Chapter 16

Appendix: The Main Problems and Methods of Evolutionary Physiology—A Lecture by Leon A. Orbeli

Additional information is available at the end of the chapter

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The following text is a lecture given at the First Conference on Evolutionary Physiology, March 7, 1956. It was originally published in Russian, in the book Evolutsiya funktsii nervnoi sistemy (Evolution of Functions of the Nervous System), Leningrad, 1958, pp. 7–17. This text was written in the Soviet epoch and therefore it contains sometimes necessary "reverences" in the direction of communistic ideology.

The text was translated by Andrey Polyanovsky.

The question of evolutionary physiology as a discipline in its own right was raised only in our country. This may have a whole number of explanations. First of all, some outstanding scientists in our country followed the evolutionary line in studying one or another physiological issue. The necessity of the evolutionary approach in physiology was accentuated by I.P. Pavlov, I.M. Sechenov and N.E. Vvedensky. From them, we got not only statements, but also fundamental papers, which predetermined further development of the evolutionary trend in physiology. This especially concerns I.P. Pavlov's studies of the higher nervous activity. I.P. Pavlov had good reasons to emphasize that studying conditioned reflexes is essentially studying reflexes in the process of their formation and development, in their beginnings and that, when studying a conditioned reflex activity, a researcher views the entire developmental continuum of reflex activity and, consequently, gets a chance to deduce from the history of conditioning the overall process of reflex activity formation during evolution. This has served a major impetus for physiologists in our country, rather than in any other, to choose the evolutionary road and to begin following the evolutionary principle.

Alongside the directions left by the coryphaei of experimental science, we have yet another, no less and may be even more important, explanation—the fact that all Soviet science is advancing under the guidance of the solely correct philosophical doctrine of dialectic materialism. The Marxist-Leninist doctrine obliges every researcher in the field of natural sciences to adhere to the principle that no one phenomenon can be understood without analyzing the history of its emergence, its development. It is the only historical method that enables correct understanding of the subject matter. Based on these two tenets—the requirements of the Marxist-Leninist philosophy and the directions by our great predecessors—we are approaching now the problems of evolutionary physiology.

It would be incorrect to say that wishes to study functions in their evolutionary history were not stated by other eminent physiologists. I remember that in 1908, the now late English physiologist Keith Lucas published his brochure entitled "Evolution of functions," in which he expressed bitter regret that the evolutionary principle, which proved to be extremely fruitful and widely used in morphological sciences,* was almost of no use in physiology. K. Lucas stated some considerations on the necessity of following the evolutionary principle in physiological studies and, furthermore, pointed out the difficulties physiologists encounter if they attempt to approach a study of the function from the viewpoint of its emergence and origin. In any case, our Soviet physiology can be presently characterized exactly as physiology imbued with the evolutionary principle. Nevertheless, the question does arise on whether it is enough for individual researchers working in the field of physiology simply to adhere to evolutionary theory, to reckon with evolutionary theory, to try applying the historic approach to solving one or another problem or to seek a new discipline entitled "evolutionary physiology" to appear and develop as an independent discipline within the system of physiological studies and biological sciences.

I can afford asserting that the time has come not simply for the evolutionary principle to become a guiding force in furthering physiological studies but for the independent discipline, evolutionary physiology, to arise as a result of the progress achieved by physiological science in general.

I must say that morphologists already pointed out the necessity of establishing evolutionary physiology along with evolutionary morphology. These statements belong to late A.N. Severtsov, who emphasized that it is time for physiologists to address the evolutionary matters and to found evolutionary physiology along with evolutionary morphology. The term "evolutionary physiology," still unknown in other countries, is our term, our proposition to single out evolutionary physiology as a discipline in its own right along with evolutionary morphology, evolutionary histology and evolutionary biochemistry.

I have to remind that in this case it is definitely not about tearing evolutionary physiology as an independent discipline from the rest of physiology. Not at all! We should consider it as a new, present-day stage in the development of physiology because evolutionary physiology can in no way be constructed in isolation from the rest of physiology. It should make maximum use of all that abundant material, which was obtained both by classical (medical) physiology and by general physiology, zoophysiology, comparative physiology and embryophysiology—all those branches of physiology that have been elaborated until now and have achieved enormous success. Evolutionary physiology should use all this material. It is a product of, a superstructure over, those physiological studies that are in progress now. But this does not deprive it of the right to put forward its own questions, to pose them as a leading line, and to select the material that helps solve the evolutionary problem.

What should be the tasks of evolutionary physiology? It seems to me that the two pivotal lines should underlie evolutionary physiology. K. Lucas grieved that there were no studies of the evolution of functions, and of course, the evolution of functions must be the first pivot of evolutionary physiology. We should strive to consider any function subjected to experimental investigation in terms of the history of its formation: how one or another function is formed in the process of evolution, how the intertwining of separate functions led to certain changes in

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each of them, resulting in the representation of each given function in certain animals exactly this way and not otherwise. This is the question of studying the evolution of functions.

Another question is whether evolutionary physiology should and could be confined to studying the evolution of functions. I do not think so. The second, no less and may be even more important task of evolutionary physiology, is supposed to be functional evolution, that is, a verification of evolutionary physiology on the basis not of morphological material and morphological methods but physiological studies.

A study of the evolution of functions will provide a certain material and open up a new avenue toward understanding why the evolutionary process was running this way, but not otherwise, and what the mainstream of the evolutionary process was in terms of the evolution of functions.

It may appear that these are one and the same. But essentially it is not true, indeed. Functional evolution is a higher stage of evolutionary physiology as compared to studying the evolution of functions. In one case, we simply track the historical developmental path of some functional relationships, while in another case we approach the understanding of what the evolutionary process is and how it formed, why the evolutionary process was running exactly this way being based on those functional rearrangements that were arising in living organisms.

Proceeding now to more specific tasks that underlie both main pivots of evolutionary physiology, we must pose a question: is it enough to study the developmental path of various functional relationships in different representatives of the animal kingdom we are dealing with, taking into account the history of the formation of these functions, or should we also set ourselves the task of elucidating the mechanisms of the evolution of functions, those specific conditions and motives that directed the process of development along one or another way? In other words, should we also study the significance of the individual factors that determined the course of evolution?

In this respect, we certainly have to reckon with the basic tenet of our science and Marxist-Leninist philosophy that organism and its environment make up a single, indivisible and interrelated whole. With this in mind and considering that the entire process of the development of different functional relationships ran in a certain environmental context, everchanging, ever affecting living organisms, it becomes clear that no one function could form and undergo any changes otherwise than under the influence of and depending on those environmental impacts that it was permanently exposed to. So, the task of studying the evolution of functions involves not only the elucidation of the course of development, developmental pattern, succession of events, but also establishing the interdependence of these events as well as the causative dependence of all changes and transformations on the environmental factors that affect living beings. We have to reckon both with the internal factors coming from the organism itself, in the form of an interaction of its separate parts, and the external factors.

As regards the problem of functional evolution, this is a much more complicated matter. Here we need to foresee the issue of what further development is supposed to be, how we could imagine the further transformation of individual functions and whole organisms under the effect of those environmental changes that are occurring right now, before our eyes, and that may become determinative for further development of functional relationships. These issues

are not only of theoretical significance. Of course, their theoretical significance is quite clear to everyone and requires no proof, but I have to remind that the conditions, under which the organisms are living at present, change substantially every day. Enormous success of science and technology, that we are witnessing now and that resulted from great progress humankind has achieved in its evolution, creates by itself new living conditions, sometimes so different from the normal that they may prove to be determinative for further development of life on Earth. From this viewpoint, we have to admit that evolutionary physiology, in the sense I have stated above, is not only a theoretical but also a strictly practical science in the sense of considering all those conditions, under which we are living now and will be living in the near future, in the light of those influences that these conditions may have on the existing organisms and their offspring, be it of human beings or the animal world.

The question arises: what methods should evolutionary physiology use to embrace the tasks I have just talked about?

Over many years, I and my fellow workers have been adhering to the viewpoint that correct understanding of the evolution of functions and mechanisms underlying evolutionary changes in functions is attainable provided that one and the same researcher uses simultaneously four methods, basically different but leading to the same goal.

The first way, as is clear to everyone, is certainly **comparative physiology**—the use of comparative physiological material in order to understand how different phyletic lines evolved under different living conditions and how the same functions developed becoming more sophisticated or, quite the contrary, dropping out in some phyletic lines depending on the specific living conditions. The question then arises as to how one and the same function undergoes changes under different conditions and, on the other hand, how the initially different functional relationships converge leading to one and the same ultimate result under the influence of environmental factors.

Evolutionary physiology should definitely be based on the ready material of comparative physiology and *zoophysiology*, but on the other hand, it should develop on its own, artificially selecting those animal samples and conditions that are of special interest from the viewpoint of the evolution of functions. Here, perhaps, we have to run counter to the views of some evolutionists. We believe that it is necessary to distinguish between three disciplines. The first is zoophysiology, that is, descriptive physiology of individual animal species, an extremely important science, which is of great theoretical and even greater practical significance. We need to know all forms of life represented now on Earth. Another thing is *comparative physiology*, which chooses from the huge material of zoophysiology only certain objects and issues that allow a comparison and elucidation of certain regularities. Yet more special and, at the same time, complex demands are made by *evolutionary physiology*, which not simply compares what occurs under different living conditions but uses the experimental method to understand how these functions formed.

The second way is **the use of ontogenetic development**, that is, studying functions not in phylogenesis but ontogenesis. Here there is less of the ready material, and we need to strain every nerve to reinforce this aspect of physiological studies because at present ontogenetic

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physiology is developed relatively poorly. We should try to embrace both the embryonic and postnatal stages of development and find out when the rudiments of different functions begin to show up, at what stage and how the function of those structures that pre-existed and developed independently changes depending on the formation of different morphological structures. This particularly concerns those tissues and organs that fall at a certain age during their development under the influence of the nervous system and endocrine factors. As a result of these effects, endocrine and neural, the developmental course itself undergoes substantial changes, and we should understand how the development would proceed without the interference of certain endocrine factors and the determinative influence of the nervous system on the development of endocrine organs as well as, vice versa, the effect of endocrine organs on the variability of the nervous system. With regard for all these features we should approach ontogenetic physiology to make it a tool for studying the evolution of functions.

Still, additional possibilities open up in front of us—**the use of clinical material**. I must say that it was not without reason that the issues of evolutionary physiology were raised by physicians, not biologists. This seems to be a paradox, but it is not true, and this is because clinical studies led to the idea that in certain cases some symptoms represent echoes of what had happened at earlier developmental stages, that in some cases of pathology, we deal with echoes of the evolutionary process, with reverting to those functional states that characterize the earlier developmental periods.

Of course, it is particularly easy to draw a comparison between clinical symptoms of different diseases and those phenomena that we observe during ontogenesis, but phylogenesis also reveals a lot in this respect.

Directly related to the use of the clinical material is **the use of special experimental methods**. These methods boil down to an artificial disconnection of individual organs and tissues from their controlling mechanisms, a disconnection inside the controlling mechanisms themselves, inside the nervous system, and a disconnection of some lower levels from the higher ones. Then follows an observation of changes that occur both in the lower parts of the nervous system depending on the loss of regulatory influences from the higher parts and, vice versa, in the higher parts as a result of the loss of those afferentations that arrive from the lower parts. In this respect, we are particularly lucky because we can afford carrying out any experimental transections in animals providing thereby new conditions for functioning of organs, tissues and parts of the central nervous system and endocrine apparatuses, which change their regulatory function under the influence of these disconnections. Hence, we can compare these data with the results of clinical pathology and those of comparative and ontogenetic physiology.

Based on these four methods of investigation, it is possible to get an idea of how the evolutionary process was proceeding and how functions were changing during their development. As a result, not only factual relationships (not merely descriptive though) would be established, but to a large extent it would be also possible to unravel the mechanisms of interaction and, hence, to a certain extent, resolve causal relationships as well. Still, that is not all. Experiments allow a special analysis of the effect of external factors. Now we have got an extremely abundant experience in the sense that modern science and technology have made it possible to generate such forms of energy that were unknown or unattainable previously. At

present, they can be generated, detected, recorded and quantitatively evaluated. It is increasingly often that we are learning about the existence of those forms of energy that we have been unaware of before.

While throughout its evolutionary and historical development and until recently humankind was aware of only a limited number of energies that affected it naturally, over the last decades we have learnt that many types of energies represented in nature are much wider than we thought. Yet recently, ultrasounds seemed to be something artificially produced by people, but now it is turning out that during the evolutionary process not only were they generated by different animals but also served as means of signaling being perceived and evaluated in the same way as we perceive sound frequencies in the narrow range of audibility. Likewise, radio waves discovered by our compatriot Popov and being widely used in television and radio turn out to be generated by the Sun as well; the Sun's rays, that we assessed previously only in terms of their energy, contain also electromagnetic oscillations of those frequencies, wavelengths, that we use in radio engineering. So that over millions and billions of years during the evolutionary process, animal and human organisms were exposed to these electromagnetic waves, and it is only now, over just the last three decades, that we have come to grips with studying ultrahigh frequencies and applying them in ambulances and clinics for treatment, diagnostics, and so on. Nevertheless, they did exist in nature and affected all of us.

So far, we studied experimentally the effect of these ultrahigh frequencies for pure pragmatic purposes—their application in technology, medicine, and so on. Now they are becoming one of the possible factors of evolution, and we should set to studying ultrasound frequencies, electromagnetic waves and ultraviolet radiation not only in terms of their impact on individual functions and organisms but also in terms of their possible role in the evolutionary process. Thereby, we should look into the influence they may have on future generations.

If we investigate varied types of energies that we receive in their natural form and that we can now generate artificially, graduate, record and evaluate quantitatively, if we find out how they are reflected in the development of different functions, then we will obtain an enormous material for understanding not only the developmental course of functions and the history of the emergence of functional relationships but also their dependence on the environmental factors. Thus, we are arriving at a proposition that evolutionary physiology, as we understand it, should encompass a wide range of studies. It will certainly be interwoven with classical, applied and comparative physiology but anyway underlain with an endeavor to comprehend the causal dependence of the developmental course of functions on the external and internal factors, to understand those major lines, along which the evolution of functions is running and which jointly led the evolutionary process to proceed exactly in the way it did, and finally, to understand the diversity of pathways the evolutionary process may proceed along depending on those conditions that will be created on our planet. Here are the main tasks and main methods of evolutionary physiology.

However, the question arises whether the abovementioned exhausts the matter. Of course not. The basic principle, which underlies the evolutionary doctrine and studies carried out by the coryphaei of our physiological science, especially I.P. Pavlov's, is that organisms undergo the process of continuous adaptation to the environment. Therefore, it is not enough just to

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understand what specifically, and under what influence, is happening. We should clarify the adaptive role of the evolution of functions, understand how life was preserved and how it assumes various forms depending on the adaptation of a living being to new conditions under the influence of the external and internal environmental factors. We ought to understand which conditions are disastrous and which prove to be surmounted or secured by certain adaptations.

Elucidation of a number of adaptive mechanisms, adaptive changes in functions should again be one of the major tasks of evolutionary physiology. In this sense, evolutionary physiology will be not only a theoretical, but also strictly practical, science, since it will lead to results, which will enable us to influence the course of evolution in the future. It is quite important for medicine and zootechnics.

Especially hard questions arise when we approach a study of the human organism. We know well that the human organism at a certain stage of evolutionary development stopped to be only a biological being and became a social being. Interrelationships among people led to the establishment of certain social relations. The latter resulted from a kind of leap, or what may seem to be a leap, because some of our immediate predecessors perished and are now inaccessible for being studied. But in any case, the fact is that humankind rose above the rest of the animal world and in many respects surpassed it, creating new forms of activity as well as new forms of relationships with the environment. Man to a certain extent became the master of nature, at least of some of its aspects; he can consciously control it being expected to intensify his activity in this direction. Humans entered into certain relationships that are lacking in other animals. Man is not only a biological, but a social being, and this, on the one hand, relates to his nervous system development and transition to other forms of existence, but, on the other hand, these new forms of existence and interaction prove to be a powerful factor, which influences the course of changes in the structure and functions of an organism.

From this viewpoint, the historical period of the human existence certainly represents an extremely important stage in the evolutionary process, and evolutionary physiology should not digress from this point.

Recently, it seemed that the relationships among people, who created social living conditions and stay under the influence of these social factors, should serve a borderline, at which a physiologist must stop. However, proceeding from the I.P. Pavlov's doctrine and Marxist-Leninist theory, we can afford asserting that physiology must not stop here. The whole human organism with all its manifestations should become a subject of physiological investigation.

This does not mean that we should reject the existence of psychology and some other humanities. Quite the contrary, our task is to tie physiological studies to psychological as closely as possible in order to understand those physiological mechanisms that provided humans with the potential to turn from pure biological beings to simultaneously biological and social beings, to understand those physiological mechanisms that provided the possibility of interrelationships among people and thereby made this possibility a factor consciously directing the development of our progeny.

If we abandon this task, then both medicine in its major part, pedagogy and art will be absolutely cut off, ejected from natural sciences and left beyond the scope of natural-scientific

investigation. This is not to be understood as an attempt to account for all social relations in terms of natural sciences. Of course, this would be incorrect, but providing a physiological basis for them should be our goal. No doubt, an exclusively important role in this respect was played by the I.P. Pavlov's doctrine about two signaling systems. If it were not for the two signaling systems, if the second signaling system were not superstructured over the first signaling system common to the animal kingdom, if those multiform influences that we widely use in fostering our children and interrelating with each other were not established, then we would have been ignorant of functional interconnections in the human organism and its relationship with the environment.

From this viewpoint, the aspiration for studying the human higher nervous activity during its formation and development is supposed to be the acme of evolutionary physiology. A comparison of the human and animal organisms shows a striking divergence in their developmental paths from the first hours of life.

When studying the postnatal development of animals and comparing it with that of human organisms, we see how considerably the range of possibilities for the nervous system development expands under the influence of the second signaling system, while the biological processes themselves become largely subjected to the influence of the second signaling system.

This stage of the evolutionary physiology formation should certainly interest us first of all, because it leads to the cognition of humankind while representing a junction between natural and social factors, which determine the development of human personality and its activity.

This is how I and a narrow circle of my fellow workers envision the tasks and methods of evolutionary physiology. I know that many of the abovementioned propositions are far from being new as they are recognized and being used for a long time. May be much of the said will prove to be worded unsatisfactorily. Anyway, underestimation of some of the points I have afforded to draw your attention to might have an unfavorable effect on the progress of evolutionary physiology.

Evolutionary physiology, as stated above, is supposed to be pivotal to independent research. It demands to enlist a number of experimental methods from physiologists, biochemists, morphologists and psychologists to create by joint efforts a science that would complement evolutionary morphology and, at the same time, provide a clear and comprehensive understanding of how the interrelationships among people and nature as well as among people themselves first formed and then altered during evolution under the effect of historic conditions. Simultaneously, such a high goal will be promoting the resolution of a whole number of practical tasks, because all our efforts to comprehend the causal dependence among functions of an organism as well as between the effect of external factors and activity of an organism will be a means of practical assistance to the population of our motherland and the whole world in defending against some adverse factors, which are present in nature, which we generate artificially and which expand their use. Without the knowledge of their role, we may prove to be helpless in combating pernicious influences. Such a science, essentially theoretical and being of profound practical importance, should become the goal of evolutionary physiologists.

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I reiterate that nowhere are the interests of theory and practice interwoven that closely as in evolutionary physiology. Not only will we be aware of how to struggle against the influence of some external factors on an organism but will obtain an enormous material to extend the range of our theoretical ideas from analyzing those conditions, under which the work is in progress at various scientific and manufacturing institutions. This unity of theory and practice should always underlie our approach to a problem and be a guiding star, allowing us not to shut ourselves off from the life practice and not to be afraid that one or another experimental path has a character of applied science. There is neither a theoretical nor practical science, there is a single science and there must be a single science. Practice must help theory and vice versa.

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