LOCAL ACCLIMATIZATION OF THE HANDS TO PROLONGED COLD EXPOSURE IN THE ANTARCTIC

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ABSTRACT. Calorimeters were used to measure the heat loss from the hands of eight subjects at frequent intervals during their tours of duty in the Antarctic. The experiments, at test temperatures of 20° and 30°C, were conducted while the subjects remained in bed after a normal night's sleep. In any series of experiments, considerable variations in heat flow were observed, both between subjects and between replicate experiments on individual subjects. Differences between experiments in room temperature, sub-clothing temperature, hand temperature and comfort were not found to exert a systematic influence upon the measured heat flows.

Statistical analysis showed no consistent differences between the measurements of heat flow at the two test temperatures. This was presumably due to interaction between the direct effect of local temperature on blood flow to the hand and the indirect effect on the temperature of arterial blood entering the hand (arising from the re-distribution of returning blood between superficial and deep veins).

Analyses of variance used to test for seasonal differences between series of experiments showed that a highly significant fall in heat flow occurred from initial control experiments to experiments in the following winter. By the succeeding summer, heat flows had returned towards control levels.

It is suggested that the observed changes in heat flow were produced by alterations in the blood supply to the hands. The modifications to the peripheral circulation were shown to occur in parallel with seasonal changes in environmental temperature. It is concluded that the increase in cold stress experienced in winter led to a seasonal reinforcement of the level of vasoconstrictor tone in the hands.

MANY workers have described evidence of adaptation to cold in Man, but reviews of the literature (e.g. Burton and Edholm, 1955; Hammel, 1964; Hampton, 1967) demonstrate a lack of agreement concerning the general mechanisms by which adaptation is achieved. There is even some doubt whether Man from temperate zones may be expected to show further adaptation to cold (Macpherson, 1958; Norman, 1965).

Investigations into the role of the peripheral organs, particularly the hands, in adaptation have yielded more positive findings. Measurements of changes in extremity skin temperatures in tests of cold adaptation following seasonal, laboratory or field exposure have implied the occurrence of modifications to the peripheral circulation (Newburgh and Spealman, 1943; Balke and others, 1944; Horvath and others, 1947; Stein and others, 1949; Daniels and others, 1951; Carlson and others, 1953; Rennie, 1957; Scholander, Hammel, Andersen and others, 1958; Kreidner and others, 1959; Davis, 1961; Milan and others, 1961; Budd, 1964; LeBlanc and others, 1964; Andersen, 1966; Budd and Warhaft, 1966).

Direct experimental evidence of changes in physiological function of the extremities after prolonged exposure has come principally from many studies of the cold-induced vasodilatation response. When the hands, or fingers, are placed in very cold water, the skin temperature is observed to fall until, at about 10°C, spontaneous re-warming occurs. Subsequently, the skin temperature alternates between periods of cooling and re-warming in the so-called "hunting" phenomenon (Lewis, 1930), usually remaining many degrees above the temperature of the water. Most subjects feel intense pain during the phases of vasoconstriction.

In subjects whose hands are habitually exposed to cold, such as fishermen, or whose hands have been experimentally acclimatized to cold, the characteristics of the cold-induced vasodilation response are frequently observed to be modified. It has been found in such subjects that the initial constriction is less intense and that the first wave of dilatation occurs earlier and at a higher skin temperature. Subsequent skin temperatures are frequently higher in adapted than in non-adapted subjects, and less pain and general discomfort are usually experienced.

This response has been obtained in Andean Indians (Baker, 1963), Eskimos (Meehan, 1955; Miller and Irving, 1962; Eagan and Evonuk, 1964), Arctic Indians (Meehan, 1954; Elsner and others, 1960), Lapps (Krog and others, 1960) and Japanese (Yoshimura and Iida, 1952). The same sensitized response has also been observed in European subjects who habitually work with their hands in cold water, for example, Gaspé fishermen (LeBlanc and others, 1960), Norwegian fishermen (Krog and others, 1960) and British fish filleters (Nelms and Soper, 1962).

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Seasonal changes in the cold vasodilatation response have been demonstrated in Japanese subjects by Yoshimura and Iida (1952) and in Gaspé fishermen by LeBlanc (1962*a*). When the test was given to the same subjects in winter and in summer, vasodilatation was found to occur earlier and at a higher skin temperature during the colder time of year.

From the relationship between cooling rate, or heat flow, and hand volume, LeBlanc and others (1960) and Miller and Irving (1962) concluded that the difference between adapted and non-adapted subjects lies in the local circulation to the hand. Krog and others (1960) confirmed this by direct measurement of hand blood flow during cold vasodilatation.

In contrast to the wealth of information describing the reactions in cold-adapted subjects after placing the hands in very cold water, similar knowledge of the function of the peripheral circulation at higher local temperatures is not well documented. The most extensive and comprehensive studies were a series of plethysmographic measurements of the peripheral circulation in the Southampton Island Eskimos (Brown and Page, 1952; Brown and others, 1953). Comparing the Eskimos with White control subjects at an environmental temperature of 20°C, these authors found that the Eskimos maintained higher blood flows in hand and forearm over a range of local temperatures between 5° and 45°C. At the lower temperatures, the blood flow in the Eskimo group was observed to fall much more slowly than in the controls. The Eskimos were also found to maintain high hand and forearm blood flows during immersion of the feet in water at 10°C (Page and Brown, 1953).

However, other experiments have failed to demonstrate similar differences in hand blood flow between Lapps and north Norwegian fishermen and controls when tested at local temperatures of 10°, 20° and 40°C (Krog and others, 1960). In these experiments, however, measurements of local blood flow were not commenced until release of general vasoconstrictor tone was indicated by the presence of slight sweating, or a hand temperature of 35°C or above.

Few authors have made direct comparisons of blood flow before and after cold adaptation has been induced. Bader and Mead (1950) could find no changes in blood flow through the finger in warm ambient temperatures after their subjects had completed a 14-day bivouac in the Arctic winter. Wood and others (1958) measured forearm blood flow at an ambient temperature of 27°C, before and after their subjects had spent 14 days in a climatic chamber, exposed naked to a temperature of 16°C. Wood and others (1958) found that the level of forearm blood flow was reduced by about 20 per cent after the period of adaptation.

The clearest evidence for local adaptation of the extremities to prolonged cold exposure has been provided by Mackworth (1955), who used a simple test of sensory discrimination. He was able to show, when the hands were submitted to a standard cooling stress, that outdoor workers became less numb than indoor workers, that seasonal changes in the index of numbness occurred and that improvements in numbness could be induced by repeated exposure of the hands to cold stress. Following this work with experiments in the Antarctic, Massey (1959) obtained similar results in induced numbness when men in their second year were compared with new arrivals. He showed that the differences disappeared within the first 6 weeks of residence in the Antarctic.

Mackworth (1955) also measured the skin temperature of the fingers before each test and, from comparisons of the temperatures measured in adapted and non-adapted subjects, he concluded that the differences in numbness originated from an increased blood supply to the hands after prolonged cold exposure. Massey (1959) did not observe that changes in pre-exposure skin temperature occurred in step with the changes in numbness; however, he did find that the pre-test skin temperatures of both groups were lower after the main sledging journeys of the winter/spring period (the time of greatest exposure to cold) than those observed at the beginning of the year.

The present study was designed to supplement knowledge of the behaviour of the blood circulation to the hands at relatively high local temperatures, during a period when prolonged exposure to cold was anticipated. Also, it was hoped that the experiments would shed light on the suggestion that improvements in finger numbness during cold exposure are associated with an increased blood supply to the hands. The experiments were carried out in 1959 and 1960 at the British Antarctic Survey station at Hope Bay (lat. 63°24′S., long. 56°59′W.), where all personnel participated in field work for 6 months in every year.

METHODS

The subjects

Details of the eight subjects are shown in Table I. Subjects A-D were studied over a period of 2 years. They also took part in experiments in the Falkland Islands before arrival in the Antarctic, and again in a final series of experiments 6 months after their return to the United Kingdom. Subjects E-H were studied during 1 year—the second year of the period for subjects A-D. For subjects E-H the first experiments took place immediately upon arrival at the Hope Bay station.

TABLE I. THE PHYSICAL CHARACTERISTICS OF THE EIGHT SUBJECTS TAKING PART IN THE CALORIMETRY EXPERIMENTS

Subject	*Age** (yr.)	*Height* (cm.)	*Average weight†* (kg.)	*Hand volume* (ml.)		*Occupation*
				Initial‡	*Final§*	
A	27	178	70·25	481	487	Wireless operator/general assistant
B	27	165	65·50	475	469	Surveyor
C	22	169	58·25	355	355	Physiologist
D	28	185	81·00	578	589	Medical officer
E	22	185	86·50	579	561	Geophysicist
F	23	185	84·00	443	441	Meteorologist
G	27	180	64·75	467	416	Meteorologist/general assistant
H	31	185	90·75	567	561	Meteorologist/general assistant

* In first year.
† Average for first year.
‡ Average of three determinations to level of styloid process; at the beginning of the subject's tour of duty.
§ As above, at the end of the subject's tour of duty.

The calorimeter

The two calorimeters (Fig. 1a and b) were based on 4-l. vacuum flasks, the design being modified from that used by Greenfield and Scarborough (1949). The vacuum flask was contained in a large wooden box and held in place by pieces of expanded polystyrene foam, which served both as protection and as an insulating material. A two-piece wooden platform, backed with foam, fitted snugly into the top of the box. One half was permanently screwed in position to form a base for the electrical stirring and measuring devices, while the other was removable to facilitate the insertion of the hand.

A 12-V electric motor turned a hollow Perspex cone, provided with a large hole at the bottom and a series of smaller holes around the circumference at the top. In motion, water was drawn in at the bottom of the cone and expelled by centrifugal force through the holes at the top. This method of stirring proved very efficient.

In the initial experiments conducted on board one of the Survey's supply vessels at the quayside in the Falkland Islands, power was supplied to the motor by 12-V lead–acid accumulators. These were kept well charged and no significant change in voltage occurred during the course of an experiment. In the Antarctic, electricity was supplied by the station's generators. To eliminate variation in heat input from the stirrer, the motor was energized via a power pack designed to give a stabilized d.c. output of 11·6 V at a maximum current of 0·9 A for an a.c. input varying from 190 to 265 V.

The temperature of the water was measured by a thermistor (Standard Telephone Company, bead type M) attached to a Perspex rod at the bottom and to one side of the flask. The thermistor was shielded from the direct influence of the hand by a copper baffle, which also acted

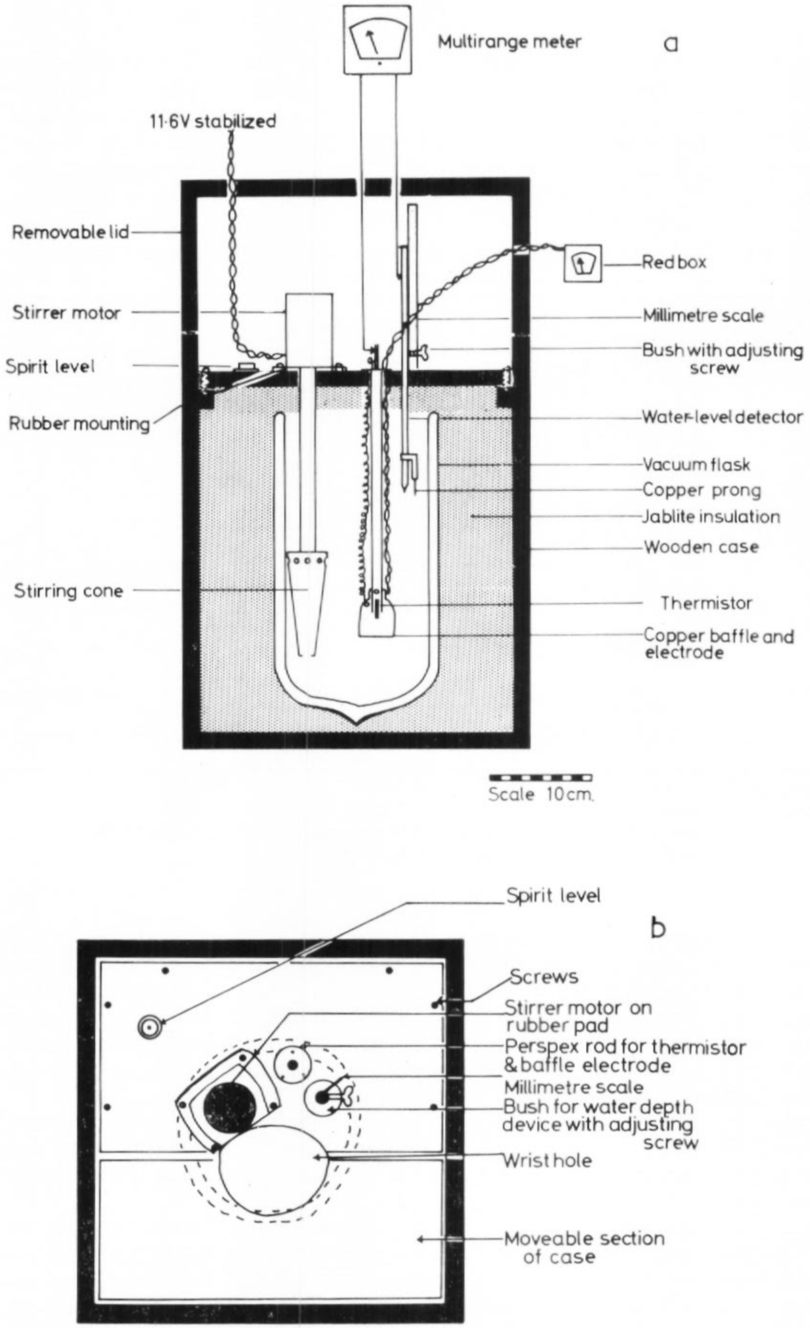

Fig. 1. The calorimeter.
a. Sectional view, showing the arrangements for stirring the water, measuring its temperature and detecting changes in the water level. "Red box" is the name given to the Wheatstone bridge circuit and galvanometer. "Jablite" is an expanded polystyrene foam. The lid was used only for protection during transport.
b. Plan view of the instrument base. Before use in an experiment, the calorimeter was levelled with the small spirit level.

as an electrode for the water-depth detecting device. The resistance of the thermistor was measured with a portable Wheatstone bridge circuit ("Red box"). For improved sensitivity, the currents passing through the galvanometer were amplified by additional transistorized circuitry. The calibration of the thermistor was checked before each series of experiments.

Changes in water temperature of 0·03°C could be detected by this method. The thermistor was therefore less sensitive than the mercury-in-glass thermometers commonly employed in calorimetric studies, but the reduced sensitivity was not important in view of the method used to calculate the heat elimination from the hand.

The immersed hand volume was also measured electrically. A long pointed alloy rod passed through a bush in the instrument base in such a way that the length immersed in the water could be adjusted and measured on a scale. 2 cm. from the pointed end of the rod, a prong made of stiff copper wire was connected to the rod through a 68 kΩ resistance. The vertical separation of the tips of prong and rod was about 1·5 mm., the copper prong being the lower. A resistance meter, set on the 100 kΩ range, was connected to the alloy rod and also to the copper baffle surrounding the thermistor, the baffle acting as the indifferent electrode. When the copper prong just touched the water surface, a deflection of about 100 kΩ appeared on the meter. When the hand displaced more water, the water level rose, passed the point of the copper prong and touched the end of the aluminium rod, causing a fall in resistance to about 40 kΩ. Conversely, if the hand withdrew from the flask, electrical continuity was lost, giving an immediate indication on the meter. In this way the volume of the hand immersed in the water could be measured and monitored during an experiment. Changes in volume of 10 ml. could be detected.

Determination of the water equivalents of the calorimeters

If the temperature of a known volume of water is raised by supplying a known quantity of heat, then (assuming no other sources of heat gain or loss)

$$A = (m+W)t \qquad \text{or} \qquad m+W = A/t,$$

where A is heat supplied (arbitrary units), m is water volume (ml.), W is water equivalent (ml.), and t is rate of rise of temperature (°C/min.).

If several different volumes of water are heated by the same supply, a plot of m against $1/t$ will intercept the m-axis at $m = -W$.

The water equivalents of the calorimeters used in the present experiments were determined by heating volumes of water, between 1,500 and 4,000 ml., with two 12-V 24-W bulbs energized via the power pack. A plot of m against $1/t$ showed the coordinates fall on a straight line, giving values for the water equivalent of 220 and 250 ml. for the two calorimeters used.

Heating or cooling corrections

To determine the heat exchange between the calorimeter and the environment, a number of experiments were conducted at ambient temperatures ranging from 0° to 10·9°C, with initial water temperatures at 20° and 30°C. During these experiments the stirrer was in operation and the hole normally occupied by the wrist was closed with insulating material. The water temperature was measured every minute for 1 hr.

When the water temperature was initially at 30°C, no change in temperature was detectable after 1 hr. in either calorimeter at any level of environmental temperature. With water initially at 20°C, one calorimeter showed a temperature rise of 0·15°C and the other of 0·30°C after 1 hr. at environmental temperatures between 5° and 20°C. These corrections were considered small and were ignored in the final calculation of the results.

Experimental method

At the Hope Bay station it was not possible to control the temperature of any room sufficiently accurately to ensure that identical conditions could be obtained throughout the year. The experiments were, therefore, performed at the subject's bedside, while the subject was still in bed, following a normal night's sleep. It was assumed that the subjects would adjust their bed clothes to create similar micro-environments in summer and winter. There is evidence that this adjustment is made by people in the United Kingdom (Goldsmith and Hampton, 1968).

The calorimeter was set up at the bedside the evening before an experiment, levelled and filled with 2·5 l. of water at a temperature slightly higher than required. Next morning the water had cooled to near the desired level and final adjustments to the temperatures were made by adding a further 500 ml. of water. The 24-W bulbs, or an ice-cold metal rod, were also available to correct the water temperature if required. The calorimeter was then allowed 15 min. to equilibrate.

These operations were carried out between 06.30 and 07.00 hr. At 07.00 hr. the subject was woken and measurements made of sub-clothing temperature (using a temperature-sensitive vest (Wolff, 1958) put on under the pyjamas the previous evening) and the temperature of the hand. To measure hand temperature the subject held a skin thermistor probe in the palm of the right hand under the tip of the third finger. The resistance of the vest and thermistor was measured with the Wheatstone bridge circuit.

The subject then turned to lie on his face and placed his hand in the calorimeter. He was instructed to immerse the hand to the level of the styloid process. The depth of immersion could not always be seen as many of the experiments were performed by torchlight while other station personnel were still asleep. However, the volume immersed could be measured accurately with the water-level detector. The subject was made absolutely comfortable with pillows, and it was ensured that he was well covered by the bed clothes. His exposed arm was covered by several towels, and the gap between his wrist and the sides of the hole in the instrument platform was filled with cotton wool. These arrangements usually took 2 min.; thereafter, the water temperature was measured as a resistance every minute for 45 min. At intervals throughout the experiment sub-clothing and room temperatures were noted. The immersed hand volume was adjusted immediately if it was observed to stray from its initial value. At the end of the experiment the subject was asked for a comfort vote (Bedford, 1936). The number of blankets on the bed was recorded, together with the pyjamas and any underclothes worn by the subject.

Heat elimination was measured during immersion of the hand at two water temperatures, 20° and 30°C. Duplicate experiments at each temperature were performed wherever possible, one each day over a period of 4 days. When two subjects were tested on the same day, the first experiments began at 06.00 hr.

The experiments were performed in the intervals between sledge journeys (Fig. 2).

Calculation of heat elimination

The resistance measurements each minute were converted into temperatures and plotted as a graph. The heat stored in the tissues of the hand was assumed to be given up to the water in the first 15 min. of each experiment (Greenfield, 1960) and to exert a negligible influence thereafter. The rate of rise in temperature between the fifteenth and thirtieth minutes was measured and used to calculate the heat elimination as follows:

$$h = 100t(m+W)/V,$$

where h is heat elimination of the hand (cal./100 ml. tissue/min.), t is observed rate of temperature increase (m°C/min.), m is volume of water in flask (ml., usually 3,000), W is water equivalent of the flask (ml.) and V is volume of hand immersed (ml.).

No corrections were made for the effect of the rise in temperature of the water during each experiment on the measured heat loss from the hands, as reductions in heat loss due to this cause are found to be small (Greenfield, 1960).

Arrangement of the results for analysis

The complex nature of the field programme at Hope Bay did not allow a schedule to be drawn up in which experiments would be carried out at regular intervals on all the chosen subjects. Instead, every opportunity was taken to conduct as many experiments as possible, when the subjects were available. In addition, the number of subjects was increased to eight in the second year. Fig. 3 shows every experiment and the month in which it was performed. For statistical analysis the experiments have been re-grouped against the month in which they were performed irrespective of the year (Fig. 4) and are seen to fall into nine series. Further justification for grouping the experiments in this way is given in the results section (p. 20-21). Together with the experiments in the Falkland Islands, and on return to the United Kingdom, these nine series of experiments were analysed as follows.

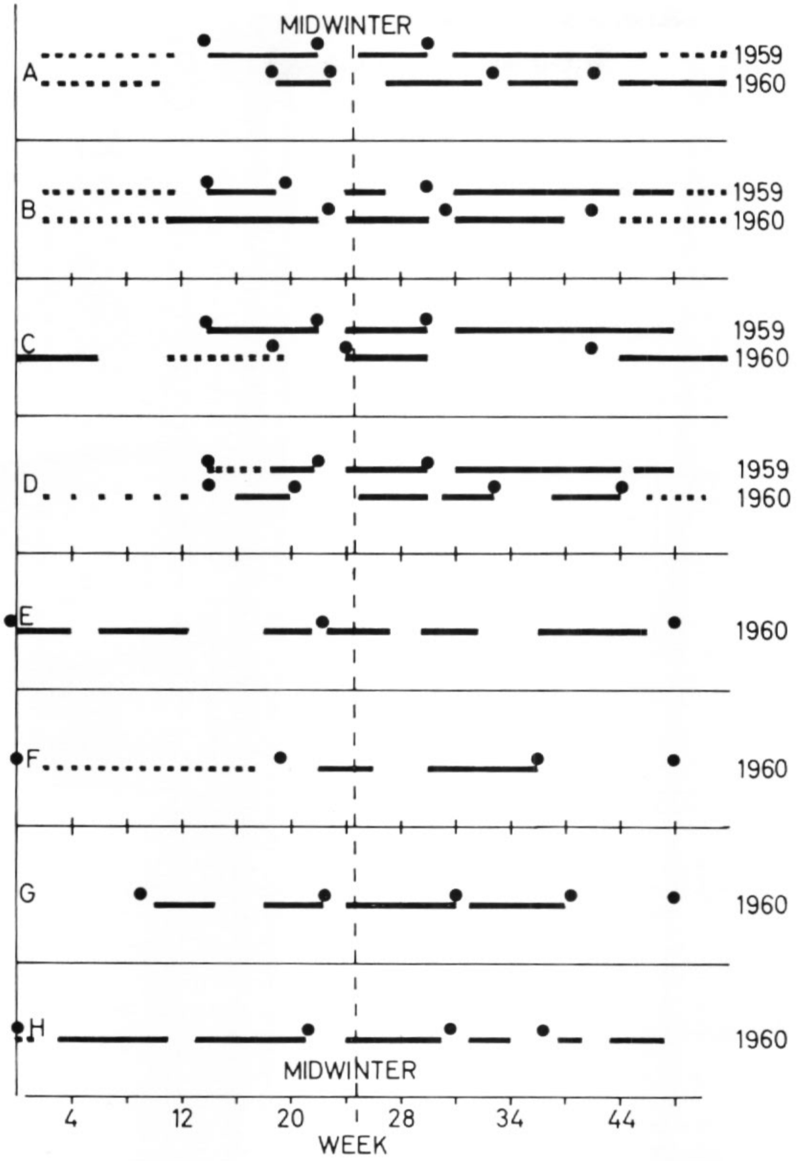

Fig. 2. The periods of the year spent in the field by each subject taking part in the calorimetry experiments.
▬ ▬ ▬ Periods away from the station and sleeping under canvas.
- - - - - - - - - - Periods of 1 or 2 days in the field, perhaps returning to the station to sleep.
● ● ● ● ● ● A series of experiments for any one subject.

The series of experiments were compared in pairs. For inclusion in the analysis a subject had to be represented in both series of experiments. Further, it was required that at least two experiments (not necessarily at the same temperature) had been conducted on a subject in any one series. No missing values were calculated for any subject.

The analysis comprised a two-way analysis of variance with replication, but sometimes with unequal numbers of replicates in the cells. The analysis gave less weight to those cells where the number of replicates was less than the maximum of four. The χ^2 values in the analyses

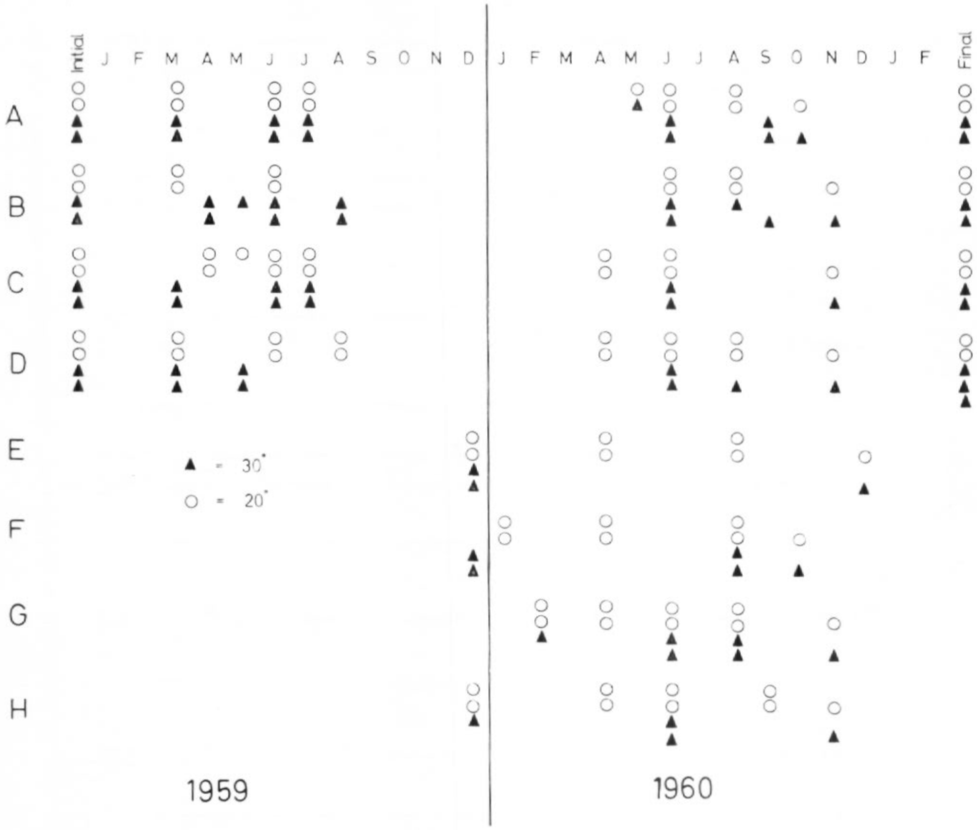

Fig. 3. The month and year in which individual experiments were performed. For subjects A–D the initial experiments were performed in the Falkland Islands before arrival in the Antarctic; the final experiments were performed 6 months after the return to the United Kingdom.

were calculated by the method of least squares, and the ratio of the χ^2 values, i.e. F, was used to test for differences between each variable. The F value, with the appropriate degrees of freedom, was referred to standard tables for significance levels.

RESULTS

The subjects' exposure to cold

It was not possible to make detailed measurements of the exposure experienced by all the subjects taking part in the calorimetry experiments. However, Fig. 2 shows information taken from the station records of the periods which each subject spent away from the station. The long continuous lines represent journeys with nights spent under canvas, the dotted segments indicate periods of travelling or field work of 1 or 2 days' duration, perhaps returning to the station to sleep. The field work was not dependent upon the season and the total amount was comparable for each subject. The time spent in the field by each subject, as a percentage of the length of his residence at the station, was: A–62, B–55, C–51, D–42, E–58, F–34, G–51 and H–42.

The broad outlines of the exposure received by these men during the periods in the field and at the station were probably not dissimilar to those observed in a detailed study of one of them (subject C; Hampton, 1967) and also to the observations made by others (Norman, 1960, 1965; Davies, 1962; Wyatt, 1963).

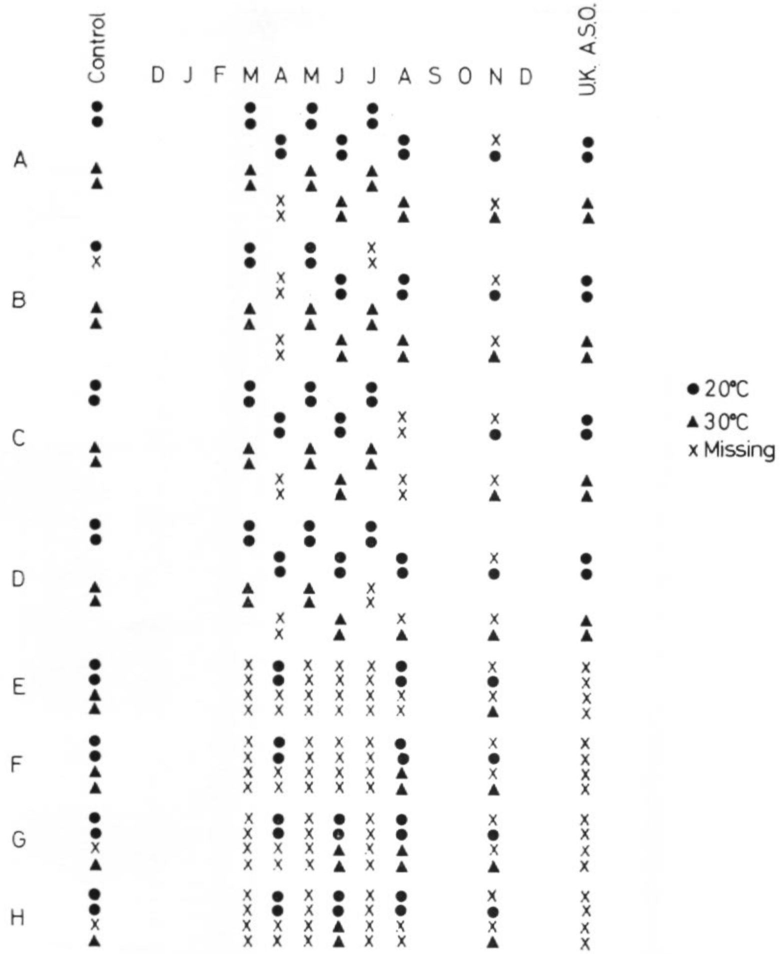

Fig. 4. The calorimetry experiments arranged in nine series against the months which they most closely represent. For subjects A–D the upper pair of experiments at each temperature was performed in 1959 and the lower pair in 1960. The experiments which would have been required to complete the matrix are shown as missing. One experiment at 20°C for subject B in the initial control is excluded as he developed a feverish illness later in the day.

Intra-individual variation in heat flow

Reference to the table of results in Appendix A shows that there were at times considerable differences between the results of replicate experiments. These differences have been summarized for individuals and they are presented in Table II. The maximum difference was 42 cal./100 ml./min., or 204·8 per cent, when the difference is expressed as a percentage of the lower figure. At best, the experiments showed good reproducibility, within 2 cal./100 ml./min. or 5 per cent, for all subjects. The average difference was 7·9 cal./100 ml./min. or 35·1 per cent.

When a pair of experiments gave widely differing results, it was seldom possible to perform a third experiment to serve as a check. (The four occasions on which a third experiment was performed, once each for subjects B and C and twice for subject D, were for reasons other than poor replication of heat flows.) On only one occasion (subject B, series 1, 20°C) was it thought fit to reject one result from an anomalous pair. The results from these two experiments were 52·4 and 140·0 cal./100 ml./min., respectively. On the day of the second experiment the subject

TABLE II. INTRA-INDIVIDUAL DIFFERENCES IN THE HEAT-FLOW MEASUREMENTS

(The table shows, for individual subjects, the average difference and range of differences between the heat flows in replicate experiments at the two test temperatures. The differences are also expressed as a percentage of the lower value of heat flow in each pair of replicates.)

Subject	*Number of pairs*	*Temperature* (°C)	*Difference between replicates* (cal./100 ml./min.)		*Difference between replicates* (per cent)	
			Mean	*Range*	*Mean*	*Range*
A	8	20	16·6	1·0–38·1	75·2	3·0–204·8
	7	30	10·6	0·8–42·0	36·5	2·2–168·0
B	5	20	6·8	1·2–12·3	42·3	9·8– 78·8
	7	30	5·3	0·6–11·9	33·5	1·4– 94·9
C	7	20	8·3	0·8–19·4	19·0	1·9– 34·8
	6	30	8·1	1·4–20·5	27·8	3·4– 97·6
D	8	20	4·7	2·0– 8·4	26·7	12·9– 38·6
	5	30	6·5	0·7–10·9	37·7	4·4–103·6
E	3	20	2·7	2·1– 3·2	9·9	6·5– 16·3
	1	30	1·9	—	7·4	—
F	3	20	3·3	0·5– 8·8	18·4	1·8– 51·2
	2	30	11·1	7·3–14·9	45·5	26·8– 64·2
G	4	20	2·5	0·0– 5·7	17·0	0·0– 46·0
	2	30	11·0	10·8–11·2	67·8	65·9– 69·7
H	4	20	9·9	3·2–22·3	32·5	8·0– 60·9
	1	30	11·3	—	40·0	—
TOTAL	73	Both	7·9	0·0–42·0	35·1	0·0–204·8

developed a heavy cold and had an elevated oral temperature. His result for that day was therefore discarded.

The variation in each pair could have arisen from three main sources: an inexact technique could have produced large differences in heat flow between replicates; the variations could be true reflections of real differences in blood flow between the two experiments arising from inadequate control of the experimental environment; the first experiment in each pair could have had a conditioning effect on the second.

To gain information on the variability of replicate experiments, in Fig. 5 the low value in each pair has been plotted against the corresponding high value. All values lie to the right of a line drawn through the origin, at 45° to the axis, and they show a linear relationship between 0 and 50 cal./100 ml./min. Above 50 cal./100 ml./min. there is much larger scatter in the relationship.

The scatter of the points on the part of the graph between 0 and 50 cal./100 ml./min. is taken to be a measure of the reproducibility of the experiments, and it shows a constant range of variability of about 12 cal./100 ml./min. for all subjects together. A dotted line drawn through the points by eye shows that the average difference between each pair was about 4 cal./100 ml./min. Individual subjects do not vary noticeably from this generalization.

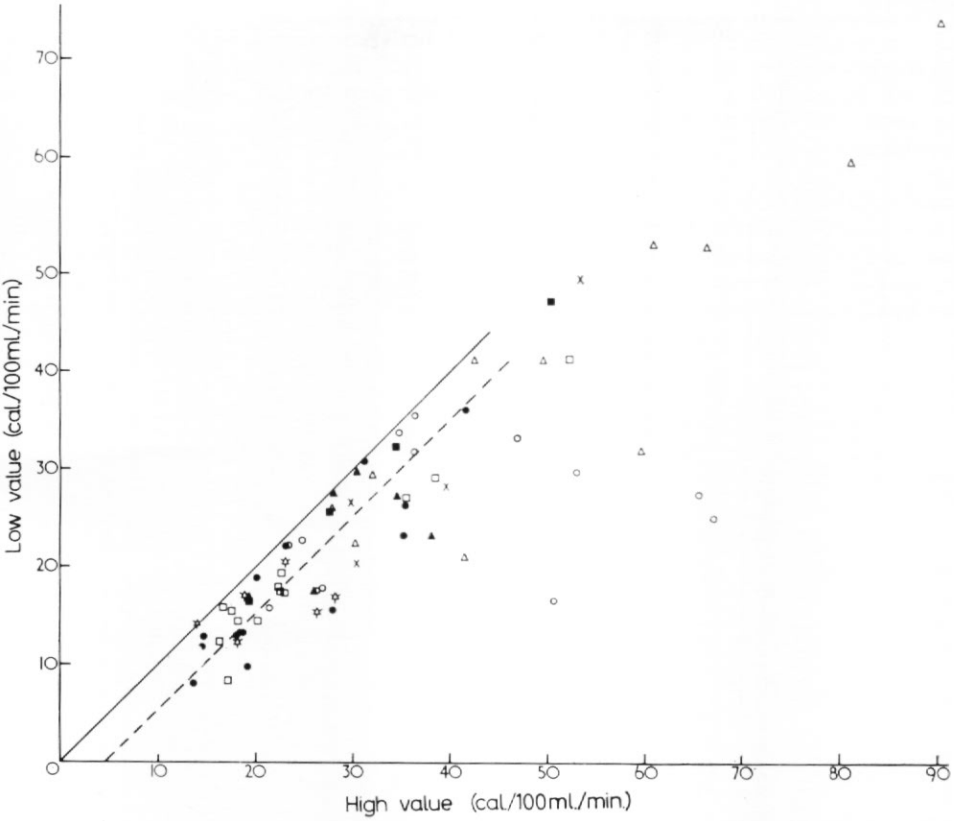

Fig. 5. The heat flows from replicate calorimetry experiments. The low value in each pair has been plotted against the high value. The solid line has been drawn at 45° to the abscissa. The dashed line has been drawn by eye through the values for heat flows between 0 and 50 cal./100 ml./min. The subjects are represented by the following symbols:
A ○; B ●; C △; D □; E ■; F ▲; G ✡; H ×.

Few experiments gave heat flows above 50 cal./100 ml./min. Above this level the greater variability within pairs was due chiefly to subject A. In only one of the pairs of experiments for this subject (16·6/50·6 cal./100 ml./min.) is there evidence of how the differences may have arisen, where the comfort vote for the low value was −1 and for the high value +1. Eleven other pairs of experiments, using this subject, gave results similar to those of the group.

It is concluded that there were real differences within pairs of experiments but that these differences were small on average and remained constant over the range of heat flows comprising the majority of the experiments. These differences were probably brought about by small uncontrolled variables in the environment, together with real physiological variation in, for example, blood flow. Had the differences been brought about by an insufficiently well-controlled technique, the variation may have been expected to be greater and the relationship more random.

In order to assess whether the first experiment in a pair had a training effect upon the replicate, the differences in each pair have been totalled for all subjects. A positive difference was taken when the second heat flow was higher than the first, and vice versa. Random differences between replicates would be expected to produce a grand total of zero. The calculation produced a grand total for all pairs of experiments of +31·5 cal./100 ml./min. or an average of 0·43 cal./100 ml./min. for each pair. This is a small figure and has been ignored in further consideration of the results. None of the totals for individuals was significantly different from zero.

Inter-individual variations

There were considerable variations in heat flow between subjects in all of the series tested. However, this was not considered to be an important aspect of the experiment as the main interest lay in the differences between series wherein each subject acted as his own control. The subjects also differed widely in physical characteristics (Table I), particularly in their hand volumes.

Seasonal variations in heat flow

Results from individual subjects. The results of experiments conducted on subjects A-D over a period of 2½ years are shown in Fig. 6. The results are plotted as a function of the months in which the experiment was performed, as shown in Figs. 2 and 3. For each subject a similar seasonal pattern of response at the two temperatures is seen. Also, during the months where

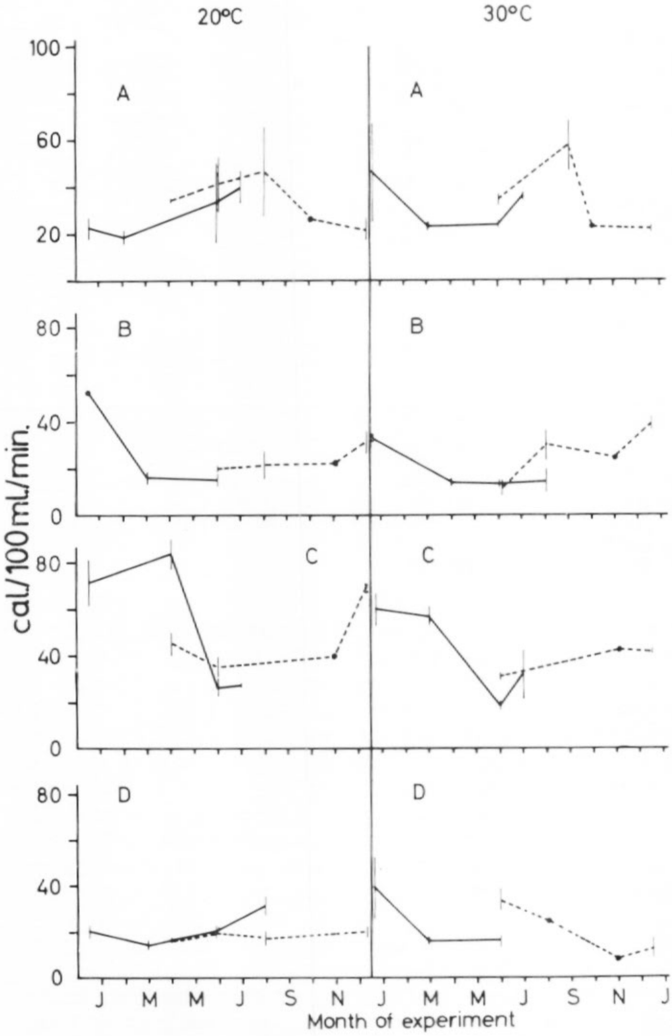

Fig. 6. The heat-flow measurements from four subjects over a period of 2½ years in the Antarctic. The vertical lines indicate the range of heat flow in replicate experiments. The solid line joins the mean of each pair of experiments in 1959, the dashed line in 1960. The results from experiments at the two test temperatures are given.

an overlap occurs the levels of heat flow are similar in the 2 years. Comparisons between the four subjects show widely varying levels of heat flow.

Subjects A, B and D all showed a fall in heat flow at both temperatures between the first and second experiments in 1959; in subject C the fall in heat flow occurred between experiments 2 and 3. In the intervening period between experiments 1 and 2, subjects A, B and D had been engaged upon ship-based field work in the Antarctic. Subject C had been resident at the Hope Bay station and had not taken part in any field work.

After this initial fall in heat flow all four subjects showed a return towards the levels observed in the first experiments. In some subjects this rise in heat flow was observed in the 1959 experiments but in others it did not occur until 1960. In either case, the pattern of the change in heat flow in individual subjects suggests that it occurred as a result of the subject's changing climatic experience during the seasons of a year, rather than as a result of a 2-year period in the Antarctic. Some subjects showed a fall in the level of heat flow in the October-November experiments of 1960 when compared to experiments earlier in the year.

Fewer experiments were performed on subjects E-H, but in general the pattern of the changes in heat flow was similar to those observed in subjects A-D (Appendix A). All four of the subjects showed an initial fall in heat flow on arrival in the Antarctic, and two subjects showed a rise in heat flow later in the year.

General pattern of the observed changes in heat flow. In Fig. 7 the heat-flow results are expressed as a percentage of the values obtained in the first experiments in the Falkland Islands, and arranged in nine separate series as shown in Fig. 4. The mean of all the heat flows measured at each series (Fig. 7d) shows a fall in heat flow between series 1 and 4, followed by a rise towards initial levels between series 4 and 7. In several subjects, particularly in the experiments at 20°C, a rise beyond control levels was observed (Fig. 7a and b).

The changes in heat flow summarized in Fig. 7d are subjected to statistical analysis on p. 27–31.

Influence of uncontrolled variables

In this study no attempt was made to control the environment in which the experiment was performed. Several factors may have influenced the results. In this section each factor is examined in turn.

Room temperature. Fig. 8 shows the mean room temperature measured at the bedside at each series, together with the mean monthly dry-bulb temperature recorded by the meteorological observers at the station. Heat flows are plotted as percentages as in Fig. 7d. For subjects B and C there was a significant relationship between heat flow and room temperature ($P < 0{\cdot}001$ and $P < 0{\cdot}01$, respectively) but subjects A and D showed no such relationship ($r = 0{\cdot}10$ and $r = 0{\cdot}23$, respectively). The correlation was significant at the 5 per cent level for subjects E, F, G and H taken together, and significant at the 1 per cent level for all subjects.

However, further information suggested that room temperature did not play an undue part in producing the observed changes in heat flow, except in so far as it reflected seasonal changes in the meteorological climate.

The records of night attire and bed clothes covering the subject at the time of the experiment showed that as the room became colder more covering was used. This relationship was significant at the 1 per cent level for seven individual subjects and highly significant for the group ($P < 0{\cdot}001$). For the group, the regression line indicated that an extra blanket was used for each 5·75°C fall in room temperature.

Sub-clothing temperature. The extra blankets used during the cold weather in winter seemed effective in preserving the micro-environment beneath the bed clothes at constant levels. Sub-clothing temperatures remained stable over a wide range of room temperatures, and no seasonal change in sub-clothing temperature was observed. The correlation between heat flow and sub-clothing temperature was not significant ($r = 0{\cdot}24$).

Hand temperature. The hand temperature measured before the experiment was not correlated with subsequent heat flow ($r = 0{\cdot}16$), although measurements of high heat flow did tend to be associated with high hand temperatures. No seasonal change in pre-experimental hand temperature was apparent.

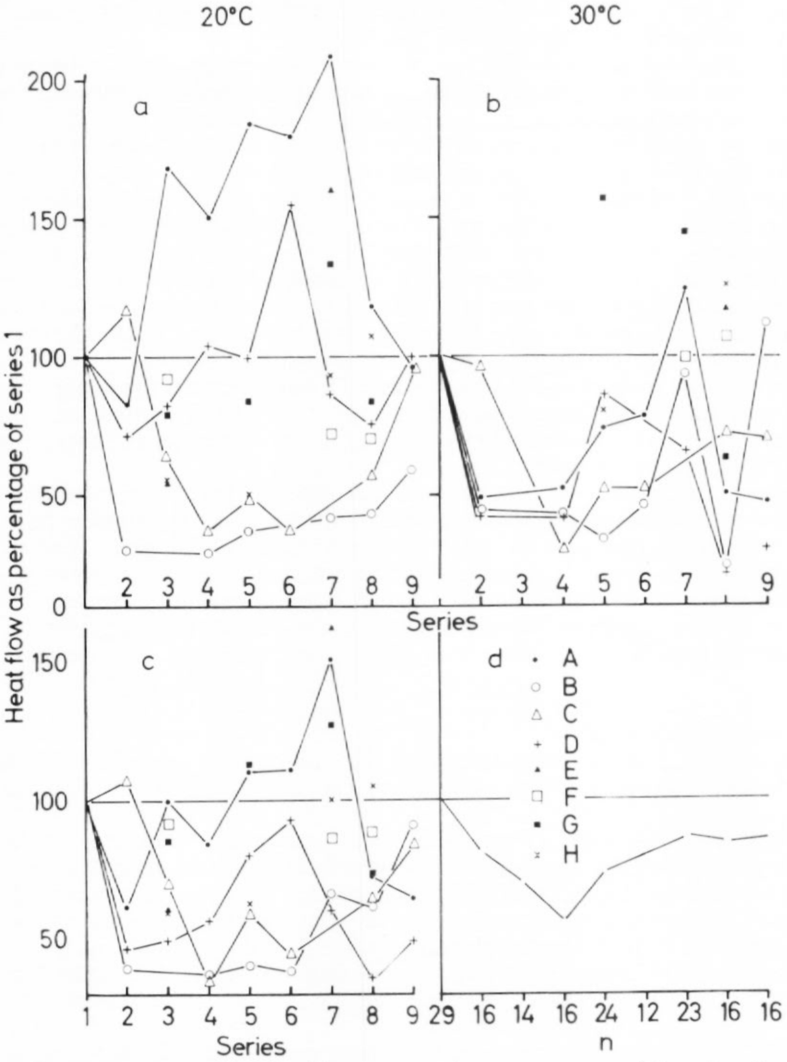

Fig. 7. The heat-flow measurements for all subjects expressed as a percentage of the values found in series 1. In a and b the mean of replicate experiments at the two temperatures is shown. In c the values from the two temperatures have been combined for each subject. In d the values from all subjects have been combined. In d each point represents the mean of individual percentage heat flows.

The lack of correlation probably arose from the high level of insulation provided by the bed clothes, which, in making the skin temperature an indeterminate point on the gradient from core to exterior, obscured the relationship between local temperature and blood flow.

Comfort. It was possible that some unmeasured variable influenced the thermal equilibrium of the body and thus affected the heat flow. Each subject was asked to describe how he felt after each experiment and the results of these enquiries are illustrated in Fig. 9. In cases where comfort was not the same in replicate experiments, the comfort vote has been plotted against heat flow for each pair of experiments. A slope upwards from left to right indicates that the heat flow was greater when the subject felt warmer.

The number of times when the subjects felt anything but comfortable was small: only 46 out of 166 experiments. A relationship between comfort and the measured heat flow was found

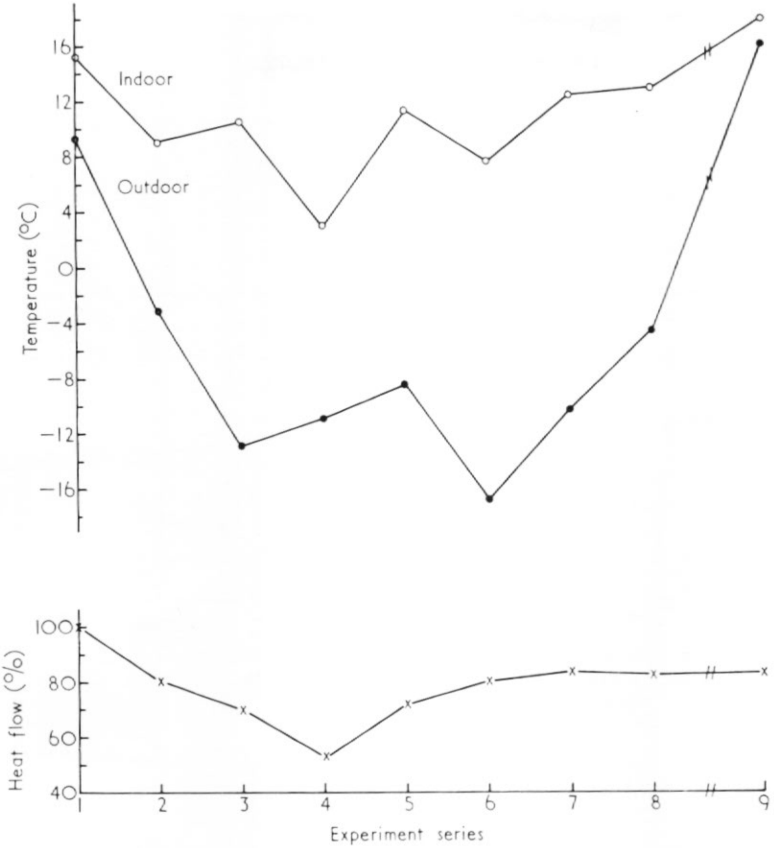

Fig. 8. Changes in heat flow and seasonal changes in room and meteorological temperature. Heat flow at each series is taken from Fig. 7d. Room temperature was measured at the bedside. Meteorological temperatures for the appropriate month were taken from the station records.

in 15 out of 23 replicate experiments. There was no statistical justification for adjusting the heat-flow results on the basis of the comfort votes.

Hand volume immersed. Every effort was made to immerse a subject's hand to the same level on each occasion, but to make the subject as comfortable as possible in each experiment small variations were permitted. The relationship of hand volume immersed to heat flow is shown for each subject in Fig. 10. The relationship is significant at the 2 per cent and 1 per cent levels for subjects A and B, respectively. In all following considerations of differences in heat flow between series, the heat flows for subjects A and B have been adjusted for volumes of 500 and 600 ml. hand volume immersed, respectively. The effect of this adjustment on the pattern of heat flow over the year is shown in Fig. 11.

Since the equation of the regression line related heat flow to hand volume and took no account of possible differences between series, the heat flows were adjusted using only the gradient of the regression line. That is, a line parallel to the regression line was drawn through the measured heat flow on the scatter diagram, the adjusted heat flow being taken as the value where the line passed through the standard hand volume.

Relationship of the results from the two test temperatures

In series where experiments at 20° and 30°C were performed on a subject, the results from the two temperatures have been compared. The mean of replicate experiments at one temperature has been compared with the mean of the replicates at the other, or with a single

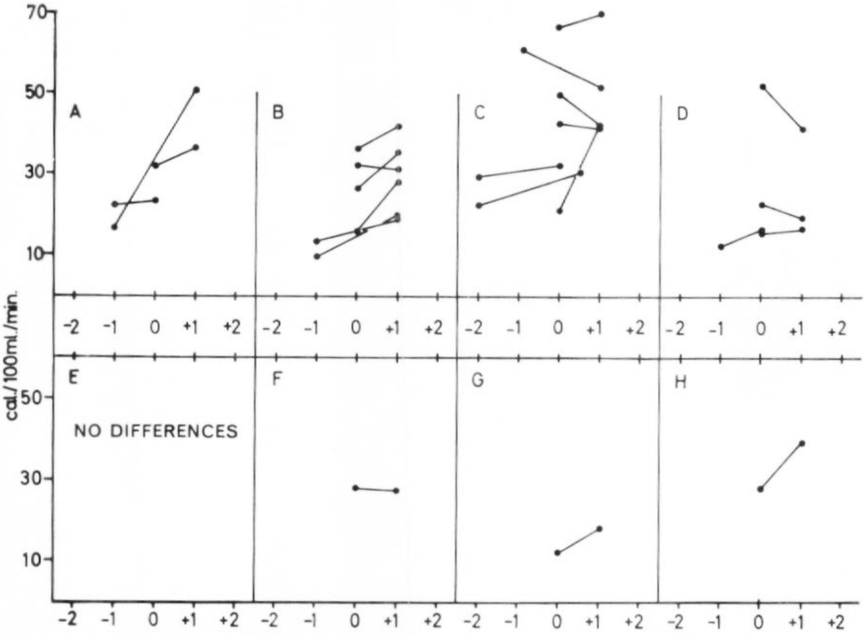

Fig. 9. Comfort and heat flow for the hand. Where comfort votes differed in replicate experiments, the heat flows measured in each experiment have been plotted against the appropriate comfort vote. In general, higher heat flows were observed when the subjects felt warmer.

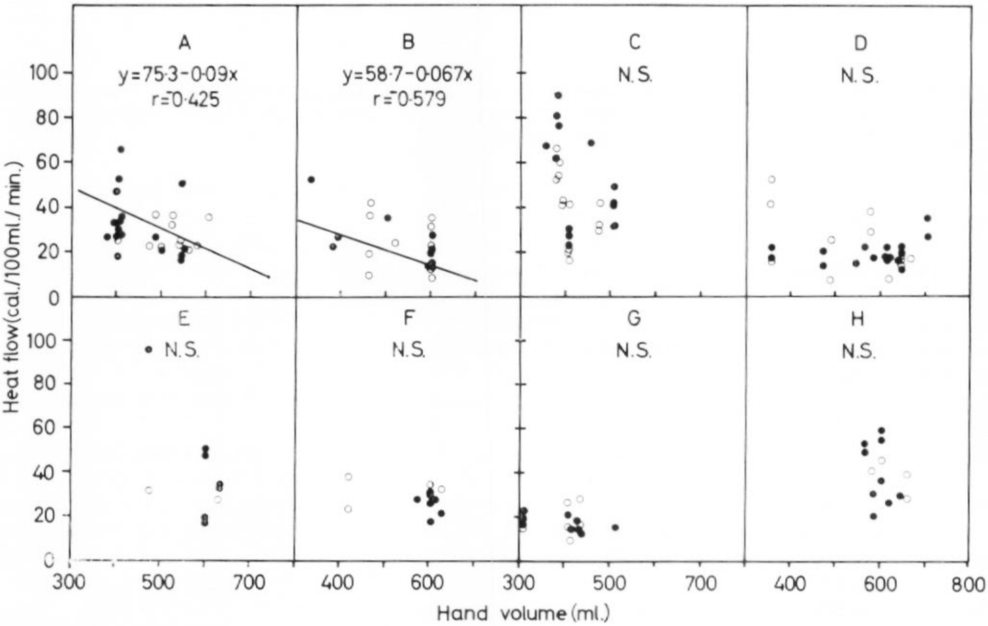

Fig. 10. Hand volume immersed in the calorimeter and heat flow from the hand.
○ Experiments at 30°C. ● Experiments at 20°C.
The relationship was significant for subject A ($P < 0{\cdot}02$) and B ($P < 0{\cdot}01$).

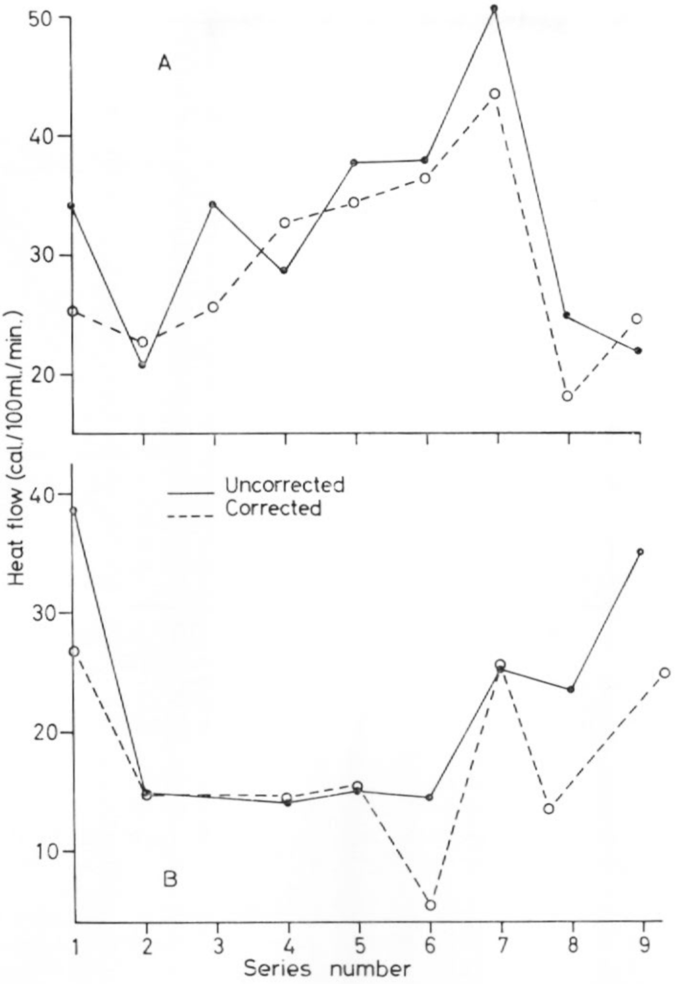

Fig. 11. Heat flow from the hand of subjects A and B adjusted to a standard hand volume. Each point represents the mean of replicate experiments at 20° and 30°C.

result where appropriate. Considering each series separately, an analysis of variance (Appendix B) showed considerable variation between subjects but no significant difference between the two temperatures. A comparison of the results from the two temperatures, taking all subjects together, showed a highly significant correlation ($r = 0{\cdot}64$, $P < 0{\cdot}001$; Fig. 12). 95 per cent confidence limits indicate the probability of a 1 : 1 relationship between the results from the two temperatures.

On the basis of this analysis, there seemed to be no justification for separate consideration of the results from the two temperatures.

Minute-by-minute calculation of heat flow

Heat flow has been calculated minute by minute for three series in which the four 2-year subjects took part. This has been carried out for the initial control experiments (series 1), a series in the middle of the Antarctic year (series 4) and the final series before leaving the Antarctic (series 8). Examples of the results of the calculation are given in Fig. 13. They show that the method of measuring temperature, which at best was sensitive to changes in temperature of about 0·03°C, was not capable of detecting a loss of heat from the hand in some

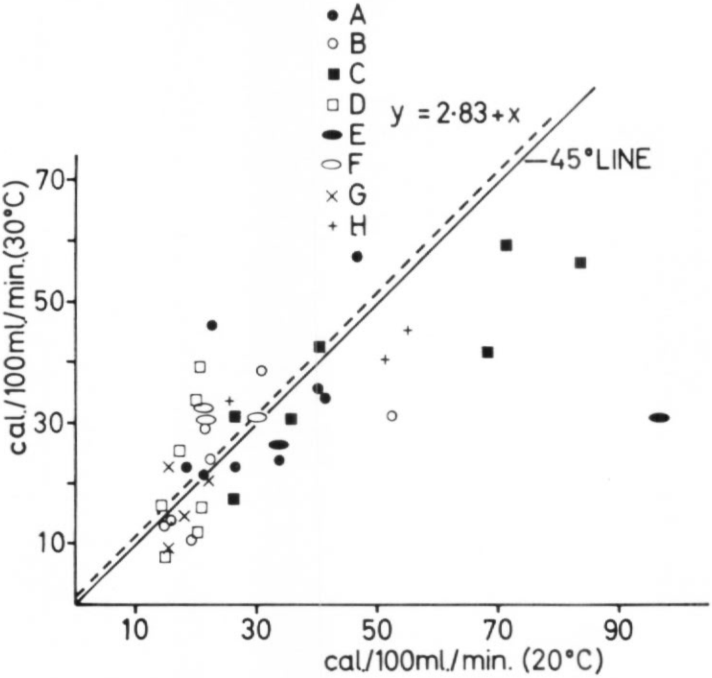

Fig. 12. The relationship between heat flow from the hand at 20° and 30°C. Each point represents the mean of replicate experiments. There is a 95 per cent probability that a 1 : 1 relationship exists between heat flows observed at the two temperatures.

minutes. In any one series, the pattern of heat loss from the hand was similar for all subjects. Comparing series, the average heat loss per minute in series 4 was smaller than in the other two.

The minute-by-minute heat losses for the two temperatures are averaged for all subjects in Fig. 14. Heat loss in the first 15 min. of the experiment, composed of heat lost from extravascular sources as well as from circulating blood, was greater in the experiments at 20°C than at 30°C, but for the remaining 25 min. heat loss was similar at the two temperatures.

Fig. 15 shows the average minute-by-minute heat loss for all four subjects at both temperatures. Before calculating the average, the heat-loss curves in individual experiments were "smoothed" by averaging the minute in which no temperature rise was observed with the heat flow in the next minute.

Heat flow is similar for series 1 and 8, particularly over the latter 25 min. of the experiment; heat flow in series 4 is consistently lower throughout.

Hand temperature and "stored heat"

Values have been calculated for "stored heat" in each experiment to investigate whether the occurrence of seasonal variations in the amount of heat stored in the tissue of the hands could be detected. The values were derived by subtracting from the total heat loss during the first 15 min. of each experiment the proportion contributed by circulating blood, i.e. the average heat flow during 15–30 min. from the graphical determination, multiplied by 15. Values for individuals are shown in Appendix C. The mean and range of the "stored heat" at the two temperatures in each series, for the four 2-year subjects, is plotted in Fig. 16. Also shown is the mean pre-experimental hand temperature. "Stored heat" at 20°C was from three to six times that at 30°C and showed a wide range of variation both within and between series. There was no obvious seasonal trend.

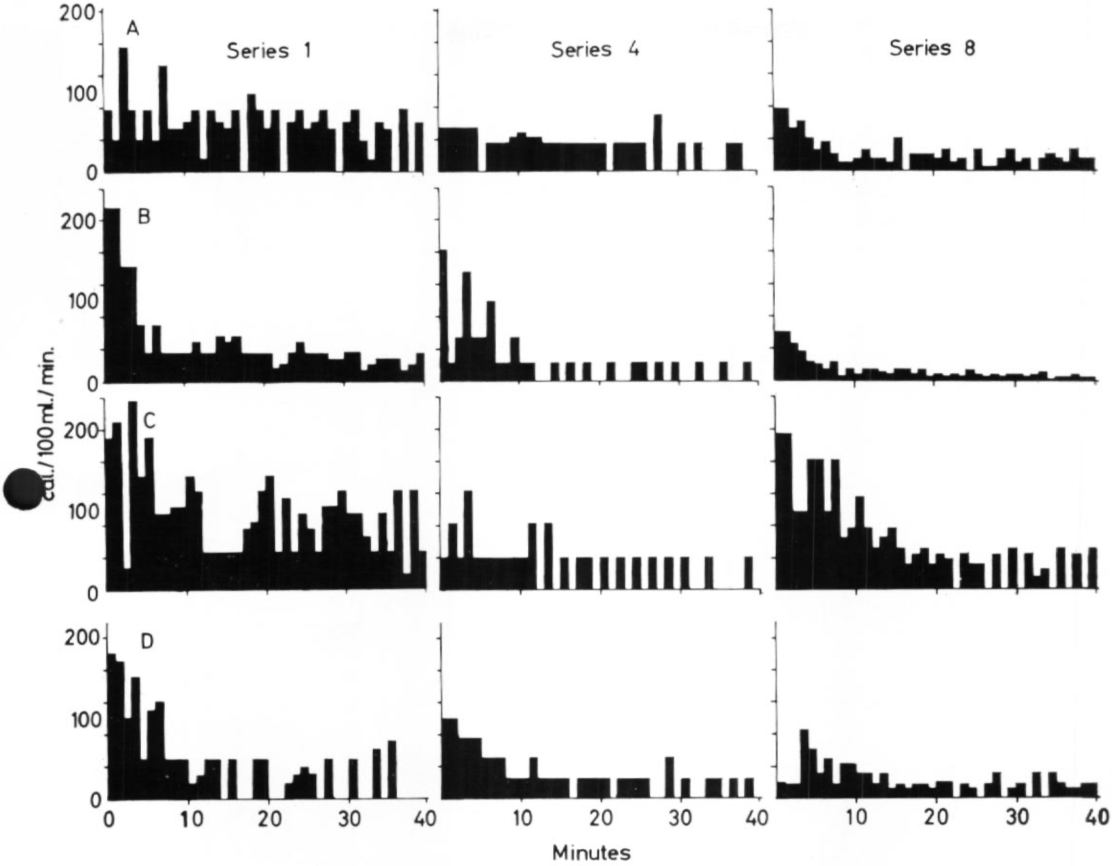

Fig. 13. Heat flow from the hand, calculated minute by minute, from typical experiments on four subjects in three series. The experiments were performed at a test temperature of 20°C and illustrate patterns of heat flow in each series.

Pre-experimental hand temperatures showed little variation either between the two types of experiment in each series or between series. The greatest difference was 0·6°C. All of the hand temperatures were high; at 35·2°C and above they were near deep body temperature, showing that the subjects maintained good insulation over the hands during the night, and sustained little heat loss.

Final analyses of differences between series

The principal findings in previous sections have been that the heat flows from the hands of two subjects were influenced by the volume of hand immersed in the water, and that no statistical difference existed between the heat flows measured at 20° and 30°C. The heat flows from subjects A and B have been adjusted to standard hand volumes, and the results from experiments at the two test temperatures have been pooled. An analysis of variance has been used to test for difference between series of experiments. Details of the analyses are given in Appendix D. The findings are summarized in Fig. 17, which illustrates pairs of series where significant differences were found to exist. All other analyses gave non-significant differences between series. These will, however, be referred to in the text.

Initial and final control experiments (*series 1–9*). An analysis of variance showed no difference between the two series, indicating that in four subjects a 2½-year period of exposure to the Antarctic environment had produced no measurable long-term effect on heat elimination from

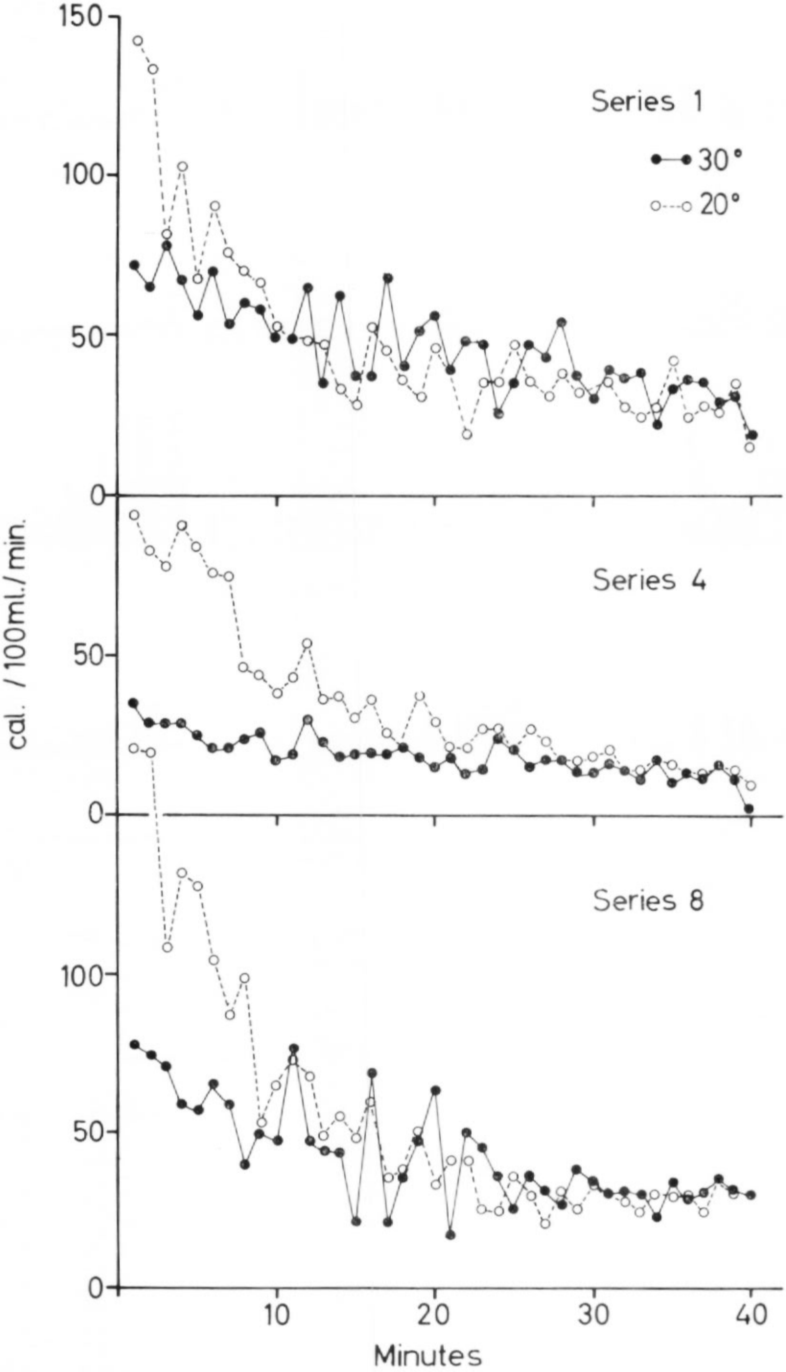

Fig. 14. Heat flow from the hand, calculated minute by minute, for all experiments at 20° and 30°C in three series. Each point represents the average heat flow in that minute from all experiments on all subjects at that temperature.

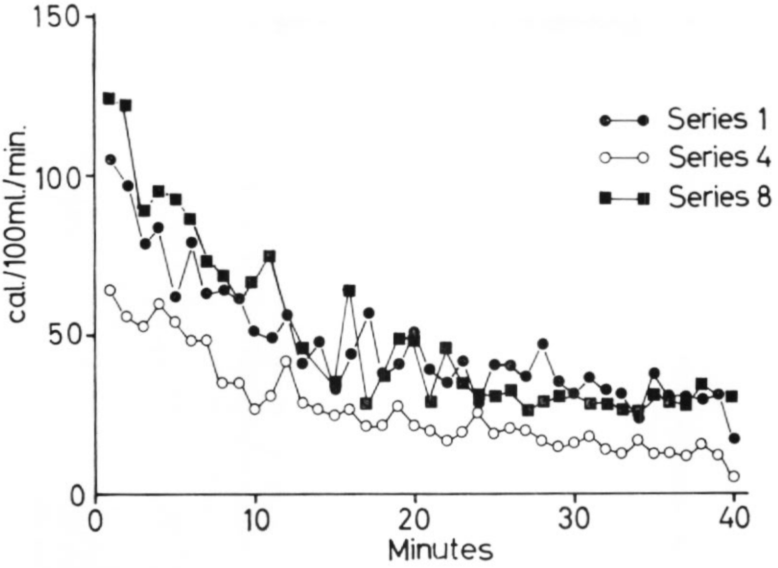

Fig. 15. A summary of the minute-by-minute heat flows in the three series. Each point represents the average heat flow in that minute from all experiments on all subjects.

the hand. The climatic exposure of the group during the month preceding the experiments was somewhat different for the two series. Before series 1 the subjects had all travelled by sea across the Equator, spending several hours each day sunbathing and working at the routine chores for shipboard life. Prior to series 9 the subjects had been in the United Kingdom for several months and had spent much of each day engaged upon office work.

Initial fall in heat flow (*series 1, 2, 3, 4*). The heat flows measured in series 2, 3 and 4 were all tested against the control values in series 1. Although heat flow declined progressively from series 1, the difference between series in the four 2-year subjects did not reach significance until series 4. The difference was then highly significant ($P < 0{\cdot}001$). If the results from the subjects

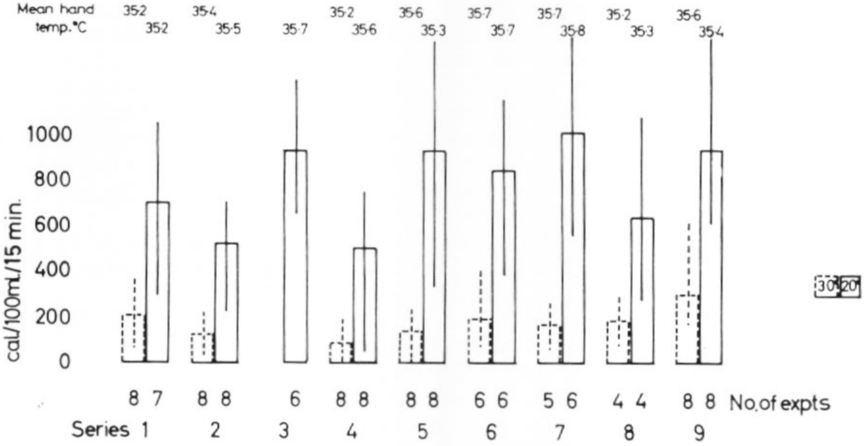

Fig. 16. Pre-experimental hand skin temperature and "stored heat" in the nine series. The rectangles show the average "stored heat" calculated at 20° and 30°C in each series. The vertical bars represent the range of "stored heat" in individual experiments.

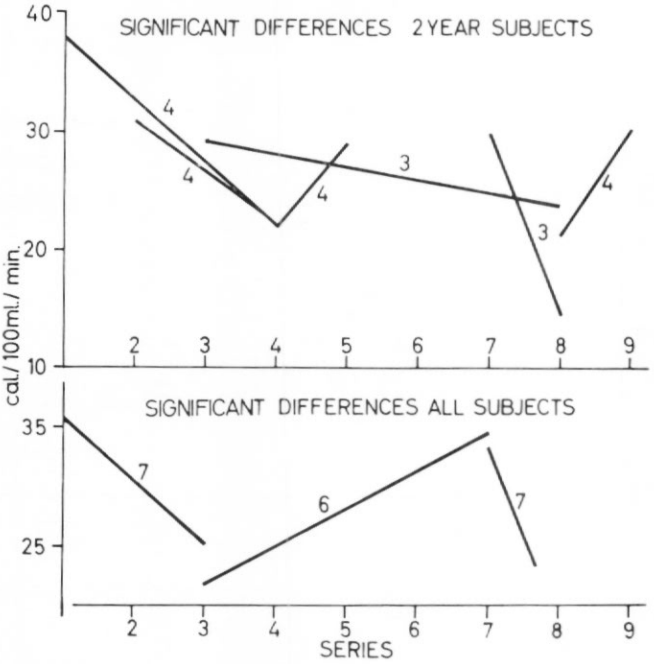

Fig. 17. Significant differences in heat flow between pairs of series. Each line joins the two series where a significant difference was found to exist. The figures indicate the number of subjects represented in each analysis.

studied during 1 year are combined with those from the 2-year men, the decline in heat flow is significant at series 3 ($P < 0 \cdot 001$). There was also a significant decline in heat flow in the four 2-year men from series 2, the first experiments performed in the Antarctic, to series 4 ($P < 0 \cdot 01$).

Subsequent rise in heat flow (*series 4, 5, 6, 7, 8*). Following the low values for heat flow observed in series 4, Fig. 7d indicates that a slow return towards control levels apparently occurred in subsequent series.

Statistical analysis provides some evidence to confirm this observation but it is not conclusive. There was no difference between series 1 to 7 for either three 2-year subjects alone, or for seven subjects when the 1-year men are included. In addition, for the six subjects available for inclusion in the analysis, there was a significant rise in heat flow between series 3 and 7. These analyses indicate that at series 7 the heat flow was at, or near, control level. However, none of the analyses of intermediate changes between series 4 and 7 gave significant results. One subject was missing from series 7 and a second subject showed a fall from series 6 to 7; these facts, combined with the slow rise of heat flow over a period of months, preclude a more positive statement of the nature of the return towards control levels.

Final changes in heat flow (*series 7, 8, 9*). Fig. 7 shows a fall in heat flow from series 7 to 8. On average the fall was a small one but in some individual subjects it was a large effect. When subjected to an analysis of variance, this fall in heat flow was significant both for three subjects in the 2-year study ($P < 0 \cdot 05$) and for seven subjects ($P < 0 \cdot 001$) when all the experiments were examined. However, less importance is attached to this comparison since there were fewer experiments in series 8 than in any other used for analysis.

Finally, for the four subjects on whom the most exhaustive series of tests was carried out, the rise from series 8 to the final controls in series 9 was just significant ($P < 0 \cdot 05$), a rise which took the heat flows of these subjects back to the pre-exposure level.

Summary of the observed changes in heat flow. The results show that a definite fall in heat flow occurred between the first control experiments and the onset of the winter months. On return from the Antarctic, heat flow had returned to its pre-exposure level, and the evidence suggests that this recovery occurred, at least in part, before leaving the Antarctic.

Relationship of heat flow to cold exposure

The previous sections have shown that, of all the measured factors which may have contributed to the results, only hand volume in two subjects had any significant effect. After adjustment for this, significant differences between series have been shown to occur.

In Fig. 18a and b the heat flows, expressed as percentage of the values observed in series 1, have been compared with meteorological temperatures taken from the station meteorological records and with derived values for windchill. In both comparisons, whether the subjects studied over 2 years are considered alone or when the heat flows from all available subjects are taken, the changes in heat flow closely follow the changes in climatic stress measured by environmental temperature or by windchill.

DISCUSSION

The method

Details of the vacuum-flask calorimeter and its use in studies of the peripheral circulation to the hand have been well documented by Cooper and others (1949), Greenfield and Scarborough (1949) and Greenfield (1960). The simplicity of the apparatus made it particularly appropriate for use in a far from ideal experimental environment, and the inability to calculate volume flow of blood created no special disadvantage. The relative insensitivity of the calorimeter to

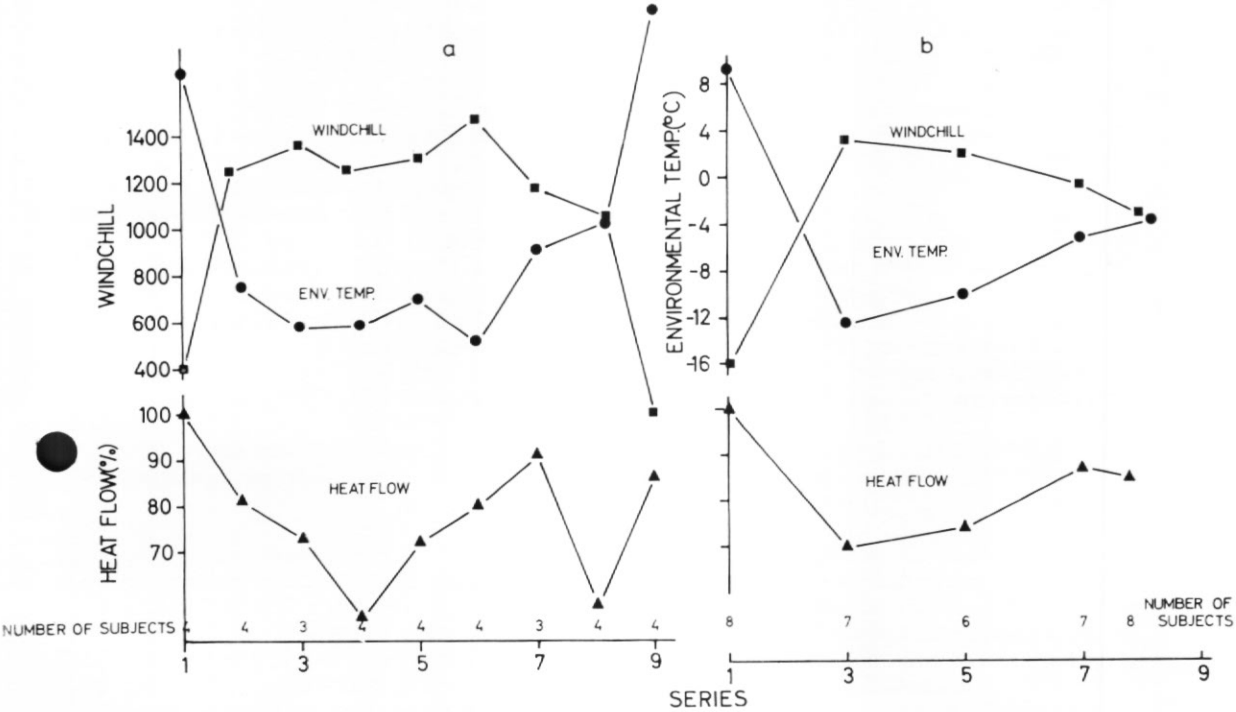

Fig. 18. Heat flow from the hand and environmental stress. In each part of the figure, heat flow is presented as an average percentage of the values observed in series 1. Environmental temperature and windchill have been taken from observations in the station meteorological records.

a. Values for the subjects studied over a period of 2 years.

b. Values for series of experiments in which at least six subjects took part.

temperature changes brought about by small random fluctuations in blood flow was a useful property of the technique when comparing experiments carried out over a long period of time.

For comparisons between experiments conducted over a span of more than 2 years, it was important to achieve as closely similar experimental conditions as possible. For this reason the response of the peripheral circulation to cool local temperatures of 20° and 30°C was chosen for investigation. In this temperature range, the spontaneous fluctuations in blood flow seen in other areas are much reduced (Barcroft and Edholm, 1943; Allwood and Burry, 1954) and interpretation of the results is not hindered by the complex origins of the cold-induced vasodilatation response (Folkow and others, 1963). Although some problems were created by conducting experiments at an early hour in the morning, after 8 hr. of warm comfortable sleep with the hand dilated (Watson, 1962; Khatri and Freis, 1967), this time did represent a repeatable basal condition for the subjects. It allowed a standard position of the arm to be easily achieved (Roddie, 1955) and avoided differences between series due to diurnal variation in peripheral blood flow (Bloch, 1964).

Results from the two temperatures

The 1 : 1 correlation of heat elimination at the two temperatures was surprising at first sight but the probable explanation became apparent upon detailed consideration of the effects of immersing the hands in water at different temperatures. A change in water temperature may have a direct effect upon the rate of blood flow and may also affect the amount of heat released by each millilitre of blood, since no account is taken of the possible re-distribution of the flow between superficial and deep vessels (Cooper and others, 1949).

It is well established that the blood flow to the fingers, hands, forearms and feet falls steeply as the local temperature is reduced from 45°C. At 29–33°C a point of inflexion occurs in the relationship and blood flow falls less steeply with temperature until, at 15–19°C, further decreases in local temperature lead to an increase in blood flow (Freeman, 1935; Spealman, 1945; Barcroft and Edholm, 1946; Allwood and Burry, 1954; Bargeton and others, 1959). Average values of hand blood flow at 20° and 30°C, taken from Freeman (1935) and Thauer's (1965) review, show that the difference may be as small as from 1–2 to 2–3 ml./100 ml./min., although at environmental temperatures of 32°C the difference in local blood flow may range from 7 to 15 ml./100 ml./min. (Spealman, 1945).

These small differences in blood flow between the two temperatures would make differences in heat loss difficult to detect by calorimetric methods even if they were the only factors involved. However, the temperature of arterial blood entering the hand may fall from 35° to 25°C when the temperature of the water is changed from 30° to 20°C (average values from Bazett, Love and others, 1948; Bazett, Mendelson and others, 1948; Bargeton and others, 1959) due to heat exchange between the blood vessels of the arm, thus leaving unchanged the maximum temperature gradient governing heat loss. The heat exchange is increased as the rate of blood flow is reduced (Aschoff, 1957) and pre-cooling may be so pronounced that the temperature gradient, and hence heat loss, is actually reduced at 20°C (Bargeton and others, 1959).

In the present experiments there are insufficient data to indicate a "between series" change in the relationship between heat loss at the two temperatures which would suggest an improvement in the counter-current heat-exchange mechanism in the arm.

Pre-exposure hand temperature and "stored heat"

Mean skin temperatures of the hand, measured immediately before each experiment, were all above 35°C, ranging from 35·2° to 35·8°C. The measurements indicated that the "base line" for the experiments remained constant throughout the year and, moreover, showed that the bed clothes used provided adequate insulation against excessive heat loss in the winter. The high degree of insulation provided by the bed clothes also probably accounted for the seasonal changes in heat loss not being reflected in parallel changes in pre-exposure skin temperature.

Heat lost to the calorimeter during the first 15 min. of an experiment was derived predominantly from heat stored in the tissues; during the fifteenth to thirtieth minutes, heat lost was assumed to have come mainly from the circulation and from metabolic processes in the hand. However, there was no sharp division between the two periods, and it was possible that changes in the "stored heat" of the tissues could have influenced the calculations of heat flow. There were large variations between subjects in the calculated values for "stored heat" in each series of experiments, and similar variations in the mean values for "stored heat" between series. The calculations showed no consistent trends over the year, however, and suggested that differences in "stored heat" were random and unlikely to have contributed to the seasonal changes in heat loss derived from the circulation.

"Stored heat" measured at 20°C was from three to six times greater than at 30°C in each series of experiments, further suggesting that the lack of a difference in heat flow between 15 to 30 min. was due to similarities in the circulatory contributions at the two temperatures rather than to a lack of sensitivity of the calorimetric method.

Interaction with other variables

The blood supply to the extremities, particularly to the hands, is a labile quantity influenced by many different factors, both physiological and psychological. The present experiments, performed over a long period of time, offered ample opportunity for interaction between blood flow and other variables.

Hand volume. Perhaps the most important of these variables is the volume of the hand immersed in the water. Burton (1939) has shown that the greater vascularity of the fingers compared with the hand stump, combined with the larger surface to volume ratio of the finger, produces an inverse relationship between hand volume immersed and measured heat flow. There was no evidence of changes in group hand volume as judged from the routine measurements made at the beginning and end of each year, but small variations in hand volume immersed did occur in individual subjects. In two subjects a significant correlation between hand volume and heat flow was observed. When the measured heat flow in these subjects was adjusted to a standard hand volume, the pattern of the differences between series was not materially affected.

General thermal state of the body. Blood flow in the hand shows a marked dependence on the general requirement of the body to conserve or to dissipate heat (Spealman, 1945; Forster and others, 1946).

In the present experiments it was not possible to standardize the environmental conditions and ambient temperature varied from below 0° to over 20°C. It is unlikely that these variations exerted a direct influence on the heat-flow results as the subjects were shown to use more bed clothes as room temperature fell, while sub-clothing temperature and hand temperature at the beginning of each experiment remained constant throughout the year. Most sub-clothing temperatures measured were in excess of 33°C, which is the mean value found for indoor activities in the Antarctic (Hampton, 1967), and all measurements were above the 27–29°C found for air temperatures between the sheets next to sleeping subjects by Macintyre (1937). Few hand temperatures below 34°C were recorded, while mean hand temperatures for any series, of 35·2°C and above, indicated minimal vasoconstrictor tone in the hand prior to a series of experiments.

Since exposure of one part of the body to cold can cause vasoconstriction in a remote area (Pickering, 1932; Bader and Macht, 1948), one cannot rule out the possibility that the response seen in the hands was provoked by excessive cooling of the face in winter, especially as vasoconstrictor control of facial blood vessels is poor (Froese and Burton, 1957; Edwards and Burton, 1960).

As mentioned earlier, the hand temperatures do not suggest any major vasoconstrictor activity in the hours preceding an experiment; also, it was remarkable to note the number of men who were able to sleep with their heads completely covered by the bed clothes during a cold night. During the course of an experiment, the subjects were always well covered, so there seems no reason to think that indirect cooling influenced the measured heat flow.

Influence of changes in physical fitness. An increase in fitness leads to a reduced fall in mean skin and extremity temperature during cooling of the nude body, a change which is also found as a response to prolonged cold exposure (Adams and Heberling, 1958; Heberling and Adams, 1961; Andersen, 1966). These results suggest that changes in heat flow from the hands could depend upon seasonal variations in fitness. In the present study no direct measurements of fitness were made but, as the sledging journeys were distributed evenly throughout the year

(Fig. 2), it is unlikely that marked seasonal variations in fitness did occur. This conclusion is strengthened by Orr's (1965) observations that the men at Hope Bay in 1959 and 1960 (including all eight men taking part in the heat-flow experiments) showed constant body weights and skin-fold thickness throughout the year, in contrast to earlier expeditions where changes in these variables were found to be related to seasonal variations in activity (Wilson, 1960). In the present study, heat flow was not related to body weight, and changes in heat flow between series were not related to concurrent changes in body weight.

Other factors. It is not likely that habituation played any part in the observed changes in heat flow as no consistent difference was found between the first and second experiment in each pair, and the changes observed between series 1 to 4 and 4 to 8 were in opposing directions.

Nevertheless, differences between replicate experiments were sometimes observed which were too large to be ascribed to the random variations associated with repeated experiments. It has been suggested elsewhere (Hampton, 1967) that the transition from sleep to wakefulness or a change in the level of attention may have influenced heat flow in the same way as bladder distension or emotional upsets have been observed to reduce the blood supply to the hands (Cunningham and others, 1953; Vanderhoof and Clancy, 1962; Cooper, 1965). There seems no reason to believe that factors such as these were encountered more at one time of year than at another.

Consideration of the heat-flow results

After taking into account all the foregoing factors, four main conclusions may be drawn from the analyses of the heat-flow results. First, in the four subjects who spent over 2 years in the Antarctic this long exposure to an unfamiliar climate produced no major change in heat elimination when the initial control experiments (series 1) were compared with the final series (series 9) performed 6 months after the return to the United Kingdom. Secondly, with the onset of winter, the heat elimination of the hands decreased to reach a nadir at the time of the coldest weather. Thirdly, there is evidence that the major part of the return of heat elimination from its lowest level to control level took place while the subjects were still in the Antarctic. These conclusions apply to results taken from the four men studied over 2 years, and also when the four men studied for 1 year are included. Finally, it seems very probable that the observed changes in heat flow represent seasonal variations in the peripheral blood flow.

In the interpretation of these results considerable importance is given to the values obtained in series 1, which are used as a basis for comparison with the Antarctic experiments. As the 2-year subjects had completed a slow sea voyage through the tropics immediately before the experiments in series 1, it is possible that they had achieved a mild degree of heat acclimatization and consequent increase in peripheral blood flow (Fox and others, 1963). An associated high value for the heat elimination observed in series 1 would affect the conclusions drawn from later experiments.

However, it is unlikely for several reasons that heat acclimatization did influence the results in the earliest experiments. On a small ship it was not possible for the subjects to engage in vigorous activity and thus induce acclimatization by the classical method, while the intensity of the solar radiation precluded prolonged sunbathing and passive elevation of body temperature.

Secondly, the results obtained in series 1 were not significantly different from series 7 (in the Antarctic) and series 9 (after 6 months in the United Kingdom), when almost certainly heat acclimatization was not present.

Finally, a progressive fall in heat elimination occurred between series 1 and 4, although it was only at series 4 that the difference became significant. This initial fall in heat elimination was also observed in the 1-year men, whose prior thermal experience at series 1 was similar to that at series 2 in the 2-year men.

The many factors which can influence peripheral blood flow have already been mentioned. In this study it is unlikely that any of them were of major importance in producing the observed results, and it is reasonable to assume that the changes in heat flow occurred in response to seasonal changes in some environmental factor not yet considered. The most likely of these is cold stress, particularly when the subjects are considered as a group, as this was the only factor which could have exerted an equal influence on all the men.

Cold exposure and physiological strain

The men departed on sledging journeys at all times of the year, and detailed studies (Hampton, 1967) showed no seasonal variations in exposure in terms of the proportion of days of outside work or the length of exposure each day. Other factors governing heat loss, such as the amount of clothing worn and the wind velocity, also remained constant, leaving meteorological temperature and solar radiation as the principal variables determining climatic stress. The measurements showed that the men were out of doors for an average of 4 hr./day during the 6 months of field work in the year. During these exposures, temperatures measured under the clothes next to the skin, and on the skin of the face, finger and toe, were on average 6°, 10°, 7° and 6°C lower, respectively, than similar measurements taken indoors. These falls in surface temperature indicate that the stress of the climate produced physiological strain which was endured for considerable periods of time. The stress was not sufficient, however, to produce the ultimate sign of strain, i.e. a fall in rectal temperature.

In Fig. 18 the seasonal changes in heat flow have been plotted together with meteorological air temperatures and windchill values for the months in which the experiments were performed. From the station meteorological records (Falkland Islands and Dependencies Meteorological Service, 1962) the values given for the length of day show that solar radiation was least effective in relieving climatic stress at the time of the lowest temperatures and greatest windchill. It seems evident that the changes in heat flow are related to changes in the level of stress, and this conclusion is supported by the fact that individual results fall more clearly into a pattern when expressed as a function of the month in which the experiment was performed (Fig. 6).

The measurements of exposure on one man (Hampton, 1967) show clearly that considerable physiological strain was experienced by the subject while out of doors. If 32°C is taken as the lower limit of sub-clothing temperature for comfort, 95 per cent of the measurements recorded out of doors were seen to fall below this level. This represented a general stimulus to peripheral vasoconstriction, lasting on average nearly 4 hr. every day. In addition, the temperatures of the three areas of skin sampled were also shown to fall on exposure to cold air. The frequency-distribution histograms for finger skin temperature showed that when inside the tent 88 per cent of the measurements lay above 30°C; outside the tent 70 per cent of the measurements were below this level.

Evidence of seasonal variations in physiological strain during the field studies was sought by comparing skin temperatures of the hand, measured when outside the tent, during the first three and the last three "travelling" days in the year, with three similar days in the winter (Table III). Skin temperatures above 30°C were not observed in the winter, while in May and September/November these temperatures predominated. 32 per cent of the hand skin temperatures observed in winter were below 20°C, but only 20 per cent of the September/November temperatures and 5 per cent of the May observations fell to this level; in each case in the spring only one layer of woollen gloves was being worn compared to leather mitts and duffel inner gloves in the winter.

The coincidence of climatic stress and physiological strain, with the lowered values of heat flow from the hands, provides good evidence that local adaptation has occurred. The results suggest that, in the zone where physical control of local heat loss is effective, prolonged exposure to cold initiates a more sensitive response to local cooling of the hands.

Heat loss, blood flow, skin temperature and adaptation to cold climates

The principal finding in this investigation indicates that at a constant local temperature the heat elimination from the hand, and probably blood flow, is reduced at the coldest time of the year. This finding conflicts with other workers. For many years, the opinion of the majority of reviewers (Carlson, 1954; Burton and Edholm, 1955; LeBlanc, 1962*b*; Hammel, 1964; Thauer, 1965) has been that an increased blood flow to the periphery is observed with prolonged exposure to cold. Only one such author (Yoshimura, 1964) has been found to hold the opposite viewpoint.

An examination of the literature shows that few studies have been concerned with the direct measurement of normal peripheral blood flow and its control mechanisms, either at different seasons of the year or in groups of subjects before and after a period of cold exposure. Broadly speaking, the majority of the evidence is derived from the cold-induced vasodilatation

TABLE III. FINGER SKIN TEMPERATURES AT THREE TIMES OF YEAR

(The number of measurements in each interval of 5°C is presented as a percentage of the total number of observations. Only measurements where the subject was wearing at least one pair of gloves have been included.)

		May	*July/August*	*September/November*
Day number		2, 8, 35	12, 13, 44	19, 32, 33
n		20	22	20
Range of meteorological temperatures (°C)		+1 to −20	−11 to −27	+1 to −11
		Occurrence of skin temperature (per cent)		
		May	*July/August*	*September/November*
Range of finger skin temperatures (°C)	35–30	60	0	35
	30–25	30	27	30
	25–20	5	41	15
	20–15	5	14	10
	15–10	0	18	10

response, from skin-temperature measurements during test exposures to cold and from comparative blood-flow studies in different ethnic groups.

Most workers are agreed that, when the hands of cold-adapted subjects are immersed in water at temperatures lower than 5°C, certain characteristic responses are seen. In view of the probable advantages of the higher temperatures in improving comfort and maintaining manual dexterity and sensitivity under local cold stress, the findings have prompted some authors to describe them as evidence of local adaptation to cold.

It should be pointed out, however, that the natural occurrence of cold vasodilatation in the hands of, for example fishermen, has not been reported. It is not certain that cold-induced vasodilatation can be expected to occur naturally, as in the circumstances where it might be anticipated the whole body is usually cold. Under such conditions the response is much depressed (Blaisdell, 1951). Studies of the temperatures occurring next to the skin under the clothes during out-of-doors exposure in the Antarctic showed that 98 per cent of the measurements lay below the mean values observed indoors, suggesting that conditions of general chill are usually experienced (Hampton, 1967). In view of the possible effect of an increase in heat loss from the hands on the heat balance of the body, it may be that the significance of the response in terms of adaptation to prolonged cold exposure should remain open to question. As Keatinge (1957) pointed out, a mechanism that protects the extremities against cold injury may have a detrimental effect upon survival.

There do not appear to have been any studies which have established a relationship between the cold-induced vasodilatation response and peripheral blood flow at higher local temperatures. Glaser and others (1959), after "habituation" of the hand to repeated cold-water immersion at 4°C, could detect no change in the heat elimination of the hand at 31°C. Thus, there seems to be no basis for the supposition that the results obtained from cold-water immersions also imply raised blood flows at the range of skin temperatures normally experienced by cold-adapted men.

The majority of the conclusions concerning the role of the peripheral circulation in adaptation to cold derive from measurements of skin temperature and conductance during exposure of the whole body to cold stress, and are based on Burton's (1934) theory of heat flow in the animal body. Widely varying groups of subjects have been studied under a variety of experimental conditions; many authors consider that their results provide evidence of an increased peripheral circulation and heat loss as a response to prolonged cold exposure (Carlson and others, 1953; Meehan, 1955; Rennie, 1957; Scholander, Hammel, Andersen and Løyning, 1958; Andersen, Løyning and others, 1960; Covino, 1961; Milan and others, 1961; Rennie and others, 1962; Elsner and Bolstad, 1963; Milan and others, 1963; LeBlanc and others, 1964; Andersen and others, 1966). On the other hand, many experiments have given contrary results and suggested that heat loss is reduced with adaptation to cold (Goldby and others, 1938; Hicks and O'Connor, 1938*a*, *b*; Newburgh and Spealman, 1943; Stein and others, 1949; Daniels and others, 1951; Scholander, Hammel, Hart and others, 1958; Hammel and others, 1959; Hammel and others, 1963; Irving and others, 1960; Ogata, 1960; Davis, 1961; Milan and others, 1963; Budd, 1964; Wyndham and others, 1964; Yoshimura, 1964; Budd and Warhaft, 1966; Wyndham, 1966).

Evidence for differences in skin temperature between adapted and non-adapted subjects during cold exposure therefore seem to be finely balanced between an increased fall in temperature on the one hand and a decreased fall on the other. Not only are these marked differences between experiments difficult to interpret, but several workers have found levels of skin temperature during cold exposure that appeared inconsistent with measured values for heat production and rectal temperature (Adams and Covino, 1958; Heberling and Adams, 1961; Milan and others, 1961; Davis, 1963; Wyndham and Plotkin, 1963). Milan and others (1961) described the paradox as an "imbalanced heat equation", and these and several other authors have brought forward explanations to equate the results with Burton's theory (Adams and Covino, 1958; Carlson, 1963).

Many of the studies consisted of short exposures to fairly severe cold, in which thermal equilibrium was rarely, if ever, attained. They therefore failed to meet the fundamental requirement of Burton's theory and it may be that the discrepancies arising from this cause are sufficient to produce the observed effects. "Stored heat" from cooling superficial tissues, for instance, might well obscure the effect upon skin temperature of a reduced rate of heat flow from deeper tissues, particularly in the early part of the exposure. In experiments in mild conditions, Ferris and others (1947) found that blood flow in the hand was almost independent of skin temperature and seemed to reflect more closely the overall need to conserve or dissipate heat.

A possible cause for paradoxical skin-temperature results could be that the areas sampled have not afforded an accurate estimate of the average skin temperature of the whole body. It is also possible that for a given skin temperature, heat loss is modified by changes in one or more of the other avenues of heat exchange between skin and environment. For example, a reduction in shivering may reduce heat loss by convection, owing to the decrease in air movement over the skin. Changes in the distribution of skin temperature may alter heat loss by convection and radiation without influencing average skin temperature.

Other factors may well influence skin-temperature measurements independently of any changes induced by prolonged exposure to cold. Adolph and Molnar (1946) noted the importance of physical fitness in the response to cold exposure. In later experiments, Adams and Heberling (1958) and Heberling and Adams (1961) showed that a physical training programme produced raised skin temperatures during cold-exposure tests and that subsequent exposures to cold produced little further change. Comparison of experiments intended to demonstrate differences in the degree of cold adaptation may therefore depend upon the relative states of physical fitness or upon the subjects' activity during the exposures (Andersen, 1966), particularly when different ethnic groups are compared (Andersen, Bolstad and others, 1960).

Of the evidence for an increased peripheral blood flow with adaptation to cold, much importance is given to the studies on the Southampton Island Eskimos by Brown and his co-workers (Brown and Page, 1952; Brown and Hatcher, 1953; Brown and others, 1953; Brown, Bird, Boag and others, 1954; Brown, Bird, Delahaye and others, 1954; Brown, 1957; Brown and others, 1963). Several features of the experiments, however, cast doubt upon the assumption that these seemingly clear-cut results can be accepted as indications of a local adaptation to cold exposure.

The experiments were conducted in a room at 20°C with the subjects clad in normal indoor clothes. At this temperature, the Eskimos were reported as comfortable (Brown and Page, 1952) or uncomfortable and perspiring (Brown, Bird, Boag and others, 1954), whereas the control subjects were chilly. This comment suggests that some degree of central drive to vasoconstrict would be present in the control subjects, in which case a reduced level of blood flow would be predicted in comparison with the Eskimos. Further, the Eskimos showed basal metabolic rates 27 per cent above the Du Bois standard compared to normal levels in the control subjects, which provides a second indication that the differences in blood flow may have been predicted. The pattern of blood flows observed was reported to be similar to that seen in patients suffering from hyperthyroidism (Brown and Hatcher, 1953; Brown, Bird, Delahaye and others, 1954). Despite the high blood flows recorded in the Eskimos, however, muscle temperatures in the Eskimos were lower than in the control subjects. The authors considered the difference resulted from efficient cooling of arterial blood by venous blood returning via the venae comitantes. This result suggests that the heat elimination from the hands of the Eskimos may have been lower than the control subjects, corresponding to the findings in the present study.

Although Krog and others (1960), in their studies of Lapps and north Norwegian fishermen, were unable to detect differences between the cold-adapted subjects and controls over a range of local hand temperatures, the levels of blood flow in the control group were, however, equal to or higher than the levels observed in the Southampton Island Eskimos, suggesting that in the latter group some centrally originating vasoconstrictor activity was present. This may mean that blood flow in the Eskimos was lower than would have been expected from their high metabolism and apparently warm state, and thus represents a reduced blood flow at any given local temperature. It would be extremely valuable to use the Eskimos as their own controls in seasonal studies to help resolve this point.

Krog and his co-workers did not measure heat elimination from the hand or deep-muscle temperatures, so it is not possible to say whether differences in counter-current heat exchange existed between the two groups in their investigation.

The absence of a centrally originating vasoconstrictor drive may explain why Bader and Mead (1950) could not find a change in blood flow through the finger in subjects who had just completed a winter bivouac in northern Canada. Their experiments were conducted at a room temperature of 32°C. The plethysmograph temperature is not reported but it is presumed to have been at ambient room temperature.

On the other hand, Wood and others (1958) have found a significant reduction in forearm blood flow following nude exposure to 16°C for 14 days. The experiments were conducted with the subjects in shorts in a room at 27°C and a plethysmograph temperature of 32°C. These results cannot represent a purely local response to cold, since, for an almost naked subject, the general level of vasoconstrictor activity must have been quite strong at 27°C; yet they are important because vasoconstrictor control of blood flow through the forearm is generally considered to be weak. An even more pronounced effect may have been observed had hand blood flow been measured. A further point of importance in the present context is that the observed changes in forearm blood flow in Wood's study must have occurred as a result of cold exposure; fitness or a calorie imbalance are unlikely to have played a part, as the subjects were sedentary and living on a normal diet.

The results obtained by Wood and his co-workers, and those found in the present study, are consistent with the findings of Budd (1962, 1964, 1965) and Budd and Warhaft (1966) that adaptation to the Antarctic environment consists of an improved ability to maintain rectal temperature under cold stress. Budd suggested that this is brought about by a decrease in heat loss from the periphery, which could be achieved by a reduced blood flow to the extremities or to improved counter-current heat exchange in the limbs.

Conclusions

Direct evidence of the role of the peripheral circulation in Man's adaptation to cold is slender; if the experiments where complex factors may be operating are set to one side, the evidence does not wholly conflict with the present finding of a decreased heat loss with acclimatization.

Although an increased blood flow to the hands in cold vasodilatation seems well established, this need not eliminate the possibility of a reduced circulatory response at higher local temperatures. If the initiation of cold vasodilatation depends upon, for example, particular temperature levels being reached in the tissues of the hand, these temperatures may be attained earlier if, after adaptation, the initial heat production is reduced.

Evidence suggesting a reduction of heat loss and peripheral blood flow as an adaptive measure in Man seems to have been neglected because of conflict with accepted opinions of the meaning of adaptation. Adaptation had been variously described as a long-term change in the reverse direction of the acute emergency reaction to cold exposure (Carlson and others, 1953), as reactions beneficial to the organism (Elsner, 1955) and improved comfort (Daniels and others, 1951). These definitions imply an increased circulation to the extremities. As Keatinge (1957) has pointed out, changes which lead to greater heat loss are of doubtful survival value, whatever short-term benefits they produce.*

Clearly much further work is required to resolve the conflict between changes which improve comfort under cold stress and those which are directed towards the maintenance of homoiothermy and an increased chance of survival.

It is possible that many of the tests employed have been so severe as to be beyond the limits to which Man can adapt, such that the differences observed may have been due to physical rather than physiological factors. In future, experiments which impose only mild stress may yield valuable knowledge of the mechanisms of Man's adaptation to cold.

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APPENDIX A

TABLES OF RESULTS OF THE CALORIMETRY EXPERIMENTS FROM EACH SUBJECT AT 20° AND 30°C

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject A (20°C)								
1	26·8	22·4	402	—	35·5	17·6	2·25	0
	17·9		402	34·5	34·5	17·7	1·75	0
2	21·4	18·6	500	35·7	35·2	10·2	5·75	0
	15·8		544	35·0	34·2	4·1	5·75	0
3	33·7	34·2	405	35·4	—	11·8	2·75	0
	34·7		405	35·9	—	11·3	3·75	0
4	16·6	33·6	544	35·5	30·0	2·8	8·00	−1
	50·6		544	35·8	35·1	6·2	8·00	+1
5	52·9	41·3	402	35·1	—	12·4	3·75	0
	29·7		402	35·2	—	11·7	3·75	0
6	46·8	40·0	400	—	34·6	6·2	6·75	0
	33·2		400	35·4	34·9	6·4	6·75	0
7	65·5	46·5	407	—	—	12·0	2·75	0
	27·4		407	36·0	—	8·9	2·75	0
8	—	26·4	—	—	—	—	—	—
	26·4		377	34·9	—	12·7	2·75	0
9	26·2	21·8	487	36·4	35·3	14·7	4·25	0
	17·5		543	35·5	35·0	14·4	4·25	0
Subject A (30°C)								
1	25·0	46·0	402	34·8	34·7	15·7	2·25	0
	67·0		402	35·6	34·8	23·2	2·25	0
2	22·1	22·7	500	35·4	34·7	13·0	5·75	−1
	23·3		544	34·8	35·2	13·4	5·75	0
3	—	—	—	—	—	—	—	—
4	22·7	23·7	544	—	34·9	5·5	8·00	0
	24·7		544	34·3	35·2	3·8	8·00	0
5	36·3	34·1	524	35·7	35·1	14·4	3·75	+1
	31·8		524	35·7	—	18·2	3·75	0
6	36·3	35·9	485	36·0	—	11·1	6·75	0
	35·5		603	35·8	—	9·8	6·75	0
7	46·5	57·2	407	35·9	—	10·1	2·75	0
	67·8		407	35·3	—	10·1	2·75	0
8	—	22·9	—	—	—	—	—	—
	22·9		473	—	—	10·9	2·75	0
9	20·5	21·7	563	36·6	34·6	18·7	4·25	0
	22·8		530	36·3	35·0	15·3	4·25	0

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject B (20°C)								
1	52·4	52·4	331	34·6	35·3	17·9	2·50	+1
	—		—	—	—	—	—	–
2	18·7	16·0	601	35·5	35·4	10·3	3·75	+1
	13·3		601	35·4	33·0	5·5	3·75	−1
3	—	—	—	—	—	—	—	–
4	12·2	15·1	601	35·3	36·0	2·2	6·75	+1
	18·0		601	35·2	34·8	3·9	6·75	+1
5	18·9	19·5	601	35·0	35·1	11·2	3·75	+1
	20·1		601	35·4	36·1	11·1	3·75	+1
6	—	—	—	—	—	—	—	–
7	27·9	21·8	603	36·4	—	19·6	2·75	+1
	15·6		603	35·5	—	10·3	2·75	0
8	—	22·4	—	—	—	—	—	–
	22·4		381	—	—	7·5	2·75	0
9	26·3	30·8	392	—	33·8	16·7	4·25	0
	35·4		503	36·3	34·4	18·6	4·25	+1
Subject B (30°C)								
1	31·2	31·5	600	34·6	36·4	19·7	3·50	+1
	31·8		331	34·3	34·2	18·8	2·50	0
2	14·7	13·8	601	35·1	35·7	12·9	3·75	+1
	12·9		601	35·3	—	7·2	3·75	+1
3	—	—	—	—	—	—	—	–
4	11·9	13·2	601	35·3	—	2·4	6·75	+1
	14·5		601	35·0	37·4	1·9	6·75	+1
5	13·6	10·8	601	35·5	—	8·2	3·75	0
	8·1		601	35·5	—	9·7	3·75	0
6	9·8	14·5	464	35·6	33·3	6·8	3·75	−1
	19·1		464	—	34·9	6·5	3·75	+1
7	23·3	29·3	603	35·9	—	16·0	2·75	0
	35·2		603	35·4	—	17·1	2·75	0
8	—	24·3	—	—	—	—	—	–
	24·3		522	—	—	16·4	2·75	0
9	41·6	38·9	464	34·0	34·6	17·1	4·25	+1
	36·1		444	34·2	36·0	17·7	4·25	0

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject C (20°C)								
1	61·6	71·3	375	35·3	34·2	23·5	2·50	0
	81·0		379	35·4	34·8	16·3	3·50	0
2	76·8	83·4	381	35·6	35·7	10·1	8·50	+2
	90·0		381	36·0	35·9	7·4	8·50	+2
3	41·1	45·3	512	35·8	—	11·4	4·75	+1
	49·5		512	35·8	—	9·8	4·75	0
4	30·2	26·3	407	35·5	36·0	2·0	5·75	+1
	22·4		407	35·8	33·9	2·1	5·75	−2
5	31·9	35·7	512	35·4	—	9·8	3·75	+1
	39·6		512	35·5	—	11·0	3·75	—
6	26·8	26·4	407	—	34·7	—	4·75	+1
	26·0		407	35·7	35·1	11·2	4·75	+1
7	—	—	—	—	—	—	—	—
8	—	40·5	—	—	—	—	—	—
	40·5		512	35·2	—	14·2	3·75	0
9	68·8	68·1	460	36·4	34·7	15·5	4·25	+1
	67·5		355	36·4	34·3	15·4	4·25	0
Subject C (30°C)								
1	66·3	59·5	379	36·0	29·3	15·5	3·50	0
	52·7		379	35·2	29·5	22·2	3·50	+1
2	52·9	56·8	381	36·0	34·1	8·9	4·75	+1
	60·8		381	35·8	34·4	3·1	8·50	−1
3	—	—	—	—	—	—	—	—
4	19·3	17·9	407	35·4	34·9	−1·1	5·75	+1
	16·6		407	35·5	35·3	1·2	5·75	+1
5	29·4	30·7	473	35·5	—	4·8	3·75	−2
	32·0		473	35·5	—	6·2	4·75	0
6	41·5	31·2	407	35·6	35·3	8·5	4·75	+1
	21·0		407	35·7	34·8	3·8	4·75	0
7	—	—	—	—	—	—	—	—
8	—	42·7	—	—	—	—	—	—
	42·7		473	35·2	—	13·4	3·75	0
9	41·1	41·8	388	35·9	—	16·2	3·25	+1
	42·5		390	36·3	—	18·8	3·25	0

Appendix A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject D (20°C)								
1	17·4	20·2	356	34·7	31·9	15·8	2·25	0
	22·9		356	35·5	34·2	17·4	2·25	0
2	16·2	14·3	648	35·2	32·0	10·9	3·75	0
	12·4		648	35·2	31·6	2·8	3·75	−1
3	17·5	16·5	628	35·9	34·0	11·7	1·50	–
	15·5		615	35·2	33·9	11·5	2·50	–
4	19·4	21·0	648	35·6	32·0	3·6	6·50	+1
	22·6		648	35·8	34·0	3·0	4·50	0
5	17·5	20·0	615	35·1	—	7·4	3·75	0
	22·4		615	35·8	—	11·9	3·75	0
6	35·5	31·3	702	35·6	34·8	6·0	4·75	0
	27·1		702	36·0	34·6	6·9	4·75	0
7	14·5	17·3	473	35·5	—	11·8	3·50	0
	20·1		473	35·5	—	9·3	5·25	0
8	—	15·1	—	—	—	—	—	–
	15·1		545	35·7	—	13·1	2·25	−1
9	22·3	20·1	566	36·8	34·5	17·8	3·25	0
	17·9		585	36·8	33·8	18·1	3·25	0
Subject D (30°C)								
1	25·9	39·1	356	35·6	34·8	21·5	2·25	+1
	52·2		356	35·3	34·1	19·2	3·25	0
2	15·9	16·3	356	35·1	34·8	12·7	3·75	0
	16·6		648	35·5	34·8	13·3	3·50	+1
3	—	—	—	—	—	—	—	–
4	14·4	16·3	648	35·3	34·2	2·6	4·75	0
	18·1		648	35·6	34·6	5·4	4·75	0
5	29·1	33·7	578	35·9	—	16·5	3·75	0
	38·4		578	35·2	—	10·1	3·75	0
6	—	—	—	—	—	—	—	–
7	—	25·5	—	—	—	—	—	–
	25·5		488	35·9	33·9	10·7	5·25	0
8	—	8·3	—	—	—	—	—	–
	8·3		488	—	—	15·0	2·50	0
9	17·1	11·9	670	36·4	33·8	19·0	1·75	0
	8·4		618	35·6	32·9	15·7	2·25	0

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject E (20°C)								
1	34·4 32·3	33·4	634 631	35·6 35·6	— —	13·2 12·0	2·25 2·25	0 0
2	—	—	—	—	—	—	—	—
3	19·3 16·6	18·0	600 600	35·8 36·0	— —	11·8 10·5	8·00 8·00	0 0
4	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—
7	47·1 50·3	48·7	600 600	— —	— —	— —	— —	— —
8	— 96·4	96·4	— 474	— —	— —	— —	— 1·75	— +1
9	—	—	—	—	—	—	—	—
Subject E (30°C)								
1	25·7 27·6	26·7	630 630	35·0 34·9	— —	11·6 12·0	2·25 2·25	0 0
2	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—
8	— 31·2	31·2	— 474	— 35·0	— —	— 11·5	— 1·75	— 0
9	—	—	—	—	—	—	—	—

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject F (20°C)								
1	29·7 30·4	30·1	601 601	34·2 33·7	— —	7·4 9·0	3·75 3·75	0 0
2	—	—	—	—	—	—	—	—
3	27·5 28·0	27·8	613 573	35·0 33·7	— —	12·8 10·5	3·75 3·75	+1 0
4	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—
7	26·0 17·2	21·6	603 603	34·6 33·9	— —	18·8 11·5	4·75 4·75	0 0
8	— 21·1	21·1	— 628	— 35·7	— —	— 10·9	— 3·75	— 0
9	—	—	—	—	—	—	—	—
Subject F (30°C)								
1	23·2 38·1	30·7	420 420	33·8 33·8	— —	11·7 12·0	3·75 3·75	0 0
2	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—
5	—	—	—	—	—	—	—	—
6	—	—	—	—	—	—	—	—
7	34·5 27·2	30·4	603 603	35·6 35·4	— —	19·5 12·8	4·75 4·75	0 0
8	— 32·7	32·7	— 629	— 35·7	— —	— 13·7	— 3·75	— 0
9	—	—	—	—	—	—	—	—

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject G (20°C)								
1	18·9 17·1	18·0	310 310	34·6 34·8	— —	13·9 10·8	3·50 3·50	0 0
2	—	—	—	—	—	—	—	—
3	14·3 14·3	14·3	418 433	33·8 34·8	— —	8·0 8·0	3·50 3·50	0 0
4	—	—	—	—	—	—	—	—
5	12·4 18·1	15·2	438 428	34·1 33·0	— —	11·6 12·2	3·50 3·50	0 +1
6	—	—	—	—	—	—	—	—
7	22·9 20·5	21·7	310 407	33·6 34·3	— —	6·2 6·7	1·50 1·50	0 0
8	— 15·2	15·2	— 515	— 34·7	— —	— 12·3	— 1·50	— 0
9	—	—	—	—	—	—	—	—
Subject G (30°C)								
1	— 14·5	14·5	— 310	— 34·0	— —	— 13·2	— 3·50	— 0
2	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—
5	17·0 28·2	22·6	438 438	34·0 34·5	— —	14·1 9·8	3·50 3·50	0 0
6	—	—	—	—	—	—	—	—
7	15·5 26·3	20·9	407 407	33·9 33·6	— —	6·3 6·8	1·75 1·75	0 0
8	— 9·1	9·1	— 415	— 34·0	— —	— 13·0	— 1·50	— 0
9	—	—	—	—	—	—	—	—

APPENDIX A—*contd.*

Series	*Heat flow* (cal./100 ml./min.)		*Hand volume* (ml.)	*Hand temperature* (°C)	*Sub-clothing temperature* (°C)	*Environmental temperature* (°C)	*Bed clothes* (layers)	*Comfort* (Bedford scale)
	Individual	*Mean*						
Subject H (20°C)								
1	53·4	51·4	567	35·1	—	9·5	3·75	0
	49·4		567	35·2	—	9·4	3·75	0
2	—	—	—	—	—	—	—	—
3	26·6	28·2	621	35·6	—	10·2	3·50	0
	29·8		646	35·7	—	8·3	3·50	0
4	—	—	—	—	—	—	—	—
5	20·4	25·5	585	31·0	—	6·3	3·75	0
	30·4		585	34·9	—	13·9	3·75	0
6	—	—	—	—	—	—	—	—
7	58·9	47·8	603	32·4	—	15·2	2·75	0
	36·6		603	34·6	—	17·4	2·75	0
8	—	55·0	—	—	—	—	—	—
	55·0		603	35·0	—	14·1	2·75	0
9	—	—	—	—	—	—	—	—
Subject H (30°C)								
1	—	40·5	—	—	—	—	—	—
	40·5		567	35·0	—	12·0	3·75	0
2	—	—	—	—	—	—	—	—
3	—	—	—	—	—	—	—	—
4	—	—	—	—	—	—	—	—
5	39·5	33·9	658	35·6	—	16·6	3·75	+1
	28·2		658	35·5	—	11·2	3·75	0
6	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—
8	—	45·5	—	—	—	—	—	—
	45·5		603	34·9	—	13·9	2·75	0
9	—	—	—	—	—	—	—	—

APPENDIX B

SUMMARIES OF THE ANALYSES OF VARIANCE USED TO TEST FOR DIFFERENCES BETWEEN THE HEAT FLOWS AT THE TWO TEST TEMPERATURES AT EACH SERIES OF EXPERIMENTS

Source	*df*	*Sum of squares*	*Mean square*	*F*	*Significance*
Series 1					
Between subjects	7	726·79	103·83	6·95	0·01
Between temperatures	1	2·11	2·11		N.S.
Residual	13	1,359·83	104·60		
TOTAL	28	8,775·01	313·39		
Series 4					
Between subjects	3	448·04	149·35	2·42	N.S.
Between temperatures	1	153·76	153·76	2·49	N.S.
Subjects × temperatures	3	32·62	10·87		
Residual	8	646·56	80·82		
TOTAL	15	1,280·98	85·40		
Series 5					
Between subjects	5	1,460·24	292·05	4·74	0·01
Between temperatures	1	11·76	11·76	<1	N.S.
Subjects × temperatures	5	469·82	93·96		
Residual	12	577·89	48·14		
TOTAL	23	2,519·51	109·54		
Series 6					
Between subjects	1	165·64	165·64	2·45	N.S.
Between temperatures	1	0·32	0·32		N.S.
Subjects × temperatures	1	40·48	40·48		
Residual	4	296·99	74·25		
TOTAL	7	503·43	71·92		
Series 7					
Between subjects	6	632·98	105·50	3·83	0·05
Between temperatures	1	114·46	114·46	<1	N.S.
Residual	9	1,459·88	162·21		
TOTAL	24	4,861·92	202·58		
Series 8					
Between subjects	7	4,794·22	684·89	2·48	N.S.
Between temperatures	1	355·32	355·32	1·29	N.S.
Residual	7	1,934·68	276·38		
TOTAL	15	7,084·22	472·28		

Source	*df*	*Sum of squares*	*Mean square*	*F Subjects × temperatures*	*F Residual*	*Significance*
Series 2						
Between subjects	3	8,553·44	2,851·15	13·30	137·01	0·01
Between temperatures	1	130·00	130·00	<1	6·25	N.S.
Subjects × temperatures	3	643·26	214·42		10·3	0·01
Residual	8	166·50	20·81			
TOTAL	15	9,493·20	632·88			
Series 9						
Between subjects	3	3,526·80	1,175·60	5·07	87·47	N.S.
Between temperatures	1	163·84	163·84	<1	12·19	N.S.
Subjects × temperatures	3	695·06	231·69			0·01
Residual	8	107·52	13·44			
TOTAL	15	4,493·22	299·55			

N.S. Not significant.

APPENDIX C

CALCULATIONS OF "STORED HEAT" FROM THE CALORIMETER EXPERIMENTS

	Subject A		*Subject B*		*Subject C*		*Subject D*		*Series*
Experiments at 20°C									
H	697	536	1844	—	1867	1799	1191	1216	1
15*h*	402	268	786	—	924	1215	261	344	
"*S*"	295	268	1058	—	943	584	930	872	
H	1030	858	507	431	1641	2040	929	729	2
15*h*	321	237	281	200	1152	1350	243	186	
"*S*"	709	621	226	231	489	690	686	543	
H	1593	1598	—	—	1357	1990	1016	891	3
15*h*	506	521	—	—	617	743	263	233	
"*S*"	1087	1077	—	—	740	1247	753	658	
H	947	1516	755	323	768	913	778	929	4
15*h*	249	759	183	270	453	336	291	339	
"*S*"	698	757	572	53	315	577	487	590	
H	2155	1554	620	862	1899	1531	936	1388	5
15*h*	794	446	284	302	479	594	263	336	
"*S*"	1361	1108	336	560	1420	937	673	1052	
H	1317	894	—	—	1361	1370	1698	1377	6
15*h*	702	498	—	—	402	390	533	407	
"*S*"	615	396	—	—	959	980	1165	970	
H	2382	1411	1858	801	—	—	1176	1036	7
15*h*	983	411	419	234	—	—	218	302	
"*S*"	1399	1000	1439	567	—	—	958	734	
H	853	—	1082	—	1693	—	510	—	8
15*h*	396	—	336	—	608	—	226	—	
"*S*"	457	—	746	—	1085	—	284	—	
H	1201	885	1106	1384	2170	2470	1486	1079	9
15*h*	393	262	395	531	1032	1013	335	269	
"*S*"	808	623	711	853	1138	1457	1151	810	
Experiments at 30°C									
H	572	1197	629	543	1257	1160	878	928	1
15*h*	375	1005	468	477	995	791	620	783	
"*S*"	197	192	161	66	262	369	258	145	
H	409	515	358	270	1020	1109	333	281	2
15*h*	332	350	221	193	794	912	239	249	
"*S*"	77	165	137	77	226	197	94	32	
	—	—	—	—	—	—	—	—	3
H	533	503	181	259	—	332	311	427	4
15*h*	341	371	179	217	—	249	216	271	
"*S*"	192	132	2	42	—	83	95	156	
H	685	721	423	269	581	581	562	579	5
15*h*	545	477	204	122	441	480	437	576	
"*S*"	140	244	219	147	140	101	125	3	
H	742	649	361	434	705	726	—	—	6
15*h*	545	532	147	287	623	315	—	—	
"*S*"	197	117	214	147	82	411	—	—	
H	963	1129	571	721	—	—	453	—	7
15*h*	698	1017	350	528	—	—	383	—	
"*S*"	265	112	221	193	—	—	70	—	
H	539	—	667	—	728	—	299	—	8
15*h*	344	—	365	—	641	—	124	—	
"*S*"	195	—	302	—	87	—	175	—	
H	539	679	826	736	1046	1264	566	309	9
15*h*	308	342	624	542	617	638	256	126	
"*S*"	231	337	202	194	429	626	310	183	

"S" $= (H - 15h)$, where "S" is "stored heat" (in cal./100 ml./15 min.), H is total heat loss in first 15 min. of each experiment (in cal./100 ml.), and h = heat loss derived from circulation (from Appendix A) (in cal./100 ml./min.).

APPENDIX D

SUMMARIES OF THE ANALYSES OF VARIANCE USED TO TEST FOR DIFFERENCES IN HEAT FLOW BETWEEN SERIES

Source	*df*	*Sum of squares*	*Mean square*	*F*	*Significance*
Series 1-9 (*Subjects A, B, C, D*)					
Between series	1	434·29	434·29	2·53	N.S.
Between subjects	3	7,272·08	2,424·03	14·09	
Series × subjects	3	421·31	140·44		N.S.
Residual	23	3,955·64	171·98		
TOTAL	30	12,083·32			
Series 1-2 (*Subjects A, B, C, D*)					
Between series	1	365·84	365·84	2·22	N.S.
Between subjects	3	11,854·57	3,951·52	24·02	
Series × subjects	3	816·02	272·01		N.S.
Residual	23	3,783·67	164·51		
TOTAL	30	16,811·10			
Series 1-3 (*Subjects A, C, D*)					
Between series	1	605·16	605·16	2·69	N.S.
Between subjects	2	3,230·73	1,615·37	71·89	
Series × subjects	2	1,251·72	625·86		N.S.
Residual	12	2,696·28	224·69		
TOTAL	17	7,783·89			
Series 1-3 (*Subjects A, C, D, E, F, G, H*)					
Between series	1	997·57	997·57	12·24	<0·001
Between subjects	6	5,170·10	861·68	10·57	
Series × subjects	6	2,001·35	333·56		<0·05
Residual	36	2,934·74	81·52		
TOTAL	49	11,103·76			
Series 1-4 (*Subjects A, B, C, D*)					
Between series	1	1,917·66	1,917·66	11·79	<0·001
Between subjects	3	2,284·81	761·60	4·68	
Series × subjects	3	2,799·10	933·03		<0·05
Residual	23	3,739·84	162·60		
TOTAL	30	10,741·41			
Series 2-4 (*Subjects A, B, C, D*)					
Between series	1	647·66	647·66	9·05	<0·01
Between subjects	3	4,958·16	1,652·72	23·08	<0·001
Series × subjects	3	4,183·09	1,394·36	19·47	<0·001
Residual	24	1,718·54	71·60		
TOTAL	31	11,507·45			
Series 1-7 (*Subjects A, B, D*)					
Between series	1	9·13	9·13	0·04	N.S.
Between subjects	2	321·29	160·65	0·67	
Series × subjects	2	952·41	276·21		N.S.
Residual	16	3,817·04	238·57		
TOTAL	21	5,099·87			

N.S. Not significant.

Appendix D—*contd.*

Source	*df*	*Sum of squares*	*Mean square*	*F*	*Significance*
Series 1-7 (Subjects A, B, D, E, F, G, H)					
Between series	1	123·36	123·36	0·93	N.S.
Between subjects	6	3,134·18	522·36	3·94	
Series × subjects	6	1,200·95	200·16		N.S.
Residual	34	4,508·55	132·60		
Total	47	8,967·04			
Series 3-7 (Subjects A, D, E, F, G, H)					
Between series	1	1,178·71	1,178·71	14·03	<0·001
Between subjects	5	1,750·28	350·56	4·17	
Series × subjects	5	899·60	179·92		N.S.
Residual	19	1,596·11	84·01		
Total	30	5,424·70			
Series 3-8 (Subjects A, C, D)					
Between series	1	87·48	87·48	7·02	<0·05
Between subjects	2	1,859·17	929·58	74·60	
Series × subjects	2	5·93	2·97		N.S.
Residual	6	74·73	12·46		
Total	11	2,027·31			
Series 3-8 (Subjects A, C, D, E, F, G, H)					
Between series	1	35·02	35·02	2·36	N.S.
Between subjects	6	3,223·83	53·73	3·63	
Series × subjects	6	725·66	120·94		<0·05
Residual	13	192·50	14·81		
Total	26	4,177·01			
Series 4-5 (Subjects A, B, C, D)					
Between series	1	379·68	379·68	4·35	<0·05
Between subjects	3	1,675·30	558·43	6·39	<0·01
Series × subjects	3 } 27	283·64	94·55 } 87·33	1·09	N.S.
Residual	24	2,074·15	86·42		
Total	31	4,412·77			
Series 4-6 (Subjects A, B, C, D)					
Between series	1	70·02	70·02	1·03	N.S.
Between subjects	3	1,879·07	626·36	9·21	
Series × subjects	3	284·28	94·76		N.S.
Residual	20	1,360·22	68·01		
Total	27	3,593·59			
Series 4-7 (Subjects A, B, D)					
Between series	1	345·52	345·52	2·85	N.S.
Between subjects	2	1,767·05	883·52	7·29	
Series × subjects	2	158·69	79·35		N.S.
Residual	17	2,060·32	121·19		
Total	22	4,331·58			
Series 5-7 (Subjects A, B, D)					
Between series	1	100·86	100·86	0·87	N.S.
Between subjects	2	1,539·39	769·69	6·67	
Series × subjects	2	330·76	165·38		N.S.
Residual	17	1,962·85	115·46		
Total	22	3,933·86			

APPENDIX D—*contd.*

Source	*df*	*Sum of squares*	*Mean square*	*F*	*Significance*
Series 5-7 (Subjects A, B, D, G, H)					
Between series	1	384·00	384·00	4·01	N.S.
Between subjects	4	2,646·49	661·62	6·92	
Series × subjects	4	239·49	59·87		N.S.
Residual	27	2,582·85	95·66		
TOTAL	36	5,852·83			
Series 6-7 (Subjects A, B, D)					
Between series	1	140·36	140·36	1·12	N.S.
Between subjects	2	1,873·65	936·83	7·47	
Series × subjects	2	391·48	195·74		N.S.
Residual	13	1,630·96	125·46		
TOTAL	18	4,036·45			
Series 7-8 (Subjects A, B, D)					
Between series	1	914·76	914·76	7·02	<0·05
Between subjects	2	611·59	305·79	2·35	
Series × subjects	2	625·69	312·84		N.S.
Residual	11	1,433·48	130·32		
TOTAL	16	3,585·52			
Series 7-8 (Subjects A, B, D, E, F, G, H)					
Between series	1	757·56	757·56	8·29	<0·001
Between subjects	6	3,915·53	652·59	7·14	
Series × subjects	6	1,000·29	166·72		N.S.
Residual	22	2,011·07	91·41		
TOTAL	35	7,684·45			
Series 8-9 (Subjects A, B, C, D)					
Between series	1	432·00	432·00	5·85	<0·05
Between subjects	3	3,779·65	1,259·88	17·06	
Series × subjects	3	804·03	268·01		<0·05
Residual	16	1,181·31	73·83		
TOTAL	23	6,196·99			