Brian K. Hall

Department of Biology, Dalhousie University, Halifax, NS, Canada B3H 4R2
E-mail: bkh@dal.ca

Homology, Homoplasy, Novelty, and Behavior

ABSTRACT: *Richard Owen coined the modern definition of homology in 1843. Owen's conception of homology was pre-evolutionary, nontransformative (homology maintained basic plans or archetypes), and applied to the fully formed structures of animals. I sketch out the transition to an evolutionary approach to homology in which all classes of similarity are interpreted against the single branching tree of life, and outline the evidence for the application of homology across all levels and features of the biological hierarchy, including behavior. Owen contrasted homology with analogy. While this is not incorrect it is a pre-evolutionary contrast. Lankester [Lankester [1870] Journal of Natural History, 6 (31), 34–43] proposed homoplasy as the class of homology applicable to features formed by independent evolution. Today we identify homology, convergence, parallelism, and novelties as patterns of evolutionary change. A central issue in homology [Owen [1843] Lectures on comparative anatomy and physiology of the invertebrate animals, delivered at the Royal College of Surgeons in 1843. London: Longman, Brown, Green & Longmans] has been whether homology of features—the "same" 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, often share gene pathways). A similar situation has been explored in the study of behavior, especially whether behaviors must share a common structural, developmental, neural, or genetic basis to be classified as homologous. However, and importantly, development and genes evolve. As shown with both theory and examples, morphological and behavioral features of the phenotype can be homologized as structural or behavioral homologues, respectively, even when their developmental or genetic bases differ (are not homologous).* © *2012 Wiley Periodicals, Inc.* Dev Psychobiol 55: 4–12, 2013.

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INTRODUCTION

Homology is the hierarchical foundation for all of biology. Consciously or unconsciously, we invoke homology whenever we compare two or more biological units, whether those units are genes, cells, tissues, organs, structures, or behaviors (Hall, 1994, 2003a; Wagner, 2007).

Much discussion about homology in the past has been mired in semantics. Along with Wake (1994), however, we can assert that homology is a central concept in biology that reflects the "hierarchical basis of comparative biology," which also is the subtitle of the volume on homology edited by Hall (1994). Homology also is a central evolutionary concept in biology (Gould, 2002; Hall, 1994, 2003a). In part because homology is a hierarchical concept and in part because homology was initially defined in non-evolutionary terms (see below), definitions of homology abound.

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Homology is variously discussed as being about sameness, identity, synapomorphy, and phylogeny, final structures (the products of evolution) and developmental processes, genes and gene networks (evolutionary processes).

RICHARD OWEN AND RAY LANKESTER'S DEFINITIONS OF HOMOLOGY

In a glossary to the published version of his "Lectures on Comparative Anatomy and Physiology of the Invertebrate Animals, Delivered at the Royal College of Surgeons," Richard Owen defined a homologue as "The same organ in different animals under every variety of form and function" (Owen, 1843, p. 379). Owen developed his definition for morphological structures not for behaviors or physiology and 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, 1843, p. 374).

For Owen, homology demonstrated the adherence of organisms to basic plans or archetypes; transformations were not possible. Although he provided what we regard as the first "modern" definitions of homology and analogy, Owen did not establish the criteria by which homology could be recognized. Owen used criteria established in the 18th century by Etienne Geoffroy St.-Hilaire. These criteria were primarily the position of the structure in the organism and the anatomical features with which it connected. As an example, the humerus of the forelimbs of all tetrapods is homologous because of its position in the upper arm and connection proximally to the shoulder girdle and distally to the radius and ulna at the elbow joint.

Owen never modified his definitions, criteria or his non-transformationist theory to accommodate Darwin's transformative theory of evolution by natural selection. Although after Darwin it could be stated that "a feature is homologous in two or more taxa if it can be traced back to the same feature in the presumptive common ancestor" (Mayr, 1982, pp. 45, 232), criteria for determining the homology of features of the phenotype remain what they were in pre-Darwinian times—position and connections.

Having accepted Darwin's theory of transformation of organisms on the tree of life published a decade before, an English anatomist and embryologist, Ray Lankester, redefined homology to take shared evolutionary ancestry into account, contrasting what he called *homogeny* (similar characters because of shared ancestry) with *homoplasy* (similar characters arising from the independent evolution of different lineages): "Structures which are genetically related, in so far as they have a single representative in a common ancestor, may be called homogenous" (Lankester, 1870, p. 36). Convinced by Darwin's evidence, Lankester saw all life as "one great genealogical tree" (p. 34) representing one history of life: "in [the various] kinds of animals and plants [we see] simply the parts of one great genealogical tree, which have become detached and separated from one another in a thousand different degrees, through the operation of the great destroyer Time..." (Lankester, 1870, p. 34). Homology has been recognized as an evolutionary concept ever since. Identification of homologues is essential when constructing the branching tree of evolution produced by evolution (Begun, 2007; Wiley, 2008).

In two recent analyses of homology, both of which used Lankester (1870) as their starting point, Gould (2002) and Hall (2003a) independently expanded the category of homology (Lankester's homogeny) to include reversals, rudiments, atavisms, and parallelisms, leaving convergence as the only class of homoplasy or independent evolution. This becomes important when we ask: "with what do we contrast homology?" Owen said analogy, Lankester homoplasy, Gould and Hall convergence (If not homology, then what? section).

HOMOLOGY AS A HIERARCHICAL CONCEPT

A hierarchical approach to homology has emerged over the past two decades (Hall, 1994; Hall & Kernery, 2012; Rutishauser & Moline, 2005). Homology has been approached at several levels, each of which places the concept at different positions in the evolutionary process. *Structural* (taxic, phenotypic) and *developmental* (transformational) *homology* are of the greatest concern when comparing behaviors between species or higher taxa and when investigating the evolution of a particular behavior.

Structural homology reflects the presence of the same character in two lineages that share a common ancestor. Structural homology, therefore, is a statement about the patterns that occur among closely related organisms as a result of shared evolutionary history. It denotes the fundamental sameness of, for example, the wing of a bird, the wing of a bat and the arm of a woman (Hall, 1994). Processes associated with producing a structural homologue need not, themselves, be homologous. Developmental homology denotes the fundamental sameness of developmental and/or genetic processes, sequences and/or mechanisms by which features are produced (Hall, 1994, 1995; Wagner, 1989a,b, 2007).

Structural and developmental homology, therefore, are at fundamentally different levels in biological

organization. Structural homology reflects the final patterns of evolution. Developmental homology reflects processes of evolution. Structural homology does not confront the issue of evolutionary changes in development that may obscure homology or appear to render the resulting structures non-homologous. This is because, as discussed below, structural and developmental homology can be uncoupled. For instance, developmental mechanisms, down to the level of gene regulation, can evolve, yet still participate in the formation of homologous features (Hall, 1995, 1999; Wagner, 2007). Non-homologous features such as vertebrate limbs and genitalia share (homologous) genetic pathways (Averof & Akam, 1996; Rosa-Molinar & Burke, 2002).

Embryonic Development and Homology

A much-debated and somewhat misunderstood issue in homology since Richard Owen coined the "modern" definition has been whether homology of features (the "same" portion of the brain in different species, e.g.) depends upon those features sharing common embryological stages—developmental pathways (Hall, 1995, 1999).

The ongoing discussion is curious when we consider that neither Owen nor Darwin required homologous development as a criterion for features of the phenotype to be homologous. Owen did observe that homologues often do share embryological development—we would now say developmental pathways and now know that gene pathways/networks also are shared. For Owen homology "is mainly, if not wholly, determined by the relative position and connection of the parts, and may exist independently of…similarity of development. There exists doubtless a close general resemblance in the mode of development of homologous parts; but this is subject to modification, like the forms, proportions, functions and very substance of such parts, without their essential homological relationships being thereby obliterated" (Owen, 1846, p. 174).

Nor did Darwin require shared development for features to be homologous: "Thus, community in embryonic structure reveals community of descent; but dissimilarity in embryonic development does not prove discommunity of descent, for in one of two groups the developmental stages may have been suppressed, or may have been so greatly modified through adaptation to new habits of life, as to be no longer recognizable" (Darwin, 1877, pp. 371–372).

We know now that, like genes and gene networks, development evolves. There can be several ways to produce a single homologous feature; bone may arise from mesoderm or from neural crest (ectoderm) and by replacement of cartilage or direct ossification of mesenchyme; electric organs in fish that share homologous features and physiology can arise from a transformation of a muscle or of a nerve; a second pair of wings can arise in *Drosophila* by homeotic mutation of Hox genes or by selection for alternate genetic pathways after genetic assimilation (Hall, 2003b; Hall & Laubichler, 2008).

Genetic Homology

With our vastly enhanced understanding of the genetic control of embryonic development, *genetic homology* has emerged as a major class of developmental homology. Genetic homology is applied to

- genes that share nucleotide sequences (orthology);
- the same genes in different animals (paralogy);
- genes that share the same function;
- genes with different functions; and/or
- similar genetic networks (Abouheif, 1999; Wagner, 2007).

These and other discoveries in developmental-evolutionary genetics have demonstrated that homologous master (controlling, developmental, or regulatory) genes can "switch on" the development of structures long regarded as non-homologous. Initiation of the development of the eyes of flies and frogs by *Pax-6* is now a classic example (Dahl, Koseki, & Balling, 1997). The lack of homology between levels focuses attention squarely on the level(s) of biological organization at which homology should be addressed. The identification of master genes involved in the formation of different structures does not require reassessing or abandoning structural homology. Seeing homology as reflecting the different hierarchical levels of biological organization we can state that features of the phenotype that are structural homologues in two taxa can develop by similar or different developmental processes or by using genes that are or are not homologous. Therefore, homology at one level in the biological hierarchy does not necessarily inform and does not negate or refute homology at other levels.

IF NOT HOMOLOGY, THEN WHAT?

Owen contrasted homology with analogy, that is, he contrasted similar structure (homology) with superficially similar features due to similar function (analogy). Although we continue to use this contrast today, rarely do we recognize that it is a pre-evolutionary comparison and rarely do we ask whether a comparison based in evolutionary theory would be more appropriate (Lauder, 1986).

Homoplasy

As first articulated by Darwin in his theory of evolution as descent by modification and as recognized by Lankester in his evolutionary approach to homology, there has been but one history of life. All organisms, and therefore all features of organisms share some degree of relationship and similarity.

Homology of a feature is recognized when two organisms share a most recent common ancestor. The humeri of apes and humans are an example. Similarity, such as that between the wings of insects and the wings of birds, reflects a deep, shared ancestry in organisms separated by hundreds of millions of years of independent evolution and today is subsumed under the term homoplasy and contrasted with homology (Abouheif, 1999; Hall, 2003a, 2012; Shubin, Tabin, & Carroll, 2009; Wake, Wake, & Specht, 2011). Lankester (1870) treated homogeny and homoplasy as reflecting features derived from common ancestry or through independent evolution, respectively. Both therefore were classes of homology for Lankester, who advocated replacing homology with the term homogeny (because of the typological connotations of homology) and replacing analogy with homoplasy because of the evolutionary basis of homoplasy. Homology and homoplasy as both reflecting evolutionary processes should resonate with late 20th to early 21st century biologists, as indeed it does (Begun, 2007; Hall, 2003a, 2007a,b; Sanderson & Hufford, 1996; Wake, 1999; Wake et al., 2011).

Parallelism and Convergence

Homoplasy is a portmanteau term for a number of patterns of evolution reflecting similarity arising through independent evolution.

Parallelism (parallel evolution) is the term used when a feature is present in closely related organisms but is not present continuously in all members of the lineage or in the most recent common ancestor of the two organisms/groups being compared. (In the latter case, the features would be homologous; Hall, 2010). Diversification of placental mammals in North America and of marsupial mammals in Australia is one of the most well studied examples of parallel evolution (Hall, 2010; Kemp, 2005).

Convergence (convergent evolution) is the term used when similar features evolve in distantly related organisms in response to similar environmental selection pressures. The evolution of wings in insects, birds, and bats is an example of convergent evolution (Hall, 2010). Convergence does not equate with analogy, which perhaps is not surprising, as one is evolutionary and the other not (Lauder, 1986). Conway Morris (2003) and others (see the chapters in Conway Morris, 2008) have analyzed the evidence for a much wider and deeper role for evolutionary convergence than previously appreciated, extending their analyses to notions of adaptation and progress in Darwinian evolution, and to the evolution of social systems and intelligence.

In a search for unity underlying homology and homoplasy and a basis for the integration of analyses of development and evolution, Gould (2002) and Hall (2003a) independently amassed the evidence for parallelism as a class of homology, leaving similarity through independent evolution (convergence) as the one class of homoplasy. This realignment facilitates the search for the common elements underlying the formation of the phenotype—what some have called the *deep homology* of genetic and/or cellular mechanisms (Hall & Kernery, 2012; Scotland, 2010; Shubin et al., 2009; Wake et al., 2011).

Convergence and Behavior

As we evaluate the application of the post-Lankesterian concept of homology to behavior we are applying an evolutionary concept whose alternative is convergence. Convergence has been demonstrated as the pattern of evolution underlying behavioral evolution in a variety of types of organisms.

As might be expected, convergence is most readily identified when the physical product of a complex set of behaviors is compared. The form of the webs built by closely related and more distantly related web-building spiders on the Hawaiian Islands provide an especially nice example. Species on different islands—sometimes referred to as ethotypes—produce very similar webs while the same species on a single island produce different webs. Because the species on different islands evolved independently of one another, Blackledge and Gillespie (2004) concluded that they evolved by convergence; the webs are homologous structures but evolved by convergent evolution of web-building behaviors.

As a second example, distantly related ants that inhabit similar habitats subject to flooding have convergently evolved the behavior of constructing levees around the entrances to their nests. Similar selection regimes have evoked the same levy constructing behavior (LeBrun, Moffett, & Holway, 2011; see also Box 2 in Toth & Robinson, 2007, for discussion of conserved and divergent components underlying convergent social evolution in insects).

Novelty

A further category of evolutionary change has emerged as a result of increasing research on the development and evolution of *novelties*.

Especially significant in the present context is the identification of novelties as non-homologies: A novelty is "a new constructional element in a body plan that neither has a homologous counterpart in the ancestral species nor in the same organism" (Müller & Wagner, 2003, p. 221); "A novelty (whether structure, function, or behavior) is a new feature in a group of organisms that is not homologous to a feature in an ancestral taxon" (Hall, 2005, p. 549). Turtle shells and tetrapod digits are prime examples of novelties, that is, of features for which no homologue exists in the most recent ancestor (of turtles or tetrapods in the two examples).

Because homology is a multilevel concept, analysis of novelty requires integrated phylogenetic, developmental, and molecular genetic analysis to determine the level at which the new feature is novel. Turtle shells and tetrapod digits are novel features of the phenotype. A novel feature may arise because of the appearance of novel developmental or genetic pathways; that is, novelty may exist at all three levels—structural, developmental, and genetic. Alternatively, preexisting gene networks and developmental plasticity involved in the formation of other features of the phenotype may be modified to provide the mechanisms responsible for the evolution of the novel feature (Bertossa, 2011; Moczek et al., 2011; Stone & Hall, 2004).

To be novel at the level of gene control, a novelty would have to be based on new (that is, previously unavailable, novel) genetic information. Such information is seen in gene co-option and neofunctionalization and in lateral gene transfer between distantly related organisms (Hall & Kernery, 2012; Tautz & Domazet-Loso, 2011) but also can arise through the evolution of new symbiotic associations, or, in social insects, through multiple, genetically distinct parents founding a colony.

Origination of the neural crest in stem vertebrates is an example of the evolution of novelty by gene co-option, in this case co-option of genes expressed in mesoderm and ectoderm in cephalochordate or ascidian vertebrate ancestors (Hall & Gillis, 2012; Meulemans & Bronner-Fraser, 2005). Origination in the cotton root-knot nematode, *Meloidogyne incognita*, of 60 new genes in six protein families that digest plant products is an example of the evolution of a novelty that followed lateral gene transfer and subsequent rounds of gene duplication (Danchin et al., 2010). An example of horizontal transfer associated with behavior is the complex behavioral interactions that occur between termites and their mutualistic fungal symbionts. Horizontal transmission of fungal symbionts occurred in the ancestral populations and is ongoing in many extant fungi and termites. Termite colonies are usually founded by at least two parental stocks, providing additional sources of horizontally and vertically transmitted genetic material of these symbioses available for selection (Aanen et al., 2002).

BEHAVIORAL HOMOLOGY

As discussed above, homology has predominantly been used by biologists to refer to morphological features of the phenotype/structures; hence structural homology. It is more inclusive and appropriate, however, to speak of *phenotypic homology* to reflect the fact that other aspects of the phenotype, including behavior, can be recognized, analyzed, and homologized. *Behavioral homology* reminds us that phenotypic homology is much broader than structural and genetic homology; homology is the hierarchical basis of comparative biology, which means biology at all levels (Hall, 2003a; Reaume & Sokolowski, 2011).

Influence of Past Attitudes to Behavior and Structures Underlying Behavior

The application of homology to behavioral features of the phenotype has been limited. In part, this is because many behavioral biologists and psychologists work with a single category of behavior—aggression, grooming or reproduction are examples—in a single species, so that a comparative and evolutionary concept—homology—has been deemed unnecessary.

The limited use of homology in behavior has a deeper basis, however. Many of those comparing behavior across taxa have taken the position developed by James Atz in a chapter in the highly influential volume "Development and Evolution of Behavior: Essays in memory of T. C. Schnierla." Atz concluded that:

> "The essentially morphological concept of homology cannot at present be applied to behavior in any meaningful (nontrite) way because of its lack of structural correlates" (1970, p. 69).

Atz was following the lead set over a decade earlier by the influential developmental psychologist Theodore Schneirla (to whom the above volume is dedicated):

> "But the concept of homology, connoting a significant evolutionary relationship between comparable mechanisms among species, has not been validated as yet for behavior and its organization" (Schneirla, 1957, 80–81).

Many behaviorists adopted this position despite Tinbergen's earlier influential outline of the study of animal behavior as the integration of evolutionary

history, adaptive function, causation, and development (Tinbergen, 1963). Behavior (ethology, psychobiology) is a discipline that can and should be approached at multiple levels in the biological hierarchy and from the perspectives of both proximate and ultimate causation, using homology as the central concept when comparative studies are undertaken (MacDougall-Shackleton, 2011; Reaume & Sokolowski, 2011).

Some seeking to apply homology to behavior have concluded that behaviors are a class of characters separate from morphology and so cannot be homologized. Homology assessment has also been regarded as not applying to behavior because behavior is regarded as subject to different modes of selection than is morphology, as more plastic than morphology, as more influenced by the environment, and as more subject to independent evolution than are morphological characters. Countering this position, Rendall and Di Fiore (2007) provide an overview of this structure–behavior dichotomy—concluding "that there is no compelling reason why behavior cannot be homologized" (p. 504)—and review evidence for the role of stabilizing selection on the genes, neural systems, morphology, and social organization associated with behavioral evolution. In his informative evaluation of the role of the environment in the generation of morphological *and* behavioral traits, Bertossa (2011) documents how "morphology and behaviour share many aspects, beginning with the importance that the environment plays for their development" (p. 2057) and how "morphology and animal behaviour could be reunited within the same framework of analysis" (p. 2063).

Homology of Behavior Does Not Require Homology of Underlying Structure

Others have been caught in the trap of mistakenly believing that homology of a behavior requires homology of underlying structure, neural control, developmental, or genetic pathways, taking the position that the structures that underlie behaviors can be homologous but behaviors cannot and so can only be analogous (Atz, 1970; Hodos, 1976; Schneirla, 1957). As outlined above, the relationship of shared or divergent structural bases to behavioral homology is similar to, and raises the same issues as the relationship of shared or divergent genes or embryonic development to structural homology. The application of homology to the various levels of biological organization and the recognition that homology at one level does not require or imply homology at other levels resolves these concerns for behavior as it does for structure.

Rendall and Di Fiore (2007) discussed these issues under the heading of "The locus of homology: Structure versus function" and provided examples in which behaviors are conserved (homologous) even when the structural basis of the behaviors is highly variable. Taxa of eutherian mammals that bury feces using the forelimbs, hind limbs, both, or neither sets of limbs are one example of a homologous behavior (burying feces) with variable structural bases. Kleisner (2008) assessed mimicry as an example of recurring evolutionary association between co-evolving species that serves the same behavioral function despite highly variable developmental origins and morphological bases. Other examples are discussed by MacDougall-Shackleton (2011) and Striedter and Northcutt (1991) who concluded "that attempts to reduce behavioral homology to morphological homologies, and morphological homology to genetic and developmental homologies, are misguided and based on a failure to recognize the hierarchical nature of biological organization" (p. 177).

Homology and the Hierarchical Organization of Behavior

Two conceptual but fundamentally interrelated issues face the behaviorist or developmental psychologist seeking to invoke homology. One is identification of the units of behavior by which behavioral features of the phenotype can be compared, broken down into component parts, homologized (behavioral homology) and through which they have evolved. The second fundamental conceptual issue comes into play when behavior is studied at multiple levels and therefore when homology is assigned at a level *other than that of the fully functional behavior.* Despite the concerns of Hodos, Atz, and others, there is no rationale for treating behavioral features as any different from morphological features of the phenotype, provided that a hierarchical approach to homology is adopted. As with structural homology, determination of behavioral homology goes beyond assigning homology to the behavior and to the structures supporting the behavior.

When we apply the evolutionary concept of homology to behaviors we have to define the hierarchical level at which homology is proposed. Behavior can be homologized at the levels of the structures that allow the behavior to be displayed, at the level of the neural control of behavior and at the levels of the developmental and genetic bases of a behavior. An example is identifications of song, wing extension, orientation, and tapping as components of courtship behavior in *Drosophila melanogaster* (Greenspan & Ferveur, 2000). Consideration of behavior at other levels—its structural, neural, developmental, or genetic basis—is not required to be able to identify courtship behavior as homologous or to compare this homologous behavior

across taxa. Just as homologous structures can arise from divergent developmental programs, so homologous behaviors need not share homology at other levels (Atz, 1970; Baerends, 1958; Bertossa, 2011; Hall, 1994; Hodos, 1976; Lauder, 1986; Stiles, 2009; Reaume & Sokolowski, 2011). In his discussion of morphology and behavior, Bertossa (2011, p. 2062) speaks of "teaching old genes (or neuronal circuits) new tricks," a phrase that captures nicely the many levels involved in the origination and evolutionary maintenance and/or diversification of a particular behavior.

Approaches to and examples of behaviors as hierarchically organized features of the phenotype that can be homologized at different levels of the biological hierarchy are becoming more numerous. Reaume and Sokolowski (2011) is an excellent source of conceptual approaches and examples drawn from a variety of behaviors in which homology at the genetic level underlies behaviors that are not homologous; homologous genes underlying non-homologous foraging behavior in nematodes, fruit flies, honey bees, and ants; Cyclic AMP signaling in sleep behavior in invertebrate and vertebrate species. Language, long regarded as the personal provenance of humans, shares a genetic homology with non-homologous behaviors—learning of song by birds and learning of motor skills by mice—via the function of the gene *Forkhead box protein P2* (*FoxP2*) (Scharff & Petri, 2011). Lest this appear to be call for an exclusively reductionist approach to behavior, the assessment of homological behavior, cognitive functions, and emotional states in social contexts provides a dynamic, interactionist dimension to behavioral homology not seen in structural or taxic homology (Clark, 2010; Griffiths, 2006, 2007; Lickliter, 2008; Moore, 2008; Wasserman and Blumberg, 2010).

CONCLUSION

Morphological and behavioral features of the phenotype can be homologized as structural or behavioral homologues, respectively, when their developmental or genetic bases differ (are not homologous). Behavior can be analyzed at levels other than as a fully formed feature of the phenotype. Homology can be assigned at those other levels and may, or may not coincide with homology of the behavior. Happily, this hierarchical approach is being adopted in increasing numbers of research programs in which the biological underpinnings of behaviors are being teased apart. Recognition of similarity and the search for the evolutionary bases of similarity are both alive and well in behavioral biology. Psychobiologists seeking a comparative and/or evolutionary context for their studies have a wealth of examples and a substantial body of evolutionary theory at hand.

NOTES

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