

Cognitive Architecture and Descent with Modification

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8 September 2005

Abstract

Against a background of recent progress in developmental neuroscience, some of which has been taken as challenging to the modularity hypothesis of Fodor (1983), this article contrasts two competing conceptions of modularity: *sui generis* modularity, according to which modules are treated as independent neurocognitive entities that owe nothing to one another, and descent-with-modification modularity, according to which current cognitive modules are understood to be shaped by evolutionary changes from ancestral cognitive modules. I argue that *sui generis* modularity is incompatible with a range of data, from the co-occurrence of deficits to the patterns of activation in neuroimaging studies, but that that same range of data is compatible with descent-with-modification modularity. Furthermore, I argue that the latter conception of modularity may have important implications for the practice and conception of fields such as developmental disorders and linguistics.

1 Introduction

In computer science and engineering, the idea of modular design is axiomatic (Baldwin & Clark, 2000). Complex systems are made up of specialized subcomponents designed for particular functions. A modern computer, for instance, includes not just a domain-general central processing unit (itself constructed out of modular subcomponents) but also a wide variety of specialized circuits dedicated to tasks like rendering graphics and producing sound effects; much the same can be said for virtually all of the world's complex computers programs.

There is ample evidences that many biological structures are similarly modular, at physiological and genetic levels (Beldade & Brakefield, 2003; Gerhart & Kirschner, 1997; Patthy, 2003; Schlosser & Wagner, 2004; Schwartz & Olson, 1999). For example, systems such as the vertebrae of the spine consist of serially-repeated subcomponents, while the body as a whole consists of specialized systems devoted to tasks such as circulation, digestion and respiration.

* The authors thank the NIH and HFSP for support, and Scott Atran, Cedric Boeckx, Clark Barrett, Noam Chomsky, Simon Fisher, Tim German, Andrew Nevins, Athena Vouloumanos, and three anonymous reviewers for helpful discussion.

Mental and neural structures¹, too, might be modular in structure (Fodor, 1983; Lenneberg, 1967; Marr, 1982), and such modularity might be an essential or highly probable aspect of the evolution of complex systems, at both cognitive (Cosmides & Tooby, 1994b; Pinker, 1997) and neural levels (Calabretta, Ferdinando, Wagner, & Parisi, 2003; Calabretta, Nolfi, Parisi, & Wagner, 2000; Redies & Puelles, 2001).²

Consistent with this idea, the brain in many ways appears to carry hallmarks of specialization. The adult human neocortex, for example, contains a large number (52 by Brodmann's count) of "areas" that can be distinguished cytoarchitecturally in terms of connection patterns and distributions of cell types. Felleman and van Essen's (1991) justly famous map of the interconnections in the visual part of a macaque brain hints at a staggering degree of highly focused connectivity. Comparable studies have not been done in infants, but the available evidence strongly suggests that basic cortical structures and pathways are largely established by birth (Bates, Thal, Finlay, & Clancy, in press; Shankle, Romney, Landing, & Hara, 1998).

Yet, the twin notions of neural and cognitive modularity have remained deeply controversial within cognitive science and cognitive neuroscience. There are ongoing debates about the definition of modules (Coltheart, 1999), and protracted debates about the empirical evidence within psychological domains such as sentence processing (Ferreira & Clifton, 1986; Spivey, Tanenhaus, Eberhard, & Sedivy, 2002; Tanenhaus, Spivey-Knowlton, Eberhard, & Sedivy, 1995), reading (Coltheart, 1999; Shatil & Share, 2003), music (Peretz & Coltheart, 2003), and navigation (Hermer & Spelke, 1996; Learmonth, Nadel, & Newcombe, 2002). Similar questions arise concerning the neural substrates for processing of faces (Kanwisher, 2000; Tarr & Gauthier, 2000). Furthermore, there are considerable debates about the extent to which any modular structure that is found in mature adults is inborn or the product of experience (Pinker, 1997; Thomas & Karmiloff-Smith, 2002; Tooby & Cosmides, 1992).

The purpose of this brief paper is not to resolve these debates, but to suggest that a perspective from biology can bring some clarity to them.

2 What this paper is not about

2.1 *Ontogenetic development.*

Before developing this argument about biology and modularity, it is important to clarify what this paper is not. It is not a paper about how putatively modular structures in adults — say mechanisms for face recognition or syntactic analysis— develop.

¹ In what follows, I will assume that neural and cognitive levels are closely correlated, although specifying the exact nature of that relation is outside the scope of the current paper.

² Although the notion of modularity in cognitive science is most often couched in terms of "classical" symbol-manipulation accounts of cognitive science, it is also compatible with connectionist accounts that seek to explain cognition in terms of the interactions between large numbers of simple processing units (Jacobs, Jordan, & Barto, 1991; Miikkulainen, 1993).

Virtually all cognitive and neural structure develops through an interaction between genes and experience (for a review, see Marcus, 2004b). If adult cognitive or neural structures is modular, it is likely to reflect the effects of both genes and experience.

For example, at the psychological level, there are powerful arguments that children have special talents for acquiring language, far in excess of their general cognitive tools (Chomsky, 1980; Crain, 1991; Pinker, 1994; Wexler & Culicover, 1980), yet it is apparent to all observers that language cannot be acquired without extensive experience. Similarly, although there may be genetic contributions to talents in domains such as music or chess, it is clear that nobody becomes expert in these domains without significant, deliberate practice (Ericsson, Krampe, & Tesch-Roemer, 1993). Likewise, it seems plausible that ecologically novel skills such as reading or chess-playing depend on experience shaping endogenous neural structures that evolved for other purposes (see for example McCandliss, Cohen, & Dehaene, 2003).

At the neural and genetic level, it is again clear that both genes and the environment make powerful contributions to development. Verhage, and colleagues, for instance (Molnar et al., 2002; Verhage et al., 2000), have shown that transgenic mice can develop largely normal brains even in the absence of synaptic transmission, supporting the importance and power of early genetic factors. Researchers such Weaver et al (2004), Francis et al (2003), and Moles et al (2004) have recently shown that molecular level processes, including gene expression itself, can be modified by early experience.

At this time, lacking precise and agreed-upon measures of what constitutes modular structure — be it cognitive or neural — it would be premature (and perhaps nonsensical) to say much more; we are simply not in a position to directly assess the relative contributions of genes and experience to any putative modular structure. In the final analysis, arguments about the nature of putatively modular structure in the adult ultimately can only be resolved by a careful understanding of both the initial state of a child (say at birth) and the mechanisms by which that child acquires and reorganizes knowledge over the lifespan.³

Despite the controversy that characterizes discussion of developmental cognitive science, there's actually some degree of consensus. Both strong "nativists" and their critics acknowledge some role for an innate underpinning: "core knowledge" that is later supplemented by "peripheral" knowledge in the more nativist language of Spelke (2000), "domain-relevant mechanisms that ... gradually become domain-specific" in Karmiloff-Smith's (1998) "emergentist" formulation.

Inasmuch as we can tentatively agree that at least some neural or cognitive structures are modular, and guided in part in their development by genes, we can temporarily put aside questions about the role of experience in order to focus specifically on that genetic contribution. We can then raise a different question: can an understanding of the underlying biology tell us anything about what kinds of modules to expect? It is the burden of this paper to suggest an answer in the affirmative.

³ A further complication, outside of the scope of the current paper, is that experience begins the womb, while genes continue to contribute to neural development and reorganization throughout life.

2.2 Evolutionary Psychology

As the argument will depend on a strand of evolutionary theory, itself an ever-controversial topic, it is important to make one more clarification about what this paper is not: it is neither a defense of (nor a critique of) “adaptationist” evolutionary psychology.

Evolutionary psychologists such as Tooby and Cosmides (Cosmides & Tooby, 1994a; Tooby & Cosmides, 1992) and Pinker (1994; 1997) have held that the nature of cognitive modules can only be understood with respect to the adaptive challenges faced by our ancestors (though see Fodor, 2000 for a counterargument). For example, Pinker (1994:420) advocated a mental taxonomy that includes modules that are separately tuned for intuitive mechanics, habitat selection, danger recognition, food recognition, contamination recognition, intuitive biology, making mental maps, monitoring well-being, tracking and selecting mates, justice, habitat selection, kinship tracking, inferring the psychology of other people, and evaluating one’s value to others.

Although it is plain that by adulthood humans have mechanisms for addressing each of the problems that Pinker delineates, in many cases, empirical evidence as to the exact underlying mechanisms is (as yet) scant, and it is unclear the extent to which some or all of these problems could instead be solved by domain-general mechanisms. For example, it is currently unknown whether the mental machinery for representing kinship relations must be explicitly genetically encoded or whether such principles could be learned from experience or acquired through cultural transmission. Likewise, to the extent that mechanisms for solving these adaptive problems might be genetically “encoded”, relatively little is known about the level of detail with which such knowledge might be innately specified.

Rather than attempting to adjudicate such debates — which clearly depend on empirical evidence that we do not yet (and in some instances may never) possess— the focus of this paper is on a different strand of the theory of natural selection: Darwin’s notion that evolution is a process of descent with modification.

3 Descent with modification

In the *On the Origin of Species*, Darwin (1859) argued that “existing forms of life are the descendants by true generation of pre-existing forms”: evolution never starts from scratch, but instead by modifying the structures of organisms already in place. Somewhat more recently the Nobel Laureate François Jacob (1977) elaborated on this idea with a illuminating metaphor of evolution as “tinkerer”, who

...often without knowing what he is going to produce, ... uses what ever he finds around him, old cardboards, pieces of strings, fragments of wood or metal, to make some kind of workable object... [the result is] a patchwork of odd sets pieced together when and where opportunity arose.

For example, the four chambers of the mammalian heart clearly bear a family resemblance to one another, presumably because they are modifications of simpler

circulatory systems such as the three-chambered heart found in amphibians and the two-chambered system found in fish. Likewise, the skeletal structures of the diverse range of forelimbs found in vertebrates — wings, flippers, arms and so forth — are plainly variations on an inherited theme.

To take another example of this phenomenon, sometimes known as “bricolage”, the thumb and index finger may look different and have distinct functions, but their distinct functions surely emerge from relatively minor tweakings of a common carpal-to-metacarpal-to-phalanx plan, and, even more radically, the wing of bird and the forearm of a human descend from a common design for tetrapod limbs. Almost nothing in evolution is without precedent; the point of descent with modification is that even the most novel elements can generally be seen as variations on pre-existing themes.

Recent work in the growing field of “evo-devo” (evolutionary-developmental biology, suggests both that the hallmarks of descent with modification can be seen at the level of individual genes and that such processes often contribute to or depend up on modular structure (Carroll, Grenier, & Weatherbee, 2001; Duboule & Wilkins, 1998; Gerhart & Kirschner, 1997; Schlosser & Wagner, 2004). To take but one example, the development of the heart can be seen as “the sum product of separable genetic modules”, such as valves, a pacemaker, and the septum that divides the heart into left and right, that were incrementally added over the course of evolution (Fishman & Olson, 1997) — a perfect illustration of the power of both modularity and descent with modification.

4 Two conceptions of neurocognitive modules

What implications does this idea have for modularity? Consider two hypothetical conceptions of modularity, which I will refer to as *sui generis* modularity (from the Latin “of its own kind”) and *descent with modification* modularity. According to the former view, each cognitive (or neural) domain would be an entity entirely unto itself. A language module (or language acquisition device), for example, would owe nothing to other cognitive devices. Audition and vision might similarly be seen as wholly separate. According to the latter theory, current cognitive (or neural) modules are to be understood as being the product of evolutionary changes from ancestral cognitive (or neural) modules.

To some extent, these labels are expository fictions. Neither term is part of the ongoing literature, and I have my doubts as to whether many practitioners would self-identify with either view. But strands of both perspectives appear implicitly in the literature, and part of my objective is to show that the two differ, and differ in their implications.

4.1 Challenges to *Sui Generis* modularity

If modules are taken to be (say) encapsulated computational devices evolved for specific functions⁴, it is natural to think of them as being separate at every level. Cosmides and Tooby, for instance, once wrote that “There is no more reason to expect any two cognitive mechanisms to be alike than to expect the eye and the spleen, or the pancreas and the pituitary to be alike.”

Nonetheless, although any two putatively distinct modules presumably must be *functionally* distinct in order to count as modules, they need not — and I will suggest should not — be presumed to be evolutionarily or genetically *sui generis*. In what follows, I will suggest that many arguments that seem to militate against modularity *per se* really argue only against an extreme, *sui generis* version of modularity, of little force against a more nuanced version of modularity.

Why should one be skeptical about *sui generis* modularity? In the first instance, even in the most “modular” of non-cognitive biological systems (such as the heart), current systems owe much to evolutionary tinkering, in many instances sharing materials (e.g., proteins and cell types) and fabrication techniques (e.g. genetic cascades for establishing positional axes) with other biological systems — and there is no principled reason to expect this to be any different in the brain. Furthermore, in comparison to the period in which (say) eye and spleen have diverged, the time course over which many putative contemporary modules (e.g., for acquiring grammar or for intuitive psychology, the assessing of the beliefs and desires of other people) might plausibly have evolved is relatively short, a time span that perhaps pointing more to shared lineage than sheer *de novo* innovation.

In keeping with this, a number of empirical facts seems to challenge the admittedly extreme *sui generis* view. For example, whatever the neural substrates of language and intuitive psychology may be, they are likely to emerge from relatively similar bits of six-layered neocortex (Brodmann, 1909). They may well occupy (partly) disjoint parts of brain tissue, but it seems likely that the neural tissue that they rely on have at least something in common. (See Kingsbury and Finlay, 2001 for a related suggestion.)

Sui generis modularity faces further empirical challenge from the fact that there is considerable overlap in sets of genes that are expressed in different cortical areas (Liu, Dwyer, & O'Leary, 2000). Distinct cortical areas are least quantitatively distinct, and may well vary both in the combinatorics of their gene expression and in their connectivity at the circuit level, but these differences appear to be superimposed upon a common background that is widely shared across the brain, and not consistent with a picture in which each neurocognitive module would be structured in ways that reflected only adaptive functional constraints that substantially differed from one module to the next.

⁴ Modules could also be taken to be devices that are innate, mandatory, fast, etc, and indeed there has been extensive discussion in the literature about what might count as a module (Carruthers & Chamberlain, 2000; Coltheart, 1999; Fodor, 1983). Because I take the current arguments here to be independent of the modularity's precise formulation, I won't rehearse those discussions here.

Likewise, few genetic disorders that have been demonstrably and uniquely associated with a single cognitive domain (Hill, 2001; Kadesjö & Gillberg, 2001; Kaplan, Wilson, Dewey, & Crawford, 1998; Karmiloff-Smith, 1998), and few cognitive disorders that can be uniquely associated with a particular genetic anomaly. The speech and language disorder found in the British KE family (Gopnik & Crago, 1991; Vargha-Khadem et al., 1998) arguably comes closest, since recent evidence directly ties that disorder to a particular gene, FOXP2 (Fisher, Vargha-Khadem, Watkins, Monaco, & Pembrey, 1998; Lai, Fisher, Hurst, Vargha-Khadem, & Monaco, 2001) but the particular disorder in that family also affects non-linguistic aspects of orofacial motor control (for a review, see Marcus & Fisher, 2003).

Furthermore, it might be argued that there is not enough room in the genome to specify the detailed circuitry of each complex human cognitive domain (e.g. language, intentional understanding, etc.) independently (Bates, 1999; Ehrlich, 2000), especially given how small the genetic difference between humans and the nearest non-speaking cousins, chimpanzees (less than 2% of genetic material: Ebersberger, Metzler, Schwarz, & Paabo, 2002; King & Wilson, 1975).

A further challenge comes from neuroimaging results. Despite fifteen years of neuroimaging (Raichle, 1998) it is difficult to uniquely identify particular neural substrates with particular cognitive tasks, and difficult, except in the lower levels of perception, to localize particular tasks to unique areas (Poeppel, 1996; Uttal, 2001). Complex tasks are often subserved by multiple areas, and individual brain regions often participate in the analysis of more than one type of content. Complex computations might consist of novel configurations of lower-level (modular) structures, rather than wholly proprietary circuitry.

Finally, although there appear to be rare cases of individuals with impaired language but intact cognition (van der Lely, Rosen, & McClelland, 1998) and cases of individuals with (nearly) normal language but significantly impaired cognition (Bellugi, Bihle, Jernigan, Trauner, & Doherty, 1990; Bellugi, Lichtenberger, Jones, Lai, & St George, 2000; Johnson & Carey, 1998), across the population at large, language and cognition are correlated. Bright people tend to be articulate, less bright people less so (Colledge et al., 2002) and people with impairments in one typically have impairments in the other (Hill, 2001), empirical facts that are not directly anticipated by the standard take on modularity.

While none of these facts is devastating to the sui generis view that the mind consists of a large number of modules each operating according to entirely different principles, each poses serious challenges.

4.2 Descent-with-modification modularity

Considerations like these might lead one to abandon modularity altogether, or to suggest that modules be seen only “as the end product of development rather than its starting point” (Elman et al., 1996) suggested.⁵ But abandoning modularity altogether

⁵ A similar view is apparently expressed by Thomas and Karmiloff-Smith (2002), in their suggestion that “genes do not code directly for high-level cognitive modules ... processing structure is emergent and experience-dependent, the *outcome* of developmental processes” (p. 731).

would leave the rare but well-documented cases of patients with genuinely selective impairment unexplained, do nothing to address why children excel at language at an age (Crain, 1991) in which they are otherwise cognitively limited (e.g., well before they can pass classical theory of mind tasks, Baron-Cohen, Leslie, & Frith, 1985), leave observations of apparent constraints in neuroanatomy (e.g. the systematicity of Brodmann's areas and the Felleman-Van Essen wiring diagram) unexplained, and suggest (with little *a priori* motivation) that the brain/mind is the only major physiological system with no internal structure.

Descent with modification offers a way out. Although modules are, by definition (Coltheart, 1999; Fodor, 1983) *computationally* distinct, they need not be genetically unrelated. Although evolutionary pressures can clearly lead distinct physiological structures to diverge and specialize, natural selection tends to be a slow process and many putative modules (e.g., a language faculty) are relatively recent, and as such might be expected to derive from common origins.

Consider by way of analogy the hand and the foot, two functionally and physically distinct systems that have diverged relatively recently from a common ancestral appendage. Through mechanisms such as “duplication and divergence” (Duboule & Wilkins, 1998; Gerhart & Kirschner, 1997; Marcus, 2004b), evolution often creates new systems by making modified copies of old systems, whether at the level of a single gene, or by the force of genetic cascade at the level of complex structures such as limbs or (it appears) brain areas (Kaas, 1987; Krubitzer, 2000). For example, some of our earliest vertebrate ancestors had only a single type of photoreceptor pigment, which sufficed for monochromatic vision. Around 400 million years ago, early in the history of vertebrates, before the modern classes like mammals, birds, and amphibians emerged, the genetic recipe for that pigment was, by sheer chance, duplicated. When one copy of the randomly-duplicated gene diverged (ie. changed slightly through some process of mutation), a new kind of pigment developed, one that was sensitive to a different part of the light spectrum. With two types, it became possible (given some further machinery to interpret the output of the photoreceptors) to discriminate shorter-wavelengths of light (like blue and purple) from longer wavelengths of light (like red and green). About 35 million years ago, one of our primate ancestors branched away from other mammals when there was a second gene duplication, this time of the genetic recipe for the long wavelength (“red”) color pigment. A third duplication and divergence led to a third type of color pigment, and what is known as trichromatic vision (Bowmaker, 1998).

The hand and the foot are similarly thought to derive from common lineage, and known to grow through largely — though by no means entirely — overlapping sets of genes (Margulies, Kardia, & Innis, 2001); an informal way to think about this is that the hand and the foot are both products of generative systems for creating vertebrate appendages.

Distinct neural modules, too, may be the product of divergent copies of ancestral cognitive systems. Such a notion, although vague, can help make sense of many of the biological considerations raised in the previous section. It leads, for instance, to the idea that distinct neuro-/cognitive modules could overlap considerably in their genetic substrates. If each module were built according to its own set of genes, it would be unexplained why there is so much overlap between genes in (say) frontal cortex and the

genes in (say) occipital cortex. If we instead think of frontal cortex and occipital cortex as diverged variation on a common theme for neural computation, the large degree of genetic overlap no longer seems surprising. (And in this light we see that genetic overlap *per se* is not a very good indicator of the extent to which the brain might or might not be modular; it would be surprising on the *sui generis* view, but is consistent with views in which there are (in human cognitive systems) no modules at all, views in which module emerge as an end product of development, and views of modules as the product of descent with modification.)

5 Evidence for modules as the product of descent with modification

Taking for granted the existence of at least some modular structure, and presupposing that genes play at least some role, several further considerations favor the descent view.

5.1 Preliminary evidence

In the first instance, descent-with-modification helps make sense of the considerable phylogenetic continuity that has been documented in recent years, in terms of comparative psychology (Cheney & Seyfarth, 1990; Hauser, 2000), comparative neuroanatomy (Gannon, Holloway, Broadfield, & Braun, 1998) and comparative genomics (Ruvolo, 2004; Waterston et al., 2002). Although humans differ enormously from chimpanzees, in their linguistic capacities (Kako, 1999; Terrace, Petitto, Sanders, & Bever, 1980), their cultural capacities (Richerson & Boyd, 2004), and (among other things) in the richness of their theory of mind (Povinelli & Giambone, 2001; Tomasello & Call, 1997), the psychology (and neurophysiology) of humans clearly also shares a great deal with chimpanzees, in psychology (Diamond, 1992) as well as biology (Carroll, 2003; Gagneux & Varki, 2001), suggesting an overall view of evolutionary innovation imposed upon a shared background.

Beyond this, we should expect evidence for descent-with-modification even *within a single species*. For example, according to the descent-with-modification view, rather than expecting each cognitive system to be a separate black box, we might expect distinct cognitive (or neural) modules to be evolutionarily and genetically related.⁶

In this way, the descent view helps make sense of the curious conjunction of selective impairment and co-morbidity. On a *sui generis* view, co-morbidity is more or less an accident; on the descent view, it's an expected outcome; at the same time the descent picture also predicts (correctly) that there should be rare cases of selective impairment.

⁶ All of these expectations should be tempered by time. Other things being equal, we should expect that systems that have diverged more recently should share more in common than those that have descended less recently. We should thus, for example, expect greater overlap between the substrates of language (which evolved relatively recently, presumably since the last common ancestor with chimpanzee some six or so million years ago, and perhaps, as some have argued, only within the last 1000 years) and general cognition than between, say the heart and the lung, which are separated by at least few hundred million years (Maina, 2002).

Cellular level analyses lend additional support. As mentioned earlier, at the neural level, the neocortex (the area of the brain most strongly associated with higher level cognition) is — to a first approximation — largely similar across its entire extent. With few exceptions, the neocortex is essentially a thin (3-4 mm) six-layered sheet, with each layer having certain characteristic properties that seem largely shared; the 4th layer takes input from the thalamus, layer 5 and 6 send output to subcortical structures. In terms of structure, layer 1 is made up largely of thin white fibers, 5 and 6 largely of pyramidal cells, and so forth (Douglas & Martin, 1998). The brain is filled with repeated motifs (Sporns, Tononi, & Edelman, 2002) such as topographic maps (essentially sets of parallel neural wiring) that occur throughout the cortex (Kaas, 1987; Kaas & Collins, 2001). Repeated structural motifs and common cellular components point to modules as different configurations of common computational stock, rather than entirely independent devices with no common components.

As Todd Preuss (2000) and others have argued, such broad similarities by no means establish complete uniformity — different cortical areas vary in quantitative factors such as thickness (Ramón y Cajal, DeFelipe, & Jones, 1988) and may well have different functions and even different microcircuitry within — but they do anchor the point that there is considerable overlap in the developmental process. Different cortical areas are, it would appear, better seen as variants on a theme than as components generated *sui generis*, independently of the evolutionary and genetic history of their neighbors.

Consistent with this, the expression of genes across cortical areas is remarkably uniform. Contemporary research has identified a unique genetic marker for the limbic system (part of the paleocortex), and several markers that are distributed in different proportion across the cortex (e.g., FGF8, distributed in greater proportion in the front of the cortex than the back, Fukuchi-Shimogori, 2001), but the vast majority of genes, perhaps more than 99%, that are expressed in any given region of cortex are expressed throughout the cortex. There may well be subtle differences in the concentrations of the protein products of those genes, but such differences once again point to parametric variation, not to entirely new suites of genes with developmental programs that are *sui generis*.

One reaches the same conclusion looking a level higher, at the distribution of cell types. Estimates about the exact number of cell types in the brain are notoriously variable, ranging from thousands to hundreds of thousands (Anderson, 1992), but to a first approximation there is again relatively little difference across the cortex. Upper bound estimates of the number of cell types in the brain rely on counting parametric variants as distinct — a neuron with a bushy dendrite is counted separately from a neuron with a sparser dendrite, and that difference is multiplied by the differences in neurotransmitters types (GABA versus glutamate, and so forth) the differences in channel distributions (sodium versus potassium or both), and so forth. However one counts, the variation among neuronal cell types can be traced to common ancestry (Striedter, 2005).

5.2 Language as case study

Further support comes from the extent to which existing candidate modules seem to share properties. To this end, consider language — the canonical putative module, and its relation to cognitive systems.

- Language, like any aspect of cognition, relies heavily on memory; the physical substrates for the memory that is implicated in language may or may not overlap with the physical substrates for memory in other content domains, but it is clear that there are many shared properties. For example, in contrast to the memory of modern digital computers which is typically addressed by location, human memory, whether for language or other domains, is addressed by content (McElree, Foraker, & Dyer, 2003). Likewise, memory in language may well be subject to the same kinds of interference effects observed in memory in other domains (Lewis, 2001). As I recently argued elsewhere (Marcus, 2004a), language may rely on a human-specific organization for memory (i.e., a new *data structure*), but the underlying mechanisms for the encoding, storage and retrieval of memory in language may overlap considerably with underlying mechanisms for the encoding, storage, and retrieval of memory in other domains that are shared across the vertebrate world.
- Language is in no small part a problem of sequencing, and it is possible that the machinery for sequencing linguistic material extends to or adapts other pre-existing machinery for sequencing. One tantalizing (albeit preliminary) bit of recent evidence suggests that training in noncognitive sequencing tasks may to some extent facilitate recovery of syntactic processing in aphasics (Hoen et al., 2003)⁷, suggesting some sort of common cognitive substrate.
- Cognitive mechanisms for spatial and temporal representation seem to run deeply through the structure of our linguistic system (Fauconnier & Turner, 2002; Landau & Jackendoff, 1993; Pinker, 1989). For example, metaphors for space and time pervade language, and map closely to our conceptions of those abstractions. (Yet spatial representations in language and cognition are not isomorphic (Munnich, Landau, & Doshier, 2001), suggesting that language makes use of mechanisms that are related to — but not identical to — those used in the representation of space and time.)
- Basic representational resources, such as the ability to represent relationships between abstract variables, distinctions between kinds and individuals, structured, hierarchical relationships are pervasive throughout both language and other domains of (human) cognition (Marcus, 2001). Machinery for combining linguistic units may be shared with or similar machinery for combining the cognitive units that underlie motor planning (Steedman, 2002).

⁷ I describe the Hoen et al study as preliminary both because it lacks a placebo control and because the results seem to indicate facilitation only for some syntactic structures but not others in ways that would not be immediately obvious from the nature of the non-linguistic training. Furthermore, additional work needs to be done to show that subjects are truly treating the linguistic materials as linguistic.

- Language may, like other domains, rely to an important extent on a process of gradual automatization through repeated practice that is akin to the automatization in other domains (Kawachi, 2002).

None of which is to say that language is *just* a product of pre-existing mechanisms, or that language simply is cognition. Just as wings build upon a common plan for vertebrate limbs by adding feathers and adjusting bone and muscle densities, the human linguistic system presumably is more than just a preexisting ancestral neurocognitive system. To whatever cognitive machinery may have already been in place, evolution may have added specialization of the vocal tract (Lieberman, 1984a), an ability to represent hierarchical or recursive structure (Hauser, Chomsky, & Fitch, 2002; Marcus, 2001, 2004b), a capacity to freely acquire new words (Jackendoff, 2002), and/or an interface between systems for communication and theory of mind (Bloom, 2000); understanding such evolutionarily recent modifications is crucial to any complete account of the human capacity for language. At the same time, as important as such new capacities are, the considerations above suggest that language does indeed borrow — sometimes with important modification, sometimes without — cognitive machinery inherited from our non-speaking primate ancestors.

6 Modules as the product of descent with modification: Implications

Construing contemporary neurocognitive modules as descendants of processes of modification, rather than as *sui generis* devices shaped purely by adaptive advantage without serious regard for developmental constraints, has a number of implications for the disciplines of cognitive science, including how we assess debates about modularity, and how we investigate putatively modular domains.

6.1 Implications for how we identify modular structure

The notion of descent-with-modification, once recognized, has significant implications for how we assess debates about modularity. Although the question of whether any particular computation is performed in modular fashion must inevitably remain an empirical one, ideas such as duplication and divergence undermine many typical arguments against modularity with particular domains.

Consider, for example, developmental disorders that affect multiple cognitive domains. To some opponents of modularity, mental disorders that affect multiple domains are *prima facie* evidence that the mind is without modules. If some disorder affects both language and general intelligence, many assume that language is simply the product of general intelligence, not an independent entity. But a finding that a given disorder affects two behaviors or neural structures doesn't mean that the two are identical — it could just mean that they are built in a similar way. If 95% of the genes involved in the circuitry for building language also participate in the constructing of other mental capacities, the vast majority of genetically-originating disorders should be expected to have broad effects. Impairments to memory, for example, ought to impair language, as well as other

domains like planning and decision-making. Disruptions to the genes that code for metabolic enzymes might be expected to affect (in some cases) the entire brain, and disruptions to genes that code for receptor proteins might have effects wherever those receptors are found. It would be a rare disorder indeed that would affect only a single aspect of cognition.

To take a concrete example, dyslexics often have a deficit not just in phonology but also in sensory-motor skills, and one might be tempted to doubt that dyslexia is a modular deficit. But the existence (and apparent frequency) of processes such as duplication and divergence make it possible that (say) two physically distinct systems could be genetically related.⁸ A finding that many dyslexics have sensory-motor difficulties doesn't mean that a single neural anomaly underlies both disorders; instead a single gene might impair some shared developmental process. Similarly, the fact that some people with language impairments are also cognitively impaired doesn't necessarily mean that language in such people is impaired *because* cognition is impaired; instead, both language and other aspects of cognition (say executive function) could be impaired by a mutation in genes that participate in the development of both. When a given disorder affects two aspects of cognition, we can't necessarily infer that the two aspects of cognition rely on a common neural or cognitive substrate.

The descent-with-modification perspective suggests caution for inferring the absence of modularity from many studies of "normal" cognition. In particular, it is often assumed that if two systems have shared properties, e.g., common learning curves, they necessarily depend on physically overlapping substrates. For example, Markson and Bloom (1997) argue against domain-specificity for word learning on the grounds that one of word-learning's hallmark traits — rapidity of acquisition — applies in other cognitive domains (e.g., associating an object with information about where it came from). A descent-with-modification view highlights the fact that such results are equally consistent with the possibility that there is a specialized architecture for word-learning that has unique physical substrates that share a common genetic heritage with other neurocognitive systems. (E.g., there could be different memory circuits involved in remembering words and "ordinary facts", but those distinct circuits might be built by common substrate).⁹ Once the logic of descent-with-modification is recognized, it becomes clear that parceling cognitive processes into underlying components is significantly more difficult than widely anticipated.

Because of the richness of gene regulation (again, see Marcus, 2004, for a nontechnical introduction), a single gene may be used multiple times in the service of radically different functions, in each copy of a serially-repeated structure (like a finger or a toe), or even in far more diverse circumstances, such as the protein product of the gene

⁸ Ramus (2004) makes a related point, arguing that two clusters of symptoms could arise from a common source. Such complexities could arise in many ways, for example single gene could take on multiple function (pleiotropy), through duplication and divergence a copy of a gene might take on new functions, or a single gene might serve a single function (say transporting a signal from a cell surface to a nucleus) that is recruited in a multiple domains. See Gerhart and Kirschner (1997) for a number of excellent examples.

⁹ Or there could be shared subcomponents used in a different ways in different systems.

Microphthalmia-associated transcription factor (MITF), which participates in eye formation, blood cell formation, and pigmentation (Gilbert, 2000). If a single brain region is heavily involved in two processes, it is commonly assumed that the two domains involve some of the same computations.¹⁰ In contrast, a single gene that is involved in two different processes does not necessarily show that the same cognitive functions are produced by the same bit of neural structure or rely on the same computational mechanisms. Apparently general processes could result from common sets of genes that contribute to multiple physically distinct substrates..

6.2 Implications for the study of linguistics

If, as argued here, modules that seem superficially different may share genes and ancestry descent-with-modification also supplies a novel argument for interdisciplinary collaboration. If two current cognitive mechanisms are, in essence, diverged copies of some single ancestral system, it follows that we may glean insight into both systems by careful comparisons of the two. For example, one might expect that the recently evolved capacity for language would draw heavily on general cognitive (or motor) resources that have been inherited from our ancestors, and hence it stands to reason that we ought to be able to gain insight in language by studying those cognitive resources.

This idea is implicit in some approaches to linguistics, such as Lieberman's (1984b; 2000) theory that language derived from ancestral motor processes, and Liberman and Mattingly's (1985) motor theory of speech perception, but has until recently been outside the mainstream of linguistics.

More recently, in a widely cited paper Hauser, Chomsky, and Fitch (2002), too, favor of an understanding of language that points to the importance of understanding general cognitive mechanisms in the service of language.. In particular, Hauser et al. advocate a distinction between what they call "faculty of language in the broad sense (FLB)" — taken to encompass a sensor-motor system, a conceptual-intentional system, and (as a proper subset of the FLB) a "narrow" faculty of language (FLN), which they describe variously as the "abstract" or "internal computational system." Although they are clear (and in my view correct) in supporting the notion that broad faculty of language can be understood in relation to ancestral systems ("because any aspect of cognition appears to be, at least in principle, accessible to language"), I would suggest that they don't in fact go far enough in appreciating the implications of descent with modification. As far I understand them, they seem to suggest that cognitive systems such as memory and categorization are to be restricted to representing ideas ("the conceptual-intentional system") — playing no role in the narrow abstract computational system.

Descent-with-modification suggests instead that we should see the hallmarks of ancestry even in the very machinery that makes abstract linguistic representation possible.

¹⁰ "Overlap in, say, brain activity at a coarse grain doesn't guarantee overlap at a fine grain;. A single voxel measured in 3 tesla magnet may capture blood flow metabolism associated with hundreds of thousands neurons, and it entirely possible that different subpopulations within are devoted to different tasks or computations.

Although the abstract computational system that allows humans to represent and process language is unique to humans, the circuitry that gives rise to that abstract computational system need not itself be entirely unique. It is possible — maybe even likely — that there is evolutionary precedent for some of the components underlying the abstract computational system.¹¹ In light of the view of evolution as a tinkerer, it is even possible that there are *no* uniquely human components, just uniquely configured components.

In any event, the degree to which the machinery for the abstract representation of language overlaps with ancestral cognitive machinery is necessarily an empirical question. For example, it is plain that we (can) talk about what we remember, but does memory play a deeper role in the abstract computational system itself? I would suggest that it must. There can be no computation with representation (Wirth, 1976), and representation inherently depends on memory. The empirical question then would be whether the memory substrates for linguistic computation evolved independently of other memory substrates, or whether those memory substrates relate to ancestral memory mechanisms.

If the abstract computational mechanism for language incorporates not just memory and recursion, but also mechanisms for (say) categorization or automating repeating actions one is led to a whole family of similar empirical questions: to what extent are the mechanisms that support linguistic representation (a) the very same mechanisms used in other cognitive computation (b) divergent copies of ancestral mechanisms that also gave rise to current cognitive mechanisms or (c) *sui generis* mechanisms with no informative ancestral history. Neuroimaging results that show significant contributions of subcortical regions (e.g., Crosson, 1992; Lieberman, 2002) and frontal areas not traditionally associated with language (e.g., Poeppel & Hickok, 2004) seem to point towards the former two possibilities, and against the latter.

In short, we may learn something about language — not just the content described by language but the very mechanisms that make it possible - by studying its relation to other cognitive systems. Such comparisons could lead to insight into the phylogenetic history of language, give pointers to what might be profitably studied using genetic (or invasive neurophysiological) techniques in animal models, and even lead to insight into the nature of language itself.

More generally, language is but one humanly-unique neurocognitive system, and none of them (e.g., the capacities to develop a rich theory of mind, to acquire symbolic systems of discrete number, or the capacity to contemplate abstract notions independent of the here-and-now) can in its current form be more than 6 or 7 millions year old. If the ideas developed here are correct, none should be studied in pure isolation. For example, in considering the plausibility and functions of putative modules for tasks such as mate-selection (Trivers, 1972), cheater-detection (Cosmides & Tooby, 1992) or theory-of-mind (Baron-Cohen et al., 1985), there may be some benefit to considering how and

¹¹ For an argument that recursion has evolutionary precedent in nonhuman primates, see Frigaszy, et al. (2002).

whether those faculties could have descended with modification from faculties possessed by recent ancestors.

6.3 Relation to Previous Work

The notion that human cognition is a tweak (or set of tweaks) on ancestral cognitive capacities is not entirely new. It occurred to Darwin, appeared in Konrad Lorenz's (1973) Nobel Prize lecture, and in various forms it has reappeared in the writings of contemporary cognitive scientists ranging from Steven Pinker (1989; Pinker, 1997) and Paul Rozin (1976) to the late Elizabeth Bates (1979). Yet the idea has largely faded from view.

In the final analysis, my goal here has not been to challenge a view that has been explicitly defended, but to call for researchers to pay greater attention to an idea that has been underappreciated. Even though upon reflection a number of cognitive scientists might endorse the notion that modern cognitive faculties must in some way represent tinkering upon ancestral cognitive capacities, there has been little day-to-day recognition of the implications of descent-with-modification. For example, although the project of relating language to psychology was once perceived as central research to both disciplines (Bever, 1970) (Halle, Bresnan, & Miller, 1978), since the mid 1970's most linguists have moved towards describing their work in terms of an abstract grammar, without making psychological commitments and many psychologists have lost interest in language as the grammatical theories have become more complex. Efforts to fully integrate the fields have faded from view. If the line advocated here is correct, there may be much to be gained in efforts to reunite the fields.

Likewise, debates in language acquisition have ricocheted between relatively extreme empiricist and nativist accounts, with neither perhaps paying sufficient attention to the compromises suggested by a perspective informed by an understanding of descent with modification. For example, Bates seemed to have recognized the importance of descent with modification in 1979, when she wrote that "language can be viewed as a new machine that evolved initially in the service of completely different functions". Yet she appears to have minimized its importance in the service of defending a more empiricist approach, in which (e.g. Dick et al., 2001) language was seen as the product of a "domain-general" processor that behaves in a particular way in light of "specific linguistic environments" (p. 759) and (merely) "quantitative adjustments [in] cortical and subcortical regions", — apparently leaving little room for qualitative or language-specific evolutionary tinkering.

As Darwin recognized, descent-with-modification can yield much more than this. Tinkering doesn't preclude qualitative or domain-specific changes— it only precludes (or more properly, renders highly improbable) starting from scratch. Wings, for instance, are plainly the product of descent with modification from ancestral appendages, yet they differ *qualitatively* from ancestral forelimbs in their ability to support flight, and are (in contrast both to ancestral limbs in general and contemporary hindlimbs) *specialized* for that function. In a similar way, at least some components of the language systems may differ qualitatively from their predecessors and/or be specialized specifically for language, even if the vast majority of components underlying language are domain-general or only quantitatively different.

Strikingly, consideration of the importance of descent-with-modification is remarkably rare even in the field of psychology most explicitly dedicated to integrating insights into evolution — evolutionary psychology. Instead, the bulk of evolutionary psychology has largely been addressed to just one strand of Darwin's thought — to the question of adaptation, of what functions various aspects of psychology might have developed *for*. Considerably less attention has been paid to the question of how current systems might have evolved through tinkering with ancestral systems. It is not uncommon, for example, to see detailed adaptationist characterizations of why some particular psychological trait might have evolved without any discussion of how the relevant neural or cognitive machinery might relate to circuits recent ancestors might already have evolved. Although I doubt that any serious evolutionary psychologist would suggest that the stock of evolutionary “spare parts” is irrelevant, few have made any direct effort to integrate such arguments, and to the extent that extant evolutionary accounts make no effort to do, they may in some instances be insufficiently constrained. Given the vast amount of recent and converging evidence from developmental biology, brain imaging, and comparative psychology, it might be time for evolutionary psychology to incorporate the notion of descent with modification more directly.

7 Afterword

Demonstrating that descent-with-modularity is not vulnerable to some of the biologically-oriented criticisms that could be leveled against *sui generis* modularity is not the same as showing that the mind (or brain) consists of modules that descended with modification. Even if the mind (and brain) descended with modification from earlier neural and cognitive architecture, it is still an empirical question whether there is any modular structure at all. Descent-with-modification suggests that there should be shared properties between modules, but if there are no modules at all, there would still be shared properties between underlying neural substrates; at best the current arguments put descent-with-modification modularity on a par with a domain-general view; they don't independently affirm it. Affirming modularity (of any sort) in any domain remains an empirical challenge.

Moreover, descent-with-modification is no panacea. It may answer some puzzles, but there are many more it cannot answer. To the extent that evolution has through descent with modification created the entire array of living organisms on the planet earth, from bacteria to worms, spiders, and human beings, descent-with-modification has not constrained biology to any single narrow niche. It is not obvious that our system for communication (say) is the only way that a linguistic system could have evolved, nor that evolution requires all intelligent life forms to reason about things in the same way. To the extent that descent-with-modification provides constraint, it is not by strictly limiting *outcome*, but by limiting process: the question is always where one could go from here (or get here in the first place), not about where one could get starting from scratch. As such, the more we know about ancestral systems the more we will be able to put the notion of descent with modification to useful work.

Finally, as always, adult cognitive (and neural) structure should still be presumed to be a reflection of both experience and genetic factors — the position I have advocated here does not in any way lessen the role of experience. But it does suggest a different way of

thinking about the nature of the genetic contribution. It entails taking anti-modularity arguments with far more caution than is customary, and perhaps most importantly it suggests we might stand a better chance of understanding cognitive and neural function if we studied particular cognitive (or linguistic, or neural) domains not as entities unto themselves, but through a comparison with other current systems that might plausibly have descended with modification from common ancestral systems.

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