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BEHAVIOR IN THE SYSTEM OF HEREDITY: A NON-REDUCTIONISTIC APPROACH

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The neo-Darwinian, paradigmatic reduction of the heredity phenomenon to the genotype-phenotype dichotomy canalized for a long time the development of the research on the heredity of behavior. In consequence, the most progressive conjecture reached by the respective neo-Darwinian workers was that most, if not all, behavioral traits are a mixture of both hereditary /i.e. genetically coded in their opinion/ and non-hereditary components.

The increasing crisis of neo-Darwinism, caused by both theoretical and empirical achievements in various biological disciplines, led in the late 1970s/early 1980s to a thorough reconsideration of the heredity phenomenon. This re-appraisal resulted in a rejection of the neo-Darwinian genotype-phenotype dichotomy and in a development of a multilevel system of heredity /e.g. Zemek, Mlíkovský, Socha 1985/. A natural consequence of the latter concept has been a reevaluation of the problem of the heredity of behavior. It is the intention of the present paper to address the latter problem in more detail. The following three questions will be in focus:

/1/ How is the behavior inherited at the behavioral level itself? What are the peculiarities of this heredity level?
/2/ What are the peculiarities of the upward causation in heredity, with respect to the behavioral level? How do other heredity levels influence the behavioral heredity level?
/3/ What are the peculiarities of the downward causation in heredity, with respect to the behavioral level? In which ways can behavior influence the other heredity levels?

Key words: multilevel heredity, heredity of behavior, Mendelian paradox, evolutionary synthesis

Ever before Darwin, it has been commonly recognized that behavioral patterns used by individuals of parental and filial generations are rather similar. Consequently, some kind of transmission of information on behavior between generations has been assumed, let it be implicitly or explicitly. Since Charles Darwin /1859/ formulated his theory of evolution, it became necessary to consider this problem also in evolutionary context and the question of how information on behavioral features can be transmitted from generation to generation arose.

Students of behavior discerned since centuries between the inherited /instinctive/ and the learned behavior /Diamond 1974/. Later, soon after the rediscovery of the Mendel´s laws of heredity and the subsequent identification of the hereditary with the genetic /Zemek 1983/, the instinctive behavior was claimed to be hereditary and the learned behavior non-hereditary. Influenced by the modern evolutionary thought rapidly developing towards the neo-Darwinian paradigm, most of the respective interest was given to genetically, or supposedly genetically, determined characters. Consequently, most of the pertinent research was aimed at discerning which behavioral patterns are hereditary, i.e. determined only genetically, and which are not.

Independently, but in spirit of his time, also Pavlov /1903, 1906/ developed his dichotomous concept of conditioned, i.e. learned, and unconditioned, i.e. instinctive, reflexes. Note, that synonymization of these terms was erroneously reversed in our previous paper /Mlíkovský and Zemek 1986/.

Studies performed during the above mentioned stage indicated that such a dichotomous classification of behavioral patterns into the hereditary, i.e. instinctive, and non-

-hereditary, i.e. learned ones is in most cases impossible /Krušinskij 1948, Schneirla 1956, Jensen 1961/. By this, another problem arose, namely, to what degree a behavioral character is determined genetically and to what degree its ontogenetic development is modified by learning or, more generally, by environmental influences.

Various experimental approaches aimed at discerning the hereditary and non-hereditary components of behavior were developed, including hybridization experiments, artificial selection for behavioral traits, comparison of monozygotic with other siblings, rearing animals in deprived environment, etc. Although it is now clear that no such experiments can prove the direct genetic control of behavioral patterns, one may agree with the fact that many behavioral patterns are influenced both by the genotype /in general sense/ of the given animal and by learning.

The third approach to the heredity of behavior consists in the recognition of a specific channel through which learned behavior, or the learned part of behavior, is transmitted from generation to generation. Recognition of this channel is implicit in the works of all researches who accept tradition /Wickler 1967/ as a phenomenon characteristic for at least some species or phyletic lines. Some authors have applied to the behavioral channel of information transmission between generations specific terms, such as social heredity, social undertaking, signal heredity, cultural heredity, or signal undertaking /see Mlíkovský and Zemek 1986/.

An important problem involved in this approach to the heredity of behavior is whether characters transmitted between generations by means of tradition may be regarded as hereditary or not. As in the frame of neo-Darwinism, in which this approach has basically developed, only information directly coded in genes was considered hereditary, the respective researchers usually concluded, that no hereditary information is transmitted through the behavioral channel. This apparent paradox was especially well expressed by Mantejfel´ /1980/, who spoke in this respect of the " 'hereditary' transmission of non-hereditary information".

The brief survey of approaches to the problem of behavior determination given above reflects intuitive efforts of the respective researchers to overcome the neo-Darwinian paradigm. Further development of this problem requires a shift from the one-level image of heredity, in which all levels of <u>internal</u> determination are reduced to one level only /see, e.g., Ho and Saunders 1984/, towards the structured, multilevel concept of heredity /Zemek et al. 1985/. Certain steps towards such a concept have been made recently also by several other authors /see Mlíkovský and Zemek 1986/.

Let us now approach the problem under discussion at a more general level. Until recently, all the research of the heredity of behavior was performed in the frame of the classical genetic thinking. Recent advances in molecular biology, especially those related to the expression of eukaryotic genes, disturbed, however, the classical gene nction /see Zemek 1983/. Consequently, Mendelian paradox could be formulated /Zemek at al. 1985/. The essence of this paradox lays in two contradictory findings: On the one hand, we know that heredity /in the sense of the Darwinian power of heredity or Mendelian genetics/ does exist at a phenomenological level, as well evidenced by hybridization experiments. On the other hand, at the DNA level, which should contain units of heredity or genes, no such atomistic units were found which could be identified with character determinants expected to be present there by classical genetists and neo-Darwinists /Zemek 1983, Zemek et al. 1985/.

Possible solutions of this paradox were indicated especially in the Dubinin's concept of the systemid gene /see Berdyšev et al. 1980/ and in Beljaev's /1981/ concept of vertical and horizontal channels of heredity. We regard both these concepts as complementary to one another and have included them into our concept of multilevel heredity /Zemek et al. 1985/.

Understanding the multilevel system of heredity requires, above all, understanding the internalization of morphogenetic factors. Morphogenetic signal of external environment /at any level/ can be substituted by new internal signals, based on different material substrates or carriers with analogical morphogenetic effect /see Zemek and Socha 1982/. Modern epigenetics is preferably aimed at studying functional constraints canalizing epigenetic pathways in a rather generally understood epigenetic landscape and at describing dynamics of character determination, but leaves out of consideration mechanisms of transmission between generations of such information, which has already been fixed. In contrast to the epigenetic approach, the multilevel system of heredity takes into account also the latter aspect and returns thus to the heredity notion its original broad meaning /Zemek et al. 1985/. From this point of view it is a solution of the above mentioned Mendelian paradox.

Let us turn now to a brief description of the properties of heredity levels. We conjecture that all of the existing heredity levels have a certain degree of autonomity, but are, at the same time, correlated inter se, building thus a complex system of heredity in each organism. Development of characters at a higher level of organization requires that lower levels of organization enable formation of building units for the development of structures at higher levels. Consequently, each character seems to be indirectly determined, or co-determined, at the DNA level. Moreover, an attribute which appears owing to the polyfunctionality or pluripotentionality of elements and structures /Zemek and Novotný in press/, can obtain an adaptive value and in this case can turn into a canalizing element in the course of genetic assimilation of morphogenetic factors.

From a certain point of view, or for solving certain tasks, the viewpoint of classical genetics is sufficient in that sense, that it may be irrelevant whether it is assumed that the unit for inheritance, splitting and combination of characters is a classical atomistic gene, or a systemic gene as a complex processual unit. The more an epigenetic pathway and, hence, a systemic gene as a projection through all heredity levels, is stabilized, or canalized in the terminology of Waddington /1957/, the more it behaves as a classical hereditary unit of the Mendelian type.

From this follow also the validity and limitations of the population genetic approach to the problem of behavior evolution and of other efforts to relate the genetic and the cultural evolution /see Mlíkovský 1986, Mlíkovský and Zemek 1986/. However, not all of characters which appear to be "non-hereditary" are formed solely by environment, but may be fixed at some other heredity level and transmitted through the corresponding heredity channel /i.e. "non-genetically"/. This applies also to the behavioral heredity level at which information is transmitted by tradition /sensu lato/.

The behavioral channel of heredity bears, in addition to the information for the modification of epigenetic pathways and for the maintenance of those which were selected during evolution as more convenient for realization of behavioral adaptations, also information on behavioral patterns as such. In this way, behavior becomes the ruling factor of adaptation and, at the same time, a channel of hereditary transmission with more grades of freedom than have the lower ones /cf. Mlíkovský 1982/.

Now we can briefly summarize the matter. The whole problem of the heredity of behavior can be divided into three basic components, namely the peculiarities of the behavioral channel itself, the influences of behavior on the lower heredity levels and, finally, the influences of the lower heredity levels on the behavioral one.

As regards the peculiarities of the behavioral channel themselves, we believe that behavioral changes, i.e. mutations in a broad sense, can arise at the behavioral level, just as at all other heredity levels. These behavioral mutations are then transmitted via tradition, are subject to natural selection and can spread through populations /see Mlíkovský 1986/.

The upward causation can be best described in terms of the role of learning in the formation of behavioral patterns. As mentioned above, no traditional experiments are able to prove the genetic basis, or the proportion of the genetic basis, of behavioral patterns. They are, however, in many cases able to discover which part of behavior is learned and which is not, i.e. which is coded at some lower heredity level. Summarizing the extensive evidence supplied by these experiments, we may briefly classify here all the possible roles of learning in the formation of behavioral patterns during ontogeny. Note, that in the following text we strongly distinguish between the self-learning and the allo-learning. In the former case, no respective interaction with other individuals is needed for a formation of normal /typical/ behavioral pattern, while such an interaction is required in the latter case.

In what follows, the necessity of learning for the formation of normal behavioral patterns during ontogeny is classified /Mlíkovský and Zemek 1986/:

1. Neither self-learning, nor allo-learning are needed.
2. Only self-learning is needed.
3. Only allo-learning is needed /it is uncertain whether this is a real variant/; and
4. Both self-learning and allo-learning are needed.

The downward causation is more complex and, hence, more difficult to assess briefly. Two basic effects can be discerned here. First, the behavior of developing individuals themselves can influence their morphogenesis, i.e. to serve as a morphogenetic signal which can be substituted during evolution by some internal factor. Second, the behavior of one or both of the parents /or unrelated individuals/ can unfluence the morphogenesis of their offspring.

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In the current literature on theoretical biology we often come across references to the wholeness of organisms, to their structural organization, to multilevel organization of the living matter, etc. The problem here is to turn from these general and often very abstract proclamations to a factual investigation of concrete structural levels, their genesis and interactions.

As behavior is an inherent function of any biological system, through which that system interacts with its environment, and which is, at the same time, an important mode of adaptation towards environment, it is necessary to devote much more attention to the study of the structure of behavior and modes of its hereditary determination than before. It also seems evident that the problem of behavior determination cannot be studied on the basis of a dichotomous distinction between hereditary and non-hereditary behavior, or behavior components, respectively, but only in frame of a revised heredity notion.

Note: This paper is based to a large extent on our previous papers: Zemek and Mlíkovský /1986/ and Mlíkovský and Zemek /1986/.

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