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Morten H. Christiansen and Nick Chater

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Authors' Response

Brains, genes, and language evolution: A new synthesis

Morten H. Christiansen[a] and Nick Chater[b]

[a]*Department of Psychology, Cornell University, Ithaca, NY 14853, and Santa Fe Institute, Santa Fe, NM 87501;* [b]*Division of Psychology and Language Sciences, University College London, London, WC1E 6BT, United Kingdom.*
christiansen@cornell.edu
http://www.psych.cornell.edu/people/Faculty/mhc27.html
n.chater@ucl.ac.uk
http://www.psychol.ucl.ac.uk/people/profiles/chater_nick.htm

Abstract: Our target article argued that a genetically specified Universal Grammar (UG), capturing arbitrary properties of languages, is not tenable on evolutionary grounds, and that the close fit between language and language learners arises because language is shaped by the brain, rather than the reverse. Few commentaries defend a genetically specified UG. Some commentators argue that we underestimate the importance of processes of cultural transmission; some propose additional cognitive and brain mechanisms that may constrain language and perhaps differentiate humans from nonhuman primates; and others argue that we overstate or understate the case against co-evolution of language genes. In engaging with these issues, we suggest that a new synthesis concerning the relationship between brains, genes, and language may be emerging.

R1. Introduction

In our target article, we argued for a number of potentially highly controversial theses concerning the relationship between human language and the cognitive and neural systems that support it. Our starting point was Chomsky's (1965; 1980) bold proposal that a core concept in linguistics and biology is Universal Grammar (UG). This species-specific innate endowment comprises a set of universal properties that allow language to develop in the mind of the child in the same biologically determined fashion that a chicken grows its wings. Crucially, the properties of UG are construed as being arbitrary, that is, as having no motivation in terms of how language functions (e.g., as a system for communication). It is from this perspective that Chomsky sees linguistics as, first and foremost, a branch of biology – because the nature of UG is presumed to characterize, albeit at a high level of abstraction, the structure of the brain mechanisms involved in language acquisition (and to a lesser extent, language processing).

UG therefore provides an explanation of the apparently neat "fit" between the structure of human languages and the processes of language acquisition. Children are able to find the "right" linguistic regularities, even in the face of linguistic data that might seem noisy and partial (according to the "poverty of the stimulus" [POS] argument; Chomsky 1980), because the "right" linguistic properties are genetically built-in, as part of UG.

The Chomskyan viewpoint constitutes an extremely strong hypothesis concerning the nature of language development, and has attracted considerable controversy (e.g., Bates & MacWhinney 1987; Pullum & Scholz 2002; Seidenberg 1997; Tomasello 2003; 2004). It is also a strong hypothesis concerning the brain basis for language and its genetic underpinnings, and here too there has been much debate (e.g., Clark & Misyak, in press; Elman et al. 1996; Müller, in press). While UG may be challenged on either of these grounds, or, indeed, concerning whether it provides the right type of theoretical framework for understanding purely linguistic data (e.g., Croft 2001; Goldberg 2006; O'Grady 2005), we argued that the UG approach runs theoretically aground when faced with *the logical problem of language evolution*[1]: that there is no credible account of how a genetically specified UG might have evolved.

Any genetically based biological structure can arise from two types of process: either through a process of (more or less) gradual adaptation driven by selection pressure, or through some non-adaptationist process, by which the structure emerges by "accident." In the target article, we argued that neither story is viable for UG as conceived in Chomsky's framework. An adaptationist account of UG cannot work, because language change is typically presumed to be far more rapid than genetic change. Hence, the linguistic environment is a "moving target," which changes too quickly for a genetically based UG to track. We also pointed out that the spread of human populations creates a further problem. If the adaptationist story is correct, each subpopulation would be expected to adapt to the local linguistic environment, resulting in different UGs across different populations. But such a conclusion contradicts the assumption that UG captures universal properties of human language. Finally, we argued that the non-adaptationist viewpoint is ruled out because the coincidence required to accidentally construct a system of the intricacy and subtlety of UG is too extreme to be credible, according to a simple information-theoretic argument.

The target article put forward a different theoretical viewpoint, which is challenged, amplified, and explored in the highly stimulating commentaries to the article. In particular, we suggested that the fit between language learners and the patterns observed in human languages – a fit which appears to be required to explain how language learning is possible – does not arise because languages are shaped by an innate UG, genetically hardwired in the learner's brain. Instead, this fit arises because languages themselves have adapted to be readily learned and processed. Rather than construing the world's languages as fixed and asking how they are learnable, we proposed that it is more appropriate to consider languages as evolving systems, which have many common patterns in part because they have adapted to common selectional pressures from human learning and processing mechanisms. From this viewpoint, the focus on

the genetic basis for language shifts from the search for genes underpinning linguistic constraints, to understanding the pre-existing neural and cognitive machinery on top of which the cultural construction of language was possible.

In responding to the commentaries here, we suggest that this viewpoint can be seen as part of a new theoretical framework for understanding the relationship between brains, genes, and language. We divide our discussion into four broad, although interrelated, themes:

1. *Rethinking classical UG*. The commentaries, and the wider current literature, indicate that theorists – except for a few holdouts (**Harnad**) – are either working outside (**Goldberg**; **Hurford**), or at minimum substantially reconceptualizing, the classic UG framework (**Barrett, Frankenhuis, & Wilke** [**Barrett et al.**]; **Piattelli-Palmarini, Hancock, & Bever** [**Piattelli-Palmarini et al.**]; **Reuland**; **Satterfield**). Somewhat to our surprise, there is relatively little argument to the effect that an evolutionary account can be offered for anything like classical UG. Nonetheless, the commentators raise a range of important issues concerning the possible innate basis for language.

2. *Too much emphasis on the brain*? The issue here is: How far can cultural learning of a system for communication explain language structure, independent of cognitive and neural constraints? Some commentators focus on the explanatory power of learning mechanisms (**Catania**), while others emphasize the mechanisms of cultural transmission (**Blackmore**; **Caldwell**; **Smith, Kirby, & Smith** [**Smith et al.**]).

3. *The biological and cognitive basis for language*. A diverse range of forces are identified, by which language may have been shaped by the brain and beyond (**Aronoff, Meir, Padden & Sandler** [**Aronoff et al.**]; **Behme**; **Brooks & Ragir**; **Corballis**; **de Ruiter & Levinson**; **Dessalles**; **Enfield**; **Fauconnier & Turner**; **Goldberg**; **Greenfield & Gillespie-Lynch**; **Landauer**; **Lieberman**; **Namy & Nygaard**; **Tallerman**; **Toscano, Perry, Mueller, Bean, Galle, & Samuelson** [**Toscano et al.**]; **Wallentin & Frith**). These proposals can also be viewed as providing a range of potentially complementary perspectives concerning what crucial neural or cognitive structures differentiate humans from nonhuman primates.

4. *When can genes and language co-evolve*? The target article makes a narrow argument: that a co-evolutionary, adaptationist account of the origin of a genetic basis for *arbitrary* linguistic constraints (as postulated in UG) is not viable. A range of commentators consider whether the assumptions of this argument apply, especially in relation to the presumed speed of language change (**Blackmore**; **Greenfield & Gillespie-Lynch**; **Pagel & Atkinson**) and level of selectional pressure (**Behme**); while others suggest that the argument cannot go through more generally (**Barrett et al.**; **Blackmore**; **Fitch**; **Hurford**), or that our arguments can be expanded to argue even against the possibility of the co-evolution of functionally relevant linguistic regularities (**Smith et al.**).

In the following sections, we discuss these themes in turn, and close by outlining open questions and challenges for future research that are raised by the commentaries. We conclude that the balance of the discussion suggests that a new synthesis concerning the relationship between brains, genes, and language may be emerging.

R2. Rethinking classical UG

The centerpiece of our argument was that there is no credible evolutionary account for a genetically based UG, throwing the classical conception of UG into difficulties. Many commentators are, largely on independent grounds, happy to accept that UG, as classically conceived, is not viable. For example, **Goldberg** argues that the traditional conception of UG should be replaced by an attempt to specify the cognitive and neural prerequisites for language, noting that recent advances in, among other things, the computational and psychological study of learning, require revisiting arguments for UG. Indeed, Goldberg and several other commentators (e.g., **Hurford**; **Wallentin & Frith**) note that Chomsky's own position can be read as rethinking the classical UG viewpoint. Thus, Hauser et al. (2002) have, as Goldberg notes, emphasized the importance of domain-general mechanisms, raising the possibility that recursion might be the only element of the "narrow faculty of language" – that is, a genetically based process, which is specific to language.

We agree with these commentators that, taken at face value, this theoretical position does seem to require letting go of core theoretical claims previously associated with UG. This move has substantial theoretical implications: It signals the need for a complete revision of the perspective that the goal of linguistics is the characterization of UG; a withdrawal of the claim that linguistics is a branch of biology; and a departure from viewing language acquisition as the "growth" of a language organ, whose blueprint is specified by the genetic constraints that encode UG. It seems, then, that Hauser et al.'s (2002) position is strongly in tension with those contemporary theorists who are committed to the view that language acquisition must be explained in terms of innate language-specific constraints, both in meta-theoretic discussions in linguistics (**Harnad**; **Reuland**; see also, e.g., Boeckx 2006) and accounts of language acquisition (e.g., Crain & Pietroski 2006).

Even if the conventional UG picture is set aside, some commentators suggest that there is, nonetheless, a role for language-specific innate constraints of some kind, especially in explaining how children can learn the enormously subtle and intricate patterns in natural language. Thus, **Satterfield** raises the point that a naive empiricist perspective on language acquisition might be expected to mirror the adult linguistic environment. But how, then, are systematic errors in children's speech to be explained? For example, how, she asks, is it possible to explain that children brought up in English-speaking linguistic environments frequently drop subject pronouns in tensed clauses (Hyams 1986), even though this is not observed in their linguistic environment? Satterfield suggests that we must look to innate language-specific biases to explain how this can occur. We agree with Satterfield that biases may be needed to explain this and other acquisition phenomena. However, whether such biases are specific to language is, of course, an empirical question. Indeed, recent analyses of children's spontaneous productions and computational modeling by Freudenthal et al. (2007) suggest that the omission of subject pronouns in English may be explained without recourse to language-specific information, by a simple developmental model incorporating cognitive processing constraints and which gradually acquires grammatical knowledge from distributional information in child-directed speech.

Also focusing on the role of innate constraints, **Reuland** provides a shortlist of requirements for an innately specified language acquisition system, going beyond the minimal conception of UG as containing only recursion (Hauser et al. 2002). These constraints appear highly language-specific in nature, such as a checking operation to compare linguistic features and a locality condition to restrict movement, depending on linguistic domains. Moreover, even if, in line with the Minimalist Program, much of the prior work of classical UG is pushed into a parameterized lexicon, non-lexical parameters are still needed in current versions of minimalist theory (Baker 2001; Boeckx 2006). Thus, despite the arguments put forward by Hauser et al. (2002), current generative accounts of language in linguistics appear to require UG to encompass considerably more abstract, language-specific properties than just recursion (at least given the current state of the Minimalist Program). As a consequence, such accounts are therefore vulnerable to the logical problem of language evolution described in the target article.

One potential way of rethinking UG is to reconceptualize it in more functional terms, which are outside the immediate scope of the arguments in the target article. **Satterfield** suggests that UG be construed as a collection of domain-general mechanisms that interact with language-specific components to help resolve the purported POS problem (see also Bever, in press). However, this perspective cannot escape the logical problem of language evolution, because of the arbitrary (i.e., nonfunctional) nature of the latter, language-specific, part of this hybrid UG. **Barrett et al.** push the reconceptualization of UG still further, proposing to conceive it simply as whatever mechanisms have evolved specifically for language – even if these should turn out to be entirely functional in nature and thus diametrically opposed to the claims of classical UG. As noted in the target article, we agree that evolution may have led to adaptations for certain functional features of language – though, as discussed further below, the extent of this is not clear (**Smith et al.**).

In contrast to these adaptationist reconceptualizations of UG, **Harnad** endorses our analyses of the problems facing adaptationist explanations of UG and instead backs a non-adaptationist account. However, as mentioned above and in the target article, this type of explanation faces a difficult dilemma. On the one hand, if UG is really so simple that it can come about through "chance" (e.g., via a single mutation), then it is not clear how it can resolve the purported POS problem, or other acquisition phenomena (as, e.g., highlighted by **Satterfield**), which are typically viewed as requiring rich language-specific innate constraints. On the other hand, if UG is permitted to have the complexity necessary to deal adequately with such acquisition issues (as hypothesized by many generative approaches), then the probability of such an intricate biological structure emerging de novo through a single macro-mutation is vanishingly small.

Also advocating a non-adaptationist perspective, **Piattelli-Palmarini et al.** suggest that we have underplayed the impact of the "evo-devo" revolution in biology for understanding how UG might have evolved by non-adaptationist means. The evo-devo approach has shown that biological evolution frequently exhibits the repetition and variation of basic "modular" structures, typically underpinned by common genetic machinery (Kirschner & Gerhart 2005).

Could this be true for UG? Chomsky (e.g., 1980) repeatedly stressed how the structure of language differs fundamentally from that observed in other cognitive domains. If this is right, it is very difficult to see how a unique, complex, and fully functioning system might spring into being as a minor variation of some existing cognitive structure. Similarly, if, as Piattelli-Palmarini et al.'s title appears to suggest, the design of language arises from optimality constraints, which might perhaps, as Chomsky (2005b) has recently suggested, be analogous to the minimum principles that give rise to soap bubbles and snowflakes, then it is unclear why special-purpose biological machinery for UG is theoretically necessary at all. In the target article, we therefore argued that the emergence by non-adaptationist means of a complex, functioning neural *system* embodying UG is astronomically unlikely. Indeed, as we read the literature, biological structures built de novo appear invariably to be shaped by long periods of adaptation (Finlay 2007). Thus, while antennae may be a modification of the insect leg (Carroll 2005), it is *not* an insect leg, or anything like one. It is exquisitely crafted to play its new role – and such apparent design is universally explained within biology as an outcome of Darwinian selection. The impact of evo-devo is to help us understand the intricate structure and constraints of the space of organisms over which the processes of variation and natural selection unfold; it is not an *alternative* to the operation of natural selection (Carroll 2001).

R3. Too much emphasis on the brain?

The title of our target article, "Language as shaped by the brain," embodies the claim that the brain, and the thought-based, perceptuo-motor, cognitive, and socio-pragmatic processes that it supports, plays a crucial role in determining the structure of natural language. Yet, as we pointed out, the influence of these processes can take a wide range of routes. Many of our commentators explore the possibility that our emphasis on the brain may be excessive (**Catania**); or that it should at minimum be supplemented with an analysis of the selective forces on language generated by its communicative function, and its transmission across networks of individuals (**Brooks & Ragir**; **Smith et al.**; **Wallentin & Frith**). According to this latter viewpoint, there may be regularities in language that can be understood independently from the details of brain mechanisms. In general, a natural challenge to our perspective on the evolution of language structure is to ask, from an explanatory point of view: How much can be explained by cultural transmission alone?

Catania suspects that, in using the brain to explain linguistic behavior, we have the cart squarely before the horse. Instead, he sees behavior as primary and argues that human learning mechanisms may be flexible enough to capture and reflect whatever patterns of behavior may be required. He uses the analogy of categorical perception (Liberman et al. 1957). While many theorists suggest that categorical perception between phoneme boundaries may arise from boundaries in the sensory input or the mechanisms of speech perception and/or production, Catania contends that it may be more productive to propose that such boundaries are not so constrained. Instead, the specific boundaries observed in categorical perception in

different languages may be determined purely by the linguistic environment (i.e., English vs. Arabic) – according to this viewpoint, the brain is not shaping language, but responding to the linguistic environment.

We suggest that this viewpoint is not adequate to explain linguistic regularities in general, however, precisely because it does *not* place constraints on the patterns of language that are viable. The challenge of understanding language structure is to explain the structural regularities that the world's languages do, and do not, exhibit; and some of the key sources of constraints are, we suggest, that languages must be easy to learn (from limited amounts of data that are available to the child), that they must be easy to process (e.g., linguistic relations will typically be local, rather than involving arbitrarily long and complex dependences between linguistic items), and that they must fit naturally with the perceptual and motor apparatus (language must be easy to decode, and easy to produce).

A lack of focus on such constraints is, we suggest, also evident in many meme-based accounts of cultural and linguistic evolution, as exemplified in the commentary by **Blackmore**. She suggests that language should be viewed as a complex of memes; and that these memes propagate in a *selfish* way – that is, the crucial factor in language evolution is the replicative power of memes, independent of any functional value that the memes may or may not have for their "hosts," that is, language users. We are wary of this perspective if taken to an extreme. We would agree that understanding which aspects of language structure will readily be transferred from one generation of language users to another is critical in understanding the selectional pressures on languages. But we see the question of the learning and processing biases of learners to be crucial in determining what is, or is not, readily transferred. That is, which structures "replicate" depends critically on the nature of the brains that propagate those structures via learning. Thus, we see the selection pressures on language as arising, to a large degree, from the properties of the brain.

Piattelli-Palmarini et al. appear to have mistaken our approach for a meme-based account (such as **Blackmore's**) and are concerned that viewing language as a cultural product means that linguistic evolution is no different, in principle, from the design of a Boeing 707. But, of course, aircraft are typically products of directed and determined efforts of design, typically by vast teams of scientists and engineers. The process of the cultural construction of language is, we suggest, a much more piecemeal, distributed, and incidental matter. In specific circumstances, with particular purposes in mind, people attempt to communicate; and the layering of such attempts, and their selective winnowing and replication, inadvertently creates a language, shaped by the brain. The putatively worrying analogy with aircraft design therefore seems remote at best.

More generally, a tendency to see processes of cultural transmission as an *alternative to*, rather than as *grounded in*, theories of brain and cognition occurs elsewhere in the literature. For example, many properties of language are viewed as arising from historical processes of language change (such as grammaticalization); and such processes are viewed as fairly independent of underlying brain mechanisms (Bybee, in press). But we argue that processes of historical language change depend crucially on the cognitive and neural machinery of the speakers involved. Even if language

is a cultural product, created by processes of cultural transmission, it is nonetheless shaped by the brains that create and transmit linguistic structure. The brain, and the cognitive and learning constraints that it embodies, is centrally important, after all. **Brooks & Ragir** generalize this line of thought to cultural products more broadly, suggesting that tool manufacture, music, and play are all likely to be shaped by an interplay of factors governing cultural transmission and the cognitive constraints of individual agents. We shall discuss later on how far the arguments of our target article, particularly concerning the non-viability of nativism with respect to apparent universals, might apply beyond language to other aspects of culture.

One way to study the interplay of constraints on learners and the structure of the cultural transmission of language is through the combination of computer simulations – where both the "cognitive machinery" of the learners and the structure of communicative interactions, including the structure of the "social network" across which information is diffused, can be directly manipulated. **Smith et al.** mention their important work in this tradition, which we shall discuss in detail later. A complementary approach is to study the diffusion of information across human agents, as outlined by **Caldwell**. She finds intriguing cases of "convergent evolution" in problem-solving tasks, when solutions are passed from "generation to generation" by gradual replacements of group members. Here, the selectional pressure (the preference for one solution over others) results from explicit reflection and discussion within the group, rather than the presumably nonconscious biases that shape many aspects of language evolution. Nonetheless, this work provides an intriguing illustration of how the properties of learners (here, their problem-solving abilities and biases) can lead to systematic regularities, which may converge across groups. Perhaps similarly, convergent evolution at the level of language change might explain some common properties across the world's languages. Thus, the interplay of computer simulations and empirical research promises to be particularly fruitful for the investigation of such convergent evolution.

R4. The biological and cognitive basis of language

In the previous section (R3), we considered commentaries that emphasize the importance of learning, communication, and properties of cultural transmission – but we have stressed that these processes are grounded in the properties of our cognitive and neural mechanisms. Here, we consider commentaries for which those mechanisms are the main focus. That is, we consider questions such as: What are the cognitive pre-adaptations that make the cultural construction of language possible? What is distinctive about human cognition? And, more broadly, how is language rooted in biology?

Before addressing these questions, it is important to distinguish the main points at issue, which concern the general biological machinery that makes language possible (which, it is typically assumed, is shared by all normally developing humans), from the question of individual variation in linguistic ability. **Pagel & Atkinson** rightly point out that human linguistic abilities, like most human cognitive differences, are quite strongly heritable, implying that these differences have a genetic basis. Such differences need not, of course, be language-specific, but might reflect general processing differences, such as variations in memory (**Landauer**; see also, e.g., Ericsson & Kintsch 1995; MacDonald & Christiansen 2002; Wynne & Coolidge 2008). Moreover, "generalist" genes may explain a broad range of learning abilities and disabilities (Kovas et al. 2007). In the target article, however, the focus is not on genes that vary between language users, but on the common genetic basis, shared across the normally developing population, that supports language acquisition and processing. The range of suggestions concerning the key biological and cognitive bases for language mentioned in the commentaries is impressively broad.

De Ruiter & Levinson argue that the key driving force behind language is *communicative intelligence*: a powerful pragmatic system for relating signals to communicative intentions. They argue that this system arose prior to language, and that this adaptation crucially distinguishes the human brain from that of other primates (for a related perspective, see Tomasello 2008). This approach provides an elegant inversion of the assumptions common in nativist perspectives on language acquisition. According to that tradition, the distinctive features of the language organ concern the abstract, structural properties of syntax and phonology; pragmatic inference is typically assumed to be continuous with general inference abilities (e.g., Fodor 1983), and hence not properly part of the language system at all, let alone part of UG. Yet, de Ruiter & Levinson take pragmatics to be the cognitively decisive mechanism for the emergence of language; and Levinson (2000) suggests, as we briefly described in the target article, that highly specific and intricate structural patterns in language, such as the binding constraints, emerge as a consequence. This concrete example of how general communicative factors can generate apparently highly arbitrary and complex syntactic phenomena illustrates the potential value of viewing language as adapted to the brain, rather than the reverse. This case is perhaps particularly interesting, given that binding constraints are often highlighted as particularly strong evidence for innate linguistic constraints (**Reuland**).

Enfield makes a related argument, focusing instead on the primacy of the speech act, a pragmatic notion concerning the unit over which communicative intentions are conveyed. He argues that the structure of communication as a series of conversational "moves and countermoves" may have strong implications for the structure of grammar. **Fauconnier & Turner**, by contrast, argue that human evolution may have undergone a qualitative and decisive *cognitive* transition involving the ability to engage in "double-scope blending." This ability permits the integration of two different representational frames, which Fauconnier & Turner take to underlie the creation of not merely language but many aspects of culture, from mathematics to religion. We suggest that the complexity and variety of cognitive machinery that presumably underlies the full range of cultural products, including language, makes the existence of a single key transition prima facie unlikely; but this bold possibility is certainly worthy of consideration in principle.

Tallerman takes up a complementary line of reasoning, in considering cross-linguistic regularities in case-marking systems. She notes that case-marking tends to be highly "economical" – that is, while a variety of possible linguistic cues

may be used to signal case, cues are used only where necessary to avoid ambiguity. Typically, overt case-marking only applies to one member of an "opposition" (e.g., between agent and patient); the identity of the non-marked case may, presumably, be "filled in" by the listener using the type of pragmatic inferences considered by **de Ruiter & Levinson**. Tallerman's account explains some of the variety of case systems observed cross-linguistically, from a purely functional standpoint (e.g., in terms of economy and avoiding ambiguity). Her arguments thus provide a counterweight to **Satterfield**'s claim that innate knowledge of case systems may have to be built into the learner. Clearly, children are able to acquire case systems for natural language – but this may be explained because case systems have evolved to be functionally effective, and, we suggest along with Tallerman, readily learned and processed. Thus, case systems, along with other linguistic regularities, will reflect whatever learning and processing biases the cognitive system embodies. But this match arises not because the learner has a language-specific innate knowledge of the case system, but instead because the case system has been selected to fit language learners and users.

Wallentin & Frith take a different tack, developing an intriguing argument. They first point out that perceptuo-motor constraints are likely to be important in constraining language, noting that imaging studies suggest that neural representations of different classes of words are located in corresponding brain areas (e.g., action words are often associated with prefrontal cortex [Hauk et al. 2004], whereas words representing spatial relations are associated with posterior parietal cortex [Wallentin et al. 2006]). Nonetheless, they note that, in many areas of classification (e.g., color names), there is considerable variation across languages, even though color names appear to be driven, to some extent at least, by considerations of perceptual optimality (Regier et al. 2007). Wallentin & Frith suggest that this may arise because the drive to align with other group members may outweigh the drive to find an optimal classification. They suggest that the goodness of a classification may partially be defined in terms of agreement with other group members, which may potentially lead to a radical and rapid runaway process. We suggest that such processes may be particularly likely where there is a large range of alternative solutions, which are roughly equally "good" from the point of view of the individual agent; and especially when it is difficult to shift from one type of solution to another. Many of the arbitrary aspects of the world's languages, ranging from the inventory of phonemes, the variety of syntactic categories, to the functioning of pronouns, seem to exhibit considerable variation. These variants are, perhaps, roughly equally good solutions; and moving between solutions is slow and difficult (although historical linguistics does sometimes indicate that change does occur between such forms; McMahon 1994). In such cases, the selection pressure on language from the brain imposes only a relatively weak constraint on the solution that is reached. Conversely, the functional pressure for the emergence of other aspects of language, such as double articulation (i.e., separate combinatorial layers of phonological and syntactic structure) or large vocabulary (**Hurford**) or compositionality (**Smith et al.**), may be so strong that these factors are not disturbed by social forces.

Greenfield & Gillespie-Lynch also consider perceptual-motor factors to be an important, but insufficient, starting point for understanding language. They argue that the structure of actions may provide an infrastructure for linguistic behavior (see, e.g., Byrne & Byrne [1993] on the complex action sequences involved in field observations of gorilla leaf-gathering). This infrastructure might be co-opted in gestural communication. Yet, like **Wallentin & Frith**, Greenfield & Gillespie-Lynch argue that social factors are likely to play a key additional role. They suggest that mirror neurons, which are phylogenetically broad, may be indicative of "intersubjectivity" (i.e., the sharing of mental states by two or more people), and that this may be crucial to language (as is indicated by, for example, work on joint attention in developmental psychology; Eilan et al. 2005). Mirror neurons appear to represent actions, whether performed by the agent or merely observed; and, suggestively, mirror neurons are located in what is arguably the homologue of Broca's area, which is important for language in humans. Differential expansion of language-related areas in the human brain may, Greenfield & Gillespie-Lynch suggest, indicate co-evolution of brain and language.

We suspect that such arguments may currently be premature. Although a number of experiments have been conducted to investigate mirror neurons in humans, the results remain unclear (for discussion, see Turella et al. in press). Another caveat is that mirror neurons were originally found in a nonhuman primate, and may even be present across a wide range of species (Hurford 2004), indicating that mirror neurons may not be a key factor in language evolution. Moreover, there are elegant statistical models that accurately show the relationship between the differential expansion of brain areas across a wide range of mammals. These models reveal no notable expansion of Broca's or Wernicke's area, as might be expected from selectional pressure for language (Finlay et al. 2001). Although these considerations caution against the specific scenario for language evolution outlined by **Greenfield & Gillespie-Lynch**, the argument of our target article does not deny the possibility of brain-language co-evolution. Rather, the logical problem of language evolution arises for *arbitrary* properties of language – because, having no "functional" anchors, these will tend to vary freely and rapidly, both across time and across populations. This would lead to a highly unstable linguistic environment, to which slow-changing language genes cannot readily adapt. But this specific argument does not eliminate all possibility of co-evolution between genes and behavior. For example, it is entirely compatible with our argument that better memory (**Landauer**) or better pragmatic skills (**de Ruiter & Levinson**; **Enfield**; **Wallentin & Frith**), might co-evolve with a language system that draws upon these skills. We shall discuss these issues in more detail, as they arise throughout the commentaries, in section R5.

Lieberman has a different proposal concerning the key neural circuitry underpinning language and a range of other human-specific behaviors, such as dance and music. He focuses on neural circuits creating bidirectional links between the cortex and basal ganglia. As also noted in the target article, the corticostriatal system is important for the learning and processing of sequential information (Packard & Knowlton 2002). Lieberman further argues that "hard" data from molecular genetics and neuroimaging suggest that these neural circuits underpin our productive syntactic capacity. For example, mutations in the FOXP2 gene, which has been shown to be crucial to the

development and function of the corticostriatal system (Lai et al. 2003), give rise to severe speech and orofacial motor problems (Lai et al. 2001; MacDermot et al. 2005). This genetic link between sequential learning and language is further underscored by recent results showing that common allelic variation in FOXP2 is associated with individual differences in performance on a sequence-learning task, which, in turn, is related to language ability (Tomblin et al. 2007). Thus, genetic research relating to brain development can readily be incorporated into the new synthesis proposed here, providing insights into the nature of the neural constraints that shape language evolution.

Emphasizing the importance of constraints arising from the human body, **Aronoff et al.** and **Corballis** explore the contribution of gesture to language evolution. Indeed, Corballis sees gesture as the origin of language, arguing that early languages may have been signed, rather than spoken. He argues that the scenario for language evolution outlined in the target article is compatible with a gestural origin of language. We see this as an important possibility. It is certainly conceivable that early language – as a cultural product – might equally well have been shaped by the mechanisms involved in the production and interpretation of gestures as those used for vocalizations. Research on modern apes suggests that vocal and manual gestures might initially have proceeded in parallel, perhaps with a more flexible use of gestures (Pollick & de Waal 2007). Subsequent changes to the human vocal tract might then have tipped the scales toward speech as the default modality for language (irrespective of whether these anatomical changes were adaptations specifically for speech [Lieberman 1984] or something else [Hauser & Fitch 2003]). We remain agnostic with regard to these questions of language origin, but we note that – perceptuo-motor differences notwithstanding – there is considerable overlap in mechanisms between spoken and signed languages that would allow for much similarity in the thought-based, cognitive, and pragmatic constraints imposed on their evolution (as outlined in the target article).[2]

Further highlighting the importance of gesture, **Aronoff et al.** point to newly emerging sign languages as a source of evidence of language evolution in vivo. Specifically, they argue that a key discontinuity between humans and other primates is *iconicity*: While nonhuman primates in the wild spontaneously gesture, they appear never to use gesture to represent external objects or events. It is interesting to ask how this difference may relate to cognitive distinctions discussed by other commentators, including **de Ruiter & Levinson**'s communicative intelligence. Perhaps the key to being able to interpret a gesture as a representation is understanding that the gesture is a signal that is intended to convey a message; and producing a gesture as a representation requires understanding that the other agent will understand this intention; and so on. A complementary suggestion is **Corballis**' proposal that "mental time travel" – the ability to mentally replay past events, or imagine future events – may underpin symbolic representation, which allows reference to items that are not perceptually present.

While **Aronoff et al.** see iconicity as a starting point for (signed) language, **Dessalles** views it as a crucial limitation. He argues that if language has been shaped by the brain, then we should expect that iconicity should be maximized, because this would make learning as easy as possible. Yet, as de Saussure (1916/1959) observed, relations between linguistic signs and their meanings are typically close to arbitrary. We believe this concern can be readily allayed by noticing that language is selected not just to be learnable, but also to be communicatively effective (that is, forms which do not successfully convey their message will be eliminated). As **Namy & Nygaard** point out, *communicative* pressures favor arbitrariness. An iconic representational system will preserve the similarity relations of the represented domain in the signs themselves. Although communication often requires distinguishing between signs for closely related things, context typically can tell us what a sign is referring to (e.g., a species of fish, a brand of car, or a TV show). An iconic system of representation will be communicatively inefficient if the signs for each type of object are highly similar, and hence contextually redundant and difficult to distinguish, both in production and perception. Developing this idea, Monaghan and Christiansen (2006) illustrate the advantages of an arbitrary, rather than a systematic, phonology-semantics mapping, in simulations with a feed-forward connectionist network. Nonetheless, the model also indicates that systematic mappings may arise in the service of learning about other aspects of language (e.g., in the form of phonological cues to lexical category; Monaghan et al. 2007). As noted by Namy & Nygaard, this illustrates the idea of language as adapting to multiple competing constraints.

Stressing the importance of communication, as well as learning, in shaping the evolution of language also resolves another of **Dessalles**'s concerns. He suggests that if languages are selected to be learnable, then linguistic complexity will gradually be stripped away, leading ultimately to a "null" language. But such a language will not evolve, precisely because it would have no expressive power, and hence would be communicatively useless. The complexity and diversity of language arise because the primary purpose of language is rich and flexible communication.

Goldberg raises a more subtle version of the same issue. Should we expect that, through successive generations, languages will become increasingly easy to learn? Might this imply, perhaps implausibly, that Creoles would be especially difficult to learn? Goldberg notes, though, that such predictions do not immediately follow, precisely because language has to simultaneously satisfy constraints concerning expressive power, and ease of learning and processing. The drive for expressive power will typically lead to greater complexity, balanced by a drive for ease of learning and processing, which pushes toward greater simplicity. Note that the constraints from learning and processing may also be in opposition – and some aspects of language change may crucially arise from this opposition. For example, historical language change involves both processes of erosion (i.e., reducing morphemes, creating irregular forms, and thus reducing the load on language production) and regularization (making learning easier) (McMahon 1994).

But how much of language change is due to child language acquisition (Bickerton 1984), or is linguistic variation primarily created and propagated through adult populations (e.g., Bybee, in press)? To the extent that child language acquisition is the major driver of change, the processes of cognitive development are likely to be important in understanding language change (**Toscano et al.**). We are sympathetic to this general perspective (cf. Karmiloff-Smith 1992), although the current state of

understanding of the learning and processing mechanisms across development may currently be insufficient to constrain closely the theory of language evolution. **Brooks & Ragir** also stress the importance of development – and in particular the prolonged neural plasticity that seems especially characteristic of humans. We see prolonged development as a consequence of the need to construct highly complex, yet flexible, cognitive functions. Indeed, to the degree that cognitive development must be responsive to the particular culture (including the particular language) to which the child must adapt, a prolonged period of learning from the environment (whether physical, social, or linguistic) is surely necessary.

Brooks & Ragir argue that our target article is insufficiently radical, however. They wish to go beyond our claim that language does not presuppose a genetically specified UG, to argue against the existence of genetically encoded cognitive pre-adaptations for language. To the extent that a pre-adaptation for language is a mechanism or process that has adapted through natural selection, but not to support language, the claim that such pre-adaptations exist seems relatively mild. Indeed, the various claims concerning cognitive and biological prerequisites for language reviewed above all seem plausibly to fall into the category of pre-adaptations. Yet we suspect that Brooks & Ragir's aim is not to deny the existence of pre-adaptations. Rather, it is to deny that the development of any specific pre-adaptation was the trigger for the creation and evolution of language. Instead, they suggest that changes in habitat, diet, and social organization might be more important. To the degree that language is viewed as a cultural phenomenon, this perspective seems plausible. Scholars do not seek to identify a crucial biological change in the hominid lineage supporting the development of agriculture, fire, or arithmetic – it may be that this is equally futile in the case of language. Nonetheless, language does appear to be uniquely human. Even if there is no single critical difference between humans and other animals, it still seems to be an important scientific project to sketch out the dimensions on which humans are biologically and cognitively special.

More broadly, the commentators on this target article have provided a rich set of hypotheses that deserve further exploration, illustrating the potential pay-off that may be obtained by attempting to understand language as shaped by the brain, and thereby countering **Piattelli-Palmarini et al.'s** concern that our approach has no explanatory bite.

R5. When can genes and language co-evolve?

Our target article makes a narrowly focused argument against the hypothesis that genes *for arbitrary features of language* (as in UG) could have co-evolved with the language itself. In a nutshell, the concern is that, lacking any functional pressure to stabilize them, and prior to the existence of putative language genes, such arbitrary features of the language will vary. Indeed, we suggest that language change is typically very much faster than genetic change, and, hence, that the linguistic environment will provide a moving target, against which biological adaptation will not be possible. We noted also that the spatial diffusion of human populations would be expected to lead to a wide diversity of languages (and, indeed, human languages appear to diverge very rapidly – Papua New Guinea was probably settled less than 50,000

years ago, and yet it contains perhaps one quarter of the world's languages, exhibiting an extraordinary diversity in phonology and syntax; Diamond 1992). Co-evolutionary processes can, of course, only adapt to the current linguistic environment – and hence the variety of languages would, through co-evolution, generate different selective pressures on "language genes." Yet modern human populations do not seem to be selectively adapted to learn languages from their own language groups – instead, every human appears, to a first approximation, equally ready to learn any of the world's languages (but see Dediu & Ladd 2007).

Although the target article is clear about the narrow scope of this argument, and, indeed, explicitly notes that it does not necessarily apply to functional aspects of language, several commentators take our argument to be rather broader: to amount to the claim that no aspect of cognition can be positively selected for language, or even that co-evolution between any pair of processes is not possible. In the light of this misreading of our argument, several points of concern from the commentators can be set aside.

In particular, **Blackmore** raises the concern that possible (although controversial, see Hauser & Fitch 2003) evidence that the larynx has been adapted to improve speech articulation would cast doubt on the viability of our argument against the co-evolution of language and language genes. Note, though, that improvements in the speech apparatus would have a positive and general functional impact on language behavior, whereas genes for UG are expressly for arbitrary features of language – and it is the latter that is the subject of our argument. **Barrett et al.**, similarly, develop an argument that language-gene co-evolution is possible, in principle. We entirely agree (see Christiansen et al. 2006, for simulations of the biological adaptation for functional features of language). Our arguments apply only to the viability of co-evolution of genes for arbitrary features of language, and Barrett et al.'s counterarguments do not address this.

Fitch puts forward what appears to be a more direct attack on our position: "If this 'logical problem of language evolution' is indeed as severe as C&C claim, it is not just linguists who should be worried: any biologist interested in adaptation to a rapidly changing environment (e.g., individual learning) or culturally transmitted system (e.g., bird or whale song) should be alarmed." The first case does not seem directly relevant. Fitch notes that adaptation to a rapidly changing environment typically leads to "generalist" species (e.g., rats) whose behavior is highly responsive to the environment; the natural parallel would be to assume that language learners would be generalists, able to deal with a broad range of linguistic environments. But, before the putative UG is established, early languages will not exhibit any specific set of arbitrary constraints – and hence, to deal with this range of languages, the generalists will not embody such constraints either. So this line of reasoning seems to lead directly to the conclusion for which we are arguing.

The case of learned bird- and whalesong appears more directly analogous to language (see also **Pagel & Atkinson**). **Fitch** points out that biologists agree that the songs of some species of birds are culturally transmitted, but within sharply defined limits. Moreover, he notes, biologists agree that birds have an innate propensity ("instinct") to acquire the song type specific to their species (Marler 1991). This seems analogous to the case of human language: Language

is culturally transmitted, and people may have an inherent disposition to acquire human languages. Fitch may perhaps suspect that we do not accept that people have any such innate propensity for language – but, in the weak sense of the term "relevant" here, our position entails that there is indeed a genetic basis for language, in the form of a range of pre-adaptations (perceptuo-motor, communicative, cognitive, and so on). We deny, though, that there is a genetically encoded language-specific UG; and we explain the viability of acquisition, and the structure of the world's languages, in the light of the adaptation *of language* to this genetic basis. **Goldberg**'s quote from Liz Bates puts the point well: "It's not a question of Nature vs. Nurture; the question is about the Nature of Nature" (Bates 1993).

Fitch goes on to develop an argument that comes dangerously close to undercutting his position. He agrees that rapid cultural changes imply that genetic changes (whether in the bird or human case) will only be positively selected for properties that are stable across that cultural environment – this is the "generalist" strategy, mentioned earlier. But *prior to the existence of language-specific genetic constraints*, arbitrary properties of language, such as those in a putative UG, will precisely not be stable: they have (by assumption) as yet no genetic basis; and (also by their presumed arbitrariness) they have no functional role to ensure they dominate the cultural environment. Hence, the arbitrary constraints of UG will be just the kinds of features that will not be genetically internalized.

Barrett et al. also observe, rightly, that co-evolution between language and genes is possible, noting that even a fast-changing environment will have statistical properties which may, to some degree, provide selectional pressure on learners. As they point out, co-evolution appears widespread in biology (e.g., Futuyma & Slatkin 1983). There are, moreover, some well-attested cases of co-evolution between culture and genes. For example, the development of arable agriculture and dairying appear to have co-evolved with genes for the digestion of starch (Perry et al. 2007) and lactose (Holden & Mace 1997). Note that these cases are examples of stable shifts in the cultural environment – for instance, once milk becomes a stable part of the diet, there is a consistent positive selection pressure in favor of genes that allow for the digestion of lactose. These cases are entirely consistent with our position: Co-evolution can and does occur where culture provides a stable target. But this could not be the case for the putative arbitrary regularities presumed to be encoded in UG. We concur with Barrett et al. that the broader project of understanding what cognitive mechanisms may have been positively selected for because of their role in language acquisition and use (e.g., **de Ruiter & Levinson**'s communicative intelligence; increased memory capacity allowing a large vocabulary [**Landauer**]; or the structure of the vocal apparatus, mentioned by **Blackmore**, and so on) is an important direction for future work.

Several commentators note that our arguments rest on the assumption that language changes more rapidly than genes and that this assumption is open to question (**Behme**; **Blackmore**). **Pagel & Atkinson** report some important recent analyses which suggest that some aspects of language may change surprisingly slowly. The Indo-European language group shows common aspects of vocabulary over many thousands of years, as shown both by traditional linguistic analysis and modern statistical methods (Pagel et al. 2007). Nonetheless, these languages have gone through spectacular divergences and reorganizations, which scarcely count as a stable linguistic environment over either time or space. Moreover, while, as Pagel & Atkinson point out, the lactose gene may have become established over a period of thousands of years, it is unlikely that a single gene would be responsible for establishing an arbitrary linguistic regularity, such as some aspect of the binding constraints. This would suggest that an even longer period of stability in the target language would be required for the relevant genes to become established. Overall, we suggest that our assumption that languages change faster than genes is a good first-order approximation – and this creates substantial difficulties for co-evolutionary accounts of the origin of UG. Nonetheless, Pagel & Atkinson's arguments raise the possibility that this assumption is not always correct, and suggest that further analysis may be required to see if there are limited circumstances where language-specific arbitrary constraints might become established.

A number of commentators point to specific evolutionary mechanisms that, they suggest, might extend or complicate our argument somewhat. **Behme** notes that our argument may be strengthened by the observation that language users need to coordinate with each other – a dramatic grammatical "advance" for a single agent might not confer selectional advantage. It would, one might say, be comparable to being the only person to own a telephone, which is useless unless there is someone with whom to communicate.

Behme further suggests that powerful forces of sexual selection may change the argument in favor of biological adaptations for language by analogy with the male peacock's impressive tail feathers (see also **Dessalles**). Indeed, the males of many species of songbirds use their vocal prowess to attract females and defend their territory, and have clearly been subject to sexual selection (e.g., Catchpole & Slater 1995). Crucially, however, such sexual selection has resulted in considerable sexual dimorphisms in the neural systems for song, with males having substantially larger brain areas for song control (e.g., MacDougall-Shackleton & Ball 1999). Similarly, sexual selection for language ability in humans would also be expected to lead to sexual dimorphisms in the brain areas involved in language, but there is no evidence for such neural differences favoring male linguistic ability. If anything, human females tend to acquire language earlier than males (e.g., Dionne et al. 2003) and to become more proficient language users (e.g., Lynn 1992). Thus, it would seem that sexual selection is unlikely to be a major determinant of any biological adaptations for language.

Hurford argues that the mechanism of "Baldwinian niche construction" may provide a route for the co-evolution of genes for some, albeit limited, language-specific knowledge or mechanisms. Perhaps some change in the structure of hominid social groups (e.g., group size) may have changed the "niche" in which communication occurs; and this might itself have altered the dynamics of language change and the selectional pressures on cognitive machinery co-opted for language processing. If this is right, then the triggers for the initial creation of language may have been social, rather than biological, change (as **Brooks & Ragir** also argue). Hurford suggests, in line with our target article, that it is possible that *functional* (rather than arbitrary) features of language might subsequently co-evolve with language, and he highlights large vocabulary, double articulation, and

long-distance dependencies as possible language-specific structures. We welcome these specific proposals, and see them as valuable pointers to guide future empirical work.

Smith et al. suggest that our argument that arbitrary aspects of language cannot become genetically fixed by co-evolution applies equally well to functional aspects of language. They cite important recent formal analyses by Kirby et al. (2007), which indicate that, if learners choose the most probable language, given the linguistic data to which they have been exposed, then the *ordering*, but not the *strength*, of their prior biases, determines the distribution of languages that arise from cultural transmission. Smith et al. raise the concern that, in this type of case, there may be no pressure of natural selection on the more "desirable" priors – and hence that genes that influence such priors may be "shielded" from processes of natural selection. We suggest that this conclusion need not follow, however. The space of possible grammars (or, more broadly, hypotheses concerning linguistic structures) is vast; and hence the number of possible orderings of prior probabilities across this space is enormous. If genes influence this ordering, rather than the precise numerical values of the priors for each element in the ordering, this gives plenty of scope for enormous genetic influences on the speed of learning, and hence provides scope for strong selectional pressure on genes. Thus, *if* functional features of language provide stable constraints on the linguistic environment, then there could, we suggest, be strong pressures of natural selection on genes determining the ordering of priors over different grammars. Hence, we currently see in principle no reason to rule out the co-evolution of language and language genes for functional (though not arbitrary) constraints on language. Nonetheless, we suggest that additional experimental, computational, and theoretical work is required to clarify the circumstances under which such co-evolution is possible.

R6. Where next?

A decade ago, Lewontin (1998) painted a bleak picture of evolutionary accounts of language and cognition as being "nothing more than a mixture of pure speculation and inventive stories" (p. 111). In the target article, we outlined the beginnings of a new synthesis for theorizing about the relationship between brains, genes, and language, emphasizing the role of cultural evolution. This perspective views language evolution as primarily a matter of cultural, rather than biological, evolution; and such evolution is seen as continuous with processes of historical language change, such that selection among linguistic forms is driven by constraints concerning cognition, communication, learning and processing, and the structure of the perceptuo-motor system. These selectional pressures can be studied directly by analyzing the neural, cognitive, and social basis of language in modern humans, by exploring the impacts of different patterns of social transmission of linguistic patterns, and by analyzing contemporary and historical language change. The positive and constructive spirit of the commentaries gives us grounds for optimism that a synthesis drawing together these, and related, perspectives, is not merely attainable in principle, but is also likely to be of considerable scientific potential. Thus, the commentaries have highlighted a range of key areas for future work, and some important theoretical challenges.

In this concluding section, we draw together these issues and identify central remaining open questions.

R6.1. Reconnecting synchronic and diachronic linguistics

We argued, in the target article, that grammaticalization and other processes of linguistic change are likely to provide much insight into language evolution. In a similar vein, we find that some of the key observations made by the commentators based on synchronic language data could be strengthened and emphasized by embedding them in a diachronic perspective. For example, **Tallerman**'s discussion of the typological patterns of case-marking as an example of linguistic adaptation could be further corroborated by incorporating diachronic data to explore the patterns of change over time, perhaps revealing more about the specific cognitive constraints involved. This point is underscored by **Aronoff et al.**, who describe how their study of in vivo changes in Al-Sayyid Bedouin Sign Language and Israeli Sign Language has highlighted the importance of body-based perceptuo-motor constraints on diachronic change. More generally, as noted in the target article, the combination of diachronic and synchronic analyses in past work has tended to show how apparently "arbitrary," language-specific linguistic universals might derive from general, cognitive constraints. The implication of this line of argumentation goes beyond theories of language evolution to the theory of language itself. For example, it seems that construction grammar may provide a much more suitable formal approach to capturing the properties of language than generative grammar in its various guises.

R6.2. Dynamics of linguistic and cultural change

Several commentators stress the importance of cultural dynamics in shaping language, some arguing that the social structures underpinning language transmissions from generation to generation may be as important as the cognitive and biological machinery of the language learner in determining the emergence and evolution of language. **Smith et al.** report computational models of language evolution, which illustrate the interdependence of assumptions about learners and mechanisms of transmission (Smith & Kirby 2008); **Caldwell** illustrates how cultural transmission can be studied in the laboratory. We suggest that there is much foundational theoretical work to be done in understanding the co-evolution of genes-for-learning and the structure of the to-be-learned domain, whether this domain is language or some other aspect of human culture. Only with such work in place will it be possible to assess the scope of the arguments presented here (e.g., whether functional aspects of language can become genetically embedded) and to determine how far our negative conclusions concerning UG might extend to putatively innate "grammars" in other cultural domains (e.g., morality; Hauser 2006). This work is required in order to extend existing theories of co-evolution (without learning or cultural change; Thompson 1994) and cultural evolution (without genetic change; Boyd & Richerson 2005).

R6.3. Relevance to language acquisition

The target article notes that language change, and consequently language evolution, may be importantly shaped

by language development, although language change in adults is also likely to be important (Bybee, in press). **Toscano et al.** and **Brooks & Ragir** elaborate on the importance of developmental processes embedded in a social context. Moreover, the target article noted that if language is shaped by the brain, the problem of language acquisition may be far less daunting than is typically assumed: Language has been shaped to be learnable from the noisy and partial input that children receive. Therefore, language will embody the (typically non-language-specific) biases or constraints the child brings to the problem of language acquisition. This dramatically reduces the impact of the POS argument, which is still used as a key motivation for UG (**Harnad**). These issues are explored in more detail in Chater and Christiansen (submitted).

R6.4. Revisiting the multiple constraints on language evolution and acquisition

The commentators elaborate and expand upon the four types of constraints (thought, perceptuo-motor, cognition, and social-pragmatic) on language evolution discussed in the target article, indicating that this framework is productive. Some highlight specific aspects of *thought* processes which may underpin language, such as mental time travel (**Corballis**) and double-scope blending (**Fauconnier & Turner**); some focus on *perceptuo-motor* constraints, including the importance of embodiment (**Aronoff et al.**) and the structure of actions (**Greenfield & Gillespie-Lynch**). **Lieberman** sees language as built upon a neural system for complex and flexible action sequences, underpinning the *cognitive* aspects of language processing and learning (**Namy & Nygaard**). Finally, several commentators stress the *social-pragmatic* forces that shape language, focusing on social interaction (**Wallentin & Frith**), communicative intelligence (**de Ruiter & Levinson**), and speech acts (**Enfield**). As noted in the target article, one of the major challenges for future research is to understand the many facets of each type of constraint, and how these constraints interact to shape the evolution of language.

R6.5. What makes humans special?

If the mechanisms shaping language evolution are to a large extent not specific to language, then what differentiates human cognition and communication from that of other primates? That is, why do humans have languages whereas other primates do not? Across the commentaries, there is a continuum of views, from the reiteration of the conventional viewpoint that grammatical information is innate and species-specific (**Harnad**; **Reuland**), across the suggestion that some such information may be a relatively small part of the story (**Barrett et al.**; **Satterfield**), to the idea that cultural and/or developmental processes are of central importance (**Brooks & Ragir**; **Smith et al.**; **Toscano et al.**). In considering human/primate differences, however, it is important to keep in mind that the absence of language-specific constraints on language does not necessarily entail the lack of species-specific constraints. Along these lines, **Hurford** and **Landauer** propose some specific cognitive features that may be uniquely human, including memory capacity sufficient to store a large vocabulary, double articulation, and combinatorial operations. Other commentators suggest

that pragmatic machinery for interpreting others' behavior may be more fundamental (**de Ruiter & Levinson**). Comparative work on primate versus human neural and cognitive mechanisms, as well as archaeological analysis and language-reconstruction to clarify the relationship between biological changes and the emergence of language, will be crucial in addressing these issues (e.g., Tomasello et al. 2005).

To conclude, we thank the commentators for providing a stimulating range of perspectives on the target article, and for their numerous constructive suggestions for directions for future research. We are optimistic that pursuing these and related lines of work, across disciplines as diverse as linguistics, primatology, developmental psychology, and neurobiology, may help construct a new synthesis for understanding the complex relationship between brains, genes, and language.

NOTES
1. Although others have used the term "the logical problem of language evolution" to point to evolutionary issues relating to UG (Botha 1999; Roberts et al. 2005), we are – to the best of our knowledge – the first to use it as an overarching label for the combined theoretical issues facing both adaptationist and non-adaptationist explanations of UG.

2. Of course, differences do exist between signed and spoken languages relating to the differences in the modality and mode of transfer of information. This raises the intriguing possibility that subtle differences in language structure and use may exist due to differences in the constraints imposed on the mechanisms subserving signed and spoken languages. For example, Conway and Christiansen (2005; 2006; in press) have shown that visual and auditory sequential learning may involve separate modality-specific, but computationally similar, mechanisms, giving rise to both qualitative and quantitative differences in the processing of auditory and visual sequences. Such differences may shape signed and spoken languages in slightly different ways so as to better fit modality-specific constraints on sequential learning.

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[The letters "a" and "r" before author's initials stand for target article and response references, respectively.]

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