BEHAVIOUR, ADAPTATION and EVOLUTION
V.J.A. Novák, V. Vančata, M.A. Vančatová
(eds.), ČSAV, Praha 1986: 33-40

HEREDITY OF BEHAVIOR IN THE CONTEXT OF THE CURRENT EVOLUTIONARY SYNTHESIS: 2. LEVELS OF BEHAVIOR DETERMINATION

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ABSTRACT - The present paper starts with a survey of historical and current alternative approaches to the problem of behavior determination. In the following text, some reasons for the failure of classical genetics and neo-Darwinism in explaining the inheritance of behavior are briefly discussed, and the multilevel concept of heredity is suggested as an at least temporarily best solution of this problem complex. Finally, a preliminary classification of the possible roles of learning in the formation of behavioral patterns during ontogeny is presented, and its meaning for the evolutionary origin of the behavioral channel of heredity is outlined.

KEY WORDS: Heredity of Behavior, Learning, Evolutionary Synthesis

INTRODUCTION

It has been perhaps never doubted that behavioral patterns used by individuals of parental and filial generations are rather similar, though not identical. Consequently, a kind of transmission of information on behavior between generations has been generally assumed, let it be implicitly or explicitly. Since Charles Darwin (1859) formulated his theory of evolution, this problem had to be considered in evolutionary context, and the question of how information on behavioral patterns can be transmitted from generation to generation arose.

While the general prerequisites for solution of this problem are discussed in the first part of this paper (Zemek, Mlíkovský 1986), this paper will focus directly on various approaches to the coding and heredity of behavior.

HEREDITARY VERSUS NON-HEREDITARY BEHAVIOR

Students of behavior distinguished since centuries between the instinctive and the learned behavior (cf. Warden 1927, Beach 1955, Diamond 1974). Later, soon after the rediscovery of the Mendel's laws of heredity and subsequent identification of the hereditary with the genetic, the instinctive behavior was claimed to be hereditary and the learned behavior non-hereditary. Influenced by the then modern evolutionary thought rapidly developing towards the neo-Darwinian paradigm, most of the respective interest was paid to genetically, or supposedly genetically determined characters. Consequently, most of the pertinent behavioral research was aimed at discerning which behavioral patterns are hereditary (i.e. determined only genetically), and which are not.

Independently, but wholly in spirit of his time, developed also Pavlov (1903,1906) his dichotomous concept of conditioned (= instinctive) and unconditioned (= learned) reflexes.

HEREDITARY AND NON-HEREDITARY COMPONENTS OF BEHAVIOR

Studies performed during the above mentioned stage yielded soon the result, that such a dichotomous classification of behavioral patterns into hereditary (instinctive) and non-hereditary (learned) ones is in most cases impossible (cf. Krušinskij 1948, 1960, Hebb 1953, Lehrman 1953, Schneirla 1956, Jensen 1961). Already Severcov (1922) anticipated this approach, but his book had remarkably little effect on the subsequent development of evolutionary ethology in general, and of hypotheses concerning the heredity of behavior in particular.

By this, another problem arose, namely to which degree is a behavioral character determined genetically and to which one is its ontogenetic development modified by learning, or, more generally, by environmental influences.

Various experimental approaches aimed at discerning the hereditary (genetic) and non-hereditary components of behavior were developed, including hybridization experiments, artificial selection for behavioral characters, comparison of monozygotic with other siblings, rearing animals in deprived environment (incl. the so-called Kaspar Hauser experiments), etc. Although it is now clear that no such experiments can prove the genetic basis of any behavioral pattern, one may agree with the fact that many behavioral patterns and in many species are influenced both by the genotype (in general sense) of the given animal and by learning. The proportion of the (supposed) hereditary component is called heritability of a character in the frame of population genetics (Falconer 1960, Whalen 1971).

TRADITION AS A SEPARATE CHANNEL FOR THE TRANSMISSION OF INFORMATION ON BEHAVIOR

The third approach to the heredity of behavior consists in the recognition of a specific channel through which learned behavior (or learned part of behavior) is transmitted from generation to generation. Recognition of this channel is implicit in the works of all researchers who admit regular learning of offspring from their parents, i.e. who accept *tradition* (see, e.g., Wickler 1967 for this term) as a phenomenon characteristic for at least some species or phyletic lines (cf. Galef 1976). Some authors applied to the behavioral channel of information transmission between generations special terms, such as *social heredity* (Baldwin 1917, and independently Dubinin 1972), *social undertaking* (Davidenkov 1947), *signal heredity* (Lobašev 1961, 1963), *cultural heredity* (Manning 1979), or *signal undertaking* (Mantejfel' 1980).

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. Because in the frame of neo-Darwinism (in which this approach basically developed) only information directly coded in genes was considered hereditary, the respective researchers concluded usually, that no hereditary information is transmitted through the channel under discussion. This is especially well expressed by Mantejfel' (1980) when he speaks of the " *'hereditary' transmission of non-heraditary information*" (p. 91).

The brief survey of approaches to the problem of behavior determination and that of attempts of conceptualization of that problem 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 internal determination are reduced, or dissolved, to one level only, towards the structured multilevel concept of heredity. Certain steps towards such a concept were made recently by several authors (Plotkin and Odling-Smee 1981a,b, Odling-Smee 1983, Odling-Smee and Plotkin 1984, Nečas 1985), and were elaborated in fuller extent by Zemek and co-workers (see Zemek et al. 1985, Zemek and Mlíkovský 1986).

BEHAVIORAL HEREDITY IN THE CONTEXT OF OTHER HEREDITY LEVELS

All heredity levels (see Zemek et al. 1985, Zemek and Mlíkovský 1986) have certain degree of autonomity, but are, at the same time, correlated *inter se*, building thus a complex system in each organism. Development of characters at a higher level of organisation requires that lower levels of organisation 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, a character which develops owing to the polyfunctionality of structures can obtain an adaptive value and turn to a canalizing element in the course of genetic assimilation of morphogenetic factors (Waddington 1957).

From a certain point of view, or for solving certain problems, the viewpoint of classical genetics is sufficient. It is irrelevant in this respect, whether it is assumed that the unit for inheritance, splitting, or combination of characters is a classical atomistic gene, or a systemic gene as a complex processual unit (cf. Zemek 1983). The more is an epigenetic pathway (and, hence, a systemic gene) stabilized, or canalized in the terminology of Waddington (1957), the more it behaves as a classical hereditary unit of the Mendelian type (cf. also Šmal'gauzen 1938).

From this follow also the validity and limitations of the population genetic approach to the problem of behavior evolution (e.g., Cavalli-Sforza and Feldman 1981), and of other efforts to relate the genetic and the cultural evolution (e.g., Pulliam, Dunford 1980, Lumsden, Wilson 1981). Not all characters which defy classical tests for genetic determination are formed solely by environment (and are, hence, non-hereditary), but may be fixed and transmitted also non-classically -- through the behavioral channel of information transmission (i.e. by tradition).

So, for certain types of problems it may be irrelevant at which level of biological determination is a given behavioral character fixed, and a simple dichotomous distinction between internal ("genetic") and external (environmental) determination may be acceptable. However, a closer analysis of the determination of behavioral characters is indispensable for solution of many other problems. So, for example, in studies of the social behavior it is necessary to dispose with means and heuristics for discerning between a mutation at the DNA level, a mutation at the somatic heredity level, or only a noise in a social channel, group tradition, etc.

Because the basis for the origin of a behavioral channel of transmission of hereditary pathways is learning, we will attempt, in the next chapter, to create a preliminary classification of the possible roles of learning in formation of behavioral patterns during ontogeny.

THE ROLE OF LEARNING IN THE FORMATION OF BEHAVIORAL PATTERNS

As mentioned above, no experiments are able to prove the genetic basis, or the proportion of a genetic basis, of behavioral patterns. They are, however, in many cases able to discover which part of behavior is learned (sensu lato) 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 (sensu lato) for the formation of normal behavioral patterns during ontogeny is classified:

(1) neither self-learning, nor allo-learning are needed;

(2) only self-learning is needed:
  - only a short-term experience is needed, e.g., imprinting to a sexual partner,
  - long-term experience is needed which leads to subsequent improvement of the respective behavioral pattern, e.g. preying technique, flight ability, etc.;

(3) only allo-learning is needed (it is uncertain whether this is a real variant);

(4) both self-learning and allo-learning are needed, but:
  - only allo-learning from parents (or supposed parents) is possible,

- only allo-learning from conspecifics (or supposed conspecifics) is possible,
- only allo-learning from other species is possible (this is probably an unreal variant),
- allo-learning from both conspecifics and others is possible, but that from conspecifics is preferred if a choise is possible,
- allo-learning from both conspecifics and others is possible, but that from others may be preferred over that from conspecifics.

CONCLUDING REMARKS

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

Because 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 to the study of the structure of behavior and modes of its hereditary determination much more attention than before. Some of the recent achievements in evolutionary biology opened new ways how to approach the mentioned problems at a more concrete level than before, and we hope that the present paper will help to coordinate them with other modern tendencies in evolutionary biology and with relevant concepts and data achieved in the past.

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