THE REGULAR CONDENSATION OF DEVELOPMENTAL STAGES AS A MECHANISM OF THE EVOLUTION OF MAN AND CULTURE.

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ABSTRACT: The ontogenetic and phylogenetic processes of the human species are observed to form a simple unitary pattern when represented on logarithmic time scales. A mathematical analysis of this pattern has indicated that it is accounted for by a regular condensation of developmental stages such that the rate of condensation of each trait is inversely proportional to the phylogenetic age of the trait. This mechanism is compatible with the organic, cultural and scientific realms of evolution within the lineage of man. The mechanism of condensation is suggested to be the result of a selection process influencing the timing of developmental actualization of inherited genome information content as well as the rate of the child's mental maturation in connection to its acquisition of cultural traits. In this way, the model accounts for the relationship between ontogeny and phylogeny.

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Introduction

Throughout the history of biology an intriguing question has been that of the relationship between an organism's individual development, its ontogeny, and the evolutionary history of its species, its phylogeny. The historic development of this question was reviewed by Gould (1977) and Patterson (1983). Gould also attempted to elucidate the mechanism of this parallelism, an attempt further elaborated by Alberch et al. (1979), Gould (1982) and McNamara (1982). In the latter papers the mechanism is discussed in terms of heterochrony, the temporal displacement of developmental characters.

A similar phenomenon is discussed in the field of psychology. Remnants of cultural and scientific history are observed in a child's mental development. A thorough investigation of this relationship was reported by Piaget and Garcia (1983).

In the present paper, I shall try to demonstrate that the two categories of parallels, i.e. parallels within the biological and cultural realms, exhibit a common and unitary structure. As a general basis for this concept I shall refer to the wide-spread view which implies that biological and cultural evolution have in common several important features (Stebbins 1982 p. 397). Cultural evolution is thus frequently included in general surveys of evolution (Young 1981, Dawkins 1976). This analogy also includes the evolution of scientific ideas. Thus Popper (1975 p. 75) suggested science may be regarded as a means used by the human species to adapt itself to the environment and asserts a fundamental similarity of the three levels of adaptation: genetic adaptation, behavioural learning and scientific discovery.

Also Kuhn (1962 p. 172) comments upon the analogy that relates the evolution of organisms to the evolution of scientific ideas but reminds us that it can easily be carried too far. But with respect to his issue of paradigms it is, as he states, very nearly perfect.

I have observed that the ontogenetic and phylogenetic processes of man, including their organic as well as their cultural and scientific manifestations, form a simple unitary pattern when represented in a bilogarithmic diagram as illustrated in Fig. 1. The aim of this paper is to call attention to this pattern and to suggest how it may be interpreted.

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Uncertainties

The conclusions which may be drawn from the present investigation stand or fall with the interpretation of the observed data. Evolutionary concepts, however, are hard to quantify and to a large extent we are compelled to rely on subjective estimates. The present investigation does however not need a strict quantification of evolutionary traits. It is sufficient that the stages of the evolutionary and developmental processes are comparable to one another. Other investigations in the field, notably the important contribution by Alberch et al. (1979) are all based on the presupposition that comparisons of evolutionary and developmental traits are possible and meaningful.

A second problem is the uncertainty of the dating of paleontological, embryological, prehistoric and mental stages. I shall in the present investigation make rough subjective estimates of these uncertainties, indicating them as line segments connected to the points plotted in Fig. 1.

Empirical data

The vertebral column appeared with the chordates nearly 600 million years ago (Young 1981 p. 50). This is supposed to correspond in the ontogenetic process to the appearance of the first somite at the embryonic age of 20 days (Hamilton et al. 1959 p. 120).

Longmore (1971) compared the embryonic development of the heart with its evolutionary stages. He demonstrated that the twenty two day old heart harks back to that of a common ancestor which appeared about 450 million years ago (ibid. p. 52). About 220 million years ago certain members of the class Reptilia developed a true four-chamber heart (ibid. p. 56). This stage is reached by the human embryo at about the thirty second day (ibid. p. 59).

The development of the kidneys proceeds through three forms, pronephros at day 22, mesonephros at day 27 and metanephros at day 32 (Hamilton et al. 1959 p. 269 - 276). The pronephros and mesonephros are found in lampreys which originated some 450 million years ago (Young 1981 p. 84). The metanephros was developed by reptiles originating 300 million years ago (ibid. p. 284).

The lungs arose in the lung fishes about 350 million years ago (ibid. p. 221). In the human embryo the respiratory diverticulum first appears in the middle of the fourth week (Hamilton et al. 1959 p. 231).

The error in the estimates of the paleontological dates of the traits discussed so far is assumed to be ± 50 million years and that of the corresponding embryonic dates ± 5 days. These errors are indicated in two of the points in Fig. 1.

The nervous system and the brain develop continuously in both ontogeny and phylogeny and no well-defined characteristics for comparison are found. In paleontology the brain size is a frequently discussed characteristic and will therefore be discussed here in this context. Brain volume increases in both ontogeny and phylogeny in S-shaped curves. In the phylogenetic process half the cranial capacity is reached some 1.5 million years ago (Stebbins 1982 p. 336) whereas the child reaches this brain volume 6 months after birth (Montagu 1981 p. 43). No error estimates are attempted for this trait.

Lieberman et al. (1972) have compared the phonetic ability and related anatomy in the newborn and adult human, the Neanderthal man and the chimpanzee. They point out 14 specific skull features of the newborn, the chimpanzee and the Neanderthal man (La Chapell-aux Saints fossil) that are similar to each other but different to that of an adult man. Casts of the nasal, oral and laryngeal cavities of the newborn human are found to display similarities to those of the Neanderthal man and the chimpanzee whereas the adult human shows divergent features.

The authors also claim that the Neanderthal man lacked the vocal tract that is necessary for the production of the vowels /a/, /i/ and /u/, a restriction

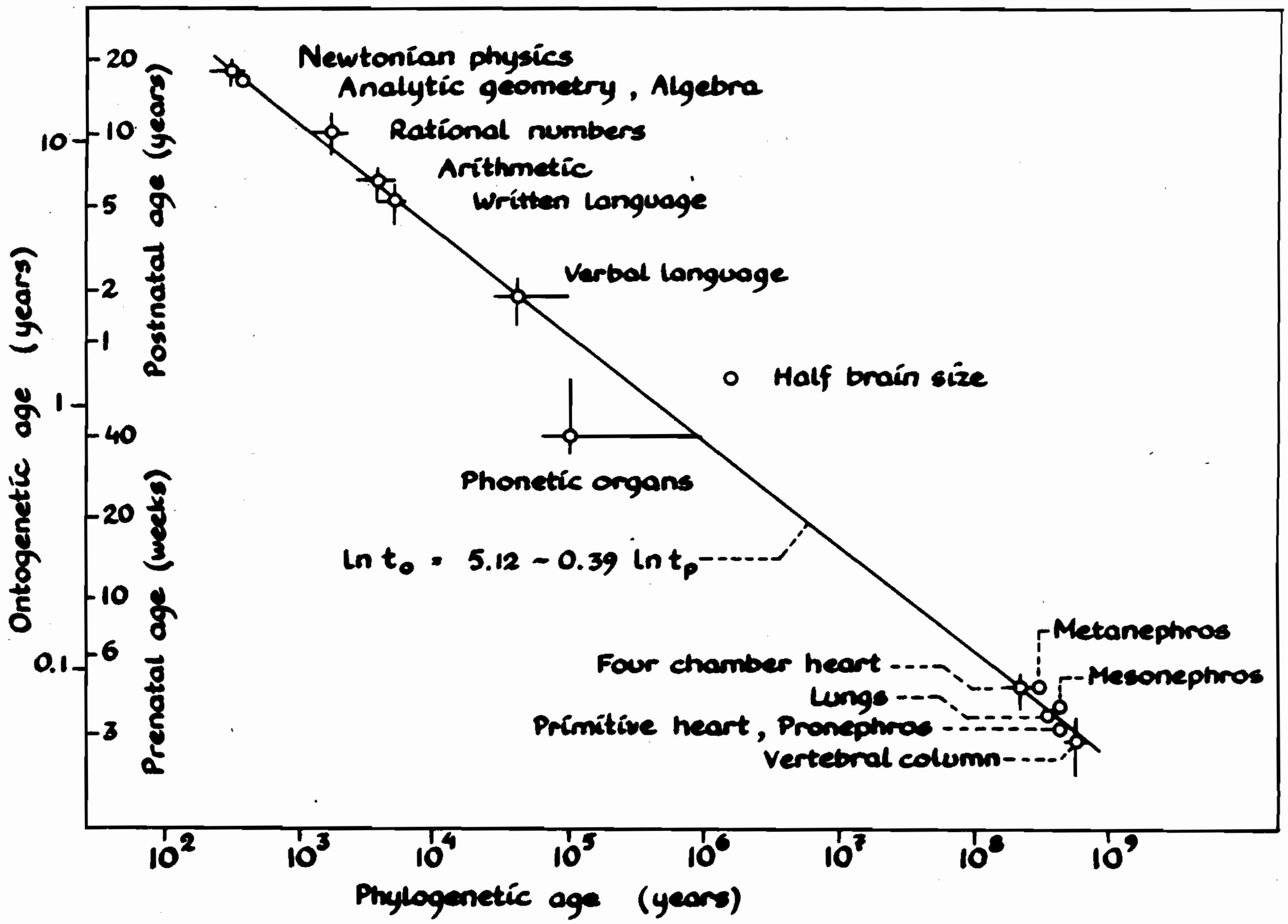

Figure 1. Diagram of ontogeny versus phylogeny in the lineage of man. The ontogenetic age, t_o, is measured from the moment of fertilization. The ordinate also gives the individual's postnatal age and fetal age. Both scales are logarithmic.

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shared by the newborn human and the chimpanzee. On this point however, the conclusions of Lieberman et al. are not accepted by other authors (Falk 1975) and therefore, for the present purpose, we may restrict our use of Lieberman's data to the specified skull features and to the cavities.

Neanderthal man existed about 100 000 years ago, and the comparisons are made with the newborn child. A point with these coordinates is plotted in the diagram. However, Neanderthal man is probably not directly related to modern man as is also pointed out by Lieberman et al. Since the chimpanzee in this respect displays features similar to those of Neanderthal man it seems probable that also other hominids, including our own ancestors, sometime in the interval between the occurrence of the chimpanzee and Neanderthal man, passed a similar stage of phonetic anatomy. This indicates that this point in the diagram should be located at a somewhat earlier phylogenetic time coordinate. The error of this trait is hard to estimate. I suggest the phylogenetic age to lie between 70 000 and 1 million years. The ontogenetic age is estimated to lie between the prenatal age of 8 months and and the postnatal age of 3 months.

As regards language development Lamendella (1976) concludes that the development of a child's language recapitulates ancestral traits in many ways.

The dating of language evolution is uncertain because of the lack of well-defined stages and of the merely indirect fossil evidence. However, according to Jaynes (1976), all indications point to the fourth glaciation during the late Pleisticene as the time during which speech evolved. This period began about 70 000 years ago and ended some 10 000 years ago.

Another estimation, based on Lieberman's investigations, was made by Fishbein (1976 p. 183). He suggested that possibly the contemporary form of language only became widespread about 40 000 years ago. According to Lamendella (1976) a child at the age of 21 months begins to acquire a communication system that qualifies as language. The last two datings are used for the point in the diagram labelled verbal language.

The uncertainty of the phylogenetic age suggests that language originated between 30 000 and 100 000 years ago. The ontogenetic uncertainty is estimated to be ± 6 months.

The use of written language first appeared in the ancient Sumerian culture 5000 (±1000) years ago. This stage is reached at the age of 5 (±1) years when the first attempts of reading and writing are made.

The Rhind Papyrus Scroll written 3700 years ago represents the oldest known document on arithmetic, a stage corresponding to an age of 6 years at which children normally begin to learn elementary arithmetic. The errors in this trait are estimated to be the same as those for written language.

As is well-known it was his expert knowledge in biology that guided Jean Piaget in his investigations on the acquisition of knowledge, on both individual and historic levels. In these studies he introduced the concept of genetic epistemology. The fundamental hypothesis of genetic epistemology is that there is a parallelism between the progress made in the logical and rational organization of knowledge and the corresponding formative psychological processes (Piaget 1970 p. 13). Piaget concludes that children are the best material for studying the development of logical, mathematical and physical knowledge.

Piaget's ideas have inspired many authors in the field of education. Thus Driver (1980) suggests that pupils in learning about the world parallel the processes scientists themselves go through.

Piaget continued these studies and, together with Rolando Garcia, he has reported a comprehensive investigation of the relationship between the child's mental development and the cultural and scientific history (Piaget and Garcia 1983). The investigation is restricted to the fields of mathematics and physics. In these fields the authors have observed surprising coincidences in method and content and very striking common features (ibid. p. 292). They conclude that their work demonstrates the role of psychogenesis and its remarkable convergence with the history of scientific thinking (ibid. p. 303). Piaget and Garcia do not make detailed temporal assertions of the coincidences discussed but nevertheless their investigation constitutes a strong general support of the present approach.

Rational numbers were introduced by Diophantus about 1700 years ago. Normally children are introduced to this type of arithmetic at the age of 10. The uncertainties are estimated to ±500 years and ±2 years, respectively.

In the history of mathematics an important step was taken by Descartes through his unification of geometry and algebra. This was 350 years ago. At about the age of 16 the basic concepts of analytic geometry are studied. The same datings can be approximately adopted for the introduction to algebra.

The next important step in the history of mathematics was the development of differential and integral calculus introduced some 300 years ago by Newton and Leibniz. Normally, the operations of derivation and integration are learned at the age of 17.

One of the most prominent paradigm shifts in the history of science is that of the Newtonian mechanics also developed 300 years ago. The stage of cognitive maturation at which Newton's concepts in mechanics are comprehended is also normally about 17.

The errors in the dating of the introduction of analytic geometry and Newtonian mechanics in the two processes are estimated to ± 100 years and ± 2 years, respectively.

A mathematical model

The traits discussed are such that the older a trait is the earlier its residual ontogenetic structure will appear during the developmental course. When these traits are plotted in a bilogarithmic diagram as shown in Fig. 1 they are found to lie near a straight line of the form

$$\ln t_o = C_2 - C_1 \ln t_p \qquad (1)$$

where t_o denotes the ontogenetic age, measured from the moment of fertilization, of each particular trait and t_p is the phylogenetic age of the trait.

Amongst the multitude of proposed evolutionary mechanisms there are two which seem to be compatible with the observed pattern. Using Gould's terminology, these are the principle of terminal addition and the principle of condensation (Gould 1977 p. 75).

The principle of terminal addition implies that, as new features are added to the end of ontogeny, the total length of the ontogeny increases whereas the length of each ontogenetic stage remains unchanged. This implies that the original length of each ontogenetic trait is such that the succession of all stages merely once forms the observed pattern and that this happens to occur just now. It thus seems improbable that terminal addition is the sole mechanism.

The principle of condensation implies that, as new traits are added to the end of ontogeny, the total length of ontogeny remains unchanged whereas each ontogenetic stage is successively shortened. In Fig.1 this means that each point drifts downwards to the right, presumably in the vicinity of the straight line. The developmental component of this displacement is what has been denoted acceleration (Gould 1977 p. 75, Alberch et al. 1979). Here, acceleration, denoted by a, is defined as

$$a = dt_o/dt \qquad (2)$$

Using the chain rule of differentiation we may write

$$a = \frac{dt_o}{dt_p} \cdot \frac{dt_p}{dt} \qquad (3)$$

and, since every trait increases its age t_p according to $dt_p/dt = 1$, one obtains

$$a = dt_o/dt_p \qquad (4)$$

Differentiation of Eq.(1) now gives

$$a = -C_1 t_o/t_p \qquad (5)$$

The acceleration of a particular stage can be considered as a result of a condensation of preceding developmental stages. Fig. 2 illuminates this concept. The figure demonstrates that the rate of condensation, q, is given by

$$q = da/dt_o \qquad (6)$$

Differentiation of Eq.(5) finally yields

$$q = -C/t_p \qquad (7)$$

where $C = C_1 + 1$.

The mathematical analysis thus implies that the observed pattern is explicable as a result of a condensation of developmental characteristics such that the rate of condensation of each trait is inversely proportional to its phylogenetic age. In spite of the fact that no information of earlier ontogenies is available I suggest as an investigative hypothesis that the suggested mechanism is a principal evolutionary mechanism that has been at work throughout the phylogenetic period comprised by the diagram of Fig. 1.

The constants C_1 and C_2 can be calculated from the straight line in Fig. 1 yielding $C_1 = 0.39$ and $C_2 = 5.12$ if time is defined in years. The acceleration and condensation can now be calculated from Eqs.(5) and (7) and, for clarity, two examples will be discussed.

The first example is the learning of Newtonian physics at the age of 17 ($t_o = 17.75$ years). The acceleration of this stage is -0.023 which implies that at present it is displaced about one year in every 40 years. The rate of condensation of the same stage is -0.005 per year. Thus this trait is at present condensed at a rate of about 5% per decade.

As a second example we may choose the onset of heart development at the embryonic age of 22 days. For this stage the present value of acceleration is found to be $-5 \cdot 10^{-11}$ or a couple of days in 100 million years. The rate of condensation of this characteristic is $-3 \cdot 10^{-9}$ per year or about 3% in 10 million years.

Due to the characteristics of logarithmic functions, it is not to be expected that Eq.(1) should be applicable to small values of t_o and t_p. It seems reasonable to assume that the applicability of the equation is restricted to the interval covered by the discussed traits. The application of Eq.(7) is also assumed not to include the most recent traits.

The mechanism of condensation alone implies, as we presumed, that the length of ontogeny is constant. This means that the embryonic period of, say, the first mammals, would be predicted to be inconceivably long. However, we may assume that terminal traits are exempted from condensation as indicated in Fig. 2. This implies, as can be seen in the figure, a certain prolongation of successive ontogenies. In the diagram of Fig. 1 this would mean that the straight line would have a somewhat lower course at earlier epochs. In other words, the constants C_1 and C_2 may be time-dependent. Since we have no information about earlier ontogenies the model can not be tested on this point. It must be emphasized, however, that a mathematical model like this one should not be carried too far. Its main merit lies in the fact that, albeit in an idealized form, it proposes strict definitions of the concepts and reveals causal and temporal relations between them which otherwise hardly would be discovered.

Discussion

A distinguishing feature of the present model is that, in spite of their greatly separated temporal regions, organic and cultural traits are aligned in a unitary pattern as demonstrated in Fig.1. This, I think, suggests the existence of a fundamental parameter of evolution common to the organic and cultural evolutionary processes. In the introduction I have referred to authors such as Popper and Kuhn who have speculated about the analogy between organic and cultural evolution. More specifically, Gatlin (1972) identified parameters common to the two realms. She showed that there are information parameters of spoken language (ibid. p. 89) and written language (ibid. p. 100) which are common to and comparable to those of the DNA molecule.

Information is coupled to complexity and, as some authors claim, also to the concept of entropy. Thus Wiley and Brooks (1982) proposed that evolution could be described in terms of entropy changes, an approach further discussed by Bookstein (1983), Wicken (1983) and Brooks et al.(1984). Thus, I think, the

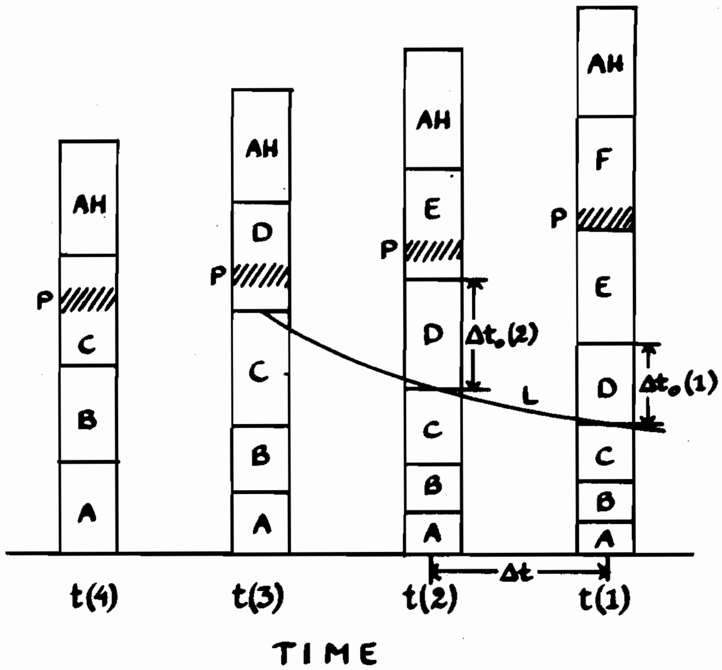

Figure 2. The diagram illustrates four ontogenies. Stage D at $t = t(2)$ has the duration $\Delta t_o(2)$, which during the interval Δt is condensed to $\Delta t_o(1)$. The relative rate of this process, condensation, is

$$q = \frac{\Delta t_o(1) - \Delta t_o(2)}{\Delta t_o(1) \cdot \Delta t} = \frac{\Delta t_o(1)/\Delta t - \Delta t_o(2)/\Delta t}{\Delta t_o}$$

Hence

$$q = \frac{da}{dt_o}$$

The acceleration corresponds to the slope of the line L. The shaded area P denotes puperty which is retarded. Stage AH denotes adulthood.

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anticipated common parameter of organic and cultural evolution may be information.

The adaptation to a changing environment and the invasion of a new ecological niche are in many cases realized by the addition of novel developmental characters. Such an addition is accompanied by an increased genome information content. We have discussed two methods by means of which the organisms cope with this situation. They may lengthen their ontogenies or they may accelerate them. As a result of the present investigation a combination of both these methods seems to be the most probable.

The proposed mechanism is explicable entirely within the concepts of neo-Darwinian theory. As regards the organic part of the developmental course each interval between the action of two consecutive regulatory genes is supposed to be subject to random variation in its length, a variation on which systematic natural selection is influencing. Regarding the mental part of the developmental course an analogous random variation in the length of each particular neural and intellectual stage is presumed as well as a systematic selection on behalf of this variation.

As a result of the selection mechanisms each stage, perhaps with the exception of the most recent, is successively condensed. The assertion that the rate of condensation for each trait is inversely proportional to the age of the trait has, as discussed above, proved capable of explaining the observed temporal correlation between ontogeny and phylogeny. The condensation of each trait gives rise to the phenomenon of acceleration. This process makes room for terminal novelties. Of course one could imagine evolutionary changes to appear at any developmental stage and not just at the end of ontogeny. However, as Maynard Smith (1983 p.41) points out, it is hard to see how viable alterations could occur except as terminal alterations or additions. Such terminal additions are in the organic realm induced by mutations and in the cultural realm initiated by intellectual innovations. These will be embedded successively in the genome of the individuals by subsequent terminal novelties. In this way information about the latter is stored in the genome of the progeny. In some instances this information is manifested in observable developmental structures and these structures thus resemble successive adult forms of precursors, a phenomenon generally designated recapitulation.

The present model thus challenges the current, wide-spread view according to which recapitulation is rejected, the concept of neoteny being regarded as the principal evolutionary mechanism. Montagu (1981 p.23) presents a list of neotenic traits the most important of which seems to be sexual maturation and the change of man's skull form. Since these traits may be regarded as contradictory to the present model they will be examined in some detail.

It has been assumed that, at the invasion of a new ecological niche, there may be selective advantage of some new characteristics. Thus let us for the moment assume that a terminal novelty is added after the main reproductive period. The selection on behalf of such a novelty would then not be a determinant of the production of offspring. Therefore, such a novelty would not be incorporated in the genome of the population. A novel trait will thus be added terminally only if the age of puperty is displaced to remain at the near-end of the developmental sequence of traits. Behavioural and cultural traits are often associated with parental care and the selection of such traits may thus be a determinant for the survival of offspring. Such traits will therefore be incorporated in the genome of the population in spite of the fact that they appear after puperty. Stage F in Fig.2 represents such a trait. As indicated in the figure, this is compatible with retarded puperty. I therefore conclude that the observed retardation of sexual maturity represents a vital facility for the incorporation of novel features in the genome of a population.

The adaptation to different ecological niches does not always require new traits. In a majority of cases, evolution proceeds through gradual changes of existing structures such as, for instance, the lengthening of the neck of the giraffe. The gradual change of man's skull form represents another example of such a process. A change of this type does not in itself necessarily increase the complexity of the system in the same sense as the four chamber heart or the ability of verbal language. Further, it is difficult to ascribe to such a trait any particular origin. Such traits are not relevant to the present model. What is claimed in the present investigation is that the mechanism of condensation will result in the observed temporal correlation between ontogeny and phylogeny only when applied to developmental traits that have once appeared as terminal, complexity-increasing novelties. Hence, recapitulation is expected to be observed only amongst such traits. This forms the principle of selection of traits applied in the present model, a principle which, it must be emphasized, is independent of the pattern claimed to be observed.

It may well be that a majority of traits are neotenic as Montagu claims but, as the present study demonstrates, a few especially important traits are not. These traits are condensed and the consequential phenomena of acceleration and recapitulation are significant for the evolutionary process towards higher degree of complexity.

There are two interpretations of recapitulation (Løvtrup 1978, Patterson 1983 p. 23). von Baerian recapitulation, which is generally accepted, is based on similarities between embryonic stages of different species. Haeckelian recapitulation, on the other hand, also acknowledges similarities between adult stages of precursors and embryonic stages of their descendents, an assertion of great controversy. Lately, genetics has entered into the focus of interest. Thus Raff and Kaufman (1983) attempted to link genetics and embryology to evolution. In the field of cultural evolution Piaget and Garcia (1983) demonstrated that the child's mental development is coupled to the history of science. However, they explicitly rejected an interpretation according to which their observations should be considered as examples of a Haeckelian ontophylogenetic parallelism (ibid. p. 80).

As an argument against recapitulation Piaget and Garcia (ibid. p. 80) assert that there is no hereditary mechanism in the field of culture. However, such a hereditary mechanism has been already discussed. Thus Dawkins (1976 p. 206) suggested cultural hereditary units to be called memes. Such hereditary units, I think, are inherent in the educational system inasmuch as teachers transfer the characteristics of preceding paradigms to their pupils.

The mechanism of condensation is considered to be a pre-requisite for the successive accumulation of novel complexity-increasing traits. Therefore, I think, the rate at which new information is incorporated in the genome is coupled to the rate of condensation. Further, since in the lineage of man the rate of condensation is found to be regular, the rate of information accumulation may also be regular. This conclusion is supported by an estimate of the number of bits of information content in genes and culture performed by Sagan (1973 p. 26). Sagan found a rough regularity of information increase when information is plotted in a diagram built on a retrospective logarithmic time scale, i.e. the same type of phylogenetic time scale as that by means of which the regular pattern of the present model was revealed.

The present interpretation is consistent with the wide-spread view according to which the direction of evolutionary change in most cases has been that towards increased complexity (Young 1981 p. 584). However, during their evolution, species seem to have deviated from the common course of increasing complexity and thus, during their ontogeny, they follow the same course of recapitulation up to the stage of their divergence into separate species. This seems to be closely related to the mechanism Løvtrup (1981) suggested to be called Spencer's Theorem. Only one species, namely that of man, persistently seems to have followed during its evolution the course of increasing complexity right up to now. On account of the present study I conclude that this evolutionary course is the specific result of the mechanism of condensation. This mechanism is based on a selection process successively influencing the timing of the developmental actualization of inherited genome information content as well as that of the child's mental maturation at its acquisition of cultural traits. The mechanism of condensation thus relates ontogeny to phylogeny and unifies the organic, cultural and scientific realms of our evolutionary history.

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