

RECENT ADVANCES IN PHYSIOLOGY

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PREFACE TO THE SEVENTH EDITION

SINCE the publication of the last edition of this book, just before the war, eleven imposing volumes of the new Annual Review of Physiology have appeared. These, added to the familiar Physiological Reviews, other periodical reviews, annual volumes of lectures, monographs, and text-books compiled from the contributions of specialists, place the physiologist in search of authoritative up-to-date information in an exceptionally favourable position. The situation of the present writer is no less favourable, for he need not, and has not troubled about committing sins of omission. An old schoolmaster used to be fond of pointing out that 'The Acts of the Apostles' should have been called 'Some Acts of Some Apostles,' and he would undoubtedly have dubbed this book 'Some Recent Advances by Some Physiologists.' Its purpose is not to impart the greatest amount of knowledge which could be introduced into its pages, but rather to indicate to the student certain modern currents of thought, anchoring him meanwhile near one of the main sources. The quantity of factual knowledge which this involves has depended on the subject, and every effort has been made to select subjects of interest and importance, to record the facts accurately, and to provide an explanatory background where necessary. The chapters, though fewer than hitherto, are all new.

It is a pleasure to acknowledge help by Dr. I. Calma in supplying practically all the material for Chapter V of which he wrote a draft. Colleagues and senior students at Liverpool and friends elsewhere have also helped by discussing subjects in which they are interested, by guiding me to the literature, or by criticising what I have written. They would probably prefer to remain anonymous lest responsibility should cling to them, but they have my sincere thanks. The sources of illustrations are gratefully acknowledged in the legends.

Finally, I would record my indebtedness to my wife, not only for reading the proofs and making the index, but for her encouragement in a much-interrupted task. The counterpart of this has been the patience of the publishers whose reminders could not have been more considerate.

W. H. NEWTON.

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CHAPTER I

THE PHYSICAL BASIS OF TEMPERATURE REGULATION

The principle of calorimeters designed to measure heat production is too familiar to require description, but during the last few years a new type of calorimetry called, by Winslow, Herrington and Gagge, 'Partitional Calorimetry' has been used to measure radiation, convection and evaporation separately. This enables the methods by which the body adjusts the balance between gain and loss of heat to be studied quantitatively. A complete survey of the results obtained by various workers is impossible in a short space, and an attempt will, therefore, be made to explain the principles and apparatus upon which such determinations are based. This requires a somewhat extended treatment of the work of Winslow, Herrington and Gagge at the expense of an evaluation of their work in relation to that of other authors. The work of Du Bois and his colleagues merits particular mention, and the reader is referred to the delightful Lane lectures given by Du Bois in 1936, and their sequel published in 1948.

The key measurement is that of the loss of heat by radiation, for evaporative heat loss can be measured by the loss of weight of the subject, corrected for oxygen intake, carbon dioxide output, etc. Knowing these two quantities the loss by convection can be derived by subtracting them from the total heat production, which is measured in the usual way. It will be seen later that Winslow and his colleagues have been able to advance further than this by taking account of the storage of heat in the body when its temperature changes, but it is first necessary to study the question of

radiation as it applies to the human body.

The perfectly-black body

An object receiving radiation obeys the same laws whether the radiation is visible or invisible: it may reflect a part, transmit a part (as glass transmits light) and absorb a part. The energy of absorbed radiation is converted into molecular motion and raises the temperature of the body. A perfectly-black body neither

reflects nor transmits incident radiation, but absorbs the whole. Now, a body freely suspended in an evacuated space attains temperature equilibrium with the walls bounding the space. In other words, the rate at which it is emitting radiation is the same as that at which it is receiving it. The intensity of emission from a perfectly-black body must, therefore, be greater than that from any other body. The Stefan-Boltzmann law states that the total rate of radiation from a perfectly-black body is proportional to the fourth power of its absolute temperature.

If the radiation from a perfectly-black body of known temperature be allowed to fall on a thermocouple, the current produced will be a function of that temperature. An instrument calibrated by exposing it to a black body at a number of different temperatures is, therefore, capable of measuring the temperature of any other black body to which it is directed. If the latter is not 'perfectly-black,' then the instrument reveals its 'black body temperature.' The black body temperature of, say, a block of hot polished copper is much less than its actual temperature. On the other hand, a cool sheet of copper may reflect intense radiation from a source of heat (concealed from the measuring instrument) without itself becoming heated (Fig. 5). Its apparent black body temperature will be greater than its actual temperature.

TABLE 1

Influence of character of surface on radiation (Hardy, 1934)

Surface	Cube Temp.	R.T.B.* Temp.	Radiat	Black body Temp.	
Cone	° C. 35;8	° C.	cal./sec./cm ² .	Per cent.	° C.
Rubber Blackened .	35.8	25.6	15.3	98	- 35 · 6
Copper .	35·8 35·8	25.6 25.6	$14 \cdot 4 \\ 1 \cdot 4$	93 10	35·0 26·5

^{*} Room-temperature black body. See text.

The influence of the nature of the surface on radiation from a body at a certain temperature is illustrated in Table 1. This refers to a cubical copper vessel filled with water at a known temperature (a Leslie cube), modified so as to present four different types of surface. In one side is inlet a cone with a blackened surface which radiates as a perfectly-black body. Part of another

side is replaced by a rubber diaphragm, a third side is blackened and a fourth left with its natural surface.

The skin as a perfectly-black body

Identity of actual temperature and black body temperature constitutes proof that a surface is a perfectly-black body at that temperature, provided the two measurements are accurate. Measurement of skin temperature for such a purpose as this is, however, difficult if not impossible. Hardy points out that surface thermometers are inaccurate because of errors from (1) calibration, during which they are usually surrounded by fluid, (2) manipulation, the reading being influenced by room temperature, the pressure exerted during application, the nature of the contact and the design of the instrument, and (3) the effect of the instrument on the surface whose temperature is to be measured. He minimises the errors of a skin thermometer by keeping the air temperature very close to the skin temperature, and under such conditions the skin temperatures as measured by a thermometer and a radiometer were identical. Further evidence is obviously necessary and is summarised below.

TABLE 2

Comparison of radiation from black body and from skin (Hardy, 1934)

Substance		Per cent. incident radiation transmitted								
		Calculated		Exptl. black body (cone of Leslie cube)			Skin -			
H-1							W ,W			
Glass				0	G		0		0	
Quartz	4.7			0		161	0		.0	
NaCl .	,			78		100	78		- 78	
KCl	,			87			88		87	
		100	- 9:				1000			

Table 2 shows what percentage of the radiation emitted respectively by skin and the cone of a Leslie cube at the same temperature are transmitted by glass, quartz, rock salt and KCl. The percentage transmission through the various substances is identical in either case with the theoretical transmission as worked out from the theoretical emission curve of a perfectly-black body at 32° C, radiating to surroundings at 22° C, and from the known transmission curves of glass, quartz, etc.

Hardy and Muschenheim (1934) studied (a) the emission spectrum of living skin, (b) the reflection spectrum of living skin, and (c) the transmission spectrum of skin from blisters and fresh amputations. All the measurements were in the infra-red, a Nernst glower being the source of radiation for the reflection and transmission experiments. The prism of the spectrometer was of rock salt, and the energy at wavelengths between 2 μ and 14 μ was measured by a thermocouple. The prism was calibrated with the aid of substances known to give peaks of emission or reflection at certain wavelengths within this range.

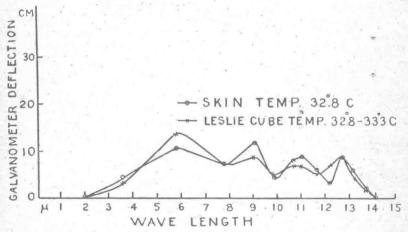


Fig. 1.—Emission spectra of skin and Leslie Cube at the same temperature. (Hardy and Muschenheim, 1934, J. clin. Invest.)

•Fig. 1 shows the emission spectra of skin and the cone of a Leslie cube at the same temperature. They are almost superimposable, and are within 1 per cent. of the theoretical curve worked out from Planck's formula, which relates the rate of radiation from a black body at a certain wavelength to its total radiation at the same temperature.

Reflection was studied by comparing that from the skin with that from a block of scraped MgCO₃, the total reflecting power of which is known. The basis of the comparison is that at any given angle of incidence, the reflected radiation is the same fraction of the total reflected radiation for each surface. At wavelengths

greater than 2 µ, 5 per cent. or less of incident radiation is reflected

from white or negro skin (Fig. 2).

Transmission through skin is negligible, even in the near infrared, though the epidermis alone may transmit 10 to 20 per cent. of rays. Hardy and Muschenheim showed later (1936) that 95 per

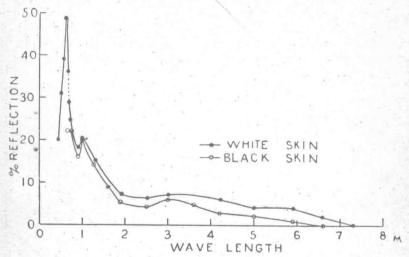


Fig. 2.—Percentage of incident radiation of various wavelengths reflected by white and negro skin. (Radiation from a Nernst glower fell normally to the surface and the energy contents of the radiations reflected at an angle of 20° into the spectrometer were measured. The total reflected radiant energy was obtained by multiplying by a factor obtained from a similar study of scraped MgCO, whose total reflecting power is known. graph shows what percentage of the incident radiation is represented by the total reflected radiation.) (Hardy and Muschenheim, 1934, J. clin. Invest.)

cent. of even the most penetrating rays were absorbed within

2 mm., of the surface, and 99 per cent. at 3 mm.

These results of Hardy confirm the conclusion of previous observers whom he quotes, that at body temperature the skin radiates as a perfectly-black body, and the wavelength of the radiation lies for all practical purposes within the limits shown in Fig. 1. The fact that white skin is a better reflector than black skin for wavelengths in the visible spectrum is irrelevant. The

same seeming paradox is encountered in the case of snow, which acts as a perfectly-black body for the wavelengths emitted by it.

The question may be asked why it is important to establish that the skin is a perfectly-black body, since in the foregoing summary we have taken for granted the use of an instrument which measures radiation directly. One reason is that the radiometer designed by Hardy, and described in the next section, owes its simplicity and practicality to the fact that it is used not as an absolute measuring instrument, but as a comparator. The standard of reference to which recourse is made before each experiment is one of temperature, so that while the calibration may be made in terms of either degrees absolute or cal. per cm.² per sec., there is no gain in accuracy by using the latter. It is more convenient to work in terms of temperatures which are in themselves of interest, and to derive the radiation from the Stefan-Boltzmann equation. In its simplest form this is

$$Q = k_R (T^4 - T_W^4)$$

where Q is the energy exchange, $k_{\rm R}$ the universal radiation constant and T and T_w respectively the absolute temperatures of the body and its surroundings. Other constants depending on the shape and 'emissivity' of the surface may need to be introduced.

The Hardy radiometer

Hardy's radiometer is claimed to be more accurate, and yet simpler and more robust than those used by previous investigators (Hardy, 1934). This is partly due to its being used as a comparator rather than as a self-contained measuring instrument; it is depicted in Fig. 3. The radiation falls on four metal quadrants, each covered with a deposit of bismuth black and each attached to a warm junction of a thermopile made from Bi-Sn and Bi-Sb alloys. The cold junctions lie outside the receiving field of radiation, but close enough to it to be subject to the same air temperature as the warm junctions, so that accidental air currents, etc., influence both junctions equally and the electric current produced is proportional to the radiant heat. The quadrants reflect about 40 per cent. of incident body temperature radiation, but the latter is concentrated 10 times by the conical silver reflector. The thermojunctions are able to exert 130 microvolts per degree, and a very sensitive galvanometer is unnecessary.

An important accessory is the 'room temperature black body' (R.T.B.) which is a black aluminium block with a thermometer embedded in it. The radiometer faces this when it is in its stand, and when in use it records the difference in temperature between the R.T.B. and the other surface to which it is exposed.

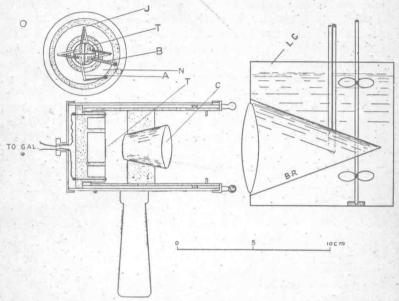


Fig. 3.—Hardy Radiometer. Vertical section (lower left) and Leslie Cube (right). Detail of thermopile construction (upper left). T, blackened tinfoil which receives radiation concentrated by silver cone, C. J, cold thermojunction outside the zone of radiation. BR, copper cone laid into side of Leslie Cube (LC). The inside of this cone is painted a dull black and it constitutes a perfect black body radiator, the temperature of which is measured by means of the thermometer submerged in the water which fills the Leslie Cube. (Hardy, 1934, J. clin. Invest.)

It will be seen from Fig. 4 that the galvanometer is used as a null instrument, the current from the thermopile being balanced by a potentiometer circuit. The alternative resistances (V, V') and the variable resistance R allow the current shown by the milliammeter per unit of potential difference across the output of the potentiometer circuit to be adjusted. In an actual calibration the potentio-

meter circuit is switched out, the radiometer exposed to the R.T.B., and the galvanometer set to read zero. The radiometer is now exposed to the conical black inlet in one face of a Leslie cube (Fig. 3) which is at a given temperature. The rate of emission of radiation from the cone to an object at room temperature can be computed from the Stefan-Boltzmann equation, and the resistances V, V' and R of the potentiometer circuit (now switched in) are manipulated so that the milliameter reads 1 ma. per 10^{-4} small cal. per sec. per cm.² The instrument is then calibrated for temperature over the range required. Using the potentiometer

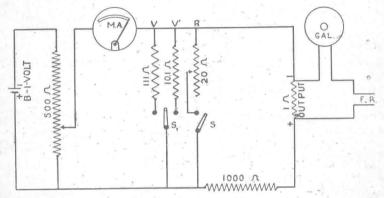


Fig. 4.—Potentiometer circuit for Hardy Radiometer. FR, leads to radiometer. For meaning of other symbols, see text. (Hardy, 1934, J. clin. Invest.)

circuit, the instrument is said to be accurate to $\pm\,0.05^\circ$ C., but direct galvanometer readings can be used over a range of 10° C. to give an accuracy of $\pm\,0.2^\circ$ C. This method of measuring surface temperature has been checked against a radiation standard of the U.S. Bureau of Standards and found to give results absolutely as well as relatively correct.

PARTITIONAL CALORIMETRY

Apparatus and methods

The chamber for controlling the radiant heat of the environment is enclosed in a larger air-conditioned chamber which is itself surrounded by a similarly conditioned air shell. Dry bulb temperatures from -10° to 55° C., and relative humidities from 15 to 95 per cent. can be maintained in the large chamber, and even in the absence of forced ventilation the air conditions within the radiation chamber do not vary far from these. The temperature range is 5° to 60° C.

The radiation chamber is illustrated in Fig. 5. It has nine sides and a ceiling, all of copper, which have a high reflectivity and from which the reflection is made diffuse by scarifying the surface. Infra-red radiation is provided by three radiant heaters A, each capable of giving 2,500 watts, above and below which air has free access to the interior of the booth. By turning up the heaters to a maximum and reducing the air temperature to a minimum, a difference of 40° between the mean radiant wall temperature (45° C.) and the ambient air temperature (5° C.) within the booth can be obtained. When the fans, J, are not in use, the hot-wire anemometer reveals a turbulent air movement of 15 to 25 ft. per min., due to convection currents and comparable with the 'still air' of an indoor space.

The air temperature is recorded by thermocouples, and the mean radiant temperature of the enclosure by a copper hemisphere E and an 80-element thermopile D. The rectal temperature is followed by means of a thermocouple, the metabolic rate by means of a Benedict-Roth apparatus and the body weight by means of the delicate vard-arm balance on which the subject's chair is supported. The subject himself exposes the Hardy radiometer to prescribed points on his body (3 on the head, 3 on the upper limb, 4 on the trunk and 5 on the lower limb), and by weighting the different areas according to certain regional factors, a figure for mean skin temperature is derived. A similar method, using the hot wire anemometer, is employed to obtain the mean air velocity, for when this is low it is turbulent and varies widely from point to point. The enclosed area of Fig. 6 represents the total range of temperatures available by the method.

Theory

Winslow, Herrington and Gagge have systematically investigated the ways in which heat is lost under a variety of conditions, the latter being chiefly remarkable for the independent variation of radiant heat and air temperature.

Since heat production, M, is known from oxygen consumption