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RELATIONSHIP BETWEEN CUTANEOUS THERMAL THRESHOLDS, SKIN TEMPERATURE AND CROSS-SECTIONAL AREA OF THE STIMULUS

BY P. P. LELE*

From the Department of Human Anatomy, University of Oxford

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In a recent investigation (Lele, Sinclair & Weddell, 1954) it was found that the threshold to a touch stimulus varied from one cutaneous test site to another. It was therefore decided to investigate the warmth and cold thresholds at various sites to determine whether or not these also show any marked variations and, if so, whether the variations run a parallel course in the case of both the warmth and the cold modalities. In addition, observations were made on the effect of alteration of the skin temperature and of the area stimulated on the thresholds thus obtained.

The thresholds were determined in two ways: (1) in terms of the smallest difference of temperature between the test object and the skin which could consistently be detected subjectively within an arbitrarily fixed period of time; and (2) the smallest area which, when suitably stimulated, gave rise to reports referable to a thermal category.

APPARATUS AND METHODS

Thermal stimuli were applied by means of circular copper tips 123, 50, 12·6 and 1·8 mm² in area, screwed into the end of a solid copper cylinder of large thermal capacity which was brought to the selected temperature by heating electrically or placing in contact with ice. Each tip carried a thermocouple which recorded its temperature correctly to ±0·25° C.

The skin temperature was measured by applying a freely suspended single thermo-electric junction of fine (40 s.w.g.) copper-constantan wire to the test site. This permitted rapid and reproducible readings (correct to ±0·25° C) to be taken without altering the skin temperature by measurable amounts. The same thermocouple was used to measure the ambient temperatures.

Both the thermocouples were connected to a short-period galvanometer which was calibrated to read 1° C/scale division. At the start, and at intervals during the experiments, the readings at two points on the calibration curve of both the thermocouples was checked.

Stimuli were also delivered to selected sites of skin by means of (i) a copper cylinder 0·78 mm² in cross-sectional area mounted at right angles to the end of one arm of a compass with sealing

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wax, and a cylinder of wood of the same cross-sectional area similarly mounted at the end of the other arm; (ii) a piece of copper wire 0·102 mm² in cross-sectional area and a piece of nylon suture material of the same cross-sectional area also mounted at right angles to ends of a pair of compass points.

Fine, drawn quartz needles from 25 to 58 μ in diameter, mounted on match sticks with sealing wax, were also used to deliver stimuli at some selected sites.

Eight healthy adult subjects (three female and five male) were used. None of them had any previous experience of sensory testing involving thermal stimuli. Circles were stamped with ink on the test sites on the left hand as shown in Fig. 1. Test sites were selected with regard to differences in the neurohistology of the skin (i.e. glabrous or hairy skin). The tests were performed

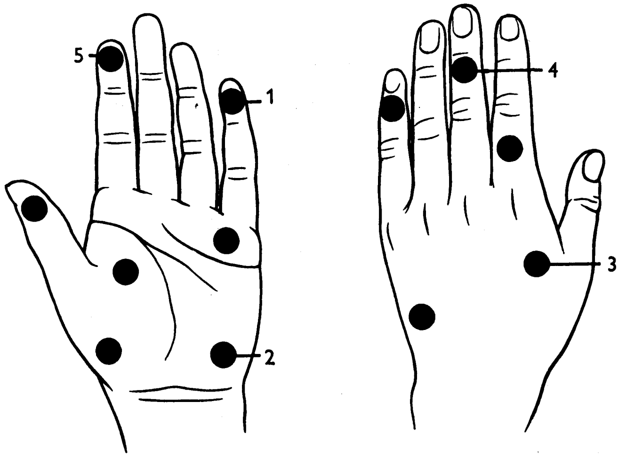

Fig. 1. Sites on left hand at which stimuli were applied.

in a small draught-free and almost sound-proof room. About 30 min were allowed for 'thermal equilibrium' to be reached and the test was started when the skin temperature at the test site had remained stable for not less than 15 min, during which time no spontaneous sensation had been reported from the test area. During the test the subject was comfortably seated with the hand suitably supported. The layout of the apparatus was such that the subject could not see the control panel or the records of the experiment.

The subject was told that the stimulus to be applied to the test area might be hot, warm, thermally neutral, cool or cold, and that he was to report the thermal status of the sensation as soon as he could after the stimulus had been applied. He was also shown how to apply the thermocouple (for measuring the skin temperature) to the test site when requested. The probe was allowed to rest on the test site at its own effective weight of about 5 g for 20 sec unless the subject declared the thermal nature of the stimulus earlier. This limit of 20 sec was imposed because it was found impracticable to maintain the temperature of the probe at the selected level for longer periods.

A pilot run of ten applications was made to get the subject used to the procedure. During this run a rough estimate of the thresholds to warmth and cold was made so that the details of the subsequent experiments could be planned.

The skin temperature was recorded before each application of the probe, the temperature of which was adjusted so as to give the selected difference between its temperature and that of the skin. This difference was in steps of 1° C. The series also included a number of thermally neutral stimuli at the skin temperature. Applications were repeated at intervals of about 4 min and the order in which the stimuli were applied was randomized. Each experiment, which normally lasted about 90 min, was frequently interrupted to avoid fatigue and was terminated if the subject felt tired or was unable to concentrate.

The least temperature difference which the subject was able to detect correctly and consistently was taken to be the threshold stimulus for that sensation. No single reply was considered to be of any significance unless the next two greater temperature differences (in the order in which they appeared in the randomization table) were also correctly interpreted. For indefinite replies such as 'on the cool side of neutral' or 'warmish neutral, I think', the threshold level was reduced by 0·5° C if the succeeding 'stronger' stimulus (as delivered in the order of randomization) was clearly and correctly reported.

Alterations of skin temperature were obtained by immersion of the hand up to the middle of the forearm in water at a suitable temperature for at least 45 min. The hand was then removed from the water and dried gently. If the subjects reported any spontaneous sensations or awareness of the hand after it was removed from the water, it was re-immersed until on further withdrawal it was found that 'thermal equilibrium' had been achieved. The skin temperature was found to change for 2–3 min, after which it remained constant for a period of about 10 min. During this time the test stimulus was applied, provided no spontaneous sensations or discomfort were reported. Immediately after each application the hand was returned into the water. Before and after altering the skin temperature in this way, the touch thresholds were evaluated by punctate and stroking stimuli delivered with a nylon thread mounted on a metal rod (Lele, Sinclair & Weddell, 1954). Every figure reported in this paper is the average derived from five or more replicates of each threshold.

In five subjects the copper and wooden stimuli of 0·78 mm^2 in cross-sectional area, both at a temperature of 19° C, were applied 10 times, each in a random order to the forehead and to the mucous membrane and the muco-cutaneous junction of the lips. The stimuli were gently lowered on to the test site so that they caused a just visible deformation at the area of contact. Each stimulus was kept on for from 3 to 5 sec. The interval between the application of successive stimuli was not less than 2 min. The stimuli were not shown to the subject who sat with eyes closed and was requested to report the nature of the sensation he experienced. An exactly comparable series of experiments was subsequently carried out on three of these subjects using the copper wire and the nylon thread.

In five additional subjects, none of whom had any previous experience of sensory testing, the quartz needles were inserted through the hairy skin of the forehead and the hand (in between the hair shafts) to depths varying randomly between 0·5 and 3·0 mm. The subjects were requested to report in their own terminology the nature of the first sensation evoked when the stimulus was delivered to the test site. They were shown the stimuli and were reassured that no portion of it would be left in their skin. They were asked to keep their eyes closed during the experiment, and stimuli were withheld in a random order to provide controls.

OBSERVATIONS

The resting skin temperatures of the various sites shown in Fig. 1 were measured after a state of 'thermal equilibrium' had been reached. These were found to vary from site to site, day to day, and from subject to subject. The lowest temperature recorded in these runs was 18° C and the highest, 35° C. On every occasion the test sites on the fingers were found to be significantly cooler ($P < 0{\cdot}001$) than those on the palm, the difference in the temperature ranging from 2 to 9° C. The thresholds for warmth and cold were determined with the 123 mm^2 tip at test sites 1 to 4 (Fig. 1) in six subjects. The order in which the sites were tested in each subject was randomized. The warmth and cold thresholds were found to vary independently of each other (Table 1). In two subjects (L.P. and J.M.G.) no consistent thresholds could ever be established at site 1, because a variable proportion (up to 30%) of the total number of responses elicited from that site were the reverse of those which might have been expected. For example, L.P. in one run reported 'stinging hot' at +7 (i.e. a stimulus temperature 7° C above the skin temperature), at −7 and −10. Cold was reported at +3 and +5; the remaining stimuli in this run being reported as neutral. In two of the other four subjects, site 1 was found to be relatively insensitive to warmth, although the cold sensitivity was of the same order as at other test sites. In these two subjects, however, site 5 was found to have reproducible warmth and cold thresholds.

TABLE 1. Warmth (*W*) and cold (*C*) thresholds in ° C above and below skin temperature (Stimulus size, 123 mm²)

Subject		Site 1	2	3	4	5
D. C. S.	*W*	+11·5	+0·4	+0·6	+2·2	−0·8
	C	− 3·6	−3·8	−2·6	−2·0	−4·4
D. A. T.	*W*	+ 0·2	+1·0	0·0	+0·5	—
	C	− 1·0	−1·6	−2·0	−1·8	—
J. M. G.	*W*	Unobtainable	+2·0	+0·8	+1·0	—
	C	Unobtainable	−1·4	−2·6	−1·2	—
L. P.	*W*	Unobtainable	+8·0	+1·8	+1·0	—
	C	Unobtainable	−2·4	−2·3	−1·4	—
R. J.	*W*	+ 1·6	+1·4	+1·0	+1·6	—
	C	− 3·6	−2·6	−2·2	−1·4	—
W. D. T.	*W*	+ 8·8	+4·4	+1·0	+1·0	+3·2
	C	− 0·8	−3·2	−3·6	−2·0	−1·6

To find out whether this variability of the thresholds was due to the influence of skin temperature or was characteristic of the site stimulated, thresholds at one site were determined at different skin temperatures and then at different sites at the same temperature in each subject.

Relationship between threshold and skin temperature

A single site in six subjects was examined in detail using the 123 mm² stimulus, the temperature of the hand being varied between 14 and 38° C in a random order by the immersion of the hand in water at a suitable temperature. During these experiments, it was found that the lowest temperatures which could be tolerated without the supervention of pain or paraesthesia varied from 13 to 20° C in different subjects. Correspondingly, the highest temperatures which could be tolerated lay between 41 and 46° C. The operative skin temperatures so obtained ranged from 14 to 18° C with cold water, and 34·5 to 38·5° C with hot water. No alterations in touch thresholds could be detected when the skin temperatures were within these limits. Since it was not possible to complete the tests in the course of one session, the reproducibility of the thresholds at many skin temperatures was checked.

Fig. 2 shows the observations made in the case of one subject (R. J. site 4), comparable observations having been made in the case of the remaining five subjects at a different site in each case. It is at once evident from this figure that the thresholds are related to the skin temperature and that this relation is different in the case of warmth and cold. At low temperatures the threshold

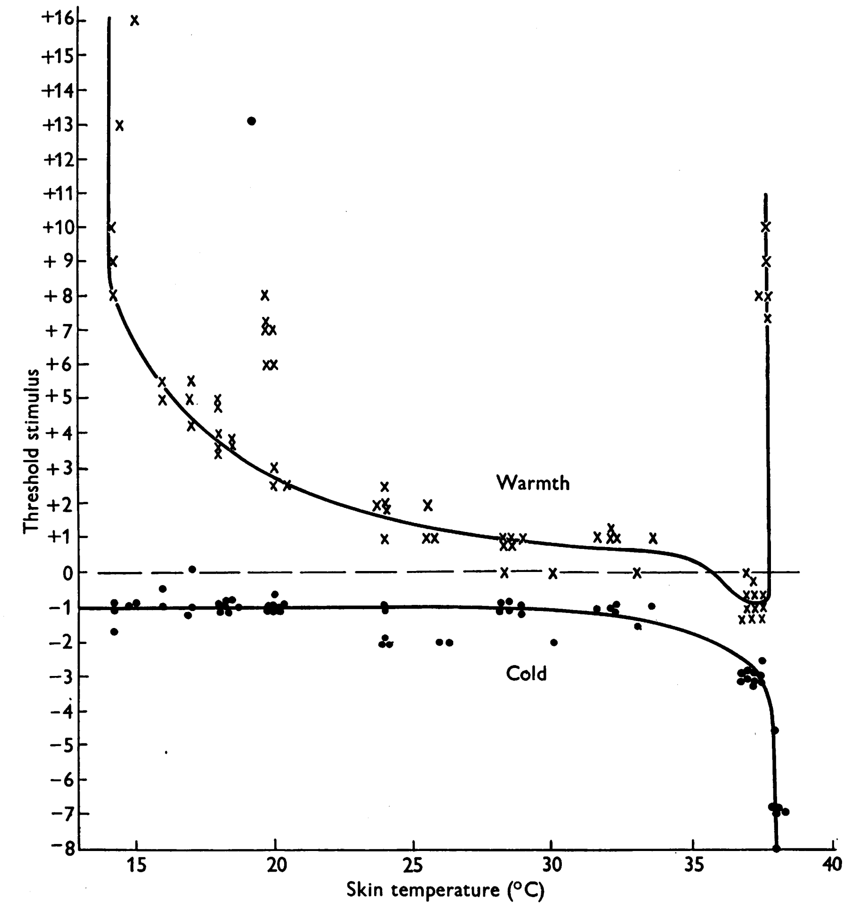

Fig. 2. Graph showing threshold stimuli for warmth and cold plotted against skin temperature in ° C.

for warmth is higher and gradually becomes lower as the skin temperature rises. This continues until a temperature of 37·5° C is reached, when the threshold for warmth is lowest. The thresholds for cold show a trend in the opposite direction, being lowest at low skin temperatures and increasing as the skin temperature rises. The neutral zone, that is the range of stimulus temperatures above and below the skin temperature in which no thermal sensation is reported, is narrowest at skin temperatures between 35 and 37° C. The threshold-skin temperature curve for warmth differs from that for cold in that it slopes more steeply. The one for cold is practically horizontal at lower skin temperatures, but since the stimulus temperatures were only varied in steps of one degree it would not in any case be possible to recognize a gradual slope, as differences of less than 1° C would not be manifest.

At skin temperatures of about 38° C, the regular change gives place to a sudden change in both the warmth and the cold thresholds. The neutral zone suddenly becomes very wide, owing to the increase of both cold and warmth thresholds. To elicit warmth, stimulus temperatures of +8 or more are necessary and for cold −6 or more. This effect on the thresholds lasted for variable periods. The cold thresholds returned to their normal level in about 1 hr. But the warmth thresholds remained abnormally high for about 3 hr. It was not possible to raise the skin temperature of this particular subject above 38° C as immersion of the hand in water at higher temperatures caused pain.

At skin temperatures below 16° C the subject remarked that the sensation of warmth was not as exact and precise as at higher temperatures, although cold was quite a definite and clear-cut sensation. He also took a longer time to respond to warm stimuli. At skin temperatures above 37·5° C the subject reported a qualitative alteration in the warmth sensation: 'warmth is felt indistinctly as if the hand was frozen in snow'. At skin temperatures of 38° C, stimuli of +8 or more gave rise to a sensation compounded of warmth, touch and pain. The sensation of warmth was very faint and vague, the chief component being touch with an addition of slight pain. Subthreshold warm stimuli applied at the test site did not arouse any pain but evoked a sensation of touch alone. These same stimuli were reported as distinctly warm or very warm on the contra-lateral test site at which the skin temperature was 35° C.

Reports which were the reverse of what might have been expected were made under certain conditions. At near-maximal skin temperature (*c.* 37° C) stimuli 1° C below the skin temperature were consistently reported as warm. On one occasion only, a warm stimulus +15 was reported as cold. This actually occurred when the skin temperature was at 20° C, 2 hr after it had been raised to 38° C. At this time the warmth threshold for the site (*c.* +3 for a skin temperature of 20° C) had not returned to its normal level.

This phenomenon of the fall in the warmth and rise in the cold thresholds with a rise in the skin temperature up to a certain maximum (where this relationship breaks down), was observed in the other five subjects. Although the slopes of the skin temperature-threshold curves and the temperatures to which the skin could be altered without causing pain varied, the comparable points on the curves lay within 1·5° C of each other. In two subjects the thresholds to warmth near to the maximal temperatures attained did not fall to below zero, but were about +1. In one subject at the highest skin temperature tested the warmth thresholds suddenly became very low instead of rising very steeply as in the other subjects. The cold thresholds, however, showed a steep rise and the neutral zone therefore remained constant and did not become wider as in the other subjects.

Variations in threshold due to site

To find out whether the variations in the thermal thresholds at different sites were entirely due to the variations in the skin temperatures at these sites, threshold determinations (using a 123 mm² stimulus) were made with the sites brought to the same temperature. The thresholds (Table 2) were still found to differ from site to site, although the pattern of cutaneous innervation (i.e. hairy or glabrous type of skin) could not be held responsible for these differences.

TABLE 2. Warmth (*W*) and cold (*C*) thresholds in ° C above and below skin temperature; test sites in the same subject at the same skin temperature

(Stimulus size, 123 mm²)

Subject		Site 1	2	3	4	Skin temp. (° C)
D. A. T.	*W*	0·0	+0·5	0·0	−0·5	33
	C	+1·0	−1·0	−1·0	−2·0	—
J. M. G.	*W*	Unobtainable	+2·5	+2·0	+1·0	31
	C	Unobtainable	+2·0	−4·0	−2·0	—
L. P.	*W*	Unobtainable	Unobtainable	+0·5	0·0	31
	C	Unobtainable	Unobtainable	−4·0	−8·0	—
R. J.	*W*	+1·5	+1·0	+1·0	+0·5	32
	C	−4·0	−2·5	−3·0	−1·5	—
W. D. T.	*W*	+4·5	+1·0	+0·5	+1·0	29
	C	−1·0	−2·0	−3·0	−0·5	—

Variations in threshold due to the cross-sectional area of the stimulus

Threshold determinations at two selected sites were made in each of four subjects, using 123, 50, 12·6 and 1·8 mm² tips in a random order. If the skin temperature changed in the course of an experiment the readings were discarded. The threshold for warmth (Table 3) was found to increase with a decrease in the cross-sectional area of the stimulus. In addition, it was found that the thresholds were more consistently reproducible when the stimuli of larger area were used and the scatter between the individual determinations was found to increase as the area of the stimulus decreased. With a stimulus 1·8 mm² two of the four subjects could not detect the thermal nature of the stimuli even at +20. They reported the stimuli to be neutral or cool until the stimulus temperature rose to the level of about 45° C when they reported pain. It is of some interest to note that this inability to detect the correct thermal status of warm stimuli was noticed in each case when the glabrous skin was being stimulated (sites 2 and 5); whereas, the warmth thresholds were always obtainable over the hairy skin (site 3).

On the contrary, the thresholds for cold (Table 3) remained remarkably constant as the area of the stimulus decreased. In only one area in one subject (J.M.G., site 2) did the cold threshold show any noticeable rise, when the smallest stimulus was being used.

TABLE 3. Warmth and cold thresholds in relation to the cross-sectional area of the stimulus

Subject	Test site	Skin temp. (° C)	Cross-sectional area of the stimulus (mm^2)	Warmth threshold (° C)	Cold threshold (° C)
D. A. T.	2	26	123·0	+1·5	−1·0
			50·0	+2·0	−1·0
			12·6	+3·5	−1·5
			1·8	Unobtainable, cannot be evoked	−1·5
	3	25	123·0	+1·0	−1·0
			50·0	+1·5	−1·0
			12·6	+1·5	−1·0
			1·8	+2·0	−1·5
E. P.	4	21	123·0	+1·0	−1·0
			50·0	+1·25	−1·0
			12·6	+2·50	−1·5
			1·8	Unobtainable 'paradoxical'	Unobtainable 'paradoxical'
	2	24	123·0	+0·5	−1·5
			50·0	+0·5	−1·0
			12·6	+4·5	−1·0
			1·8	Unobtainable 'paradoxical'	−1·0
J. M. G.	3	25	123·0	0·0	−1·0
			50·0	0·0	−2·0
			12·6	+2·0	−2·0
			1·8	+3·0	−2·0
	2	24	123·0	+2·0	0·5
			50·0	+3·5	−2·0
			12·6	+4·0	−2·0
			1·8	Unobtainable, cannot be evoked	−4·5
J. G.	5	20	123·0	+1·0	−3·0
			50·0	+1·0	−3·0
			12·6	Unobtainable, not consistent	−3·0
			1·8		Unobtainable
	4	22	123·0	+1·0	−1·0
			50·0	+1·0	−1·0
			12·6	+1·5	−1·0
			1·8	+2·0	−1'0

Stimulation with the 1·8 mm^2 tip was often followed by an 'after-glow' which was initially thermal in nature and then became tactile, fading gradually in 10–15 sec. It was also noticed that the stimulus had to be kept on to the test site for a certain minimum duration below which even the supra-threshold stimuli did not evoke any sensation. A further study relating to this point is in progress.

When the copper cylinder of 0·78 mm² at 19° C was applied to the forehead and lips, 98 % of the reports elicited were 'cold like metal' whereas 95 % of the reports following stimulation with the wooden cylinder of the same cross-sectional area and also at 19° C were 'touch—neither warm nor cold'. These observations were confirmed in three of these subjects using the copper wire and nylon thread, both 0·102 mm² and at 19° C on the lip and in some cases on the forehead and hairy skin of the hand, but none of the subjects reported 'cold' when the stimulus was applied to the test sites 1, 2 and 5 on the palm of the hand.

TABLE 4. Responses of subjects on penetration with the quartz needles into hairy skin

Subject	Prick and sting	Touch	Tickle	Warmth	Cold	Nothing	Itch	Total
A. W. D.	45	54	1	Nil	Nil	6	Nil	106
F. B.	54	67	2	Nil	Nil	5	Nil	128
B. P.	85	98	1	Nil	Nil	24	Nil	208
J. G.	38	17	32	Nil	Nil	3	13	103
A. S.	76	83	3	Nil	Nil	19	6	187

Following these experiments two subjects volunteered the information that even the application of a pin point to the forehead or the lip aroused a sensation of cold. To test the contention that a pin point could arouse such a sensation by direct stimulation of 'cold nerve-endings', quartz needles were inserted into the hairy skin of the forehead and of the hand to depths varying from 0·5 to 3·0 mm in a random order in five additional unsophisticated subjects. In each subject over 100 stimuli were delivered and the subjects were requested to report in their own terminology the nature of the first sensation in the test area of which they were aware. The results analysed in Table 4 show that reports referable to the warmth and cold modalities were absent.

DISCUSSION

In the past, most investigators imbued with the conception that the cutaneous sensory unit is a modality specific point (a natural outcome of the von Frey theory of punctate sensibility, 1895) chose thermal stimuli of the smallest possible dimensions, for the investigation of thermal sensibility. The use of such minute and unnatural stimuli in untrained subjects led to experimental results which were usually variable, often discrepant, and sometimes even conflicting (Blix, 1882; Goldscheider, 1911; Bing & Skouby, 1949). This is no longer surprising in view of the fact that the scatter of the results is large when the stimulus size is small and falls rapidly with an increase in the cross-sectional area of the stimulus. This has recently been demonstrated both for tactile (Lele, Sinclair & Weddell, 1954) and radiant thermal stimuli (Wright, 1951; Lele, Weddell & Williams, 1954). For this reason, a stimulus 123 mm² in cross-sectional area (the largest size which could conveniently rest on the smallest test site) was selected for use in the quantitative aspects of this investigation.

In addition, many of the earlier investigators in their preoccupation with the physical attributes of the stimulus, i.e. the shape, size, duration, thermal state, etc., have neglected to take into account the state of the receptor organ, the skin. Moreover, no attention seems to have been paid to the second law of thermodynamics and no attempts were made to measure the temperature of the skin before applying the stimulus. The resting skin temperature measured in the preliminary runs in this investigation was found to vary between 18 and 35° C at thermal 'equilibrium'. An analysis of the literature shows that in sensory testing experiments various stimulus temperatures from 34 to 43°C have been used to test for warmth and temperatures up to 30° C for cold, regardless of the skin temperature (Lowenstein & Dallenbach, 1930). Since the skin temperatures have not been taken into account it is probable that some fallacious results have been reported. For instance, at a skin temperature of 20° C a 'cold' stimulus of 24° C would be recorded as an instance of 'paradoxical' warmth.

The alterations in skin temperatures induced by immersion in water were within the physiological range as they did not exceed the limits of 'normal' skin temperatures obtained in the preliminary experiments by more than ±2° C in all but a few experiments. And, since in our experiments the tests were carried out only when the skin temperature was stable and only in the absence of subjective sensory phenomena and of any changes in touch thresholds (Marshall, 1953), it seems reasonable to conclude that the results relative to thresholds and skin temperature reflect the mechanism underlying thermal sensibility under physiological conditions. Under these experimental conditions it has been demonstrated that warmth and cold thresholds are not fixed quantities but vary independently of each other, from subject to subject and from site to site, and are related to the temperature of the blood and the ambient temperature. Since threshold is a measure of the degree of excitability of nerve endings, this means that the activity of the nerve endings subserving temperature sensibility must be directly related to the state of their thermal environment. However, it is evident (Fig. 2) that a sensation of warmth was reported when the sum of the skin temperature and stimulus difference lay between wide limits, i.e. approximately 21 and 35° C. Thus it is unlikely that nerve endings subserving thermal sensibility *in the test sites examined*, behave as 'thermometers' giving rise to impulses only when brought within the temperature range to which they are specifically sensitive (Hering, 1877). The results reported by Lele, Weddell & Williams (1954), who used radiant thermal stimuli, confirm the observation that nerve terminals related to thermal sensibility do not behave as 'thermometers'. Again, with reference to previous investigators not cognizant of the fact that the threshold for warmth is high at low skin temperatures, inadequate 'warm' stimuli in this range would appear to yield a dissociated anaesthesia for warmth where none in fact existed. Clearly, therefore, skin temperature and the threshold variability will have to be taken into account in future physiological and clinical studies concerned with thermal sensibility.

The only other attempt to investigate the variability of temperature thresholds is that of Ebaugh & Thauer (1950) and Thauer & Ebaugh (1952) who exposed two subjects to varying environmental temperatures for 20–30 min during which time, presumably, 'thermal equilibrium' occurred (though surprisingly enough they did not mention anything about this). They then measured warmth thresholds by exposing the test site (i.e. the forehead) to a block of dry ice. They reported no changes in warmth thresholds though the cold thresholds increased with rising skin temperature. The range of skin temperatures attained in their study was from 30 to 34° C. It is clear from Fig. 2 that within this range of skin temperatures, although cold thresholds increase slightly, the warmth thresholds change very little, if at all. It is not surprising therefore that Ebaugh & Thauer overlooked changes in the warmth threshold although they detected an increase in the cold thresholds with a rise in skin temperature.

Even when the skin temperatures at different test sites were the same, the thresholds for warmth and cold (using 123 mm^2 stimulus) are seen to vary independently of each other within wide limits at different sites. Some areas are found to be comparatively insensitive to cold, to warmth or to both. However it is not possible to ascribe this to any distinct difference in the pattern of innervation of the test sites, i.e. to glabrous or hairy type of skin. There is no reason to suppose that this state of affairs is restricted to the hand and does not apply to other regions of the body. Thus, because of the variability of the skin temperatures and of the thresholds, it is apparent that a given stimulus which is adequate to evoke a thermal sensation at one site on one occasion may be inadequate at another site or at the same site on another occasion.

Paradoxical is a word derived from the Greek, meaning 'incredible' or 'occurring at variance with the normal rule'. Hence 'paradoxical' cold would mean the sensation of cold elicited when a warm stimulus has been applied. In the present context a warm stimulus is any stimulus at a higher temperature than the skin surface. Similarly, 'paradoxical' warmth would be the sensation of warmth evoked by a stimulus at a lower temperature than the skin surface. Defined thus, paradoxical sensations were not infrequently noticed in the course of this investigation. The incidence of paradoxical sensations was much greater in some subjects and at certain sites. At site 1, even using a stimulus size of 123 mm^2, it was not possible to establish consistent thresholds in two subjects, because in a number of runs as many as 30 % of the responses elicited were paradoxical. At this site, the change in skin temperature did not materially alter the number of such responses. Some other sites which had consistent reproducible thresholds also yielded consistent paradoxical responses when the skin temperature was within a certain range, e.g. at site 4 at a skin temperature between 32 and 35° C a stimulus of -1 was consistently reported warm. However, all sites gave a large number of paradoxical responses for up to 3 hr after immersion in water at the highest temperatures that could be tolerated without pain.

Paradoxical sensations have been described by many workers such as Strümpell (1881), Blix (1882), Goldscheider (1911) and, more recently, Jenkins (1938); and they have been used by some to formulate hypotheses about the depths at which heat and cold receptors lay. Von Frey (1895), because of his belief in the specific and punctate nature of the cutaneous unit of sensibility, laid down that for a sensation to be termed 'paradoxical', a single modality-specific end-organ must be stimulated by a specific temperature and a response of the opposite sign obtained. However, since doubt has been cast on the morphological specificity of the encapsulated nerve endings, many of them having been demonstrated to be histological artifacts owing to imperfect technique (Weddell, Pallie & Palmer, 1954), the suspicion arises that many 'paradoxical' responses may have been functional artifacts owing to imperfect experimental design. It is probable, however, that some of the consistently recurring instances of paradoxical sensation encountered in this investigation and those of Sinclair & Hinshaw (1951) are of significance in relation to the mechanism of sensibility.

The variability of the thresholds in relation to the cross-sectional area of the stimulus clearly indicates that the site of the stimulus is an important factor in thermal sensibility and particularly so in investigations of a quantitative nature. The fact that the thresholds, as well as the scatter of the observations, rise with decreasing stimulus size makes it necessary to use stimuli of relatively large cross-sectional area if consistent results are to be obtained.

Warmth thresholds show a marked fall as the cross-sectional area of the stimulus increases from 1·8 to 123 mm^2 and this is evidence of spatial summation for warmth within this range. On the other hand, in the case of cold stimuli of the same cross-sectional areas there is no clear-cut evidence in favour of spatial summation. Of particular interest is the fact that in certain regions (always provided there is a reasonable difference of temperature between the stimulus and the skin) the cross-sectional area of the stimulus necessary to arouse a report of cold is so small as to lead the subject into the belief that a point 'cold' source is an adequate stimulus; moreover, it appears that there is virtually no region on the lips or the forehead which, when stimulated with a point 'cold' source, does not evoke a report of cold. This effect is somewhat less marked on the back of the hand and is not demonstrable in certain regions on the palm and fingers. It is also clear that the point 'cold' source is, in effect, an object which can conduct heat from the skin, for cold is never reported when a non-conductor is employed under similar circumstances. Presumably, it might be argued that there are end-organs which give rise to impulses in response to 'cold' just beneath the skin surface and that the more available they are to stimulation (i.e. the thinner the cornified layer) the more the skin surface as a whole gives rise to reports of cold when stimulated. In other words, it might seem that endings for 'cold' are very numerous and cold 'spots' are due to the relative accessibility of specific 'cold nerve endings' rather than the absence of such endings in between 'cold spots'.

If this argument were true, then it should be possible to insert needles into the skin and stimulate endings or nerve fibres to arouse reports of cold and warm as well as other modalities commonly reported as being 'felt in the skin'. Woollard, Weddell & Harpman (1940) claimed that this could be done; however a re-analysis of their observations (in consultation with Dr Weddell), with particular reference to their methods, shows that thermal sensations were only aroused when fine *steel* needles were used. The needles were prepared by etching so that surmounting the shaft there was a fine (20–80 μ) tip of approximately uniform diameter from 1 to 4 mm in length. Reports of cold and warmth sensations were few and far between, and occurred only when the whole of the tip had been inserted into the skin. The present observations show that, during over 700 penetrations, all the sensations reported in Table 4 could be aroused except those of a thermal nature when *quartz* needles were used. The critical difference between these two sets of experiments is the thermal conductivity of the material from which the needles were made. These observations in conjunction with those of Bishop (1943) strongly suggest that the various reports elicited, including those relating to the temperature mode, are related not to the stimulation of specific endings but to the manner in which non-specific nerve endings or fibres in the skin are stimulated. These observations, together with those of Woollard *et al.* (1940), suggest that cold stimuli are more likely to affect non-specific nerve endings lying in strata more accessible and therefore usually more superficial than those related to the warmth mode.

SUMMARY

1. The skin temperatures at various test sites on the hand vary between 18 and 35° C even when the subject is in thermal equilibrium at a constant ambient temperature.

2. The thresholds (defined as the least temperature differences which can be distinctly perceived) to contact warmth and cold stimuli vary from subject to subject, and from site to site, and do so independently of each other. They are, however, consistently related to the skin temperature at the site under test. The warmth thresholds are high at low skin temperature and decrease as the skin temperature rises. The cold thresholds are lowest at low skin tem-

peratures and increase when the skin temperature rises above 35° C. The variation of the thermal thresholds with skin temperature is far more pronounced for warmth than for cold, and persists till the skin temperature reaches the upper limit of the physiological range.

3. The thresholds vary from site to site even when the sites are at the same temperature, and this variability is not correlated with the neurohistological pattern of the skin, viz. glabrous or hairy skin.

4. The thresholds also vary in relation to the cross-sectional area of the stimulus in the range studied, the warmth threshold rising as the cross-sectional area decreases. Cold thresholds do not show a comparable increase as area decreases.

5. A cold sensation can be elicited by areas of the size of a pin point provided the stimulus is able to conduct heat rapidly. No thermal responses are elicited when the skin is pierced for up to 3 mm by fine quartz needles, although touch, prick, itch, tickle and no sensation are reported. It is suggested that cold stimuli are more likely to affect non-specific nerve endings lying in strata more accessible and therefore usually more superficial than those related to the warmth mode.

6. The importance of these facts in relation to clinical sensory testing is evident.

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