THE PART PLAYED BY THE SKELETAL MUSCLES IN THE CHANGES IN GASEOUS EXCHANGE IN HYPER- AND HYPOTHERMIA

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Cooling human beings and animals causes the development of weak electrical activity in "resting" muscles, a condition which has been referred to as thermoregulatory tone. The effect was first discovered by Burton and Bronk [9], and the work was extended by other investigators [2, 3]. It is thought that the electrical activity of the muscles during their apparent resting condition indicates changes in muscular metabolism, and constitutes an important mechanism of chemical thermoregulation.

The present work describes a parallel study of gaseous exchange and electrical muscular activity at different body temperatures reached initially by the application of heat and then by the induction of deep hypothermia.

Variations in gaseous exchange at different body temperatures have been studied by several investigators [2]. In white rats, the corresponding changes in oxygen consumption have been studied in detail in our laboratory by A. Izbinskii [4] and A. I. Shcheglova [7]. Because the muscles play an important part in chemical thermoregulation, an attempt to relate changes in gaseous exchange to variations of the electrical activity in the muscles is extremely important. (After our work had been completed, a report was published by I. S. Repin [5] describing thermoregulatory tone in cooled rabbits.)

METHOD

The work was carried out on white rats weighing 180-200 g. The animals were placed in narrow cages having wire sides and top and a wooden floor. Such an arrangement limited their movements, and enabled any necessary manipulations to be carried out while a normal body position was maintained. Measurements were made of the electrical activity of the muscles of the thigh, and in some cases of those of the back, neck and head. The apparatus and method for recording the muscular potentials has been described in detail previously [2, 3]. Gaseous exchange was determined in pneumatically sealed chambers of 15 liters capacity. Air samples were analyzed by means of a Haldane apparatus. Body temperature was measured by a thermocouple inserted 2.5 cm into the rectum.

The rats were placed in a hermatically sealed chamber which was initially at 35°. When the temperature in the rectum reached 38.5-40°, the chamber was ventilated and the gaseous exchange and electrical muscular activity were determined. The animals were left in the room for 20-25 minutes. The next experiment was carried out in the same way at a temperature of 19-22°, the temperature in the rectum being 35-36°; the temperature of the chamber was then reduced to $8-10\frac{1}{9}$ when the rectal temperature fell to 29-32°.

For greater cooling, the rats were immersed for a few seconds in water, and then transferred to a refrigerator at -5° . When the temperature in the rectum had fallen to $26-17^{\circ}$, gaseous exchange and electrical muscular activity

The Changes in the Oxygen Consumption in White Rats at Different Body Temperatures

	Body temperature				
Number of animals	39—40°	35—36°	29—32°	19—22°	18—17°
	Oxygen consumption (in ml/g/hr for mean)				
1 2 3 4 5 6 7 8 9		1,81 1,80 2,10 2,61 2,03 2,22 2,15 1,34 2,74 2,00	2,96 3,27 — 2,90 4,11 3,09 3,75 3,69 2,62	1,20 1,73 1,04 1,11 1,45 1,85 1,21	0,88 0,73 0,52 0,65
Average	0,94	2,08	3,29	1,19	0,57

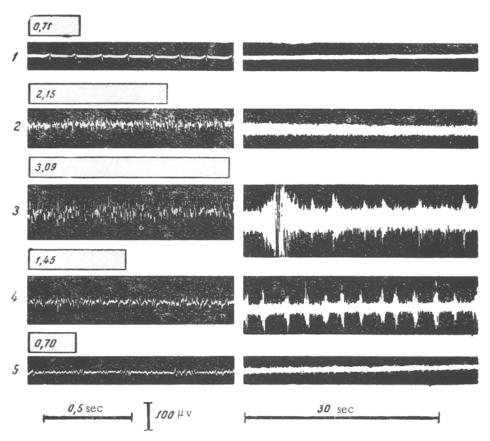


Fig. 1. Change in the oxygen demand and in muscular electrical activity in the thigh muscles of the rat at different body temperatures. 1) At a rectal temperature of 39.2° (the electrocardiogram is shown); 2) at 34.9° 3) at 31.4°; 4) at 21.5°; 5) at 18.5°. The electrocardiogram record was taken at a paper speed of 50 mm per second (on the left) and at a speed of 2 mm per second (on the right). The oxygen consumption (shown by the horizontal columns placed above the electrocardiogram) is given in m1 per g per hour.

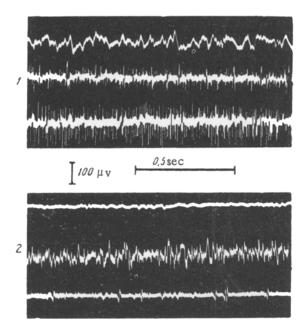


Fig. 2. Change in the electrical activity of the cerebral cortex and muscles in the hypothermic white rat. 1) Record taken for rectal temperature of 35.4°, temperature of temporalis muscle 34.4°, of the thigh muscle 34.1°; 2) after cooling to a rectal temperature of 11.5°, temperature of temporalis muscle 15.8°, thigh muscle 10°, and brain 15.9°. Curves from above downwards: potentials from cerebral cortex, from temporalis muscle, and from the thigh muscle.

were again measured. In this case the temperature of the gaseous-exchange chamber was 18-20°.

In other experiments, the electrical activities in muscles and in the cerebral cortex were recorded simultaneously. For this purpose the animals were fixed to a stand, and after the fur had been moistened with water they were surrounded by finely crushed ice. Platinum electrodes were introduced into the brain to a depth of 1-1.5 mm. Temperature measurements were made of the rectum, muscles, and brain. In all, 140 experiments were performed on 34 rats.

RESULTS

As can be seen from the table and from Fig. 1, for a body temperature of $38.5-40^{\circ}$, the minimum value of the gaseous exchange is attained when there is practically no electrical activity in the muscles. At a body temperature of $35-36^{\circ}$, the greater oxygen demand coincides with a comparatively feeble but maintained muscular electrical activity. This phenomenon of thermoregulatory tone is not associated with any movements, but may be observed during the whole of the experiment, while the animals remain motionless. The smallest observable movement of the rat causes a momentary burst of potentials of large amplitude (up to $300-600\,\mu\,v$ or more).

At a rectal temperature of 29-32°, the oxygen consumption increases shaprly. Thermoregularoty tone increases to a maximum. In addition, shivering commences,

and is indicated on the electromyogram by periodic bursts of potentials of large amplitude (up to 300-500 μ v). Cooling the body until the rectal temperature falls to 22-19° causes a reduction in gaseous exchange and a depression of the electrical activity of the muscles. As can be seen from Fig. 1., there is then no appreciable change in the shivering, and at the same time the thermoregulatory tone is decreased. There is a reduction in the frequency and the voltage of the separate potential excursions. The peaks become rounded. Further cooling to a rectal temperature of 18-17° causes a marked reduction in gaseous exchange. The electrical activity of the distal parts of the body (hind legs and back) is depressed. However, some electrical activity is maintained in the muscles of the head and neck, and, as our subsequent experiments showed, there is even a depression of the cerebral potentials. We found that the potentials developed in the cerebral cortex disappeared at a brain temperature of 16-17°. The temperature in the rectum, in the muscles of the thigh, and in the temporalis muscle then were 11-15°, 10-14°, and 16-17°, respectively. In our experiments, the temperatures of the brain and of the temporalis muscle were always a few degrees higher than in the thigh and rectum (Fig. 2).

It was therefore found that the oxygen consumption and electrical activity of the main mass of skeletal muscles of the white rat were altered in the same direction over a range of temperatures extending from hyperthermia to profound hypothermia (while the animal remained apparently completely at rest).

There are two kinds of electrical activity which develop as a response involving chemical thermoregulation. The first kind is the well-known cold shivering, which takes place only after considerable cooling has occurred. The second kind consists of thermoregulatory tone, which is a more precise method of chemical thermoregulation. During a gradual transition from a raised body temperature to a very low one, thermoregulatory tone is initiated considerably earlier than cold shivering, and disappears earlier too.

It is clear that different physiological mechanisms underlie the two processes.

It appears that the muscular system plays a definite part in thermal regulation, even where extreme body

temperatures are concerned. Thus, for instance, the complete absence of electrical muscular activity during raised body temperature must be interpreted as an adaptive mechanism which reduces the formation of heat in muscle to a minimum. On the other hand, a certain degree of electrical activity is maintained in some muscles at very low temperatures. This result confirms the view of A. D. Slonim [6], A. Izbinskii [4] and Giaja [11] who maintain that the constant-temperature body mechanisms continue to operate even in profound hypothermia. It is interesting that the body's response to cooling is maintained even after the higher nervous centers have been put out of action. This effect is precisely the opposite of that which we observed in our experiments on hypoxia, when thermoregulation failed comparatively early, and muscular electrical activity was completely suppressed, although cerebral electrical activity was well maintained [2].

It is important to note that during progressive cooling, activity is maintained longest in the proximal parts of the body. It would appear that we are here concerned with a mechanism of "regional" thermoregulation which has the effect of maintaining the highest temperatures in the most important parts of the body. "Regional" thermoregulation occurs in all homothermic animals, and results in only certain of the organs and tissues (brain and viscera) having a constant temperature, while the temperature of the peripheral parts of the body varies greatly with the temperature of the surroundings [8, 12 and others]. Regional thermoregulation is particularly well developed in hybernating species on awaking from the winter sleep. During the warming up period, the temperature in the mouth may be 10-15° higher than that in the rectum (review and original observations by Eisentraut [10]). This interesting observation requires further study.

SUMMARY

Gaseous exchange and electrical activity of skeletal muscle were studied in white rats at rest. The rectal temperature varied between 38.5°-40° and 18-11°. It was shown that when the body temperature was high gaseous exchange was minimal and there was no electrical activity in the muscles. When the body temperature fell, both gaseous exchange and muscular electrical activity first rose and then fell. At very low body temperatures, only the muscles of the proximal parts of the body continued to manifest some electrical activity.

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