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The development of the concepts of homeothermy and thermoregulation

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Abstract

The adjuncts to the existing determinations of homeothermy are made on the basis of available and new data, the principles of temperature adaptation of humans and homeothermal animals are given. The main purposes of the thermoregulation system of homeothermal animals and humans during various temperature excesses are formulated. The arguments are advanced in favor of the fact that in the thermoneutral zone the thermoregulation system goes from the principles of regulating the temperature homeostasis by one or several temperature points of a body to the regulation by the fluctuations of the total heat content of an organism, which increases the sensitivity and the accuracy of the thermoregulation system operation. The physiological mechanisms are described of determining (measuring) the total heat content of a body.

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1. Homeothermy

The most important marker of homeothermy, which has as yet no scientific explanation, is a high level of energy exchange. It exceeds the corresponding values in vertebrate poikilothermal animals by a factor of 5–10 (given the same mass and the body temperature). Such a great difference demonstrates a profound "break", which occurred in the evolution between these two highly developed groups of animals. These differences touch upon other large problems of energetics of the living organisms, such as, for example, the differences in the energy consumption per unit of the body mass between the newborn and adult organisms, between very small and very big mammals. The elucidation of the reasons for such differences is the fundamental problem of modern energetics of the living organisms. It may lay with the changes in the efficiency of various kinds of biological work, which determines the intensity of energy consumption in an organism and its heat production. There can be other mechanisms.

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Another most important marker of homeothermy consists in a constant comparatively high body temperature. For all the groups of homeothermal organisms this temperature lays in a comparatively narrow range between ~36 and 42 °C. A constant body temperature for various species (a species body temperature) is maintained under adequate conditions within even narrower ranges, comprising only several tenths of °C. The deviations from this temperature result in the thermoregulation reactions. Sometimes this gives rise to a belief that homeothermy restricts the "freedom of life". Such a simple conclusion does not reflect an important role of homeothermy in the development of the animated word. The matter is that a constant comparatively high body temperature and an intensive metabolism provide a rapid development of the central nervous system and acquisition of complex progressive forms of behavior for the homeothermal organisms (Burton and Edholm, 1955). That is why the progressive biological evolution always goes together with the development of homeothermy.

The origin of homeothermy in the biological evolution of vertebrates is associated with the tendency of maximal increase in the heat production level and of increasing the body temperature in various species of animals. This is necessary for the development and maintenance of complex functions of the central nervous system. In modern homeothermal animals the energy sources and the rate of the energy exchange reactions allow a continuous increase in the heat production by a factor of 1.5–2 at the expense of decreasing the efficiency of ATP resynthesis in the tissues. The existence of such biochemical mechanism is proved theoretically (Porter and Brand, 1993). We observed such an effect in a homeothermal animal as a whole and in the isolated organs (Ivanov, 1989). In such a case a question arises: why for the mammal organisms the body temperature of 37–39 °C is the upper temperature limit of life. This limit appears to depend on the protein thermal resistance. As the temperature increases, the rate of the protein denaturation increases, and the rate of their restoration decreases. When the temperature of a cell exceeds 40 °C, the cell membranes get "destroyed" and the organism dies (Bowler and Manning, 1994). The upper temperature limit of life is the most rigid biological constant. The animals do not overcome it. In any living organism the protein plays the most important role in the structure and functions of the cells. Hence the existence of a homeothermal organism near the upper temperature limit of life allows the highest level of metabolism to be achieved. Such is the special feature of homeothermy.

Another special feature of homeothermal organisms is their ability to preserve their viability during deep cooling. This is the inheritance of poikilothermal ancestors. Moreover, with the help of changing the ion composition of the blood the vital activity of a homeothermal organism can be restored without rewarming at such a low temperature, which is inherent only to poikilothermal animals (Ivanov, 1997, 2000; Ivanov et al., 2005).

2. Two purposes of thermoregulation

In humans and homeothermal animals the thermoregulation functions are distinctly divided into two parts by their physiological purposes and physiological mechanisms.

First, this is thermoregulation that counteracts strong or "crude" external and internal temperature excitations, which are capable of serious disruption of temperature homeostasis of an organism and of imposing a danger for life. Under ordinary adequate conditions of homeothermal organism life such severe temperature excesses occur rarely. However, just these reactions are the main subject of thermoregulation studies up to now (Hales, 1997; Cabanac, 1997; Lomax and Schounbaum, 1997; Boulant, 1999; Griffin, 2004, etc.).

Second, this is a special type of thermoregulation, its purpose consisting of leveling comparatively small but continuously arising internal and external temperature excitations. Such fluctuations occur even in the region of thermoneutral zone (for humans in the zone of temperature comfort) and are an inherent part of the normal active life

of animals and humans. Under adequate conditions in the absence of abrupt temperature excesses this is just the main function of thermoregulation system in humans and homeothermal animals. Bligh (1966) was the first to pay attention to the existence of such principal differences in the types of thermoregulation. However, the study and a detailed examination of the physiological significance of the second type of thermoregulation have started only recently. The numerical proofs in favor to this point of view will be given below.

3. The main thermoregulation reactions

During the threat of overcooling in humans and animals the skin vessels become contracted to a greatest extent and the heat production increases. There are two mechanisms of increasing the heat production. The first is the thermoregulatory muscle "tone" (Ivanov, 1989). It consists in irregular frequent contractions of separate motive units of the skeletal muscles. In the electromyogram it looks like a continuous sequence of biopotentials from 10 to 50 µV and can be registered only with the help of a highly sensitive electromyograph. This type of muscle activity increases the heat production of the whole organism by 15–50%. It is of principal significance since it goes together with all the cases of chemical thermoregulation and shows that the contractile activity of the muscles always provides the basis for the thermoregulatory increase in the heat production of an organism. If the cooling increases, the thermoregulatory tone transforms into the cold shivering, which increases the heat production of a homeothermal organism by 200-250%. For a man this is the maximal thermoregulatory increase in the heat production. The physiological protection from overheating in humans and homeothermal organisms has been much studied. Such a protection attains its greatest power on water evaporation from the surface of a body (thermal sweating) or from the mucosa of respiratory ways (thermal panting).

We emphasize that the efficiency of the above listed thermoregulatory reactions is limited. A naked man, for example, dies at the temperature of still air of $+1\,^{\circ}$ C or even $+2\,^{\circ}$ C (Burton and Edholm, 1955). The evaporation reactions against overheating have a large power and efficiency. However, they are not able to protect an organism against overheating for any prolonged time, since they require a large amount of energy and water. The latter is most difficult, since a high environmental temperature and an intensive insolation as a rule go together with a deficit of water in the habitat. A limited efficiency of ordinary thermoregulation reactions is of importance for understanding the mechanisms of prolonged (lifelong) temperature adaptation.

4. Mechanisms of temperature adaptation

The study of the mechanisms of human and animal adaptation to a continuous living under conditions of an

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