

Title of Talk: Assessing homology at different levels of the biological hierarchy

Brian K. Hall

"I will grant that someone might be able to generate an original thought concerning homology, but I doubt it." (Wake, 1999, p. 24)

Submitted Abstract:

A **central issue** in homology since Richard Owen coined the modern definition of the term in 1844 has been **whether homology of features** (a similar portion of the brain in different species, for example) **depends upon those features sharing common developmental pathways**. Owen did not require this criterion, although he observed that homologues often do share developmental pathways (and we now know, gene pathways). A similar situation has been explored (to some extent) in the origin of behaviours, especially, **whether homologous behaviours must share a common structural basis**. However, development evolves, and we now know there can be several ways to produce a single homologous feature; a bone may arise from mesoderm or from neural crest (ectoderm); electric organs in fish that share homologous features and physiology can arise from a transformation of a muscle or of a nerve. I will discuss the problem of **how homology is translated across levels of the biological hierarchy** and apply these findings to developmental psychology. Historically, I will touch on the work of James Baldwin who related evolutionary transformations and the origin of new features to environmental adaptations based on learning, and Jean Piaget who transferred the concept (and processes) of epigenetics from biology to psychology.

The abstract submitted to the organizers is above, with central questions/issues highlighted. The paper below covers all but the last sentence of the abstract: I have more research to do to get up-to-speed on the application of my talk to psychology; Indeed, I expect to be working on this section until the day before we meet.

Introduction

Homology is the hierarchical foundation of all biology. Consciously or unconsciously, we invoke homology whenever we compare two or more biological units, whether those units are genes, cells, tissues, organs, structures, behaviour or individuals.

Much of the discussion about homology in the past has been mired in semantics. I hope that, along with David Wake (1994) we can agree that homology is "the central concept for *all* of Biology" and move on. Despite the importance of homology as the "hierarchical basis of comparative biology" (the subtitle of the volume edited by Hall, 1994) and its central place with evolution in biology, definitions of homology abound. Wake (1994) concluded that: "...I found no reason to change my personal definition of homology (which is not worth repeating, since I cannot even convince students in my own lab of the correctness of my position)." During our discussions I am sure we will see homology as sameness, identity, synapomorphy, a statement about final structures, a statement about developmental processes and/or about genes, and we will have discussed whether homology is (or should be) hierarchical.

Owen's (and the modern/current) definition of homology

In 1843 Owen defined a homologue as; "The same organ in different animals under every variety of form and function." Owen contrasted homology with analogy ("A part or organ in one animal which has the same function as another part or organ in a different animal"). Owen never modified his definitions to accommodate Darwin's theory of evolution by natural selection. In 1870, Ray Lankester redefined homology to account for shared evolutionary ancestry, contrasting what he called **homogeny** (similar characters because of shared ancestry) with **homoplasy** (similar characters arising in different lineages). Lankester stressed that both homogeny and homoplasy are forms of homology, because all life is a single tree. Recent independent analyses of homology, both beginning with Lankester, led Gould and Hall to an expanded category of homology to include reversals, rudiments and atavism, leaving convergence as the only classes of homoplasy or independent evolution (Gould, 2002; Hall, 2003).

Homology as a hierarchical concept

Until recently, homology has been approached at two levels: structural and developmental. Structural homology reflects the presence of the same character in two lineages that share a common ancestor (a synapomorphy/symplesiomorphy), while developmental homology pertains to the same developmental mechanisms producing a shared character. Structural homology need not always equate with developmental homology. For instance developmental

mechanisms, down to the level of gene regulation, can evolve, despite forming structurally homologous features.

Finding in genetics in which equivalent (homologous) master genes 'switch on' the development of structures long regarded as non-homologous — the eyes of flies and frogs, for example— have focused attention squarely on the issue of the level(s) of biological organization at which homology should be addressed. I will discuss homology on at least four levels — structural, genetic, developmental and behavioural.

Structural or phenotypic homology regards homology as a statement about the final pattern produced by evolution; the wing of a bird, the wing of a bat and the arm of a woman. How does structural homology deal with evolutionary changes in development that may obscure homology without rendering the resulting structures non-homologous?

Genetic homology as been applied to

- the 'same' genes as nucleotide sequences;
- the same genes in different animals (paralogy and orthology);
- the same genes that share the same function;
- the same genes with different functions and/or
- similar genetic networks (discussed by Abouheif)?

Does the identification of master genes (controlling, developmental or regulatory genes) require a reassessment of structural homology or can we have different conceptions of homology at the genetic/developmental and phenotypic levels? Features of the phenotype that are structural homologues in two species develops can develop by different developmental processes or by using genes that are not homologous. The same genes/genetic pathways homologous genes are utilized in the production of non-homologous structures within an individual and across species. Homology at one level in the biological hierarchy of organization does not require homology at other levels. Homology reflects evolution caught in the act.

Embryonic Development and Homology

A central issue in homology since Richard Owen coined the modern definition of the term in 1844 has been whether homology of features (a similar portion of the brain in different species, for example) depends upon those features sharing common developmental pathways. Owen did not require this criterion, although he observed that homologues often do share developmental pathways (and we now know, gene pathways). A similar situation has been explored (to some extent) in the origin of behaviours, especially, whether homologous behaviours must share a common structural basis. However, development evolves, and we now know there can be several ways to produce a single homologous feature; a bone may arise from mesoderm or from neural crest (ectoderm); electric organs in fish that share homologous features and physiology can arise from a transformation of a muscle or of a nerve. Identifying novel features requires assessments of similarity (homology and homoplasy), of relationships (phylogenetic history) and of shared developmental and genetic pathways or networks.

Behavioural homology

Homology has predominantly been used for structures; hence structural homology. It would be more inclusion to speak of phenotypic homology to reflect the fact that other aspects of the phenotype, such as homologous behaviours, can be recognized and analyzed. Behavioural homology reminds us that homology is much broader than structural and genetic homology. **Homology is the hierarchical basis of comparative biology and that means biology at all levels.** The relationship of shared or divergent structural bases to behavioural homology is similar to, and raises the same issues, as the relationship between shared or divergent genes or embryonic development and structural homology. Just as homologous structures can arise from divergent developmental programmes, so homologous behaviours need not share a common structural basis.

Here is where I move into material not yet prepared: I will discuss the problem of how homology is translated across levels of the biological hierarchy and apply these findings to developmental psychology. Historically, I will touch on the work of James Baldwin who related evolutionary transformations and the origin of new features to environmental adaptations based on learning, and Jean Piaget who transferred the concept (and processes) of epigenetics from biology to psychology.

Some literature

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