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Evolution

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The following description of evolution concentrates on an approach that most connects with comparative psychology, and therefore differs from standard accounts, which readers may like to consult for a more general picture. The entry in *Encyclopedia Brittanica* written by Sewell Wright (1965) is especially commendable. It is thought-provoking, balanced and comprehensive, running well over 12 pages of closely printed text. The present account is much more limited in scope, and is mainly concerned to bring out those areas of convergence between contemporary evolutionary theories and comparative psychology that may be fruitfully explored in future.

Lamarck, Darwin and the neo-Darwinian Synthesis

Evolution refers to the natural (as opposed to supernatural) origin and transformation of the living inhabitants of the planet earth throughout its geological history to the present day. Many have speculated on evolution since the time of the Greeks. The ideas which have come down to us, however, originate in the European Enlightenment. This period saw the beginning of Newtonian mechanics, mathematics and other modern scientific developments, including John Ray's species concept and C. Linnaeus' system for classifying organisms. The power of rational thought in science to explain the material universe presented a deep challenge to received wisdom, especially the biblical account of creation according to the Christian Church. Evolution by natural processes -- as opposed to special creation by God -- was already on the mind of most educated people. Linnaeus came to accept a limited transformation of species later in his life; other prominent figures who wrote on the possibility of evolution include the naturalist, G.L. Buffon and Charles Darwin's grandfather, Erasmus Darwin.

The first *comprehensive* theory of evolution is due to Jean Baptiste de Lamarck (1809) who was very much a product of the Enlightenment, both in his determination to offer a naturalistic explanation of evolution and in his systems approach. Thus, he dealt at length with physics, chemistry and geology before embarking on presenting evidence that biological evolution has occurred. He also suggested a mechanism of evolution, whereby new species could arise through changes in the relationship between the organism and its environment in the *pursuance of its basic needs*, which produce new modifications in its characteristics that become inherited after many successive generations.

Lamarck's theory was widely misrepresented to be merely "the inheritance of acquired characters", or caricatured as changes resulting from the "wish" fulfillment of the organism. Half a century later, Charles Darwin was to include a number of Lamarck's ideas in his own theory of evolution by natural selection. The theories of evolution and heredity are closely intertwined in their historical development. Just as evolutionists needed a theory of heredity, so plant breeders in the eighteenth century who inspired Mendel's discovery of genetics were motivated by the question as to whether new species could evolve from existing ones. In accounting for change or transformation, it is also necessary to locate where constancy or stability resides.

Darwin's (1859) theory of evolution by natural selection states that, given the organisms' capability to reproduce more of their numbers than the environment can support, and there are variations that can be inherited, then, within a population, individuals with the more favourable variations would survive to reproduce their kind at the expense of those with less favourable variations. The ensuing competition and "struggle for life" results in the "survival of the fittest", so that the species will become better adapted to its environment. And if the environment itself changes in time there will be a gradual but definite "transmutation" of species. Thus, nature effectively 'selects' the fittest in the same way that artifical selection practised by plant and animal breeders ensures that the best, or the most desirable characters are bred or preserved. In both cases, new varieties are created after some generations.

In *addition* to natural selection, Darwin invoked the effects of use and disuse, and the

inheritance of acquired characters in the transmutation of species. It is clear, however, that those Lamarckian ideas do not fit into the theory of natural selection, and Darwin's followers all regard the lack of a theory of heredity and variation as the weakest link in the argument for natural selection. When Mendelian genetics was rediscovered at the turn of the present century and Weismann identified the material basis of heredity as the "germplasm" in germ cells which became separate from the rest of the animal's body in the course of early development, it seemed to offer a perfect explanation of how Mendelian genes could be passed on unchanged from one generation to the next. Darwinism was promptly reinterpreted according to the gene theory in the 'neo-Darwinian synthesis' from the 1930s up to the 1950s and 60s. This coincided with an extremely productive and exciting period in the history of biology as the gene theory itself continued to inspire a series of discoveries that culminated in the DNA double helix and the genetic code.

The neo-Darwinian synthesis began with the mathematical representation of genes in populations and in plant breeding (biometrical genetics), which, together provide a rigorous theory of Darwinian natural selection in terms of genes for both discontinuous and continuously varying characters. Systematics and paleontology for their part, defined phylogenetic relationships and 'adaptive radiations' of the major groups in accordance with Darwin's dictum of 'descent with modification'. At the same time, the detailed study of chromosomes together with mutational and other cytogenetic analyses eventually clarified the molecular basis of Mendelian genes, which are located to linear arrays on chromosomes. Heritable variations are generated by random mutations in these genes, different forms (alleles) of which are subject to natural selection via the different characters they determine, As the genes, according to Weismann, are insulated from environmental influences, they are passed on unchanged to the next generation, except for rare random mutations.

With the identification of DNA as the genetic material and the cracking of the genetic code in the 1950s and 60s, the 'central dogma' of molecular biology came to be accepted by most biologists. It states that the sequence of bases in each DNA is faithfully transcribed into RNA, and the RNA translated into a specific sequence of amino-acids of a protein in a one-way information flow; and no reverse information-flow is possible. This strengthens "Weismann's barrier", which is supposed to strictly forbid environmental influences, or any experience in the life-time of the organism to directly, i.e., predictably, affect its genes. In the new orthodoxy which reigned over the next 20 years, the organism tended to be seen as no more than a collection of genes, its development, the unfolding of a 'genetic programme' encoded in the genome. Random mutations give rise to mutant characters and natural selection allows the fittest mutants to survive and reproduce. Environmental changes give new selective forces and evolution is thereby guaranteed. Dawkins (1976) has pushed this reductionistic trend to its logical conclusion in proposing that organisms are automatons controlled by 'selfish genes' whose only imperative is to replicate at the expense of other 'selfish genes'. E.O. Wilson (1975) extended neo-Darwinian theory to animal and human societies to define the new discipline of sociobiology, which poses the paradoxical question (i.e., paradoxical *within* neo-Darwinism): how could altruistic behaviour evolve (given that genes, and the behaviour they control are fundamentally selfish)?

This paradox disappears, of course, when one rejects the ungrounded assumption that selfishness or competitiveness is fundamental to the living world. Animals engage in competitive or aggressive acts, but that does not mean there are inherent qualities of

competitiveness and aggressiveness which can account for those acts. Furthermore, examples of cooperation among animals far outstrip those of competition. Kropotkin (1914) has given abundant evidence of the natural sociality of all animals which is independent of genetic relatedness. Thus, one could invert E.O. Wilson's question and ask, why do animals compete, given their natural sociality? This highlights the sociopolitical underpinnings of all scientific theories. Darwinism is no exception, for it is all of a piece with the Victorian English society preoccupied with competition and the free market, with capitalist and imperialist exploitation.

Darwin and Lamarck, The Genetic versus the Epigenetic Paradigm

History has the habit of creating heroes and anti-heroes, and so Darwin triumphed while Lamarck bore the brunt of ridicule and obscurity. The reason is that the theories of the two men are *logically* diametrically opposed. Darwin's theory is natural *selection*, and selection entails a separation of the organism from its environment. The organism is thus conceptually closed off from its experience, leading logically to Weismann's *barrier* and the central dogma of the genetic paradigm, which is reductionistic in intent and in actuality. Lamarck's theory, on the other hand, is of *transformation* arising from the organism's own experience of the environment. It *requires* a conception of the organism as *open* to the environment -- which it actually is -- and invites us to examine the dynamics of transformation, as well as mechanisms whereby the transformation could become 'internalized'. Hence it leads logically to the epigenetic approach, which embraces the same holistic, systems thinking that Lamarck exemplifies (Burkhardt, 1977).

The Genetic Paradigm and neo-Darwinism

Neo-Darwinism is a theory based on genes, G.C. Williams (1966) states explicitly, ". . . In explaining adaptation, one should assume the adequacy of the simplest form of natural selection, that of alternative alleles in Mendelian populations." (p.4) Natural selection on alternative alleles can only be a valid description of reality when the following abstractions of the genetic paradigm are assumed to be true: **(a)** genes determine characters in a straightforward and additive way, **(b)** they are stable and, except for rare random mutations, are passed on unchanged to the next generation, and **(c)** there is no feedback from the environment to the organism's genes. All three assumptions have been demonstrated to be false.

Assumption **(a)** was known to be false since the beginning of the neo-Darwinian synthesis, and to some of the most prominent 'architects' of the grand synthesis such as Sewell Wright (1969; 1978) and Ernst Mayr (1963). Wright argues that *selection relates to the organism as a whole, or to the social group, not to single genes except as a net resultant*. He saw that the major source of variability is in the recombination of already existing genes into a great number of different genotypes, many of which would occupy equivalent "adaptive peaks" in a "fitness landscape". Mayr, on the other hand, insists that natural selection acts on "co-adapted gene complexes" as a whole, and remains highly critical of 'beanbag

[population] genetics' such as that of R.A. Fisher (1930) and J.B.S. Haldane (1932), which deals with selection of single genes. However, that still leaves both the "fitness landscape" and the "co-adaptive gene complex" undefined, and with little impact on the study of evolution in the mainstream, where it is customary to identify a character, then assume there is a hypothetical gene (or set of genes) responsible for it, which may be selected in isolation from everything else.

Critics point out that the mapping between genes and the organisms' characters (phenotype) in development is nonlinear and non-additive (as it would already be when one takes Wright and Mayr seriously), and that the organism as a dynamical system is subject to universal generative principles not immediately dependent on the genes. Neo-Darwinists counter that these are only "developmental constraints" which limit, to some extent, the action of natural selection, but that natural selection still plays the creative role in evolution (Bonner, 1982). There have been serious attempts to use developmental findings to trace phylogenetic relationships (Humphries, 1988; Wake, 1990; D.B. Wake, 1991) although the theoretical relationship between ontogeny and phylogeny is still not adequately understood by most systematists (Ho, 1988a; Wake, 1994).

Assumptions **(b)** and **(c)** effectively separate the organism from the environment, which has the role of the 'selector'. Of course, most people accept that the environment also interacts with the organism, causing changes in its characteristics. However, it is supposed that the environment as 'interactor' can be neatly separated from the environment that selects, for so long as the germline genes are stable, and do not change with the environment, then it is irrelevant how the rest of the body is affected. As only the genes are passed on in evolution, it also means that evolution is separate from development. Maynard Smith and Holliday (1979) have indeed declared that the gift of Weismannism to evolutionary (i.e., neo-Darwinian) theory is that development can be safely ignored. As we shall see, these assumptions are no longer tenable.

The demise of the genetic paradigm and revival of the epigenetic approach

The assumptions that genes are stable, and that they are insulated from environmental influences, are pivotal to the genetic paradigm and neo-Darwinian theory. They were inspired by Weismann's theory of the germplasm which, however, has been flawed from the start. Plants do not have separate germ cells at all, for every somatic cell is potentially capable of becoming a germ cell, and that is why plants can be propagated from cuttings. Most animals also do not have germ cells that separate from the rest of the body early in development (Buss, 1987). Furthermore, there is no evidence that the genes in germ cells are stable, or immune from environmental influences once they have separated from the rest of the body. Evidence that genes are neither stable nor immune from direct environmental influence has been accumulating over the past 20 years in the findings of molecular genetics. They reveal hitherto unsuspected complexity and dynamism in cellular and genic processes involved in gene expression, many of which serve to destabilize and alter genomes within the lifetime of all organisms (Steele, 1979; Pollard, 1984; Ho, 1987; Rennie, 1993). This is in direct contradiction to the static, linear conception of the central dogma that previously held sway.

A complicated network of feed-forward and feedback processes has to be traversed just to express one gene or synthesize a single protein (reviewed by Rennie, 1993; Kendrew, 1995). For a gene is not a continuous sequence of DNA which can be transcribed and translated mechanically with fidelity. It is actually interrupted in many places, and the bits must be properly joined together in order to make a functional protein. Instead of a linear causal chain between DNA and protein, there is a bewildering profusion of other proteins regulating transcription, and alternative starts and stops are often involved just to produce the RNA, which is then subject to a vast array of alternative choppings and changings or further editing by yet other proteins, before it is ready to be translated. Translation is similarly subject to its own batallion of regulatory factors, and the genetic code itself can be recoded or read in alternative ways by the cellular machinery to make the protein. After that, a spectrum of post-translational processings intervene before the finished product is ready for transport to its final destination accompanied by still other proteins acting as 'chaperones'. It is clear that no gene ever functions in isolation. It becomes increasingly difficult to define and delimit *a* gene, as multitudinous causal links criss-cross and interramify throughout the entire epigenetic net, ultimately connecting the expression of each gene with that of every other.

The genome itself is embedded within the epigenetic net, and is far from stable or insulated from environmental exigencies. A large number of processes appear to be designed especially to destablize genomes during the life-time of all organisms, so much so that molecular geneticists have been inspired to coin the descriptive phrase, "the fluid genome". Mutations, insertions, deletions, amplifications, rearrangements, recombinations, gene-jumpings, and gene-conversions keep genomes in a constant state of flux in evolutionary time (Dover and Flavell, 1982). Genes are found to jump between species that do not interbreed, being carried by mobile genetic elements, viruses or microorganisms, which can exchange genes at a prolific rate, as witnessed by the rapid horizontal spread of antibiotic resistance in bacteria. Parasites that infect more than one species are also vectors for horizontal gene transfer. A particular genetic element -- the P-element -- has spread to all species of fruitflies in the wild within the span of less than 50 years, probably carried by a parasitic mite (Rennie, 1993). These 'fluid genome' processes are by no means entirely stochastic or meaningless, but are subject to physiological and cellular control. Gene jumping, recombination and other alterations of the genome are frequent responses to stress or starvation in non-dividing cells that enable them to adapt or adjust to new situations.

Similarly, cellular processes regularly inactivate whole batteries of genes by chemically marking them during normal development, or imprint them with binding proteins that alter the expression of the genes (Sapienza, 1990). Some of these marks and imprints are created early in development and may be passed on to the next generation via the germ cells. These instances of 'epigenetic inheritance' already constitute a substantial body of literature (comprehensively reviewed by Jablonka and Lamb, 1995).

Epigenetic inheritance is just one aspect of the (previously forbidden) reverse information flow -- from the environment to the genomes -- of which there is now abundant evidence. The genomes of higher organisms contain a high proportion of both functional and nonfunctional (pseudo)genes that have arisen by reverse transcription of processed and mutated RNA sequences back to DNA which is then re-inserted into the germline genome. This process was predicted long ago by Nobel laureate, Howard Temin (1971), who discovered the reverse transcription enzyme in a large class of RNA retroviruses that are

related to the mobile genetic elements present in all genomes. The immune system may be particularly active in using this mechanism to incorporate, into the germline, new antibody genes that have been generated by mutations in somatic cells during immune responses against foreign antigens (Rothenfluh and Steele, 1993).

Despite the correlation of genetic changes with physiological or cellular states, many still regard these genetic changes to be the result of random mutations which are then subject to internal or external selection. 'Internal' selection is merely another name for physiological interactions that ultimately give the required change, which is often highly predictable and repeatable. Plants exposed to herbicides, insects to insecticides and cultured cells to drugs, are all capable of changing their genomes repeatably by specific mutations or gene amplifications that render them resistant to the noxious agent (Pollard, 1988). Starving bacteria and yeast cells respond to the presence of (initially) non-metabolizable substrates by greatly enhanced, specific mutational changes in the required enzymes compared to other 'non-selected' enzymes. They are hence referred to as "directed mutations" (Foster, 1992; reviewed by Symonds, 1994). Finally, selection in any form has been ruled out in the predictable and repeatable genetic changes which occur simultaneously and uniformly in *all* the cells of the growing meristem in plants exposed to fertilizers, which are then stably inherited in subsequent generations (Cullis, 1988). The genetic paradigm has collapsed under the weight of its own momentum in the burgeoning new genetics. With the demise of the genetic paradigm, neo-Darwinian theory has likewise lost its foundation.

Beginning in the early 1970s and just before the recent revelations in molecular genetics, there has already been a general revival of the epigenetic approach. This comes from workers in divers disciplines, all focussing on the development of the organism as the key to understanding evolution (Lovtrup, 1974; Gould, 1977; Ho and Saunders, 1979; 1984; Alberch, 1980; Webster and Goodwin, 1982). Many share Lamarck's holistic conception of the organism developing and evolving in concert with its ecological (biosocial and physicochemical) environment; a few even recognized that the mutual feedback interrelationships between organism and environment may extend to directed genetic changes. The new genetics seems to bear out Lamarck's basic propositions, although the precise cellular or epigenetic mechanisms mediating non-random, directed genetic changes are not yet understood.

Epigenetic Theories of Evolution

There are a number of different epigenetic theories of evolution, some predating the neo-Darwinian synthesis. One common starting point for all epigenetic theories is the developmental flexibility of all organisms. In particular, it has been observed that artificially induced developmental modifications often resemble (*phenocopy*) those existing naturally in related geographical races or species.Thus, it seems reasonable to assume that evolutionary novelties first arose as developmental modifications which somehow became stably inherited (or not, as the case may be) in subsequent generations.

An early proponent of an epigenetic theory was Baldwin (1896) who suggested that modifications arising in organisms developing in a new environment produce "organic

selection" forces which are internal to the organism, and which act to stabilize the modification in subsequent generations. Another notable figure was Richard Goldschmidt (1940), who questioned the orthodox neo-Darwinian account that new species originate as the result of the accumulation, by natural selection, of small single gene effects over geological time, for he saw abundant evidence of 'unbridgeable [genetic] gaps' between natural species. He proposed therefore, that evolutionary novelties arise from time to time through *macromutations* producing "hopeful monsters" that can initiate new species. In his defence, he was at pains to point out that monsters are hopeful because of the inherent *organization* of the biological system that tends to 'make sense' of the mutation. More recently, Lovtrup (1974) advocates a similar theory of evolutionary novelties, or major phyletic groups, coming into being by macromutations.

One important reason for focussing on development is that developmental changes are far from random or arbitrary (Ho and Saunders, 1979; 1984; Alberch, 1980; Webster and Goodwin, 1982). Instead, they are determined by the dynamics of developmental (epigenetic) processes which are amenable to mathematical description. The set of possible transformations is highly constrained so that particular transformations may be predictably linked to specific environmental stimuli. This is the basis for 'structuralism in biology' (Webster and Goodwin, 1982; Lambert and Hughes, 1984; Goodwin *et al*, 1989), or 'process structuralism' (Ho and Saunders, 1984; Ho, 1988a) which proposes a rational taxonomy of biological forms and a natural system of classification based on the dynamics of processes that generate the forms (Ho, 1990; Ho and Saunders, 1994). The dynamics of the processes are themselves subject to contingent complexification in the course of evolution, by virtue of the lived experience of the organisms themselves. We cannot go into details about that here, except to point out that directed genetic changes in given environments are proving to be just as nonrandom as morphological changes, and hence, possibly subject to comparable systemic constraints (Ho, 1987).

Waddington's theory of genetic assimilation

The most influential recent figure among the 'epigenetic evolutionists' is Waddington (1957), who attempted to accommodate 'pseudo-Lamarckian' phenomena within neo-Darwinism in his theory of genetic assimilation. Like all Darwinian and neo-Darwinian evolutionists, he wanted to explain the origin of *adaptive* characters, i.e., characters that seem to be fitted to the functions they serve.

First, Waddington conceptualizes the flexibility and plasticity of development, as well as its capacity for regulating against disturbances, in his famous 'epigenetic landscape' -- a general metaphor for the dynamics of the developmental process. The developmental paths of tissues and cells are seen to be constrained or *canalized* to 'flow' along certain valleys and not others due to the 'pull' or force exerted on the landscape by the various gene products which define the fluid topography or structure of the landscape (Fig. 1). Thus, certain paths along valley floors will branch off from one another to be separated by hills (thresholds) so that different developmental results (alternative attractors) can be reached from the same starting point. However, some branches may rejoin further on, so that different paths will nevertheless lead to the same developmental result. Genetic or environmental disturbances

tend to 'push' development from its normal pathway across the threshold to another pathway. Alternatively, other valleys (developmental pathways) or hills (thresholds) may be formed due to changes in the topography of the epigenetic landscape itself.

The importance of the epigenetic landscape is that its topography is determined by *all* of the genes whose actions are inextricably interlinked, and is not immediately dependent on specific alleles of particular genes (Ho and Saunders, 1979). This is in accord with what we know about metabolism and the epigenetic system, particularly as revealed by the new genetics. Hence, it has evolutionary consequences other than those predicted by the selection of individual genes. The epigenetic landscape captures the complex nonlinear dynamics of the developmental process, which has been explored mathematically in greater detail since, and its evolutionary consequences made explicit (Saunders, 1992). For example, it accounts for 'punctuated equilibria' (Eldredge and Gould, 1972) -- the observation in the fossil record of evolutionary stasis over long geological periods punctuated by the sudden appearance of new species or of rapid morphological change. It also shows how large organized changes can occur with a relatively small disturbance, or how continuously varying environmental parameters can nevertheless precipitate discontinuous phenotypic change.

Thus, when a population of organisms experience a new environment, the following sequence of events may take place.

a. A novel response arises during development in *a large proportion of* the organisms in a population exposed to a new environmental stimulus.

Because the topography of the landscape is not the property of specific alleles of individual genes but the collective property of all the genes, it is expected that a large proportion of the population will respond. This corresponds to the normal developmental pathway being 'pushed' over a threshold, or a new pathway appearing by a change in topography of the epigenetic landscape.

b. If this response is adaptive, then there will be natural selection for its "canalization", i.e. it deepens in intensity and becomes regulated so that a more or Iess uniform response results from a range of intensity of the environmental stimulus. This involves a change in the epigenetic landscape so that the valley constraining the new developmental path deepens and regulates against disturbances.

c. After some generations, the response becomes genetically assimilated, in that it arises even in the absence of the stimulus. This would entail a further change in the topography to bias the original branch point in favour of the new pathway, so that the new phenotype will persist in the absence of the environmental stimulus.

Waddington was not very specific as to the mechanisms involved either in canalization or in genetic assimilation, except to argue that because they are advantageous there would be selection for them presumably through suitable "modifier" genes, i.e., genes which modify the expression of the character (or the topography of the epigenetic landscape). He and his colleagues have carried out experiments showing that artificial selection for the new character could result in canalization and genetic assimilation.

Ho *et al* (1983) questioned the assumption that genic selection is necessary for canalization and genetic assimilation, and in a series of experiments, demonstrated that heritable cytoplasmic effects may be involved in canalization in the *absence* of selection *for* the new character. Heritable cytoplasmic effects were first demonstrated by Jollos (1921) early this century. Developmental biologists are also familiar with observations indicating that changes in cytoplasmic organization could be stably inherited independently of nuclear or cytoplasmic DNA (Malacinski, 1990). Recently, Chow *et al* (1994) demonstrated that heritable cytoplasmic effects are induced by a low serum culture medium which predispose entire populations of cultured cells to malignant transformation in subsequent generations. However, these studies do not give any clue to the mechanisms involved in cytoplasmic effects. Cytoplasmic effects may be due to a dynamic equilibrium of genic and cellular processes (a cellular or gene expression state) that is a property of the *whole* system, in which case, they may prove elusive to conventional methods that attempt to identify single, localized molecular causes. They may involve (many) genes being marked and other epigenetic inheritance of varying memory spans, as Jablonka and Lamb (1995) suggest.

Heredity and evolution in the light of the new genetics

How should we see heredity in the light of the new genetics? If the genome itself is so dynamic and fluid, where does heredity reside? It is clear that heredity does not reside solely in the DNA of the genome. In the first instance, it resides in an epigenetic cellular state -- a dynamic equilibrium between interlinked genic and cellular processes. But even that is an abstraction and reification. It cannot be assumed that heredity is exhausted at the boundary of cells or organisms. For as organisms engage their environments in a web of mutual feedback interrelationships, they transform and maintain their environments which are also passed on to subsequent generations as home ranges and other cultural artefacts (Oyama, 1986; Gray, 1988). Embedded between organisms and their environment are social habits and traditions, an inseparable part of the entire dynamical complex that give rise to the stability of the developmental process, and which we recognize as heredity (Ho, 1988b). Heredity is thus distributed over the whole system of organism-environment interrelationships, where changes and adjustments are constantly taking place, propagating through all space-time scales in the maintenance of the whole, and some of these changes may involve genomic DNA. Thus, the fluidity of the genome is a *necessary* part of the dynamic stability, for genes must also be able to change as appropriate to the system *as a whole*.

What implications are there for evolution? Just as interaction and selection cannot be separated, so neither are variation (or mutation) and selection, for the 'selective' regime may itself cause specific variations or 'adaptive' mutations. The organism experiences its environment in one continuous nested *process*, adjusting and changing, leaving imprints in its epigenetic system, its genome as well as on the environment, all of which are passed on to subsequent generations. Thus, *there is no separation between development and evolution*. In that way, the organism actively participates in shaping its own development as well as the evolution of its ecological community.

While the epigenetic approach fully reaffirms the fundamental holistic nature of life, it can give no justification to *simplistic* mechanistic ideas on arbitrary effects arising from use and disuse or the inheritance of acquired characters. Organisms are above all, complex, nonlinear dynamical systems (Saunders, 1992), and as such, they have regions of stability and instability that enable them to maintain homeostasis, or to adapt to change (or not as the case may be). The appearance of novelties and of mass extinctions alike in evolutionary history are but two sides of the same coin, we cannot be complacent about the capacity of organisms to adapt to any and all environmental insults that are perpetrated. The dynamics of the developmental process ultimately holds the key to heredity and evolution, in determining the sorts of changes that can occur, in its resilience to certain perturbations and susceptibility to others.

Genetic and epigenetic paradigms in the study of behaviour

We are now in a position to examine the parallels in the study of animal behavior, where a similar divide between the genetic and epigenetic paradigms occurs. In the classical view due to Lorenz (1965), which is shared to some extent by Tinbergen (1963), the development of behaviour consists of a largely autonomous sequence of maturation of central neural mechanisms controlling the animal's behavioural repertoire. The environment, insofar as it enters in development, does so in the form of specific stimuli serving to release preformed patterns of behaviour from central inhibition. A strict dichotomy is thereby maintained between the 'innate' and 'acquired' components of behaviour, the 'innate' being equated with species-typical or instinctive behaviour. This fits easily within the genetic paradigm in terms of genes controlling behaviour in a more or less straightforward and mechanical manner. Much of the theorizing in sociobiology is based on just such an assumption, despite apologies to the contrary. In opposition to the theory of Lorenz, comparative psychologists such as Lehrman (1956) and Schneirla (1965 ; 1966), have shown that the 'innate' and 'acquired' are inextricably confounded. And that applies even to so-called instinctive behaviour.

In a classic study on the chick, Kuo (1966) showed how the embryonic heartbeat is instrumental in stimulating and entraining the raising and lowering of the head (resting on the heart), whose movements extend to the beak opening and closing, then to swallowing the amniotic fluid later on. The embryo not only develops an integrated sense of itself, but also a series of coordinated movements that are the tangible precursor of so-called instinctive behaviour. Similarly, Gottlieb (1963) showed how isolated wood ducklings learn to recognize the call of its conspecifics at hatching simply through hearing its own call while still in the egg. Thus, there is no preformed set of behaviour encoded in the genes waiting to be released. Even an isolated animal is subject to self-stimulation arising from its own activities beginning early in embryogenesis, which in turn generates complex behavior. (This demonstrates the fallacy of isolation experiments that are still carried out by ethologists and sociobiologists to-day in an attempt to prove that particular behaviours are innate or instinctive.)

The aim of comparative psychology, according to Schneirla, is to discover the similarities *and differences* between phylogenetic levels in how behavior is organized. This requires careful studies on the ontogeny of species-typical behaviour which deal with the problem of organization. Maturational (biological) processes are inextricably linked with the experiential, each in turn defining and transforming the other. Through the interplay of maturational and experiential processes, the physiological and 'meaningless' become psychological and meaningful by social reinforcement. There is thus a continuum linking the genetic/metabolic with the social and pyschological. A full understanding of how organisms evolve must ultimately take on board the whole spectrum of interrelationships (Tobach and Greenberg, 1984; 1988).

Comparative psychology is thoroughly epigenetic in its holistic attention to many levels of living organization, and its emphasis on how complex behaviour is *generated* during development through the *formative* influence of experience. Recently, Gottlieb (1992) has extended comparative psychology to consider how new behaviour defines new functions, and hence, new morphologies in evolution. This same step has been taken by developmental psychologist Piaget some years ago.

Piaget (1979) rejected the idea that there is an innate cognitive structure which allows us to make sense of reality. Instead, much of his prodigious volume of work is devoted to showing how cognitive abilities are developed through the child's own activities in exploring and experiencing the world. One of his preoccupations in biology is to undertand why form is so-well suited, or adapted to the 'function' it serves. In his last works, Piaget (1979) returned to the study of biology in order to consider the evolutionary problem which he regards as insoluble within the neo-Darwinian framework: how is it that the form of an organ is invariably accompanied by the behavioural repertoire appropriate to its use? It stretches credulity to imagine, for example, that the woodpecker first got a long beak from some random mutations followed by other random mutations that made it go in search of grubs in the bark of trees. The only explanation for this coincidence of form and behaviour in the execution of function is that the two must have evolved together through the organisms' experience of the environment.

Experience, as we have seen, never involves the organism in a purely passive role. Organisms generally *act* (more than just *behave*) so as to give themselves the greatest chance of survival. This is brought about by various means ranging from avoidance reactions in unicellular organisms to the purposive or directed explorations of higher organisms. Thus, a change in habit may be the efficient cause of the change in form, which in turn accounts for the fit between form and function. If it is true that organisms generally act so as to maximize their prospects for survival, it follows that the resulting modification of form will most likely be 'adaptive'. The 'adaptation' will involve feedback effects on its physiology, which include changes in gene expression, or in the genes themselves. On the other hand, organisms may also act and develop 'maladaptively', as human beings, in particular, seem capable of doing.

The epigenetic approach, dynamic holism and the new organicism

The epigenetic paradigm which encompasses both comparative psychology and biology may be broadly characterized as follows:

1. Development occurs by epigenesis, in which the experience of the organism's environment enters as necessary *formative* influences, there being no preformation or predetermination in the genes.

2. Evolutionary changes are initiated by developmental changes.

3. These developmental changes are non-arbitrary, being determined by the dynamics of the epigenetic system itself.

4. Developmental changes may be assimilated into the new organism/ environmental system as a whole, which set the parameters for further evolution.

5. Epigenesis mediates between the biological and social levels serving to integrate the two into a structural and functional whole.

6. Development and evolution are continuous, with the organism participating in shaping its own developmental and evolutionary history.

Schneirla shared obvious sympathies with the work of epigeneticists such as Waddington, Kuo, and Lehrman. However, he chose to refer to his own approach as "dynamic holism", with emphasis on the concept of 'integrative levels': the idea that there are behaviors or activities specific to levels of integration which cannot be reduced to the components at a lower level. For example, Schneirla (1966) points out that ants are capable of situation-specific behavior which gives rise to the *social* level of organization, while mammals exhibit an integrative solution of problems which is characteristic of the *psychosocial* level of organization. This recognition of level-specific phenomena does not imply a separation of distinct, disconnected levels. On the contrary, it acknowledges the continuity between them and behoves us to pay attention to all levels and their interconnections.

In reaction to the recent spread of neo-Darwinian genetic determinism into the social sciences, many sociologists and psychologists have argued that the social and psychological are separate and independent of the biological. I have shown how neo-Darwinian genetic determinism is no longer tenable within biology, while an alternative approach explicitly recognizes the mutually dependent, mutually defining and transforming relationship between the biological and the psychosocial.

The epigenetic paradigm has transformed into a contemporary movement in what I shall refer to as the 'new organicism'. It attempts to connect biology with non-equilibrium physics, chemistry and mathematics, offering greater precision to ideas of living organization, of organic wholeness and complexity (Nicolis and Prigogine, 1989; Saunders, 1992; Ho, 1993; Kaufman, 1993; Goodwin, 1994). In particular, the organism is seen as a *coherent* domain thick with activities over all space-time scales which are interlocked and intercommunicating; hence the organism itself has no levels nor *preferred* levels (Ho, 1993), 'levels' being our own construct for making sense of the entangled whole. A new alliance between psychology and organicist biology is timely in presenting a picture of evolution that is consonant with empirical findings as well as with our deepest experience of nature's unity.

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Figure 1. The epigenetic landscape.

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