

Importing the homology concept from evolutionary biology into developmental psychology
5-page synopsis for Developmental Homology Workshop

Ever since Richard Owen defined “homology” in 1843 as referring to “the same organ in different animals under every variety of form and function” (p. 374), the concept has proven invaluable to evolutionary biologists. Although homologous body parts often appear similar to one another, Wagner (2007) and Griffiths (2007) have both stressed that homologues arise as a result of a process of *copying*, so that their relationship is better characterized as “the same” than as “similar.” In particular, homologues are versions of the same thing because they are present in animals that are both descendants of an ancestor that possessed that very same character. In Wagner’s words, “Sameness, then, by the definition of homology, does not refer to similarity of structure or function as such, but to historical continuity...In other words, the homology concept can be applied to anything that forms a lineage” (p. 473). If we take “lineage” to mean “descent in a line from a common progenitor,” this concept should be relevant to both phylogeny—descent from a common ancestor—and to ontogeny—descent from a common progenitor cell (a zygote). Therefore, although developmental psychologists rarely make use of the homology concept, it could be as valuable for developmentalists as it has been for evolutionists. To help introduce this potentially useful notion into developmental psychology, this talk will introduce some of the concepts and distinctions biologists and philosophers of biology use to study homology, as well as some of the unresolved issues related to this idea.

Homologues can be detected on several levels of analysis, including four that I will consider here. Homology of structures—the first level I will consider—can be observed both across and within organisms. Such morphological homologies across organisms (e.g., the similarity of a dog’s femur and a human’s femur) are typically explained as reflecting descent from a relatively recent common ancestor; this is known as “taxic” homology. In contrast, morphological homologies within a single organism (e.g., the similarity of two of a whale’s vertebrae) are typically explained as reflecting descent from a common developmental precursor; this is known as “serial” homology. We can also detect homology at a second level of analysis, namely at the level of DNA. These so-called genetic homologies can be of three

different subtypes, two of which are analogous to taxic and serial morphological homologies, respectively. The third subtype of genetic homology—resulting from lateral transfer of DNA from one species to another contemporaneous species—has no morphological counterpart, but might provide an interesting way for psychologists to think about learning. At a third level of analysis, we can detect behavioral homologies; these have been the focus of much less study than structural or genetic homologies, but recent work in philosophy makes it clear that there are no insurmountable obstacles to using the homology concept to consider psychological phenomena (Clark, 2010; Ereshefsky, 2007; Love, 2007). Finally, at a fourth level of analysis, ontogenetic homologies identify developmental *processes* that are the same, either in individual organisms or across related organisms. So to summarize, homology can be identified at the structural, genetic, behavioral, and/or ontogenetic levels (and possibly at other levels as well). Furthermore, it should be possible to identify psychological or behavioral homologies across different species (taxic), across two individuals in the same species (taxic), within an individual at a given developmental moment (serial), and even across developmental moments in the same individual (serial). Finally, in addition to being able to identify such homologies in behavioral or psychological states, we might also be able to identify homologies in the developmental *processes* responsible for the emergence of these states.

Interestingly, it has become clear that homologies at these various levels of analysis may be independent of one another. This is true for genes that contribute to the development of bodily structures, for neural circuits that contribute to conceptual structures, for conceptual structures that contribute to behaviors, and so on. Thus, homologous genes can contribute to the development of non-homologous phenotypes (Griffiths, 2006), and non-homologous genes can contribute to the development of homologous phenotypes (Wray and Abouhelf, 1998). Likewise, non-homologous neural circuits can underlie homologous behaviors or psychological processes (Ereshefsky, 2007), and non-homologous behaviors can be subserved by homologous neural circuits (Bergeron, 2010). Finally, homologous *processes* can lead to the development of non-homologous phenotypes, and non-homologous developmental processes can lead to the emergence of homologous phenotypes (Hall, 2007). As a result

of this state of affairs, one of the challenges facing developmentalists interested in using behavioral homology concepts will be to delimit the phenomena to which these concepts can be applied.

Fortunately, in the 1950's Remane identified specific criteria that could be used to recognize morphological homologies, and these criteria will be helpful to psychologists interested in behavioral and/or ontogenetic homologies as well. Remane first recommended looking at the relative (spatial) position of the body parts in question in the arrangement of two organisms; when seeking behavioral homologies, Ereshefsky (2007) and Love (2007) recommend taking a similar approach involving looking for behaviors' relative (temporal) positions in an overall behavioral pattern. Remane's second criterion requires evaluation of the extent to which a bodily structure is "special." In explaining this criterion, Griffiths (2007) noted that if a characteristic "cannot be explained by the role of a part in the life of the organism," it is special in the way Remane meant; "The fact that in the vertebrate eye the blood supply to the retina lies between the retina and the source of light is a famous example of a 'special quality'" (p. 648). Applied to behavior, this criterion has been used to identify "the web weaving behaviors of different spider taxa as distinct behavioral homologies" (Ereshefsky, 2007, p. 665). Finally, Remane's third criterion entails the tracing of a bodily structure through evolutionary intermediates. Here, too, behavioral homology could be ascertained if particular behaviors within or across organisms could be linked to one another either in ontogenetic or phylogenetic time.

Importing the concept of homology from evolutionary biology into developmental psychology could help address specific questions of interest to behavioral scientists. For instance, thinking in terms of homology could help developmentalists address the question of whether or not developmentally early-appearing and developmentally late-appearing versions of particular psychological characteristics can properly be considered to be "the same" as one another; examples of such characteristics might include neonatal and adult facial imitation, or number processing in infants and adults. Thinking in terms of homology could also contribute to understanding in a more general way; as Matthen (2007) notes,

Homology thinking is adopted in a particular domain because it is thought to be the best theoretical approach to the explanation of a certain set of features in that

domain, given empirical facts about it. For example, it is adopted as a way of identifying a dog's physical gesture as one of submission...because grouping these things together with others of common origin explains their morphology, system connectivity, functional role, and adaptive function better than alternative taxonomical approaches. (p. 677)

One interesting product of thinking in terms of homology has been the realization that homologies can reasonably be thought of as biological 'building blocks.' A number of theorists (e.g., Brigandt, 2007) consider them to be natural kinds—"carved" at nature's joints, in some cases literally—and their appearance across multiple species confers a kind of perception-independent reality on them. For similar reasons, Wagner (1996), too, considers homologues to be "modular units of evolutionary transformation" (p. 36). So, one of the reasons homology thinking could be helpful for psychologists is because such an approach might help us identify behavioral "units" that could be considered natural kinds and/or that could be subjected independently to selective pressure. These would be the building blocks of behavior, cognition, or affect.

Finally, thinking in terms of homologies could help with the identification of psychological characters as distinct from character *states*. Morphological homologues are discrete characters that are the same structure across different species (Brigandt, 2007; Fitch, 2000; Wagner, 2007), but in those different species, they can sometimes be in extremely different states. For example, birds' outer wings are homologues of human hands, but in a highly modified form; although their appearances are rather different, the bones that make up human hands and the bones that make up birds' outer wings are both variations of the same bones that were present in the forelimbs of our common tetrapod ancestor. Hence, the characters—in this case, the digits at the distal ends of the forearms—can be in any of several continuously varying states, and the characters themselves can be thought of as abstractions across those several states. If, by analogy, we wanted to bring this approach to bear on a behavioral phenomenon, we would be faced with an immediate question. Fearfulness, for example, could be construed as either a character or a character state (e.g., a state that an emotional response system might be in), and it is not

immediately clear which of these two ways of thinking would be more helpful. Remaining cognizant of extant work on other types of homology could help psychologists as they think through such questions.

Although the work of biologists can be of help to developmental psychologists in such ways, developmental perspectives can also contribute to biologists' understandings of behavioral and morphological homologies. Biologists' explanations of taxic morphological homology have typically sidestepped the question of how characters present in ancestors are transmitted—sometimes in a radically altered form—to their descendants (Griffiths, 2006); what has been missing is a developmental account of the presence of these characters. Serial homologies in particular cannot be explained simply with reference to common evolutionary descent, and because several of the behavioral homologies we will likely be considering in this workshop will be of that variety, focusing on ontogeny will certainly be as important for us as focusing on phylogeny. As Griffiths (2006) has pointed out, “homology...is a phenomenon that stands in need of explanation...It has been clear since Darwin that a critical part of that explanation is provided by common descent. However, ...it is [now] clear that developmental biology is another critical component of the explanation” (p. 11). Consequently, an interdisciplinary approach to the study of homologies is likely to contribute significantly to our understanding of the development of both biological and psychological characters.

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