

## **The concept of homology in the development of behavior**

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I study the development of human handedness - a species-typical behavior pattern that exhibits similarities across species (in the form of preferred limb-use) and similarities across development within an individual. Handedness is associated also functional differences (associated with the control of speech and visual-spatial skills) between the cerebral hemispheres in humans. Handedness is also an aspect of the functional differences between the hemispheres. I depend on the concept of homology when I extrapolate from the neural mechanisms involved in the control of limb use in certain model animals (chimpanzee, rhesus monkey, rat, and mouse) to differences in how the preferred and non-preferred hand are controlled in humans. Thus, I infer from the structures involved in controlling hand use in specific primate models that these same structures are involved in controlling hand use in humans. My intention in this essay is to examine the use of the concept of homology in the study of the development of human handedness. To do so, I will need to sketch the history of the concept of homology and its companion concept analogy, the role of these two concepts in systematic and developmental biology, and finally the use of homology in the Ethological study of animal behavior. Each of these sketches will reveal the problems encountered with the homology concept. Nonetheless, I will argue that developmental biology can serve as a frame for generating important questions for behavioral development (especially human behavioral development) that have not been employed by developmental psychologists.

Toward the end of this essay, I will attempt to provide answers to the challenge questions posed by the hosts for this workshop: How might developmental psychologists use the homology-analogy distinction that has proven so useful to biologists? How might we determine if a characteristic present in adults is homologous—or merely analogous—to a characteristic present earlier in development? How can we use the concept of homology to help developmental psychologists formulate novel, empirical research questions? With my answers to these questions, I hope to convince the reader that these questions will not be easily answered.

### **Concept of Homology**

The concept of homology was proposed originally by Owen in the 19<sup>th</sup> C as part of a debate about the classification of species (Gilbert and Epel, 2009). During the 18<sup>th</sup> and 19<sup>th</sup> C, the classification of animals and plants was divided by two major approaches: one approach was represented by the work of Saint-Hillaire and later Owen, who classified species according to a notion of “unity of type” (i.e., similarities among organisms that were believed to reflect the idealized forms upon which the Creator designed individual species). Thus, Owen’s original notion of homology was that it represented those similarities across the variation of species’ forms that reflected an idealized form (a Platonic ideal). The other approach to classification, represented by Cuvier and Bell, focused on differences in form across species because these differences reflected how each species was matched to the conditions of existence (adaptation). Both of these positions represented a desire to create higher order classifications of species (i.e., genera, family, class) that were not simply the products of human decision making. As Griffiths (2007) has noted, a science appears to be valid if the inferences that it draws are “based on categories that correspond to some inherent structure in the subject matter – not the whim of the person who creates the category”. Natural science seeks natural categories.

During the 18<sup>th</sup> and 19<sup>th</sup> C, it was generally believed that species were natural units but that higher order classification techniques (including the Linnaean) could be influenced by faulty reasoning processes (human whim). To be a science, systematics needed to identify a natural factor for combining species into larger and larger groups. Similarities alone would not work because it was recognized that similarity among species was more often confusing than clarifying (dolphins and sharks are similar in some ways but not in many other ways because their similarities match the conditions of their existence). Owen’s concept of homology seemed to provide a natural basis for the classification of species. The organization of species into larger groups was best accomplished by noting an underlying pattern in their form. Mammals have a particular pattern of organization that seems to be shared across species and distinguishes them from birds and reptiles. Similarly, birds and reptiles have a pattern of organization of structures that links them with mammals but distinguishes them from fish and frogs and so on. Indeed, even those species of mammal, bird, and reptile occupy an entirely aquatic habitat, retained the forms that distinguished them from one another and from fish and amphibians despite the shared habitat.

Owen also distinguished between serial and archetypical homology. Archetypical homology referred to the apparent hierarchical (or nested) similarity of form among species. Serial homology referred to the apparent repetition pattern of organization within the organism. Tetrapod forelimbs are serially homologous with tetrapod hindlimbs. Each vertebra in the vertebral column is homologous with the other vertebrae in the column. Bilateral organisms exhibit an anterior-posterior segmentation that reflects a serial homology.

Owen (1843) defined homology as “the same organ in different animals under every variety of form and function.” This definition underscores the irrelevance of form and function of the structures (organs) that were compared. The definition also emphasizes the comparative character needed for classification by homology. The underlying geometry of the organism sets the potential archetype of which any particular structure could be a variant. Of course, Owen’s definition requires a precise definition of “same”. Owen proposed the criterion of relative position as the definition of “same”.

Subsequently, traits had to meet the following three criteria to be identified as homologous:

1. Criterion of position: Homology results from the same position in comparable systems of structures (this represents Owen’s underlying geometry).
2. Criterion of special quality: similar traits can be homologized without regard to position if they agree in several unusual characteristics. The greater the complexity of the trait and the greater the degree of correspondence in the comparisons, the greater the confidence in the judgment that the traits are homologous.
3. Criterion of constancy or continuity: Even dissimilar and differently located traits can be homologous if intermediate, connecting traits (with intermediate connections based on criteria 1 and 2) can be shown to exist. The connecting traits may be ontogenetic stages or members of taxonomic groups.

Thus, the humerus bone is identifiable in cetaceans, pinnipeds, cheroptera, and primates by its position in the skeletal structure of these mammals, by its continuity across taxonomic groups, and in its order of appearance in the ontogenetic stages of these species. Similarly, the pineal gland in mammals and the pineal eye in reptiles are homologous by position, continuity across taxonomic groups, and ontogenetic stage.

I used the word “traits” deliberately in describing the three criteria for identifying homology instead of the usual words “structures” and “forms” because although the construct of homology was established to characterize morphological structures and forms organisms can be similar across more dynamic traits such as physiology and behavior. However, behavior (and other dynamic traits) creates special problems of measurement that are more serious than for structure (Atz, 1970). What part of the organism’s repertoire should be recorded and measured and how should this measurement be done? How can the events be described in reasonable and pertinent detail sufficient for persons who have never previously witnessed them to recognize them upon initial witnessing? Moreover, there are problems of distinguishing among acts (the problem of continuity across actions), dealing with both within and between individual variability (the problem of variability), dealing with an extended ontogeny (the problem of identifying and measuring both stability and change in the behavioral trait as these occur often throughout the lifespan), and, finally, dealing with the ephemeral character (each behavioral act exhibits an evanescence of appearance and disappearance during the repertoire of performance). Therefore, underlying all attempts to homologize traits (even static traits) are the questions of how the trait is described and defined.

Darwin altered the character of homology by conceptualizing it historically and removing it from the realm of metaphysics (idealized forms). Darwin perceived of species, not as natural units but as pockets of relative commonality in a sea of diversity. The apparent unity of type was explained as representing descent from a common ancestor (not an idealized form) and the variations fitting the conditions of existence were explained by natural selection; hence, the Darwinian theory of descent with modification. Thus, the homologies used for nesting the taxonomic grouping of organisms represented the historical lineage of their evolution.

The meaning of homology is partly dependent on the meaning of analogy. Similarity of form based on analogy derives from limited solutions to a common condition of existence (e.g., natural selection for convergence). Dolphins, ichthyosaurs, and sharks are similar, in part, because of the water medium of their existence constrains the range of variations that operate effectively. In addition, the modern concept of “homoplasy” refers to similarity that is the result not of simple ancestry (homology), but of either reversal to an

ancestral trait in a lineage or of independent evolution (Wake, Wake, & Specht, 2011). Independent evolutionary convergence is similarity resulting from different developmental mechanisms (usually involving gene activation); whereas, independent evolutionary parallelism is similarity resulting from the same developmental mechanisms (usually involving gene activation). Because morphological variation is limited by constraints dependent on lineage, developmental, physical and biochemical mechanisms, not all possible morphologies for a particular organism are realized or expressed. This inherent limitation on form increases the likelihood of homoplasy. For Wake, et al. (2011), developmental research must be conducted within a context of knowledge of the organism's taxonomic status. Comparative developmental research (not of model organisms but of taxonomically related organisms) is essential for identifying and defining the processes responsible for similar phenotypes across diverse taxa. Modern developmental research has demonstrated that the mechanisms responsible for generating phenotypic similarity can be found at different organizational levels - the phenotypic or whole organismal level, developmental, epigenetic, and genetic levels.

Darwin incorporated developmental phenomena into the notion of homology by proposing that adaptations that depart from type develop later, with the stage of appearance representing the lineage of the species. Common descent was observed by homologies in the specific pattern of developmental transformations and any modification in these transformations revealed how development was altered to produce diverse adaptive structures. Darwin proposed developmental processes as the means for producing the variations on which natural selection could operate. Nevertheless, he did not have an adequate theory for how developmental processes could be transmitted across generations to ensure the shaping of characteristics to their environments.

In mid-20<sup>th</sup> C, the "modern synthesis" of genetics with evolution also did not provide an adequate explanation for the production of the phenotypic variation upon which natural selection operates. Instead, a "blue-print" notion of genetics was proposed in which genes contain instructions for the construction of a phenotype and developmental biology was simply an expression of those instructions. Natural selection then became the preservation of one set of instructions over other sets identified by differential reproductive success. Gene mutations, gene recombination, and the combining of genes in sexual reproduction were the only

processes that could produce the variations of phenotype. Of course, modern molecular genetics has effectively challenged these simplistic notions (Michel, 2010). The four assumptions of the modern synthesis were:

1. All evolutionarily significant variation is heritable and can only be caused by genetic variation in alleles.
2. Organisms are genetically single individuals; hence the focus of natural selection is the individual.
3. The environment is a selective agent but does not contribute to the construction of the phenotype.
4. Evolution is the slow accumulation of small differences in the genome.

However, it has long been acknowledged that natural selection cannot explain the occurrence of variations and those variations in the genome (mutations, recombination, and sexual combination) did not provide a mechanism for how such changes created phenotypic variations. The discoveries of modern cellular biology and molecular genetics have refocused attention on the processes and mechanisms of development (or the transformation of a genotype into a phenotype). Only by including developmental biology (involving information about developmental changes in gene activity and developmental plasticity) can evolutionary theory account for the occurrence of phenotypic variations.

### **Evo-Devo: the modern synthesis extended.**

In the last two decades biologists have combined evolutionary biology with developmental biology to create what some consider a successor to the modern synthesis (Pigliucci, 2007), an evolutionary developmental biology (evo-devo). From the evo-devo perspective, developmental genetics reveals three types of variation that are important in evolution: allelic variation of genes providing information for the specification of particular proteins (structural genes), allelic variation of regulatory loci that affect the expression of structural genes, and plasticity-derived epigenetic variation that affect the expression of genes during development. Evo-devo has revealed how many of the important differences among species depend on which, where, when, and how much genes are activated during development. Major phenotypic changes can be associated with changes in patterns of activation of regulatory genes. These changes in activation are influenced by epigenetic processes during development which can be transmitted across generations.

Evo-devo explains biodiversity in terms of variations in developmental trajectories. The focus is on how changes in development create novel phenotypes, how development constrains certain phenotypes from arising, and how developmental mechanisms evolve. Evo-devo also examines how the environment plays a role in regulating developmental processes and how organisms evolved to incorporate environmental signaling.

Consequently, evo-devo adds important qualifiers to the four assumptions of the modern synthesis:

1. All evolutionarily significant variation is heritable and can only be caused by genetic variation in alleles.  
**Epigenetic variation that plays a role in the development of a phenotype can be transmitted across generations.**
2. Organisms are genetically single individuals; hence the focus of natural selection is the individual.  
**Organisms are like ecosystems, composed of numerous genotypes that interact with one another. Natural selection favors “teams” rather than particular individuals; consequently, this privileges relationships as a unit of selection and opens the way to examining the influence of natural selection on populations.**
3. The environment is a selective agent but does not produce the phenotype. **The environment can instruct which phenotype can be produced from the genetic repertoire.**
4. Evolution is the slow accumulation of small differences in the genome. **Evolution can be marked by relatively quick changes resulting from relatively small differences in the expression of genomic processes during development.**

The new evolutionary synthesis based on evo-devo added additional constructs to evolutionary theory which derive from developmental biology (Gilbert & Epel, 2009). These constructs build on concepts proposed during the modern synthesis but were not incorporated as fully into evolutionary theory as they must be now. One concept, the “norm of reaction” for a given genotype (Dobzhansky, 1955), derived from the recognition that the relationship between the genotype and the phenotype was complex (Johanson, 1909). The investigation of the effects of different environmental conditions on the phenotype led to the notion that there is a range of phenotypes that can be expressed from any given genotype (“the norm of reaction”). In addition, the construct

warned that the particular phenotype expressed is not predictable from knowledge of the environment, the genotype, or their simple interaction. Rather, the variation in phenotype from a particular genotype derives from developmental plasticity. Phenocopies are examples of such environmentally produced phenotypes that mimic phenotypes associated with changes in alleles. Indeed, the construct of phenocopy raises the question of whether the similarities in traits across members of a species (all genetically somewhat disparate) are simply examples of phenocopies. It is always presumed that the similarities in the genome of species members is responsible for their similarity of traits. However, the same trait seems to be able to develop from different genes and the same gene seems to permit the development of different traits (Minelli, 2009).

The notion of developmental plasticity permitted early theorists (Spalding, 1873, Morgan, 1896, and Baldwin, 1896) to propose it as a mechanism for evolution. Later, Waddington (1956) coined the term “genetic assimilation” to represent a process whereby there is a genetic stabilization of an initially environmentally induced phenotype. As a result of such assimilation, over many generations, the phenotype will come to be more tightly associated with the genotype (Waddington’s canalization). Thus, the evolution of novel traits may be facilitated by developmental plasticity involving mutual adjustment (without genetic change) among variable aspects (modules) of the phenotype during development.

Development is a modular process in which different loci of the organism exhibit differences in rate and extent of cellular transformations. However, the transformations operating in these loci are not independent from one another but rather are interactive and integrated. Alterations in one module can prompt adjusted alterations in other modules (Minelli, 2009). West-Eberhard (2003) noted that if an environmental change produces a change in the which, where, when, and how much of development in any locus, then the regulative plasticity of organism (the interactive and integrated aspects of the loci) ensures some form of adjustment to the new environmental challenge (otherwise the development is ended by the loss or ineffectual functioning of the organism). Such regulative plasticity leads to a new trait. If the initial change is induced by a fairly widespread environmental event, the new trait will have occurred for a portion of the population sufficient enough for the availability of mates for those individuals with the new phenotype (this means that there are no hopeful



monsters). Subsequently, relatively random processes of allelic variation, recombination, and sexual combination along with natural selection will eventuate in genetic assimilation so that the trait eventually occurs irrespective of the presence of the environmental inducer.

Thus, the reciprocal developmental induction of modules during development is responsible for developmental plasticity. Such developmental plasticity ensures that a novel structure/trait can be complex and adaptive immediately and without requiring small changes. Typically, genetic assimilation represses plasticity (canalization); however, there also can be an increase in plasticity. Species inhabiting several environments, in which one variant is not optimal over all habitats, can be subject to increased developmental plasticity. Consequently, for some organisms, developmental plasticity is retained by natural selection to permit environmental information to help direct appropriate developmental processes and transformations across the lifespan. Moreover, genetic assimilation across generations will eventuate in the trait of developmental plasticity being retained irrespective of the presence of environmental variability. Developmental parameters of plasticity can permit faster evolution of traits and since this plasticity is responsive to environmental information it can account for the apparent directedness of evolution. Thus, since development is the cascade of events linking genotype with phenotype, evolutionary theory needs to incorporate the mechanisms of development.

“Heterocyberny” is a construct coined by Gilbert and Epel (2009) to capture the influence of four developmental genetic mechanisms underlying macroevolutionary change. These are: heterotopy, heterochrony, heterometry, heterotypy. In the first three of these “heteros”, the regulatory regions of the genome are affected. That is, the gene’s product remains the same although it may be synthesized in a new place in the developing organism (heterotopy), at a different time during development relative to other developmental events (heterochrony), or in different amounts (heterometry). Heterotypy is a change in the proteins that bind to these regulatory regions thereby altering their relation to other modules.

To these mechanisms, Gilbert and Epel (2009) add ecological contributions to developmental biology. Developing organisms can produce environmental factors that alter the development of other organisms which,

in turn (via reciprocal interactions) produce environmental factors that alter the development of the original organism. This plasticity of the habitat permits niche construction during development. Niche construction is the idea that emphasizes the capacity of organisms to modify selection pressures and act as co-directors of their own evolutionary biology (Lewontin, 2002). Organisms fit their world so well because they have constructed it. When organisms alter their development in response to environmental cues so that they fit the environment better, that is adaptive developmental plasticity. When a developing organism induces changes in its environment in ways that make the environment more fit with the organism, that is niche construction.

Developmental biology has illuminated the meaning of homoplasy via a concept of “deep homology”. Common developmental genetic mechanisms have been shown to underlie features that long were considered classic examples of convergent evolution. The paired appendages of tetrapods (e.g., salamanders, lizards, mammals) and arthropods (e.g., flies, lobsters, spiders) evolved independently, but the integration of phylogenetics, development, and genetics into their investigation shows that homologous gene clusters sharing ancient common ancestry are responsible for the initial outgrowths from the body that become patterned along body axes (front to back, top to bottom, etc.) in both vertebrates and arthropods. Patterning in tetrapod appendages, despite considerable variation among taxa, is largely governed by relatively late expression of long-conserved homologous Hox genes during development. The same developmental genetic process might control even relatively terminal portions of the development of fish fins and tetrapod limbs. Thus, while the morphological structures expressed in adults (e.g., legs of flies and legs of humans, or digits of salamanders and fin rays of zebrafish) are not homologous (because they were not present in a shared ancestor), homology may lie within the organization of Hox genes and their regulatory networks (although specific genes might have different patterns of expression).

All eyes, invertebrate and vertebrate, develop through a cascade of similar transcription factors despite vast phylogenetic distances. These networks include genes (e.g., Pax6) that have been deployed in different ways at different times, and specific molecular signaling pathways that have re-evolved in different lineages. The networks and cascades, which contain homologous genes and members of the same gene families, are not

genetically identical. Thus, the end phenotypes might be general homologs at the level of a very remote common ancestor but convergent with respect to end phenotype and more recent phylogenetic ancestor. Indeed, what has historically been termed “convergence” and attributed to independent evolution in unrelated taxa often has a common genetic system associated with trait development. However, comparing underlying genetic mechanisms alone is insufficient if they are not integrated appropriately in developmental and phylogenetic information. Morphologically disparate taxonomic groups that are only remote relatives can share toolkits of morphogenesis. Such general morphogenetic themes reflect constraints on variation and these constraints can produce homoplastic traits. Identification of such homoplastic traits and the examination of the developmental mechanisms constraining their development will illuminate the limits on phenotypic evolution, the nature and reasons for biases in its direction, and why “descent with modification” may follow predictable pathways (Wake, Wake, & Specht, 2011).

Developmental constraints on morphogenesis are of three sorts: Physical, morphogenetic, and phylogenetic. The number and forms of possible phenotypes that can be created are limited by the interactions that are possible among molecules (physical constraint) and between modules (biochemical constraint). It is physically impossible to evolve a wheeled vertebrate because blood cannot circulate through a rotating organ. Chemical principles such as those represented by a reaction-diffusion model seem to govern the architecture of the limb. Therefore, spatial features of limbs that cannot be generated by reaction-diffusion model will not be able to occur. The notochord degenerates in vertebrates but it is transiently necessary for specification of the neural tube in vertebrate embryos (a phylogenetic constraint). As genes become involved in the activity of more than one developmental module, they become more difficult to change. This ability of a gene to play multiple roles in different developmental modules (pleiotropy) results in the interconnectedness of modules and the interdependence of developmental processes.

### **Homology of behavior.**

Since, in practice, the animal behaviorist works with animals that have already been phylogenetically classified, the distribution of behavior patterns across species may be used as evidence for or against any

proposed behavioral homologies without the problem of circularity. However, a monkey's arm, whale's fin, bird's wing, and salamander's forelimb are all indubitably homologous but homologizing their behavior would be misleading at best. Convergence can occur in unrelated groups in response to similar environmental conditions. Strong selection pressures, especially those associated with rigorous environments tend to promote convergences. For example, unlike Australian marsupials (who share homologous traits and who are distinct from other mammalian species), all indigenous species of Australian birds appear to share many features in common with species of birds in Eurasia and the Americas. It appeared as though separate waves of immigration brought birds to Australia from these disparate places. Until the examination of their genomes, there did not seem to be any common ancestry that could link these indigenous species. However, genomically, they clearly all evolved from a common Australian ancestor and not from Eurasian or American ancestry.

Early Ethologists proposed specific criteria for the identification of behavioral homologies.

1. Peripheral structures. Movements employing homologous structures in similar ways may be considered homologous (Tinbergen , 1962). However, nonhomologous behaviors may be based on homologous structures (Atz, 1970). The anal fins of poeciliids and anablepids are homologous as fins but not a gonopodia. Baerends argued that for homology of behavior the patterns of muscle contraction should be largely identical. If these show important differences then homology is less likely. However, very few behavioral studies have included analyses of muscle function and Atz argues that this may be because there is no reason to believe that muscles exhibit any more fixed evolutionary relationship to associated behavior than do any other structures.
2. Nervous system. Although it is possible to establish homologous regions of the brains of animals as diverse as fish and mammals, this has not solved the problem of homology of behavior for these animals. The neurobehavioral organization of birds is so unlike that of the mammal that any similarities in behavior between them must be convergence, despite a homology among neural tissues. Nevertheless, Pribram (1958) simply pronounced that when behavior is served by homologous neural structures those behaviors must be considered homologous until proved otherwise.

In the next sections I will use the study of handedness and limb preference to illustrate the problems associated with using neural structure as the source of homologous behavior. I also will propose that developmental cascades make similarities in behavior across the lifespan appear to be homologous when they are merely developmental derivatives. Finally, I will propose how a specific conduct of developmental research will provide for scientific understanding of human development that accounts for the uncannily complex repetitions among human cultural groups (human universals), who have long been isolated, without appeal to a naturally selected human nature. Rather these similarities may be a product of a contingent history from a founding group.