Cultural Recycling of Neural Substrates
during Language Evolution and Development

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Abstract

Cultural evolution has emerged as a key source of explanation for the emergence of complex linguistic structure in the human lineage. In this chapter, we argue that the cultural evolution of language has been shaped by non-linguistic constraints deriving from the human brain. By analogy to reading, novel cortical networks for acquiring and using language are suggested to have emerged through the cultural recycling of pre-existing neural substrates. These language networks inherited the structural properties and limitations of their component cortical circuits. In support for this perspective on the neurobiology of language, we discuss evidence regarding the multi-function nature of Broca's area—often considered to be a canonical language region—and the distributed nature of lexicosemantic representations. We conclude by noting that more research is needed to explore how the cultural evolution perspective may provide new insights into the neurobiology of language.

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Introduction

Research on language evolution aims to answer some of the most fundamental questions about the nature of our linguistic abilities: Why is language the way it is, and how did it come to be that way? Fueled by theoretical constraints derived from recent advances in the brain and cognitive sciences, the past couple of decades have seen an explosion of research on language evolution. This research was initially prompted by Pinker and Bloom's (1990) groundbreaking article arguing for the natural selection of biological structures dedicated to language. The new millennium, however, has seen a shift toward explaining language evolution in terms of cultural evolution rather than biological adaptation. Nonetheless, although the cultural evolution of language has had a substantial impact on the cognitive sciences, it has received relatively little attention within cognitive neuroscience (though see e.g., Arbib, 2010; Deacon, 1997, for exceptions).

In this chapter, we outline how the cultural evolution of language may be consistent with recent thinking about the cognitive neuroscience of language. First, we discuss the logical problem of language evolution faced by theories proposing biological adaptations for arbitrary features of language. As an alternative, we argue that the cultural evolution of language provides a solution to this problem, indicating how we can explain the close fit between the structure of language and the mechanisms employed for acquiring and using language. We then review recent proposals about neuronal recycling and how they may provide a neural foundation for the cultural evolution of language by

analogy with a human skill that we know is the product of cultural evolution: reading. Finally, we discuss some of the implications for the neurobiology of language, by highlighting specific non-linguistic neural substrates that provide the bases upon which language networks emerge during development.

A Solution to the Logical Problem of Language Evolution: Language Shaped by the Brain

The acquisition of language is subject to a number of biological, species-specific constraints. After all, only humans have language; no other animal communication system comes close to the complexity and diversity of forms we see in human language (e.g., Evans & Levinson, 2009). A key question is, however, whether these biological constraints necessarily have to be specific to language, or whether they may be broader in nature, deriving from constraints on non-linguistic neural mechanisms that have been pressed into use in language.

A longstanding influential approach is to assume that language acquisition is constrained by a Universal Grammar (UG): a genetic language-specific neural system analogous to the visual system (e.g., Maynard-Smith & Szathmáry, 1997; Pinker, 1997). As such, UG provides a possible explanation for the close fit between the structure of language and how it is acquired and used. But the idea of linguistically-driven biological adaptations as the origin of a genetically specified UG faces a *logical problem of language evolution* (Christiansen & Chater, 2008). UG is meant to characterize a set of universal grammatical principles that holds across all languages (e.g., Chomsky, 1981). It is a central assumption that these principles are *arbitrary*, and not determined by

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functional considerations, such as constraints on learning, memory, cognitive abilities, or communicative effectiveness. This creates an evolutionary problem because any combination of arbitrary principles will be equally adaptive. A possible solution is to construe the principles as constituting a communicative protocol by analogy with inter-computer communication: it does not matter what specific settings (principles) are adopted as long as everyone adopts the same set of settings (Pinker & Bloom, 1990). However, this solution faces three fundamental difficulties relating to the dispersion of human populations, language change, and the question of what is genetically encoded (Christiansen & Chater, 2008).

First, the problem of divergent populations of language users arises across a range of different scenarios concerning language evolution and human migration. In all cases, it would seem that the evolution of UG would require a process of gradual adaptation prior to the dispersion of human populations and an abrupt cessation of such adaptation afterwards to avoid genetic assimilation to diverging local linguistic environments (Baronchelli, Chater Pastor-Satorras & Christiansen, 2012). Second, the adaptationist account of UG faces the problem that within a single population, linguistic conventions change much more rapidly than genes thus creating a "moving target" for natural selection. Computational simulations have shown that under conditions of relatively slow linguistic change, arbitrary principles do not become genetically fixed—even when the genetic make-up of the learners is allowed to affect the direction of linguistic change (Chater, Reali & Christiansen, 2009). Third, natural selection produces adaptations designed to fit the specific environment in which selection occurs. It is thus puzzling that an adaptation for UG would have resulted in the genetic underpinnings of a system

capturing the abstract features of all possible human linguistic environments, rather than fixing the superficial properties of the immediate linguistic environment in which the first language originated.

It remains possible, though, that language did have a substantial impact on human genetic evolution. The above arguments only preclude biological adaptations for arbitrary features of language, whereas there might be features that are universally stable across linguistic environments (such as the need for enhanced memory capacity, or complex pragmatic inferences, Givón & Malle, 2002) that might lead to biological adaptation (Christiansen, Reali & Chater, 2011). However, these language features are likely to be functional, to facilitate language *use*—and thus would typically not be considered part of UG.

But without UG, how can we explain the apparent close fit between the structure of language and the mechanisms by which it is acquired and used? Instead of asking how the brain may have been adapted for language, we suggest that we may get more insight into language evolution by asking the opposite question: How has language been adapted to the brain? This question highlights the fact that language cannot exist independently of human brains. Without our brains, there would be no language. Thus, there is a stronger selective pressure on language to adapt to the human brain than the other way around. Processes of cultural evolution involving repeated cycles of learning and use are hypothesized to have shaped language into what we can observe today. The solution to the logical problem of language evolution is, then, that cultural evolution has shaped language to fit the human brain (Christiansen & Chater, 2008).

The last decade has seen a growing body of work suggesting that language may have evolved primarily by way of cultural evolution rather than biological adaptation. Evidence in support of this perspective on language evolution comes from computational modeling, behavioral experimentation, linguistic analyses, and many other lines of scientific inquiry (see Dediu et al., in press, for a review). A key hypothesis emerging from this work is that the cultural evolution of language primarily has been shaped by non-linguistic constraints deriving from neural mechanisms existing prior to the emergence of language (see Christiansen & Chater, 2008, for a review of the historical pedigree of this perspective). Language is viewed as an evolving complex system in its own right; features that make language easier to learn and use, or are more communicatively efficient, will tend to proliferate, whereas features that hinder communication will tend to disappear (or not come into existence in the first place).

Christiansen and Chater (2008) describe four different types of constraints that act together to shape the cultural evolution of language. One source of constraints derives from the perceptual and motor machinery that supports language. For example, the serial nature of vocal (and sign) production forces a sequential construction of messages with a strong bias toward local information due to the limited capacity of perceptual memory. The nature of our cognitive architecture provides a second type of constraints on the cultural evolution of language through limitations on learning, memory and processing. E.g., limitations on working memory will constrain the number and length of dependencies between nonadjacent elements in a sentence. The structure of our mental representations and reasoning abilities constitutes a third kind of constraints on language evolution. For instance, human basic categorization abilities appear to be reflected in the

structure of lexical representations. Finally, socio-pragmatic considerations provide yet another source of constraints on how language can evolve. As an example, consider how a shared pragmatic context may lighten the informational load on a particular sentence (i.e., it does not have to carry the full meaning by itself). Importantly, these four types of constraints do not act independently of one another; rather, specific linguistic patterns arise from a combination of several of these constraints acting in unison. Individual languages emerge through a gradual historical process of tinkering, recruiting different constellations of constraints, and thus give rise to the diversity languages.[1]

The idea of language as shaped by cultural evolution to fit pre-existing constraints from the human brain also promises to simplify the problem of language acquisition. When children acquire their native language(s), their biases will be the right biases because language has been optimized by past generations of learners to fit those very biases (Chater & Christiansen, 2010; Zuidema, 2003). This does not, however, trivialize the problem of language acquisition but instead suggest that children tend to make the right guesses about how their language works—not because of an innate UG—but because language has been shaped by cultural evolution to fit the non-linguistic constraints that they bring to bear on language acquisition. A key remaining question, though, to which we turn next, is whether it is possible to provide a more detailed account of the neural bases supporting the development and cultural evolution of language.

Cultural Recycling of Neural Substrates during Development

Over the past decade, a new perspective on the functional architecture of the brain has emerged (see Anderson, 2010, for a review). Instead of viewing various brain regions as

being dedicated to broad cognitive domains such as language, vision, memory, or reasoning, it is proposed that low-level neural circuits that have evolved for one specific purpose are redeployed as part of another neuronal network to accommodate a new function. This general perspective has been developed independently in a number of different theoretical proposals, including the "neural exploitation" theory (Gallese, 2008), the "shared circuits model" (Hurley, 2008), "neuronal recycling" hypothesis (Dehaene & Cohen, 2007), and "massive redeployment hypothesis" (Anderson, 2010). The basic premise is that reusing existing neural circuits to accomplish a new function is more likely from an evolutionary perspective than evolving a completely new circuit from *de novo* (cf. Jacob, 1977)

If this hypothesis is correct, we should expect most brain areas to participate in multiple, potentially diverse behavioral functions. Supporting this prediction, Anderson (2010) reviews results from 1,469 subtraction-based fMRI studies involving eleven different task domains, ranging from action execution, vision, and attention to memory, reasoning and language, finding that any given cortical region is typically active for most of these task domains. That is, a specific neural circuit that is active in a particular cognitive task, such as language, is generally also active for multiple other tasks.

The cultural recycling hypotheses further predicts that cognitive functions that have emerged more recently in human evolution should be more widely distributed across the cerebral cortex than older ones. This is because these more recent traits will be able to rely on a wider variety of cortical circuits with different, potentially useful properties in order to produce the most optimal network for this novel function, and there is no *a priori* reason for why these neural circuits should be placed next to one another

(Anderson, 2010). Thus, if the neural mechanisms involved in language are primarily the product of recycling of older neural substrates, as proposed by cultural evolution theorists, then we would expect to find the brain areas involved in language to be widely distributed across the brain. Analyzing the co-activation of Brodmann areas for eight different task domains in 472 fMRI experiments, Anderson (2008) found that language was the task domain for which co-activation patterns were the most widely scattered across the brain. Following language in terms of the degree of distribution of neural co-activation patterns came reasoning, memory, emotion, mental imagery, visual perception, action and, lastly, attention. Indeed, language was significantly more widely distributed than the latter three task domains: visual perception, action and attention.

Importantly, as existing neural circuits take on new roles by participating in new networks to accommodate novel functions, they still retain their original function (though, the latter may in some cases be affected by properties of the new function through developmental processes[2]). The limitations and computational constraints of the original workings of those circuits will therefore be inherited by the new function, creating a "neuronal niche" (Dehaene & Cohen, 2007) for cultural evolution. In other words, the emerging new function will be shaped by constraints deriving from the recycled neural circuits as it evolves culturally. Thus, this is the sense in which we argue that language has been shaped by the brain through the cultural recycling of pre-existing neural substrates.

Reading as a Product of Cultural Recycling

Writing systems are only about 7000 years old and for most of this time the ability to read and write was confined to a small group of individuals. Thus, reading is a culturally evolved ability for which humans would be unlikely to have any specialized biological adaptations. This makes reading is a prime candidate for a cognitive skill that is the product of cultural recycling of prior neural substrates.

Dehaene and Cohen (2007) argue that skills resulting from culturally mediated neuronal recycling, such as reading, should have certain characteristics. First, variability in the neural representations of the skill should be limited across individuals and cultures. With regard to reading, the visual word form area, which is located in the left occipito-temporal sulcus, has been consistently associated with word processing across different individuals and writing systems. Second, there should be considerable similarity across cultures in the manifestation of the skill itself. Consistent with this prediction, Dehaene and Cohen (2007) note that individual characters in writings systems across the world consist of an average of three strokes, and the intersection contours of the parts of these characters follow the same frequency distribution (e.g., T, Y, Z, Δ). Third, there should be some continuity in terms of both neural biases and abilities for learning in non-human primates. That reading might build (at least in part) on the recruitment of evolutionary older mechanism for object recognition is supported by recent results from a study of orthographic processing in baboons (Grainger et al., 2012) indicating that they were able to distinguish English words from nonsense words.

The available data regarding the neural representation of reading, combined with analyses of writing systems and experiments with non-human primates, suggest that writing systems have been shaped by a neuronal niche that includes the left ventral

occipito-temporal cortex. Next, we extend this argument to include language more generally, outlining the neuronal niche within which language has evolved by cultural evolution.

Non-linguistic Neural Constraints on Language

Evidence predominantly drawn from functional neuroimaging in adults supports the hypothesis of language having adapted to the brain. We discuss two important sources of evidence, one related to the functional diversity of Broca's area, the other to the distributed brain organization for lexicosemantic representations.

Broca's area (comprising Brodmann areas [BAs] 44 and 45 in the left inferior frontal gyrus [LIFG]) is considered crucial among the 'language regions' of the human brain (Price, 2010). Some proposals even assign an exclusive linguistic or syntactic role to LIFG (e.g., Grodzinsky, 2000). As described above, however, exclusive language specialization would be unexpected from an evolutionary perspective. Such proposals also overlook extensive neuroimaging evidence (reviewed in Müller, 2009). Here, we focus on one example, the role of LIFG in motor-related processing and action perception.

Outside neurolinguistics, Broca's area is often considered a premotor (rather than a language) region (e.g., Curtis & D'Esposito, 2003). Indeed, postmortem cellular evidence shows that BA 44 is 'dysgranular' cortex (containing few cells with sensory afferents in cortical layer IV), a feature shared with primary motor cortex (Amunts et al., 1999). Unsurprisingly, the role of LIFG in language has been related to its motor specialization (Rizzolatti, Fogassi, & Gallese, 2002). Relevant evidence originates from

monkey studies (Rizzolatti & Gentilucci, 1988). Specifically, neurons in monkey area F5, which may correspond to human BA 44 (Rizzolatti & Arbib, 1998), respond to object-directed action when presented visually or auditorily, *in the absence* of any motor response (Kohler et al., 2002). Since these *mirror neurons* are not directly involved in motor execution, they are considered important for imitation as well as for detecting and recognizing the actions of others (Rizzolatti & Craighero, 2004). These functions are supported by connectivity between ventral premotor and inferior parietal cortex (Fabbri-Destro & Rizzolatti, 2008), with possible additional participation of the superior temporal sulcus (Rizzolatti & Craighero, 2004).

Ample imaging evidence suggests that the mirror neuron system (MNS) exists in the human brain in regions corresponding to those identified in monkey studies, i.e., bilateral IFG and inferior parietal cortex (Molenberghs, Cunnington, & Mattingley, 2012), possibly suggesting some role in the emergence of language (Arbib, 2010; Rizzolatti & Craighero, 2004). From this perspective, the existence of mirror neurons in Broca's area is not a coincidence, but indicates a crucial role for imitation and action recognition as building blocks of language (Nishitani, Schurmann, Amunts, & Hari, 2005). In the framework of the cultural recycling model, this implies that LIFG is not a 'language area' that happens to also play a role in other, apparently non-linguistic functions. Rather, LIFG had initially developed action-related functions, which secondarily made it suited for its role in language emergence. Indeed, it has been suggested that LIFG's action-related functions develop early in infancy through associative learning (Cook, Bird, Catmur, Press & Heyes, in press) – prior to the development of language. This view of sequence and causality can be applied both to

child development, where action recognition and imitation may be considered building blocks of language acquisition (Glenberg & Gallese, 2012), and to evolution (Corballis, 2010), where the existence of the MNS in 'pre-verbal' nonhuman primates is known (as described above)[3]. However, while the MNS and the imitative abilities and action recognition it affords may be necessary phylo- and ontogenetic conditions for the emergence of language, they cannot be sufficient: Macaque monkeys (as studied by Rizzolatti and colleagues) possess an MNS, but never developed language. Language evolution must therefore rely on other building blocks beyond imitation and action recognition, including brain connectivity.

The relevance of connectivity for functional specialization in cortical regions, such as LIFG, is fundamental. As proposed by Passingham et al. (2002), the functional role of each brain region may be largely determined by its afferent and efferent connectivity patterns, i.e., by which other brain regions it 'hears from' (receives synaptic input from) and 'talks to' (sends axons with synaptic terminals to). The connectivity-based principle implies that local specializations in cortex are not arbitrary. This is well understood for sensorimotor regions (e.g., primary visual cortex has visual functions because it receives input from the retina via the thalamus), but specializations of association cortices are often not understood in analogous ways. For example, why is a major 'language region' located in LIFG?

As mentioned, a neural action recognition system is not a sufficient condition for language. Correspondingly, the connectivity of IFG is far more complex than described above in the context of action recognition (Anwander, Tittgemeyer, von Cramon, Friederici, & Knosche, 2007). While the arcuate fasciculus indeed connects IFG with

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inferior parietal and lateral temporal regions in posterior perisylvian cortex (Catani, Jones, & ffytche, 2005), the functional relevance of these connections goes beyond those ascribed to the MNS, relating, for example, to spatial processing and attention (Sack, 2009) and auditory processing, auditory-visual integration, and face processing (Hein & Knight, 2008). IFG furthermore connects with both the dorsal stream, crucial for visuospatial processing and visuomotor coordination (Goodale & Westwood, 2004), and the ventral stream (Saur et al., 2008), which provides meaningful interpretation of visual and auditory stimuli (Grill-Spector & Malach, 2004). Although not all of these functions may appear immediately relevant to language emergence, the status of Broca's area as a convergence zone (Mesulam, 1998; Meyer & Damasio, 2009), where connections with numerous other sensorimotor and association cortices come together, provides a promising neuroscientific account of its crucial role in language.

Related to connectivity-based functional specialization, a second example of 'language adapting to the brain' concerns lexicosemantic organization. Beyond LIFG and its crucial role in lexicosemantic representations (Binder, Desai, Graves, & Conant, 2009), the distributed organization of semantic representations is reflected in the principle of category-specificity, which was first observed in patients with semantic deficits that differentially affect specific classes of objects. Some patients, for example, show dissociations between impaired animate and retained inanimate items (Mahon & Caramazza, 2009). Warrington and McCarthy (1987) point out that sensory features are important for distinguishing between living items, while action semantics are more important for inanimate items, like tools; loss of sensory or action knowledge could therefore differentially disrupt the semantic representations of living and non-living

items, respectively. Crucially, category-specificity does not reflect impaired processing of sensory input or motor output, but impairment at the conceptual level (Mahon & Caramazza, 2009).

The clinical evidence of category-specificity is supported by imaging findings in healthy adults. For example, the processing of semantic representations related to action and function is associated with activation in left (pre)motor cortex (Chao, Weisberg, & Martin, 2002; Lubrano, Filleron, Demonet, & Roux, 2012; Goldberg, Perfetti, & Schneider, 2006) and left posterior middle temporal cortex (Chao, Haxby, & Martin, 1999; Hwang, Palmer, Basho, Zadra, & Müller, 2009) – the latter being important for non-biological object motion perception (Beauchamp, Lee, Haxby, & Martin, 2003). Conversely, animate categories are linked to activations in visual cortices, such as the fusiform gyrus (Chao et al., 2002) and the superior temporal sulcus (Chao et al., 1999; Tyler et al., 2003), an area involved in the perception of biological motion (Pelphrey, Morris, Michelich, Allison, & McCarthy, 2005).

A meta-analysis (Chouinard & Goodale, 2010) corroborated activation differences for naming of animals (temporo-occipital regions) vs. naming of tools (left prefrontal, premotor, and somatosensory regions), highlighting the role of sensorimotor cortices in lexicosemantic representations. Examples are premotor and primary motor cortex (Chao & Martin, 2000; Hauk et al., 2004), visual cortices in fusiform gyrus and occipital lobe (Goldberg et al., 2006; Pulvermüller & Hauk, 2006), and orbitofrontal olfactory regions (Goldberg et al., 2006; Gonzalez et al., 2006). Action words related to different body parts (face, arms, legs) are associated with patterns of activation corresponding to the somatotopic organization in primary motor and somatosensory

cortices (Carota, Moseley, & Pulvermüller, 2012), further supporting the sensorimotor bases of lexicosemantic representations.

Several theoretical models have been developed to account for the lesion and imaging evidence. According to sensory/functional (Warrington & McCarthy, 1987) and sensorimotor models (Martin, 2007), semantic representations are distributed throughout the brain as a reflection of sensorimotor processes crucial to their *acquisition*, with weighted participation based on the relative importance of each sensorimotor region. Alternatively, the domain-specific hypothesis (Caramazza & Mahon, 2003) proposes that differential brain organization is based on evolutionary importance – for example, animals forming a separate category because they may be predators or prey and are thus crucial for survival. However, both of these approaches, as well as the related theory of 'grounded cognition' (Barsalou, 2008), are in agreement that lexicosemantic representations and the underlying object knowledge do not constitute separate brain systems, but are intimately tied to sensorimotor systems. This implies a hierarchical principle, but one without strict division between sensory and conceptual realms.

Semantic representations (possibly with the exception of abstract words, see Shallice & Cooper, 2013) can thus be considered highly complex sets of sensorimotor-based representations, whose complexity is reflected in distributed brain organization. This implies that the lexicosemantic system adapts to pre-existing brain systems that support sensorimotor and other nonverbal functions. It also illustrates biological and evolutionary economy. Thus, the emergence of language in hominid evolution did not require the launch of an entirely novel set of brain 'modules', as suggested by Chomsky

(e.g., 1972) and followers (Fodor, 1983), but made use of existing neural machinery, i.e., brain systems for sensation, perception, and motor functions.

Conclusion

Much recent work on the evolution of language has focused on the role of cultural transmission across language learners and users in the emergence of complex linguistic structure. This work has suggested that much of language may have been shaped by neural mechanisms predating the origin of language (e.g., Christiansen & Chater, 2008). In this chapter, we have sought to understand the evolution of language in terms of the cultural recycling of neural substrates, suggesting that language may have "recruited" pre-existing networks in development to support the evolution of various language functions. Just as our reading ability relies on a network of cortical circuits that existed before the invention of writing systems, so – we argue – has language largely come to rely on networks involving brain mechanisms not dedicated to language. However, much work still needs to be done and we hope that the present chapter might serve a starting point for future cognitive neuroscience research on the cultural evolution of language.

Notes

1 A possible reason for why extant non-human primates do not have language may be that humans have gone through a number of biological adaptations, most of which are not specific to language, but which provided the right kind of perceptuo-motor, cognitive, conceptual, and socio-pragmatic foundations for language to "take off" by way of cultural evolution.

2 For example, exposure to the specific patterns of occurrence of center-embedded clauses in German, appear to affect sequential learning of nonadjacent dependencies, more generally (de Vries, Geukes, Zwitserlood, Petersson & Christiansen, 2012).

3. Importantly, though, we see this perspective as being agnostic with regard to the question of whether language originated in the gestural or vocal modality.

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