

FUNCTIONAL HOMOMOLOGY AND FUNCTIONAL VARIATION IN EVOLUTIONARY COGNITIVE SCIENCE

Author: Claudia Lorena García

Abstract: Most cognitive scientists nowadays tend to think that *at least some* of the mind's capacities are the product of biological evolution, yet important conceptual problems remain for all of them in order to be able to speak coherently of mental or cognitive systems as having evolved naturally. Two of these important problems concern the articulation of adequate, interesting and empirically useful concepts of homology and variation as applied to cognitive systems. However, systems in cognitive science are usually understood as *functional* systems of some sort. Thus, talking about functional systems' being homologous requires one's having a solid, adequate and empirically articulated concept of functional homology—and the same is true of functional variation. Here I construct an original concept of functional homology that, in my view, adequately systematizes a number of the actual uses of the word 'functional homology' in a variety of biological disciplines and in ethology. I also propose a number of criteria for the empirical application of the concept that are analogous to the criteria that are actually used in comparative biology, ethology, and (possibly) molecular developmental genetics. Then I construct a concept of functional variation on the basis of this concept of homology.

Keywords: Evolution of mind, descent with modification; cognitive science; functional systems; morphology; molecular developmental genetics.

Although most cognitive scientists nowadays tend to think that *at least some* of the mind's capacities are the product of biological evolution, there are important differences among them—some thinking that most of those capacities naturally evolved, while others proposing that only the mind's so-called peripheral (e.g., sensory) capacities are the result of evolution. But no matter how this controversy is decided—and who, in the end, is likely to be in the right—important conceptual problems remain for *all of them* in order to be able to speak coherently of mental or cognitive systems as having evolved naturally. Two of these important problems concern the articulation of adequate, interesting and empirically useful concepts of homology and variation as applied to cognitive systems.

However, systems in cognitive science are usually understood as *functional* systems of some sort—e.g., either as classical systems or as neural networks. Thus, talking about functional systems' being homologous requires one's having a solid, adequate and empirically articulated concept of functional homology—and the same is true of functional variation. And although it is true that some molecular biologists and some developmental biologists sometimes talk about some entities' being functionally homologous to other entities, there does not appear to be a consensus among them concerning what this talk of functional homology amounts to, or how to ground it in an empirical sense.

Here I construct a concept of functional homology that, in my view, adequately systematizes a number of the actual uses of the word 'functional homology' in a variety of biological disciplines and in ethology. I also propose a number of criteria for the empirical application of the concept that are analogous to the criteria that are actually used in comparative biology, ethology, and (possibly) molecular developmental genetics. Then I construct a concept of functional variation on the basis of this concept of homology.

I shall proceed as follows: First I explain the concept of morphological homology and its associated criteria concerning which there is some consensus among biologists. Then I articulate a concept of homology as applied to functional systems, and propose the corresponding criteria for it. Then I briefly present some of the more important problems and questions that are still formulated in connection with the concept of homology in morphology, and briefly examine how some resolutions to these controversies can impact our concept of functional homology. Next, I examine in some detail certain proposals to define a homology concept in connection with some entities in molecular developmental genetics, and argue that my proposed concept (with its associated criteria) are preferable over those for various reasons. Finally, I give some

reasons why I think my proposal sheds an entirely new and fresh light on certain evolutionary questions with respect to cognitive systems.

I. Morphological Homology.

Before Darwin's theory came along, Richard Owen (1804-1892) had already made a distinction between homology and analogy by saying that a homologue is "the same organ in different animals under every variety of form and function. . . . [In contrast, an analogue is a] part or organ in one animal which has the same function as another part or organ in a different animal" (Owen 1843, 379 and 374).

With Darwin, the intuitive idea surrounding the traditional concept of homology (as opposed to analogy) became that a historic-evolutionary line exists among certain structures or organs of organisms belonging to diverse species, even though those parts or structures are morphologically and/or functionally dissimilar. The intuitive idea underlying homology is that of *sameness due to common ancestry*; homologous traits are said to be *the same (type of) trait* because they have a common ancestor. Thus, if two traits T1 and T2 of two distinct species S1 and S2 are homologous in this sense, then there is a common ancestor of both S1 and S2 which had a trait T3 in such a way that T1 and T2 are said to be the same (type of) trait because they are *modifications* of T3.

For example, bones of the middle ears of mammals are homologous with the bones of the lower jaws of reptiles, although the former are neither structurally nor functionally similar to the latter (Hall 1994). In contrast, an example of an *analogy* is given by the wings of insects and the wings of birds—they have the same function but are not homologous.

Furthermore, the notion of variation and that of homology are intimately connected. The former also is central to evolutionary theory since, according to it, some populations of a certain species sometimes give rise to other species in the following manner: The traits or characters of the individuals of that population present *modifications or variations*. Then individuals with the most adaptive combination of those variations normally are the ones that survive long enough to reproduce, and pass on those variations (those that are heritable) to their descendants, and so on But, the variations that we are talking about are variations *of the same trait*. Thus, to be able to reconstruct an evolutionary story, one has to be in a position to recognize when two traits are *the same trait (or of the same type)*, and when we are looking at different traits--and that is given by the notion of homology.

There are various epistemological criteria that are presently used in the identification of morphological homologies. These are derived mainly from the work of two key researchers in the 1950's: Adolf Remane (1952) and Willi Hennig (1950).¹ These criteria are *epistemological* in the sense that they state the kinds of evidence that count in favor of hypotheses of homology; they are necessary since the mere characterization of homology—as the same part or organ under every variety of form and function, a sameness due to common ancestry—does not give a clue as to what kinds of empirical evidence are admissible when attempting to determine whether two parts, traits or characters are (or are not) homologous—i.e., whether they can (or cannot) be said to be the same (type of) character *due to common ancestry*. The criteria in question are classed into two groups or steps, known as ‘Primary and Secondary homologies’ (DePinna, 1991). These steps indicate how to proceed in the confirmation (or disconfirmation) of a certain hypothesis that asserts that two given traits or characters are homologous:

- A. *Primary Homology*: In this step three criteria are used to identify homologies. It involves certain kinds of comparisons between *two* traits of two different organisms. The resulting homology hypotheses are still tentative.
- B. *Secondary Homology*: This step involves the use of cladistic analysis as applied to the hypotheses of the previous step, and it consists basically in establishing comparisons between *many* traits of two different organisms. The criterion that consists in the application of cladistic analysis is also known as the ‘*criterion of congruence*’. The final hypotheses produced in this step are considered stronger than those of the previous step.

Let us look at each of these steps in more detail. Concerning *Primary Homology*, we mentioned that there are three criteria for identifying homologies:

1. *Relative position*: Two parts or organs are considered as homologous when they occupy the same relative position in the respective organisms—where ‘same position’ means same morphological, physiological or topological position. The idea is that there is good evidence that two traits, T1 and T2, of two organisms are homologous when one can find sufficient topological, morphological and physiological correspondences between many *other* organs and parts of those organisms, since it would be very implausible that too many correspondences evolved separately.

¹ For a fuller account of the history of the homology concept, and of its associated empirical criteria, see Laubichler (2000).

2. *Special quality*: this refers to the complexity or distinctness of a certain trait; the idea is that the more specialized and/or complex two traits are, the less likely it is that the traits evolved independently, and the more likely that we are indeed dealing with the *same (type of)* trait--i.e., with a homology.
3. *Remane's continuity*: this criterion is satisfied when the trait in question is placed within an evolutionary series of traits starting with a relatively simple trait and going towards increasingly more complex traits. The idea is that one's ability to place some traits on a gradual evolutionary continuum, is evidence that such traits are homologous.

In *ethology*, a criterion analogous to the criterion of *relative position* in morphology is used for behavior, as follows: two behaviors are homologous when they occupy the same position in a more general pattern of behavior—e. g., two different forms of tail wagging in two types of birds are homologous when they occur in the same “place” in the corresponding courtship rituals (Wenzel 1992, 366). *Special quality* is also used in ethology as a criterion for behavioral homology. For example, the different web weaving behaviors of spiders belonging to different taxa are so unique and distinctive that they are considered as homologous. Ritualized behaviors (such as mating behaviors) are often considered as homologous, due to their complexity, when they achieve the same function albeit using very different motor patterns (Ereshefsky 2007, 665; Wenzel 1992, 366). Finally, the criterion of continuity is used in ethology to determine homologies (Wenzel 1992, 368-69), as well as the *polarity* of a trait in a series of traits; the idea is that the simpler forms of the trait are evolutionary older than the more complex forms. In ethology, this criterion is also used for ordering the *ontogeny* of behavior. Again, the assumption is that the ontogeny of a homologous behavior becomes more complex as the behavior evolves (*Biogenetic Law*). (Ereshefsky 2007, 665).

Concerning *secondary homology*—the second step in the confirmation of hypotheses of homology—DePinna says that these hypotheses are the “result of an analysis of pattern detection” (DePinna 1991, 382), called ‘cladistic analysis’, which partially involves a method for the construction of cladograms—i.e., tree-like structures—and the application to these of a principle of *parsimony*.

The cladistic principle of parsimony holds that, among the different tree-like structures that can in principle be construed for a group of taxa, one should pick the one “that requires that we postulate the lesser number of evolutionary changes.” (Futuyma 1998, 97). This principle allows us to pick, among all the possible cladograms that can be constructed for certain traits in a group of taxa, the cladogram(s) that

“maximizes propositions of homology.” (De Pinna 1991, 383). The result of applying cladistic analysis by using the principle of parsimony is a general phylogenetic pattern that seeks to maximize the *congruence* of a great number of traits of a group of organisms—ideally, traits that have already satisfied the criteria of Primary Homology.

In ethology, both Konrad Lorenz and Niko Tinbergen used the criterion of congruence—the construction of cladograms using parsimony—to reconstruct phylogenies and to confirm hypotheses of homology as applied to behavior.

A final and most important point for this section: the criteria listed above for confirming homology hypotheses—whether in the Primary or in the Secondary homology steps—*are not thought of as necessary and sufficient conditions for homology*; rather, the more such criteria are fulfilled (and in a clearer fashion), the *more confirmed* the corresponding homology hypothesis is considered.

II. Functional Homology: My Proposal.

Here I will simply assume that any acceptable evolutionary cognitive science that irreducibly postulates cognitive systems in their explanations of behavior will have to construct a notion of *homology that applies to cognitive systems or mechanisms*.² In other words, an acceptable evolutionary cognitive science that irreducibly postulates cognitive systems, cannot produce acceptable evolutionary explanations of behavior having a notion of homology that applies to morphology only, and not a wider notion of homology that also applies to cognitive systems.

However, cognitive systems—however one conceives them, whether they are thought of as Turing Machines, neural networks, or the like—are *functional entities, entities that are individuated in terms of some of their functions, where ‘function’ is understood here in the widest possible sense*. Roughly speaking, cognitive systems *are* entities that do some things and in certain ways. Furthermore, cognitive systems are functional entities *distinct from behaviors*, that are sometimes some of their *actual causes*. It follows that, to construct an adequate notion of homology that can apply to cognitive systems involves the construction of a suitable notion of *functional homology*.

² Here I will not argue for this assumption, although I am inclined to think that one can construct a number of plausible conditional arguments in its favor. I say a bit more about this issue in Section V of this paper.

Remember that there is an agreement among most biologists to understand (morphological) homology as: *the same organ or part under every variety of form and function; a sameness explained in terms of common ancestry*--this is Owen's classical definition as seen through a Darwinian lens. But what would the analogue be for *functional* homology? Would it be: *the same function* under every *variety* of form and *function*, (a sameness that is due to common ancestry)? How could this be? What is required here is a way to *characterize functional differences that are at the same time classified as of the same function*. Thus this requirement *appears* to be contradictory!

The same *apparently* contradictory requirement is involved in an attempt to give a characterization of functional variation: they would have to be understood as different functions in the same function! How can the same function be at the same time different functions? What should we do? There are two options: either abandon the task of constructing coherent notions of functional homology and functional variation; or else attempt to explain away the appearance of contradiction.

Here I will attempt the second option.³ Indeed, there are some good reasons to try to avoid the first one:

1. The concept of functional homology is already in use in various biological disciplines, principally in molecular developmental biology (Love 2007).
2. Many psychological categories are functional categories (from behavior to cognitive systems), and so at least some of them must be construed as functional homologies if an evolutionary project of any kind is to work in the cognitive sciences (e.g., Ereshefsky 2007).
3. A substantive and consistent concept of functional variation must be construed if we are to make sense of the idea that some cognitive mechanisms and processes are more *evolvable* than others. (García 2007)
4. Generally, the study of the ways in which a cognitive mechanism—i.e., a functional system of sorts—varies in a population is essential to the study of its evolution. And this requires an interesting and coherent notion of functional variation.

³ Alan Love (2007) has recently proposed another interesting solution to this problem in connection with functional homology; a way to skirt the inconsistency that appears to threaten this concept. I will discuss Love's proposal in section IV of this paper.

My proposal would be to articulate a concept of functional homology as applied to functional systems—and then, on this basis, to construct a notion of functional variation. A *functional system* is an entity that performs at least one function. It may or may not have an internal functional structure--i.e., it may or may not be constituted by functional *subsystems*. If it is, we shall call it, a '*structured system*'; if it is not, then it will be called an '*unstructured system*'.

Secondly, the heart of my proposal hinges upon an attempt to cash out the pretheoretic idea that there is a distinction between *what something does*, and *how it does it*. This idea will be differently articulated as applied to structured as opposed to unstructured functional systems. Concerning *structured* functional systems, to the question, '*What does S do?*', the answer is 'F', whenever F is one of the functions that S as a whole performs. On the other hand, to the question, '*How does S do F?*', the answer consists in detailing each of the functions that each of the functional subsystems of S performs--functions that are necessary for S to perform F.

Concerning *unstructured* functional systems, the answer to the question, '*What does S do?*' is 'F', whenever F is one of the functions S performs. Additionally, to the question, '*How does S do F?*', the answer consists in detailing the way in which S's performance of F is implemented at a lower level of description--say, at the level of motor patterns, or at the cellular level. Once we have these background concepts, I can articulate my proposal as follows:

Two functional systems, S1 and S2, are *homologous* when:

- a. S1 and S2 perform the same function, albeit possibly in different ways, i.e., whether differently implemented (in the case of both structured and unstructured systems) or subsystemically differently performed (in the case of functionally structured systems only), and
- b. S1 and S2 have a common ancestor.

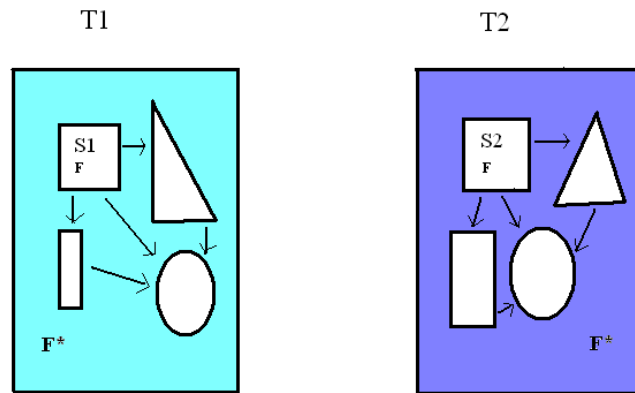
The question now concerns the criteria for functional homology. In other words, the question is: what can count as evidence that two functional systems—two behavioral or cognitive systems—are functionally homologous? Let us first look at the criteria of Primary homology:

1. Relative Position

We have two functional systems, S1 and S2. They are either unstructured or structured. Both perform a function F, perhaps differently—whether subsystemically or implementationally in a different manner. This criterion tells us to regard these two functional systems as homologous when

- (a) they are functional parts of two other larger functional systems, T1 and T2 respectively, both of which perform the same function F^* ($F^* \neq F$), possibly in a different manner (whether at the implementational or the subsystemic level), and
- (b) there are certain subsystemic *functional similarities* in the way in which T1 and T2 perform F^* --similarities in the subsystemic form of operation of each of them, and the temporal pattern of occurrence of their subsystems. This is necessary because the criterion of relative position tells us that it is precisely the existence of such organizational (functional and morphological) similarities between T1 and T2 that leads us to expect that S1 and S2 are homologous--i.e., perform the same function *due to common ancestry*.

Criterion of Relative Position



S1 and S2 would be considered functionally homologous, under this criterion, when they both fulfill the same function F, and are subsystems of larger functional systems T1 and T2 which also perform the same function F^* , perhaps differently, although there are certain functional and morphological similarities between T1 and T2.

In order to better understand this criterion, let us examine a clear example of functional homologues and of the manner in which the ethological analogue of the relative position criterion (i.e., relative position criterion)

is applied. We saw that, in ethology, two different forms of tail wagging are considered homologous when they occur in the same “place” in courtship rituals. The behaviors in question (i.e., tail wagging, courtship ritual, etc.) are functionally characterized; certainly they are not identified as particular motor patterns, or as specific physical motions. What we have here then is two larger functional systems *T1* and *T2* (i.e., those that output courtship rituals), and two functional subsystems S1 and S2 (outputting tail wagging behaviors) that are parts of *T1* and *T2*. Although the functional subsystems, S1 and S2, have the same functional characterization (i.e., produce tail wagging), they are not identical in all respects; for example, they may each consist of different motor patterns and/or physical motions. Something similar can be said of the larger functional systems, *T1* and *T2*, that output courtship rituals.

The criterion of relative position then tells us that we have evidence to consider S1 and S2 as homologous whenever they are parts of larger functional systems performing the same function (courtship of a possible mate), **and** whenever S1 and S2 (both of which are forms of tail wagging) occur in the same “place” in the corresponding courtship rituals (*T1* and *T2*). But for it to even make sense to talk about two component processes being in the “same place” within two larger processes, *some structural, functional and temporal correspondences have to exist between the two larger processes*--and this is precisely what our criterion of relative position requires.

Notice that one of the advantages of our characterization of functional homology and of its associated criterion of relative position is that it can be applied to *any* functionally characterized entity—not only to functionally described behavior, but also to cognitive systems of any sort (whether these are thought of as Turing machine-like, or as neural nets, etc.)

2. Special Quality

As applied to morphological traits, this criterion refers to the complexity or distinctness of a certain trait; the idea is that the more specialized and/or complex two traits, the less likely the traits evolved independently, and the more likely that we are indeed dealing with the *same (type of) trait*--i.e., with a homology. Talking about functional systems S1 and S2, this criterion refers either to the specificity of the function that S1 and S2 perform, or to the complexity of their subsystemic operation (if any).

3. Remane’s Continuity

With respect to morphological traits, this criterion is satisfied when the trait in question is placed within an evolutionary series of traits starting with a relatively simple trait and going towards increasingly more complex traits. The idea is that one's ability to place some traits on a gradual continuum, is evidence that such traits are homologous. In connection with functional systems, this criterion will be satisfied when one can find a gradual continuum of functional systems--all undertaking the same function--but in increasingly complex ways, at either the subsystemic and/or the implementational level. Let us now consider the criterion of Secondary Homology.

We saw above that cladistic analysis together with the Principle of Parsimony, constitutes the Criterion of Congruence in the *Secondary* step for morphological homology. Indeed, Konrad Lorenz himself used this Criterion to confirm some hypotheses of homology in connection with animal behaviors. Although I do not include here the details of my proposal as to how to understand and apply this criterion to any two functional systems, say S1 and S2, the general idea is to do the following:

- a. Whenever possible, apply the three criteria of homology constitutive of Primary Homology—to wit, relative position, special quality and continuity—to S1 and S2.
- b. Describe the subsystemic and/or implementational characters or traits of S1 and S2 (especially those whose homologies are already known, if any).
- c. Describe other relevant functional systems of O, distinct from S1 and S2 (especially those that more directly interact with S1 and S2 respectively, and those whose homologies are already known).
- d. Construct the corresponding cladogram using the principle of parsimony using all of the characters, and functional systems or subsystems described in b and c, respecting as much as possible the statements of homology already known.

We are now in a position to say when two functional systems are *variations* of the same type of functional system:

s1 and s2 are *functional variations* of each other in population P only if

- a. s1 and s2 are numerically distinct particular systems occurring in members of P;
- b. s1 and s2 are functionally homologous;
- c. therefore, s1 and s2 both perform the same *function* F; and

d. s1 and s2 do perform F --either implementationally or subsystematically--differently.

III. Controversies surrounding the Concept of Homology.

There is a number of contemporary discussions in biology involving the concept of morphological homology and other concepts that are intimately connected to that one. How these disagreements are eventually resolved will have an impact on any proposal like mine to fashion a clear concept of functional homology.

- (1) First of all, there is a controversy concerning whether the application of any of the criteria for morphological homology mentioned in Section I above—i.e., the criteria of Relative Position, Continuity, Special Quality, and the criterion of Secondary Homology—indeed allows us to obtain evidence to accept a homology hypotheses to the effect that two characters *derive from a common ancestor*, or whether the criterion in question is spurious because it relies on presuppositions that are, in the best of cases, unproven and speculative. For example, there is a discussion concerning whether or not the criterion of Secondary Homology presupposes that evolution itself is parsimonious—an huge presupposition that is unacceptable as a ground for using the Parsimony Principle to decide the fate of hypotheses of homology because such a use would simply beg the question concerning whether evolution generally—or always—is dynamically parsimonious (Rieppel 2007).

And although there appears to be an almost universal consensus concerning the acceptability of the aforementioned criteria of homology, this discussion is ongoing and its status may change. If so, then this will clearly also have an effect on the status of the corresponding criteria here proposed for functional homology.

- (2) Secondly, biologists disagree with respect to whether the concept of morphological homology should (or should not) have a *causal grounding*; that is to say, some of them accept while others reject the view that any two traits or characters must share an *underlying structure or mechanism* in order to be homologous. Until now, the characterization of homology as sameness due to common ancestry does not provide us with sufficient elements to conclude that this sameness must be grounded in a deeper structural sameness. In fact, it could well be the case that the only thing that homologous characters have in common is the fact that they have a common ancestor. However, some

biologists deny this; they argue that, were the concept of homology to lack a suitable underlying causal base, then it would also lack theoretical—possibly also practical and heuristic—interest (e.g., Müller 2003 and Laubichler 2000). For example, Gunther Wagner argues that two characters are homologous when the same set of regulatory genetic networks are part of their ontogenetic development (Wagner 2007, p. 473), while Gerd Müller thinks that the deeper structure underlying homologous characters is of a more general organizational sort. He calls it ‘organizational homology’, and says: “Homologues are autonomized elements of the morphological phenotype that are maintained in evolution due to their organizational roles in heritable, genetic, and structural assemblies.” (Müller 2003, p. 65). However the interest of these proposals, there is not as yet a consensus among biologists concerning the acceptability of these and other proposals concerning a putative causal base to the concept of homology (Rieppel 2007, Müller 2003, Striedter and Northcutt 1991).

Notice that my proposal in the direction of a concept of functional homology may suffer different fates depending upon which causal base theory for morphological homology is ultimately accepted by most biologists (if any). If, for example, Wagner’s proposal is accepted then, for various reasons I cannot go into here, I find it very unlikely that a uniform regulatory genetic base exists for what may turn out to be functional homologues in my theory—or at least, its application to most of cognitive science. On the other hand, Müller’s wider proposal may fit, if only partially, my notion of functional homology because his proposal goes in a direction similar to mine: if I understand him correctly, both our proposals go in the direction of understanding homology in terms of the sameness of organizational place and role that a morphological (in my case, a functional) element has in certain kinds of assemblies, including assemblies at lower levels of description.

- (3) Furthermore, there is a debate surrounding the question as to whether the individuation of characters is irremediably subjective—and, if it is not, then how one *should* go about individuating characters when constructing phylogenies and, thus, when determining the acceptability of certain hypotheses of homology. This discussion is of cardinal importance

to the issue concerning the degree of objectivity that can or cannot be achieved in the discovery of homologies, and concerning the existence or inexistence of a causal base for homology. As we saw in Sections I and II above, the Principle of Parsimony is of central importance in the construction of cladograms that are used in the Secondary Homology step when determining the acceptability (or inacceptability) of certain hypotheses of homology. This principle tells us that, among all of the possible cladograms that can be constructed for a group of taxa, we must choose the one that postulates the least number of evolutionary changes—and this cladogram will be the one used to determine the acceptability of a homology hypothesis. But, as Richards explains,

The number of evolutionary changes required by an hypothesis is . . . a consequence of the number of characters that change. (Richards 2002, p. 4).

In other words, two different character individuation strategies often support different and equally parsimonious cladogram structures leading to the acceptance of two different and *incompatible* homology hypotheses. And different pedagogical and disciplinary traditions frequently adopt different ways of individuating characters (see also Griffiths 2006). But Richards does not stop here; he further argues that there is no reason at all to think that there will be a unique individuation procedure, or that any such procedure *should* exist (cf. Rieppel and Kearney 2007). He says: “the application of the parsimony principle is ultimately indeterminate because the choice and individuation of characters that figure in parsimony computations are indeterminate” (Richards 2002, p. 1).

The question as to the individuation of characters, in the context of *functional homology*, involves very difficult issues concerning the individuation of functional systems and their ontological status—i.e., issues as to what makes one functional system different from another, what the epistemological criteria are for their identification, whether and when one can regard the postulation of a functional system as ontologically substantial. These are real issues that are much discussed in various philosophical and psychological contexts. Unfortunately, the consideration of these discussions and their plausible resolution

in connection with our concept of functional homology, albeit very necessary, cannot be undertaken here due to obvious limitations of space.

IV. Functional Homology and Molecular Developmental Genetics.

In this section, I show how my proposal would work in the field of molecular developmental genetics, and why it is to be preferred over other characterizations of functional homology in the field. As far as I know, there are only two explicit proposals to characterize functional homology in connection with some of the entities studied at the molecular developmental genetic level. These proposals are made by Ehab Abouheif (1999) and Alan Love (2007). Let us examine each in turn.

Abouheif (1999) proposes some homology criteria for regulatory gene networks (RGNs). An RGN is constituted by a functionally individuated set of genes and their interactions. At a first pass, he characterizes homology for RGNs as follows: “For two regulatory networks to be homologous, all the genes and their interactions must be derived from a network in the most recent common ancestor.” (Abouheif 1999, p. 208). He also fashions an additional *novel* category, which he calls ‘*partial homology*’ for RGNs:

For networks to be partly homologous, some genes and their interactions must be derived from the most recent common ancestor, whereas others must have been recruited into the pathway since the divergence of the species being compared. (Ibid., p. 209)

So, for two RGNs to be homologous, two conditions have to be fulfilled: First, all of their constitutive *genes* have to be homologous; and secondly, all of the *interactions* among their genes must also be homologous. Now, two genes are homologous when they are orthologues of each other—i.e., they are gene copies resulting from speciation (Abouheif, *et al.*, 1997). On the other hand, concerning the homology of the genetic interactions constitutive of two RGNs, say S1 and S2, Abouheif proposes the following criteria: (1) the biochemical and the developmental *functions* of the genes of S1 are *similar* to those of S2; and (2) the relative spatial positions in which the corresponding genes are expressed are similar as well. If these criteria are fulfilled, says Abouheif, then there is some evidence to think that R1 and R2 are homologous.

However, just as in the case of morphological homology, the most important test for the homology of RGNs for Abouheif consists in the application of the criterion of congruence: “all of the genes and [their] interactions in the network should be analysed individually and defined as discrete taxonomic characters”

(Abouheif 1999, p. 214); then a phylogenetic tree for those characters must be constructed using the Principle of Parsimony.

Let us now compare Abouheif's proposal with ours. In our proposal, two distinct levels are involved in determining whether two RGNs are (or are not) homologous:

- (a) There is the level of genes and their biochemical and developmental functions (i.e., their interactions); and
- (b) there is also the level of RGNs and their functions.⁴

Indeed, our analysis directs us to consider RGNs as functional systems. We also consider as functional systems those which include particular genes and their biochemical functions. Suppose we are considering two RGNs, S1 and S2, in two classes of organisms, and are trying to determine whether or not they are homologous. The first two minimum necessary conditions to be fulfilled for S1 and S2 to be homologous are the following:

1. There is a function F which both S1 and S2 fulfill (perhaps in a different manner at the subsystemic level); and
2. S1 and S2 are functional parts of two larger functional systems, T1 and T2 respectively, which fulfill the same function F*.

To be a bit more specific, S1 and S2 fulfill the same biochemical function—albeit differently at their subsystemic (genetic) levels—while being parts of two corresponding larger RGNs, T1 and T2, which undertake the same function (perhaps differently) within a larger developmental process in the developing embryo.

Furthermore, to be homologous, S1 and S2 have to fulfill to an appropriate degree some (or, if possible, all) the Primary Homology criteria for functional systems, and then the Secondary Homology cladistic criterion of Congruence. For example, our criterion of Relative Position for functional systems tells us to look for significant similarities between the larger T1 and T2 (of which S1 and S2 are parts) at the subsystemic functional level—and this will instruct us to go one level down to determine whether there are

⁴ Although Abouheif agrees that RGNs constitute “a distinct level of biological organization” (Ibid., 212), he does not incorporate this idea into his statement of the criteria for homology of RGNs, since his criteria only require one to determine homology for the entities in level (a)—i.e., genes and their functions—and not for those in level (b), to wit, the RGNs themselves.

interesting similarities between the constitutive genes of each of the subsystems of T1 and T2, their functions, and the manner in which they are integrated to fulfill developmental function F*.

Notice that our criteria for functional homology *do not* require that, if S1 and S2 are homologous, then they must be identical in all of their subsystemic or implementational details—i.e., they do not require that they have the exact same genes with the exact same biochemical and developmental functions carried out in the exact same manner—neither does it require that the larger systems T1 and T2 are subsystemically or implementationally identical. In contrast, Abouheif's analysis does seem to require this. He says:

Some members of a genetic network may be obligately linked . For example, tissues or cells expressing the signaling molecule *hedgehog* can, as far as known, only be perceived by the receptor molecule *patched* . . . Currently the only clear examples of obligate linkage are between genes that transmit signals within and between cells, particularly, ligands and their receptors. The more obligate linkages there are in a regulatory gene network, the more likely it is to be conserved. (Abouheif 1999, p. 209)

In other words, the more the regulatory linkages in an RGN are obligate (i.e., linkages where there can be no functional substitution of a gene or molecule of one kind for another of a different kind), the more such an RGN is likely to be conserved through evolutionary changes, such as speciation, and thus the more likely they are to remain *homologous* across different taxa. On the other hand, Abouheif adds, an RGN that contains many linkages that are not obligate but facultative will tend to experience functional gene substitutions through important evolutionary changes, and thus will at most remain *partially* homologous to its ancestors.

Thus, for Abouheif, if two RGNs are (fully) homologous, their linkages and their genes must be identical—there appears to be little room in his analysis for interesting (subsystemic and/or implementational) differences between homologous RGNs. Indeed, in the discussion that follows Abouheif's paper, a number of well-known biologists such as Wray, Wagner, Striedter and Hall, mention this consequence as a shortcoming of Abouheif's analysis (Abouheif 1999, pp. 222-225). My analysis, in contrast, does not have any such consequence.

Let us now turn to examine Alan Love's (2007) proposal. He has recently proposed an interesting characterization of functional homology—or, as he calls it, '*homology of function*'—and some criteria for it. He starts out by explaining his distinction between two senses of 'function': *activity-function* (what something

does), and *use-function* (what it is for). An activity-function is a ‘mere activity’ whose description “does not invoke a specific variety of functional contribution.” (Love 2007: 696). Under *use-function*, Love subsumes most of the concepts of function that have been proposed by philosophers of science—principally, of biology and psychology. Love distinguishes at least three types of *use-function* concepts:

- (a) *causal role* concepts, referring to the contribution to a capacity;⁵
- (b) fitness advantage or *viability* concepts; roughly, they emphasize the value of having something;⁶ and
- (c) *selected effect* or etiological concepts, which involve reference to the origination and maintenance via natural selection (Love 2007, p. 696).⁷

Then Love argues that

only an activity interpretation (‘what something does’) accents the ‘function’ itself, apart from its specific contribution to a systemic capacity and position in a larger context. Therefore, the appropriate meaning for ‘homology of function’ is activity not causal role, since activity can remain constant ‘under every variety of form and function’. (Love 2007, p. 695)

Indeed, Love’s central proposal is that the most appropriate notion of functional homology must be characterized as “the same *activity-function* in different animals under every variety of form and *use-function*.” (Ibid., p. 696).

Concerning the criteria one can use to identify sameness of activity-functions in different organisms, Love starts out by reminding us that, in the case of structural homology, “correspondence relations among structurally homologous features are established by criteria such as relative position and/or connection, similarity of structural detail, special quality and embryological origin.” (Ibid., p. 700) He then suggests that we seek out “a criterion [for activity-function homology] that plays a role analogous to that of relative position in structural homology judgments.” (Ibid.), and proposes *organization* as a criterion. According to him,

Organization refers to how activities are arranged so as to contribute to causal roles, . . .

Organization also takes into account same level and inter-level relationships, . . . ‘Component’ activity-functions are homologous because of *interconnected interdependencies within a larger*

⁵ Robert Cummins (1975) has the best known account of function of this kind.

⁶ Concepts such as these have been defended by a number of philosophers of biology, e.g., John Bigelow and Robert Pargetter (1987).

⁷ A concept of this sort was originally proposed by Ruth Millikan (1989).

system, including both structural organization (e.g., part-whole hierarchies) and functional organization (e.g., temporal hierarchies). (Ibid., my emphasis).

However, the very distinction between activity and causal-role functions in Love seems to me to be *ungrounded*. To speak of the activity of a thing is already to speak of the causal effects (however immediate) that thing brings about in other things; doing something is bringing something about, that is, *having a certain causal role*, however local. The examples Love considers as characteristic activity-functions such as the biochemical function of a regulatory gene (Love 2007, p. 697), the visceral mesoderm specification function of the homeodomains for vertebrate *Nkx2-5* and *Drosophila tinman* (Ibid., p. 698), the firing of an individual muscle, the beating of the heart, or capillary diffusion (Ibid., p. 701), are all cases where some effect is brought about—in some cases, a temporally/spatially immediate effect, in others an effect not so immediate. But if so—if the description of any activity of any entity always makes reference to one or more of the effects that that entity brings about, i.e., always makes reference to either its local or its larger causal role—then there is no principled distinction between activity and causal role.

Perhaps Love would be prepared to accept this consequence.⁸ However, there is another consequence of Love's proposal that, I think, flies off in the face of what one would want to say concerning any interesting homology concept—morphological, functional, or otherwise.

The core idea of any homology concept as applied to entities S1 and S2, is that they can differ considerably among themselves (at one or more levels of description) and yet be *the same*, because they derive from a common ancestor. But, as we explained, there is the additional and more interesting issue of the criteria for homology: how one can go about recognizing homologies *in the present*. Concerning morphological homology there is some sort of a consensus concerning the criteria of Primary and Secondary homology. The criterion of Relative Position in *morphology*, for example, indicates that evidence that two traits T1 and T2 are homologous can be found if one can establish sufficient correspondences between (a) the network of spatial, physiological and morphological relations of trait T1 with other traits in the appropriate organism, and (b) the same network of relations of T2 with other corresponding traits in the other organism.

⁸ For example, Love points out that the same process involving a certain item can be considered both as its activity-function and as its use-function, depending upon the level of organization at which one is looking. He says: "the capacity defining the use-function of a regulatory gene at one level of organization, such as axial patterning, must be considered as an activity-function itself at another level of organization, such as the differentiation of serially repeated elements along a body axis." (Love 2007, p. 698)

So, one has to consider the one trait T1 and the manner in which it relates spatially, physiologically, etc., with other traits T1₁, . . . , T1_n in the same organism—and the same for T2. The *network*₁ of suitable relations of T1 with T1₁, . . . , T1_n in the first organism is then compared with the *network*₂ of suitable relations of T2 with T2₁, . . . , T2_n in the second organism. If there are strong and relevant similarities between those networks, then the criterion is met. We can now appreciate that our criterion of relative position for *functional homology* is structurally very similar to the one accepted in the field of comparative morphology—but Alan Love’s criterion of ‘organization’ is not. Let us see.

As we saw, he characterizes homology of function as ‘the same activity-function in different animals under every variety of form and use-function’ (Love 2007, p. 696). He then states his ‘criterion of organization’ as follows:

‘Component’ activity-functions are homologous because of *interconnected interdependencies within a larger system*, including both structural organization (e.g., part-whole hierarchies) and functional organization (e.g., temporal hierarchies). (Ibid., p. 700, my emphasis)

Although it is far from clear what Love is saying here—e.g., what role do these ‘interdependencies in a larger system’ play in the determination of homology?, do they have to be similar?, can they be different?—his meaning seems to get clearer once we realize that he wants to allow for the possibility that the activity-functions—i.e., the biochemical functions—of two genes are homologous, for example, even though their use-functions—i.e., their developmental functions in larger functional systems—are very different. For example, he says that

Biochemical *activity*-functions of genes are often conserved (i.e., homologous), while simultaneously being available for co-option to make causal role contributions (*use*-functions) to distinct developmental processes. The same regulatory genes are evolutionarily stable in terms of activity-function and evolutionarily labile in terms of use-function. (Love 2007, p. 697)

But this appears to go directly against the spirit of the aforementioned criterion: as we saw, this criterion directs us to find evidence for the homology of two entities—in this case, the functional systems S1 and S2 that include certain homologous genes and their biochemical effects on one or more other proteins or molecules—by locating them as parts of *larger functional contexts* T1 and T2 that are *functionally (and thus subsystemically and implementationally) similar in important respects*—in our case, as parts of larger similar

RGNs or other developmental processes. But this means that to find evidence that two such genetic systems, S1 and S2, are homologous, they need to be embedded within larger functional systems T1 and T2, that are functionally *similar* in important respects—although they may differ in certain other respects.

Thus, according to our relative position criterion, there are *restrictions* as to how much T1 and T2 can differ functionally—subsystemically and implementationally—for S1 and S2 to be still considered as functionally homologous—there are *restrictions*, in other words, as to how different two larger functional (e.g., developmental) contexts can be in which the corresponding gene's same biochemical functions are inserted, for those biochemical functions still to be thought of as homologous. Love does not seem to think that these restrictions are necessary: “Biochemical *activity*-functions of genes are often conserved . . . , while simultaneously being available for co-option to make *causal role contributions (use-functions) to distinct developmental processes.*” (Love 2007, p. 697; my emphasis)—and this, I have argued, constitutes an important *disanalogy* with the criterion of Relative Position whose idea is that one has to look at the larger—in our case, functional—context to find evidence in favor of a homology hypothesis.

Love can respond that, if one understands the criterion of relative position as I do, then it has almost no application to molecular developmental genetics, given that the functional phenomena studied in this field rarely have the ontological structure required by my criterion. As he put it above: it is often the case that a regulatory gene or set of genes have their “activity function” conserved while their contribution in a larger developmental functional context changes—or, to put it in the terminology of functional systems: oftentimes, the functional system consisting of a regulatory gene (or set of genes) reappears in many *functionally distinct* larger (developmental) systems in different organisms. What is conserved is the gene (or set of genes), what tends to change is the larger functional developmental context in which the gene makes its subsystemic contribution.

If Love is right in thinking that this is how most of the phenomena in molecular developmental genetics behave—and Abouheif (1999, p. 211) appears to agree with him on this—then my criterion of relative position simply has no application in this field. But note that, if Love and Abouheif are right, then their corresponding criterion of homology for two genetic functional systems cannot appeal to similarities between the larger functional contexts in which each of them appears, and thus it boils down to saying that—*independently of their larger functional contexts—they are homologous simply when they consist of the same*

genes having the same functions. The worry is that this move reduces the concept of homology to something rather uninteresting—a worry that, as we saw, was voiced by the biologists discussing Abouheif’s proposal.

Of course, this discussion is by no means over; much more can be said on either side. All I want to say at this point is that, if Love and Abouheif are right concerning the behavior of molecular developmental genetic phenomena, then my proposal with respect to the criterion of relative position with respect to functional systems will have no application in this discipline. If they are right, however, the consequence also follows that there appears to be no way to articulate an interesting concept of homology in molecular developmental genetics—where an interesting homology concept in this field would be one which would allow for two genetic functional systems—say, two RGNs—*to be somewhat different at the subsystemic and/or implementational level, and yet in some sense be the same type of phenomenon—i.e., be homologous.*

V. Functional Homology in Evolutionary Cognitive Science.

In section III, I gave a very sketchy idea as to how the concept of functional homology—as I articulated it—can apply to the study of behavior in ethology, when that behavior is described in some functional manner. There is, however, a great deal of discussion in ethology concerning the manner in which the behavior of an organism should be described when studying its evolutionary history, i.e., whether it should (or should not) be characterized simply as a set of physical motions, or also in terms of some of the behavior’s physical effects on the organism’s environment—and if so, which of the many effects of the behavior, etc. There is also a discussion concerning whether—and if so, when—one should postulate internal cognitive mechanisms in order to explain a behavior or set of behaviors. Many ethologists—e.g., those working on spiders, ants, arthropods in general, fish, and some birds—tend to conceive of behaviors (as much as possible) as sets of stereotypical physical motion patterns, and to determine the homology of behaviors in a way that includes their immediate salient physical effects (e.g., nests, webs, etc.); they try to skirt (as much as possible) the description of behavior in functional terms. Furthermore, they avoid any talk of internal cognitive mechanisms, and thus any talk of the homology of such things (de Queiroz, *et al.*, 1993; Lee, *et al.*, 1996; Bosch, *et al.*, 2001; Benjamin, *et al.*, 2004). In other words, ethologists of this persuasion try to conceptualize behavior as morphological characters as much as possible. This approach, however, would be extremely limited when studying human behavior—indeed, it is extremely limited when applied to the study of the more interesting behaviors of birds and mammals.

These last two points can be—and have been exhaustively—argued throughout the history of a number of disciplines (from cognitive ethology, psychology, cognitive science, philosophy of mind and of psychology, etc.) during this and last centuries. For one, the virtual absence of stereotypical behaviors (behaviors that consist in roughly the same patterns of the same physical motions) in many relatively complex biological organisms capable of cognition, radically restricts the applicability of such an approach. What this means is that a concept of homology as applied to behaviors-as-patterns-of-physical-motions would have virtually no applicability in the study of most behaviors of those cognitively complex organisms. A functional description of behaviors becomes inescapable in these cases.

Furthermore, talking about homology in connection with functionally described behaviors will probably not be sufficient to appreciate the full extent to which cognitive traits have been conserved throughout the evolution of cognitively complex organisms. We also need to look at the level of *cognitive systems*, and fashion a concept of homology that will allow us to detect those cognitive capacities that have somehow been evolutionarily conserved (with modifications), and those that are evolutionarily novel—and this is precisely what we have been trying to do here: fashioning such a concept.

Questions such as whether the capacity for language in humans is an evolutionary novelty—or whether there is a capacity in bonobos or the other great apes that is somehow homologous to our language capacity (or to parts of it)—questions like this, I say, can be answered only when we have a good, clear concept of functional homology (and its associated criteria). If our proposed concept is accepted, then saying that both the communicative capacity in bonobos and the linguistic capacity of humans could not have descended (with modifications) from a communicative capacity in a common ancestor because the bonobos' capacity is—implementationally and/or subsystemically—different from the human linguistic capacity (*and it is*), is not enough—it would be like saying that the bones of the jaws in reptiles and the bones of the middle ears of mammals are not the same trait (that the latter are evolutionary novelties) because they are morphologically and functionally so different! In our case, one has to make further, larger functional systemic comparisons (as in our criteria for functional homology: relative position, continuity, etc.) as well as the congruence test for the corresponding functional cognitive systems taking into account many of the subsystemic and implementational characteristics of each, as we have suggested in Section III. And after all

this is done, the answer may be affirmative; it may be that those two communicative capacities—in bonobos and in humans—albeit ostensibly different in various respects, are nonetheless homologous.

But let me be clear: I am not saying that those capacities are homologous—neither am I saying that it is likely they are. All I am saying is that questions concerning whether two cognitive capacities are (or are not) the same—whether or not they are homologous—cannot be resolved simply by looking at the functional similarities and differences among those two capacities in isolation from the rest of the cognitive capacities of the organisms in question, their implementation in their brains, their functional subsystemic structure, etc.

VI. Conclusions.

Much more work needs to be done to make my proposal clearer and useful in practice. So far, I have only provided the abstract conceptual background needed to articulate homology hypotheses relative to cognitive systems—and to get some ideas concerning how the corresponding empirical criteria could be understood.

Whether my proposal is applicable in the field of molecular developmental genetics remains to be seen; if so, then interesting functional homology assertions can be made in this context and their evidence found.

Furthermore, my proposed concept of functional homology can be applied to animal behavior in fields such as cognitive ethology, so long as behavior is characterized functionally.

BIBLIOGRAPHY

Benjamin, S. P. and S. Zschokke (2004), “Homology, Behaviour and Spider Webs: Web Construction Behavior of *Linyphia hortensis* and *L. triangularis* (Araneae: Linyphiidae) and its evolutionary significance” *Journal of Evolutionary Biology* 17: 120-130.

Bigelow, John and Robert Pargetter (1987), “Functions” *The Journal of Philosophy* 84: 181-196.

Bosch, Jordi, Yasuo Maeta, and Richard Rust (2001), “A Phylogenetic Analysis of Nesting Behavior in the Genus *Osmia* (Hymenoptera: Megachilidae)” *Annals of the Entomological Society of America* 94: 617-627.

Brigandt, Ingo and Paul E. Griffiths (2007), “The Importance of Homology for Biology and Philosophy” *Biology and Philosophy* 22: 633-641

Cummins, Robert (1975), “Functional Analysis” *The Journal of Philosophy* 72: 741-765.

de Pinna, Mario G. G. (1991), “Concepts and Tests of Homology in the Cladistic Paradigm” *Cladistics* 7: 367-394.

de Queiroz, Alan, and Peter H. Wimberger (1993), “The Usefulness of Behavior for Phylogeny Estimation: Levels of Homoplasy in Behavioral and Morphological Characters” *Evolution* 47: 46-60.

Ereshefsky, Marc (2007), “Psychological Categories as Homologies: Lessons from Ethology” *Biology and Philosophy* 22: 659-674.

- Futuyma, D. (1998). *Evolutionary Biology*. Third edition. Sunderland, Massachusetts: Sinauer Associates, Inc.
- García, C. L. (2007), "Cognitive Modularity, Biological Modularity and Evolvability" *Biological Theory: Integrating Evolution, Development and Cognition*, 2 (1), pp. 62-73.
- Griffiths, Paul E. (2006), "Function, Homology and Character Individuation" *Philosophy of Science* 73: 1-25.
- Hall, Brian K. (1994), "Introduction". In Brian K. Hall (ed.), *Homology: The Hierarchical Basis of Comparative Biology*. San Diego, California: Academic Press, pp. 1-19.
- Hennig, Willi (1950), *Grundzüge einer Theorie der Phylogenetischen Systematik*. Berlin, Deutscher Zentralverlag.
- Laubichler, Manfred D. (2000), "Homology in Development and the Development of the Homology Concept" *American Zoologist* 40: 777-788.
- Lee, Patricia L. M., Dale H. Clayton, Richard Griffiths, and Roderick D. M. Page (1996), "Does Behavior Reflect Phylogeny in Swiftlets (Aves: Apodidae)? A Test Using Cytochrome *b* Mitochondrial DNA Sequences" *Proceedings of the National Academy of Sciences USA* 93: 7091-7096.
- Love, Alan (2007), "Functional Homology and Homology of Function: Biological concepts and Philosophical Consequences" *Biology and Philosophy* 22 (5):
- Millikan, Ruth Garrett (1984), *Language, Thought, and Other Biological Categories* (Cambridge, Massachusetts: The MIT Press).
- Müller, Gerd (2003), "Homology: The Evolution of Morphological Organization". In: Gerd B. Muller and Stuart A. Newman (eds.), *The Origination of Organismal Form: Beyond the Gene in Developmental and Evolutionary Biology*. (Cambridge, Massachusetts: The MIT Press), pp. 51-69.
- Remane, Adolf (1952), *Die Grundlagen des natürlichen Systems, der vergleichenden Anatomie und der Phylogenetik*. Akademische Verlagsgesellschaft, Leipzig.
- Owen, Richard, (1843), *Lectures on the comparative anatomy and physiology of the invertebrate animals*. London: Longman, Brown, Green and Longmans.
- Richards, Richard (2002), "Kuhnian Values and Cladistic Parsimony" *Perspectives on Science* 10 (1): 1-27.
- Rieppel, Olivier (2005), "Modules, Kinds and Homology" *Journal of Experimental Zoology (Mol Dev Evol)* 304B: 18-27.
- Rieppel, Olivier (2007), "The Nature of Parsimony and Instrumentalism in Systematics" *Journal of Zoology, Systematics and Evolution Res* 45 (3): 177-183.
- Rieppel, Olivier and Maureen Kearney (2007), "The Poverty of Taxonomic Characters" *Biology and Philosophy* 22: 95-113.
- Striedter, Georg F. and R. Glenn Northcutt (1991), "Biological Hierarchies and the Concept of Homology" *Brain, Behavior and Evolution* 38: 177-189.
- Wagner, Gunther (1989), "The Biological Concept of Homology" *Annual Review of Ecology and Systematics* 20: 51-69.
- Wagner, Gunther (2007), "The Developmental Genetics of Homology" *Nature Reviews: Genetics* 8: 473-479.
- Wenzel, John W (1992), "Behavioral Homology and Phylogeny" *Annual Review of Ecology and Systematics* 23: 361-381.