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A STUDY OF TEMPERATURE CONTROL IN THE HUMAN BODY BY EXPERIMENT AND COMPUTER SIMULATION

Arthur Reginal Atkins

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ABSTRACT

The dynamic temperature response of the human body is studied by analysing the thermoregulatory mechanism. By subjecting man to a large number of step disturbances and comparing his transient response with that of a mathematical model it is possible to identify the control characteristics quantitatively over a wide range of environments. The analysis shows that both proportional and rate control actions occur, the reaction to an increase in heat stress is different to that of a decrease in heat stress. Control is initiated by thermo-sensors of identical characteristics in the core, hypothalamus, muscle and skin. Thermo-sensors in the muscle provide a rapid change in sweat control action when man starts working. Control is based upon the non-linear characteristics of the thermo-sensors and not upon a set point.

Thermoregulation Simulation Biological models

Heat physiology

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A STUDY OF TEMPERATURE CONTROL IN THE HUMAN BODY BY EXPERIMENT AND COMPUTER SIMULATION

A. R. ATKINS

I hereby state that:

a) unless reference is made in the text of other persons, this is my own work;

b) none of this work or any part of it has been submitted in the past or is being or is to be submitted for a degree in any other university;

c) ideas for this work were obtained at informal discussions and lectures at the university and at the Human Sciences Laboratory of the Chamber of Mines of South Africa, the source of any other information is referred to in the text.

A.R. ATKINS

ARA/MS
29th September, 1975.

CHAPTER 1

INTRODUCTION

The study of the thermal response of man to thermal stress has been of interest to physiologists, ventilation engineers, industrialists, miners and space scientists for many years. With a knowledge of the thermal behaviour of man it is possible to design the most suitable ventilation system for a particular environment or to predict the maximum amount of work a man may perform in a given environment.

Unlike physical systems, this study is hampered by inter - and intra-individual variability, the degree of acclimatisation, the day to day variability of the body, the complex shape of the body and the difficulty of making detailed accurate measurements. Nevertheless, heat physiologists have acquired a great deal of knowledge on the thermal behaviour of man and are capable of predicting his steady state of response to almost any environment. Little is known, however, of the transient response of man when he is subjected to a change in environment because the precise function of the thermo-regulatory mechanism of man during thermal transients is unknown. One of the reasons is the lack of, and the difficulty of obtaining accurate experimental results.

There are few laboratories which are equipped with a climatic chamber capable of direct calorimetric studies on men who are in a natural upright position and are able to work.

Heat physiologists have followed other disciplines by using models to describe their problem. The first simple, yet very valuable, electrical model of thermal control was suggested by MacDonald and Wyndham (1950).

This original idea has sparked off a host of ideas. Models are invaluable in the study of any complex system. The purpose of this first model was described as "an aid to the systematic analysis of the complex physiological data and should not be mistaken for a mere electrical analogy."

This thesis describes a study of the dynamic thermal behaviour of man. In place of the usual examination of steady state data, the transient behaviour of man to changes in environment is analysed for the purpose of evaluating the thermal control characteristics. Under severe heat stress or during exposure to cold, man seldom is in a state of thermal equilibrium and it is therefore important to understand his dynamic behaviour.

Seven questions were selected as the objectives, namely:

1) What is the precise function of each control action and how effective is it in controlling body temperature when the body is subjected to a thermal stress?

2) It is possible to identify a quantitative relation between the control actions and body temperature?

3) Do both proportional and rate control actions take place?

4) Is it necessary to have thermo-receptors distributed throughout the body or are those which have been located in the core and in the skin sufficient for control purposes?

5) Is the very rapid increase in sweating, recorded after a man starts working, initiated by a non-thermal control action or can it be initiated by a rapid change in body temperature?

6) How accurately and in what environmental conditions can the body temperature be predicted?

7) Under what conditions does the body attain a steady state and how long does this take after a thermal disturbance?

This thesis commences with a review of the subject of thermoregulation in man.

Chapter 3 describes the two major components of the thermoregulatory mechanism, namely, the controller and the controlled system. Each component is examined and then the information required for this study is defined.

Chapter 4 describes the experiments for studying the thermal responses of man in the climatic chamber. A summary of the experimental results are included in this chapter. A detailed description of the climatic chamber, the experimental equipment and the results are given in the Appendix.

The experimental tests on men in the climatic chamber show rather simple smooth temperature response curves and therefore suggest that a very simple behaviour model of the controlled system may be used to analyse and identify the control characteristics of a resting man. Chapter 5 examines the thermoregulatory mechanism of a man exposed to a heat stress and Chapter 6 examines the response of a man exposed to a cold stress by analysing the response of a simple model.

In case there is any doubt that the control characteristics derived from the simple model are not applicable to a 'distributed body', Chapter 7 shows that a more complex model, with the same control characteristics as those derived from the simple model, behaves in a similar manner to the experiments in the

climatic chamber. The detailed model is used to examine the control characteristics of a working man and to complete the study of the objectives.

The study of the objectives is reviewed in Chapter 8.

All the experiments described in this study were performed in the Chamber of Mines Research Laboratories calorimetric wind tunnel. The author of this thesis represented the research team which was responsible for the development of the climatic chamber, as an electronics engineer. His tasks were

a) to provide the necessary electronic instrumentation for the measurement of the physiological data, and
b) to study the thermoregulatory control of man and to design a simulator which could predict man's responses in as wide as variety of environments as possible.

Unless reference is made to other workers, the analysis which follows is due entirely to the author.

CHAPTER 2

HEAT TRANSFER AND TEMPERATURE CONTROL OF THE HUMAN BODY: A REVIEW

2.1 Introduction

2.2 Metabolism and body temperature

2.3 Heat transfer

2.3.1 Heat transfer within the body

2.3.2 Heat transfer between the body and its environment

2.4 Thermal stress and the control of body temperature

2.4.1 Thermo-sensors and neuro-transmitters

2.4.2 Control of sweating

2.4.3 Control of blood flow

2.4.4 Control of heat production

2.5 Mathematical and physical models of thermoregulation

2.6 Conclusions

2.1 Introduction

The biological importance of the regulation of temperature for survival has been known for centuries. In 1797 James Currie wrote: "If a definition of life were required, it might be most clearly established on that capacity by which the animal preserves its proper heat under the various degrees of temperature in which it lives." It was Claude Bernard (1879) who first formally stated these requirements. Early work was done on the thermal response of man to various environments by Bazett (1933, 1938, 1949), Burton (1934), Du Bois (1937), Gagge (1949), Hardy (1938,1949), Herrington (1949), Robinson (1949) and Winslow et al.(1949). The words 'temperature control' appear in the literature as early as 1933. A book by Newburg (1949) contains early reviews of many of the important topics related to heat physiology, namely heat transfer, body temperature, thermal comfort, blood circulation and thermal sensation. It was,however,only after Wiener's classic book entitled 'Cybernetics', published in 1948, that interest in the feedback control processes in living systems was aroused.

The subject soon became divided. One group of investigators followed the path on the neuronal level, concerning themselves with locating and testing the function of neurons and synapses, while the other group was more concerned with the overall biophysical aspects of thermo-regulation. Ventilation engineers avoid this subject and confine their interest to comfort and stress indices.

This chapter reviews the literature relevant to the subject of heat transfer in, and temperature control of the body. An attempt is made to clarify the present state of knowledge of biothermal temperature regulation. The review commences with the source of heat in the body which causes an elevation of temperture . The temperature zones, which are of interest in this study, are described. The heat produced in the body must be transferred from sites of generation to the

skin before it can be lost to the atmosphere. The review follows the same order. The need for, and the method of stabilising body temperature is described; the subject starts with neuro-temperature-sensors and leads on to the control actions. Finally, a few types of bio-thermal models used for assisting with the study of this subject are described.

2.2 Metabolism and body temperature

The energy requirements of the body are met through metabolism, the combustion of foodstuffs with oxygen. The whole life process is, infact, a form of slow combustion which supports the production of heat and work. There are definite quantitative relationships between the intake of food and oxygen with the production of work and the liberation of heat, as was first realised by Lavoisier and L place (1783).

The minimum metabolism required to preserve life of a resting man in a comfortable thermal environment is known as basal metabolism. A typical value is 100 watts. Approximately 70 per cent of this heat is thought to originate from part of the viscera, the weight which comprises less than 8 per cent of the total body weight (M.Nielsen, 1971). Less than 20 per cent of the basal metabolism is contributed by the muscle and skin. The metabolic rate of heat production includes that due to physical activity and the metabolism of digested food.

The mechanical efficiency of physical activity is low and varies from zero to 20 per cent , depending upon the activity (Williams, 1966). A moderate rate of work will increase the metabolism from 100 watts to approximately 250 watts. Man is capable of performing useful work at the rate of 350 watts for short periods, and at this rate his rate of metabolic heat production can be as much as 1 200 watts (Wyndham et al., 1959).

The metabolism of a resting subject is constant over a wide range of temperatures. It has been noted that there is

a slight increase at very high ambient temperatures (Winslow and Herrington, 1949). A substantial increase in metabolism is caused by shivering during exposure to cold (Burton, et al. 1955).

It is man's metabolism which elevates his body temperature to some level above average ambient temperature. The temperature varies considerably from one part of the body to another. The temperature of the skin and of the extremities of the limbs vary with the environment, whereas the temperatures of the deeper structures in the trunk and head, particularly the vital organs such as the brain, kidney and liver are fairly stable. Muscle will have a temperature between those of the deeper structure of the trunk and the skin. The temperature of large muscles reaches the highest level after heavy work (Saltin et al., 1966, 1968, 1970; Aikas et al. , 1961).

In the field of temperature regulation the body is often divided into two major temperature zones; the core representing the greater portion of thermal mass of the body, and the skin. The boundary between these two zones is in the region of the dermis where there is a very large temperature gradient. The core is represented by a single temperature, which should be the mean temperature of that zone, and the skin is represented by the mean surface temperature.

The author (Atkins, 1960) suggested that the body should be divided into at least four concentric temperature zones if one is examining a working man, the zones are

a) the core representing the skeleton, viscera and deep fatty tissue,

b) the muscle,

c) the skin, and

d) the circulatory system which includes the thermal mass of the blood in the heart and lungs (Atkins, 1962).

With these four zones it is then possible to identify

muscle temperature with a zone other than the core. The temperature of the circulatory system is represented by the arterial blood temperature, that is the temperature of the larger arteries and the temperature of the blood in the heart and lungs. The arterial blood temperature is often associated with core or deep body temperature. This is not always correct for reasons explained later in Section 2.3.

The term'mean body temperature'is often referred to in texts. True mean body temperature may be defined as the mean of all the temperature components of the body weighted according to their thermal masses. In a two zone analogy the core represents the majority of the thermal mass and therefore the mean body temperature will be almost identical to the mean core temperature. Mean body temperature is sometimes expressed as a function of rectal and skin temperature,(Snellen,1966; Stolwijk et al.1966; Colin et al.,1971)

Because of thermal gradients within the core of the body,it is difficult to find a convenient site for measurement of a representative core temperature. The two most accessible places are the rectum and the mouth. The latter is severely influenced by rapid respiration (Strydom et al., 1956). The rectal temperature has been used traditionally for experimental measurements of deep body or core temperature. It is slightly higher than most other temperatures which have been measured in the body of a resting subject (Minard and Copman, 1963), and is therefore a better indication of the temperature at the centre of the core rather than the average core temperature. However, if the temperature gradient across the core is not large, rectal temperature is a reasonable indication of core temperature. Because the rectum is surrounded by a large thermal mass, the rectal temperature, like the mean core temperature, has considerable thermal inertia.

The oesophageal temperature, measured just above the level of the diaphragm, is regarded as being closely representative of the arterial temperature (Nielson and Nielson, 1962 ; Snellen, 1969; Cooper and Kenyon, 1957). A very useful comparison between oral, rectal and arterial temperature has been

given by Cranston (1966) and Eichna et al.,(1951). Minad and Copman (1963) have reviewed the literature and provide a table which lists the internal temperature gradients in resting human subjects related to rectal temperature. Temperatures vary by + 0,4 °C to - 0,45 °C. The mean deviation is - 0,2 °C.

A few physiologists favour tympanic temperature measured in the ear cavity as an indication of arterial temperature (Benzinger, 1960, 1963). One of the reasons for this choice is the fact that it responds rapidly to forced internal heat loads. Nadel and Hovarth (1970) have shown that tympanic temperature is influenced by the temperature of the skin, and Greenleaf and Castle (1972) have stated clearly that tympanic temperature is not suitable as a measure of core temperature.

Muscle temperatures have been measured during exercise with very fine thermocouple wires (Saltin et al.,1968;Buchthal 1944). This method causes considerable discomfort and is therefore not undertaken in the experiments in the climatic chamber at the Human Sciences Laboratory.

The skin is the interface at which there is an exchange of energy between body and environment and its temperature is therefore of considerable importance. Radiation thermography has shown that the temperature varies by several degrees at different sites on the body surface (Whipple, 1964). The temperature of the skin is governed by the adjacent peripheral blood distribution, the velocity and temperature of the blood and by the mode of exchange of heat with the environment (Mitchell, 1972; Murlin,1939; Stoll, 1960). There is a large and varying gradient in the temperature of the tissue beneath the skin. This aspect is discussed in detail in the following section.

The main problems in measuring skin temperature are not to disturb the adjacent peripheral blood flow or to shield the skin from radiative and evaporative heat losses. The techniques

and difficulties of measuring skin surface temperature are well described by Mitchell (1966,1972). The subject was pioneered by Hardy and Stoll who developed both radiometer and direct thermocouple probes (Stoll and Hardy, 1949; Stoll and Hardy, 1950; Hardy, 1953; Stoll, 1954).

A mean value of skin temperature is required in calculations of the total heat loss from the body. The sites at which the representative temperature is measured, The minimum number of sites required and their corresponding weighting factors have been investigated in detail (Hardy et al.1938; Teichner, 1958; Ramanathan, 1964; Mitchell, 1972). The fifteen point technique used in the Human Sciences Laboratory is described in Chapter 3.

In Table 2.1 are presented typical steady state body temperatures which have been measured in men during periods of rest and work in a comfortable environment.

TABLE 2.1

Comparison of body temperatures during rest and work in an ambient temperature of 30 °C.

	Rest	Work
Mean skin	33 °C	34 °C
Subcutaneous tissue	33,5 °C	35 °C
Muscle	35 °C	38 °C
Arterial	36,8 °C	37,6 °C
Rectal	37 °C	37,4 °C

2.3 Heat transfer

A stable mean body temperature is attained when heat production balances heat loss. The metabolic heat must be transferred from sites of generation to the skin before it can be lost to the atmosphere. If all the metabolic heat input is not lost to the environment homeostasis does not occur and the body temperature will increase.

2.3.1 Heat transfer within the body

Direct heat conduction through tissue accounts for about 20 per cent of the basal metabolic heat and a negligible proportion during exercise (Atkins, 1969). Most of the metabolic heat is transferred by vascular convection in blood flowing to the skin surface.

Arterial blood entering a capillary bed in the region of high temperature caused by metabolic heat production, has a temperature lower than that of the tissue. Because of good thermal contact with the tissue, the blood accumulates heat and it is assumed that the venous blood leaving the tissue has a temperature close to that of the tissue (Atkins, 1962; Stolwijk, 1966). Venous blood from different areas is mixed in the heart and lungs. Since part of the venous blood returning from the periphery is cooler than that of the regions of high metabolism, the mean venous temperature has a value between the temperature of the metabolic region and the periphery (Atkins, 1962). The blood is mixed thoroughly in the heart and lungs. The temperature of the blood leaving this zone, that is, the arterial temperature, is therefore almost equal to the mean venous temperature at steady state. The difference between the arterial temperature and the mean venous temperature during homeostasis is due to the loss of a small quantity of heat through respiration in the lungs (Mitchell, 1972). The arterial blood entering a metabolically

inactive peripheral capillary bed will have a temperature higher than that of the tissue and heat will therefore be transferred from blood to the tissue.

The net result is a transfer of heat from regions of active metabolism in the core and muscle to the blood in which the heat is carried, via the heart and lungs, to the peripheral capillary beds.

The arterial temperature is clearly lower than the temperature of metabolically active areas of the core of a resting man otherwise there would be no vascular convection. When the body is undergoing heavy physical activity the muscle temperature is higher than the rectal temperature and the arterial blood temperature can exceed the rectal temperature but it will be lower than the muscle temperature. The arterial temperature is therefore dependent upon both the distribution of blood in the body and the temperature of the body components. The thermal inertia of the circulatory system is much smaller than the core or muscle and the arterial temperature will therefore have a much faster time response than the core temperature.

Unless the circulatory system is treated as a separate thermal zone, as suggested by the author, care should be taken when associating arterial blood temperature with core temperature, particularly during a transient state.

There is uncertainty concerning countercurrent heat exchange between arteries and veins in regions where these vascular channels are in fairly close proximity. Bazett et al. (1948) examined the arms and legs of a man and suggested that countercurrent heat exchange might take place. Mitchell and Myers (1968) analysed the possibility of countercurrent heat exchange between adjacent larger arteries and veins and concluded that this is negligible. Keller and Seiler (1971) suggested that countercurrent heat exchange might be effective

in local regions near the surface where smaller arteries and veins which distribute blood for local perfusion, pass close together.

The peripheral capillary beds where the arterial blood 'disposes of' the heat are an important region and worthy of closer examination. The capillary beds are close to the skin surface and do, in fact, invaginate into the epidermis. Because of the complex nature of the skin and adjacent tissue there is little detailed information regarding the distribution of heat and the thermal gradient in this area, particularly for different parts of the body.

Stoll (1960) has stated that the skin may vary in thickness from 0,5 mm to 5 mm and suggested that heat transfer should be treated differently according to which of the two layers of the skin heat is transferred, namely,

a) the inner section containing small peripheral blood vessels, and

b) the outer bloodless tissue through which heat is transferred by conduction only.

The inner section of the skin contains many arterioles, venules and capillaries. (Refer to Figure 2.1) The capillaries loop out towards the skin forming a link between the arteriolar plexus and the superficial venous plexi (Kenshalo and Nafe, 1962). The flow of blood through the capillaries is determined by the state of the pre-capillary sphincter, which is either open or closed. There are also arterio-venous anastomoses, which are direct shunts with contractile walls between arterioles and venules (Greenfield, 1963).

Bazett (1949) has made a detailed study of the temperature gradient near the surface of the skin of the forearm. He measured the temperature profile to a depth of 6 mm at 0,25 mm intervals. Depending on air temperature, the difference

between the temperature at the surface and at this depth varied from one to two degrees centigrade. A distinct peak was noticed at a depth of 0,8 mm followed by a trough at 1,5 mm. The peak is attributed to the presence of an arteriolar network or plexus. Bazett gives a very good illustration (see Figure 2.1) which shows the possible reason for this peak.

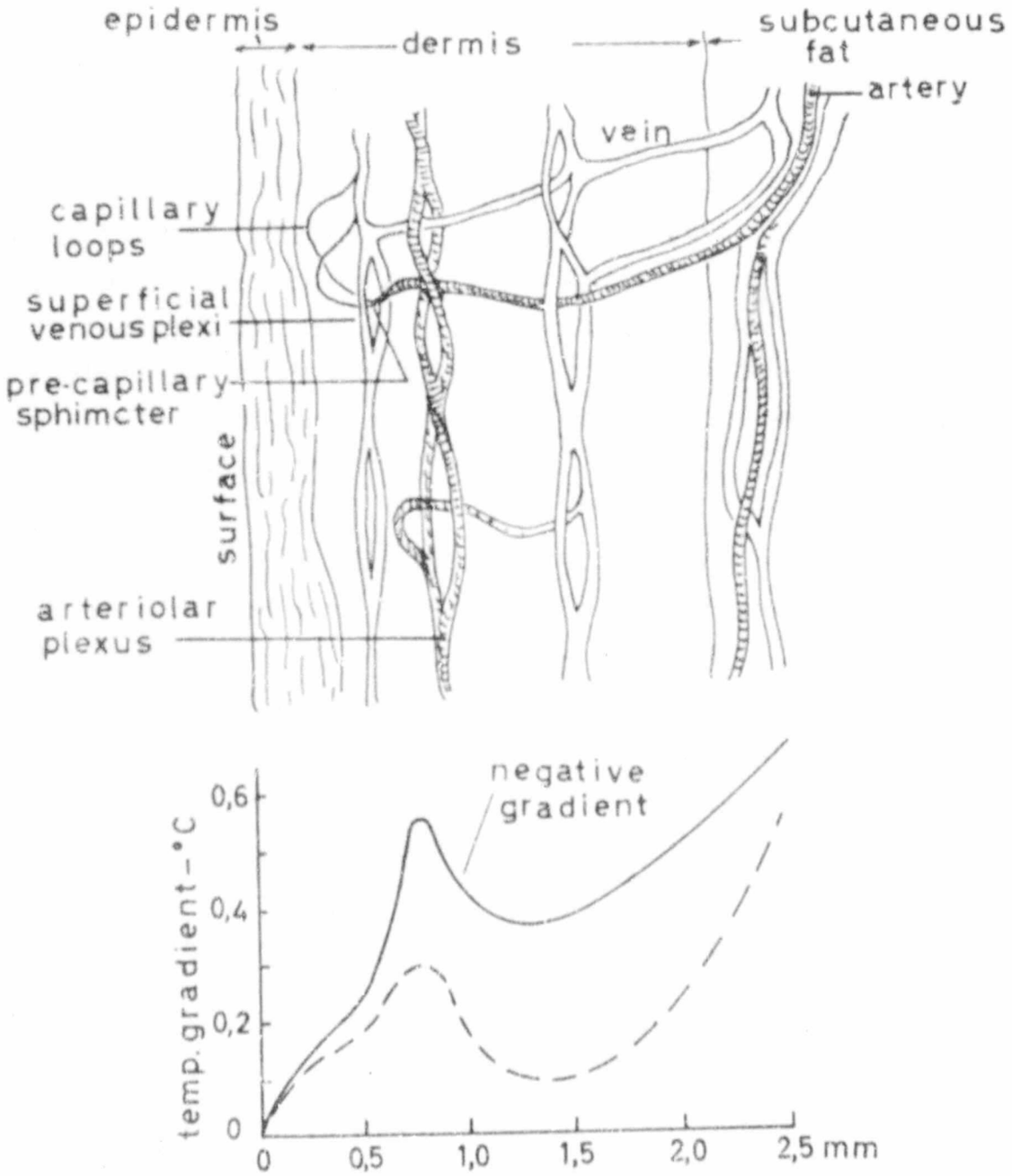

FIGURE 2.1

A sectional schematic representation of the skin. The temperature gradient is shown below the schematic diagram.

B. Nielson (1969) has also examined the temperature gradient beneath the skin with the object of determining at what depth "an operational average deep-skin temperature should be measured." This temperature might represent the temperature of the nerve endings of the peripheral thermal receptors. Temperatures were measured at 1 mm intervals to a depth of 6 mm.

Because fewer measuring intervals were used than those of Bazett, the thermal gradient is not as clearly defined as that given by Bazett. A slightly negative gradient, in a direction towards the centre of the body was measured when the body was at rest, whereas a positive gradient of 2,5 °C per mm was measured at high work rates. Nielson did not detect the peak and trough in the skin temperature gradient noted by Bazett, partly because fewer measuring intervals were used and partly because the ambient temperature was higher.

The most important aspect of Nielson's data is that the temperature gradient between the surface and a depth of 3,5 mm was 5 °C for a working subject. Assuming a typical skin temperature of 33 °C, the tissue temperature would be 38 °C. Clearly, the peripheral capillary bed must, therefore, lie within a few millimetres of the skin surface and range from 0,5 to 4 mm in depth.

2.3.2 Heat transfer between the body and its environment

Heat transfer between man and his environment occurs mainly by radiation, convection and the evaporation of sweat. The mechanism of heat exchange obeys rigorous physical laws and is essentially the same as that for inanimate bodies (Mitchell, 1972). Respiratory heat loss is significant only in cases of high ventilation rates in a dry atmosphere.

There are difficulties in applying the laws of heat loss on account of the very irregular shape of the body. Direct calorimetry has made it possible to verify these laws experimentally and to produce reliable expressions for the three modes of heat exchange. Early work may be credited to Gagge et al., (1937); Hardy (1949); Machle and Hatch (1947); Kerslake and Waddell (1958); Woodcock (1965); and the Fort Knox Laboratories (1946). At two modern calorimetric wind tunnels (Colin and Houdas, 1967; Colin et al., 1971 and Mitchell et al., 1969) the subject has been studied in great detail. The most recent and perhaps the most accurate work on this subject has been done at the Chamber of Mines Laboratories (Mitchell, 1972). Mitchell was able to measure radiative, convective and evaporative heat loss directly. The theoretical analysis of heat exchange from the body is described in Chapter 3.

2.4 Thermal stress and the control of body temperature

If any passive body is subjected to a change in ambient temperature, the temperature within the body will change by an equal amount, given sufficient time. This is not so with the human body which is equipped with an active thermoregulatory mechanism which is capable of maintaining a near-constant core temperature and which thus minimises the thermal strain. The main sources of thermal stress are environmental temperatures and the increase in metabolism due to physical work. The body can make four corrective actions of which three are involuntary:

1. The rate of sweat secretion on the skin surface is adjustable.

2. The distribution and rate of blood flow in the periphery and splanchnic bed are adjustable.

3. The rate of heat production within the body is adjustable.

4. The body may take on or remove protective clothing and seek a more suitable environment.

Hardy (1971) has shown that involuntary or physical regulation will protect man in an environment temperature ranging from 0 °C to 50 °C whereas behavioural regulation can protect a man in temperatures ranging from - 200 °C to + 800 °C.

The reason why temperature regulation is necessary has not been determined. Most physiologists agree that it is probably the temperatures of the organs and of the brain which require this stable temperature for survival. Bligh (1966), in an excellent review, states: "The control of heat production and heat loss so that the deep-body temperature remains more or less constant is a property of most mammals - the great mass of evidence accumulated over more than a century gives general support to this interpretation."

It has been shown, however, that the organs of some animals can be subjected to a much wider temperature variation without noticeable harm (Mitchell, 1972). Snellen (1972) has suggested that it is not the body temperature but body heat content which is controlled. In this thesis it will be assumed that it is the core temperature, in particular the temperature of the viscera, which requires control.

If one has to control the temperature of an insulated waterbath, it is natural to do so by means of a thermostat in the waterbath. The thermostat has a reference or setpoint temperature and should the temperature of the bath fall below this setpoint, some corrective action is taken to restore the bath temperature to its required value. This basic concept

of control has led physiologists to try to locate the source of temperature sensors and also the setpoint.

2.4.1 Thermo-sensors and neuro-transmitters

The reflex response of the skin to changes in tem era-ture was first noted by Francois-Frank. Pickering (1932) provided the first conclusive evidence that a thermo-regulatory action results from a change in either the skin or core temperatures. Bazett (1949) stated that there is little doubt that the hypothalamus is the temperature-sensitive region in the core.

The relative importance of either the skin and core temperature in initiating control was a popular research topic for many years. Burton and Edholm (1955), Randall et al. (1963) and van Beaumont and Bullard (1967) considered the skin temperature to be important while Benzinger (1963) attributed all control to the core temperature. Wyndham et al.(1965) have shown clearly, the relative importance of both skin and core temperatures.

Hensel (1973) has recently written a comprehensive review of the neural processes in thermoregulation. He states that there is little direct evidence of the location of central temperature receptors in man. On the basis of the results of experiments with animals, the hypothalamus and spinal cord are regarded as the area with the highest con-centration of thermo-receptors. It has been suggested, though there is no proof, that thermo-receptors might be situated in the large veins of the legs and in the muscle of man (Gisolfi and Robinson, 1970; Saltin and Gagge, 1971 and Saltin et al. 1971).

The introduction of the single-unit recording techniques for the study of thermo-sensitive neurons by Birzis and Hemingway (1957) opened a new door to the study of thermo-

regulation. Micro-electrode techniques enable single cell activity to be observed and provide a valuable method of locating thermo-sensitive neurons. The experiments have confirmed the presence of highly thermo-sensitive cells in the spinal cord, the preoptic and posterior areas of the hypothalamus, the abdomen, veins and the skin of animals (Hensel, 1973).

The early work of Nakayama et al.(1961, 1963) located neurons in the hypothalamus which were sensitive to heat only. Later work by Hardy et al.(1964), Eisenman and Jackson (1967), Cabanac (1968) and Hensel and Wurster (1969) revealed certain neurons sensitive to cold and others sensitive to heat. It is now an accepted fact that there are two types of thermo-sensors, namely 'warm sensors' and 'cold sensors'. It is interesting to note that, so far, only a few cold and no warm receptors have been identified by electrophysiological methods in the skin of human subjects (Hensel, 1973).

The average static frequency- temperature characteristics of warm and cold nerve fibre populations, taken from the nasal area of a cat, are given by Hensel and Kenshalo (1969). These curves are illustrated in Figure 2.2. They compare favourably with rat scrotal (Iggo, 1969) and cat spinal cord (Simon and Iriki, 1971) thermosensitive units.

Hensel and Huopaniemi (1969) noted another important characteristic of neuron activity in the nasal region of a cat. They found the impulse frequency of the nerve fibres to be very dependent on the rate of change of temperature. The peak impulse frequency is about three to five times the static frequency following a step change in temperature. The settling time is approximately twenty seconds. The dynamic sensitivity is bi-directional: warm receptors are excited by a rise in temperature and inhibited by a fall in temperature. Cold receptors respond the opposite way.

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