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Evolutionary Cognitive Science: Constraints and Unification

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*“Grading the evolutionary constraint is deeply problematical
(...)the best we can do is ask loosely how the theory relates to
evolutionary and comparative considerations”*
Anderson & Lebiere (2003, 5)

Abstract

The present paper proposes an evolutionary constraint on theories of cognitive architecture. The framework proposed dispels some pessimistic assessments concerning the feasibility of such project and criticizes some current evolutionary thought in cognitive science. Implications of the constraint are also discussed.

Keywords: evolutionary psychology; phylogeny; theory-choice.

Introduction

Most theories in Cognitive Science, and specially in the field of Evolutionary Psychology (Cosmides & Tooby (1992), Buller (2005)) have exposed the idea that compromises with the independently motivated framework of the modern, Neo-Darwinian theory of evolution imply an acceptance of specific “design features” for the organization of cognitive architectures. Foremost among these is innate modularity (Samuels (1998); Buller (2005; chap. 4)). In order to show the fragility of this line of reasoning it would be enough to point out that for other researchers, the same chain of reasoning leads to the exact opposite: massive-action distributed systems and “constructivist modularity”, if any (Buller (2005), von der Malsburg (1996)). But the plot deepens¹.

The unifying core of modern evolutionary theory is the theory of population genetics (Fisher (1930), Beatty (1986), Sober (1986)) or its extensions to non-genetic or optimality models in behavioral ecology (e.g., Maynard Smith (1982), Grafen (1991)). In its own terms, the theory makes no definite, *a priori* assertions on which are and which are not the evolvable phenotypes. The theory deals with forces impinging on populations, shifting the relative frequencies of hereditary factors or with predictions that *may* be true of the design of physiological, morphological or behavioral traits of the organisms subject to study, given some set of specifiable selective pressures and trade-offs. Indeed, the same framework has been carried to the study of the dynamics of very different factors from those commonly

studied by zoologists and in other fields of biology, often as brief suggestions (Dawkins (1976)) or within more articulate and formal theories (Boyd & Richerson (1985)).

Given this state of affairs, how could we overcome the pessimistic assay of Anderson & Lebiere (2003) presented in the epigraph to this paper and devise some workable and conceptually sound “evolutionary criterion” on theories of cognition? How could we work out some operational research program to include the vast array of methodologically and theoretically insulated researchers working with “evolutionary concerns” on cognition and behavior? How can we make sense of the huge body of available data on the cognitive and behavioral capacities of human and non-human animals? In the next section we will provide a sketch for a program of research that may help in the attainment of these goals.

1. The Framework

Our main idea, to be explained in the remaining of the paper, is that studies on the evolution of cognition should stick fiercely to the methods and concerns of the field of *phylogenetic analysis*, in a complementary approach to that commonly employed to study adaptation in cognition and behavior, exemplified by experimental research in Evolutionary Psychology (Buss & Haselton (2005)) and in Behavioral Ecology (e.g., Hill & Hurtado (1996)) and as an implementation of an evolutionary constraint on theories of cognition.

Although many authors have expressed cogent views on the importance of a phylogenetic or general “historical” outlook on these matters (cf. e.g., Byrne (2000), Povinelli (1993), Foley (1996)) none has, in our view, explored these tools with the due depth nor have any of these authors established a link with broader concerns in the Cognitive Sciences, such as theory choice. Nevertheless, many researchers (Foley and Byrne included) have stressed the dependence of Evolutionary Psychology on comparative and historical considerations in their “reverse engineering” of the mind, for example, as related to the critical notion of EEA (Environment of Evolutionary Adaptedness, Tooby & Cosmides (1990)). Not surprisingly, there are some dissenting voices arguing that Evolutionary Psychologists

¹ It should be clear at this point that we are not downplaying *any* imaginable way to justify the hypothesis of modular organization, but only this particular *a priori*, evolutionary argument.

have not paid attention to such issues properly (Daly & Wilson (1999), Heyes (2000)).

As a flagrant measure of how poor is the general understanding of the phylogenetic approach to evolutionary psychology, Buller (2005) in his throughout critique of some particular strains of thought in the field makes the following remark at page 96:

“nonhuman primate species differ considerably with respect to foraging, parental care, and mating system. So we face the problem of which nonhuman primate to take as our model of Pleistocene humans (...) Rather, similarity of ecological conditions is a more important determinant of similarity of behavioral traits than is degree of relatedness.”

The striking point missed by Buller is that *no* approach to matters of phylogeny reconstruction takes any single species as a “model” for the inference of ancestral states. Even those researchers that have not explored in great depth the tools of phylogenetic analysis could not endorse such a simplistic position (Povinelli (1993), Byrne (2000)). This process of ancestral state estimation is, to the contrary, a much more complex intermingling of statistical methods operating on comparative data and with explicit assumption concerning the evolutionary processes that could have lead to the observed comparative patterns (Hansen & Martins (1996), Schultz *et al.* (1996)).

The field of phylogenetic analysis is also more inclusive than that of “comparative considerations” mentioned in the Anderson & Lebiere (2003) epigraph. It does not bother only to describe and code for the similarities and differences among different species, but crucially, with the inference of evolutionarily significant information from the observed patterns, based on a definite theory about which processes played a role in bringing the observed outcomes about. This includes the postulation of ancestral states, the particular forces that lead to differentiation or convergence among related groups or, in a nutshell, it deals with the inference of evolutionary causes from extant patterns and auxiliary assumptions (Kemp (1985), Kluge (2001)). As the study of evolutionary relations from comparative data is a broad and fascinating field, as old as the discipline of evolutionary biology, we will concentrate on those aspects which stand out as more relevant for our purposes.

A number of different phylogenetic comparative methods (PCMs) work in a very similar way: observable properties of related species are coded in some form (e.g., in a binary code of character states of ‘absence’ (0) or ‘presence’ of a given trait (1), or in terms of multi-state characters represented by positive integers) and then used to describe the groups (*taxa*) under study. The distribution of character states is used to describe the pattern in terms of optimally-simple hierarchies of characters (*cladograms*) which actually split the space of characters under scrutiny in the set of *primitive* and *derived* character states. Of course that the Devil lies in the details about which optimality criteria is used in selecting among alternative cladograms. For reasons of editorial brevity we can only point out that, given our

present purposes, those criteria dependent on particular evolutionary assumptions are clearly the most relevant (cf. e.g., Kluge (2001))¹. From these “data-driven” or apparently objective initial steps, a number of manipulations of the data can be made in order to infer biologically significant relationships among the represented groups, such as the existence of putative adaptive radiations that lead to the observed patterns, the existence of phyletic lines of “least resistance” (where differentiation has been greater) or even the inference of ancestral (non-observable) states for particular character in putative ancestors.

In the last two decades, the field of phylogenetic analysis went through a revolution in the application of differing statistical methods, and has overcome a number of misguided assumptions concerning the extent of their role in understanding evolution. One standard opinion is that the study of phylogenetic and historical patterns is at a “different level of analysis” from the study of adaptation (cf. Tooby & Cosmides (1989)). Modern PCMs do embody mechanisms for the extraction of information on microevolutionary patterns affecting particular lineages, for example, through the decomposition of observed variance in continuous variables in terms of phylogenetic variance (or ‘phylogenetic signal’, that is, the patterns in data that can be accounted for in terms of common descent) and “error” in the test of this null-hypothesis that can be assigned to other forces, such as natural selection (Cheverud *et al.* (1985)). Likelihood ratio tests can also be used to compare models of phylogenetic evolution with observed data (Baum & Donoghue (2001)). The development of such models also dispels the idea that the only approach to the evolution of adaptive traits in phylogenetic analysis is the equation of derived and species-specific character-states with adaptation (Reeve & Sherman (1993)).

A number of functions of comparative data can be quantitatively derived, such as measures of variance or covariance or measures of phenetic distance (overall similarity). Based on measurements such as these, Hansen & Martins (1996) proposed a model where information on evolutionary processes can be quantitatively estimated on the basis of comparisons between “expected data matrices” derived from specific evolutionary models and the observed patterns. In figure 1 below, we expect a matrix of expected values for variances and covariances in comparative data, given particular phylogenies and assumptions on the processes leading to the observed patterns (cf. Martins (1995)). The matrix for phylogeny A gives the predicted values for the variances in each of six species that diverged once from a common ancestor and experienced equal evolutionary change thereafter. Phylogeny B assumes less branching in a first speciation event and further branching events leading to three clades of closely related pairs of species, ((A, B), (C, D), (E, F)).

¹ It should also mentioned at this point, and this will be clear in the following paragraphs, that the algorithms and methods better suited for those with evolutionary concerns in mind operate upon continuous rather than discrete data.

Theoretical syntheses of predicted patterns of comparative data, such as those in figure 1, are used to estimate the extent to what extent the observed data fit the predictions embodied in the phylogenies and evolutionary processes assumed.

phylogeny A						
	A	B	C	D	E	F
A	V_A	0	0	0	0	0
B	0	V_A	0	0	0	0
C	0	0	V_A	0	0	0
D	0	0	0	V_A	0	0
E	0	0	0	0	V_A	0
F	0	0	0	0	0	V_A

phylogeny B						
	A	B	C	D	E	F
A	V_B	C_B	0	0	0	0
B	C_B	V_B	0	0	0	0
C	0	0	V_B	C_B	0	0
D	0	0	C_B	V_B	0	0
E	0	0	0	0	V_B	C_B
F	0	0	0	0	C_B	V_B

Figure 1: Expected Data Matrices (see text)

2. Ranking Theories

The specific proposal made in our paper concerning the evolutionary constraint and its function in theory-choice in cognitive science is based on the following remark: both the problem of theory choice (inference to the best explanation or “non-demonstrative inference”) and the problem of finding the correct depiction of evolutionary relations among observed and ancestral taxa, are what statisticians call *inverse problems* (Evans *et al.* (2006)). So, instead of walking through a space of competing theories with some “grading function”, we could assign different theories the task of providing existing PCMs with characters (“cognitive states”) and watching how well they fare. That is, the evolutionary constraint is formalized as a *test* proposed to competing theories, and the criterion for grading is provided by the way they are able to cope with the independently motivated body of explicit, formal methods of phylogenetic analysis.

To take an example on how this might work, consider the (non-trivial) problem of character choice and coding. It is not the case that every trait seen in the individuals of a population or species is equally useful for phylogenetic analysis. Good characters vary more between species than intraspecifically; show high heritability (h^2) estimates; are quantifiable; are independent units and can be compared in different species, so that preliminary hypotheses of homology (identity through common descent) can be framed. At this preliminary stage, it is not difficult to see that theories will differ on how well phylogenetic analysis can be carried along with the characters they are able to furnish. Chomskyan-like linguistic theory, for example, would fare very poorly, mainly because it works with cognitive capacities that show little if any variation in the

species (so that h^2 estimates cannot be made; or rather, the theory is unable to account for existing variation (Bishop (2003)) and because even analogs of syntactic competence are hard to come by in comparative data. ACT-R on the other hand, would fare much better (especially in its “neurally realistic” variants). Many of the parameters in the learning equations of ACT-R can be inferred for a number of motor and perceptual tasks in different species. Features of the architecture can be related with its neural substratum (e.g., the loop involved in the selection of production rules and frontostriatal systems) and experimental measures can be related to these parameters of the architecture (e.g., the time to select a production rule can be related to the density of striatal connections or to mean axon diameter; cf. Roth & Dicke (2005)). This sort of tight relation between differing levels of analysis opens the way for phylogenies based on neurocognitive characters which may furnish information (predictions) on other characters (in this case, behavioral measures). This property of “informativeness” is also necessary for a good phylogeny (Mayr (1969)). Alternatively, a number of semi-continuous characters related, for example, to the complexity of declarative chunks or the mean number of parallel subcortical features, can be used for the derivation of measures such as phenetic distances or inter-specific variances, useful in a number of PCMs for the assessment of microevolutionary causal processes (Hansen & Martins (1996)).

In synthesis, our proposal grades alternative theories in terms of their ability to provide adequate data (characters) for phylogenetic comparative methods (PCMs). The fact that different data sets differ in their usefulness relative to these methods and that different theories vary in the kind of data they can provide (as we purported to show in the previous discussion) provides the criteria for theory-choice on the basis of this constraint. There are, to be sure, other steps involved in the development of phylogenies beyond character choice and the determination of their usefulness. These further steps may also be included within the constraint. The determination of character polarity (primitive-derived relations among character states) lies among these. To this end, comparisons with more distant taxonomic groups (*outgroup comparison*) or the use of fossil and developmental data is employed, at least heuristically. It is again not difficult to see that not all theories will fare equally well in meeting these conditions. The important point is, however, that the evolutionary significance of these theories is being subject to test in term of their interaction with a body of complex methods independently justified for their capacity to promote our understanding of similar evolutionary relations holding between slightly different characters: physiological processes, anatomical structures and behaviors (Lauder (1986)). It is a natural extension to consider their significance to the study of cognition in order to proceed beyond “loose evolutionary and comparative considerations” as suggested by Anderson & Lebiere (2003)).

3. Integration

A crucial property of our proposal is its “therapeutic” qualities relative to current approaches to the evolution of cognition. Mainstream hypothesis on evolutionary cognitive science could be aptly seen as almost literary, lacking explicitness and often getting lost in a huge amount of disconnected data (e.g., Donald (1991)). The perspective of phylogenetic analysis allows one to focus on manageable problems, to make explicit its assumptions on the nature of the relevant evolutionary processes, to integrate in a single framework of formal methods a number of distinct data sets often discussed in loosely ways (fossil data, developmental mechanisms; e.g. Mithen (1996)) and to answer different questions (niche specific effects and resulting adaptations, measurement of phylogenetic signal, etc).

The adoption of the methodology of PCMs for evolutionary cognitive science also paves the way for fruitful interactions between comparative studies and equilibrium-based or dynamic models of evolutionary process, such as Artificial Life models (Christiansen & Kirby (2003)) and Game-Theoretic approaches (Nowak & Komarova (2001)). It is well-known, for example, that many complex evolutionary games show multiple ESS (Maynard Smith (1982: 126)). This means that an understanding of the initial conditions of a population may be critical for framing empirical hypothesis.

The way the application of PCMs to matters of cognitive and behavioral evolution relates to other expanding fields of research, such as Evo-Devo, or to models of cultural evolution and non-genetic inheritance seems to be more complex and problematic. Development as a dynamic and highly interactive process is poorly understood and has not been properly integrated into evolutionary theory, due to a number of factors (cf. Maynard Smith (1982), Wilkins (2001), Turkheimer (1998), (2000)). Questions regarding development are virtually untouched by studies confined to estimating genetic contributions to phenotypic variance in particular traits (Turkheimer (1998)) even tough measures such as heritability are among the relevant variables for character choice in phylogenetic analysis (Lieberman (1999)). It should also be mentioned that within the field of developmental science (and specially in developmental social psychology) there is a huge methodological gulf insulating human and non-human studies (and the data derived thereof) due to obvious ethical constraints on the permissible experimental designs applicable to humans (Turkheimer (2000)). This gulf shrinks to a considerable degree when we abstract from matters of development and consider what, from this perspective, we could call “ideal” cognitive architectures, especially in the context of efforts to integrate the traditional field of animal learning psychology with computational theories endemic to cognitive science (Gallistel (2003), Ristau (1991)).

As it seems to be clear by now, notwithstanding the comments of the previous paragraph, the relative dependence of particular psychological traits on culture or

social learning is built in our proposal during character choice and the weighting of particular characters on the basis of its heritability estimate. Characters that show up with low heritability factors when things like shared/non-shared environment are controlled for are less suitable for phylogenetic analysis. We acknowledge the problems immanent in behavior genetics, but the fact that the field is taken as a useful platform for a more significant and exhaustive developmental science (Wahlsten (2003)) fuels optimistic prospects of better understanding.

4. Final Discussion

In this work it was presented a preliminary discussion of an ongoing project of devising an explicit, formal and conceptually sound evolutionary constraint on theories of cognition. A tentative conclusion that seems to stem from these proposals seems to be that low-level, neurobiologically constrained theories and architectures would be selectively preferred under this constraint. Such theories can provide conceptual tools to assess fine-grained inter-individual variation, may furnish continuous or semi-continuous characters (to which most PCMs show greater sensitivity) and may be used in comparative research. This result offers another reason to embrace approaches based on the burgeoning field of computational neuroscience (Quartz & Sejnowski (1997), Churchland & Sejnowski (1992)).

To the extent that this result can be justified, some other interesting, broader effects can be seen in the theoretical landscape of the cognitive sciences. First, it provides another motivation for the increasing effort in developing biologically realistic connectionist models (Churchland & Sejnowski (1992), Crick (1989)). Second, it can converge with some strains of thought in Cognitive Science which acknowledge the role of higher level symbolic accounts of cognitive processes but assign full causal power in generating actual behavior to sub-symbolic processes (Smolensky, Legendre & Miyata (1992)). That is, a single descriptive framework could be applied to proximate questions (causation of behavior) and to ultimate questions (evolutionary characterization).

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