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Research Article

On the Mechanisms of the Emergence of the Adaptive Phenotypes: Organism-centric View

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Abstract

According to Modern Synthesis the material sources of adaptive phenotypes are random mutations of DNA and chromosomes to the new habitat conditions. In particular, the adaptive phenotypes are considered the changes only at the level of genic part of DNA (gene-centric view). However, this approach did not lead to the disclosure of the mechanisms of origin of phenotypic complexity. It is this point of view that seems to us an obstacle in comprehending the mechanisms of the emergence of adaptive phenotypes. The point is that the question of the place and role in the origin of biological adaptation of non-coding DNAs (ncDNAs), which, for example, make up 98% of the human genome, remains out of sight. This question should find its place in evolution, if only because Homo sapiens is the only animal that managed to populate the entire landmass of the Earth while remaining a single tropical biological species. Therefore, in order to get out of this deadlock, it is proposed to review our attitude to gene-centric view and replace it with organism-centric view. It is proposed that, as with the emergence of nucleosomes, cell nucleus, mitotic chromosomes, biological sex, species, the Cambrian Explosion, multicellular and homoeothermic organisms, including modern humans, ncDNAs played a leading role in the emergence of adaptive phenotypes.

Key words: adaptive phenotypes; origin of adaptive phenotypes; gene-centric view; organism-centric view; non-coding DNAs; heterochromatin regions; cell thermoregulation; chromocenters

Introduction

Although a great deal of research has been done on the mechanisms of evolution, one question remains to be fully elucidated: how do adaptive phenotypes arise? In particular, a critical question is the processes of interaction between the genome and the new habitat conditions that ultimately lead to the emergence of phenotypic complexity. Also unclear is what factors direct cells to perform specific adaptive tasks so that their metabolism, transcription, physiology, and morphogenetic competencies work in favor for the formation of the desired adaptive anatomical novelty. In this regard, very stimulating ideas have emerged in recent years.

The material basis and mechanisms of the emergence of adaptive phenotypes are still under debate. According to Modern Synthesis the material sources of adaptive phenotypes are random mutations of DNA to the new habitat conditions. Currently, the main mechanism of development of adaptive phenotypes are considered the changes only at the level of genic part of DNA (gene-centric view). It is this point of view that seems to us an obstacle in comprehending the mechanisms of the origin of new adaptive phenotypes. For example, the role of non-coding DNAs (ncDNAs), which constitute 98% of the human genome, in adaptation is still unclear. This question should receive a rational explanation also because *Homo sapiens* is the only higher eukaryote that managed to populate the entire Earth's landmass while remaining a single tropical species.

Before outlining our position on possible mechanisms of adaptive phenotype emergence, we found it necessary to briefly highlight alternative concepts to the Modern Synthesis. Fortunately, these concepts, thanks to the initiative of the Biological Journal of the Linnean Society, are collected in a special issue under the general title "Teleonomy in Living Systems" [4]. The following are key generalizations taken from this issue. For example, Vane-Wright [14] states, “Organisms have disappeared as fundamental entities, as basic unities, from contemporary biology because they have no real status as centres of causal agency. Organisms are now considered to be generated by the genes they contain”. Noble & Noble [10] argue, all living systems are continuously creative in the process of maintaining their integrity. Of necessity, they have to adapt to the ongoing, incessant changes that affect the ‘conditions of life’. They characterize physiology as ‘the study of purposeful living function’, where function necessarily implies purpose. Heylighen [5] writes about the concept of concerted action which implicitly encompasses the notion that

goal-directed behavior requires the coordinated activity of a broad repertoire of actions, aspects and components of the system. Babcock & McShea [1] maintain that their externalist account of teleology whereby living systems are 'guided' by external fields, is consistent with conventional physical determinism, but does not thereby 'threaten the existence of purpose, teleology or freedom'.

There are a number of important ideas regarding the origin of evolutionary novelty. As is well known, Lamarck believed that animals had common bonds (roots) and evolved from each other. He attributed evolution and changes in animal species mainly to changes in the conditions of existence (climate, food, etc.) and to efforts on the part of the animals themselves, which led to modifications and could be inherited. Population geneticists, proponents of Modern Synthesis, define evolution as change in gene frequency. In particular, they suggest that spontaneous mutations under the constant pressure of natural selection promote the development of more adapted phenotypes, eliminating or reducing the frequency of those genes that lead to less adapted forms.

The proponents of the new approach (purposiveness "teleonomic" view) consider that there to be other, different sources and mechanisms of novelty that can be important steps in the genesis of evolutionary change. For example, Moscek [8] regarding the origins of novelty and the evolution of innovation considers that it is the genesis of new, complex traits as a key problem in organic evolution. In particular, he believes that, faced with new or stressful conditions, the development of an organism shifts towards the production of functionally integrated phenotypic forms. At the same time, existing developmental pathways are part of the formation of such renewed evolutionary changes. Shapiro [11] emphasizes, "The capacity of living organisms to alter their own heredity is undeniable. Our current ideas about evolution have to incorporate this basic fact of life. Author of the concept "natural genetic engineering" continues the challenge to the Modern Synthesis the vision of gradual change brought about by natural selection acting on random mutations as the primary source of evolutionary novelty. Continuing to challenge neo-Darwinism, Shapiro notes that animal and plant breeders have yet to develop new species solely by artificial selection. However, such selection alone rarely, if ever, produces new species and concludes that "the best-documented path to the origin of species we have is an inherited biological process, not a series of accidents". Clawson & Levin [3] continue the search for the origin of evolutionary novelty and have sought "deep design principles of life". Their findings indicate that goal-directed behavior is a universal property of all such beings and see teleonomy as a unifying framework for understanding all possible agents. Editors of the special issue of the Journal concluded: "In sum, what the contributors to this volume have collectively shown is that living systems exhibit/demonstrate an evolved, means-ends purposiveness (teleonomy), in a myriad of different ways. This arises from, and is necessitated by, the fact that all living organisms are contingent dynamic (and kinetic) systems that must actively seek to survive and reproduce in their many different, often changing environments. Their "agency" derives from this unavoidable "struggle for existence"—in Darwin's famous characterization. Teleonomy in living systems is not, after all, only "apparent." It is a fundamental fact of life" [4].

Thus, new views on the emergence of the adaptive phenotypes, different from the Modern Synthesis, seem to us to open a new way to search for possible mechanisms of the emergence of adaptive phenotypic complexities. In other words, the recognition of 'teleonomy in living systems' makes it possible to prioritize the organism-centric view instead of the generally accepted gene-centric view, which allows us to include ncDNAs as an important component (material) of the genome in biological adaptation. Below we will attempt to outline our understanding of the mechanisms of the emergence of the adaptive phenotypes derived from studies of chromosomal heterochromatin regions, which are the highest form of organization of ncDNAs, on the example of adaptation of human populations to the extreme conditions of high mountains and the Far North of Siberia.

Mechanisms of the Emergence of the Adaptive Phenotypes: Organism-centric View.

As is known, Darwin paid great attention to the problem of species and speciation. It is not by chance that the title of his work contains the words "origin of species". The task of evolutionary theory is to explain the mechanism of the origin of life and changes in the actual species of animals and plants inhabiting the Earth. We adhere to the view that evolution begins with the emergence of an adaptive phenotype, which in time may culminate in the emergence of a new species. A new species is a consequence (not always inevitable) of the emerged adaptive phenotype, which, due to the rearrangement of the genome (most often at the level of chromosomes), led to reproductive isolation with all the ensuing consequences [23; 25; 26; 34].

Let us start with the question: what is necessary for a new adaptive phenotype to emerge? If we make a simple analogy, as, for example, with construction, it requires at least three conditions: building materials, purpose, and performers. The first condition is satisfied with the ingestion of food, from which the necessary building materials and energy are extracted. The second condition, from our point of view, is determined by the organism itself, which can be labeled as the organism-centered arguments. The third condition implemented with the help of already existing genes and ncDNAs in the genome. In this case, genes are used as labor forces for the formation of adaptive phenotypes, and ncDNAs for the regulation of gene expression, the packaging of genetic material and the regulation of temperature homeostasis in the cell. While we have a more or less clear view on the first condition, and the second condition is outlined above within the concept of "teleonomy in living systems", there are fundamentally different views on the third condition (see above).

Obviously, proteins will be required for the formation of an adaptive phenotype. Where do they come from? Perhaps, the emergence of an adaptive phenotype does not necessarily require genes that do not exist in the genome of a given species or in animals in general. For example, the human body contains more than twenty thousand different proteins that control muscle contraction, digest food, form bones, receive signals from the environment and relentlessly process hundreds of small molecules in cells, which is quite enough for the formation of phenotypic complexity or anatomical novelty of any complexity in the organism. The fact is that until recently scientists had assumed that the same gene, no matter where found, always had the same phenotypic effect. However, developmental geneticists have now shown that this is not necessarily so. The same gene may have rather different expressions in annelids (Polychaeta) and arthropods (Crustaceans). Organisms seems to be able to recruit genes in new developmental processes that previously had seemed to have other functions.

Denis Noble [9] has argued, following West-Eberhard [14] that the genes have often been the followers rather than the leaders in evolutionary change. Although this is a different generalization from Modern Synthesis, it still lacks some details. In recent years, the molecular basis of phenotypic evolution has become one of the most important areas of study in the post-synthesis era. Moreover, evolution is no longer seen as "a change in gene frequencies, as is claimed so often, but a change of phenotypes, in particular the maintenance (or improvement) of adaptedness and the origin of diversity. Changes in gene frequency are a result of such evolution, not its cause" [7].

We believe that ncDNAs, not genes, are the leaders in the emergence of adaptive phenotypes, and here is why. As we know, the genome of all cells in an organism is the same. Nevertheless, at the same time, different genes work in different types of cells depending on the functions they perform in the organism. The question of what determines this state of affairs is in general terms more or less known: the regulation of gene expression and the packaging of genetic material determines the chromatin in the cell nucleus. However, what hides under the vague concept of chromatin, except for the terms eu- and heterochromatin, is difficult to define, especially when it comes to specific mechanisms of regulation of gene function. Regarding leadership: why it is not genes but chromatin that decides what phenotype to

be, if they do not carry any genetic information there is no generally accepted concept yet.

The Essence of the Proposed Hypothesis.

According to our hypothesis, the origin of adaptive phenotypes schematically looks like:

(a) A change in the physicochemical and biotic conditions of the habitat of the population is so strong that it poses a direct threat to the realization of vital needs of the organism (nutrition, reproduction or defense against predators);

b) In this situation, the organism will be forced to strengthen or increasing existing structures or functions by intensifying the activity of already functioning genes or mobilizing "silent" genes necessary for;

c) In order to mobilize the required genes, chromatin is rearranged so that its ncDNAs regulate the gene expression and the packaging of genetic material to shape the required adaptive phenotype;

d) A new center of biochemical activity appears in the cell, which inevitably leads to excessive temperature in the nucleus, threatening its normal function;

e) To remove the excess heat the cell nucleus resorts to merging of new biochemically highly active chromatin sites into chromocenters using chromosome heterochromatin regions to preserve temperature homeostasis in the cells;

(e) With time these epigenetic changes in chromatin can result in translocation of heterochromatin regions involved in the formation of chromocenters from one chromosome to another, which could lead to reproductive isolation using meiotic mechanisms with all the ensuing consequences (for details see [16; 17; 27-29; 33;35]).

Our long-term studies of human populations permanently living in extreme climatic conditions show that *Homo sapiens* can adapt even without the involvement of genic parts of their genome. Thus, for example, the human populations can adapt to cold and high-altitude hypoxia by changing the amount of chromosomal Q-heterochromatin regions (Q-HRs), which consist mainly of highly repeated sequences of ncDNAs, not capable to encode proteins and enzymes known in the science. In particular it is turned out that chromosomal Q-HRs are distributed in human genome not accidentally. Specifically the amount of chromosomal Q-HRs in human population genome depends on climate and geographical conditions of permanent residence and not their ethnic and racial peculiarities. The largest amount of chromosomal Q-HRs are found in the genome of populations living in low altitude subequatorial Africa and India, and the least - in Northern Siberia aborigines, as well as indigenous people of Tien-Shan, Pamir and Эфиопского нагорья (for details see [15; 28; 33]).

Discussion.

We have already repeatedly discussed the leading role of ncDNA in the origin of nucleosomes, cell nucleus, mitotic chromosomes, biological sex, species, the Cambrian explosion, multicellular and homoeothermic organisms, including modern humans (for details, see [16-24; 26-27; 30; 32]).

The fact is that the possibility of origination of complex adaptive forms only because of random mutations at the gene level is not proved yet. Ernst Mayr [7], who repeatedly rejected reductionism in evolutionary biology, argued 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-centered view of evolution, insisting, “a gene is never visible to natural selection and in the genotype”. In particular, he wrote: “Evolution deals with phenotypes of individuals, with populations, with species; it is not a change in gene frequencies." … “It is the phenotype that is exposed to natural selection and not individual genes directly”. ”Not its genes or genotype, because these are not visible to selection, but rather its phenotype. The word phenotype refers to the totality of morphological, physiological, biochemical, and behavioral characteristics of an individual by which it may differ from other individuals”.

We believe that it is ncDNAs in chromatin that can determine the question of which genes should work in a given cell. Let us try to express our understanding of the problem using a well-known example. As it is known, Jean-Baptiste Lamarck proposed the idea that is now called the inheritance of acquired traits in which he suggested that maybe the experience of an organism in one generation could somehow lead to changes in the progeny that would benefit them in the next generation. He famously thought that the giraffe‘s neck had been extended by reaching higher and higher into trees for nutrition.

Organisms react to changes in the external environment so that to minimize their impact. This phenomenon is called homeostasis. The lack or absence of food perhaps is the most important factor that disturbs homeostasis. Let us imagine such hypothetical situation in the example of a giraffe. The climate of the African savannah began to change rapidly, trees became less and less, and for giraffes became harder and harder to get the leaves, most of which were located on the upper levels of plants. Since to hunt for food is a vital need, then animals mobilize all the possibilities of their organisms.

At the same time, it remains unclear: what factors direct organisms to perform specific adaptive tasks so that their metabolism, physiology and morphogenetic competences work to form the required adaptive anatomical novelties. If we look for an answer to this situation within the concept of 'teleonomy in living systems', then the picture will probably look like this: disturbance of homeostasis forces chromatin in the nucleus to organize chromocentres using chromosomal heterochromatin regions and move there genes that work in favor of the formation of a long neck. From their point of view, an organism facing a new challenge shifts its development towards the production of functionally new integrated phenotypic forms [8]. Noble & Noble [10] state, “All living systems are continuously creative in the process of maintaining their integrity. Of necessity, they have to adapt to the ongoing, incessant changes that affect the conditions of life”. Clawson & Levin [3] point to goal-directed behavior as a universal property of all living beings and see teleonomy as a unifying framework for understanding all possible agents? In other words, for adaptive phenotypes to emerge, an organism must face a choice: to be or not to be. Only those organisms in the population, which due to favorable circumstances were able to rearrange chromatin so that genes started working in the right place and at the right time will survive and leave offspring. Apparently, the formation of adaptive phenotypes is an extremely difficult task and it is possible for very few individuals in the population, as evidenced by the fact that 99.99% of the organisms that have ever existed on Earth have not survived.

From our point of view, adaptive phenotypes in humans include a large neocortex, a hairless skin, skin colour, variability of body heat conductivity, ability to long-distance running and a very high physiological plasticity. Clearly, this is far from being a full list of traits characteristic of *H. sapiens* and may include others [20-26; 28]. Common to all these traits is their ability to be inherited. In this sense, we should not consider as adaptive phenotypes such acquired traits that are the result of, for example, learning (speech, writing ability, sports and artistic achievements, etc.), because they are not inherited and are reversible processes.

Apparently, for important acquired traits to be inherited it is necessary to rearrange the chromatin of the nucleus, as, for example, in position effect variegation, but not structural genes. The point is that the genic part of DNA is very conservative and even if they change, these changes are rarely passed on to offspring because they occur mainly in somatic cells. Whereas chromatin rearrangement requires such stressful situations when the organism can no longer continue to exist within the framework of the previous developmental programme. Since the absence of such acquired traits as speech, learning or artistic and sporting achievements are not matters

of life or death; they are apparently not capable of chromatin destabilization, although they are certainly important for survival, including the acquisition of food, successful reproduction and defense against predators.

Thus, it would be more correct to understand unidirectional, non-reversible evolutionary processes by adaptation. It is for this reason that we consider the so-called adaptive genes and genotypes found in the genome of some high-altitude populations of Tibet, the Himalayas, and the Ethiopian Plateau not as the result of adaptive evolution (the emergence of an adaptive phenotype), but as a manifestation of acclimatization, a reversible response of the genome to a new condition of existence (for details see [21; 23; 27; 34]).

There is another point worthy of discussion. It can be considered established that the most complex organisms, such as humans and other mammals are the most highly evolved organisms. It turned out that the more complex the organization of an animal is, the more and clearer densely packed chromosome regions (G-, Q- and R-bands) composed mainly of ncDNAs are manifested. Using special methods of differential staining, the clearest chromosome bands are found in humans, then in higher primates, and worse in other primates and mammals. For example, the methods of differential staining (G-, Q- and R-staining) that reveal densely packed sections of metaphase chromosomes are weakly expressed in reptiles, amphibians and fish, but absent in plants. Chromosomal constitutive heterochromatin (C-heterochromatin) is detected by differential C-staining only in higher eukaryotes [28-31].

In this regard, Shapiro [11] wrote "...the most complex organisms have the largest amounts of repetitive and non-coding DNA in their genomes. In other words, the organisms we assume to be the most highly evolved have apparently gained much of their complexity by accumulating non-coding DNA content rather than increasing the protein-coding capacity". Thus, the more complex the organism, the more and more clearly expressed are the chromosome C-, G-, Q- and R-bands. We interpret this fact in the following way: the larger and clearer the chromosome bands, the more densely packed condensed chromatin is around the nucleus, which is involved in the removal of excess metabolic heat from the cell nucleus. We believe that this circumstance directly affects cell thermoregulation, which phenotypically manifests itself in the form of body heat conductivity (for details see [28-31; 33]).

Finally, the leading role of ncDNAs in the evolution of eukaryotes is evidenced by modern prokaryotes. Microbes are known to have arisen about 3.5 billion years ago and have not changed significantly during this time, except for the strains that appear, for example, under the influence of antibiotics. The reason seems to be that new strains of microbes arise only due to gene mutations, since the proportion of ncDNAs in their genomes is negligible or absent. Since, as we believe, cell nucleus, mitotic chromosomes, biological sex, species, the Cambrian explosion, multicellular and homoeothermic organisms, including modern humans arose due to long evolution and the leading role of ncDNAs, it is not unexpected that prokaryotes were incapable of forming complex adaptive phenotypes, i.e. evolution (for details see [19-26; 28]). It is hard to imagine that the above features of eukaryotes have arisen through gene accumulation and/or their favorable mutation. Genes, for all their importance, need leaders, and they cannot determine where, when and what to do by themselves. All they can do is determine the synthesis of functional RNA molecules.

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