

Gerhard Medicus

Forschungsstelle für  
Humanethologie in der  
Max-Planck-Gesellschaft,  
Andechs, Germany, and  
Landes-Nerven-Krankenhaus,  
Hall in Tirol, Austria  
gerhard.medicus@tilak.at

## The Inapplicability of the Biogenetic Rule to Behavioral Development

.....  
**Key Words:**

Ontogeny,  
Phylogeny,  
Recapitulation,  
Biogenetic rule,  
Psychology,  
Ethology,  
Behavior.

.....

**Abstract**

The biogenetic rule states that ontogeny repeats phylogeny. The validity of this rule for behavioral ontogeny has never been proven. Few developmental psychologists or ethologists have committed themselves on the issue. A clear position, based on empirical data, is needed. The present interdisciplinary article offers cogent reasons why the biogenetic rule has no relevance for behavioral ontogeny.

We know that the order in which many anatomical characteristics develop in an individual from conception to maturity (ontogeny) may, in general terms, repeat the evolutionary history of its species (phylogeny). Therefore, phylogenetically older characteristics very often develop earlier during ontogeny and more recent phylogenetic characteristics often develop later. This tendency is known as the biogenetic rule.

This connection between phylogeny and ontogeny can be demonstrated by comparing, for example, the embryogenesis of different vertebrates. Humans have a shorter common phylogeny with fish than they do with any other mammal. The more distant the relationship between two species (e.g., fish and humans), the shorter the sequence of early similar characteristics. Conversely, the closer the relationship (e.g., any mammal and humans), the longer the sequence of similar characteristics developed during ontogeny. Karl von Baer [1828, p. 224] observed that 'characteristics shared by large animal groups [mostly] develop earlier in an embryo than unique characteristics'. This is known as von Baer's rule of embryonic resemblance. Charles Darwin [1859/1979, p. 427] claimed, 'the structure of the embryo ... reveals the structure of its progenitor'. Von Baer's observation and Darwin's interpretation were subsequently examined in detail by Haeckel [1866].

The anatomical similarity between the ontogenetic development of different species implies

that shared characteristics can be traced back to roots in a common ancestor and can be classified as homologous. For example, all vertebral columns are homologous, as are all feathers. When two structures of different species are similar but have not evolved from the same similar ancestral structure, one speaks of convergence or analogy. One example of such an analogy is the 'camera-eyes' of cephalopods and vertebrates.

Inferences can thus be made from phylogeny to explain peculiarities of ontogeny [Gould, 1977; Haeckel, 1866; Osche, 1982; Riedl, 1975]. Conclusions drawn from ontogeny and applied to unknown phylogeny, however, are only valid given specific restrictions. It is sometimes possible to draw conclusions about phylogenetic succession by knowing several anatomical characteristics in adults of related species and by knowing the sequences of their homologous ontogenetic characteristics. Such reconstructions at best allow us to better understand the chronology of phylogenetic emergence of characteristics of related species. The search for the phylogenetic missing links remains hypothetical [Osche, 1982].

Consequently, the biogenetic rule is not a law. It is not a 'must', but a 'may be' [Raff and Wray, 1989]. In the field of comparative anatomy, there exists a wealth of literature [reviewed by Gould, 1977; Osche, 1982; Riedl, 1975] that affirms the usefulness of the biogenetic rule, and several theories have been proposed to explain why ontogeny generally recapitulates phylogeny.

The biogenetic rule has also been applied to psychology. At the turn of the century, Hall [1904] was one of the leading psychologists who believed that the behavioral development of a child conforms to the biogenetic rule. On the basis of this reasoning, some races were judged more 'childlike' than others. Thus, the concept of mental differences between human races received 'scientific' (biogenetic) backing, providing a basis for judgments regarding the value of different races. For example, 'savages' were equated with children or children with savages. Yet as soon as the 'neoteny'<sup>1</sup> of humans was taken into greater consideration, the 'higher' races were seen as the childlike. Piaget [1971] saw some parallels between the phylogeny of human behavior and the ontogeny of children's behavior, but he did not see direct causal connections between phylogeny and ontogeny, as Haeckel [1866] did in the case of anatomy. The most renowned psychologist to apply the biogenetic rule to (bio-) psychological ontogeny was Freud [1914/1953]. For example, he linked oral and anal sexuality to quadrupedal ancestry and considered neuroses as fixated ancestral characteristics.

Today, most developmental psychologists no longer see a place for the biogenetic rule in psychology [Lerner, 1976], although some do not declare any definite position on the issue and others do not give good reasons for their positions. Gould [1977], for example, is one who does not believe in behavioral recapitulation, but he does not offer substantiation for his position. In contrast, many biologists accept the rule with respect to behavioral ontogeny in animal species. The question of the validity of the biogenetic rule for psychology remains of interest, since ethological theory and data more and more frequently enter into the field of psychology [see, for example, Charlesworth et al., 1986]. The purpose of the present article is to make the argument, on the basis of data from different disciplines, that application of the biogenetic rule in ethology, developmental psychology, and developmental neurology can no longer be regarded as valid.

## Ontogeny and Phylogeny in Anatomy

Phylogeny can be seen as a sequence of progressive stages. Many fossils show characteristics which were evolutionary stages (or *metaphenes*<sup>2</sup>) for later phylogenetic characteristics. Metaphenes

usually are of adaptive value with respect to the environment of the individual. For example, in the ancestor of amphibians (an early bony fish, *Osteichthyes*), gills were breathing organs. In these fish, gills were metaphenes - they were the basis for further phylogenetic development throughout tetrapods (i.e., vertebrates with four legs).

During phylogeny, metaphenes (with an environmental or *external* adaptive value) can additionally come to have an *internal* adaptive value as stages (or *interphenes*<sup>2</sup>) necessary to induce subsequent developmental characteristics. These induced developmental characteristics are usually phylogenetically later than the inducer. In other words, during anatomical embryogenesis, early developmental stages of organs, which are homologous with phylogenetically older stages, often induce transformation into later developmental stages, homologous with phylogenetically more recent stages. Thus, many phylogenetically older stages (in Haeckel's terms, *palingenetic* characteristics) are indispensable during the physiological process of anatomical ontogeny. Without them, subsequent characteristics could not develop. Ontogeny is a hierarchical sequence involving many prerequisite formative steps. In general terms, ontogeny recapitulates the phylogeny of the species. During further phylogeny, the external (environmental) adaptive value can become lost, while the internal value as developmental inducer can remain.

## Ontogeny and Phylogeny in Ethology and Psychology

Although the biogenetic rule has certain validity for anatomy, its application to the functional development of anatomical structure (e.g., behavioral ontogeny) is invalid for the following reasons.

### (1) *Interphenes Lacking in External Adaptive Value*

If a characteristic has developed a function as an interphene during phylogeny, it can lose the original function (i.e., adaptation to the environment) that it had as a metaphene. Consider, for example, the gill arches in mammal embryos. Originally these arches developed in response to the environment. Now they are only observable as embryological interphenes necessary for the subsequent development of the auditory bones and certain laryngeal structures. They no longer have an ontogenetic gill-breathing function. Here, the interphene function appears to be the only reason that gill arches have been retained during the

---

<sup>1</sup> 'Neoteny' in its widest sense is the maintenance of juvenile characteristics in the adult. For example, in humans, curiosity is not only a juvenile characteristic but also (sometimes) one of an older person.

---

<sup>2</sup> The terms *metaphene* (phylogenetic precondition) and *interphene* (ontogenetic prerequisite carrier unit, which is homologous with an ancestral metaphene) were introduced by Riedl [1975].

phylogeny of amniotes (higher vertebrates, i.e., reptiles, birds, and mammals). The only 'burden' [Riedl, 1975] imposed on interphenes is to fulfill certain internal ontogenetic requirements. Thus, anatomical ontogeny usually recapitulates phylogenetically ancestral characteristics, not because of their original function as metaphenes, but because of their phylogenetically later function as interphenes. In view of this fact, one should not expect the function of anatomical substrata (e.g., behavior) to develop during ontogeny according to the biogenetic rule.

A contrasting example is the ontogenetic appearance and disappearance of an antiquated characteristic that functions not as an interphene but as an environmental adaptation. The (distal) tadpole tail develops because of its function in swimming and not in order to induce a subsequent characteristic. The neotenus species (i.e., species whose ontogeny terminates with sexual maturity at a larval stage of their ancestors, e.g., in the axolotl) serve as another contrasting example. Here interphenes can be retained in the adult. In addition, characteristics such as the umbilical cord are special ontogenetic adaptations (in Haeckel's terms, *caenogenetic* characteristics). In their approximate relation to the organism, they usually do not develop according to the biogenetic rule, as palingenetic characteristics do.

### (2) *Anatomical Recapitulation with Simultaneous (Parallel) Functional 'Recapitulation'*

As mentioned above, an anatomical interphene rarely shows its original (environmental) function as a metaphene. When it does, functional and anatomical ontogeny recapitulate phylogeny *simultaneously* (see point 4). In this case, the inductive carrier function is achieved by the anatomical structure itself and not by the process of functioning (see point 5). This occurrence can be illustrated by two examples. First, the symmetrical larvae of flat fishes (*Pleuronectiformes*) move like most other fish larvae. During metamorphosis, the flat fishes become asymmetrical and develop their characteristic shape as fish adapted to living on the sea floor. As a second example, in the adult lancelet (*Amphioxus*, *Branchiostoma*, a chordate) and in the larvae of lampreys (*Ammocoetes* larva or *Petromyzonta*), the endostyle serves in ingestion [Hertwig, 1906]. During the lamprey's metamorphosis to maturity, however, the endostyle becomes the thyroid gland. The endostyle was a metaphene in an adult chordate ancestor; in the lamprey larva it is an interphene. But in lampreys, during the ontogeny of the thyroid gland, the *anatomical* recapitulation has a specific and *simultaneous* equivalent in the *functional* recapitulation. Here the functions of the endostyle,

both before and after metamorphosis, are adaptive to the environment. The original metaphene function of the endostyle has remained throughout the phylogeny of the lamprey larva until the present day. The situation is similar with respect to the amphibian gills.

### (3) *Primordial Behavior without Interphene Function*

During the behavioral ontogeny of certain species (in contrast to anatomical ontogeny), only a few 'primordial' behavior patterns can be observed [Baerends, 1958; Eibl-Eibesfeldt and Wickler, 1962; Wickler, 1961a], which mostly seem to be phylogenetically more recent characteristics. On the basis of similar behavior patterns of more original (primitive) extant and related species, these primordial behavior patterns can be traced back to an archetypal form in a common ancestor, i.e., they can be recognized as homologous. The few examples cited (see below) do not suffice to support a biogenetic rule for behavioral ontogeny. Yet there is no evidence that these behavior patterns function also as interphenes during ontogeny (see point 5). During ontogeny, primordial behavior must have causes other than primordial characteristics during anatomical recapitulation (see point 4). (a) The tetrapodlike walking of certain juvenile nestling birds and of juvenile desert jerboas (*Notiosorex*) appears homologous with the way their reptile ancestors walked. However, examination shows that it is an inefficient pattern of locomotion due to the immature spatial orientation of these juveniles. (b) Generally adult arctic skuas (*Stercorariidae*; suborder gulls) do not hunt their prey themselves, but are specialized in snatching prey away from other birds. Juvenile arctic skuas, while playing, swoop down on things drifting in the sea. On this basis it has been argued that they show primordial behavior of independent food acquisition. But components of this behavior are later used by the bird in other ways and in other situations and therefore it can be seen as part of the bird's learning process. (c) Many tetrapods (e.g., reptiles) scratch their heads with their hindlegs, while their forelegs remain on the ground. Similarly, some birds scratch their heads while lowering their wings as if the wing were still a foreleg (version 1). In other species the wing remains in the resting position on the body (version 2, most likely the more recent version phylogenetically). With respect to the biogenetic rule, newly hatched birds of some species develop their head-scratching in the 'wrong' order. Some species start scratching during ontogeny with version 2 and end with version 1, but as far as known no species develops its scratching in the contrary order [Lorenz, 1937; Wickler, 1961b]. The succession of these behavioral steps apparently does not allow conclusions regarding phylogenetic emergence, as is possible in comparative anatomy. The two manners of

scratching appear to be functionally almost equivalent. (d) Young primates cling to the fur of the carrying parent. Premature and mature human babies still show the corresponding (homologous) grasping reflex [Prechtl, 1953]. This grasping reflex is an ontogenetic adaptation, i.e., a caenogenetic trait. Even though it might sometimes have little adaptive value for the human baby, it can be seen as a behavioral rudiment. With further maturation, the frontal lobe of the brain usually inhibits this reflex. In the case of neurological disturbances of the frontal lobe (e.g., in some senile atrophical processes), the grasping reflex can again be released, i.e., frontal-lobe syndrome.

#### (4) *No Subsequent Recapitulation, First of Anatomy, Then of Function*

The anatomical embryogenesis of the human brain occurs in accordance with the biogenetic rule. By birth, all parts of the brain (old and new) have developed macroscopically. The main part of the maturation of human feeling, thinking, and behavior occurs after birth, through myelination of nerve cells, growth of dendrites, and establishment of synapses (mainly on the microscopic level). Once the anatomical development of the nervous system has been completed in accordance with the biogenetic rule, a second, subsequent (not simultaneous, see point 2) period of behavioral development also following this rule appears improbable, since interphenes induce the development of anatomical structures.

A (mainly postnatal) sequence of hypothetical behavioral interphenes would have to induce, step by step, the development of macroscopic structures that had anatomically developed previously (prenatally). Thus, with respect to phylogeny, a twofold recapitulation of similar developmental levels within one individual or organ (first macroscopic anatomically, then functionally, and in both cases according to the biogenetic rule) appears impossible [Medicus, 1987]. If phylogenetically older parts of the brain mature before more recent ones, this happens because older parts are often prerequisites for the function (brain-computation) of newer ones.

#### (5) *No Behavioral Interphenes*

As could be expected from the previous points, no 'behavioral interphenes' have been identified thus far. When the function of anatomical interphenes is disturbed, anatomical malformations result [Hall, 1984; Müller, 1989]. But there are no behavioral disturbances known that have resulted from the disturbances of hypothetical behavioral interphenes. The following empirical data support this claim. (a) During ontogeny, physical restriction

of movement does not result in behavioral disturbances. For example, babies who have had their pelvises and thighs in a cast to treat congenital dislocation of the hip joint learn to walk without disturbance, despite having been in the cast for months. In birds, newly hatched chicks whose wings are strapped from hatching until the normal age of flying are still able to fly instinctively when released [Grohmann, 1939]. Simply the fact that both 'mature' non nestling birds and 'immature' nestling birds exist makes recapitulation of phylogeny unlikely to hold true for the ontogeny of ground locomotion in non nestling birds. (b) Xylocain, an anesthetizing agent, was added to the water of developing amphibians, from the earliest egg stage until the yolk sack of the larva was consumed. Because of this agent the amphibians had no sensory input and could not move. After xylocain was withdrawn, the amphibians showed no significant behavioral disturbances [Carmichael, 1926, 1927; Model et al., 1971]. (c) An ontogeny of behavior in accordance with the biogenetic rule is unthinkable in metamorphosing species. In insects, for example, grubs 'close for reconstruction' by building a cocoon (*chrysalis*), and then for many stages show no behavioral development. (d) Courtship behavior can be composed of behavioral characteristics that have different phylogenetic ages, for instance dominance and affiliative behavior [Eibl-Eibesfeldt, 1990; Medicus and Hopf, 1990]. Yet an ontogenetic recapitulation of phylogeny cannot be observed in courtship behavior. In many species courtship behavior is only performed under specific endocrinological conditions [Balthazart, 1983]. In some vertebrate species, artificial application of testosterone (a male sexual hormone) induces male courtship behavior in females, but again without an associated recapitulation of phylogeny. An imprinting on the sex partner [Lorenz, 1935] occurs in some species during early ontogeny long before the respective courtship behavior is performed. This time interval between imprinting and courtship behavior does not conform to the biogenetic rule. However, it must be admitted that exceptions to the biogenetic rule can also be observed in comparative anatomy. (e) As a final example, it is interesting to note that, at least in mammals, sensory perceptions of the environment influence the maturation of certain parts of the central nervous system in an essential and vital way [Riesen, 1960; Wiesel and Hubel, 1963]. A search for an ontogenetic repetition of the natural history of certain aspects of sensory input of the species would be absurd. Furthermore, children born deaf and blind would be unable to develop normal thinking, feeling, and behavior.

## Conclusion

In contrast to anatomical ontogeny, in the case of behavioral ontogeny there are no empirical indications of 'behavioral interphenes, that developed phylogenetically from (primordial) behavioral metaphenes. A few behavior patterns observable during ontogeny can be interpreted as phylogenetically 'primordial'. These few primordial

behavioral characteristics observable during the ontogeny of some species can be either adaptive or neutral. In the latter case, the characteristics might be byproducts of maturation of the nervous system, but, as far as is known, without (inductive) interphene function. These facts lead to the conclusion that attempts to establish a psychological theory on the basis of the biogenetic rule will not be fruitful.

## References

- Baer, K. E. v. (1828). *Entwicklungsgeschichte der Thiere Beobachtung und Reflexion* [Development of animals: Observation and reflection]. Königsberg: Bornträger.
- Baerends, G.P. (1958). Comparative methods and the concept of homology in the study of behavior. *Archives Neerlandaises de Zoologie*, 13, 401-417.
- Balthazart, J. (1983). Hormonal correlates of behavior. In D.S. Farner, J.R. King, & K.C. Parkes (Eds.), *Avian biology* (Vol. VII, pp. 221-365). New York: Academic Press.
- Carmichael, L. (1926). The development of behavior in vertebrates experimentally removed from the influence of external stimulation. *Psychological Review*, 33, 51-58.
- Carmichael, L. (1927). A further study of the development of behavior in vertebrates experimentally removed from the influence of external stimulation. *Psychological Review*, 34, 34-47.
- Charlesworth, W.R., Costall, A., & Ghiselin, M.T. (1986). Darwin and developmental psychology. *Human Development*, 29, 1-35.
- Darwin, C. (1859). *The origin of species* Reprint from 1979 (J.W. Burrow, Ed.). Harmondsworth: Penguin Books.
- Eibl-Eibesfeldt, I. (1990). Dominance, submission and love. In J.R. Feerman (Ed.), *Pedophilia: biosocial dimensions* (pp. 150-175). New York: Springer.
- Eibl-Eibesfeldt, I., & Wickler, W. (1962). Ontogenese und Organisation von Verhaltensweisen [Ontogeny and organization of behavior patterns]. *Fortschritte der Zoologie*, 15, 354-377.
- Freud, S. (1953). Three essays on the theory of sexuality. In *Standard edition of the complete psychological works of S. Freud* (Vol. VII). (J. Strachey, Ed.). London: Hogarth Press.
- Gould, J.S. (1977). *Ontogeny and phylogeny* Cambridge MA: Harvard University Press.
- Grohmann, J. (1939). Modifikation oder Funktionsreifeung? Ein Beitrag zur Klärung der wechselseitigen Beziehungen zwischen Instinkthandlung und Erfahrung [Modification or maturation of functions? A contribution to clarify the reciprocal connections between instinct and experience]. *Zeitschrift für Tierpsychologie*, 2, 132-144.
- Haeckel, E. (1866). *Generelle Morphologie der Organismen* [General morphology of organisms]. Berlin: Georg Reimer.
- Hall, B.K. (1984). Developmental mechanisms underlying the formation of atavisms. *Biological Review*, 59, 89-124.
- Hall, G.S. (1904). *Adolescence: its psychology and its relations to physiology, anthropology, sociology, sex, crime, religion and education* (2 vols.). New York: Appleton.
- Hertwig, O. (1906). *Handbuch der vergleichenden und experimentellen Entwicklungslehre der Wirbeltiere* [Manual of comparative and experimental embryology of vertebrates]. Jena: Gustav Fischer.
- Lerner, R.M. (1976). *Concepts and theories of human development* Reading MA: Addison-Wesley.
- Lorenz, K. (1935). Der Kumpan in der Umwelt des Vogels. *Journal für Ornithologie*, 83, 137-215 & 289-413. Translated in English (1957) as: Companionship in bird life. In C.H. Schiller (Ed.), *Instinctive behavior* (pp. 83-128). New York: International Universities Press.
- Lorenz, K. (1937). Biologische Fragestellungen in der Tierpsychologie [Biological questions in animal psychology]. *Zeitschrift für Tierpsychologie*, 1, 24-32.
- Medicus, G. (1987). Toward an ethopsychology: A phylogenetic tree of behavioral capabilities proposed as a common basis for communication between current theories in psychology and psychiatry. In J.R. Feerman (Ed.), *The ethology of psychiatric populations Ethology and sociobiology*, 8(3S), 131S-150S (suppl.).
- Medicus, G., & Hopf, S. (1990). The phylogeny of male/female differences in sexual behavior. In J.R. Feerman (Ed.), *Pedophilia: biosocial dimensions* (pp. 122-149). New York: Springer.
- Model, P.G., Bornstein, M.B., Crain, S.M., & Pappas, G.D. (1971). An electron microscopic study of the development of synapses in cultured fetal mouse cerebrum continuously exposed to Xylocaine. *Journal of Cell Biology*, 49, 362-371.
- Müller, G.B. (1989). Ancestral patterns in bird limb development: a new look at Hampe's experiment. *Journal of Evolutionary Biology*, 2, 31-47.
- Osche, G. (1982). Rekapitulationsentwicklung und ihre Bedeutung für die Phylogenetik. Wann gilt die „Biogenetische Grundregel“ [Recapitulation and its implications for phylogeny. When is the biogenetic rule valid?]. *Verhandlungen des Naturwissenschaftlichen Vereins in Hamburg (NF)*, 25, 5-31.
- Piaget, J. (1971). *Biology and knowledge*. Chicago: University of Chicago Press.
- Precht, R.F.R. (1953). Stammesgeschichtliche Reste im Verhalten des Säuglings [Phylogenetic relics in behavior of babies]. *Umschau*, 21, 656-658.
- Raff, R.A., & Wray, G.A. (1989). Reterochrony: Developmental mechanisms and evolutionary results. *Journal of Evolutionary Biology*, 2, 409-434.
- Riedl, R. (1975). *Die Ordnung des Lebendigen. Systembedingungen der Evolution*. Hamburg: Parey. Translated in English (1978) as: *Order in living organisms: a systems analysis of evolution*. Chichester: Wiley.
- Riesen, A.R. (1960). Effects of stimulus deprivation on the development and atrophy of the visual sensory system. *American Journal of Orthopsychiatry*, 30, 23-36.
- Wickler, W. (1961a). Ökologie und Stammesgeschichte des Verhaltens [Ecology and phylogeny of behavior]. *Fortschritte der Zoologie*, 13, 303-365.
- Wickler, W. (1961b). Über die Stammesgeschichte und den taxonomischen Wert einiger Verhaltensweisen der Vögel [About phylogeny and taxonomic value of some behavior patterns in birds]. *Zeitschrift für Tierpsychologie*, 18, 320-342.
- Wiesel, T.N., & Hubel, D.R. (1963). Effects of visual deprivation on morphology and physiology of cells in the cat's lateral geniculate body. *Journal of Neurophysiology*, 26, 978-993.

Copyright © 1992 S. Karger AG, Basel

This article is only meant for the personal use of students visiting the lecture "Introduction to Human Ethology" in Innsbruck and must not be passed on.

Der Artikel ist nur für den persönlichen Gebrauch der Studenten der Innsbrucker Vorlesung „Einführung in die Humanethologie“ bestimmt und darf nicht weitergeleitet werden.