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Functional Complexity in Organisms: Parts as Proxies

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Abstract. The functional complexity, or the number of functions, of organisms has figured prominently in certain theoretical and empirical work in evolutionary biology. Large-scale trends in functional complexity and correlations between functional complexity and other variables, such as size, have been proposed. However, the notion of number of functions has also been operationally intractable, in that no method has been developed for counting functions in an organism in a systematic and reliable way. Thus, studies have had to rely on the largely unsupported assumption that number of functions can be measured indirectly, by using number of morphological, physiological, and behavioral "parts" as a proxy. Here, a model is developed that supports this assumption. Specifically, the model predicts that few parts will have many functions overlapping in them, and therefore the variance in number of functions per part will be low. If so, then number of parts is expected to be well correlated with number of functions, and we can use part counts as proxies for function counts in comparative studies of organisms, even when part counts are low. Also discussed briefly is a strategy for identifying certain kinds of parts in organisms in a systematic way.

Key words: complexity, evolution, function, modularity, parts

1. Introduction

Cats seem to be more capable animals than clams, on the whole. That is, a cat seems to have a greater range of abilities, to be able to perform more functions.[1] But how would one demonstrate this? No list of functions has been compiled for any organism, nor does any reliable, systematic method for compiling such a list exist. Function in organisms is understood (in one sense; see below) to be the product of natural selection, and without knowing the selective forces that have operated on an organism over its evolutionary history, it is hopeless to try to identify and count functions directly (Brandon 1999). Nor could we with any confidence compile a list based on *a priori* considerations of what functions are required, of what an organism must be able to do to survive and reproduce. Clams may have vast numbers of functions in dimensions that our immersion in our own ecology makes it difficult for us to see, or even to imagine.

One possible practical approach is to use number of different morphological structures, physiological cycles, or behaviors as an indirect measure of number of functions. Or, in the terms I will use in this paper, we might assume that number of different "parts" is a good proxy for number of different functions, or "functional complexity." Indeed, at least impressionistically, cats do seem to have more internal structures and larger behavioral repertoires than clams.[2]

This use of parts as a proxy for functional complexity has figured prominently in certain empirical work in evolutionary biology. For example, Bonner (1988) speculated that selection for greater efficiency should favor increased division of labor within organisms, and therefore lead to an increase over the history of life in the number of different internal functions an organism is able to perform.[3] He used number of cell types as a proxy for number of internal functions, and argued that the upper limit on number of cell types for metazoans has tended to increase (see also Valentine et al. 1993). And Bell and Mooers (1997; also Bonner 1988) demonstrated a correlation between organismal size and number of internal functions, also using number of cell types as a proxy.

Cisne (1974) proposed that increasing taxonomic diversity should produce an increase in the complexity of ecological roles, and that organisms with a greater number of different morphological "tools" should then evolve to fill those more complex roles. In present terms, the argument seems to be that increasing diversity demands increasing functional complexity, which in turn will be reflected in greater numbers of parts. (A similar argument was discussed briefly by Waddington [1969]; see also Darwin's Notebook E [Barrett et al. 1987].) A connection between phenotypic and functional complexity has also figured in certain theoretical work; for example, Godfrey-Smith (1996) proposed that environmental heterogeneity is correlated with behavioral complexity, which he understood as a kind of functional complexity.

Undeniably, these studies have taken some imaginative approaches and produced some provocative findings. But shadowing this work have been two serious concerns. First, the assumption that number of types of morphological, physiological, and behavioral parts in organisms is well correlated with number of functions, and therefore can be used as a proxy for it, is undemonstrated. The assumption might sound reasonable, but it is not obvious that it must be so. Functional units in organisms do not always coincide with discrete structures or behaviors. And it is at least conceivable that many or even most functions might ignore part boundaries and instead be distributed more globally, as the so-called fight-or-flight response seems to be, or at a smaller scale, as memory seems to be within the brain.

Second, the use of the part-types proxy presents difficulties of its own. The empirical approaches discussed have shrewdly made use of cases where parts are obvious (e.g., cells), and where counting types is fairly uncontroversial. But this opportunistic approach leaves the relevant conceptual issues unresolved. What are parts, in principle? And on what basis can we identify them in cases where their distinctiveness as part is not obvious?

Here I offer a rationale for why, given certain assumptions, number of part types should be well correlated with numbers of functions, and therefore part-type counts can be used as proxies in making comparisons in functional complexity among organisms. Stated more cautiously, my purpose is to make explicit an argument and set of assumptions that would be sufficient to establish a good correlation between parts and functions. One virtue of this explicitness is that it makes a careful examination of the assumptions – and perhaps even empirical testing of them – possible.

Briefly, the argument is this: I define a part as a system that is highly connected or integrated internally and also isolated to some degree from its surround, a definition which corresponds fairly well to our intuitive understanding of the term. I then argue that a functional system requires both internal integration, in order to achieve the coordination required for function, and external isolation, to minimize outside interference with that coordination. Therefore, in the evolution of organisms, natural selection can be expected to have localized functions in parts to some extent.

This is not to say that number of parts ought to equal number of functions. As I will try to show, a number of distinct functions may use, or overlap in, the same part. Nevertheless, I will argue, number of part-types should be well correlated with number of functions. And therefore in comparisons among organisms, number of part-types ought to be a reasonable proxy for number of functions.

The argument is based on and extends theoretical work on integration and isolation by Bonner (1988), Olson and Miller (1958), and Mishler and Brandon (1987); on modularity by Wagner and Altenberg (1996), Mittenthal et al. (1992), and Raff (1996); on criteria for entities by Campbell (1958); on complex systems decomposition by Simon (1969), Levins (1973), and Wimsatt (1974); and on hierarchy by Salthe (1985, 1993). And it complements theoretical work suggesting possibly-analogous relationships between parts and functions at higher levels of organization, for example, between functional complexity and morphological division of labor in colonies (e.g., Wilson 1968; Schopf 1973; Oster and Wilson 1978), and at the ecological level between environmental heterogeneity and specialization (e.g., Levins 1968).

In the discussion that follows, I first examine function, explaining how for present purposes functions are to be understood and considering the theoretical and practical difficulties involved in counting them. Next I do the same for parts. Then follows a more detailed version of the argument that parts and functions should be well correlated, along with a brief discussion of the relationship between the present argument and a related one concerning developmental modules by Wagner and Altenberg (1996). Finally, I attempt to show in a cursory way how the parts in an organism – or at least a representative sample of them – can be counted in practice.

2. Functional complexity

Various conceptual problems arise in connection with the notion of "number of functions." Some will be discussed shortly, and hints will be offered for how they might be handled in principle. However, most can be left unresolved. For present purposes, little more is required than to explain how the word function is being used and to establish a sense in which one organism may be said to have more or fewer functions than another.

A clarification is necessary first: at issue is the number of *different* functions and later, the number of *different* parts. Thus, for example, a cell with 100 mitochondria might have the same number of different function types as an otherwise identical cell with only 10. (Of course, in principle, the former could be understood to have more if *degree* of function is thereby enhanced, but here functions are treated as discrete, as either present or absent; see below.) However, for both functions and parts, it will frequently be convenient to omit the word "types."[4]

2.1 *Function*

Two views of function in organisms have been acknowledged (Brandon, in press). In what has been called the etiological, or historical, view, the function of an organismal structure is the job or task for which it was designed by natural selection acting in the past; in other words, functions are "selected effects" (Neander 1991). In the ahistorical view, the function of a structure is its present contribution to some capacity of the organism, or the structure's present "causal role," regardless of its selective history (Amundson and Lauder 1994). Here I adopt the "selected effects" view, because it makes the argument connecting parts and functions more straightforward. However, the argument could be modified, I believe, to accommodate a causal role view.

Thus, the functional complexity of an organism is simply the number of different tasks it has been selected to perform. Unfortunately, no clearcut illustrative comparisons – say between a functionally simple and a functionally complex organism – are available in biology. The reason is that, as discussed, for any particular species, we are quite ignorant of the selective forces that have acted on it.

For illustrative purposes, however, we can turn to human technology. For example, a Swiss Army knife is functionally more complex than an ordinary screwdriver. Most screwdrivers are designed exclusively to install screws, but a typical Swiss Army knife has been engineered to function as a can opener, a knife, a saw, and so on, as well as a screwdriver. Notice that design has taken the place of selection as the cause of function, and that is why we can be fairly confident that our lists of actual functions for both devices are correct.

2.2 *Refinements and difficulties*

An understanding of functional complexity as a count of selected (or designed) capacities will be sufficient to establish a connection with parts. A more formal treatment of functional complexity would need to address certain theoretical issues, which here I will only raise.

2.2.1 *Efficaciousness*

Black bears can climb trees and may well have been selected for their ability to do so. But grey squirrels are better climbers and likely more functional in this respect than bears. Arguably, a proper measure of functional complexity would weight each function by the efficaciousness with which it is performed.

2.2.2 *Independence*

In primates, feeding and propulsion seem to be more or less independent. If so, and if both are true functions, then in a tally of functions for a primate, each would count as one. But in baleen whales, feeding and propulsion are linked, in that effective filtering of food from sea water by the baleen requires forward motion. Thus in these whales, the two functions may not be entirely distinct, and if so it would seem to follow that feeding and propulsion together should count as more than one but less than two functions. More generally, an appropriate measure of functional complexity would be one that factors out redundancies resulting from overlap among the selective forces that have acted. Thus, in a formal treatment, functional complexity would be treated as an analogue measure, and we would more properly speak of an organism's "quantity of function," than its "number of functions." For present purposes, however, the clearer discrete notion suffices.

2.2.3 *Functional hierarchy*

It seems clear that propulsion by coordinated limb movement is a function for an organism as a whole, but that a muscle contraction is a function only for a limb. In other words, at the scale of the organism, a muscle contraction is a kind of "subfunction." And a myofibril might perform a sub-subfunction. Given this hierarchy of function, at least two approaches to counting are possible. We might try to count all functions at all levels below that of the organism. But for complex organisms, this would be an enormous undertaking.

Alternatively, we might limit counts to functions that affect organismal performance directly, that is, ignoring all subfunctions, sub-subfunctions, and so on. In principle, this might be done in a consistent way using the notion of "screening off," a concept which has proved useful in distinguishing levels of selection (Brandon 1996; Roth 1991). For example, the function of the circulatory system as a whole can be said to screen off, to some extent, the function of many of the smaller blood vessels that constitute it. This is so insofar as the failure of a single small blood vessel (e.g., by occlusion) does not impair the function of the circulatory system as a whole, which has some capability to revascularize tissues deprived of sufficient blood supply. (See Brandon [1996] for a more formal treatment of screening off.) Limiting counts to organism-level functions is the approach adopted later, in the discussion of parts counting in practice. Its main virtue is that it limits counts in a consistent way and thus make counting more feasible.[5]

2.2.4 *Biases*

One might reasonably worry that because function is neither tangible nor directly observable (at least not as structure is), our perception of it in nature is prone to certain biases. For one thing, as mentioned earlier, we may be biased by our first-hand knowledge of our own anatomy and ecology and therefore somewhat blinkered in our view of function in other species. Also biasing us may be our familiarity with machines, in which function has been engineered in cognitively congenial ways; the organization of function in organisms may be radically different.

In principle, these are not problems: here functions are by definition the product of selection, thereby locating the actual standard for what constitutes a function (and for pinning down its proper hierarchical level) not in ourselves, but in nature. However, in practice, these biases may be reasons not to try to count functions directly, that is, not to try to compile a list of functions for an organism based on *a priori* considerations of what it must be able to do for itself. Oddly enough, indirect counts based on structure, using parts as proxies, may be more reliable.

2.2.5 *Arbitrariness*

It is difficult to escape the feeling that number of functions is arbitrary in the sense that it is a consequence of our choice of descriptive frame. “Chewing” sounds like a single organismal function, but what is to prevent us from arbitrarily breaking it down into two functions, say chewing vegetation and chewing insects? Again the answer is that true functionality is a product of selection, not of our arbitrary choices. To put it more precisely, in order for a described capability to count as a function, there must have been independent, heritable variation in performances efficacy at some point in the organism’s evolutionary history. For example, if there had been heritable variation in, and selection on, tooth morphology affecting ability to chew vegetation and independent variation in and selection on some other aspect of tooth morphology affecting ability to crush insects, then the two would be independent functions. Chewing by itself could be a function only if selection had acted on variation in some aspect of chewing ability that is independent of food type.

3. Parts

A part, as I use the word here, is a system that is both connected or integrated internally and disconnected or isolated with respect to its external surround (cf. Olson and Miller 1958; Simon 1969; Bonner 1988).[6] A crystal, such as a diamond, is a part. Ordinarily, a free chunk of diamond is integrated internally, in that the atoms comprising it are tightly bonded to each other. It is also isolated, in that the bonds connecting those atoms to molecules in the surrounding air are much weaker or non-existent. A cell is a part. And within a cell, a mitochondrion is a part. However, parts need not be spatially localized: a simultaneous, joint telephone conversation among a number of people who are widely scattered geographically – a conference call – is a part. Similarly, a pattern of neural and muscular activation might be a part, even if the nerve and muscle cell bodies involved are widely separated from each other; in other words, a behavior can be a part. Likewise, a physiological cycle, such as the Krebs cycle, might be a part.[7]

Both internal integration and external isolation are crucial. A set of marbles scattered on the floor is isolated from, say, other sets of marbles that are not present, but it is not internally integrated and therefore not a part. A system consisting of three out of the four people involved in a conversation is also not a part. This arbitrary subset is internally integrated but not isolated from its surround (because the surround, by assumption, includes the fourth person).

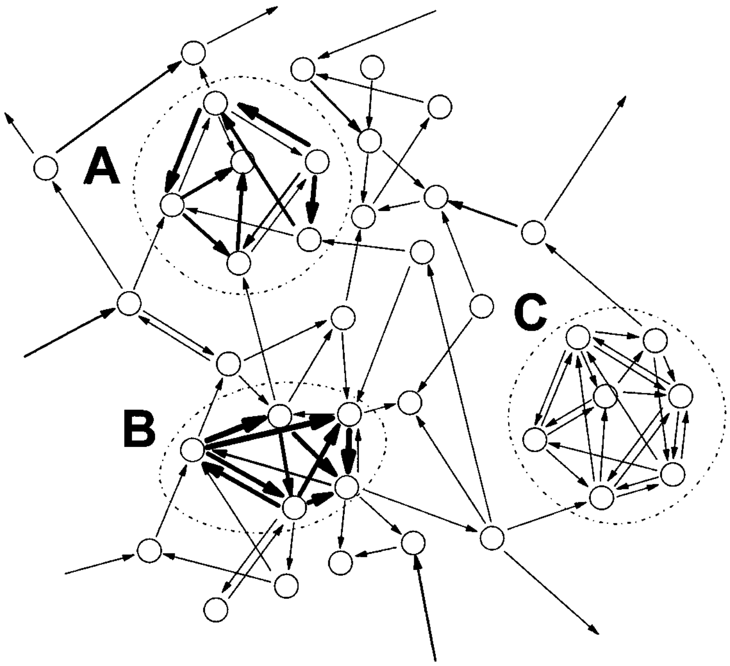

Figure 1. Three parts. Small circles are components, and arrows show interactions among them. Thickness of arrows corresponds to the strength or intensity of the interactions. Parts are indicated with large dashed circles/ovals.

Both integration and isolation are joint functions of numbers and intensity of interactions. Figure 1 shows a system in which arrows represent interactions between components and the thickness of the arrows indicates the strength or intensity of the interactions. Dashed circles or ovals circumscribe three parts. What characterizes each part is the large number of interactions and/or their greater intensity relative to the number and intensity of interactions with the surround. Part B has few internal interactions, but they are strong relative to its weaker interactions with external components. Part C has weak internal interactions but they are many relative to its external interactions. Part A is intermediate.

Notice that the extent to which a system is a part may be a matter of degree (Campbell 1958). Measures of degree of "partness," could be devised, but are not needed here. Also, partness is time-scale dependent, in that the degree of integration may vary with the length of time over which interaction is considered. Thus, a system of components may be a part on one time scale and not on another.

Notice also that partness is conceptually independent of function. A liver is both a part and functional. A rock, however, might be a part but not functional (although a rock that is used to grind corn is at least temporarily functional). Likewise, the Krebs cycle is functional, but a conference call might not be, if for example it results from an electronic malfunction producing an accidental multiple connection among strangers. The accidental conference is no less a part for all the pointless confusion it generates. Ultimately, the point here will be to argue that parts and functions ought to be closely related in organisms; in order to do so, it is necessary to keep the two notions conceptually distinct, at least initially.

Finally, none of the familiar reductionism-holism issues arise here. Parts may, but need not, have emergent properties; their status as parts is independent of such properties.

3.1 *Integration*

As indicated, systems are integrated to the degree that interactions among components are many or strong or both. In turn, an interaction between the two components is marked by the correlation it produces in their behavior (Campbell 1958), although the precise form of the correlation – such as whether it is linear or non-linear – is not important here. Further, no distinction is made between the simple correlations among components produced by cohesive forces and those produced by complex dynamical interactions (cf. Mishler and Brandon 1987). Thus, a diamond is integrated in the same sense as (and probably to a greater degree than) an *Amoeba*.

Two types of integration can be distinguished, developmental and operational. Developmental integration is the degree of interactiveness among components in the process that generates some larger system, for an organism, its ontogeny (Olson and Miller 1958; Wagner 1996; Wagner and Altenberg 1996; Cheverud 1996; Zelditch 1996). In contrast, operational integration refers to interactiveness among components independent of development, ordinarily after the system has been generated. (Obviously the distinction is not a perfectly clean one, but it is sufficiently so for present purposes.) Crucially, operation includes *all* non-developmental interactions that occur, not just the functional ones. For example, any side-reactions closely associated with the Krebs cycle are aspects of the cycle’s integration even if they are deleterious. (Thus, operational integration is not the same as what has been called “functional integration,” in the sense of Cheverud [1996] and Olson and Miller [1958].) Here, the term integration refers to operational integration, unless otherwise indicated.

3.2 *Isolation*

Isolation is the opposite of integration. In parts, isolation may be achieved by a specialized structure, a boundary, as in a gas-filled balloon or a cell. But it may also simply be the result of a termination of integration, as in a diamond.

In diamonds, balloons, and cells, the region of integration is spatially unified and demarcated. Such parts correspond to what we normally think of as objects. But in some parts, spatial unity is absent, because isolation is achieved by specificity of interaction, as in a conference call or the hormone-mediated signaling pathways of an endocrine system. Indeed, where specificity is high, the components of a part can physically intermingle with the components of another part, with little or no reduction in the mutual isolation of the two parts.

3.3 *Hierarchies of parts*

Parts may be composed of internally integrated and externally isolated sets of smaller parts, or what might be called subparts. And these subparts may in turn be composed of internally integrated and externally isolated sub-subparts, and so on. (Here, I have mostly referred to the entities comprising parts as components, rather than subparts, because their formal status is not important.) Thus, parts, like functions, may be counted at any hierarchical level, in principle; as discussed, the focus here is on parts at the level just below the organism. Of course, in organisms, the nesting of parts is not always especially neat, in that parts often overlap levels, existing partly at one level and partly at another, so to speak (Wimsatt 1974; McShea and Venit, in press). Still, considerable hierarchical structure can ordinarily be discerned and used to identify hierarchical level of parts (McShea and Venit, in press; also see below).

4. Functions and parts

In organisms, selection is expected to localize functions to some extent within parts. The reason is that a structure that is functional needs to be integrated internally in order to achieve the coordination of internal activity that function demands. And it also needs to be isolated externally to limit interference from other functions. For example, in a mammal, chewing and locomotion both require coordinated activity in a number of components (including muscles, nerves, bones, etc.), and this coordination doubtless requires considerable integration among these components. But the systems also need to be isolated from each other if, for example, a mammal is going to be able to eat and walk at the same time.

Of course, internal integration is not expected to be complete; a condition in which every component affects every other component is more likely to produce chaos than coordination (Kauffman 1993). Nor is perfect isolation expected; a part that functions in total isolation within an organism cannot coordinate its activity with other functions.[8]

4.1 *State cycles and functional overlap*

This argument might seem to predict that each function must have its own part, and therefore to predict a perfect 1:1 relationship between parts and functions. If that were the case, number of parts would be a very direct measure of number of functions. However, it seems clear that in organisms, multiple functions do overlap within the same part. In tetrapods, the vertebral column, including bones and associated ligaments, muscles, and perhaps nerves, is probably a part in which both the locomotion and support functions overlap. In some cases, the overlap may be nearly complete, with multiple functions performed almost entirely by one part. For example, a shell in a freshwater mollusc might function simultaneously for defense, ballast, calcium storage, and so on. In general, some overlap is expected in organisms in that it allows them to make more economical use of parts, and therefore it ought to be favored frequently by selection.

What makes overlap possible is that, under certain conditions, isolation can be imperfect without interference. To see this, it helps to understand functions as “state cycles” (Kauffman 1993). Figure 2 shows a state cycle schematically: a single part, represented by a large circle, undergoes a series of transitions in the course of executing some single function. The smaller, interior circles are the components of the part; the interactions among them are not shown. The shading within each small circle shows the condition of each component, its “state,” at each time. (An assumption is that every part-type has a single, unique state cycle; parts with different state cycles are considered different part types.)

Each component also has its own “state cycle.” The component located at about one o’clock (inside the large circles) has a moderately long cycle in which it assumes a total of three different states, and the sequence in which it passes through them has a moderately complex pattern. Specifically, it remains in the same state for times 1 and 2 (hatched), then switches to a different state at time 3 (shaded), and then to a third state at time 4 (clear). In contrast, the component at three o’clock has a very short and simple cycle in which it remains in the same state (solid) at all times.

Less abstractly, chewing in mammals is typically accomplished with a state cycle in which the lower jaw, the dentary, first undergoes orthal retraction, in which food is pierced; then follows a buccal phase, in which shearing

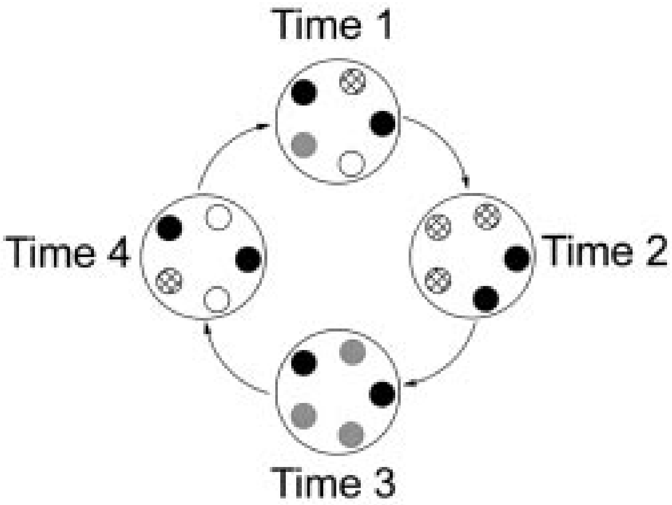

Figure 2. Schematic diagram of a state cycle for a single function (large circles). Here, five components (small circles) interact (arrows not shown) over four time steps in the performance of some function. In the course of a cycle, each component goes through some consistent sequence of state changes (shown as changes in shading) as a result of its interactions.

occurs; and finally a lingual phase, for grinding (Gingerich 1984). We might think of the two jaws and their associated teeth and muscles as components (small circles in a state-cycle diagram), and the entire ensemble as a single part (a large circle). Also suppose that the state of the components is their position in space, perhaps relative to some common reference point. Therefore, in a schematic representation of chewing, the changes in shading of the components would represent the changing positions of components as the lower jaw cycles.

Returning to the abstract discussion, Figure 3 shows how functional overlap may succeed and also how it may fail. Figure 3A shows two functions, both with state cycles of length four as in Figure 2. One function requires two components and the other requires three. The figure illustrates a situation in which the two functions are independent, meaning that they correspond to very different organismal capabilities, and in which they are also isolated from each other, meaning that they operate entirely within different parts. In Figure 3B, the two functions have been reconfigured so that they share a component, the filled circle, and thus neither is completely isolated in its own part. In this case, both functions still “work,” because the state cycle of the shared component is compatible with both. An example might be the oxygen supply requirements for locomotion and respiration.

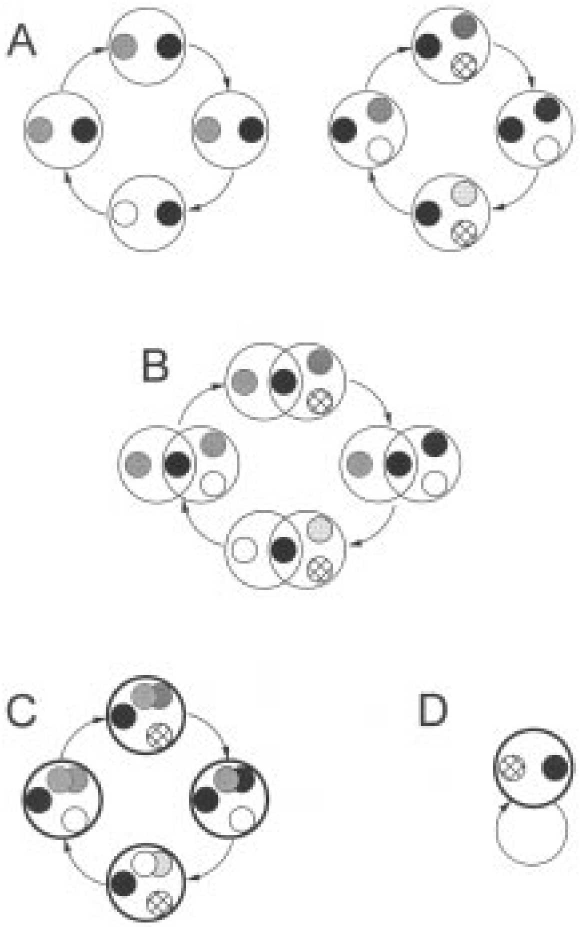

Figure 3. Sequence showing the consequences of functions “attempting” to overlap in the same part. A: State cycles for two independent functions, one with two components (left) and one with three (right). B: Two functions (same ones as in A), one component shared (solid circle). C: Two functions (same as in A), complete overlap attempted (thicker border on large circles indicates two functions present). D: Two-component functions, one state each (state cycle length one indicated by looped arrow), complete overlap.

Both functions require a constant supply of oxygenated blood and thus a single circulatory system can be used by both.

With greater overlap, consistency may become more difficult to achieve. In Figure 3C, two functions are attempting to operate entirely within the same part (represented by drawing the large circle with a double-thickness line), but neither is successful, because their demands on one of the shared components are conflicting (indicated with the overlapping small circles). In this case, the conflict is serious, with the two functions making incompatible demands on the state of that component at every time interval.

Figure 3D shows a situation in which two functions are able to operate compatibly while sharing all of their components. They can do so only because both require few components (two), and the state cycles for all components are short (length one) and simple (one state each). In the shell of the freshwater mollusc, defense, ballast and calcium storage could be single-state functions. Defense might require only that the shell remain intact and rigid at all times, while ballast and calcium storage might make completely compatible demands on the shell's composition. Even more functions might be accommodated if they can be accomplished with the same structure and if their state-change requirements are few.[9]

More generally, given this model of function, the ease with which any two functions may overlap in the same part – or to put it another way, the probability of their being able to doing so – is expected to depend on at least three factors: 1) The number of components to be shared. The more components shared, the greater the likelihood of conflict. 2) The length of the state cycles of the shared components. The longer the state cycle of a shared component, the greater the likelihood of conflict. 3) The complexity[10] of shared-components' state cycles.[11]

Further, other things being equal, the probability of compatible overlap is expected to decline rapidly, indeed exponentially, as number of components shared and state cycle overlap increase. To put it another way, given some number of functions "attempting" to overlap in the same part, and given that overlap is required to occur in some fixed set of components, each with some arbitrary and fixed cycle length and complexity, the probability of successful overlap is expected to decline exponentially as number of functions increases.

An important caveat is relevant here: notice that this argument regarding overlap applies only in cases where multiple functions make demands on the same component *at the same time*. Where demands are asynchronous, so that a common component cooperates in multiple functions in a kind of time-sharing arrangement, true overlap does not occur. For example, in humans, the trachea is used in both the breathing and sound generation functions, but ordinarily we do not breathe and speak at the same time, so there is no real overlap.

4.2 *Number of functions per part*

We can now predict certain aspects of how functions will be distributed among parts. Figure 4 is a hypothetical distribution showing frequency of parts (ordinate) in which a given number of functions (abscissa) overlap. That is, it shows the number of parts with zero functions, the number with only one function, the number in which two functions overlap, the number in which three overlap, and so on. The figure can be understood to represent a *possible* distribution for organisms generally.[12]

Little is known about the actual form of this distribution for real organisms, of course. For example, we do not know that it has a single mode, as the hypothetical distribution does. However, certain features of it can be inferred from first principles and from the preceding discussion. First, we can say that the distribution will have a lower limit at or close to zero, in that few if any parts will have a negative function. A part with a negative function would be one that destroys, or interferes with, function in the positive-function parts. Obviously function-destroying collections of components would be opposed by selection when they arise. But even if they arise and persist, perhaps owing to developmental constraints, they are not expected to be organized as parts. Recall that the integration and isolation that characterizes parts is expected to be the product of selection, for the most part (although see footnote 8).

Returning to the hypothetical distribution (Figure 4), we can further say that zero-function parts should also be few, by the same argument as above, although they will likely be much better tolerated than negative-function parts (again see footnote 8). Finally, to the extent that overlap is difficult, i.e., that selection forces parts to be mutually isolated, the expectation is that few parts will participate in more than one function and that frequencies will decline rapidly as number of functions increases. Two predictions follow: (1) The mean of the distribution will probably be greater than one. (In the figure, the mode is placed somewhat arbitrarily at one, and the mean is not shown.) And (2) the variance will be low.[13]

For present purposes, the second prediction is especially important. Because the variance of the distribution is expected to be low, the correlation between number of parts and number of functions in an organism is expected to be quite good. To put it another way, suppose that the distribution of functions among parts for organisms generally is constrained by selection to be similar to that shown in Figure 4, and that the parts in each species are a sample drawn from that distribution. Then, in comparisons among a number of species, number of parts should be well correlated with – and therefore should be a good proxy for – number of functions, i.e., for functional complexity.[14]

Finally, notice that *some* correlation between parts and functions would exist even if the variance were high. Suppose, for example, that the distribution of functions among parts were flat, so that parts with up to 100 functions occurred just as frequently as parts with one function. Then, in organisms, numbers of parts and numbers of functions would still be correlated (with a mean of 50 functions per part). Indeed, for organisms with many parts,

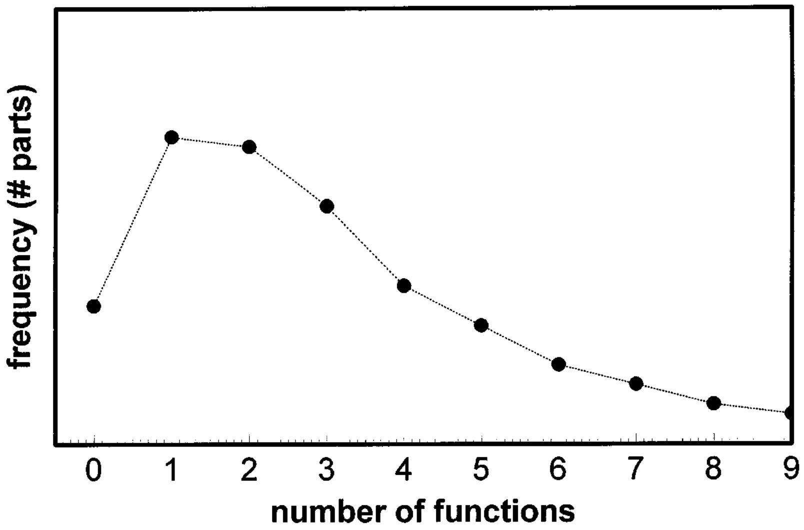

Figure 4. Hypothetical distribution showing frequency of part types in an organism (ordinate) in which a given number of functions overlap (abscissa).

the correlation would be a good one (D. Raup, personal communication). Thus, the point of the state-cycle argument is actually somewhat narrower than might be supposed; it is simply that selection against functional overlap keeps the variance low, thereby insuring that the correlation will be a strong one. If true, then we can use part counts as proxies for function counts *even for organisms with few parts.*

4.3 *An alternative version*

Presenting the argument in a different way may help to clarify exactly what is being claimed. Suppose that functions were randomly distributed among parts. More specifically, suppose that an organism has N parts and is selected to perform F functions. Also assume that each function has some fixed probability, p, of making use of (or overlapping in) each part. In that case, the distribution would be binomial, with mean number of functions per part equal to Fp, and variance equal to Fp $(1 - p)$. In this model, high variance occurs when functional demands are many (F is high) and where p $(1 - p)$ is large, i.e., at or near $p = 0.5$. However, at these parameter values, functional overlap would be considerable. If F is high, then the mean number of functions per part, Fp, would be high also. More concretely, at $p = 0.5$, an organism with only 9 functions ($F = 9$) would have three or more functions overlapping in more than 90% of its parts. The argument above maintains that this will typically be opposed by selection, and therefore that the variance cannot be high.

This model also reveals three logically possible routes to low variance:

1) F might be low. In other words, a good correlation between functions and parts is expected even if functions are distributed randomly, provided that number of functions is low, as it might be perhaps for organisms living in selective regimes that are in some sense uncomplicated.
2) p might be high and close to one, with F at some moderate or intermediate value. However, this case is forbidden by the argument against functional overlap.
3) Finally, p might be low and close to zero, again with some intermediate value of F. This occurs when functions are diffusely distributed among parts, with little overlap. In this case, we can say that if N were very low, then many functions would by chance end up assigned to no part at all; in other words, many functional demands would not be met. Also if N were very high, then many parts would have no function, which presumably would be opposed by selection. Thus, in these circumstances, an intermediate value of N would seem to be favored.

The entire range of possible cases – that is, of possible combinations of values of F, N, and p – might be worth closer investigation.

4.4 *Another route to parts: Selection for evolvability*

Wagner and Altenberg (1996; see also Wagner [1996]) have argued that selection for evolvability is expected to produce modularity in developmental systems. That is, evolvability demands that structures involved in different functions be independently modifiable, and therefore selection tends to organize development so that functionally independent structures are also produced more or less independently in ontogeny. In Wagner's (1996) example, selection in birds might be expected to have minimized developmental interactions between structures involved in beak and wing, so that, for example, beak size and wing shape can be modified independently.

Modifying Wagner and Altenberg's argument, selection for evolvability predicts functional parts, as well as developmental modules (Wagner, personal communication; Brandon 1999). That is, evolvability requires isolation of functions in their operation, as well as in their development. Where two functions are not isolated, an evolutionary change in one might produce a situation in which its operation interferes with that of the other. Conceivably, an evolutionary modification of the pharynx to improve breathing efficiency (or to reduce probability of choking) might compromise its effectiveness as a food conduit.

My own argument was largely inspired by Wagner and Altenberg's but differs from it, and from the modified version of it discussed, in that it invokes only selection for present function, not selection for evolvability. Thus, the functional units corresponding to beak and wing would be expected to be isolated from each other as different parts even if neither were independently modifiable in evolution. Modifying Wagner's example, a bird whose wing convulsed every time its beak closed on an insect would be functionally compromised whether wing and beak were developmentally modular or not.

4.5 *Apparent difficulties*

4.5.1 *Differing theoretical perspectives*

In the present scheme, parts are defined as patterns of integration and isolation. Thus, if we had a complete "wiring diagram" for an organism – a kind of map showing all interactions among all components, including their intensities, at some time scale – we would know all of the parts (at that time scale), including their hierarchical levels. To put it another way, at a given time scale, every system has a single, unique decomposition into parts, subparts, and so on. However, Wimsatt (1974) pointed out that the decomposition of organisms into parts seems to vary with theoretical perspective. For example, viewed as a device for locomotion, a tetrapod limb is decomposable into one set of parts, but viewed as a device for thermoregulation, it might have a different set, and the two sets might well have non-coincident boundaries (Wimsatt 1974). Actually, this raises no problem for present purposes. These different theoretical perspectives are essentially different functional decompositions, and the fact that a system has several non-coincident functional decompositions does not deny that it has a single "interactional" decomposition, a single pattern of integration and isolation. Granted, parts may overlap in their use of components, as discussed, and may also be difficult to discern if time-sharing occurs and components are spatially distributed.

4.5.2 *A multiplicity of processes*

A related issue has to do with the multiplicity of physical processes in which parts may emerge. Parts may occur as internally integrated and externally isolated units in chemical-bond networks, chemical or electrical signaling networks, fluid networks, and so on. Again, this presents no problem in principle; parts produced by all physical processes are equally legitimate. But it does suggest that no one physical method for identifying parts is likely to detect more than a fraction of them.

4.5.3 *Two contrary predictions*

Oster and Wilson (1978; see also Wilson 1968) analyzed the relationship between castes and tasks in social insects and offered two models, both of which could be construed to contradict the central argument here. The first predicts that, in the absence of constraints, the ratio of castes to tasks will be 1:1, with each caste performing one task. Arguably, their model ought to apply at the organism level as well, with tasks corresponding to functions and castes to parts; if so, then the ratio of parts to functions in organisms ought to be 1:1, contrary to one of the conclusions reached earlier. In fact, a 1:1 caste-to-task ratio is never realized in social insects; even in the eusocial species, each caste performs many tasks. One reason is that, as Oster and Wilson pointed out, number of castes is limited by various constraints, such as allometric growth relationships that limit the range of morphologies that can be produced. Similar constraints at the organism level might limit the number of part types that can be produced. Also, the Oster and Wilson model assumes that selection acts to minimize number of individuals, or to maximize what they call the “ergonomic efficiency” of the colony. The assumption is not unreasonable, even at the level of the individual; such selection could well be complemented by selection for economical use of parts, which would tend to encourage multiple uses of parts, and perhaps even to maximize overlap of functions within parts.

To explain the low number of castes in social insects, Oster and Wilson developed a second model based on the distribution of castes and tasks in morphospace. This model predicts that maximum number of castes will be proportional to the logarithm of number of tasks. Applied at the organism level, the prediction would seem to be that $N \alpha \ln(F)$, i.e., that individuals with many functions should have few part types, and therefore overlap of functions within parts should occur. Indeed, when number of functions is large, the overlap is expected to be massive, a conclusion which contradicts the state-cycle argument above.

However, the model also predicts that number of castes will be inversely proportional to what Oster and Wilson call the “behavioral flexibility” of the caste, or in present terms, the ability of a part to accomplish multiple functions. Thus, if the argument based on state-cycles is correct, then selection against state-cycle mismatches will tend to keep part flexibility low, number of parts high, and overlap low. In other words, massive overlap is not necessarily a consequence of the Oster and Wilson model. In fact, in social insects, the overlap is only apparent. Workers perform most tasks one at a time, so in effect the arrangement is a time-sharing one. In other words, a caste is not a single part type, but rather many part types.

5. Counting parts in practice

Identifying all of the parts in an organism, even a relatively simple one, would seem to be out of the question. However, we might be able to identify a subset of all parts, a representative sample, and use that sample as a proxy for all parts, which in turn is a proxy for functions. For example, we might limit ourselves to "object parts," or parts that are spatially localized and marked by morphological boundaries (McShea and Venit, in press). The assumptions would be that the appearance of an object is usually a consequence of the relatively tight integration among a set of components, that the limits or boundaries of objects correspond to reductions in integration; and further that object parts are a representative sample of all parts, including the behavioral and physiological ones. Alternatively, we might count behaviors (e.g., Cole 1985), on the assumptions that discrete behaviors correspond to internally integrated and externally isolated patterns of neural and muscular activation; and further that behavioral parts are a random sample of all parts. In either case, the likelihood that either sample will be representative is greater if the comparison is limited to closely related species.

A similar tactic is employed in most phylogenetic analyses, in which hypotheses about phylogenetic relationships are based on samples of characters. Further, most studies rely exclusively on one kind of data, morphological or behavioral (or in recent years, molecular), and the (usually implicit) assumption is that one type is sufficiently representative that it will yield the correct pattern of relationships (see De Queiroz and Wimberger 1993).

In a recent study, McShea and Venit (in press) developed protocols for identifying object parts and for assessing their hierarchical levels, along with an application of the protocols to produce a list of parts in bryozoans – more specifically, in the individuals, or zooids, that make up a broyozoan colony. (In this case, object parts might be considered especially appropriate as a proxy for all parts in that bryozoans are sedentary organisms with limited behavioral repertoires.)

The goal was to compile a list of object parts at a hierarchical level just below that of the zooid, in other words, a list of parts but not subparts, sub-subparts, etc. In practice, we limited ourselves to the object parts that were visible in dissections, photographs, and anatomical drawings at a magnification that is low relative to the size of the organism. In assessing hierarchical level, the primary criterion was nestedness. In other words, objects nested within the zooid were parts, while objects nested within parts were subparts (or belonged to some lower level). The assumption is that patterns of functional screening off map well onto a hierarchy of physical nestedness.

This strategy requires certain approximations. For example, lacking operational measures of degree of partness, we settled instead for binary approximations; a given structure either counted as a part or it did not. In effect, partness was discretized. Also, the strategy is prone to certain kinds of error. First, very small objects will not be visible at low magnification and will be overlooked. Second, the existence of spatially distributed parts (e.g., certain physiological parts) means that the hierarchical level of some object parts will be misidentified; that is, some apparent object parts will actually be subparts. Finally, some objects will not be true parts at all, because integration will sometimes cross object boundaries. See McShea and Venit (in press) for a longer discussion of assumptions and limitations.

Unavoidably, even the identification of object parts relies to some extent on our various precognitive perceptual mechanisms, that is, on gestalts. However, there is some reason to think that our gestalts will be fairly reliable. Our perceptual systems are probably designed to recognize such parts, because historically they have been reliable features of our evolutionary environment (Campbell 1958). And if the argument here is correct, they have also been the locus of function in other organisms, and therefore have been highly relevant features.

6. Discussion and summary

The argument here is that a functional system needs to be both integrated internally and isolated from its surround, and therefore in organisms, functions are expected to be localized, to some extent, in parts. Further, most parts will participate in few functions, and few parts will have many functions overlapping in them. Thus, the variance in number of functions per part will be low, and number of parts is expected to be well correlated with number of functions. It follows that we can use part counts as proxies for function counts in comparative studies of organisms, even when part counts are low.

There is a widely shared intuition that the organization of organisms into parts is significant and that this significance has to do with function. Parts are quite salient in organisms, especially the physically bounded parts. Indeed, it would be difficult to describe organisms in any other terms than parts. Further, parts are generally assumed to have a connection with function; phrases of the form, “The function of the spleen is to . . . ,” are commonplace in anatomy texts. On the other hand, we know that functions do overlap, that the relationship between parts and functions is not one-to-one. And one might reasonably worry that the apparent significance of parts is a consequence of some bias (perhaps of our familiarity with machines), and that functions in organisms are actually distributed more globally. The argument here backs our first intuition.

Establishing a connection between numbers of parts and functions also helps to make sense of the entire literature on the evolution of morphological complexity, dating back to Lamarck (1809; for a review, see McShea 1996). In considering that literature, some have undoubtedly wondered why morphological complexity is considered important, why it is expected to be significant in organisms. One answer is that, in most empirical studies, morphological complexity has been treated as a function of number of part types (e.g., Cisne 1974; Schopf et al. 1975; Saunders and Ho 1976, 1981; Bonner 1988; McShea 1993; Valentine et al. 1993; Saunders and Work 1997), which should – if the present argument is correct – reflect number of functions. Presumably functional complexity, in turn, is controlled to some extent by natural selection, and therefore might be expected to have interesting evolutionary properties.

Ultimately, the test of the proposed correlation between parts and functions must come from empirical studies. And obviously the ideal test would involve a direct comparison of part counts and function counts in various organisms. However, we do not know how to identify functions in any systematic way, and therefore we have reason to worry that direct counts – perhaps based on intuitive notions of what functions an organism requires – would not be meaningful.

An alternative approach would be to test for correlations between part counts and other predictors of functional complexity. For example, I have examined in a preliminary way the hypothesis that the number of functional demands on a cell in a multicellular organism ought to be fewer than on a free-living cell, because in the former, many functions are assumed by the organism as a whole (McShea, in press). If true, then the functional complexity of free-living cells – and therefore their part counts – should be higher. Consistent with the hypothesis, in a small sample, free-living cells had more object parts, and the difference was statistically significant. The finding, if supported by larger samples and further analysis, could be construed to support both correlations simultaneously. That is, it would be consistent with both: (1) the hypothesized (negative) correlation between the emergence of multicellular existence and functional complexity at the cell level; and (2) the (positive) correlation proposed here between functional complexity and object-part counts.

The argument here has the virtue that it is fairly simple and its conclusion is plausible. Its major fault or limitation, in my view, is that it is still mainly theoretical. A constraint on organisms – that number of parts must be well correlated with number of functions – has been bootstrapped up, so to speak, from a number of reasonable but empirically unsupported assumptions and principles, notably the principle of limited functional overlap. And we know that organisms often find ingenious ways to thwart or to avoid such theoretical limitations. As a result, the conclusion could be wrong. Or it could be right in certain cases, say, for certain kinds of parts, or in certain groups of organisms, but wrong in general. Thus, pending one or more strong tests, considerable skepticism is appropriate. A major purpose of this paper is to motivate such tests.

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Notes

[1] In fairness to molluscs, not all mammal-mollusc comparisons would have been so clearcut. For example, it does not seem quite so obvious that a squirrel has more functions than a squid, or an otter than an octopus.

[2] Just as it reasonable to doubt that cats have more functions than clams, it is also reasonable to doubt that they have greater morphological complexity. Our intuitions on both issues is subject to a variety of biases (McShea 1991). On the other hand, the claim about morphology has some objective basis. Schopf et al. (1975) measured morphological complexity as number of anatomical terms, and estimated that we have about 300 terms for clams and about 1000 for mammals. Normalizing for taxonomic diversity within the groups, mammals have about 0.33 terms per genus and 3.5 terms per family, while the values for clams are 0.09 and 1.5, respectively.

[3] Heylighen (in press) predicts that functional complexity should tend to increase on different grounds, namely that organisms with more functions are better able to accommodate more dimensions of environmental adversity, or take advantage of opportunities in more dimensions. In other words, increased functional complexity is advantageous in all or most lineages, and therefore will tend to increase, on average.

[4] Two further clarifications might be helpful. First, it will occasionally be convenient to refer to the functional complexity *of* organisms. By this I mean the number of functions that the parts of an individual perform, *not* the number of functional roles filled by an individual as a unit in some larger whole, such as a colony. Of course, selection produces functionality at various levels, including the colony, and where it does, the argument here could be applied, albeit with some translation. (See discussion in the text of a colony-level model developed by Oster and Wilson 1978.)

Second, the phrase functional complexity is sometimes used in another sense, having to do with the complexity of spatial relationships and interconnections among the anatomical elements involved in producing one or a small number of organismal functions (e.g., Lauder 1981; Friel and Wainwright 1998). For example, one might be interested in the functional complexity of the feeding apparatus in a fish. A connection may well exist between functional complexity in this sense and the total number of functions in an organism, but that is beyond the scope of the present discussion.

[5] Wimsatt (1994) argued that organisms seem to be designed so that variation at the genetic level tends *not* to propagate to higher levels, or in present terms, such variation is screened off from selection at the organism level. This is why, he points out, an organism tends to resemble its parents, despite the enormous genetic differences between them. The assumption here is that considerable variation at all levels below that of parts is screened off in this way. See also discussions of independence among levels in Simon (1969) and Salthe (1985, 1993).

[6] Parts correspond closely with Simon's (1969) "subsystems." In other words, parts are the units into which Simon argues many natural systems are – in his famous phrase – "nearly decomposable."

[7] The choice of the word "part" over alternative near-synonyms, such as individual, module, entity, component, system, and structure, requires some explanation. "Individuals" usually refers to organisms (e.g., Buss 1987; although cf. Hull 1980), and many parts, as defined above, are not organisms. "Module" might be acceptable, but it has come to be used mainly for integrated and isolated *developmental* entities (Wagner and Altenberg 1996; also see below). Terms like entity, system, structure, and component are quite vague, which in turn makes them useful here in cases where ambiguity is helpful and no technical meaning is intended. Also, the correspondence between the present technical definition of parts and its colloquial meaning is imperfect. We generally think of parts as physically bounded entities, as objects, in which the isolation is visually (or tactilely) evident. Some parts are bounded in this way, like the diamond, but some – like behaviors – are not. Also colloquially the term is restricted to entities within larger wholes, those that are *part of* something. But under the technical definition, (facultatively) stand-alone entities, like the Solar System, count as parts whether or not we choose to see them as components of larger wholes.

[8] The prediction is only that functions will tend to be localized in parts, not that all parts will be functional. A network of components in which connections and their strengths were assigned randomly would, by chance alone, contain some parts, and most of these would probably be non-functional. Also, parts produced by selection may become non-functional when the selective regime changes. In other words, some zero-function parts are expected in organisms. Selection for economy may tend to eliminate them, but developmental constraints may maintain a great number of them. Nor is it the case that organisms must consist entirely of well-defined parts. Parts organization may be weak among components which are not subject to strong selection. Again, the existence of such components may be opposed by selection for economy but maintained by developmental constraints.

[9] In the earlier example involving the shared circulatory system, the demands made on the component were not only compatible but identical. In the hypothetical freshwater mollusc, the various demands on the shell are different, and take advantage of different properties of the shell, but are compatible with the shell remaining in a single state.

[10] A full discussion of what state-cycle complexity might mean is not possible here. For present purposes, it will suffice to say that it is some increasing function of the improbability, or the difficulty, of a sequence of state transitions. Thus a two-state repeating sequence (e.g., ABABAB . . . , where the letters represent different states) is simple, while a sequence with no pattern (e.g., ACBADCCB . . .) is complex. An information-theoretic understanding (and

measure) of complexity would be applicable here (Chaitin 1975; Crutchfield and Young 1989); see also the various measures of configurational complexity (McShea 1996). In any case, the crucial point is that the more complex the state cycle required by one function, the less likely that the same state cycle will happen to meet the requirements of another function.

[11] Other variables could be implicated as well, such as degree of compatibility of the various functional demands that will be made on components. Here, average values for such variables are assumed to suffice; in other words, these factors are treated as constants.

[12] It would not be hard to devise a simple model to investigate how the shape of this distribution depends on how number of components required, state-cycle lengths, etc., are distributed among functions.

[13] A possible objection is that state-cycle mismatches are not ruled out by selection, that instead selection forces compromises in which mismatches occur and performance is simply rendered suboptimal. The result of overlap then would be a reduction in the *degree* of functionality in the overlapping functions rather than a reduction in the *number* of functions overlapping. This objection could be accommodated simply by reformulating the argument in analogue terms – in terms of “quantity” rather than “number” of functions. Then the claim would be that selection against overlap limits the quantity of function per part rather than the number of functions per part. In any case, a low variance is still expected.

[14] Notice that a further assumption is implicit, namely that the distribution of functions among parts is approximately the same in the organisms compared, i.e., that a shared distribution of the same general form as that in Figure 4 in fact exists. The assumption does not seem implausible, and indeed seems likely when the organisms compared are closely related and broadly similar in their morphology, physiology, and behavior. In any case, the assumption can be relaxed somewhat: suppose that each species has its own unique distribution, with the mean number of functions per part varying systematically with, say, number of parts. In particular, suppose that organisms with more parts also have different rules governing overlap, so that they tend to have slightly higher means. Provided that all means and variances remain fairly low, parts and functions would still be strongly correlated across species. Of course, the correlation might no longer be linear.

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