppression of neural activity when the thermode warmed the skin to the adapting temperature following the cool stimulus.

Warming the SA I receptors by 6° C suppressed the steady-state neural activity which reappeared after the skin stabilized at the higher temperature. The steady-state frequency was higher following warming than it was prior to the warm stimulus as shown to the right of Text-fig. 2*b* and *d*. This is because steady-state activity increased, in general, as a function of increased skin temperature.

Text-fig. 3 shows post-stimulus time histograms that resulted from the computer analysis of the SA I units shown in Text-fig. 2. The programme provided measurements of the steady-state and peak frequencies, latency of the peak frequency, and impulse counts following stimulation for the first sec, the first 15 sec, and the second 15 sec. All quantitative information reported here is based on similar computer displays for each condition of thermal stimulation.

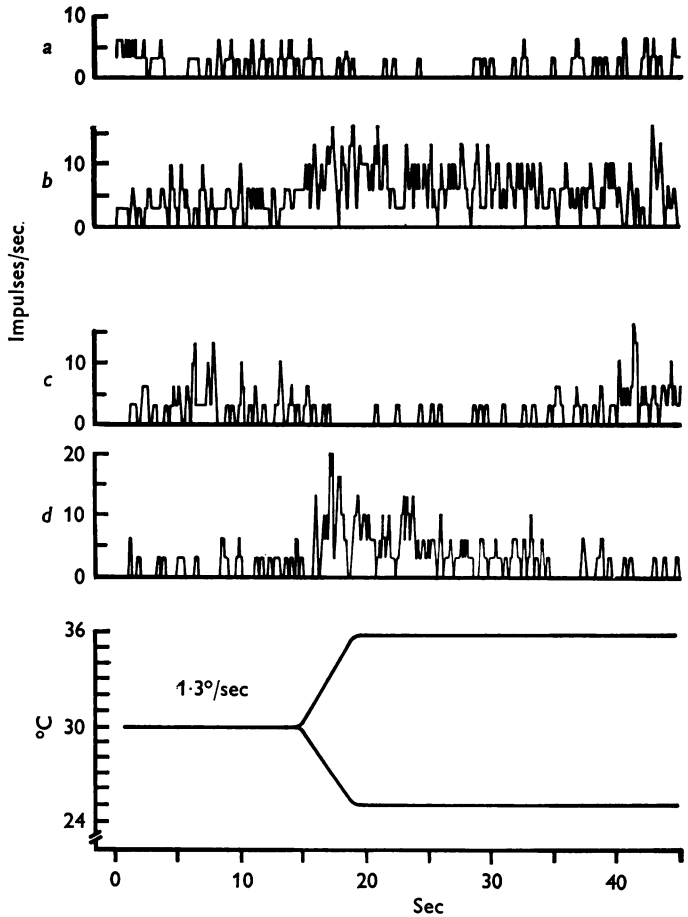
Response variability to thermal stimuli. Others (Hunt & McIntyre, 1960; Iggo, 1966; Iggo & Muir, 1969; Werner & Mountcastle, 1965; Witt & Hensel, 1959) have observed that skin temperature has a highly variable influence on the steady-state activity of SA I units. The variability of the SA I receptor steady-state activity to static temperatures will be described later. We are concerned here with the variability of the dynamic responses to temperature changes of fixed intensity.

Eight, 2° C cool stimuli of 35 sec duration separated by 1 min at the adapting temperature (33° C) were given to each of 5 cat SA I units. The mean peak frequency of the forty responses was 21·08 impulses/sec. Analysis of variance (Edwards, 1963) allowed the total variance of the peak frequencies to be partitioned into the variance due to the units of 392·53 (S.D. = ± 19·81) and the variance due to stimuli of 40·4 (S.D. = ± 6·37). The pronounced differences in the peak frequency of response between SA I units to 2° C cooling is characteristic and has been noted by Werner & Mountcastle (1965). However, when between-unit-variability was excluded the variability of the peak frequencies of response to 2° C

cooling was close to that obtained by Iggo & Muir (1969) for the variability of neural responses of a single SA I unit to repeated mechanical stimulation.

A part of the between units variance may have resulted from differences in the pressure of the thermode on the skin. Variations in mechanical displacement of SA I receptor influenced the steady-state response (Werner & Mountcastle, 1965) and may have, in turn, affected the dynamic sensitivity to temperature changes. This has not been systematically investigated.

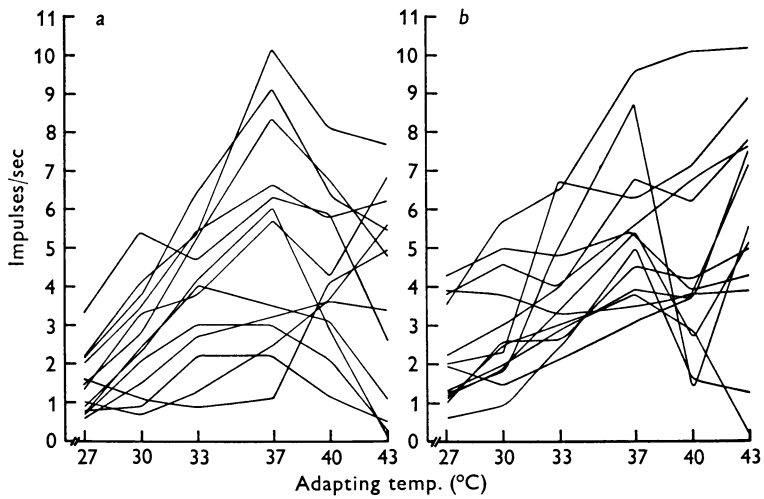
A second variable may also have contributed to the between units variance. Even though body core and thermode-skin interface temperatures were controlled, large differences in limb temperature still could



Text-fig. 3. Post-stimulus time histograms plotted by the computer for the neural activity shown in Text-fig. 2 for the cat (*a*, warming; *b* cooling) and the monkey (*c*, warming; *d*, cooling). The composite temperature trace is shown beneath the histograms.

have occurred. This would have resulted in differences in the temperature at the receptor site. However, we think the magnitude of such an effect, if present at all, is likely to be small because the nerve terminal elements of the SA I receptor are no more than 20 microns beneath the epithelial surface (Iggo & Muir, 1969).

The effect of the temporal order of warm and cool stimuli upon peak frequency and latency was also investigated. In seven of the cat units, 2° cooling for 35 sec was followed in 60 sec by either 5° C cooling or 6° C



Text-fig. 4. The individual unit steady-state frequencies as a function of the adapting temperature of the 13 Type I slowly adapting mechanoreceptor units from the cat (*a*) and from the monkey (*b*).

warming for 35 sec and then 60 sec later a second 2° C cooling stimulus was given. The adapting temperature was 33° C. There was no discernible effect on the peak frequencies of response to the 2° C cool stimuli by the interposition of either 5° C cooling or 6° C warming. The short duration of the warm and cool stimuli and the 60 sec at the adapting temperature allowed sufficient recovery time so that the dynamic responses were not affected by prior stimulation.

No detectable differences in the steady-state or dynamic responses of the units were found that could be attributed to the adapting temperature sequence.

Steady-state response to temperature. Steady-state activity was sampled for 15 sec immediately before each of the four cool stimuli at each adapting temperature for the thirteen cat and thirteen monkey SA I units. Means of the four, 15 sec samples of steady-state activity were used to construct the individual unit steady-state curves shown in Text-fig. 4. The differences

between the steady states of the individual units are the most distinctive feature of the Figure. While the units differed markedly, one from another, analysis of variance showed that repeated measurements of the steady state within units was considerably more stable. Estimates of the variance due to steady-state variability within each of the cat SAI units were an increasing function of adapting temperature from 0·126 (S.D. = ± 0·11) at 27° C to 4·95 (S.D. = ± 2·22) at the 43° C adapting temperature. Variance estimates due to differences between the cat's SAI units also increased with adapting temperature, from 2·06 (S.D. = ± 1·42) 27° C to 27·42 (S.D. = ± 5·24) at the 43° C adapting temperature. Both Werner & Mountcastle (1965) and Iggo & Muir (1969) have observed similar increases in variability in steady-state activity of the cat SAI units at higher static skin temperature.

The variability of the steady-state responses of the monkey SAI units at the six adapting temperatures followed a pattern similar to that of the cat SAI units except that the variances were somewhat larger.Variance estimates due to steady-state variability within each of the monkey SAI units ranged from 0·18 (S.D. = ± 0·42) at 27° C to 36·05 (S.D. = ± 6·00) at the 43° C adapting temperature.

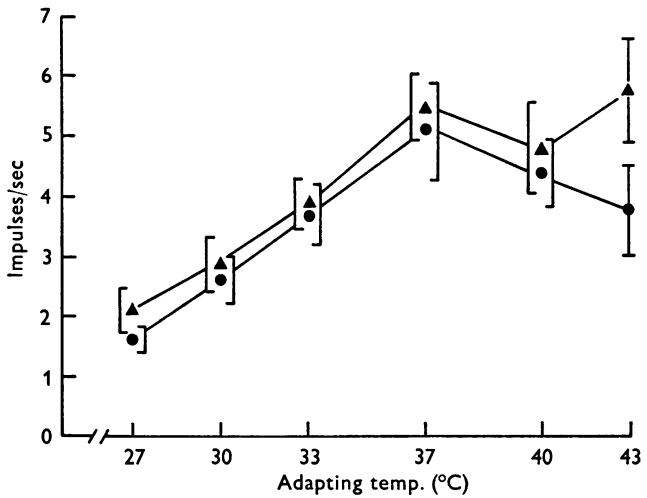
Variations in thermode pressure between preparations may have been responsible, in part, for the large differences in steady-state activity between units. However, thermode pressure remained constant within a preparation, yet the variance within each unit, as well as that between units increased as the adapting temperature increased. It is apparent, that while some inter-unit variability may have resulted from differences between units in the thermode pressure, much of the variability is an inherent characteristic of the units themselves.

The mean steady-state activities of the thirteen cat and the thirteen monkey units at each adapting temperature are shown in Text-fig. 5. The steady-state activity of both the cat and the monkey units increased with higher adapting temperatures at a rate of 0·3 impulses/sec ° C to peaks of about 5·4 impulses/sec at the 37° C adapting temperature. At the 40° C adapting temperature both the cat and the monkey units showed a reduced steady-state activity. At 43° C the cat units continued to decrease while the monkey units reached a second peak of 5·8 impulses/sec. At a 50° C adapting temperature the units from both species were silent.

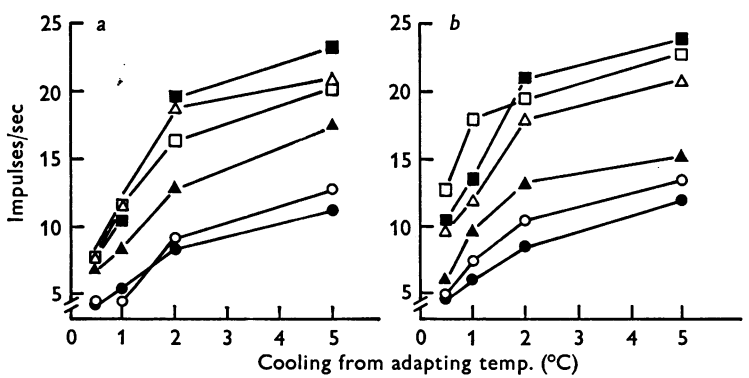
The difference in steady-state activity between the cat and the monkey units at 43° C adapting temperature probably does not represent a real species difference because the F ratio from the analysis of the variance failed to reach statistical significance ($0{\cdot}10 > P > 0{\cdot}05$).

Dynamic response to cooling. Cooling the skin in the area of the receptor(s) by as little as 0·5° C, without exception, produced a phasic increase in the

frequency of discharge of the SA I units of both the cats and the monkeys. Cumulative post-stimulus time histograms for each intensity of cooling at each adapting temperature for the thirteen units from the cat and the thirteen units from the monkey were computed to assess the dynamic responses to cooling. The peak frequencies of the cumulative responses to the four intensities of cooling at the six adapting temperatures for the cat

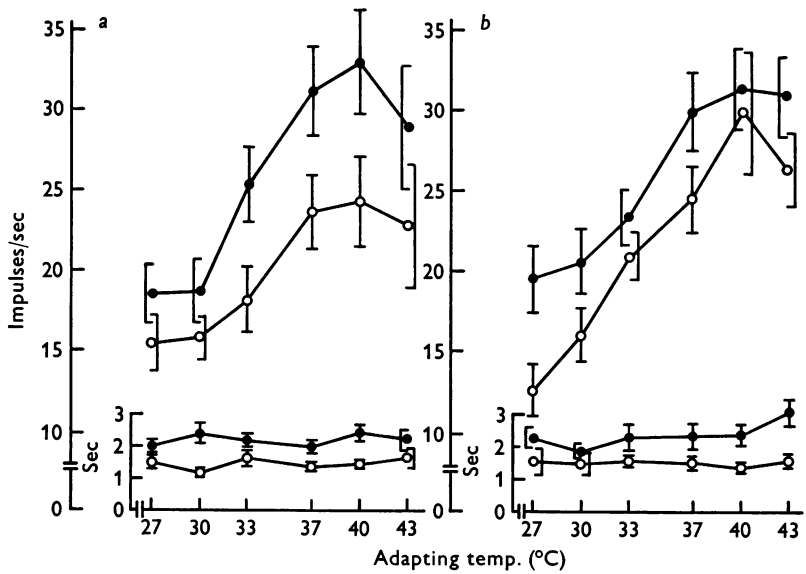


Text-fig. 5. The mean steady-state frequencies as a function of the adapting temperature for Type I slowly adapting mechanoreceptor units from the cat (●—●) and from the monkey (▲—▲). The brackets indicate the size of the standard error of each mean.



Text-fig. 6. Cumulative peak frequencies of activity obtained from the cumulative post-stimulus time histogram as a function of the intensity of the cooling stimulus from adapting temperatures of 27° C (●—●), 30° C (○—○), 33° C (▲—▲), 37° C (△—△), 40° C (■—■) and 43° C (□—□) for Type I slowly adapting mechanoreceptor units from the skin of cats (*a*) and monkeys (*b*).

and the monkey are shown in Text-fig. 6. The dynamic cool responses of the cat units do not differ appreciably from those of the monkey. Dynamic cool sensitivity roughly paralleled steady-state sensitivity except that both the cat and the monkey showed cumulative peaks of dynamic activity to cooling by 2 and 5° C from a 40° C adapting temperature. The fact that the



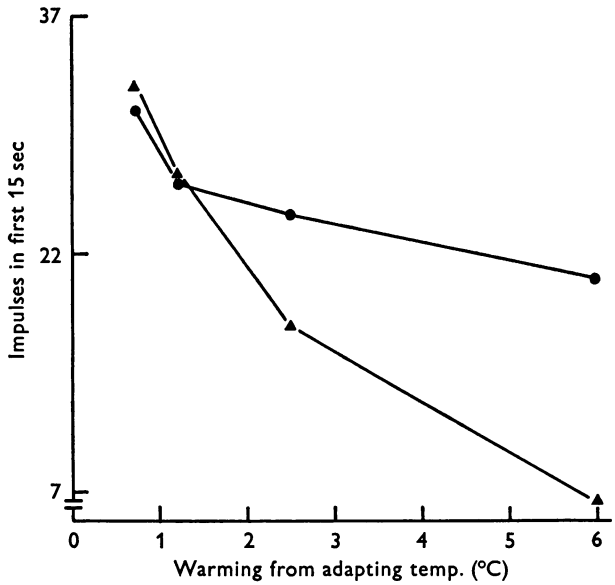
Text-fig. 7. Mean peak frequencies of activity and peak latencies obtained from individual post-stimulus time histograms for 2° C (○—○) and 5° C (●—●) cooling from each adapting temperature of Type I slowly adapting mechanoreceptor units from the skin of cats (*a*) and monkeys (*b*). The brackets indicate the size of the standard error of each mean.

peak dynamic sensitivity occurred at 40° C was expected since cooling from 40 to 38 or 35° C moved the skin temperature through the peak steady-state sensitivity of the receptors.

The greatest increase in the dynamic response occurred to cool stimuli up to 2° C in intensity. More intense cooling at an even faster rate resulted in little additional increase in the cumulative peak dynamic responses. Cooling intensities of 2° C increased the discharge frequency by 6 impulses/sec.° C. In contrast, cooling by 5° C increased the peak frequency of discharge by only 7 impulses/sec.° C (adapting temperature 40° C). Similar results have been reported by Leftwich & Kenshalo (1970). Total impulse counts for 4 sec and for 15 sec following the onset of cooling yielded similar results.

Text-fig. 7 shows the mean peak frequencies of the responses of SA I units to 2 and 5° C cooling from the six adapting temperatures. Also shown

are the mean latencies of the peak measured from the onset of cooling. The general shapes of these curves are the same as those obtained if the data of Text-fig. 6 were plotted on these co-ordinates. However, the mean peak frequencies are higher than those of the cumulative post-stimulus time histograms, shown in Text-fig. 6, because of the smearing effect of variable latencies of the peaks in the cumulative post-stimulus time histograms.



Text-fig. 8. The mean number of impulses during the first 15 sec following onset of several intensities of warming from an adapting temperature of 30° C for the thirteen Type I slowly adapting mechanoreceptor units from the skin of cats (●—●) and monkeys (▲—▲). The values were obtained from the cumulative post-stimulus time histograms. The cumulative steady-state activities for the 15 sec before warming were 39 and 43·5 impulses for the cat and monkey units, respectively.

The highest dynamic frequency in any of the units was 60 impulses/sec to 5° cooling from a 40° C adapting temperature. This was observed in one unit, each, from the cat and the monkey.

Measurements of the latency of the peak frequencies, shown in Text-fig. 7, were stable at all adapting temperatures, as shown by the relatively small standard errors of the means. There was no apparent orderly change in peak latency across the adapting temperatures. The mean peak latency occurred at about 2 sec for the 5° C, and at 1·3 sec for the 2° C cool stimuli, regardless of the adapting temperature. These stimuli were presented at rates of 1·3 and 1·0° C/sec, respectively, which means that the frequencies peaked well before the end of the cooling stimulus. It further shows that

the acceleration in discharge was a monotonic function of the adapting temperature up to 40° C.

Dynamic response to warming. Warm stimulation invariably resulted in a decrease or complete suppression of the steady-state activity in the SAI units from both the cat and monkey. Warming by 6° C, from a 30° C adapting temperature, caused all units to become silent for 8–10 sec following the onset of warming. Activity gradually increased to a higher steady-state level, equal to that at a 36° C adapting temperature, within 20–25 sec after that temperature was attained.

Text-fig. 8 shows the cumulative decrease in steady-state activity to the several intensities of warming. The decrease is represented as the total impulses during 15 sec immediately after the onset of warming. This method of representation confounds the amount by which activity was suppressed with the duration of the suppression. Nevertheless, it shows that the major part of the decrease in activity due to warming the SAI receptors of the cat occurred at intensities of less than 1·2° C. Higher intensities of warming produced relatively little further decrease in activity during the 15 sec post-stimulus period. In the monkey SAI receptors, however, intensities of warming higher than 1·2° C produced additional reductions in the activity of the units. This resulted from longer periods of complete suppression of activity and slower recovery to the new activity level in the monkey than in the cat units.

In the cat units there appeared to be a maximum period of between 10 and 12 sec during which steady-state activity of the SAI units can be completely suppressed by warming. When the units were warmed by 15°, at a rate of 1° C/sec from a 30° adapting temperature, the units were silent for 10–12 sec after which activity reappeared and increased rapidly even though warming had not yet reached its final temperature of 45° C.

Heat resistance of SA I receptors. The impairment by heat of the response of the SAI receptors to cooling and mechanical stimulation was invesgated in the 26 units included in this report. There were no apparent differences between the cat and the monkey units so they are considered together. After heating the units from 43° to about 51° C for 35 sec they could not be excited by rapid cooling nor did the maintained pressure of the stimulator elicit a steady-state discharge at any one of the lower adapting temperatures. A tap on the stimulator produced a small burst of activity which also disappeared after the units had been heated to about 53° C for 35 sec. Sensitivity to either cool or mechanical stimulation did not reappear after more than one hour at a 30° C adapting temperature. In a single monkey unit the response to cooling and mechanical stimulation remained apparently unimpaired until the skin had been heated to 58° C for 1 min. Then only the response to cooling disappeared. The

receptor of this unit was located on the foot at the edge of the hairy skin. The corneum was probably thicker there than on the arm or leg which could account for the greater heat resistance of this unit than that found in the others.

Radiant stimulation. Radiant energy was used to try to initiate activity in 15 SAI units of the cat. Three of the 15 responded with 3–5 irregularly spaced impulses following exposure to radiant cold. Radiant heat was ineffective in initiating activity in any of the units.

DISCUSSION

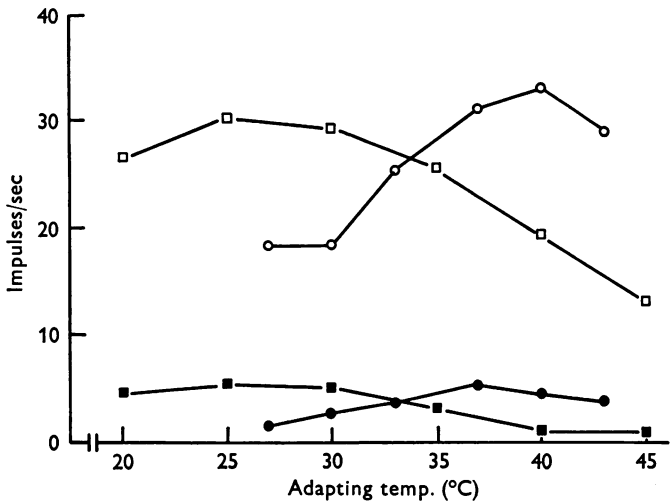
There were few differences that could be found between cat and monkey SAI receptors. The most pronounced differences were anatomical. The epithelial domes with their vascularized core, readily identifiable in cats' skin, were difficult to identify in the monkey's skin. Not only were the domes smaller in the monkey but the vascularization of the dome was not apparent even under high ($\times 45$) magnification. The india ink perfusion that showed the vascular reticulum in the cat SAI receptors failed to show a similar vascular reticulum in the monkey SAI receptors.

Differences in the responses of cat and monkey SAI receptors to thermal stimulation were insignificant. There was a tendency for the monkey SAI receptors to show a higher steady-state activity at the 43° C adapting temperature and to recover steady-state activity more slowly following warming stimuli.

The SAI mechanoreceptors show a negative coefficient to temperature change as do specific cold units. Both show a phasic increase in impulse frequency to transient skin cooling and a phasic decrease in frequency to skin warming. The similarity between SAI units and specific cold units to temperature change ends here. The SAI units are characteristically silent in the absence of intentional mechanical stimulation of the receptor. A steady-state discharge can be produced by constant pressure on the SAI receptive fields and the frequency of this pressure induced discharge can be changed by changing the adapted skin temperature. Radiant energy is generally ineffective in stimulating SAI units that are not already active to constant pressure. However, radiant energy may modulate the low discharge frequency of SAI units active in the absence of intentional mechanical stimulation. All specific cold units show a steady-state discharge at skin temperatures between 20 and 30° C. They are unaffected by even strong mechanical stimulation of their receptive fields.

Text-fig. 9 shows the differences in steady state and phasic responses to temperature change of specific cold units (Kenshalo, Hensel, Graziadei & Fruhstorfer, 1971) and the SAI receptors described here. The cold unit

steady-state activity peaked at a static skin temperature of 29° C whereas the pressure induced SAI receptor steady-state activity peaked at 37° C. The peak activity to 5° C cooling occurred at an adapting temperature of 25° C for specific cold units whereas it occurred at an adapting temperature of 40° C for the SAI units. These clear-cut differences in responses of the SAI units and specific cold units to cool stimulation leaves small reason to confuse them.



Text-fig. 9. The mean steady-state (filled symbols) and peak dynamic (open symbols) responses of thirteen Type I slowly adapting mechanoreceptor units (◑—◑) and 23 specific cold units (◨—◨) from cats. The peak frequencies of the dynamic responses were to 5° C cooling from each adapting temperature. The rate of cooling used with the specific cold units was 0·4° C/sec. That used for the SAI units was 1·5° C/sec (specific cold unit data from Kenshalo, Graziadei, Hensel & Fruhstorfer, 1971).

Although it cannot be stated positively, the available evidence indicates that SAI units do not contribute to thermal sensations, nor does their excitation by thermal stimuli give rise to sensations in the thermal mode. This conclusion is based on two lines of evidence. First, the SAI receptors are not readily stimulated by radiant cooling yet the radiant cooling used was more than sufficient to elicit cool sensations in human skin. Furthermore, threshold cool sensations produced by radiant cooling are approximately equal to those produced by conducted cooling (thermode resting on the skin), considering the area of skin simulated (Ebaugh & Thauer, 1950; Hardy & Oppel, 1938). It might be argued, as did Jenkins (1951), that threshold measurements to radiant and conducted energy show different results and this difference could be attributed to the added information provided by SAI receptor activity. However, when skin area

stimulated is held constant there is no basis to contend that one heat energy form yields results that differ from those obtained by the use of other forms of the energy (Kenshalo, Decker & Hamilton, 1967).

The second line of evidence that excludes SA I units from a role in thermal sensations derives from a comparison of psychophysical measurements of the cool threshold as a function of skin temperature with both steady-state and dynamic activity of specific cold units as compared to SA I units. Psychophysical measurements of the cool threshold as a function of adapting temperature showed that the cool threshold increased progressively as the skin was adapted to temperatures of 36° C and higher (Kenshalo, 1970). This suggests that the cold sensing mechanism became less sensitive at the higher adapting temperature. Similar results were obtained by use of radiant cold stimulation (Ebaugh & Thauer, 1950). Such an increase in threshold at high adapting temperature is consistent with the decreased dynamic sensitivity of specific cold units at high adapting temperatures, but is difficult to reconcile with the increased dynamic sensitivity of SA I units at these same high adapting temperatures.

Dr Duclaux was a Fulbright–Hays Scholar and was supported in part by NSF grant GU 2612 while this research was in progress. The research was supported by USPHS Grant NS-02992. We thank Dr Pasquale Graziadei for providing the Plate figures.

REFERENCES

BROWN, A. G. & IGGO, A. (1967). A quantitative study of cutaneous receptors and afferent fibres in the cat and rabbit. *J. Physiol.* **193**, 707–733.

CASEY, D. E. & HAHN, J. F. (1970). Thermal effects on response of cat touch corpuscle. *Expl Neurol.* **28**, 35–45.

CATTON, W. T. (1970). Mechanoreceptor function. *Physiol. Rev.* **50**, 297–318.

EBAUGH, F. G. & THAUER, R. (1950). Influence of various environmental temperatures on the cold and warmth thresholds. *J. appl. Physiol.* **3**, 173–182.

EDWARDS, A. L. (1963). *Experimental Design in Psychological Research.* New York: Holt, Rinehart and Winston.

HARDY, J. D. & OPPEL, T. W. (1938). Studies in temperature sensation. IV. The stimulation of cold by radiation. *J. clin. Invest.* **17**, 771–777.

HUNT, C. C. & MCINTYRE, A. K. (1960). Properties of cutaneous touch receptors in cat. *J. Physiol.* **153**, 88–98.

IGGO, A. (1966). Cutaneous receptor with a high sensitivity to mechanical displacement. In *Touch, Heat, and Pain*, pp. 237–256, ed. DEREUCK, A. V. S. & KNIGHT, J. Boston: Little, Brown.

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

JENKINS, W. L. (1951). Somesthesis. In *Handbook of Experimental Psychology*, pp. 1172–1190, ed. STEVENS, S. S. New York: Wiley and Sons.

KENSHALO, D. R. (1963). Improved method for the psychophysical study of the temperature sense. *Rev. scient. Instrum.* **34**, 883–886.

KENSHALO, D. R. (1970). Psychophysical studies of temperature sensitivity. In *Contributions to Sensory Physiology*, vol. 4, pp. 19–74, ed. NEFF, W. D. New York: Academic Press.

KENSHALO, D. R., DECKER, T. & HAMILTON, A. (1967). Spatial summation on the forehead, forearm, and back produced by radiant and conducted heat. *J. comp. physiol. Psychol.* **63**, 510–515.

KENSHALO, D. R., HENSEL, H., GRAZIADEI, P. & FRUHSTORFER, H. (1971). On the anatomy, physiology and psychophysics of the cat's temperature sensing system. In *Mechanisms of Oral-Facial Sensation and Movement*, chap. 3, pp. 23–45, ed. DUBNER, R. N. & KAWAMURA, Y. New York: Appleton–Century–Crofts.

KENTON, B. & KRUGER, L. (1971). Information transmission in slowly adapting mechanoreceptor fibres. *Expl Neurol.* **31**, 114–139.

LEFTWICH, M. S. & KENSHALO, D. R. (1970). Temperature sensitivity of the Type I slowly adapting mechanoreceptors. *Fedn Proc.* **29**, 522 abst.

LINDBLOM, U. & TAPPER, D. N. (1966). Integration of impulse activity in a peripheral sensory unit. *Expl Neurol.* **15**, 63–69.

PINKUS, F. (1902). Über einen bisher unbekannten Nebenapparat am Haarsystem des Menschen: Haarscheiben. *Derm. Z.* **9**, 465–469.

STRAILE, W. E. (1969). Encapsulated nerve end-organs in the rabbit, mouse, sheep, and man. *J. comp. Neurol.* **136**, 317–336.

TAPPER, D. N. (1965). Stimulus-response relationships in the cutaneous slowly-adapting mechanoreceptor in hairy skin of the cat. *Expl Neurol.* **13**, 364–385.

WERNER, G. & MOUNTCASTLE, V. B. (1965). Neural activity in mechano-receptive cutaneous afferents: Stimulus-response relations Weber functions, and information transmission. *J. Neurophysiol.* **28**, 359–397.

WITT, I. & HENSEL, H. (1959). Afferente Impulse aus der Extremitätenhaut der Katze bei thermischer und mechanischer Reizung. *Pflügers Arch. ges. Physiol.* **268**, 582–596.

EXPLANATION OF PLATE

Fig. 1. A scanning electron micrograph of the skin surface over a Type I slowly adapting mechanoreceptor from a cat. The texture of the corneum over the dome is markedly different from that of the surrounding epithelium. It is characterized by a cobble stone-like appearance. In the surrounding areas the corneum is corrugated in appearance. Some tissue shrinkage resulted from the initial fixation in 10% formalin. This may have exaggerated the surface features somewhat. The horizontal bar represents 100 μ.

Fig. 2. A scanning electron micrograph of the skin surface over a Type I slowly adapting mechanoreceptor from a rhesus monkey. The surface characteristics of the corneum over the receptor are markedly different from those seen in cat's skin. Furthermore, the diameters of the domes, when found in the skin of monkeys, were smaller than those found in the skin of the cats. The horizontal bar represents 100 μ.

Fig. 3. A photomicrograph of the vascularization in a Type I slowly adapting mechanoreceptor in the skin of cat. The hind limb was perfused through the femoral artery with a solution of isotonic saline, heparin and india ink. Skin samples were fixed in 10% formalin, cleared in cedar-wood oil and then photographed. The ghost of the epithelial dome is just visible over the vascular arborization. The horizontal bar represents 100 μ.

Fig. 4. A photomicrograph of the superficial vascularization of a skin sample containing a Type I slowly adapting mechanoreceptive structure from a rhesus monkey. The tissue was prepared exactly as that of the cat, shown in Fig. 3. The vascular arborization, so clearly present in cat's skin, was nowhere to be seen in monkey's skin. The horizontal bar represents 100 μ.