38

Language Evolution

C. Boeckx

ICREA, Universitat de Barcelona, Barcelona, Spain

38.1 An Evolving Landscape

There has never been a better time, in my opinion, to work on the topic of language evolution. The field of "evolutionary linguistics," as one may call it, used to be plagued by lack of relevant data and therefore constituted a forum for all kinds of speculation. Such just-so stories were denounced most forcefully in a famous essay by Lewontin (1998). Unfortunately, they continue to this day. However, next to, and slowly supplanting this literature, a body of knowledge is emerging that holds great promise. It is a body of knowledge that is the epitome of interdisciplinarity, bringing together scholars from evolutionary biology, genetics, linguistics, cognitive neuroscience, and developmental psychology. This growing body of knowledge, which is the focus of this chapter, rests on several foundational assumptions:

1. Any evolutionary account of the human language phenotype will have to take into account both the species-specific biological endowment and the powerful structuring forces of culture and social interactions. The human language phenotype is too complex to capture by means of single-level, unidimensional, one-magic-bullet explanations.

2. Any account intended to appeal to biological mechanisms, including cultural accounts that of course must recognize the human biological commitment to culture, will have to center its efforts on the brain. There is simply no alternative to linking genotype and phenotype. Accordingly, cognitive descriptions will have to be linked to neural circuit mechanisms prior to being linked to genes.

3. Any approach aiming to characterize the evolutionary trajectory of human language will have to be Darwinian. This (hopefully) sounds like a no-brainer, but it is worth stressing that for an account to be properly Darwinian, it must at the very least take the notion of "descent with modification" seriously.

This means that it must strive to exploit as broad a comparative database as possible (in the case of humans, focus on the lessons one can derive from other animals) and avoid resorting to "special" explanations (be they in terms of special brain regions, mechanisms, etc.). No matter how modestly "linguistic" nonhuman creatures appear to be, the Darwinian logic of descent requires us to be able to discern an evolutionary path from there (them) to here (us). That is, ultimately, the human language phenotype must be rooted in nonstrictly human and nonstrictly linguistic cognition. "Only us" approaches just will not do. (To be clear: this is not to say that there is no specialization at the brain level. There is. But specialized regions follow principles of the surrounding brain circuits and work in an integrated fashion with less-specialized circuits.)

It seems to me that the field of evolutionary linguistics has matured enough now to demand that points (1)–(3) be present in any study falling under its scope. In particular, it simply will not do to state (as has all too frequently been the case until recently) that "we know so little about the brain," or that "some cognitive process (ultimately implemented in neural hardware) is encoded in our genes," or that "animal studies are not useful to capture the core human language phenotype because language is something unique to humans."

Of the three guidelines just listed, I take (2) to be the most important one: evolutionary linguistics is a brain initiative. As Marcus (2004) put it, genes do not build behavior or cognition. They code for and regulate the expression patterns of proteins that build neural building blocks that assemble into circuits, whose (environment-dependent) activities amount to processing information— that is to say, computing—that we can describe in cognitive terms and take to underlie behavior. There is no way around this long chain of inferential steps from genotypes to phenotypes. Each

and every one of these steps is necessary and equally important, and moving from one level of description to the next requires a specific linking hypothesis. (For a very clear discussion of this issue with respect to the first gene causally related to some aspects of language, FOXP2, see Fisher, 2015.)

For several decades, the field of linguistics has been dominated by debates concerning "nature" or "nurture," until at some point advocates of the "rich and domain-specific biological endowment" camp (typically associated with work from the generative grammar tradition most closely connected to Noam Chomsky) realized that they were probably making too many demands on said biological endowment (demands that it could not possibly meet, especially given the assumption that human language evolved recently). They then began cutting down on the cognitive apparatus they relied on. This in turn led them to realize that this trimmed-down apparatus was incapable of capturing all the subtleties of linguistic knowledge. As a result, they began to delegate, explicitly or more often implicitly, some (indeed, much) of the mechanisms supporting adult linguistic knowledge onto the learning task and on the context in which learning takes place. In other words, the learning component came to play a much more important role. In so doing, they converged with advocates of the strong cultural component school (for more detailed discussion, see Boeckx, 2014). Interestingly, some of the strongest results of the latter school emerged in the context of evolutionary studies (see Kirby, 2013). Such studies, which formed the bulk of works presented at all the Evolang meetings (the major forum for studies on language evolution), demonstrate that generations of language learners, equipped with generic learning biases, shape the grammatical profile of the languages they learned. If this is true, then it would be mistaken to insist on building these aspects of grammatical knowledge into the initial substrate/biological endowment. Rather, these attractors populating the grammar space emerge from learning and communicative pressures. As a result, the focus, for the biologically inclined, should not only be on tracing down the origins of these generic biases in other animals, but also on our inclination to engaging in learning and communicating (verbally).

Following authors such as Michael Arbib (2002), I like to distinguish between the evolution of language and the evolution of the language-ready brain. The term "language-ready brain" not only draws attention to the centrality of the brain (cf. point (2) mentioned earlier), but also stresses the distance we ought to expect between what we will find at the neural level and what we can observe in the linguistic phenotype (adult linguistic knowledge).

The distinction between language and language-ready brain should not, I think, be conflated with the distinction between either of these terms and the notion of "protolanguage." The latter, exhaustively reviewed in Fitch (2010), refers to a stage (or multiple stages) in language evolution that is intermediate between what we can reasonably infer about the linguistic capacity of the last ancestor we shared with great apes from the behavior of living great apes and our species-specific linguistic capacity. Some scholars, such as Arbib (2002), take whatever degree of grammatical complexity that may exist between modern language and protolanguage to be a matter of culture. Others, such as myself, while recognizing the importance of cultural learning and transmission, still allow for significant changes at the level of the brain between a protolanguage user and a full-fledged, modern-language user. In other words, just as one distinguishes between language and protolanguage, it may be worth distinguishing between a protolanguage-ready brain and a language-ready brain. The difference between the two may just be a matter of degree of commitment to culture, but it would still be reflected in our biology, and need not be regarded as less significant than the step that led to the emergence of protolanguage.

The position just outlined appears to match the model insightfully sketched by Scott-Phillips and Kirby (2010). They observe that "[w]e can characterise the study of language evolution as being concerned with the emergence of language out of non-language. This involves two main processes of information transmission and change: a biological one (…) and cultural one (…). Prior to the existence of a culturally transmitted communication system, we can consider only the various preadaptations for language (e.g. vocal learning, conceptual structure [etc.]). Once cultural transmission is in place, then it might operate simultaneously with biological evolution in a co-evolutionary process and/or there might be cultural evolution alone [reference omitted]. In either case, we urgently need a better general understanding of how cultural transmission and social coordination shape language if we are to achieve a complete picture of the evolution of language. Once language has emerged, further changes can and do occur. This is the domain of language change and historical linguistics." What this passage makes clear is that the distinction between "phylogeny" (evolution of language; genetic evolution) and "glossogeny" (evolution of languages; cultural evolution), introduced by Hurford (1990), is not as clear-cut as it may be, given the recognized role of culture in adding complexity and structuring the linguistic phenotype.

The passage quoted from Scott-Phillips and Kirby (2010) also allows me to address another, related point.

They talk about "the emergence of language out of nonlanguage," but just to be clear: the Darwinian logic of descent forces us to recognize a continuum, at some level, between these two states. If, as is generally recognized, we must ground aspects of our linguistic capacity into the brains of nonlinguistic creatures, calling these creatures nonlinguistic is a bit misleading. This is exactly the issue that Hauser et al. (2002) addressed in a widely cited article. In an attempt to capture both the species-specific character of language and the roots of aspects of our language faculty in other species, they distinguished between the faculty of language in the narrow sense (FLN, corresponding to what makes us unique) and the faculty of language in the broad sense (FLB). In this way, nonhuman animals could be called broadly linguistic creatures, but not narrowly linguistic creatures, a term that should be reserved to us.

Unfortunately, instead of focusing on the fact that this distinction drew attention to the roots of aspects of language in other species and called for renewed appreciation for the promises of comparative cognition, many scholars, especially linguists, used the FLN-FLB distinction to stress what made humans different. In other words, instead of focusing on FLB, they focused on FLN. Specifically, they tried to provide content to FLN (something which, incidentally, Hauser, Chomsky, and Fitch invited by hypothesizing that FLN consisted of "recursion and its mapping to the sensorimotor and conceptual interfaces") and looked for some unique traits. In so doing, they not only departed from the Darwinian logic of descent but also departed from the consensus in current biology that "phenotypic novelty is largely reorganizational rather than a product of innovative genes" (West-Eberhard, 2003). It seems to me that statements such as West-Eberhard's demand that the idea that what makes human language unique is the way it organizes or collects attributes that individually can be rooted in nonhuman cognition be taken as the default hypothesis. Of course, once collected under a single roof ("language-ready brain"), these traits may give rise to nonlinear, "emergent" effects. Likewise, as Fujita (2016) has stressed, when placed in the context of the human brain, "old" pieces may acquire new roles that transform their nature (the sort of feedback loop familiar in biology). So, in the end, as I already expressed in Boeckx (2013), the FLN-FLB distinction does not strike me as the most felicitous way of capturing the continuum that the Darwinian logic of descent demands between our linguistic capacity and nonhuman cognition. I prefer the perspective advocated in Petkov and Jarvis (2012) and Arriaga and Jarvis (2013).

As a final note on this continuum, let me point out that continuum need not mean "scale." Rather, following François Jacob's well-known tinkering metaphor, we should think of our language-ready brain as a mosaic or patchwork, composed of parts (possibly, multiple protolanguage components) that do not fit neatly a cognitive *scala naturae* but rather display deep homologies with capacities found in a variety of species. Of course, our language-ready brain evolved from a primate brain, but the latent potential of subtle tinkering events, as I will show later, need not always be best understood by examining primate behavior and studying primate cognition (for more on this way of understanding cognitive phylogenies, see Theofanopoulou and Boeckx, 2015).

38.2 Deep Homology

Until recently most language-oriented books on comparative cognition just had one message: animals do not have the cognitive capacities necessary to acquire language (see Anderson, 2004 for a particularly clear example of this). But the tides have changed. De Waal and Ferrari (2010) put it best: "Over the last few decades, comparative cognitive research has focused on the pinnacles of mental evolution, asking all-or-nothing questions such as which animals (if any) possess a theory of mind, culture, linguistic abilities, future planning, and so on. Research programs adopting this top-down perspective have often pitted one taxon against another, resulting in sharp dividing lines. Insight into the underlying mechanisms has lagged behind … A dramatic change in focus now seems to be under way, however, with increased appreciation that the basic building blocks of cognition might be shared across a wide range of species. We argue that this bottom-up perspective, which focuses on the constituent capacities underlying larger cognitive phenomena, is more in line with both neuroscience and evolutionary biology."

In the domain of language this bottom-up perspective is best illustrated in the context of birdsong studies. There is now an extensive literature documenting parallels between birdsong and aspects of human language (not just speech, as I will discuss later) at various levels of description: development, neural basis, and evolution (for a recent state-of-the-art survey, see Bolhuis and Everaert, 2013). Both birdsong and human language are vivid illustrations of what Peter Marler (2004) called the "instinct to learn." Both show strong evidence for the need to have a brain configured in a particular way to engage in vocal learning (Jarvis, 2004) and at the same time highlight the importance of the environment in shaping the structure of the songs. Thus, like humans, songbirds raised in isolation, without any conspecific adult models during the critical period for song learning, never recover. They never move much beyond the babbling stage called "subsong." But Feher et al. (2009) showed that in a colony of songbirds founded

by an isolate, normal song structure reemerges over the course of a few generations, in a way strongly reminiscent of what happens with creole languages.

Like language users, then, birds demonstrate that possessing a song-ready brain is not enough. Rather, learning, taking place over several generations, is required for the song to develop completely. The birdsong literature also demonstrates that specific environmental circumstances, such as domestication (crucially, not targeting song structure per se), can lead to a complexification of the song phenotype (Okanoya, 2012), raising the possibility that self-domestication processes often mentioned in the context of recent human evolution (see Thomas, 2014; Benitez-Burraco et al., 2016) may have also played a role in structuring the human language phenotype, an issue I will return to later.

Arguably the biggest advance coming from the birdsong literature concerns the neurobiological basis of vocal learning. The literature of the past 20 years has accumulated robust findings concerning the brain pathways necessary for vocal learning and the molecular underpinnings of said pathways. Vocal learning abilities in birds depend on two main pathways: a nidopallial-striatal-thalamic loop responsible for the acquisition of new vocalizations, known as the anterior pathway, and a posterior pathway directly connecting the arcopallium and the syrinx, which controls intentional vocal production. Translating this to humans, a corticobasal ganglia-thalamic loop, along with a direct connection between the motor cortex and the larynx, appears to be the required neurological substrate for vocal learning (see Jarvis, 2004 and much subsequent work since). Analyzing the rudimentary substrates for vocal learning found in a non–vocal-learning suboscine, the eastern phoebe, Liu et al. (2013) suggest that the posterior pathway is probably the first step in achieving a vocal-learning readiness.

More remarkably, in addition to uncovering these neural pathways, birdsong scholars were capable of canalizing the genomic revolution to uncover deep homologies at the molecular level, so much so that comparisons of brain transcriptomes of song-learning birds and humans relative to vocal nonlearners identified convergent gene expression specializations in specific song and speech brain regions of avian vocal learners and humans (Pfenning et al., 2014). In particular, the forebrain part of the vocal-learning circuit that makes a robust direct connection to brain stem vocal motor neurons in independent lineages of vocal-learning birds (songbird, parrot, and hummingbird) was shown to have specialized regulation of axon guidance genes belonging to the SLIT-ROBO molecular pathway (Wang et al., 2015). Wang et al. showed that, unlike in mice and non–vocal-learning birds, in vocal-learning birds, SLIT1 was differentially downregulated in the motor song output nucleus that provides a direct link between the bird equivalent of the motor cortex and the syrinx, whereas SLIT1's receptor ROBO1 was developmentally upregulated during critical periods for vocal learning. Interestingly, the SLIT-ROBO pathway has been associated with a range of disorders in humans where language is affected (see references in Boeckx and Benítez-Burraco, 2014b). In addition, SLIT1 is a direct target of FOXP2 (Vernes et al., 2007; Konopka et al., 2009). Thus, Wang et al.'s finding is directly related to the remarkable literature on FOXP2 and its role in language that was built on Lai et al.'s (2001) landmark association between a mutation affecting this transcription factor and a development language disorder.

This is not the place to provide an extensive review of the FOXP2 literature (for excellent recent overviews, see Fisher, 2016; Fisher and Vernes, 2015; Graham and Fisher, 2015). Suffice it to say that this literature has provided a unique point of entry into the molecular basis of the neural implementation of aspects of the human language capacity. Especially worthy of note are (1) discoveries pertaining to the neural function of FOXP2; (2) the strong expression profile of FOXP2 in subcortical circuits; and (3) the recent evolutionary changes affecting FOXP2. Let me touch on each of these briefly.

Following Lai et al.'s discovery that heterozygous mutations of the human FOXP2 gene cause a monogenic speech and language disorder (reviewed in the overviews cited earlier), intensive work has uncovered that reduced functional dosage of the mouse version (Foxp2) causes deficient corticostriatal synaptic plasticity and impairs motor-skill learning and that the songbird orthologue appears to be critically important for vocal learning. Significant research has been made in delineating the gene's interactome, which has led to results such as Vernes et al. (2011), where Foxp2 was shown to regulate gene networks implicated in neurite outgrowth in the developing brain by directly and indirectly regulating mRNAs involved in the development and plasticity of neuronal connections. In another study, Tsui et al. (2013) concluded that FOXP2 regulates genesis of some intermediate progenitors and neurons in the mammalian cortex and suggested that the evolution of the gene may be associated with the expansion of the human cortex.

One of the most robust findings in the FOXP2 literature concerns the gene's strong expression in subcortical structures such as the basal ganglia, the thalamus, and the cerebellum (Vargha-Khadem et al., 2005; Haesler et al., 2004; Teramitsu et al., 2004). This has led to the renewed interest in these structures for language and has led to the reappraisal of models that attribute a key role, both ontogenetically and phylogenetically, to

subcortical structures (eg, Jarvis, 2004; Lieberman, 2006; but see also Boeckx, 2013; Boeckx and Benítez-Burraco, 2014a,b; Barton, 2012; among others).

In terms of impact, the evolutionary history of FOXP2 cannot be matched. FOXP2 is a highly conserved gene, with only two amino acids separating the human version from the chimpanzee version, and only three amino acids separating the human version from the mouse version. Needless to say, the discovery of two recent changes in the otherwise remarkable stable history of the gene has led to a lot of speculation concerning language evolution (speculation unfortunately rarely accompanied by detailed linking hypotheses between these mutations and neurobiology). The discovery that the Neanderthal genome contained the two key mutations found in modern humans (Krause et al., 2007) led to the claim that language has a deeper history than most scholars claimed (for the most compelling case in favor of this position, see Dediu and Levinson, 2013). Although hard to prove at this point, independent data suggest that this position is worth taking very seriously (although it is also important to bear in mind the evidence pointing to species-specific regulation of the gene; cf. Maricic et al., 2013). The SLIT-ROBO GTPase activating protein 2 (SRGAP2) is duplicated three times in the human genome compared to the chimpanzee genome, and one of the partial duplicated copies partially suppresses SLIT protein activity, thereby causing slower forebrain dendritic pruning, leaving more and longer dendrites (Charrier et al., 2012; Dennis et al., 2012). Crucially, the relevant duplications are not only specific to our species but are also part of the Neanderthal genome. Given that the SLIT-ROBO pathway appears to be significant in the context of vocal learning, and that the SRGAP2 duplication is not unique to the genome of anatomically modern humans, it is tempting to claim that some of our extinct ancestors were, if not equipped with all aspects of the modern language faculty, at least capable of complex vocal learning.

Independent evidence for this position may come once again from the birdsong literature. Liu et al. (2013) point out in their analysis that "vocal learners share relatively small body size, which may allow these birds (and their ancestors) to better manoeuvre flight and create more ecological niches for foraging (nectar feeding, flying-insect catching) and aerial vocal display. Such elaborate flight manoeuvreing may require a better coordination or reconfiguration of respiratory control from the forebrain. The forebrain respiratory control may subsequently integrate pre-existing motor pathway in the arcopallium for the control of flight, jaw, and vocal movement, and/or auditory relays, and lead to evolution of vocal learning (see a similar view proposed by Janik and Slater (1997) for vocal learning in mammals)." Although, as Liu et al. point out, this "respiratory control" hypothesis is highly speculative, it is worth bearing in mind, in line with Levinson (2016), that the African variety of *Homo erectus* (*c*.1.6 My) appears to have lacked the breathing control necessary for modern speech. By contrast, the last common ancestor between anatomically modern humans and Neanderthals appears to have had all the physiological prerequisites. Levinson suggests, reasonably, that by that time communication was predominantly vocal, as opposed to gestural.

This reasoning is to be placed in the context of the motor theory of vocal learning put forth by Feenders et al. (2008). This theory states that the "cerebral brain pathways for vocal learning in distantly related animals evolved independently as specializations of a preexisting motor system inherited from their common ancestors" and is based on gene expression in very closely located brain circuits responsible for activities such as hopping and signing. Plausibly, as discussed by Chakraborty and Jarvis (2015), the pathway critical for vocal learning may have evolved by duplication and then divergence from the motor pathways regulating nonvocal motor behaviors.

Chakraborty and Jarvis (2015) have also argued for another duplication event, responsible for the type of advanced vocal imitation found in parrots. By means of baseline gene expression, singing-driven gene expression, and neural connectivity tracing experiments, Chakraborty et al. (2015) demonstrated that the parrot brain contains what looks like a song system within another song system. The inner song system, which they call "core," appears similar to other vocal-learning birds, whereas the outer system, called "shell," appears unique. Chakraborty et al. propose that it is this shell pathway that is responsible for their imitative abilities compared to other vocal-learning bird lineages. As Chakraborty et al. observe, the connectivity of the shells had some significant differences to the core nuclei. Also, the size of some of the shells, contrary to what happens in the case of cores, seems to scale allometrically with brain size and positively correlates with both vocal and cognitive complexity in different parrot species. I find the latter finding of great interest, as Deacon (1989, 1997) suggested that one of the factors allowing for the establishment of the vocal learning circuit is encephalization. Deacon points out that when space is sparse, the innate, noncortically controlled vocalization circuit outcompetes the cortical connections making intentional vocalization possible. But as brains expand, space is created for both systems to be maintained. The vocal-learning literature in birds does not seem to support a strong version of this hypothesis, as vocal learning does not seem to require big brains, although there are two caveats to be made in this context. First, encephalization appears to be a factor for shell systems,

and it is precisely in those birds with shell systems that we see a richer semantics associated with vocal output. Second, although absolute size may not be a factor, neuron number may be. That is, it has recently been shown by Olkowicz et al. (2016) that bird brains pack more neurons in the same brain space as mammals, and vocal-learning birds have an even higher packing density than other bird species and twice as many neurons as some nonhuman primate brains bigger than theirs.

In this context, it is also worth pointing out, following Hillert (2015), that the timing of the duplication events (Dennis et al., 2012) of the SRGAP2 gene mentioned earlier coincides with landmarks of neocortical expansion in the transition from *Australopithecus* to *Homo*. This suggests to me that a better understanding of the functional consequences of the peculiar evolution of SRGAP2 may bear directly on the vocal-learning system we possess(ed).

Be that as it may, Chakraborty et al.'s work highlights the relevance of complexity in vocal learning that complements the notion of complexity that emerged from, eg, the work of Okanoya (2012) on the complexification of songs in the context of domestication. [I should note that there may be different kinds of complexity, as discussed in Deacon (2006), just like there are different degrees of novelty/complexification in an organism; cf. Müller (2010).] There appear to be (possibly not unrelated) environmental and neural factors contributing to the range of vocal-learning capacities. In fact, Petkov and Jarvis (2012) and Arriaga and Jarvis (2013) propose that vocal-learning abilities are distributed along a continuum. Thus, instead of thinking of vocal learning as a relative rare trait found only in three distantly related groups of mammals (humans, bats, and cetaceans) and three groups of birds (parrots, hummingbirds, and songbirds), we may conceive of vocal learning as more widespread. According to this view, the degree of voluntary control that an animal has over its vocalizations is primarily determined by the robustness of the cortical−laryngeal (or equivalent) pathway, very weak in mice and nonhuman primates, but very strong in canonical vocal learners. This continuum hypothesis makes it possible to study a wider range of species to reveal the neurobiological substrates of vocal learning and parallels attempts to decompose the human language faculty into more basic building blocks that can be studied in a wide range of species (see, eg, Samuels, 2011 for a detailed attempt in the context of phonology).

The ultimate lesson I want to highlight from the literature on vocal learning in birds (which I suspect will soon be enriched by work on bats; see Rodenas-Cuadrado et al., 2015) is that solid progress and formulation of testable hypotheses in understanding the evolution of aspects of language must go hand in hand

with a very precise characterization of the neural basis of these cognitive/behavioral capacities.

38.3 Primate Ancestry

Whereas the previous section provided a survey of substantial results building on more than a decade of sustained work on the neurobiology of vocal learning, this section will focus on an equally important, but less well understood, topic in the domain of language evolution: the cognitive abilities we inherited from our primate ancestry.

Until recently, researchers disregarded nonhuman primates in the context of evolutionary linguistics because unlike vocal-learning birds, the imitative abilities of our closest living relatives, especially their vocal imitative abilities, were far from remarkable. In addition, experimenting with nonhuman primates is far more challenging when it comes to neurobiological issues than it is with birds or mice. But as I hope to convey in this section, we can still gather valuable information concerning our primate ancestry; in fact, in the few cases where investigating the neural basis of their behavior, primates have been shown to shed light on the evolution of human language, so much so that I anticipate significant progress in this area in the near future.

There is very good evidence of a rich cognitive life among our primate relatives. Works such as Cheney and Seyfarth (1992, 2008), Hauser (2001), and, especially Hurford (2007) have documented a wide range of behaviors that strike me as providing solid grounds for trusting in Darwinian descent when it comes to "semantics." This is not to say, of course, that there was no innovation in this domain when full-blown language emerged, but in the domain of semantics, and in fact language as a whole, the gap between "them" and "us" has not infrequently been exaggerated by the fact that our own behavior was described in extremely rich, domain-specific computational terms, but not so for our relatives. When less "intellectualized" descriptions of our behavior are provided, the gap is considerably reduced, and the plausibility of descent reinforced. To my mind the clearest demonstration of the statement just made comes from the work of Moore (2016a,b) on intentional communication and its cognitive prerequisites. Often described in uniquely human terms (semantics/pragmatics), it turns out that more "minimalist/elementary" descriptions can be offered and shown to be adequate.

The reason I will not discuss semantics/pragmatics much here is because even for humans, the neurobiological basis of these abilities is not well understood. It is often said that semantics remains the "last frontier" for both neurolinguistics and evolutionary linguistics, but

I think that it is especially in the context of neurolinguistics that insight is lacking. Evolutionary speaking, one can be fairly confident that a rich conceptual basis, "waiting" to be modified, was in place millions of years ago. Hopefully, the growing appreciation for the cognitive sophistication of parrots and corvid songbirds (Emery and Clayton, 2004) will also provide additional insights into this area, following the logic of deep homology discussed in the previous section.

The question I will focus on in the rest of this section is, how did this rich conceptual structure we have every reason to believe was present in our last common ancestor with great apes, got to be paired with a vocal-learning ability? Put another way, how did we come to take volitional control of our vocalizations?

It is not the case that the auditory processing system of primates is poor. In fact, Bornkessel-Schlesewsky et al. (2015) and Wilson et al. (2015) have revealed substantial homology in this domain, with both a ventral and dorsal pathway linking up the frontal and temporal cortex to organize auditory perception at various scales. Rather, the issue pertains to vocal imitation.

To address these questions, recent work has focused on several areas and primate behaviors. One has been to show that primate calls, though not learned, have a richer internal structure than one may have suspected, with some scholars seeing the seeds of compositional semantics in them (Arnold and Zuberbühler, 2008 et seq.; work which incidentally led to a reexamination of combinatorial meaning in birds' vocal output; Engesser et al., 2016).

Another line of research has focused on the ways in which primates get around the poor control of their vocal apparatus. Consider, for example, the way in which orangutans achieve the desired modification of their calls by manipulating leaves (Hardus et al., 2009; Lameira et al., 2012): by positioning a hand or holding leaves in front of their lips, orangutans lower the maximum frequency but maintain other parameters of the call similar. This is a bit like playing music with a wind instrument. More interestingly still, when orangutans modify their calls in this way, they sound as if their body size is bigger than it actually is, which has obvious functional consequences. Since size exaggeration has also been claimed to be at the heart of the evolution of a descended larynx (Fitch, 2000; Fitch and Reby, 2001), it is tempting to see these modified calls by orangutans as a solution forced upon them by the lack of laryngeal control.

Yet another line of research has identified sophisticated vocal behaviors in primates such as the elaborate songs in gibbons (Koda et al., 2012 and references therein). These have been shown to engage in duets and perform sophisticated movements of the vocal apparatus (very reminiscent of human soprano singers) to propagate their long-distance vocalizations.

These cases aside, studies on primate communication have focused on the fact that primates may be poor vocal learners but far better gesture users. There is a rich literature showing the complexity of primate gestures (see, eg, Roberts et al., 2014), with very clear evidence of intentionality in them (Genty and Zuberbühler, 2014, 2015). This has often been used as evidence for the primacy of a gestural protolanguage (see, eg, Arbib, 2002) and claims that human languages are not always a matter of sounds, but signs (sign languages). In fact, the very term "protolanguage" was first used by Hewes (1973) with a gestural protolanguage in mind. But it seems to me that the question is not so much whether sounds or signs were first, but how sounds and signs were paired to achieve a multimodal signal like human language. This is so because (1) if we set aside sign language for a moment, it is clear that sounds and signs are paired very early in ontogeny in humans (Esteve-Gibert and Prieto, 2014) and are always coupled in adults (speakers gesturing and deaf signers vocalizing) and (2) the motor theory of vocal learning put forth by Jarvis et al. for birds, which I discussed in the previous section, suggests that gestures may well have provided a first evolutionary step, but the crucial leaning step came afterward [inspired by the work on vocal-learning birds, Fitch (2011) suggests that the direct corticolaryngeal connection key to vocal learning exapted from the corticospinal pathway for nonvocal motor production]. One has to bear in mind that speech does not go away as a linguistic medium, except in extreme situations.

It is for these reasons that I find particularly illuminating studies that identify multimodal signals in nonhuman primates. I am certainly not the first to call for a multimodal study of nonhuman primate communication (see Waller et al., 2013; Zuberbühler, 2015), but it is quite likely that many previous studies missed valuable information by focusing on one or the other modality. Recent work (Liebal et al., 2004; Micheletta et al., 2013; Genty et al., 2015; Taglialatela et al., 2015) has tried to correct this bias and has suggested that the activation of the homologous Broca area in chimpanzees in both attention calls and gestures points to a multimodal origin of language (Taglialatela et al., 2011).

As a matter of fact, multimodal communication appears deeply rooted in evolutionary history. Bass and Chagnaud (2012) identified shared developmental and evolutionary origins of neural basis of vocal-acoustic and pectoral-gestural signaling present in vocalizing fishes. In a similar vein, Lawton et al. (2014) has revealed a conserved role of *Drosophila melanogaster* FoxP

(FOXP2's homolog) in motor coordination and courtship song. Male flies with reduced FoxP expression exhibit decreased levels of courtship behavior, altered pulse-song structure, and sex-specific motor impairments in walking and flight. Multimodal communication has also been found in birds (Pika and Bugnyar, 2011; Bostwick and Prum, 2005; Hoepfner and Goller, 2013; Williams, 2001; Soma and Mori, 2015), where wing movement, beak movement, and even feet movement accompany song in a synchronized fashion.

All in all, it seems to me that the study of multimodal communication holds great promise for the study of human language evolving, breaking free of the somewhat sterile debate between musical and gestural protolanguage (incidentally, song and dance might be just another instance of multimodal communication whose evolutionary history may be worth elucidating).

Among the instances of multimodal communication in primates, there is one that I wish to highlight: lip smacking. Lip smacking is an affiliative facial expression observed in many primates, and it has been the focus of intense and very productive research recently (Ghazanfar et al., 2012). The reason researchers were drawn to it is because although it is not "vocal" (with at least one exception to which I return later), it constitutes a case of "silent" vocalization and provides one of the best precursors for aspects of human speech. Lip smacking is made up of regular cycles of vertical jaw movement and is clearly directed toward a conspecific. During the lip-smacking act, the lips, tongue, and hyoid have been shown to move at 4—5 Hz (Ghazanfar et al., 2012), which is exactly within the range of the universal rhythm of speech and distinct from the rhythm of chewing movements in both monkeys and humans. In addition, (aspects of) speech and lip smacking appear to be dependent on homologous cortical circuits (unlike innate calls, they are cortically controlled) (Ghazanfar et al., 2010) and display a remarkably similar developmental trajectory (Ghazanfar et al., 2013; Ghazanfar and Takahashi, 2014). All these parallelisms suggest that aspects of human speech, most specifically the syllabic envelope, evolved from the rhythmic facial expressions of a common ancestor to both humans and macaques (Ghazanfar and Poeppel, 2014a; MacNeilage, 2010). In my view, the lip-smacking studies by Ghazanfar and colleagues offer us the strongest parallelism with human speech in the nonhuman primate domain, only surpassed by work on vocal-learning birds.

Remarkably, gelada baboons have been shown to pair lip smacks and vocalizations, in a way even more similar to human syllables (Bergman, 2013; Richman, 1976). This is not to say, of course that these "syllables" uttered by geladas are identical to syllables produced by humans (on these differences, see Martins and Boeckx, 2014), but it reinforces the idea that some aspects of human vocal behavior can be found in nonhuman primates, exactly as the Darwinian logic of descent leads us to expect.

Pursuing this hypothesis, Lameira et al. (2015) have looked at other possible precursors of aspects of human speech in great apes, beyond lip smacks, and have documented orangutan calls at a speechlike rhythm, coined "clicks" and "faux speech." They suggest that "like voiceless consonants, clicks required no vocal fold action, but did involve independent manoeuvring over lips and tongue." And "in parallel to vowels, faux speech showed harmonic and formant modulations, implying vocal fold and supralaryngeal action." They conclude that great apes may be less respiratorily, articulatorily, or neurologically constrained for the production of consonant- and vowel-like calls at speech rhythm than previously thought. Certainly, as Lameira et al. (2014) point out, there seems to be growing evidence for evolutionary continuity within the great apes as far the control of the supralaryngeal vocal tract. Thus, they argue, control of the vocal folds (that key aspect of vocal learning we understand well from vocal-learning birds) evolved as a subsequent step (see Levinson, 2016 for a similar historical reconstruction based on a comparative study of turn taking).

In a related line of research, Pisanski et al. (2016) offer an impressive review arguing that "the ability of humans to flexibly control the size-related source—filter dimensions of our vocal signals (i.e., vocal control) is likely to predate our ability to articulate the verbal dimensions of speech and therefore may provide an evolutionary pathway from nonhuman primate vocal communication to human speech." Pisanski et al. present a range of evidence, most of it from the past 5 years or so, that nonhuman primates may share our capacity to modulate F0 and formants to perhaps a greater extent than previously thought. As an example, they mention cases of chimpanzees producing "novel and apparently flexible attention-seeking grunts toward humans." They point out that although it does not occur in the wild, this type of vocal behavior demonstrates "a latent capacity to control vocal fold adduction and airflow that is required to produce sustained laryngeal vibration." Thus, among nonhuman primates, manipulation of the larynx and vocal tract may be more flexible than once thought. I personally anticipate more evidence in favor of this position in the near future, especially from bonobos, where evidence for functional flexibility is accumulating rapidly (Clay et al., 2015). Pisanski et al. conclude their review by pointing out that "vocal flexibility in nonhuman primates suggests that other species have

greater neuroanatomical elaboration of the direct lateral motor cortical route than previously thought or, alternatively, may be achieving flexibility with older neural structures." This I take to be a crucial issue in the domain of the evolution of the neurobiology of language that hopefully will be the focus of intense research in the years to come.

To conclude this brief survey of our primate ancestry when it comes to vocal behavior, I would like to highlight current work on marmoset and the evolution of turn taking. Levinson (2016) has made a strong case for it being a crucial trait of human verbal communication, one that can be found among our closest living relatives, the bonobos and chimpanzees (Fröhlich et al., 2016). As a highly vocal primate, marmosets offer a rich source of data concerning turn taking. In fact, Takahashi et al. (2013) argue that the turn-taking behavior of marmosets is so similar to what is found in our behavior that this is yet another piece of evidence that our primate ancestry may have been rich enough to provide a foundation from which human cooperative vocal (and not only gestural) communication could have evolved.

Takahashi et al. (2016) investigated the ontogeny of this behavior in marmosets and were able to show how engaging in vocal turn taking with parents at a very early age shapes vocal acoustics in infant marmoset monkeys. Reviewing a related study by Zhang and Ghazanfar (2016), Tchernichovski and Oller (2016) offer a very interesting scenario for the evolution of vocal communication. They suggest that, at first, slow fluctuations in respiratory rate are mirrored in the rate of vocalization. As the channel evolves, according to them, "additional physiological variables start affecting acoustic features until, eventually, fine forebrain control drives differentiation of syllable type, producing vocal sequences, which may carry rich information about behavioral state."

I find this hypothesis interesting, not because it suggests that the cortex may have taken control over emotional vocalizations, but because it means that emotional vocalizations controlled by the limbic system in nonvocal learners, including mice, could provide a rich source of aspects of human linguistic behavior (see Theofanopoulou, 2016 for interesting suggestions in this direction).

As should be obvious, the neurobiology of nonhuman primates (with the possible exception of lip smacking) is nowhere nearly as precisely understood as the neural (and molecular) underpinning of vocal learning in birds, but, as I hope to have shown, recent work has taken the crucial step of showing that nonhuman primates can provide a rich evolutionary substrate for human language, which is an important departure from what was received wisdom only a few years ago.

38.4 Tinkering With Our Inheritance

Up until now I have been keen to stress descent, because it has been minimized for too long, and it offers genuine results and promises for the field as a whole. But the Darwinian logic of descent comes jointly with that of "modification," and this is the issue I want to address in this section. What got modified in our recent history that matters for the evolution of our linguistic capacity? Even granting, as I think we must, the real possibility that our ancestors became vocal learners long ago, were there further modification steps that took place more recently in our lineage that may be cognitively relevant?

Recall from the discussion in Section 38.2 that the vocal learning literature, especially that focused on birds, has identified at least two ways in which vocal-learning capacities can be enhanced. One is via domestication, the other via the elaboration of shell structures on top of the core vocal-learning circuit, which seems to go hand in hand with brain growth.

I believe that both processes were critically involved in the emergence of our species. In particular, the fossil record, enriched by discoveries made possible by the successful retrieval of ancient DNA (Pääbo, 2014), suggests that the brain growth trajectory in our species departed significantly from that our extinct ancestors, early in life. There is every reason to believe that although infants do not produce grammatically complex expressions at that time, the first months after birth constitute a critical period for subsequent language (and indeed, cognitive) development. Although much work that adopted the concept of critical period for language development in the wake of Lenneberg (1967) usually refers to a period from birth to puberty, a closer examination reveals that there are, in fact, several critical periods for different aspects of language development, and many of these periods are much shorter than anticipated. As reviewed by Friedmann and Rusou (2015), the acquisition of some of the most distinctive properties of language such as complex syntax has a critical period that ends during the first year of life, and children who missed this window of opportunity later show severe syntactic impairments. Early postnatal life is also a critical window during which many neurodevelopmental disorders, such as autism, develop (though some of them, such as schizophrenia, may only manifest themselves later in life). As LeBlanc and Fagiolini (2011) write in their review article on whether autism should be seen as a "critical period disorder," brain circuits that are key to language and higher-order cognition are refined by experience during critical periods early in postnatal life, and even slight dysregulations can have large-scale effects.

It is for this reason that I find it extremely interesting that a series of work (Neubauer et al., 2010; Gunz et al., 2010, 2012; Scott et al., 2014; Hublin et al., 2015) has shown on the basis of data from living primates as well as computer-assisted reconstructions of brain developments from Neanderthal skulls that anatomically modern humans, with their globularized braincases, follow an early postnatal brain growth trajectory that sets us apart from our closest extinct and extant relatives. Although Neanderthal brains were significantly bigger than what we can observe from our closest living primate relatives, their brain growth trajectory was essentially a "blown-up" version of a chimpanzee brain development. Ours, by contrast, follows a different course that is reflected in our basketball-like head shape. Interestingly, it is during this very same period (first months postnatally) that the growth pattern of our faces also departs from that of our closest extinct and extant relatives (Lacruz et al., 2015).

I have argued in a series of articles (Boeckx, 2013, 2017a; Boeckx and Benítez-Burraco, 2014a) that this globularization phase must have been significant for understanding the evolution of our cognitive capacities, including language. If the brain grows differently, it wires differently, because growth and wiring are two sides of the same coin. These two units coevolve. And if we believe that different connectivity patterns give rise to distinct circuits with functional consequences, then globularizing a brain at such a critical period must have been cognitively significant.

I recognize that we cannot yet be sure about the precise consequences of globularization, because we do not yet understand fully how different brains can produce different cognitive modes. But the long list of disorders displaying both craniofacial and cognitive/linguistic deficits (Boeckx and Benítez-Burraco, 2014a) can help in this regard. Furthermore, Gunz et al., as well as Bruner (2010) et seq., have provided us with important information: the globularization of the human brain reconfigures the seat of cognition in several ways. It has been claimed to affect most clearly the parietal lobe, the cerebellum, and the frontal pole; plausibly as well, it affects the temporal lobe and the olfactory bulbs. This much can be inferred from fossilized crania. But our knowledge of brain development leads us to suspect that more deeply embedded structures that do not leave obvious marks on bones must have also been affected, be it in terms of volume or wiring diagrams (or both): the thalamus, the hippocampus, and other subcortical structures that strongly interact with regions of the brain most visibly affected by globularization. Many of these regions have not traditionally been associated with neural circuits thought to be responsible for language but in the next section, I will list a series of reasons to doubt the classical neurolinguistic models.

Work on archaic genomes has provided us with lists of genes that were modified in the course of evolution of our species since the separation from the Neanderthal lineage. Several of these changes appear to be related to brain development and function (as well as to craniofacial bone development; see Boeckx and Benítez-Burraco, 2015). In work in progress I am exploring the possibility that quite of few of these changes were in fact connected and caused the globularization of the brain (case) by affecting neural processes that delayed neurogenesis and influence brain growth (affecting most clearly the subventricular zone), generating a brain that matured more slowly (essentially a remarkably neotenous brain), and as a result a brain that was more dependent on the environment. Such a brain had to be a better "language-learning" brain. Accordingly, structures traditionally responsible with learning and memory, both cortical and subcortical, came to play an even more salient role in our species.

Apart from allowing us to detect a different brain growth trajectory, the fossil record also leads us to suspect that our species underwent an intensification of what amounts to a self-domestication process (as Benitez-Burraco et al., 2016 discuss, globularization and self-domestication may in fact be linked). As reviewed in Thomas (2014), several scholars have long entertained the idea that anatomically modern humans were self-domesticated. Behavioral similarities (as well as neurobiological similarities, see Rilling et al., 2012) between us and bonobos, who have also claimed to be self-domesticated (Hare et al., 2012), reinforce this idea (MacLean, 2016). The idea of self-domestication will be obvious to anyone who recognizes the heavy dependence of ours species on its sociocultural environment. This is the cooperative spirit that seems to make us so special among our closest relatives (Tomasello, 2009).

But behavior is not the only source of evidence, which is a good thing given the notorious difficulty of reconstructing behavior from the fossil record. As stressed in Theofanopoulou and Boeckx (2016a), several anatomical characteristics (as well as emerging molecular data) of our species are reminiscent of what one finds in the context of domestication, especially when contrasted with what we know about Neanderthals (taken as a representative example of archaic *Homo*). As reviewed under the rubric of the "domestication syndrome" by Wilkins et al. (2014), domesticated species display a range of characteristics that set them apart from their wild counterparts: the suite of characteristics that signals domestication includes depigmentation, floppy, reduced ears, shorter muzzles, curly tails, smaller teeth, smaller brain/cranial capacity, neotenous (juvenile) behavior, docility, and reproductive cycle changes (more frequent estrous cycles). Of course, not all of these characteristics are found in all domesticates, but most of

them are indeed present in all domesticates. Theofanopoulou and Boeckx (2016a) note that many of these changes match fairly well some of the well-known anatomical differences between anatomically modern humans and Neanderthals. I will review some of their observations here: first, the distinct ontogenetic trajectories discussed earlier under the rubric of globularization (Hublin et al., 2015; Lacruz et al., 2015) result in craniofacial differences that invariably lead to a more "gracile," "juvenile" profile in anatomically modern humans. This profile is sometimes considered "feminized" (Cieri et al., 2014) and is associated with an overall reduction of sexual dimorphism, which also appears to be a trait associated with domestication (Hare et al., 2012). Incidentally, Theofanopoulou and Boeckx point out this process of "feminization" (reduction of androgen levels, rise of estrogen levels; see Cieri et al., 2014 for references) is often associated with a reduced reactivity of the hypothalamus—pituitary—adrenal axis (Trut et al., 2009), a physiological trait also associated with domestication (Kunzl and Sachser, 1999).

Returning to craniofacial considerations, it is well established that prognathism is significantly reduced in our species (Maureille and Bar, 1999; Lacruz et al., 2015). Browridges and nasal projections are smaller in us than in our most closely related (extinct) relatives (Cieri et al., 2014), as is our cranial capacity (Mellars et al., 2007), and our tooth size (Zilberman and Smith, 1992). Differences in other traits associated with domestication may also exist, but there are either confounding factors (eg, geography for pigmentation) involved or the data are subject to more controversial interpretation (eg, Knight et al., 1995 in the case of reproductive cycle changes) than the anatomical record we just reviewed briefly. What is clear is that on balance we appear to bear more anatomical characteristics associated with domestication than Neanderthals.

Surprisingly, proponents of the self-domestication hypothesis have not always been explicit about what species they were comparing anatomically modern humans to in order to make their case. Comparison with more distantly related species, such as chimpanzees (taken as proxy for the last common ancestors they shared with us), strikes me as inherently less compelling, as there are just too many anatomical differences (and thus, confounding factors) involved. In addition, the domestication process is supposed to be rapid and, as such, fits better with a Neanderthal/anatomically modern human comparison. It is also unlikely that the self-domestication process took place after the emergence of anatomically modern humans (contra Cieri et al., 2014), because some of the traits associated with a domestication process are already present in the earliest specimens of our species, although of course it is very likely the case that this self-domestication process intensified after our species emerged.

What is most important for present purposes is that much like changes at the level of brain growth, domestication and concomitant-relaxed selection have been claimed to lead to an enhancement of complexity in vocal learning (Okanoya, 2012; Deacon, 2010), so that if the anatomical record (as well as the emerging molecular evidence, which I have not reviewed here) is anything to go by, it is quite plausible that early anatomically modern humans were biologically committed to a greater dependence on culture and learning, which naturally led to a more complex grammatical mind (and maybe a greater dependence on activity-dependent genes, which appear to be important in all vocal learners).

38.5 Updating the Neurobiological Model for Human Language

Apart from the fact that many scholars have insisted too much on the species uniqueness of our language capacity, the lack of a comprehensive neurobiological model for said capacity has certainly played a major role in keeping the evolution of human language shrouded in mystery. In the absence of an adequate neurobiological target for evolutionary studies, the temptation to bypass the brain and spin evolutionary tales is just too great.

For over a century, researchers stuck to the classical model derived from the work of Broca and Wernicke. This is not, of course, to say that the classical frontotemporal cortical circuit makes no contribution to high-level linguistic processing. But it is equally clear that language processing recruits a far more widely distributed network (Fedorenko and Thompson-Schill, 2014; Blank et al., 2016; Friederici and Singer, 2015; Hagoort and Indefrey, 2014; Poeppel et al., 2012), drawing on multiple brain rhythms to provide a rich enough oscillatory regime for such a complex task (Theofanopoulou and Boeckx, 2016c; Lam et al., 2016). At the same time, an increasing number of papers on subcortical structures such as the hippocampus or the cerebellum start with statements such as "a growing body of work suggests [x; a subcortical structure] contributes to a variety of cognitive domains beyond its traditional role in [y; a very basic function not part of any core description of language]" (see Jarvis, 2004 on the forebrain broadly, Marien and Manto, 2016 for the cerebellum; Theofanopoulou and Boeckx, 2016b for the thalamus; Kurczek et al., 2013 for the hippocampus).

In the remainder of this section, I would like to highlight a few research paths and trends that strike me as worth pursuing, since they provide a window of

opportunity to tackle, productively, very difficult questions about the evolution of human language.

Most of these highlights bear on semantic cognition, rather than vocal learning in the narrow sense (although I repeat that I do not think one should draw a sharp distinction between the two), because I think that this is the domain that we understand the least, precisely because comparative studies are so hard [in the domain of vocal learning, Jarvis (2004) offers a compelling candidate model]. Incidentally, what I call "semantic cognition" likely falls under the rubric of syntax for most researchers. This is because decades of work in theoretical linguistics have made clear that syntax cannot be dissociated from (structural) semantics.

The first trend I would like to discuss is the importance of the temporal lobe. In my experience, when people think of higher-order (linguistic) cognition, they immediately associate it with the frontal lobe and, more specifically, Broca area. No doubt, Broca area is an important node of the language network, but it is certainly not the more central one, at least when the construction of compositionally interpreted structures (ie, syntax/semantics) is concerned. True, as revealed by Schenker et al. (2010), Broca area has expanded sixfold compared to what we find in chimpanzees (Brodmann areas 44 and 45 that make up most of Broca region appear to be the most greatly expanded cortical areas yet identified in humans), but a growing number of experiments have revealed that the temporal lobe, traditionally associated with "memory" and "the lexicon," plays an equally, if not more, important role in cognition (on the possible role of Broca region, see Boeckx et al., 2014; Bornkessel-Schlesewsky et al., 2015; Fitch and Martins, 2014). For instance, work by Pylkkänen and colleagues has focused on the contribution of the left anterior temporal lobe to combinatorial processing. Together with the ventromedial prefrontal cortex, the angular gyrus, and the medial parietal cortex, the left anterior temporal lobe plays a central function in the compositional interpretation of hierarchically structured expressions (Pylkkänen, 2015; Westerlund et al., 2015).

A recent study by Davey et al. (2016) points to the role of another temporal region, the posterior middle temporal gyrus in semantic cognition. The latter appears to function as a hub within a large-scale network that allows the integration of automatic retrieval in the default mode network with demanding, goal-oriented cognition. In terms of connectivity, this temporal region appears to be uniquely placed to link two macrocircuits, the default mode network, thought to be the seat of "self-generated thoughts," and a frontoparietal "multiple-demand"/"executive control"/"dorsal attention circuit." As reviewed in Buckner and Krienen (2013), cortical association regions spanning the frontal and parietal cortices are disproportionately expanded

in humans compared with other primates. They mature late in development and are often disrupted in mental disorders (Sato et al., 2016). They appear to impose order on the self-generated thoughts by the default mode network.

A more deeply embedded temporal structure, the hippocampus is a core member of the default mode network. Recently, and largely thanks to the work of Duff and colleagues, its potential role in linguistic cognition has been reappreciated (see Alamri, 2016 for a more extensive review and discussion). Kurczek et al. (2015) have highlighted the significance of the hippocampus in the neural network that supports a range of abilities including remembering the past, thinking about the future, and introspecting about oneself and others, abilities that are often said to be human specific and shown to break down in a range of mental disorders where language is also affected (eg, schizophrenia, see Wible, 2012). Studies involving individuals with hippocampal amnesia, such as Duff et al. (2013), show that quintessentially human behaviors, such as the creative use of language as evidenced in verbal play, is severely damaged, which serves to highlight the interdependence of language and memory. Like evolution, language appears to make new use of old parts, so memorized units are as important as novel combinations, and in recent years scholars have been calling for a renewed appreciation of memory as an integral component of online information processing (see Hasson et al., 2015). Traditional divisions like declarative versus procedural memory systems may have to make way to a more integrated system that recognizes a strong hippocampal—striatal axis (prototypical declarative vs. procedural memory hubs) in learning, prediction, and goal-directed behavior (Pennartz et al., 2011). In this context, it is worth mentioning that mice endowed with the humanized version of Foxp2 have been claimed to accelerate learning by enhancing transitions from declarative to procedural performance (Schreiweis et al., 2014).

As Rubin et al. (2014) write, the frontal lobes have figured prominently in most studies of flexible or goal-directed behavior, but the hippocampus appears to play an equally important role by "forming and reconstructing relational memory representations that underlie flexible cognition and social behavior." Recently, Ellamil et al. (2016) showed how the hippocampus is recruited in the spontaneous generation of thoughts. As they point out, "[i]n contrast to the connectivity of other cortical areas, where short-distance synapses to nearby neurons predominate and long-distance connections are rare, neurons within a large part of the hippocampus are equally likely to connect to nearby or distant neighbors (Buzsaki, 2006). This highly variable microcircuitry may facilitate the creation of arbitrary or unlikely

connections between groups of neurons that otherwise encode distinct memories or experiences (Buzsaki, 2006)." This description fits quite well with the core creativity function often attributed to language (see, eg, Boeckx, 2014). Such a generation of thought would have to be regulated by circuits responsible for dorsal attention, but it may be that the source of novel combinations may not lie in the neocortex. If true, this would be excellent news for evolutionary linguistics, for the hippocampus is one of the most closely scrutinized brain structures in neuroscience. Perhaps, some of our higher-order cognitive functions were indeed exapted from basic circuits associated with memory and spatial cognition. At the very least, this possibility reinforces the need to adopt a much broader conception of the neural circuits responsible for linguistic cognition.

As a final note on the possible hippocampal involvement in language, I would like to comment in the fact that it is usually the temporal cortex that is taken to provide the basis for linguistic memory ("the lexicon"), not the hippocampus. But the two structures clearly interact and may play complementary roles. When Teyler and DiScenna (1986) put forth their "hippocampal memory indexing theory," they suggested that the role of hippocampus may be "to form and retain an index of neocortical areas activated by experiential events," serving to "establish a cortically based memory trace." This role of the hippocampus as a "pointer" to more elaborate conceptual structures fits well with descriptions of word meaning (Pietroski, 2007) and could explain how hippocampal lesions need not completely abolish linguistic output, as the matured cortex could supplement it.

This raises an important issue, I think. Many brain structures have often been discarded as peripheral for language because of lesion studies showing how linguistic cognition can be preserved after seriously damaging them. But this sort of conclusion is often arrived at by studying the language system in adults, as opposed to asking how the system developed in the individual. It may well be that some structures were once critical, but their roles can be transient (and harder to detect, like the Wittgensteinian ladder that got used to climb and was then kicked off). Too often, the frontotemporal cortical circuit is studied once it is fully in place, but this may just reflect a specialization (modularization or routinization) lying at the confluence of broader, more distributed corticosubcortical circuits engaged in more generic functions. Instead of viewing the "core language circuit" in isolation, ontogenetic as well as phylogenetic considerations force us to view it as part and parcel of a broader cognitive basis. (I think this is consistent with the high degree of functional specificity for high-level linguistic processing in the adult human brain described in Fedorenko et al. (2011).)

As a final topic for this section, I would like to touch on the role of the parietal lobe in the context of language. I do so because this is the most conspicuous brain structural change that can be associated with the emergence of anatomically modern humans from the fossil record (Bruner, 2010). As I point out in Boeckx (2017b), there is evidence of significant "parietalization" of certain neural circuits highly relevant for language. For instance, Kumar et al. (2016) suggest that the enhanced laryngeal motor cortex—parietal connections in humans could provide the right neural substrate for more complex synchrony of higher-order sensorimotor coordination, proprioceptive and tactile feedback, and modulation of learned voice for speech production.

I also argued that the expansion of the parietal region played a role on the "semantic" side. Bruner (2010) reviews studies that point to the hub status of the parietal lobe for functions associated with the default mode network, which I already alluded to in the context of the hippocampus. Moreover, there is a range of studies that have documented a human-specific modification of how Broca region and Wernicke region are connected with one another through white matter pathways. In addition to a direct connection that is shared with nonhuman primates, there is also an indirect pathway, through the parietal lobe in humans (Catani and Jones, 2005; Dick and Tremblay, 2012; Hecht et al., 2013; Mendoza and Merchant, 2014; Catani and Bambini, 2014). Although this remains to be confirmed, it is plausible to envisage that this indirect connection may provide the basis for richer representational capacities. For instance, it could be that the formation of a frontoparietotemporal loop allows for the formation of recursive representations, since both frontoparietal and frontotemporal networks are routinely associated with processing sequences, and recursive representations are, at some level of description, sequences of sequences. Several authors have independently stressed the relevance (both ontogenetically and phylogenetically) of an indirect, frontoparietotemporal pathway (Friederici, 2012; de Diego-Balaguer et al., 2016) for language tasks, and so evolutionary studies stand to benefit from future investigations of the role of what is sometimes called Geschwind territory, next to the more familiar Broca and Wernicke regions.

38.6 Conclusion

To summarize the main message of this chapter, like vocal learning in birds, human language is a highly complex, polygenic trait that recruits numerous brain regions, over and above the classical language regions, to provide a computational regime supporting linguistic cognition. Strong adherence to the Darwinian logic of

descent, with its emphasis on a rich cognitive life for nonhuman species, offers the hope to shed light on what looks like a very human-specific, domain-specific capacity like language. Such an approach requires studies that embrace the multifactorial (not only genes, not only environment), multidimensional (genome, connectome, "dynome," "cognome") nature of the capacity to master grammatical systems of the kinds we do.

There is no doubt in my mind that a richer data set thanks to the genomic revolution, and a broader comparative basis adopting a bottom-up approach to study primate cognition guarantees that in the very near future a much more elaborate, and more precise picture of language evolution will be available than the one I have offered here. But even the present one strikes me as a far cry from claims not so long ago that we would never find out.

Acknowledgments

References

Alamri, S., 2016. The Role of the Hippocampus in Language Processing. PhD. Universitat de Barcelona (in progress).

Anderson, S., 2004. Doctor Dolittle's Delusion. Yale University Press, New Haven.

Arbib, M., 2002. How the Brain Got Language. Oxford University Press, Oxford.

Arnold, K., Zuberbühler, K., 2008. Meaningful call combinations in a non-human primate. Curr. Biol. 18 (5), R202–R203.

Arriaga, G., Jarvis, E.D., 2013. Mouse vocal communication system: are ultrasounds learned or innate? Brain Lang. 124 (1), 96–116.

Barton, R.A., 2012. Embodied cognitive evolution and the cerebellum. Philos. Trans. R. Soc. B 367 (1599), 2097–2107.

Bass, A.H., Chagnaud, B.P., 2012. Shared developmental and evolutionary origins for neural basis of vocal–acoustic and pectoral–gestural signaling. Proc. Natl. Acad. Sci. U.S.A. 109 (Suppl. 1), 10677–10684.

Benitez-Burraco, A., Theofanopoulou, C., Boeckx, C., 2016. Globularization and domestication. Topoi 1–14.

Bergman, T.J., 2013. Speech-like vocalized lip-smacking in geladas. Curr. Biol. 23 (7), R268–R269.

Blank, I., Balewski, Z., Mahowald, K., Fedorenko, E., 2016. Syntactic processing is distributed across the language system. Neuroimage 127, 307–323.

Boeckx, C., Benítez-Burraco, A., 2014. The shape of the human language-ready brain. Front. Psychol. 5, 282. https://doi.org/10.3389/fpsyg.2014.00282.

Boeckx, C., Benítez-Burraco, A., 2014. Globularity and language-readiness: generating new predictions by expanding the set of genes of interest. Front. Psychol. 5, 1324.

Boeckx, C., Benítez-Burraco, A., 2015. Osteogenesis and neurogenesis: a robust link also for language evolution. Front. Cell. Neurosci. 9, 291. https://doi.org/10.3389/fncel.2015.00291.

Boeckx, C., Martinez-Alvarez, A., Leivada, E., 2014. The functional neuroanatomy of serial order in language. J. Neurolinguist. 32, 1–15.

Boeckx, C., 2013. Biolinguistics: forays into human cognitive biology. J. Anthropol. Sci. 91, 63–89.

Boeckx, C., 2014. Elementary Syntactic Structures. Cambridge University Press.

Boeckx, C., 2017a. The language-ready head: evolutionary considerations. Psychon. Bull. Rev. 24 (1), 194–199. https://doi.org/10.3758/s13423-016-1087-5.

Boeckx, C., 2017b. A conjecture about the neural basis of recursion in light of descent with modification. J. Neurolinguist. 43, 193–198.

Bolhuis, J.J., Everaert, M., 2013. Birdsong, Speech, and Language: Exploring the Evolution of Mind and Brain. MIT Press.

Bornkessel-Schlesewsky, I., Schlesewsky, M., Small, S.L., Rauschecker, J.P., 2015. Neurobiological roots of language in primate audition: common computational properties. Trends Cogn. Sci. 19 (3), 142–150.

Bostwick, K.S., Prum, R.O., 2005. Courting bird sings with stridulating wing feathers. Science 309 (5735), 736.

Bruner, E., 2010. Morphological differences in the parietal lobes within the human genus. Curr. Anthropol. 51, S77–S88. https://doi.org/10.1086/650729.

Buckner, R.L., Krienen, F.M., 2013. The evolution of distributed association networks in the human brain. Trends Cogn. Sci. 17 (12), 648–665.

Buzsaki, G., 2006. Rhythms of the Brain. Oxford University Press, Oxford.

Catani, M., Bambini, V., 2014. A model for social communication and language evolution and development (SCALED). Curr. Opin. Neurobiol. 28, 165–171.

Catani, M., Jones, D.K., 2005. Perisylvian language networks of the human brain. Ann. Neurol. 57 (1), 8–16.

Chakraborty, M., Jarvis, E.D., 2015. Brain evolution by brain pathway duplication. Philos. Trans. R. Soc. B 370 (1684), 20150056.

Chakraborty, M., Walløe, S., Nedergaard, S., Fridel, E.E., Dabelsteen, T., Pakkenberg, B., Jarvis, E.D., 2015. Core and shell song systems unique to the parrot brain. PLoS One 10 (6), e0118496.

Charrier, C., Joshi, K., Coutinho-Budd, J., Kim, J.E., Lambert, N., De Marchena, J., Polleux, F., 2012. Inhibition of SRGAP2 function by its human-specific paralogs induces neoteny during spine maturation. Cell 149 (4), 923–935.

Cheney, D.L., Seyfarth, R.M., 1992. How Monkeys See the World: Inside the Mind of Another Species. University of Chicago Press.

Cheney, D.L., Seyfarth, R.M., 2008. Baboon Metaphysics: The Evolution of a Social Mind. University of Chicago Press.

Cieri, R.L., Churchill, S.E., Franciscus, R.G., Tan, J., Hare, B., 2014. Craniofacial feminization, social tolerance, and the origins of behavioral modernity. Curr. Anthropol. 55 (4), 419–443.

Clay, Z., Archbold, J., Zuberbühler, K., 2015. Functional flexibility in wild bonobo vocal behaviour. PeerJ 3, e1124.

Davey, J., Thompson, H.E., Hallam, G., Karapanagiotidis, T., Murphy, C., De Caso, I., Jefferies, E., 2016. Exploring the role of

the posterior middle temporal gyrus in semantic cognition: integration of anterior temporal lobe with executive processes. Neuroimage 137.

de Diego-Balaguer, R., Martinez-Alvarez, A., Pons, F., 2016. Temporal attention as a scaffold for language development. Front. Psychol. 7, 44.

De Waal, F.B., Ferrari, P.F., 2010. Towards a bottom-up perspective on animal and human cognition. Trends Cogn. Sci. 14 (5), 201–207.

Deacon, T.W., 1989. The neural circuitry underlying primate calls and human language. Hum. Evol. 4 (5), 367–401.

Deacon, T., 1997. The Symbolic Species. Norton, New York.

Deacon, T.W., 2006. Emergence: the hole at the Wheel's Hub1. In: The Re-emergence of Emergence: The Emergentist Hypothesis from Science to Religion: The Emergentist Hypothesis from Science to Religionvol, vol. 159, p. 111.

Deacon, T.W., 2010. A role for relaxed selection in the evolution of the language capacity. Proc. Natl. Acad. Sci. U.S.A. 107 (Suppl. 2), 9000–9006.

Dediu, D., Levinson, S.C., 2013. On the antiquity of language: the reinterpretation of Neandertal linguistic capacities and its consequences. Front. Psychol. 4, 397.

Dennis, M.Y., Nuttle, X., Sudmant, P.H., Antonacci, F., Graves, T.A., Nefedov, M., Curry, C.J., 2012. Evolution of human-specific neural SRGAP2 genes by incomplete segmental duplication. Cell 149 (4), 912–922.

Dick, A.S., Tremblay, P., 2012. Beyond the arcuate fasciculus: consensus and controversy in the connectional anatomy of language. Brain 135 aws222.

Duff, M.C., Kurczek, J., Rubin, R., Cohen, N.J., Tranel, D., 2013. Hippocampal amnesia disrupts creative thinking. Hippocampus 23 (12), 1143–1149.

Ellamil, M., Fox, K.C., Dixon, M.L., Pritchard, S., Todd, R.M., Thompson, E., Christoff, K., 2016. Dynamics of neural recruitment surrounding the spontaneous arising of thoughts in experienced mindfulness practitioners. Neuroimage 136.

Emery, N.J., Clayton, N.S., 2004. The mentality of crows: convergent evolution of intelligence in corvids and apes. Science 306 (5703), 1903–1907.

Engesser, S., Ridley, A.R., Townsend, S.W., 2016. Meaningful call combinations and compositional processing in the southern pied babbler. Proc. Natl. Acad. Sci. U.S.A. 113, 201600970.

Esteve-Gibert, N., Prieto, P., 2014. Infants temporally coordinate gesture-speech combinations before they produce their first words. Speech Commun. 57, 301–316.

Fedorenko, E., Thompson-Schill, S.L., 2014. Reworking the language network. Trends Cogn. Sci. 18 (3), 120–126.

Fedorenko, E., Behr, M.K., Kanwisher, N., 2011. Functional specificity for high-level linguistic processing in the human brain. Proc. Natl. Acad. Sci. U.S.A. 108 (39), 16428–16433.

Feenders, G., Liedvogel, M., Rivas, M., Zapka, M., Horita, H., Hara, E., et al., 2008. Molecular mapping of movement-associated areas in the avian brain: a motor theory for vocal learning origin. PLoS One 3 (3), e1768.

Feher, O., Wang, H., Saar, S., Mitra, P.P., Tchernichovski, O., 2009. De novo establishment of wild-type song culture in the zebra finch. Nature 459 (7246), 564–568.

Fisher, S.E., Vernes, S.C., 2015. Genetics and the language sciences. Annu. Rev. Linguist. 1, 289–310.

Fisher, S.E., 2015. Translating the genome in human neuroscience. In: Marcus, G., Freeman, J. (Eds.), The Future of the Brain: Essays by the World's Leading Neuroscientists. Princeton University Press, Princeton, NJ, pp. 149–159.

Fisher, S.E., 2016. A molecular genetic perspective on speech and language. In: Hickok, G., Small, S. (Eds.), Neurobiology of Language. Elsevier, Amsterdam, pp. 13–24.

Fitch, W., Martins, M.D., 2014. Hierarchical processing in music, language, and action: Lashley revisited. Ann. N.Y. Acad. Sci. 1316 (1), 87–104.

Fitch, W.T., Reby, D., 2001. The descended larynx is not uniquely human. Proc. R. Soc. Lond. B Biol. Sci. 268 (1477), 1669–1675.

Fitch, W.T., 2000. The evolution of speech: a comparative review. Trends Cogn. Sci. 4 (7), 258–267.

Fitch, W.T., 2010. The Evolution of Language. Cambridge University Press, Cambridge.

Fitch, W.T., 2011. The evolution of syntax: an exaptationist perspective. Front. Evol. Neurosci. 3 (9).

Friederici, A.D., Singer, W., 2015. Grounding language processing on basic neurophysiological principles. Trends Cogn. Sci. 19 (6), 329–338.

Friederici, A.D., 2012. Language development and the ontogeny of the dorsal pathway. Front. Evol. Neurosci. 4 (3).

Friedmann, N., Rusou, D., 2015. Critical period for first language: the crucial role of language input during the first year of life. Curr. Opin. Neurobiol. 35, 27–34.

Fröhlich, M., Kuchenbuch, P., Müller, G., Fruth, B., Furuichi, T., Wittig, R.M., Pika, S., 2016. Unpeeling the layers of language: bonobos and chimpanzees engage in cooperative turn-taking sequences. Sci. Rep. 6.

Fujita, K., 2016. On certain fallacies in evolutionary linguistics and how one can eliminate them. In: Fujita, K., Boeckx, C. (Eds.), Advances in Biolinguistics: The Human Language Faculty and its Biological Basis. Routledge.

Genty, E., Zuberbühler, K., 2014. Spatial reference in a bonobo gesture. Curr. Biol. 24 (14), 1601–1605.

Genty, E., Zuberbühler, K., 2015. Iconic gesturing in bonobos. Commun. Integr. Biol. 8 (1), e992742.

Genty, E., Neumann, C., Zuberbühler, K., 2015. Bonobos modify communication signals according to recipient familiarity. Sci. Rep. 5.

Ghazanfar, A.A., Poeppel, D., 2014. The neurophysiology and evolution of the speech rhythm. In: Gazzaniga, M.S., Mangun, R. (Eds.), The Cognitive Neurosciences V. MIT Press.

Ghazanfar, A.A., Takahashi, D.Y., 2014. The evolution of speech: vision, rhythm, cooperation. Trends Cognitive Sci 18 (10), 543–553.

Ghazanfar, A.A., Chandrasekaran, C., Morrill, R.J., 2010. Dynamic, rhythmic facial expressions and the superior temporal sulcus of macaque monkeys: implications for the evolution of audiovisual speech. Eur. J. Neurosci. 31 (10), 1807–1817.

Ghazanfar, A.A., Takahashi, D.Y., Mathur, N., Fitch, W.T., 2012. Cineradiography of monkey lip-smacking reveals putative precursors of speech dynamics. Curr. Biol. 22 (13), 1176–1182.

Ghazanfar, A.A., Morrill, R.J., Kayser, C., 2013. Monkeys are perceptually tuned to facial expressions that exhibit a theta-like speech rhythm. Proc. Natl. Acad. Sci. U.S.A. 110 (5), 1959–1963.

Graham, S.A., Fisher, S.E., 2015. Understanding language from a genomic perspective. Annu. Rev. Genet. 49, 131–160.

Gunz, P., Neubauer, S., Maureille, B., Hublin, J.-J., 2010. Brain development after birth differs between Neanderthals and modern humans. Curr. Biol. 20, R921–R922. https://doi.org/10.1016/j.cub.2010.10.018.

Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., Hublin, J.-J., 2012. A uniquely modern human pattern of endocranial development. Insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. J. Hum. Evol. 62, 300–313. https://doi.org/10.1016/j.jhevol.2011.11.013.

Haesler, S., Wada, K., Nshdejan, A., Morrisey, E.E., Lints, T., Jarvis, E.D., Scharff, C., 2004. FoxP2 expression in avian vocal learners and non-learners. J. Neurosci. 24 (13), 3164–3175.

Hagoort, P., Indefrey, P., 2014. The neurobiology of language beyond single words. Annu. Rev. Neurosci. 37, 347–362.

Hardus, M.E., Lameira, A.R., Singleton, I., Morrogh-Bernard, H.C., Knott, C.D., Ancrenaz, M., Wich, S.A., 2009. A description of the

orangutan's vocal and sound repertoire, with a focus on geographic variation. Orangutans: Geographic Variation in Behavioral Ecology and Conservation, pp. 49–64.

Hare, B., Wobber, V., Wrangham, R., 2012. The self-domestication hypothesis: evolution of bonobo psychology is due to selection against aggression. Anim. Behav. 83 (3), 573–585.

Hasson, U., Chen, J., Honey, C.J., 2015. Hierarchical process memory: memory as an integral component of information processing. Trends Cogn. Sci. 19 (6), 304–313.

Hauser, M.D., Chomsky, N., Tecumseh Fitch, W., November 22, 2002. The faculty of language: what is it, who has it, and how did it evolve? Science 298 (5598), 1569–1579. https://doi.org/10.1126/science.298.5598.1569.

Hauser, M.D., 2001. Wild Minds: What Animals Really Think. Macmillan.

Hecht, E.E., Murphy, L.E., Gutman, D.A., Votaw, J.R., Schuster, D.M., Preuss, T.M., Orban, G.A., Stout, D., Parr, L.A., 2013. Differences in neural activation for object-directed grasping in chimpanzees and humans. J. Neurosci. 33, 14117–14134.

Hewes, G.W., 1973. Primate communication and the gestural origin of language [and comments and reply]. Curr. Anthropol. 5–24.

Hillert, D.G., 2015. On the evolving biology of language. Front. Psychol. 6.

Hoepfner, A.R., Goller, F., 2013. Atypical Song Reveals Spontaneously Developing Coordination between Multi-Modal Signals in Brown-Headed Cowbirds (Molothrus ater).

Hublin, J.J., Neubauer, S., Gunz, P., 2015. Brain ontogeny and life history in Pleistocene hominins. Philos. Trans. R. Soc. 370, 20140062. https://doi.org/10.1098/rstb.2014.0062.

Hurford, J., 1990. Nativist and functional explanations in language acquisition. In: Roca, I.M. (Ed.), Logical Issues in Language Acquistion. Foris Publications, Dordrecht, The Netherlands, pp. 85–136.

Hurford, J.R., 2007. The Origin of Meaning. Oxford University Press.

Janik, V.M., Slater, P.B., 1997. Vocal learning in mammals. Adv. Study Behav. 26, 59–99.

Jarvis, E.D., 2004. Learned birdsong and the neurobiology of human language. Ann. N.Y. Acad. Sci. 1016 (1), 749–777.

Kirby, S., 2013. Language, culture and computation: an adaptive systems approach to biolinguistics. In: Boeckx, C., Grohmann, K.K. (Eds.), Cambridge Handbook of Biolinguistics. Cambridge Handbooks in Language and Linguistics. Cambridge University Press.

Knight, C., Power, C., Watts, I., 1995. The human symbolic revolution: a Darwinian account. Camb. Archaeol. J. 5 (01), 75–114.

Koda, H., Nishimura, T., Tokuda, I.T., Oyakawa, C., Nihonmatsu, T., Masataka, N., 2012. Soprano singing in gibbons. Am. J. Phys. Anthropol. 149 (3), 347–355.

Konopka, G., Bomar, J.M., Winden, K., Coppola, G., Jonsson, Z.O., Gao, F., Geschwind, D.H., 2009. Human-specific transcriptional regulation of CNS development genes by FOXP2. Nature 462 (7270), 213–217.

Krause, J., Lalueza-Fox, C., Orlando, L., Enard, W., Green, R.E., Burbano, H.A., Bertranpetit, J., 2007. The derived FOXP2 variant of modern humans was shared with Neandertals. Curr. Biol. 17 (21), 1908–1912.

Kumar, V., Croxson, P.L., Simonyan, K., 2016. Structural organization of the laryngeal motor cortical network and its implication for evolution of speech production. J. Neurosci. 36 (15), 4170–4181.

Kunzl, C., Sachser, N., 1999. The behavioral endocrinology of domestication: a comparison between the domestic Guinea pig (Cavia aperea f. porcellus) and its wild ancestor, the cavy (Cavia aperea). Horm. Behav. 35, 28–37.

Kurczek, J., Brown-Schmidt, S., Duff, M., 2013. Hippocampal contributions to language: evidence of referential processing deficits in amnesia. J. Exp. Psychol. Gen. 142 (4), 1346.

Kurczek, J., Wechsler, E., Ahuja, S., Jensen, U., Cohen, N.J., Tranel, D., Duff, M., 2015. Differential contributions of hippocampus and medial prefrontal cortex to self-projection and self-referential processing. Neuropsychologia 73, 116–126.

Lacruz, R., Bromage, T., O'Higgins, P., Arsuaga, J.L., Stringer, C., Godinho, R., Carbonell, E., 2015. Facial ontogeny in Neanderthals and their ancestors. Nat. Commun. 6.

Lai, C.S., Fisher, S.E., Hurst, J.A., Vargha-Khadem, F., Monaco, A.P., 2001. A forkhead-domain gene is mutated in a severe speech and language disorder. Nature 413 (6855), 519–523.

Lam, N.H., Schoffelen, J.M., Uddén, J., Hultén, A., Hagoort, P., 2016. Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations. Neuroimage 142, 43–54. https://doi.org/10.1016/j.neuroimage.2016.03.007.

Lameira, A.R., Hardus, M.E., Wich, S.A., 2012. Orangutan instrumental gesture-calls: reconciling acoustic and gestural speech evolution models. Evol. Biol. 39 (3), 415–418.

Lameira, A.R., Maddieson, I., Zuberbühler, K., 2014. Primate feedstock for the evolution of consonants. Trends Cogn. Sci. 18 (2), 60–62.

Lameira, A.R., Hardus, M.E., Bartlett, A.M., Shumaker, R.W., Wich, S.A., Menken, S.B., 2015. Speech-like rhythm in a voiced and voiceless orangutan call. PLoS One 10 (1), e116136.

Lawton, K.J., Wassmer, T.L., Deitcher, D.L., 2014. Conserved role of Drosophila melanogaster FoxP in motor coordination and courtship song. Behav. Brain Res. 268, 213–221.

LeBlanc, J.J., Fagiolini, M., 2011. Autism: a "critical period" disorder? Neural Plast. 2011.

Lenneberg, E.H., 1967. Biological Foundations of Language. Wiley, New York.

Levinson, S.C., 2016. Turn-taking in human communication – origins and implications for language processing. Trends Cogn. Sci. 20 (1), 6–14.

Lewontin, R., 1998. Evolution of cognition. In: Scarborough, D., Sternberg, S. (Eds.), Questions We Will Never Answer. An Invitation to Cognitive Science., Methods, Models, and Conceptual Issues, vol. 4 MIT Press.

Liebal, K., Pika, S., Tomasello, M., 2004. Social communication in siamangs (Symphalangus syndactylus): use of gestures and facial expressions. Primates 45 (1), 41–57.

Lieberman, P., 2006. Toward an Evolutionary Biology of Language. Harvard University Press.

Liu, W.C., Wada, K., Jarvis, E.D., Nottebohm, F., 2013. Rudimentary substrates for vocal learning in a suboscine. Nat. Commun. 4.

MacLean, E.L., 2016. Unraveling the evolution of uniquely human cognition. Proc. Natl. Acad. Sci. U.S.A. 113 (23), 6348–6354.

MacNeilage, P.F., 2010. The Origin of Speech. Oxford University Press.

Marcus, G., 2004. The Birth of the Mind. Basic Books, New York.

Maricic, T., Günther, V., Georgiev, O., Gehre, S., Ćurlin, M., Schreiweis, C., de la Rasilla, M., 2013. A recent evolutionary change affects a regulatory element in the human FOXP2 gene. Mol. Biol. Evol. 30 (4), 844–852.

Marien, P., Manto, M., 2016. The Linguistic Cerebellum. Academic Press.

Marler, P., 2004. Innateness and the instinct to learn. An. Acad. Bras. Cienc. 76 (2), 189–200.

Martins, P.T., Boeckx, C., 2014. Attention mechanisms and the mosaic evolution of speech. Front. Psychol. 5, 1463.

Maureille, B., Bar, D., 1999. The premaxilla in Neandertal and early modern children: ontogeny and morphology. J. Hum. Evol. 37 (2), 137–152.

Mellars, P., Boyle, K., Bar-Yosef, O., Stringer, C.H.R., 2007. Rethinking the Human Revolution. McDonald Institute Monographs, Cambridge.

Mendoza, G., Merchant, H., 2014. Motor system evolution and the emergence of high cognitive functions. Prog. Neurobiol. 122, 73–93.

Micheletta, J., Engelhardt, A., Matthews, L.E.E., Agil, M., Waller, B.M., 2013. Multicomponent and multimodal lipsmacking in crested macaques (*Macaca nigra*). Am. J. Primatol. 75 (7), 763—773.

Moore, R., 2016. Gricean communication and cognitive development. Philos. Q. (in press).

Moore, R., 2016. Gricean Communication, Joint Action, and the Evolution of Cooperation. Topoi (in press).

Müller, G.B., 2010. Epigenetic Innovation. Evolution: The Extended Synthesis. MIT Press, Cambridge, MA, pp. 307—328.

Neubauer, S., Gunz, P., Hublin, J.-J., 2010. Endocranial shape changes during growth in chimpanzees and humans: a morphometric analysis of unique and shared aspects. J. Hum. Evol. 59, 555—566. https://doi.org/10.1016/j.jhevol.2010.06.011.

Okanoya, K., 2012. Behavioural factors governing song complexity in Bengalese finches. Int. J. Comp. Psychol. 25 (1).

Olkowicz, S., Kocourek, M., Lucan, R.K., Portes, M., Fitch, W.T., Herculano-Houzel, S., Nemec, P., 2016. Birds have primate-like numbers of neurons in the forebrain. Proc. Nat. Acad. Sci. U.S.A. 113 (26), 7255—7260.

Pääbo, S., 2014. The human condition—a molecular approach. Cell 157 (1), 216—226.

Pennartz, C.M.A., Ito, R., Verschure, P.F.M.J., Battaglia, F.P., Robbins, T.W., 2011. The hippocampal—striatal axis in learning, prediction and goal-directed behavior. Trends Neurosci. 34 (10), 548—559.

Petkov, C.I., Jarvis, E.D., 2012. Birds, primates, and spoken language origins: behavioral phenotypes and neurobiological substrates. Front. Evol. Neurosci. 4, 12.

Pfenning, A.R., Hara, E., Whitney, O., Rivas, M.V., Wang, R., Roulhac, P.L., Jarvis, E.D., 2014. Convergent transcriptional specializations in the brains of humans and song-learning birds. Science 346 (6215), 1256846.

Pietroski, P.M., 2007. Systematicity via monadicity. Croat. J. Philos. 7 (3), 343—374.

Pika, S., Bugnyar, T., 2011. The use of referential gestures in ravens (*Corvus corax*) in the wild. Nat. Commun. 2, 560.

Pisanski, K., Cartei, V., McGettigan, C., Raine, J., Reby, D., 2016. Voice modulation: a window into the origins of human vocal control? Trends Cogn. Sci. 20 (4), 304—318.

Poeppel, D., Emmorey, K., Hickok, G., Pylkkänen, L., 2012. Towards a new neurobiology of language. J. Neurosci. 32 (41), 14125—14131.

Pylkkänen, L., 2015. Composition of complex meaning: interdisciplinary perspectives on the left anterior temporal lobe. Neurobiology of Language. Elsevier, New York.

Richman, B., 1976. Some vocal distinctive features used by gelada monkeys. J. Acoust. Soc. Am. 60 (3), 718—724.

Rilling, J.K., Scholz, J., Preuss, T.M., Glasser, M.F., Errangi, B.K., Behrens, T.E., 2012. Differences between chimpanzees and bonobos in neural systems supporting social cognition. Soc. Cogn. Affect. Neurosci. 7, 369—379.

Roberts, A.I., Roberts, S.G.B., Vick, S.J., 2014. The repertoire and intentionality of gestural communication in wild chimpanzees. Anim. Cogn. 17 (2), 317—336.

Rodenas-Cuadrado, P., Chen, X.S., Wiegrebe, L., Firzlaff, U., Vernes, S.C., 2015. A novel approach identifies the first transcriptome networks in bats: a new genetic model for vocal communication. BMC Genom 16 (1), 836.

Rubin, R.D., Watson, P.D., Duff, M.C., Cohen, N.J., 2014. The role of the hippocampus in flexible cognition and social behavior. Front. Hum. Neurosci. 8, 742.

Samuels, B., 2011. Phonological Architecture. Oxford University Press, Oxford.

Sato, J.R., Biazoli, C.E., Salum, G.A., Gadelha, A., Crossley, N., Vieira, G., Anés, M., 2016. Connectome hubs at resting state in children and adolescents: reproducibility and psychopathological correlation. Dev. Cogn. Neurosci. 20, 2—11.

Schenker, N.M., Hopkins, W.D., Spocter, M.A., Garrison, A.R., Stimpson, C.D., Erwin, J.M., Sherwood, C.C., 2010. Broca's area homologue in chimpanzees (*Pan troglodytes*): probabilistic mapping, asymmetry, and comparison to humans. Cereb. Cortex 20 (3), 730—742.

Schreiweis, C., Bornschein, U., Burguière, E., Kerimoglu, C., Schreiter, S., Dannemann, M., Groszer, M., 2014. Humanized Foxp2 accelerates learning by enhancing transitions from declarative to procedural performance. Proc. Natl. Acad. Sci. U.S.A. 111 (39), 14253—14258.

Scott, N., Neubauer, S., Hublin, J.J., Gunz, P., 2014. A shared pattern of postnatal endocranial development in extant hominoids. Evol. Biol. 41 (4), 572—594.

Scott-Phillips, T.C., Kirby, S., 2010. Language evolution in the laboratory. Trends Cogn. Sci. 14, 411—417.

Soma, M., Mori, C., 2015. The songbird as a percussionist: syntactic rules for non-vocal sound and song production in java sparrows. PLoS One 10 (5), e0124876.

Taglialatela, J.P., Russell, J.L., Schaeffer, J.A., Hopkins, W.D., 2011. Chimpanzee vocal signaling points to a multimodal origin of human language. PLoS One 6 (4), e18852.

Taglialatela, J.P., Russell, J.L., Pope, S.M., Morton, T., Bogart, S., Reamer, L.A., Hopkins, W.D., 2015. Multimodal communication in chimpanzees. Am. J. Primatol. 77 (11), 1143—1148.

Takahashi, D.Y., Fenley, A.R., Ghazanfar, A.A., 2016. Early development of turn-taking with parents shapes vocal acoustics in infant marmoset monkeys. Philos. Trans. R. Soc. B 371 (1693), 20150370.

Takahashi, D.Y., Narayanan, D.Z., Ghazanfar, A.A., 2013. Coupled oscillator dynamics of vocal turn-taking in monkeys. Curr. Biol. 23 (21), 2162—2168.

Tchernichovski, O., Oller, D.K., 2016. Vocal development: how marmoset infants express their feelings. Curr. Biol. 26 (10), R422—R424.

Teramitsu, I., Kudo, L.C., London, S.E., Geschwind, D.H., White, S.A., 2004. Parallel FoxP1 and FoxP2 expression in songbird and human brain predicts functional interaction. J. Neurosci. 24 (13), 3152—3163.

Teyler, T.J., DiScenna, P., 1986. The hippocampal memory indexing theory. Behav. Neurosci. 100 (2), 147.

Theofanopoulou, C., Boeckx, C., 2015. Cognitive phylogenies, the Darwinian logic of descent, and the inadequacy of cladistic thinking. Front. Cell Dev. Biol. 3, 64.

Theofanopoulou, C., Boeckx, C., 2016. Molecular Footprints of the Self-Domestication Process in *Homo sapiens* (Submitted MS).

Theofanopoulou, C., Boeckx, C., 2016. The central role of the thalamus in language and cognition. Advances in Biolinguistics: The Human Language Faculty its Biological Basis.

Theofanopoulou, C., Boeckx, C., 2016. (Neural) syntax. In: Martin, R., Gallego, A. (Eds.), Language, Syntax, and the Natural Sciences. Cambridge University Press, Cambridge (to appear).

Theofanopoulou, C., 2016. Implications of oxytocin in human linguistic cognition: from genome to phenome. Front. Neurosci. 10, 271.

Thomas, J., 2014. Self-domestication and Language Evolution. PhD, University of Edinburgh.

Tomasello, M., 2009. The Cultural Origins of Human Cognition. Harvard University Press.

Trut, L., Oskina, I., Kharlamova, A., 2009. Animal evolution during domestication: the domesticated fox as a model. Bioessays 31, 349.

Tsui, D., Vessey, J.P., Tomita, H., Kaplan, D.R., Miller, F.D., 2013. FoxP2 regulates neurogenesis during embryonic cortical development. J. Neurosci. 33 (1), 244—258.

Vargha-Khadem, F., Gadian, D.G., Copp, A., Mishkin, M., 2005. FOXP2 and the neuroanatomy of speech and language. Nat. Rev. Neurosci. 6 (2), 131—138.

Vernes, S.C., Spiteri, E., Nicod, J., Groszer, M., Taylor, J.M., Davies, K.E., Fisher, S.E., 2007. High-throughput analysis of promoter occupancy reveals direct neural targets of FOXP2, a gene

mutated in speech and language disorders. Am. J. Hum. Genet. 81 (6), 1232−1250.

Vernes, S.C., Oliver, P.L., Spiteri, E., Lockstone, H.E., Puliyadi, R., Taylor, J.M., Nicod, J., 2011. Foxp2 regulates gene networks implicated in neurite outgrowth in the developing brain. PLoS Genet. 7 (7), e1002145.

Waller, B., Liebal, K., Burrows, A., Slocombe, K., 2013. How can a multimodal approach to primate communication help us understand the evolution of communication? Evol. Psychol. 11 (3), 538−549.

Wang, R., Chen, C.C., Hara, E., Rivas, M.V., Roulhac, P.L., Howard, J.T., Jarvis, E.D., 2015. Convergent differential regulation of SLIT-ROBO axon guidance genes in the brains of vocal learners. J. Comp. Neurol. 523 (6), 892−906.

West-Eberhard, M.J., 2003. Developmental Plasticity and Evolution. Oxford University Press.

Westerlund, M., Kastner, I., Al Kaabi, M., Pylkkänen, L., 2015. The LATL as locus of composition: MEG evidence from English and Arabic. Brain Lang. 141, 124−134.

Wible, C.G., 2012. Hippocampal temporal-parietal junction interaction in the production of psychotic symptoms: a framework for understanding the schizophrenic syndrome. Front. Hum. Neurosci. 6, 180.

Wilkins, A.S., Wrangham, R.W., Fitch, W.T., 2014. The "domestication syndrome" in mammals: a unified explanation based on neural crest cell behavior and genetics. Genetics 197 (3), 795−808.

Williams, H., 2001. Choreography of song, dance and beak movements in the zebra finch (*Taeniopygia guttata*). J. Exp. Biol. 204 (20), 3497−3506.

Wilson, B., Kikuchi, Y., Sun, L., Hunter, D., Dick, F., Smith, K., Petkov, C.I., 2015. Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in macaques and humans. Nat. Commun. 6.

Zhang, Y.S., Ghazanfar, A.A., 2016. Perinatally influenced autonomic system fluctuations drive infant vocal sequences. Curr. Biol. 26 (10), 1249−1260.

Zilberman, U., Smith, P., 1992. A comparison of tooth structure in Neanderthals and early *Homo sapiens sapiens*: a radiographic study. J. Anat. 180 (Pt 3), 387.

Zuberbühler, K., 2015. Linguistic capacity of non-human animals. Wiley Interdiscip. Rev. Cogn. Sci. 6 (3), 313−321.

Further reading

Bastir, M., Rosas, A., Gunz, P., Peña-Melian, A., Manzi, G., Harvati, K., Hublin, J.J., 2011. Evolution of the base of the brain in highly encephalized human species. Nat. Commun. 2, 588.

Benítez-Burraco, A., Boeckx, C., 2015. Possible functional links among brain- and skull-related genes selected in modern humans. Front. Psychol. 6, 794. https://doi.org/10.3389/fpsyg.2015.00794.

Ghazanfar, A.A., Poeppel, D., 2014. The Cognitive Neurosciences V.

Lewontin, R., 2000. The Triple Helix: Gene, Organism, and Environment. Harvard University Press, Cambridge, MA.

Theofanopoulou, C., 2015. Brain asymmetry in the white matter making and globularity. Front. Psychol. 6, 1355. https://doi.org/10.3389/fpsyg.2015.01355.