Review Article

On the Origin of Homeothermic Animals

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Abstract:

Temperature has a fundamental influence in all chemical and biochemical reactions and physiological processes. Maintaining the relative constancy of the internal temperature (temperature homeostasis) is a necessary condition for normal life. Mammals and birds as well as humans have been found to be able to maintain a temperature homeostasis in the body (homeothermic animals). However, it is unknown the origin of homeothermic animals. It is assumed that homeothermy is not the result of the evolution of the central organ-based physiological mechanisms of thermoregulation. Homeothermy is the result of the evolution of some part of non-coding DNAs in the genome of the higher eukaryotes that led to the emergence of chromosomal heterochromatin regions (HRs). Chromosomal HRs are capable to form the condensed chromatin around the nucleus, which underlie the material basis of cell thermoregulation and responsible for dissipating excess heat energy from the nucleus into the cytoplasm. Homeotherms are animals in whose cells chromosomal HRs are able to form the densest layer of condensed chromatin with high thermal conductivity capable efficiently removing excess heat from the nucleus to ensure the implementation of a very high level of cellular metabolism.

Key words: origin of homeothermic animals; chromosomal heterochromatin regions; condensed chromatin; cell thermoregulation; non-coding DNA

Introduction

Some living beings maintain temperature homeostasis in the body due to external sources of energy (poikilothermy), others due to the energy of food consumption (homeothermy). Despite the fundamental similarity of the mechanisms of the central organ-based physiological thermoregulation, even among the higher vertebrates exists poikilothermic and homoeothermic animals.

Homeothermy ('warm-bloodedness') is the ability of an animal to maintain a relatively constant core temperature for an indefinitely long time, regardless of fluctuations in environmental temperature. Warmbloodedness is maintained endothermically, i.e. by-product of metabolic heat. In poikilothermic animals, in contrast to homoeothermic animals, body temperature passively follows the change of the environment temperature.

It is known that homeothermy takes place when living beings has a high level of cellular metabolism to maintain the necessary body temperature by producing heat energy from the consumed food, i.e. it is based on a high and regulated level of metabolism. Thus, in contrast to poikilothermic organisms, homeothermic animals build their heat exchange based on their own heat production, which makes them independent of external temperature fluctuations. As a result, the temperature range of life activity of homeothermic animals practically coincides with the range of temperatures carried by living organisms.

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Thus, heat generation is a basic property of endothermic homeotherms. However, the cause of this high metabolic rate remains a source of controversy. In particular, processes such as high ionic permeability of plasma and mitochondrial membranes and high fluidity of proteins and membranes have been suggested to underlie this phenomenon. It is also known the role of feathers and fur, as well as a layer of subcutaneous fat and high body mass, which significantly reduce resting heat loss to the environment. For example, the thermal conductivity of reptile coverings is so great that they cannot ensure the preservation of endogenous heat at rest at any body temperature. A reptile "dressed" in bird or mammalian coverings could retain heat at maximum aerobic muscular activity and body temperature as in homeothermic animals [1-3].

Thus, physical thermoregulation combines a complex of morphophysiological thermal insulating mechanisms that determine the overall level of heat dissipation at the level of the organism of homeothermic animals (feathers and hair). The significance of thermal insulation is that, by reducing heat loss, it contributes to the maintenance of homeothermy with less energy expenditure. This is particularly important when inhabiting persistently low temperatures. Adaptive changes in the heat-insulating function of the coverts are reduced to a reorganization of their structure, including the ratio of different types of hair or feathers, their length and dense arrangement. The pilomotor form

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of regulation of heat dissipation acts mainly at low temperature of the environment, requiring less energy expenditure. However, it should be remembered that insulating structures (feathers, hair) do not cause homeothermy, as is sometimes thought.

Origin of homeothermic animals

In the literature, we failed to find special theories or hypothesis about the origin of homeothermic organisms. Works devoted to this problem are limited to descriptions of chemical and physiological mechanisms of maintenance of relative constant temperature in a body with indication of pros and cons of homeothermy for organisms. Regarding the possible genetic mechanisms of homeothermy there is no information at all [4].

The existing hypotheses do not answer the questions: where, why and how did the phenomenon of homeothermy arise? The absence of transitional forms among modern species and the lack of paleontological evidence make understanding the origin of homeothermy difficult and ambiguous. If we assume that homeothermy occurred as part of the evolution of the central organ-based system of physiological thermoregulation in higher eukaryotes, then the question remains unanswered: why did it happen only in birds and mammals? Besides, higher vertebrates do not differ fundamentally in the organ-based system of physiological thermoregulation.

We suggest that homeothermy is not the result of the evolution of central organ-based physiological mechanisms of thermoregulation. Homeothermy is the result of the evolution of some part of non-coding DNAs in the genome of the higher eukaryotes that led to the emergence of chromosomal heterochromatin regions (HRs). Chromosomal HRs are capable to form the condensed chromatin around the nucleus, which underlie the material basis of cell thermoregulation and responsible for dissipating excess heat energy from the nucleus into the cytoplasm. Homeothermics are animals in whose cells chromosomal HRs are able to form the densest layer of condensed chromatin around the nucleus with high thermal conductivity capable efficiently removing excess heat from the nucleus to ensure the implementation of a very high level of cellular metabolism.

To better visualize this viewpoint, it is necessary to recall what chromosomal HRs, condensed chromatin and cell thermoregulation are. Briefly, chromosomal HRs are the highest form of organization of non-coding DNAs, consisting of short repetitive sequences of nucleotides, which constitute the bulk of DNA in the genome of higher eukaryotes and especially in birds and mammals. In humans, non-coding DNAs make up about 98% of their genome and 15%-20% of them form chromosomal HRs. In the interphase cell, chromosomal HRs form a layer of condensed chromatin around the nucleus, which is characterized by the highest density [5].

Based on study of distribution of chromosomal HRs in human populations living under different climate and geographic conditions, in norm and at some forms of pathology the hypothesis about thermoregulation existence at the cell level has been presented. The essence of hypothesis of cell thermoregulation (CT) is elimination of the temperature difference between the nucleus and cytoplasm when the nucleus temperature becomes higher than in the cytoplasm. The higher eukaryotes use a dense layer of peripheral condensed chromatin (CC) as heat conductor for a more efficient elimination of the temperature difference between the nucleus and cytoplasm. The CC localized between a nucleus and cytoplasm is made of chromosomal HRs. The phenotypic manifestation of CT is the level of body heat conductivity of the individuals in the population with all the ensuing consequences for the organism [5-8].

The mechanism of cell thermoregulation is schematically represented as follows: if for one or another reason the temperature in the nucleus begins to exceed the temperature of the cytoplasm, the second law of thermodynamics comes into force. But it is not just the transfer of heat from the nucleus to the cytoplasm in general that is important here. What matters here is speed and safety. By the latter, we mean the integrity and functional safety of the nuclear envelope, which, like all cell membranes, is very sensitive to high temperature. Without going into details, let us only note that for safe removal of excessive heat energy, special temporary structures (nuclei, chromocentres and other nuclear bodies) are formed in the nucleus to localize and direct the 'heat flow' in an organized manner into the cytoplasm for the safety of the nuclear envelope. It is not difficult to imagine that excessive heat energy of the nucleus at uniform exposure of the nuclear envelope can affect its structural integrity and functional abilities (for details see [5-9].

The sources of temperature rise in the cell are more or less clear: all metabolic processes are associated with energy transformations, and they are invariably accompanied by heat release. However, it seems to us highly probable that the temperature rise in the cytoplasm and nucleus must have some peculiarities. In the cytoplasm, the generation of ATP through glycolysis or oxidative phosphorylation leads to an increase in its temperature, and it is removed into the intercellular space and further carried away by the circulation system. Complex processes also take place in the nucleus. Chromosomes have both internal (repair, recombination, rearrangement, modification, restriction) and external (replication, transcription, packaging, organized movement) molecular activities, which are accompanied, inter alia, by some heat output, which can lead to the appearance of excessive temperature. However, this temperature is carried out into the intercellular space not directly but through the cytoplasm, which is not so easy and may require the help of temporary heat dissipating structures in the nucleus (see above).

We believe that the temperature in the nucleus will be higher and rise faster than in the cytoplasm for the following reasons: a) the volume of the nucleus is not comparably smaller than that of the cytoplasm. Therefore, even at the same intensity of metabolism in all parts of the cell, the nucleus should overheat faster and more strongly than the cytoplasm; b) the heat-producing structures of the cytoplasm (mitochondria, ribosomes, etc.) are not gathered in one place as in the nucleus, but are scattered more or less evenly throughout the cytosol, which allows them to dissipate heat relatively easily by diffusion and conduction through the cytoskeleton and ER [5-9].

Thus, the nucleus can conduct heat only in the cytoplasm (in case the nucleus temperature, for this or that reason, exceeds the temperature in the cytoplasm). With this, the nucleus has two options for the dissipation of heat surplus: either by increasing its volume or increasing the heat conductivity of the nuclear envelope. As the first option is limited and the second one is difficult due to the vulnerability of cell membranes to temperature changes, apparently the higher eukaryotes took advantage of the opportunity of a dense layer of peripheral condensed chromatin as heat conductor for a more efficient elimination of the temperature difference between the nucleus and cytoplasm [4-8].

The role of the circulatory systems (CS) very important in maintaining temperature homeostasis on the organism level. However, the CS cannot influence directly to the temperature inside the cells (except for endothelial cells lining the intima of blood vessels), as they are linked with the CS indirectly - through the intercellular space. Thus, the CS influence on inner cellular temperature homeostasis is limited and its effect, in general, comes to transferring surplus heat from the intercellular space. That is why it seems that the problem of maintaining the inner cellular temperature homeostasis is solved by cells themselves, and we call it the cell thermoregulation [5,8].

Evidences for a possible role of cell thermoregulation in the origin of homeothermic animals

Over the years, several methods cell temperature measurements have been developed, each with its advantages and limitations. Broad categories include contact probes, offering direct but potentially invasive measurements; infrared thermography, which is non-contact and useful for surface temperature mapping; and fluorescence-based thermometry, providing high sensitivity and specificity (see review [10]). Thanks to these methods, it was found that heat is not evenly distributed in the cell. It turned out that there are areas in the cell that are characterized by high temperature: nucleus, mitochondria, ribosomes and ER. So, for example, Nakano et.al. [36] show differences of $2.9\pm0.3^{\circ}$ C in the temperature across individual cells, between cytosol and nucleus areas. It is not yet known how heat is distributed in the nucleus. Having no direct experimental data yet, we still assume that heat in the nucleus, as well as in the cytoplasm, is distributed unevenly. Nuclei, chromocentres and other membrane less nuclear bodies should have the highest temperature.

Adaptation of a human to different climatic and geographical conditions has two principal features: a) only man managed to master the entire land of the Earth, while remaining a single, tropical biological species; b) in contrast to animals, human colonization of all climatic-geographical provinces, including the extreme ones (Far North and high-altitude), occurred in a very short period of time. It remains unclear how it all was managed by a human. Regarding genetic mechanisms, the main question is not clarified: did a human adapt only with the help of genes or did he use a means inherent only in H. sapiens? The data obtained when analyzing the genomes of populations living in different high-altitude provinces (Tibet, the Andes, and the Ethiopian Plateau) turned out to be extremely contradictory [11-19]. Without going into long discussions, we decided to limit ourselves here to the well-known remarks of E. Mayr [20], who rejected reductionism in evolutionary biology, arguing that 'evolutionary pressures act on the whole organism, not on single genes, and that genes can have different effects depending on the other genes present'. He rejected the idea of a gene-centred view of evolution, insisting 'a gene is never visible to natural selection and in the genotype'.

If not genes, then what? Our experience in the search for the genetic basis of human adaptation to some extreme natural conditions in Eurasia (the Extreme North of Eastern Siberia, the Pamir and Tien-Shan high-altitudes) shows that, apparently, chromosomal HRs is the sought genetic material. We believe that this is a highly probable response; in adapting to a climate different from that of East Africa, humans have used a non-genic part of their genome (chromosomal HRs), known for its high mobility and neo-conservatism in individual development and evolution (for details see [21-29]).

It is well known that only man is capable of endurance running and, in this sense, he has no equal among animals. There are different answers. Walking upright has allowed us to become some of the best distance runners, but at the expense of speed. It is also believed that to run long distances on the African savannah man needed to have an effective cooling system and it is believed that man has developed one.

We believe that there is another important factor unique to man, which ultimately allowed him to occupy the top of the food chain. This factor is the peculiarity of the heat-conducting ability of the human body. Man became a good long-distance runner because among animals he has the most highly heat-conducting body, which allowed him to effectively dissipate excess heat outside the body [30].

When running, especially for long distances, a person faces the main threat: overheating of the body. It is known that for this purpose a man uses two ways of heat dissipation: evaporation of moisture from the body surface and respiratory tract. However, we believe that humans must possess an additional, perhaps inherent only to the species *H. sapiens* means of combating overheating of the organism. By this, we mean its heat-conducting ability [31].

It has been experimentally shown that the effect of CT can be indirectly assessed by the level of the body heat conductivity (BHC). In particular chromosomal Q-HRs, which along with C-HRs are present in the human karyotype influence on the level of the human BHC [31]. We have shown in our time that the greatest number of chromosomal Q-HRs are contained in the genome of indigenous people of subequatorial Africa [24]. Since there is a close relationship between the level of human BHC and the Auctores Publishing LLC – Volume 24(4)-701 www.auctoresonline.org ISSN: 2690-4861

quantitative content of chromosomal Q-HRs in its genome, there is nothing unexpected in the fact that athletes from subequatorial Africa (e.g. marathon runners from Kenya and Ethiopia) differ in sports that require, among other things, effective heat dissipation outside the body. Indeed, a sportsman with high heat conductivity cannot make much progress in mountaineering and water sports because their body cools rapidly. However, this sportsman can be more successful in sports, which require effective heat-loss [34].

Discussion

Homeothermy is a pronounced aromorphosis - a progressive evolutionary change leading to an overall increase in the level of adaptation of an organism to changing environmental temperature conditions. Numerous studies have shown that birds and mammals use an order of magnitude more energy to maintain their vital activity and, consequently, consume more of it. It is known that the reptiles have survived to the present time mainly by lurking predators and only a small number of herbivorous forms, almost all of them living in 'warm' regions. At the same time, homeothermic animals have conquered practically the entire livable part of the biosphere, canalized new energy flows and displaced reptiles from the main niches.

Let us look at how homeothermic animals live in reality. We will try to illustrate of this issue by the example of two organisms, comparable in size, human and crocodile, typical homeothermic and poikilothermic organisms. Let us start with how they eat. As known, at one time crocodiles can eat up to 23% of their body weight. Crocodiles are well adapted for long-term fasting. Without food, adult crocodiles can live about one year. While the mammal predators of the same size as crocodiles daily require approximately 5–10 times more food. At the same time, about 90% of the calories obtained from food are spent on maintaining a constant core temperature in the body. It seems to us that the level of intracellular metabolism is not determined by the ability of animals comparable in mass to generate a lot of energy or its availability. The ability of cells to remove excess heat from the nucleus to the cytoplasm in a timely manner is extremely important in order to avoid undesirable consequences of high thermal energy for such vital genetic processes as repair, recombination, replication, transcription, rearrangement, packaging etc. of DNA. And this is possible only through CT using a dense layer of CC in interphase cells [4-6].

Nevertheless, this does not mean that CT is an effect exclusively of chromosomal HRs. As is known, in the chromosomes of higher eukaryotes except HRs there are G+ bands, which make up more than half of their length. It is believed that in the composition of chromosomal G+ bands can be heterochromatin materials, the so-called intercalary heterochromatin. Even if G+ bands do not contain HRs, the fact that they are tightly packed in the body of mitotic chromosomes convinces that they can also participate in CT as part of CC [7].

We believe that the CC should be the densest domain in bird and mammal interphase cells among higher vertebrates. This confidence is due to the fact that the clearest differentials staining (C-, G - and Q-bands) give the human mitotic chromosomes, then other higher primates, and then the rest of the mammals. Bad or not differential staining gives chromosomes of reptiles and amphibians. By the way, only C-bands can be obtained on plant chromosomes. Referring to the ability of chromosomes to give a differential staining, we have in mind the well-known fact that C+, G+ and Q+ bands represent the densest areas of mitotic chromosomes, enriched with heterochromatin and other types of non-coding high repetitive DNAs, which constitute the physical basis of CC. Our assumption about the highest density of CC in human cells among mammals is due to the fact that: a) the human genome has all known types of constitutive heterochromatin (C - and Q-HRs); (b) among the higher primates, the highest amount of chromosomal C-HRs is found only in the human karyotype [6,7,21-29].

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We assume that the chromosome segments of the higher eukaryotes have undergone their own evolution in the direction: C-heterochromatin \rightarrow G+ and Q^+ bands $\rightarrow Q$ -heterochromatin as response of a cell nucleus for the demand of multicellular organisms in denser packaging of non-coding DNA for the increase of the heat-conducting effect of CC between the nucleus and cytoplasm [6,7]. For example, at a later stage of evolution of the mammals in Africa in the ancestors of three higher primates (Homo sapiens, Pan troglodytes and Gorilla gorilla) besides C-heterochromatin, a new type of constitutive heterochromatin, Q-heterochromatin, appeared [6]. Obviously, this is related to the increase of the metabolism intensity in their organism, and, accordingly, the further improvement of the cell thermoregulation. In this case the Q-heterochromatin is not only a new type of constitutive heterochromatin, but possibly an additional 'center of compactization and attraction' for more dense packaging of adjacent inactive chromatin, thus, increasing the heat conducting effect of CC in the interphase cell of three higher primates [4,7].

If our reasoning really has to do with real events in animal evolution, then for example, it is not difficult to explain why the crocodile did not become a homeothermic animal. It seems to us highly probable that the main cause of poikilothermy in a crocodile is the peculiarities of its karyotype; as in all reptiles' crocodile chromosomes, give a bad differential staining. This means that in such cells the density of CC is low, which complicates the effective transition of excess metabolic heat from the nucleus to the cytoplasm. Perhaps a crocodile lies for so long after the reception of the next portion of food not because of problems associated with digestion (for example: lack or few of food processing enzymes), and because excessive physical activity may cause a risk of overheating of the body. Homeothermic animals solve this problem by efficient removal of excess metabolic heat from the interphase nucleus to the cytoplasm with a dense layer of CC, that is, they have a more perfect cell thermoregulation.

Of course, there will be opponents who believe that mechanisms of physiological thermoregulation, for example, in human are perfect: otherwise, he could not master almost all the land on Earth so rapidly and effectively. We suppose that during his evolution man, possibly owing to chromosomal Q-HRs, had an additional and very flexible tool to ensure more effective thermoregulation, allowing him to master almost all the oykumene [31,32]. In essence, all that was said comes to one simple thought: how does man as a homeothermic being differ from other mammals as concerns preservation of temperature homeostasis. As far as we know, H. sapiens is not only devoid of a more or less large anatomic structure, but also has no protein or enzyme that has no analogue in the animal world. The fundamental structural characteristic of man is the presence of chromosomal Q-HRs in its genome, which he has inherited together with the chimpanzee and the gorilla - from one common ancestor. In this context, the only difference of H. sapiens is the wide quantitative Q-HRs variability in his genome [5].

Conclusion

Every form of cell activity, like cell division, gene expression, enzyme reaction, metabolism and pathological states are marked by temperature changes. In fact, the heat energy released by individual cells as a by-product of their vital activity is very small. However, the approximately 37 trillion cells in the human body together have been shown to be capable of maintaining his core temperature at 37 °C. This macroscopic outcome of the cell thermoregulation is the most important and only function of heat.

Birds and mammals have become homeothermic animals, perhaps not because they have the most developed systems of physiological thermoregulation. Their homeothermy is due to the evolution of noncoding DNAs, chromosomal HRs and chromosomal bands (G + and Q +), which have proven to form the densest layer of condensed chromatin around the nucleus among existing animal cells. Due to this, the removal of excess thermal energy from the nucleus has become more effective than that of poikilothermic animals with all the ensuing consequences.

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Essentially homeothermic organisms can be seen as energy conversion entities governed by the second law of thermodynamics [35].

Apparently, the physiological thermoregulation functions relatively independently from CT as evolutionally new adaptive system. From our point of view, CT can be the missing link, which should fill the "gap" between the thermoregulation systems, functioning at the molecular level and the whole organism (for details see [5,32,33]).

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