Neurological Foundations of Language: Emerging Perspectives

Constantina Theofanopoulou[1], Pedro Tiago Martins[2], Javier Ramirez[3], Elizabeth Zhang[1], Gonzalo Castillo[1], Edward Shi[1], Saleh Alamri[1], Anna Martinez Alvarez[1] & Evelina Leivada[1]
[1]University of Barcelona, [2]Pompeu Fabra University, [3]University of Girona

Recepció: 31/01/2015, acceptació 20/05/2015

Abstract: Recent advances in the context of the biological studies of the human language capacity make it clear that a successful marriage of the relevant disciplines—linguistics and biology, broadly construed—will require a serious rethinking of the neurobiological foundations of language. It is our aim in this paper to give a flavor of some of the results of current investigations carried out by our research group that we think contribute to this emerging neurobiology of language.

Keywords: Broca's area, biolinguistics, globularity, laterality, oscillation, evolution

Fonaments neurològics del llenguatge: perspectives emergents

Resum: Els avenços recents dins del context de l'estudi biològic de la capacitat humana del llenguatge han fet palès que la unió reeixida de les disciplines rellevants —lingüística i biologia, enteses àmpliament— requerirà una seriosa revisió dels fonaments neurobiològics del llenguatge. El nostre objectiu en aquest article és oferir un esbós d'alguns dels resultats d'investigacions actuals dutes a terme pel nostre grup de recerca que creiem que poden contribuir a aquesta neurobiologia del llenguatge emergent.

Paraules clau: Àrea de Broca, biolingüística, globularitat, lateralitat, oscil·lació, evolució.

Fundamentos neurológicos del lenguaje: perspectivas emergentes

Resumen: Los avances recientes en el ámbito del estudio biológico de la capacidad humana del lenguaje han puesto de manifiesto que la unión exitosa de las disciplinas relevantes —lingüística i biología, entendidas en un sentido amplio— requerirá una seria revisión de los fundamentos neurológicos del lenguaje. Nuestro objetivo en este artículo es ofrecer un esbozo de alguno de los resultados de las investigaciones actuales llevadas a cabo por nuestro grupo de investigación que creemos que pueden contribuir a esta neurobiología del lenguaje emergente.

The present work was made possible through a Marie Curie International Reintegration Grant from the European Union (PIRG-GA-2009-256413), a grant from the Generalitat de Catalunya (2014-SGR200) and grants from the Spanish Ministry of Economy and Competitiveness (FFI-2013-43823-P and FFI-2014-61888-EXP).

Palabras clave: Área de Broca, biolingüística, globularidad, lateralidad, oscilación, evolución.

1. Introduction

Recent advances in the context of the biological studies of the human language faculty make it clear that a successful marriage of the relevant disciplines—linguistics and biology, broadly construed—will require a serious rethinking of the neurobiological foundations of language (Poeppel 2014). The age of the "classical model" of brain and language, developed in the 19th century by pioneers like Broca, Wernicke and Lichtheim is well over. The traditional division along the axis of language production and language comprehension does not seem to be warranted. Instead, for central aspects of language processing neural infrastructure is shared between production and comprehension (Hagoort 2014). Equally importantly, more areas than Broca's and Wernicke's regions are involved in language. As reviewed in Petersson et al. (2012), the language network is more extended than the classical language regions and includes, next to Broca's region, adjacent cortex in the left inferior and middle frontal region, substantial parts of superior and middle temporal cortex, inferior parietal cortex, as well as subcortical structures such as the thalamus, the basal ganglia, the hippocampus, and the cerebellum. Whereas prior investigations of functional specialization focused on the response profiles of particular brain regions, it seems necessary to reframe issues of the mind/brain in terms of dynamic brain 'networks', which are to be understood as collections of regions jointly engaged by some mental process (Fedorenko and Thompson-Schill 2014).

As it slowly replaces the classical model, the emerging outline of this new 'neurobiology of language' (Poeppel et al. 2012) approximates distributed networks more generally involved in cognition (working memory models, the default network, the multiple demand system, the global neuronal workspace model, etc.; see Boeckx and Benítez-Burraco 2014, Ramírez, Theofanopoulou and Boeckx 2015), thereby becoming a better candidate for the hypothesis that language-readiness is central to modern cognition, as opposed to just another encapsulated module of the mind. In other words, an important conclusion of this new neurobiology of language is that "none of the language-relevant regions and none of the language-relevant neurophysiological effects are language-specific" (Petersson et al. 2012 :1972). Rather, the neurobiological architecture that makes our brain language-ready is embedded within an infrastructure that allows researchers to formulate evolutionary scenarios fully consistent with the Darwinian logic of descent with modification.

It is our aim in this paper to give a flavor of some of the results of current investigations carried out by our research group that we think contribute to this emerging neurobiology of language. In addition to highlighting a few preliminary results, we also want to point to important conclusions that follow naturally from the sort of work we are engaged in.

2. DECOMPOSITION

Boeckx, Martínez-Alvarez and Leivada (2014) focus on a *locus classicus* like Broca's area to argue that the attempt to figure out how linguistic computations are implemented in the human brain requires us to go beyond the standard model, and to recognize that regions like Broca's region are (i) far from monolithic, (ii) just one node in a complex functional network, (iii) unlikely to be exclusively dedicated to certain cognitive domains.

Specifically, they highlight the benefits of decomposing both anatomical regions like 'Broca's area' and computational operations such as 'linearization' in language in order to formulate productive linking hypotheses across the fields of neuroscience and linguistic theory.

In full agreement with David Poeppel in several publications (Poeppel, 2005, 2011, 2012; Embick and Poeppel 2005, 2014), there is an urgent need to adopt new perspectives both in linguistics and neuroscience to overcome the challenge of interdisciplinary exchange. Regarding linguistics, this means: "[providing] a decomposition (or fractionation) of the particular linguistic domain in question (e.g., syntax) into formal operations that are, ideally, elemental and generic. [...] Generic formal operations at this level of abstraction can form the basis for more complex linguistic representation and computation" (Poeppel, 2005: 11). For neurolinguists, there is a need to take seriously the receptoarchitectonic analyses that have shown a subdivision of Broca's region itself as well as a subdivision of both 44 and 45 areas (see e.g. Amunts et al., 2010; Zilles & Amunts, 2009; Neubert et al., 2014). These subdivisions are likely to be dedicated to distinct computational functions.

Boeckx, Martínez-Alvarez and Leivada (2014) show that without the decomposition of formal operations (in this particular case, linearization) it would not be possible to relate them to what our current knowledge of the brain's functional anatomy suggests. At the same time, failure to decompose standard areas like Broca's region would make it difficult to map formal operations onto brain junctures. To summarize, parallel decomposition appears to be required to reach the relevant level of granularity at which one can begin to formulate (and subsequently, to test) linking hypotheses between formal linguistic theory and neuroscience. It bears emphasizing that the decomposition of formal operations should not be seen as a purely theoretical exercise. Rather, it should be guided from 'the bottom up', building on the sort of computational capacities we already know the brain can perform (specifically, oscillation-based computations, which will be addressed below).

A natural consequence of this decomposition strategy is that it is likely, given the generic character of the computations we will ascribe to these sub-areas, that they are not exclusively linguistic in nature, and that domain-specificity is the result of the context of (dynamic) connectivity in which these computations take place.

3. MIND/BRAIN

As Boeckx and Theofanopoulou (2014) point out, linguists have disregarded for too long what is known about the brain, claiming that we still known so little about it that, so far, it is pointless to try to relate mind and brain. In our opinion, this view must be abandoned. While we acknowledge that not everything about the brain is known, we believe enough information is known in order to support the articulation of fruitful hypotheses linking mind and brain. Specifically, it is fairly well-established that information processing at the brain level is achieved by a meaningful interaction of oscillations at various frequencies generated by populations of neurons (Buzsaki 2006).

We therefore urge linguists to frame their discussion in light of this working hypothesis about brain rhythms and offer concrete proposals that can be translated into rhythmic terms.

For example, Boeckx (2013) proposes that we view syntax as an unbounded merge operation, regulated by cyclic applications of a process called "Spell-Out". Spell-Out-regulated Merge amounts to an iterative application of a generic combinatorial operation (set-formation), coupled with a periodic forgetting of material already combined. This is not the place to justify this model (see Ramírez, Theofanopoulou and Boeckx 2015 for extensive discussion and refinements). Suffice it to say that all it needs are elements that can freely combine (so-called lexical items, the precursors of "words"), an active memory buffer (technically known as the division between the "phase edge" and "the phase complement" in the recent generative literature), and the right balance between a process of combination (Merge) and a process of deactivation (De-Merge or Spell-Out). This balance is fairly close to an optimal chunking strategy familiar to cognitive scientists.

Interestingly, in the literature on brain rhythms, it has been claimed that flexible frequency control of cortical oscillations enables computations required for working memory. In particular, Dipoppa and Gutkin (2013) provide a model where individual frequency bands implement elementary computations constitutive of cognitive tasks. When looked at from a linguist's perspective, such elementary computations look a lot like those discussed in the previous paragraph concerning syntactic computations. Dipoppa and Gutkin (2013) claim that rapid memory access and load is enabled by the beta/gamma oscillations, maintaining a memory while ignoring distractors by the theta, rapid memory clearance by the alpha rhythm. One may think of memory access and load as accessing lexical items and merging them; of maintaining a memory in terms of the syntactician's memory buffer, and of memory clearance as Spell-Out. What this suggests to us is that if one is willing to decompose specific linguistic operations like Merge in more generic terms, one can already take advantage of the existing literature to translate these operations in terms of neuronal dynamics (interactions among brain frequencies). To put it another way, we want to urge linguists to frame their theories not just in neural anatomical terms, but specifically in light of what we know about distributed oscillatory, dynamic networks. Our discussion of Dipappa and Gutkin's work also suggests that domains like language and working memory can be brought closer together, reinforcing the erosion of domain specificity. In this particular case we think that it would be particularly interesting to examine more closely the traditional Y-model of grammar (Chomsky 1995) and that of working memory (Baddeley 2012) and see if the similarities are deep or merely superficial.

Another positive aspect of the decomposition approach that we would like to briefly mention here is that it can lead to the rejection of otherwise well-established theoretical notions. Thus, as an example of this shift of perspective from domain-specific atomic units to neurally more plausible generic primitives, Boeckx and Theofanopoulou (2014) examine the nature of the linguistic notion of 'parameter', which is meant to underlie the psychological mechanism of language acquisition. As they show, the central commitment of cognitive science to link mind and brain necessarily implies the abandonment of atomic units like parameters, and favors implementational solutions that are much closer in spirit to the theoretical vocabulary employed by theoretical traditions like cognitive linguistics, as well as representational options that are plausibly shared across species. It is this latter point that we'd like to emphasize here.

The 'divide-and-conquer' approach stands to offer valuable benefits by allowing researchers to exploit results from what are standardly regarded as non-linguistic creatures. This is an unavoidable path if one is to understand the evolution of a complex trait such as language: one must study the evolution of the simpler mechanisms that underlie it. Comparative work will help determine which of these mechanisms are shared, which are unique, and which have evolved independently in different, distant species as recurrent solutions for recurrent challenges. Thus, the study of the behavior, cognition and neurobiology of different species well beyond our closest relatives will help in arriving at a decidedly intricate but biologically informed "cognitive phylogeny" for language.

For example, recent progress in understanding the neurobiology of birdsong suggest that, despite major differences in brain anatomy, shared mechanisms may underlie vocal learning in birds and humans (Jarvis, 2004). (Incidentally, this literature reinforces the need to take sub-cortical structures into account.) Likewise, the introduction of a humanized version of the Foxp2 gene into mice shows clear brain-related differences, specifically, alterations of the cortico-basal ganglia circuits (Enard et al. 2009), which has been suggested to allow for a faster information transfer between systems responsible for procedural memory (e.g., basal ganglia), and systems responsible for declarative memory (e.g., hippocampus) (Schreiweis et al. 2014).

While such studies enable us to explore plausible paths of descent, fully in line with the underlying Darwinian logic of evolution, they also beg the question of what it is specifically about the human brain that makes it possible for us, but not others animals, to acquire grammars of natural languages.

Building on Broca's writings (see Harrington, 1989), it has often been hypothesized that lateralization patterns are central to characterize the language-ready brain (Crow, 2008). Although we believe that hemispheric asymmetries certainly play a role in characterizing linguistic competence at the brain level, at least two considerations convinced us that laterality cannot be as central as it is often taken to be. First, the distinctive pattern of lateralization observed in human adults appears to be acquired through linguistic interaction (Minagawa-Kawai et al., 2011). Second, brain laterality is an aspect of many species. As such, it cannot be taken to be 'the' trait that explains language emergence. Laterality is salient, for example, in non-human vocal learners like birds (Moorman et al., 2012). Our conclusion is also in line with more recent studies casting doubt on a direct link between laterality and language as a whole (see, among others, Benítez-Burraco and Longa, 2012; Bishop, 2013; Cochet and Byrne, 2013; Fitch and Braccini, 2013; Gómez-Robles et al., 2013; Greve et al., 2013; Hancock and Bever, 2013).

Rather than laterality, we hypothesize that the relevant autapomorphy is one that has so far received no attention in the context of biolinguistics, and that is most visibly expressed in the globular aspect of the human endocranial morphology, particularly salient in early postnatal development (Vannucci et al., 2013). As Boeckx and Benítez-Burraco (2014) have argued, there are several reasons to claim that the neuroanatomical and physiological properties giving rise to globularity, not only at the cortical level, but also and crucially at the sub-cortical level, contributed significantly to making our brain language-ready. How this globularity pattern interacts with the pronounced hemispheric asymmetries we find in humans is likely to become a topic of intense investigation for us in the near future. But we regard the coincidence of the emergence of globularity in the fossil record with the origin of language as significant. This coincidence, then, seems to be an important part of the evolutionary (evolution of) language puzzle.

5. Conclusions

It is clear that a successful marriage between linguistics and biology requires a deeper understanding of the neurological foundations of our language faculty. While it is already obvious that notions like syntax or semantics or phonology are not to be found in the brain as such, it should be equally obvious that all linguistic notions must be well grounded in brain-terms if we are to understand them at a satisfactory level.

It is also clear that a deeper understanding of the neurological foundations of our language faculty would provide us with a more solid basis to approach problems such as language acquisition and language evolution.

5. References

AMUNTS, KATRIN; LENZEN, MARIANN; FRIEDERICI, ANGELA D.; SCHLEICHER, AXEL; MOROSAN, PATRICIA; PALOMERO-GALLAGHER, NICOLA; ZILLES, KARL (2010). "Broca's region: novel organization principles and multiple receptor mapping". *PLoS Biology*, 8(9), 1-16.

BADDELEY, ALAN (2012). "Working memory: theories, models, and controversies". *Annual review of psychology*, 63, 1-29.

BISHOP, DOROTHY VM. (2013). "Cerebral asymmetry and language development: cause, correlate, or consequence?". *Science*, 340, 6138.

BENÍTEZ-BURRACO, ANTONIO; LONGA, VICTOR M. (2012). "On the inference 'Neanderthals had FOXP2= they had complex language'". *Evolution of Language. Proceedings of the 9th International Conference (Evolang9)*, 50-57.

BOECKX, CEDRIC (2013). "Merge: Biolinguistic considerations". *English Linguistics*, 30(2), 463-484.

BOECKX, CEDRIC; BENÍTEZ-BURRACO, ANTONIO (2014). "The shape of the human language-ready brain". *Frontiers in psychology*, 5, 282.

BOECKX, CEDRIC; MARTINEZ-ALVAREZ, ANNA; LEIVADA, EVELINA (2013). "The functional neuroanatomy of serial order in language". *Journal of Neurolinguistics*, 32, 1-15.

BOECKX, CEDRIC; THEOFANOPOULOU, CONSTANTINA (2014). "A Multidimensional Interterdisciplinary Framework for Linguistics: The Lexicon as a Case Study". *Journal of Cognitive Science*, 15, 403-442.

BUZSÁKI, GYORGY (2006). *Rhythms of the Brain*. Oxford: Oxford University Press.

CHOMSKY, NOAM (1995). *The minimalist program*. Cambridge: Cambridge University Press.

COCHET, HÉLÈNE; BYRNE, RICHARD W. (2013). "Evolutionary origins of human handedness: evaluating contrasting hypotheses". *Animal cognition,* 16(4), 531-542.

CROW, TIMOTHY J. (2008). "The ' big bang' theory of the origin of psychosis and the faculty of language". *Schizophrenia research*, 102(1), 31-52.

DIPOPPA, MARIO; GUTKIN, BORIS S. (2013). "Flexible frequency control of cortical oscillations enables computations required for working memory". *Proceedings of the National Academy of Sciences*, 110 (31), 12828-12833.

EMBICK, DAVID; POEPPEL, DAVID (2014). "Towards a computational(ist) neurobiology of language: correlational, integrated and explanatory neurolinguistics". *Language, Cognition and Neuroscience*, pub ahead-of-print, 1-10.

ENARD, WOLFGANG; GEHRE, SABINE; HAMMERSCHMIDT, KURT; HÖLTER, SABINE M.; BLASS, TORSTEN; SOMEL, MEHMET; BRÜCKNER, MARTINA K.; SCHREIWEIS, CHRISTIANE; WINTER, CHRISTINE; SOHR, REINHARD; OTHERS (2009). "A humanized version of Foxp2 affects 9 cortico-basal ganglia circuits in mice". *Cell*, 137(5), 961-971.

FEDORENKO, EVELINA; THOMPSON-SCHILL, SHARON L. (2014). "Reworking the language network". *Trends in cognitive sciences*, 18(3), 120-126.

FITCH, W.; BRACCINI, STEPHANIE N. (2013). "Primate laterality and the biology and evolution of human handedness: a review and synthesis". *Annals of the New York Academy of Sciences*, 1288(1), 70-85.

GÓMEZ-ROBLES, AIDA; HOPKINS, WILLIAM D.; SHERWOOD, CHET C. (2013). "Increased morphological asymmetry, evolvability and plasticity in human brain evolution". *Proceedings of the Royal Society B: Biological Sciences*, 280(1761), 20130575.

GREVE, DOUGLAS N.; VAN DER HAEGEN, LISE; CAI, QING; STUFFLEBEAM, STEVEN; SABUNCU, MERT R.; FISCHL, BRUCE; BRYSBAERT, MARC (2013). "A surface-based analysis of language lateralization and cortical asymmetry". *Journal of cognitive neuroscience*, 25(9), 1477-1492.

HAGOORT, PETER (2014). "Nodes and networks in the neural architecture for language: Broca's region and beyond". *Current opinion in neurobiology*, 28, 136-141

HANCOCK, ROELAND; BEVER, THOMAS G. (2013). "Genetic factors and normal variation in the organization of language". *Biolinguistics*, 7, 75-95.

HARRINGTON, ANNE (1989). *Medicine, mind, and the double brain: A study in nineteenth-century thought*. Princeton: Princeton University Press.

JARVIS, ERICH D. (2004). "Learned birdsong and the neurobiology of human language". *Annals of the New York Academy of Sciences*, 1016(1), 749-777.

MINAGAWA-KAWAI, YASUYO; CRISTIA, ALEJANDRINA; DUPOUX, EMMANUEL (2011). "Cerebral lateralization and early speech acquisition: a developmental scenario". *Developmental cognitive neuroscience*, 1(3), 217-232.

MOORMAN, SANNE AND GOBES, SHARON MH AND KUIJPERS, MAAIKE AND KERKHOFS, AMBER AND ZANDBERGEN, MATTHIJS A AND BOLHUIS, JOHAN J. (2012). "Human-like brain hemispheric dominance in birdsong learning". *Proceedings of the National Academy of Sciences*, 109(31), 12782-12787.

NEUBERT, FRANZ-XAVER; MARS, ROGIER B.; THOMAS, ADAM G.; SALLET, JEROME; RUSHWORTH, MATTHEW FS. (2014). "Comparison of human ventral frontal cortex areas for cognitive control and language with areas in monkey frontal cortex". *Neuron*, 81(3), 700-713

PETERSSON, KARL-MAGNUS; FOLIA, VASILIKI; HAGOORT, PETER (2012). "What artificial grammar learning reveals about the neurobiology of syntax". *Brain and language*, 120(2), 83-95.

POEPPEL, DAVID (2005). "The interdisciplinary study of language and its challenges". *Jahrbuch des Wissenschaftskollegs zu Berlin*, 1-14.

POEPPEL, DAVID (2011). "Genetics and language: a neurobiological perspective on the missing link (-ing hypotheses)". *Journal of neurodevelopmental disorders*, 3(4), 381-387.

POEPPEL, DAVID (2012). “The maps problem and the mapping problem: two challenges for a cognitive neuroscience of speech and language”. *Cognitive neuropsychology*, 29(1-2), 34-55.

POEPPEL, DAVID (2014). “The neuroanatomic and neurophysiological infrastructure for speech and language”. *Current opinion in neurobiology*, 28, 142-149.

10

POEPPEL, DAVID; EMBICK, DAVID (2005). “Defining the relation between linguistics and neuroscience”. Cutler, Anne (ed.). *Twenty-first century psycholinguistics: Four cornerstones*. Psychology Press, 103-118.

POEPPEL, DAVID; EMMOREY, KAREN; HICKOK, GREGORY; PYLKKÄNEN, LIINA (2012). “Towards a new neurobiology of language”. *The Journal of Neuroscience,* 32(41), 14125-14131.

SCHREIWEIS, CHRISTIANE; BORNSCHEIN, ULRICH; BURGUIÉRE, ERIC; KERIMOGLU, CEMIL; SCHREITER, SVEN; DANNEMANN, MICHAEL; GOYAL, SHUBHI; REA, ELLIS; FRENCH, CATHERINE A.; PULIYADI, RATHI; OTHERS (2014). “Humanized Foxp2 accelerates learning by enhancing transitions from declarative to procedural performance”. *Proceedings of the National Academy of Sciences*, 111(39), 14253-14258.

RAMIREZ, JAVIER; THEOFANOPOULOU, CONSTANTINA; BOECKX, CEDRIC (2015). “A hypothesis concerning the neurobiological basis of phrase structure building”. Ms. Universitat de Girona/Universitat de Barcelona/ICREA.

VANNUCCI, ROBERT C.; BARRON, TODD F.; HOLLOWAY, RALPH L. (2013). “Frontal brain expansion during development using MRI and endocasts: relation to microcephaly and Homo floresiensis”. *The Anatomical Record*, 296(4), 630-637.

ZILLES, KARL; AMUNTS, KATRIN (2009). “Receptor mapping: architecture of the human cerebral cortex”. *Current opinion in neurology,* 22(4), 331-339.