The Emergence of Modern Communication in Primates: A Computational Approach

Antonio Benítez-Burraco, Ana Mineiro and Alexandre Castro-Caldas

Abstract It is biological structures (and their activities), and not the diverse functions they contribute to (i.e., forms of behavior), that evolve. We believe that the long-lasting controversy around when modern language appeared would benefit from a shift of focus, from "communication" to "computation." Computation is the activity performed by specific neural devices. Computational devices (and their neurobiological correlates), but not communication devices, have a common evolutionary history. We further expect that computational devices are functionally coupled to different interface systems, thus rendering diverse kinds of outputs and eventually contributing to different functions (forms of behaviors). Multiple evidence (genetic, neurobiological, clinical, archeological, fossil, and ethological) suggest that the computational device of human language (the faculty of language in the narrow sense, after Chomsky) is an evolutionary novelty that appeared along with anatomically modern humans. Importantly, this does not preclude that other extinct hominins had "language." It is just that the strings of symbols they were plausibly able to produce lacked certain structural properties that we can only find in extant oral or sign languages. Hominin oral "languages" (or better perhaps, "protolanguages") could have replaced signed "languages" at some early period during hominin evolution. Nonetheless, the gestural "languages" (or better, "protolanguages") hypothetically employed by other extinct hominids would have been less structurally complex than extant human languages are.

Keywords Computation • Hominin • Language evolution • Language modalities • Syntax

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A. Benítez-Burraco (✉)
Department of Spanish Philology and Teaching,
University of Huelva, Huelva, Spain
e-mail: antonio.benitez@dfesp.uhu.es

A. Mineiro · A. Castro-Caldas
Institute of Health Sciences, Portuguese Catholic University, Lisbon, Portugal

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1 Introduction

Not surprisingly, when it comes to the origin of social communication systems within primates, it is human language that has spilled the greatest amount of ink. Initially, the analysis of language evolution mostly relied on linguistic evidence, as provided by language contact studies, historical linguistics, and the like. Nowadays, this has also become an important concern for researchers with very different backgrounds (anthropologists, primatologists, or archeologists, but also molecular biologists and geneticists). The field has greatly benefited from this multidisciplinary approach. At the same time, the need for such an approach clearly reflects the complexity of the task.

There is an intense dispute around when and how modern language has evolved, and above all, what language has evolved from (and what for). To begin with, it is hotly disputed whether language has evolved by descent with modification (Brandon and Hornstein 1986; Pinker and Bloom 1990; Hurford 1992; Dunbar 1993; Newmeyer 1998; Donald 1999) or is instead an exaptation (Calvin and Bickerton 2000; Chomsky 1982, 1988; Gould 1991; Lieberman 1984; Piatelli-Palmarini 1989; Wilkins and Wakefield 1995). The latter possibility could imply that most components of language evolved to fulfill other functions (i.e., are preadaptations), but also that some of them (or even language itself) could be afunctional, non-specific, or dysfunctional by nature (Chomsky 1988; Piatelli-Palmarini 1990; Lightfoot 1999). As a consequence, it is also disputed whether language has evolved in a gradual fashion (from oral or even manual communication devices) (Newmeyer 1998; Corballis 2002; see also Calvin and Bickerton 2000), or if it instead suddenly appeared (Berwick 1998; Chomsky 2010). Another topic of interest is whether language exhibits continuity with other primate communication systems or instead derives from ape cognition (or from both) (Aitchison 1998; Ulbaek 1998; Bickerton 1990, 2009). A last concern is what language evolved for (assuming that it is an adaptative trait). Diverse evolutionary advantages have been suggested for language: (1) the optimization of hunter-gatherer abilities (Cziko 1995); (2) technological development (Gibson 1990; Ambrose 2001); (3) sexual selection (i.e., courtship and mating optimization) (Aiello 1998; Miller 1999; Wildgen 2004); (4) the improvement of child care and teaching (King 1996); or (5) the enhancement of social interactions within larger groups (Dunbar 1996, 1998; Dessalles 2000; Tomasello et al. 2005). Conversely, for researchers who argue that the (computational) device needed for language processing can be detached from the functions language ultimately fulfills (e.g., Chomsky), language could have arisen in neutral conditions.

2 The Evolutionary Puzzle

The analysis of language evolution primarily relies on two kinds of complementary evidence: comparative (that is, homologous faculties existing in other extant species) and fossil (that is, intermediate stages in the evolution of the faculty).

When it comes to living species, we run into the discontinuity problem. In a nutshell, no extant species has a communicative system that is endowed with the same combinatorial complexity and the symbolic nature as that of humans. In fact, we find more symbolic complexity in phylogenetically distant species, at least in natural conditions. For instance, non-combinable symbolic elements seem to be more common among *Cercopithecidae*. Hence, vervet monkeys or Diana monkeys make use of them to point to some of their predators (Cheney and Seyfarth 1990). Similarly, we find more complex (sound) strings in phylogenetically distant species, at least in natural conditions. Paradigmatically, some birdsongs can be described in terms of syllables, motifs, and song bouts, which suggest that some kind of sequential rules (or syntax) regulate their arrangement and combination (Marler 1970; Todt and Hultsch 1998; Okanoya 2002). Among extant primates, it is among *Hylobatidae* (Geissmann 2000) and *Cercopithecidae* (Ouattara et al. 2009) where we usually find sounds combined in different fashion. It is not entirely evident which animal faculties are homologous to human language. It could be either animal cognition (e.g., symbolic behavior) or oral communication [see Bickerton (1990, 2009) for a comprehensive discussion].

With regard to fossil evidences of language, they could also be essentially uninformative regarding the emergence of complex language. Fossil evidence is basically of two kinds: evidence of the auditive/vocal systems and evidence of symbolic behavior. Concerning the first kind of evidence, it could be problematic because of what we elsewhere have called the “form-function” problem [see for instance Balari et al. (2011, 2013)]. This problem has two sides. On the one hand, modern functions cannot be automatically inferred from human-like, language-related biological structures. A classic example is the descended larynx, which is also present in other, non-linguistic mammals (Fitch and Reby 2001; Fitch 2002). Moreover, linguistic units are not physical, but cognitive by nature. That is, being able to categorically perceive two different sounds [as most primates do (Zayan and Vauclair 1998; Thompson and Oden 2000)] does not entail being able to distinguish them as two different phonemes, that is, as sounds with contrastive meaning in a word. On the other hand, modern functions can exist even when some human-like, language-related biological structure is absent. Paradigmatically, in our species, sign languages are as grammatically complex as oral languages, although they use different reception and transmission channels (Sandler 2006; Sandler and Lillo-Martin 2006).

Concerning evidence of symbolism, there is an ample consensus in paleoanthropology in the sense that complex symbolic behavior implies language (Mellars 1996a, b; McBrearty and Brooks 2000). But, by *language,* we are referring here to a language endowed with semantic compositionality and productivity. It is this kind of language that enables to go beyond the “here and now” and to create displaced conceptual representations, both in time and space (Jerison 1985; Bickerton 1990; Dennett 1996). Evidence of symbolism per se in other extinct species are controversial, even among Neanderthals (Mithen 1996, 2006; Mellars 1996a, b; Tattersall 1998). Actually, other extant primates can learn and use symbols (Premack 1971; Savage-Rumbaugh 1986; Gardner et al. 1989). In truth, the hallmark of human language is not *symbolism* per se, but the fact that symbols are arranged in strings exhibiting certain formal properties. If we could eventually prove that some extinct hominins had a symbolic culture, we could not automatically infer that they were endowed with a modern faculty of language. Symbolic cultures are opaque by nature (Eco 1976), while linguistic meaning is open and productive by nature.

3 What Evolves in Language Evolution

It is not always clear which entity we are referring to when we talk about language evolution. Here, caution is in order. In fact, this is an important concern if we want to properly address this evolutionary conundrum. Firstly, we should not conflate *language* with one of the functions it fulfills, namely *communication*. Human language is a tool subservient to many other functions besides communicating (e.g., thinking and reasoning, marking social identity, expressing emotions, playing, etc.). As a consequence, when discussing language evolution, it seems more appropriate to focus on structural properties of language [to some extent some structural properties of language are said to be motivated by the functions it fulfills (Croft 1995)]. Secondly, we should not equate *language* with a *code* either. From a semiotic perspective, human languages are indeed codes (Morris 1946). But, natural languages are not merely sets of symbols that are arbitrarily associated with a plurality of meanings to allow a communicative interaction between partners. As we pointed out at the end of Sect. 2, these symbols are arranged in very specific ways. Hence, it is compositionality, productivity, recursion, binding, and the like that are the idiosyncratic features of human languages at the structural level. As a consequence, we further contend that it is not just structural properties of language that matter, but specifically how linguistic structures are generated. In other words, when asking about how language evolved, we should give priority to the questions of why modern humans (and only they) are able to generate such linguistic structures and how this capacity has evolved in our lineage.

In our opinion, this shift of focus is supported by current theoretical paradigms in biology. Modern biology claims that only biological structures evolve, but not the uses they are ultimately given as a consequence of their connections with other structures and the relationships existing between the organism and the environment [see Love (2007) for a discussion]. Ultimately, the evolution of biological structures results from the evolution of the developmental systems that control their growth. As noted by Raff (2000: 78), "(e)volution is biased by development."

4 The Computational Hypothesis: Overview

In Sect. 3, we argued that functional rationales for language ("communication," "symbolic behavior," and the like) are not entirely illuminating with regards to language evolution. In fact, neither "communication" nor "symbolic behavior" are natural classes with a common evolutionary history [see for instance Hauser et al. (2002)]. In Sect. 3, we concluded as well that it would be perhaps more informative to explore the way in which linguistic structures are generated. In fact, some linguists (e.g., Chomsky) have characterized *language* as a computational device: “A person’s language is a computational system of the mind/brain that generates an infinite array of hierarchically structured expressions” (Chomsky 2005: 45). This computational system interfaces with a conceptual system (a set of symbols for concepts) to produce sentences, which are in turn exteriorized either acoustically (speech) or visually (signs). Notice that to compute is just to sequence and to relate groups of elements. Importantly, *computation* is the activity performed by specific sets of neurons. That means that computational systems are biological structures belonging to a natural class with a common evolutionary history. We thus arrive at our computational hypothesis: “language evolution is explained above all by the evolution of the neural substrate of the computational system employed for language processing.” Eventually, this implies that it is neither animal communication nor animal cognition, but computational abilities that language has evolved from. Similarly, when analyzing the fossil register, it is not evidence of auditive or vocal systems, or of modern (i.e., “symbolic”) behavior that matters, but of computational abilities (see below).

In order to implement our hypothesis, we will rely on a classic depiction of computational systems posited by Chomsky in the 1950s (Chomsky 1956, 1959). According to his Hierarchy, different formal languages are needed to handle different sorts of computational problems. Specifically, linguistic structures involving cross-serial dependencies suggest that natural languages should be characterized as Type 1, or context-sensitive languages within this hierarchy. It has been argued that formal grammars cannot satisfactorily apprehend all the complexities inherent in natural languages (Rogers and Pullum 2011) and specifically, that Chomsky's Hierarchy may be "too weak and too strong" when applied to human languages (Berwick et al. 2002: 2). Nonetheless, we think that they can illuminate their most basic properties. More importantly, this Hierarchy has a neurobiological correlate. Our ultimate contention will be that it is this neural architecture that can actually illuminate how human language evolved. In a nutshell, the automaton in Chomsky’s Hierarchy equates to a computational device integrated by a pattern generator (or sequencer) and a memory “stack.” Simply put, more memory resources allow the automaton to generate more complex structures. According to Ullman (2001) or Lieberman (2002), the neural substrate of the sequencer is the basal ganglia, although this patterning activity plausibly emerges from the coordinated activity of diverse subcortical and cortical areas, perhaps involving the cerebellum and the thalamus as well (Murdoch 2010; Barbas et al. 2012). In turn, the memory "stack" may be equated to the working memory that plausibly relies on the activity performed by diverse cortical areas. Given that systems of computation are a natural class with a common evolutionary history, the question of how language evolved can be reformulated in terms of how this neural substrate has evolved. It is evident that speaking (or signing) entails much more than just computing. For language to exist, this computational system must be coupled to a dictionary of symbols (aka *lexicon*) and to some device that allows to exteriorize and to interiorize the strings of symbols it ultimately generates (speech organs or signing mechanisms).

However, these interfaces are secondary to language. Once again, if language is to be merely characterized as a gestural or oral symbolic communication system, then ape strings of signs or lexigrams, such as those generated by some individuals reared in captivity (Gardner et al. 1989; Savage-Rumbaugh and Lewin 1994; Savage-Rumbaugh et al. 1998), should be regarded as *sentences*. However, these strings lack key properties of human sentences, namely, recursion or bound anaphora (i.e., binding or control relations). In the same vein, if it is exteriorizing mechanisms that matter, sign languages as employed by deaf people could not be regarded as natural languages. Nonetheless, their central properties parallel those of spoken languages [see Sandler and Lillo-Martin (2006) for a comprehensive characterization]. Hence, signs in signed languages also belong to lexical categories like noun, verb, adjective, adverb, pronoun, and determiner. Sign languages possess as well a lexicon of sign forms and a system for creating new signs in which meaningful elements (morphemes) are combined. Certainly, the combinatory system results more from non-concatenative processes (in which a sign stem is nested within various movement contours and planes in space). But, similarly to spoken languages, signed languages are also governed by constraints on morpheme combination and application of rules to particular forms. At the syntactic level, sign combination to form sentences is governed as well by phrase structure rules and syntactic principles. Sign languages follow universal constraints on syntactic form that have been proposed on the basis of data from spoken languages (for instance, constraints on co-reference and embedded structures). All signers can distinguish grammatical from ungrammatical combinations of signs in their language. Moreover, signs are not holistic gestures, but are composed of a finite inventory of contrastive meaningless units that resemble the phonemes of spoken languages (handshape, location [or place of articulation], and movement [orientation of the handshape]). Ultimately, sign languages are acquired by the child in the same fashion than oral languages (Newport and Meier 1985; Mayberry and Squires 2006), and similar brain areas are involved in processing both modalities (see Sect. 5 below).

We think that all these circumstances qualify our computational hypothesis.

5 The Computational Hypothesis: Comparative Evidence

When we look at "animal communication" with the Chomsky's Hierarchy lens, we only find T3 systems (i.e., regular grammars) among extant species. Some species [as Gentner's starlings (Gentner et al. 2006)] could perhaps access T2 systems, but only in experimental conditions [but see van Heijningen et al. (2009) and Berwick et al. (2011) for a critical view]. Conversely, we actually find T1 systems in nature, but they do not interface with conceptual capacities or with sound exteriorising devices. For instance, weaving is a motor activity that seemingly demands a context-sensitive computational system [see Lorenzo (2012) and for a comprehensive characterization]. What if this ability is more informative than "communication" per se for unraveling language evolution? In fact, comparative evidence ultimately suggests that the interface between a T1 computational system, a conceptual system, and a vocal–auditory system in our species is a contingent fact. For instance, in weaver birds, this enhanced, T1-type computational capacity has plausibly interfaced with a dictionary of "movemes" [i.e., motor primitives, after Del Vecchio et al. 2003] and with some mechanisms controlling movements. Of course, this possibility is nicely illustrated by sign languages too, in which an enhanced, specifically human T1 system has interacted with a gestural-visual exteriorizing/interiorizing device.

Not surprisingly, the comparative analysis of the neural substrate of the computational system of language in diverse species allows to find evolutionary continuity and real language homologs. This substrate seems to be a quite ancient neural circuitry similarly designed in birds and mammals (Teramitsu et al. 2004; Bolhius et al. 2010; Berwick et al. 2012). However, while the sequencer component is highly preserved, working memory exhibits a lower degree of evolutionary continuity, ultimately suggesting that cortex evolution is the key step for computational systems to evolve (Balari and Lorenzo 2013; Balari et al. 2013). Moreover, although they are peripheral with regards to the emergence of modern language (but not of language per se), both the conceptual system and the externalization/internalization systems exhibit a long evolutionary history too, also linked to the evolution of cortical areas.

It is not only comparative evidence that seemingly corroborates the functional unspecificity of the computational system of language (in the sense that it can interface with different systems rendering different outputs), and ultimately, the suitability of our computational approach to language evolution. In our own species, two lines of evidence also confirm this possibility. On the one hand, it is not just language, but motor or cognitive disorders that can be conceptualized as *constructional* disturbances. For instance, drawing disorders do not only entail a disturbance in single motor movements, but also in the planning of motor sequences per se. In fact, as pointed out above, motor sequences seem to be decomposable into primitives that are arranged according to combinatorial or syntactic rules (Flash and Hochner 2005, and references cited therein). Importantly, neuroimaging analyses suggest that brain areas involved in language processing greatly match brain areas involved in motor processing (Makuuchi et al. 2003; Makuuchi 2010). Actually, the brain seems to rely on basic neural "binding mechanisms" to generate any kind of composite objects at the representational level (Flash and Hochner 2005), thus eventually explaining why the same areas are activated. Importantly also, just as we considered the lexicon and the exteriorizing/interiorizing devices as peripheral regarding language, convergent evidence similarly suggests that biomechanical factors play a subsidiary role in movement, with movements being controlled by a "central" device (Dipietro et al. 2009). On the whole, this probably explains the comorbidity frequently observed between motor and language disorders. Hence, whenever one of these brain areas performing some basic computation (relevant for both language and motor planning) is affected, both motor and linguistic disturbances simultaneously appear. For example, dyslexia is sometimes comorbid with drawing deficits, to the extent that a visuoconstructive deficit has been claimed to occur in dyslexics (Eden et al. 2003; Lipowska et al. 2011). Moreover, it has been suggested that dyslexia could be caused by a general deficit in the rule abstraction mechanism inherent to sequential learning, which would simultaneously impair both visuomotor tasks and syntax (Vicari et al. 2005; Pavlidou et al. 2010). Similarly, linguistic and motor deficits co-occur in Huntington's disease, a neurodegenerative condition caused by the selective atrophy of the basal ganglia (Teichmann et al. 2005, 2008; Robins Wahlin et al. 2010).

On the other hand, recent research has revealed that (spoken) language areas within the left hemisphere are also recruited for sign language production and comprehension. Concerning production, the involved neural systems seem to be quite the same as in oral languages. So, despite the considerable differences between articulators (vocal tract vs. hands), the functional specialization of the neural system does not depend on the nature of the motor system involved (Emmorey 2002). It is true that some dissociation seems to exist at the neural level between signs and pantomime gestures. For instance, Corina et al. (1992) reported left-hemisphere dominance for linguistic signs (of American Sign Language [henceforth, ASL]) but no lateral effect when subjects had to produce gestures like waving good bye. At the same time, the systems involved in the motor planning needed for signing and the systems involved in producing non-linguistic signs may not be completely autonomous (Corina et al. 1999). Hence, recent research also conducted by Corina et al. (2000) with PET technology suggested that cortical regions involved in everyday perception of human actions is also recruited in linguistic processing by deaf native signers. Concerning comprehension, Neville et al. (1998) found that Broca's and Wernicke's areas, but also the superior temporal sulcus and the angular gyrus (the latter usually implicated in reading in hearing people) are activated in hearing and deaf native signers when asked to watch ASL sentences (the activation of critical left-hemisphere structures during sign language processing in both groups further suggests that this cannot be the result of a neural reorganization due to a "lack of auditory input"). Conversely, some differences can be observed regarding the localization of the lexicon. Hence, deaf and hearing native signers showed distinct patterns for open (in essence, derivational and constructional "productive" words such as nouns, verbs, or adjectives) and for closed (in essence, "dead words" in terms of lexical productivity such as articles, conjunctions, auxiliaries) ASL sign classes when compared to English speakers (Neville et al. 1997). Regarding English speakers, the event-related potential (ERP) response to closed class words was left lateralized, and for the native ASL signers, it was bilateral. In sum, the brain areas involved in language computation are conceived to welcome the information within the linguistic processing, independently of the modality (oral vs. signed). In other words, the brain seems to respect function rather than form (Emmorey 2002). In the same vein, Hickok et al. (1996) have claimed that left-hemisphere specialization for language is due to the "linguistic nature of the systems" rather than the sensorial features of the linguistic signal or the motor aspects of language production. Probably also, it is not the motor system or the perceptual mechanisms (audition vs. visuospatial processing) that guides the brain organization for language. It is possible then to consider the left hemisphere as specialised in the control of complex motor movement independently of whether those movements are linguistic or not.

In fact, the hypothesis that neural devices performing specific activities can be functionally coupled to different interface devices (thus contributing to diverse functions) is the mainstream approach to brain function in current neurobiology. For instance, Poeppel and Embick (2005) have claimed that "(t)he natural assumption is that the differently structured cortical areas are specialized for performing different types of computations, and that some of these computations are necessary for language but also for other cognitive functions" (p. 112) and that "(o)perations of a specific type have uniform computational properties, and it might be expected that certain brain regions are specialized to perform this type of computation" (p. 116).

6 The Computational Hypothesis: Fossil Evidence

This computationally oriented view of language evolution supports our previous criticism of the fossil evidences commonly used for inferring the presence of modern language in other hominin species (see Sect. 2). Accordingly, if they are essentially uninformative, it is basically because they are related to the so-called external systems [after Chomsky (Hauser et al. 2002)], that is, the externalization/internalization systems (speech/signing organs) and the conceptual system (dictionary of symbols). Again, this does not entail that they are uninformative with regard to language evolution (or the emergence of communication) per se among primates.

As the very existence of other full-fledged linguistic modalities besides spoken languages (paradigmatically, sign languages) already suggested, fossil evidence also confirms that the interface between a T1, human-like computational system, a conceptual system, and a vocal–auditory system (as observed in our species) is a contingent fact. On the one hand, this circumstance supports the view that some hominin species could have relied on other mechanisms (alternative to speech) for interiorizing/exteriorizing the "linguistic" (or rather perhaps, protolinguistic) sequences they were able to generate (see Sect. 8 below for a more detailed discussion about this possibility). On the other hand, it also validates the search for other, "non-linguistic" fossil evidence of language evolution, namely, evidence related to the computational system of language itself. In doing so, one ought to, of course, leave in second place the functions this system ultimately fulfills when it is attached to other devices. As we discussed in previous sections, it is neuronal structures (and their activities) that matter in evolution; moreover, it is the achievement of an enhanced computational system what would ultimately explains the emergence of modern language.

We have suggested two different evidences of this type (but we expect many others) (Balari et al. 2013). Knots are the first one. Remember that weaving or knotting demands a context-sensitive computational system (see Sect. 5). It seems plausible that whoever made knots could think in context-sensitive terms as well (and plausibly could also externalize that kind of thought), thus having modern language [see Camps and Uriagereka (2006), or Balari et al. (2011) for more comprehensive defenses of this view]. In the fossil register, knots are attested only from 27 Kya (=kiloyears) BP (=before present) (Soffer et al. 2000), although they can be inferred from about 75–90 Kya BP. Crucially, they are only associated with anatomically modern humans (henceforth, AMH) (d'Errico et al. 2005; Henshilwood and Dubreuil 2009). Lithic industries are the second kind of such evidence. Contrary to the static nature of prior hominin techno-complexes, including the Mousterian industries associated with Neanderthals, the AMH register shows a very quick succession of lithic industries that are more and more complex in time (Mithen 1996; Tattersall 1998; Mellars 2002, 2005; Wynn and Coolidge 2004). Complex language seems a key requirement for non-static cultures. (Non-static) culture can be construed as a continuous, self-feedbacked process of change (Dennett 1995; Dunbar et al. 1999; Levinson and Jaisson 2006). Above all, it is modern, syntactically complex language that fuels this endless change, given that it allows to explore virtually (and to transmit efficiently) new possibilities (Dennett 1995, 1996). For example, only modern language allows for achieving mental representations that can be displaced both spatially and temporally or that lack a real correlate (Jerison 1985; Bickerton 1990; Dennett 1996). Perhaps more importantly, non-static cultures demand an enhanced working memory (Coolidge and Wynn 2005; Wynn and Coolidge 2007). As we discussed in Sect. 4, the more memory resources available to the sequencer, the more complex strings the computational system is able to generate. If it is the case that only AMHs are endowed with an enhanced working memory, it is plausible as well that only they have had a T1 computational system. This ultimately implies that some important cortical reconfiguration occurred in our species, but not in other extinct hominins, allowing modern syntax to emerge (see Sect. 7 below).

On the whole, these two kinds of different non-linguistic evidence support the view that only AMHs among the hominins have complex language. Again, this does not entail that other hominins lacked language. It is just that their (proto)languages had been less structurally complex than AMH languages. Quite probably, they were endowed with regular, ape-like grammars (see below Sect. 8 for a more detailed discussion).

7 The Computational Hypothesis: Neurobiological Evidence

The discussion above implicitly entails a specific model of brain evolution within our clade. This mode of change had prompted the emergence of modern language only in our species. Under our view, some cortical reconfiguration occurred in our species that increased our working memory capacity and eventually allowed the resulting (and enhanced) computational system to interface with the "external systems." We think that this model is supported by diverse paleoneurobiological and genetic evidence.

In the last few years, language evolution has also been discussed from a neurobiological perspective. However, the search for homologs of the neuronal substrate of language has been focused on the attribution of functional equivalences to some of the "classical" language areas, particularly, to Broca's area. However, this can be problematic. As we discussed above, modern functions cannot be automatically inferred from human-like, language-related structures (we called this "the form-function problem"). Hence, although Broca's areas in monkeys and humans perform the same *activity* (i.e., they are *homologs*), they are not *functionally* equivalent, given that in apes it controls grasping and manipulation (interestingly, it also discharges when the monkey observes a conspecific making similar actions) (Rizzolatti and Arbib 1998).

Another common proxy for (modern) language is *lateralization*. A growing corpus of evidence suggests that the left hemisphere plays an important role in producing and understanding linguistic utterances. Lesions occurred in the perisylvian area of the left hemisphere provoke different types of language disorders, namely aphasias. In Paleoanthropology, left-lateralization patterns are usually inferred from handedness ratios. On the whole, the full inference is as follows: if some hominin species had a right-handedness ratio similar to living people, then it would have also had a human-like pattern of brain lateralization and, ultimately, have been endowed with linguistic abilities similar to AMHs [see for instance Frayer et al. (2010) on Neanderthals]. Many circumstances make this inference problematic [see Benítez-Burraco and Longa (2012) on this extinct species]. Briefly, the link between right-handedness, (structural and functional) brain lateralization, and language is not as straightforward as assumed, even within our own species. On the one hand, the correlation between handedness and verbal skills is weak to say the least (Natsopoulos et al. 2002; Nettle 2003), even at the brain level (Szaflarski et al. 2002; Selnes and Whitaker 2006). On the other hand, non-left lateralized brain configurations (as those exhibited by some left-handed people or some hemispherectomized subjects) do not compulsorily entail an impaired or disordered faculty of language (Foundas et al. 1994; Liégeois et al. 2008). Lastly, in "crossed aphasia," language deficit can occur in right-handed people after right-brain damage (Castro-Caldas et al. 1987; Falchook et al. 2013). In truth, the "linguistic brain" might not be as left lateralized as currently assumed (even in right-handed people), given that some key areas seem to be right lateralized [i.e., the caudate (Ifthikharuddin et al. 2000; Watkins et al. 2001)] and that different cortical areas of the right hemisphere are regularly recruited for language processing (Just et al. 1996). Additionally, from a phylogenetic perspective, both right-handedness and brain lateralization seemingly predate the evidence for (modern) language. For example, according to Holloway (1996), *Homo erectus* already showed a modern, right-handed pattern. In fact, it has been suggested that both human and ape handedness patterns are similarly influenced by task complexity (Uomini 2009). Moreover, structural and functional brain asymmetries predate the evidence for (modern) right-handedness (and of course, for language) in our clade.

Again, this is true both for extinct (Holloway 1981; Kyriacou and Bruner 2011) and extant primates (Holloway and De La Costelareymondie 1982; Cantalupo and Hopkins 2001). Eventually, it is possible that brain lateralization is only indirectly related to language. As Cochet and Byrne (2013) have pointed out, "there is some evidence that tool use served as a preadaptation for left-hemisphere specialization for language." In the same vein, "a growing body of work suggests that features of intentionality and hierarchical structure may explain the functional origin of cerebral and manual asymmetries." Incidentally, this possibility reinforces the convenience, when discussing language evolution, of detaching neural structures and their activities from the functions they ultimately contribute to. On the whole, language at the brain level seems to depend more on a particular connectivity pattern between different areas (performing basic types of computations) than on a specific pattern of structural and functional lateralization of the brain. Laterality might be primarily related to speech (i.e., the externalization of linguistic expressions), as Broca himself pointed out in his seminal work (Broca 1861: 334). After all, the articulators must perform symmetrically, and we cannot use them independently. But, as we have sufficiently argued, speech is a peripheral component of the human faculty of language.

On the contrary, it has been usually assumed that brain size constitutes too rough a proxy for language evolution [see Falk (1990) or Ayala and Cela Conde (2006), among many others]. However, when brains grow, structural changes (in the form of internal reorganization) occur that presumably give rise to functional changes with crucial consequences for language evolution. On the one hand, brain allometry changes, because late-maturing brain areas usually grow larger (Finlay and Darlington 1995). On the other hand, a more areas or activity nuclei appear, and they show a higher degree of lamination (Ebbesson 1980; Strausfeld et al. 2000). Finally, the mutual invasion of these areas and nuclei of activity (aka *connectional invasion*) is favoured (Deacon 1990a, b). We have hypothesized that some crucial steps for the emergence of a modern computational system (and ultimately, of modern language) can be a by-product of the increment of brain size occurred during our speciation (see Balari et al. 2013 for details). Hence, the more cortical resources, the more working memory available for computing (a key step for achieving a full-fledged computational system). Similarly, the more cortical resources, the more long-term memory available for storing information and ultimately, for having larger lexicons). Additionally, the connectional invasion of disjoint areas would have allowed different systems to interface (this is crucial for constructing a functional module from different computational devices, otherwise functionally non-specific by nature). In a similar vein, Boeckx (2012) has argued that the more globular configuration of (adult) AMH brains (compared to that of other extant hominins), with the thalamus located in a more central position and with neurons establishing more long-distance connections, created a new neuronal workspace that allowed for more efficient connections and information exchanges to take place and, eventually, for an enhanced computational efficiency. According to him, this new mode of combination, which allows for the formation of potentially unbounded hierarchical structures (Boeckx has called it *unbounded* *merge*), is not radically new. What is new is the fact that it is not constrained. As a consequence, it can combine any sort of elements. Of course, we do not rule out the possibility that some AMH-specific interconnection patterns have also contributed to these changes and, ultimately, to the emergence of modern language. For instance, the temporal lobe projection of the human arcuate fasciculus seems to be absent (or to be much smaller) in non-human primates (Rilling et al. 2008). Obviously, it is very difficult to infer brain connectivity from hominin endocasts, given that brain nerve tracts do not fossilize.

In turn, we expect that these changes in brain size (and connectivity) resulted from the modification of genes controlling neural proliferation. In fact, some of these genes have been positively selected in our clade and some substitutions or insertions/deletions have specifically occurred after our split from Neanderthals. It is plausible then that these changes could account for (some of) the observed differences in brain ontogeny between both species (Gunz et al. 2012). These dissimilar ontogenetic trajectories plausibly entail different patterns of brain connectivity and of the interface between processing devices, and ultimately, different faculties of language. For instance, *MCPH1* encodes a protein involved in DNA repair and in chromosome condensation during the cellular cycle (Trimborn et al. 2004; Xu et al. 2004). Its mutation gives rise to microcephaly, an atavistic condition characterised by a reduced cortical volume resulting from a decrease in the number of neurons (Woods 2004). Although the strongest signals of positive selection on this gene predate the split between Old World monkeys and great apes (Evans et al. 2004; Wang and Su 2004), AMHs bear a derived allele in some positions of the gene compared to Neanderthals (Green et al. 2010). In a similar vein, Boeckx (2012) has linked the emergence of his unbounded merge to some change in a gene (or genes) controlling the development of the brain (and the skull).

We cannot rule out the possibility that some of the changes that brought about modern language affected to genes involved in other processes, such as neural differentiation, migration, or interconnection. We will refer here to these genes as “language genes” in the plain sense that their mutation usually gives rise to clinical conditions in which language is impaired (of course, there is no such thing as language genes stricto sensu: genes are not blueprints!). Under our computational hypothesis, these genes would have stabilised and consolidated the reorganizational processes concomitant with brain growth. One of these “language genes” is *FOXP2*. This gene encodes a transcription factor that promotes the neuronal differentiation necessary for the development and the activity of cortico-thalamic-striatal circuits involved in motor planning, sequential tasks, and procedural learning (Vargha-Khadem et al. 2005; Fisher and Scharff 2009). In the human lineage, the protein FOXP2 has undergone two key changes (Enard et al. 2002), although these changes predate the split between Neanderthals and AMHs, about 300–400 Kya BP (Krause et al. 2007). However, an AMH-specific single nucleotide change (SNC) has been recently found within a regulatory region of the gene. This change may have modified its expression pattern in our species (Maricic et al. 2012). In the same vein, the Denisovan (the hominin species closest to Neanderthals) *CNTNAP2* shows a fixed ancestral SNC compared to the AMH gene (Meyer et al. 2012). *CNTNAP2* is one of FOXP2's targets and also a candidate gene for specific language impairment and autism (Alarcón et al. 2008; Bakkaloglu et al. 2008; Vernes et al. 2008). However, *Foxp2* mutations impair auditory-motor association learning in mice (Kurt et al. 2012). Therefore, this gene could actually be related to the externalization of language (i.e., speech), and not (at least directly) to the development of the computational system of language. Consequently, it seems necessary to still look for other substitutions and insertions/deletions that have occurred within the human lineage that have affected other different genes involved in neural proliferation, migration, specialization, or interconnection. Notice, however, that phenotypic innovations can arise in neutral conditions too (that is, without involving gene mutations), due to the very dynamics and the generative properties of developmental systems (Müller and Newman 2005; West-Eberhard 2005; Walsh 2007). That means that two species could eventually exhibit different faculties of language even if they are endowed with the same "linguistic genotype," particularly if environmental conditions bring about divergent brain ontogenies that give rise to different patterns of brain connectivity and ultimately, of interface between processing devices.

8 The Computational Hypothesis: Constraints on Language Evolution

Our last concern is how our hypothesis, if correct, constrains previous (and future) models of language evolution.

As we have suggested elsewhere in this paper, our view that a modern faculty of language (this primarily meaning a modern system of computation) is an evolutionary novelty of AMHs does not preclude the possibility that other extinct hominins had "language," i.e., that were able to productively combine symbolic elements into strings that were ultimately uttered or signed. It is just that these strings probably lacked certain structural properties that we can only find in current oral or sign languages (specifically, dependencies acting at an arbitrarily long distance). At the same time, language "sophistication," as posited by Corballis (2002), did not probably increase in a smooth way. As we discussed in Sect. 4, although syntax is not an all-or-nothing matter, it is not a continuum either. If our hypothesis is correct, the "languages" (or protolanguages) of other hominins would have been endowed with regular grammars (as ape "languages" are) or perhaps with context-free grammars.

The modality of these hominin "languages" or protolanguages (that is, the way in which linguistic sequences were ultimately transmitted, either orally or gesturally) is also a controversial point. For example, according to Corballis (2002: 123), "the facts of primate evolution favor an origin (of the language instinct) in manual gestures." Our evolutionary model is compatible with Corballis's "from hand-to-mouth" hypothesis, because of the functional independence of the computational system of language, the role played by "language areas" in extant primates (paradigmatically, by Broca's area), and the very existence (and properties) of sign languages, which suggest that orality is not a prerequisite for language. In fact, speech organs seem to have evolved quite slowly. Hence, modern vocal tracts and modern auditory systems are already attested in *Homo heidelbergensis* (Martínez et al. 2004; Martínez and Arsuaga 2009). This suggests that oral "language" predates the emergence of modern syntax within our lineage. Maybe this modern, enhanced-for-speech audio–vocal device already interacted with a conceptual system (responsible for thought) in other hominin species (it surely did in Neanderthals). In other words, the closest species to us would have probably been endowed with oral, symbolic communication systems, although less complex grammatically. Concerning more distant species, they could have been endowed with gestural "languages" or protolanguages, as Corballis suggests, but very probably, these communication devices would have been less complex than human languages. According to Boeckx (2012), the conceptual systems of other hominins (and even the putative "words" or signs they used) would not have been identical to ours, given that our enhanced syntactic capacity very likely reshaped them. Putting it differently, hominin semantics and phonology were not exactly the same as ours.

Finally, the hypothesis that orality replaced gestuality sometime after the split of our lineage from extant apes is also compatible with our model. However, co-evolution and co-intervention between both modalities is also plausible. After all, sign languages and oral languages have a common neural substrate (see Sect. 5). Probably, in the latest extinct hominins sign "languages" and oral "languages" would have coexisted as they do in modern humans.

9 Conclusions

To summarize, we contend that if we want to improve our research on communicative abilities in primates, we should redraw ongoing studies on language evolution by giving pre-eminence to computational issues and by diminishing the importance given to communication (and in fact, to any other function of language). In particular, we should acknowledge that:

- the faculty of language is, above all, a natural system of computation
- language functions are orthologous to this faculty
- in our species, it is the case that this system of computation interacts with a conceptual system and a vocal–auditory system (and occasionally, with a gestural-visual system)
- language (in a broad sense) arises from the interface between these three components
- each component can functionally interface with other devices (at the same time, the output of this interaction, even being non-linguistic by nature, can illuminate their properties)
- these components have a long-lasting evolutionary trajectory, with homologs (and perhaps analogs) in other extant species

- human-like language is not possible without an enhanced (i.e., human-like) computational system
- within our lineage this enhanced computational system is an AMH autapomorphy (that is, a derived trait), but has probably evolved in other vertebrate lineages too.

If we proceed in this way, we will be able to find real (that is, informative) language homologs in other extant species and also real (again, informative) language fossils from extinct species. Ultimately, we will obtain a more accurate, biologically grounded view of how communication evolved in our clade.

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