Why Brain Oscillations are Improving Our Understanding of Language

Antonio Benítez-Burraco[1] and Elliot Murphy[2]

1. Faculty of Philology, University of Seville, Seville, Spain

2. Division of Psychology and Language Sciences, University College London, London, UK; Department of Psychology, University of Westminster, London, UK

Abstract: We review the potential that brain oscillations have for improving our understanding of the processing, evolution and development of natural language. The different 'grammars' of brain rhythms can account for different perceptual and cognitive functions, and we argue that this includes language. We aim to address six distinct questions – the What, How, Where, Who, Why, and When questions – pertaining to oscillatory investigations of language. We review how language deficits found in clinical conditions like autism, schizophrenia and dyslexia can be satisfactorily construed in terms of an abnormal, disorder-specific pattern of brain rhythmicity. Lastly, we argue that an eco-evo-devo approach to language is compulsory.

Keywords: Oscillations, gamma, delta, theta, cross-frequency coupling, schizophrenia, autism, Neanderthals

1. Introduction

During the last 150 years, neurolinguistic research has mostly focused on mapping language to the brain. The advent of various neuroimaging facilities (MRI, EEG/MEG, PET) has allowed neurolinguists to draw very precise maps of the 'language-ready' brain (that is, our species-specific brain configuration that allows us to learn and use language), both in pathological and neurotypical populations. It is now evident that language results from the coordinated activity of several widespread brain networks, encompassing different areas of both hemispheres (e.g. Poeppel et al., 2012; Chai et al., 2016, among many others). Nonetheless, as Poeppel (2012) has often stated, "mapping is not explaining".

Research into neural oscillations can allow us to circumvent this crucial limitation of neurolinguistics and provide robust, motivated explanations of how the brain processes language. Oscillations enable the construction of coherently organised neuronal assemblies through establishing transitory temporal correlations. They reflect synchronised fluctuations in neuronal excitability and are grouped by frequency, with the most common rhythms being delta (δ: ~0.5-4Hz), theta (θ: ~4-8Hz), alpha (α: ~8-12Hz), beta (β: ~10-30Hz) and gamma (γ: ~30-150Hz). These are generated by various cortical and subcortical structures, and form a hierarchical structure since slow rhythms phase-modulate the power of faster rhythms (see Buzsáki and Draguhn, 2004; Buzsáki and Watson, 2012).

There are many reasons why oscillations are a promising candidate in this respect; for instance, they are primitive components of brain function and appear to be both domain-general (that is, individual oscillations intervene in different cognitive and perceptual

functions) and domain-specific (that is, there exists a specific pattern of coupling between oscillations related to, and explaining, each cognitive function) (Hancock et al. 2017, Murphy 2018). Importantly, too, the different "grammars" of brain rhythms accounting for different perceptual and cognitive functions are believed to be species-specific, but the atoms encompassing these grammars (that is, the individual rhythms) are shared across many species (Buzsáki et al., 2013; Brincat and Miller 2015; Esghaei et al. 2015; Kikuchi et al. 2017; Murphy and Benítez-Burraco, 2018). This circumstance grants a noteworthy evolutionary continuity to cognitive functions, which is particularly important in the case of language; meaning, certain elementary computational processes seem to have oscillatory implementations, and as such small tweaks to their phasal and coupling properties can yield modifications to their scope and format (Figure 1).

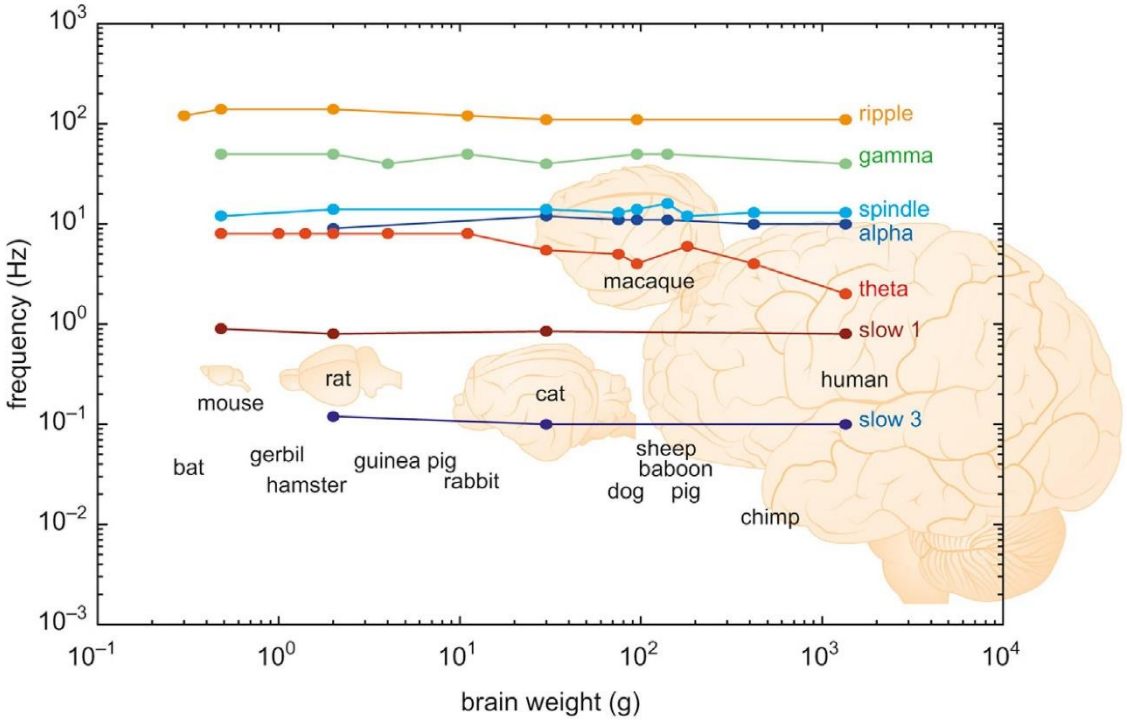

Figure 1: The 'What' Question: Different types of brain oscillations account for the activity of cortical and subcortical structures. Each mammalian species makes use of a different combination (or 'grammar') of a common set of brain oscillations (reproduced from Buzsáki et al. 2013; Figure 2B).

2. Brain Oscillations and the Linguistic Brain

As also discussed extensively by Poeppel (e.g. Poeppel and Embick 2005), current neurolinguistic studies suffer from two crucial shortcomings. On the one hand, they rely on broad distinctions between components of language (syntax vs. semantics, morphology vs. syntax, etc.), which actually involve multiple neural components, computations, and representations. On the other hand, the core elements of linguistic theory (like parts of speech, syntactic operations and the like) do not map onto the core biological elements identified by neuroscience (neurons, columns, and the like). It is consequently urgent for us to present a model of language in computational terms that can be processed by specific parts of the brain in real time.

Distilling language into a specific pattern of coupling between different brain oscillations appears feasible. Importantly, this approach satisfactorily accounts for core facets of language according to consolidated linguistic theories. For instance, the combinatorial power of merge (the basic operation in the modern generative approach to language, which combines two syntactic objects to form a new syntactic unit) and the cyclic power of phrasal labeling (the operation which chooses the lexical features to be assigned to the merged syntactic unit) are able to be implemented via various oscillatory interactions such as forms of cross-frequency coupling (Murphy 2015, 2018, Meyer 2018). In the most recent and comprehensive oscillatory model of language comprehension defended in Murphy (2016, 2018) (which goes considerably beyond the discussion of combinatorics, representational accommodation, and prediction presented in Meyer 2018), empirical and conceptual motivations are presented to defend the idea that δ-θ phase-amplitude coupling constructs multiple sets of linguistic syntactic and semantic features, with distinct β and γ sources also being embedded within θ for, respectively, syntactic prediction and conceptual binding. This provides a specific neural code for *recursive hierarchical phrase structure*, the core distinctive feature of human language (reapplying the set-forming operation to its own output), with α also being involved in the early stages of binding (Pina et al. 2018) to synchronize distant cross-cortical γ sites required for the 'θ-γ code' of working memory and to modulate attentional resources (Figure 2).

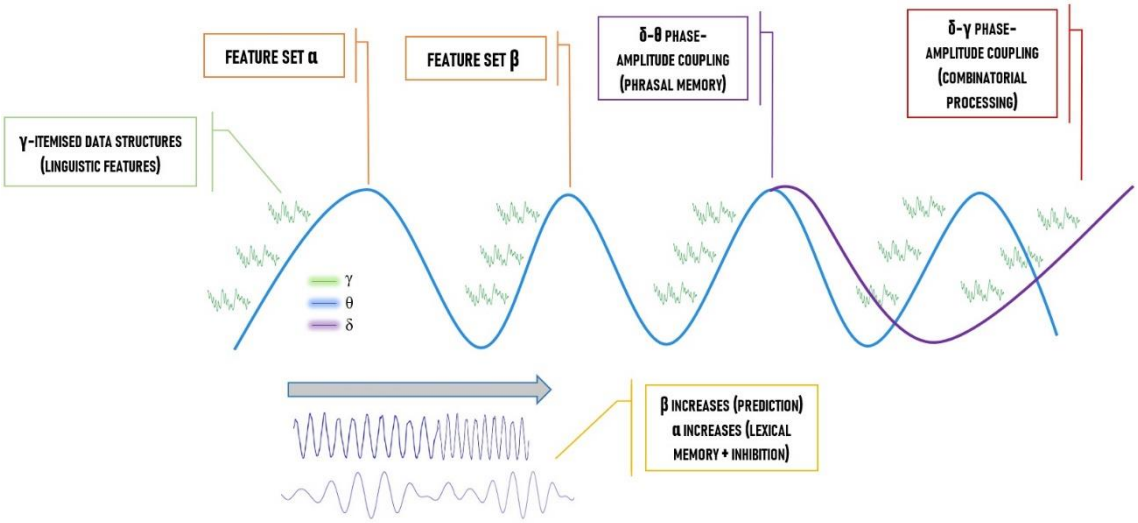

Figure 2: The 'How' Question: A neural code for language, representing the various cross-frequency coupling interactions proposed to implement hierarchical phrase structure building.

Importantly, Murphy (2018) also discusses the high likelihood that travelling oscillations are involved in language comprehension. These are oscillations which move across the brain; meaning, the spiking of neural clusters is coordinated not just across two fixed points (e.g. hippocampus-and left inferior frontal cortex phase-amplitude coupling) but across a particular extended path. These travelling oscillations have recently proven to coordinate neural activity across widespread brain networks and across different temporal windows, and ultimately, to support brain connectivity and function (Zhang et al., 2018). Accordingly, δ waves could cycle across the cortex, building up the syntactic representation phrase-by-phrase and potentially being endogenously reset by a newly constructed phrase, and being coupled to traveling θ waves which perform the same

function. Traveling δ waves could be responsible for patterning spiking from single- to multi-unit lexical structures in each δ cycle. As such, δ would coordinate the phrasal construction while θ-γ interactions would support the representational construction of linguistic feature-sets. Lastly, as Gągol et al. (2018) reveal, δ-γ coupling is involved in fluid intelligence (solving problems using a range of cognitive faculties on the fly, spontaneously), whereby δ embeds cross-cortical γ rhythms depending on the cortical areas needed for the particular task, i.e. geometric reasoning, visual processing etc. Murphy (2018) proposes that δ-γ coupling may be a generic combinatorial process, combining representations from within and across domains (Figure 3 contrasts the classical 'language areas' with the model we are proposing, revealing a considerably greater degree of complexity).

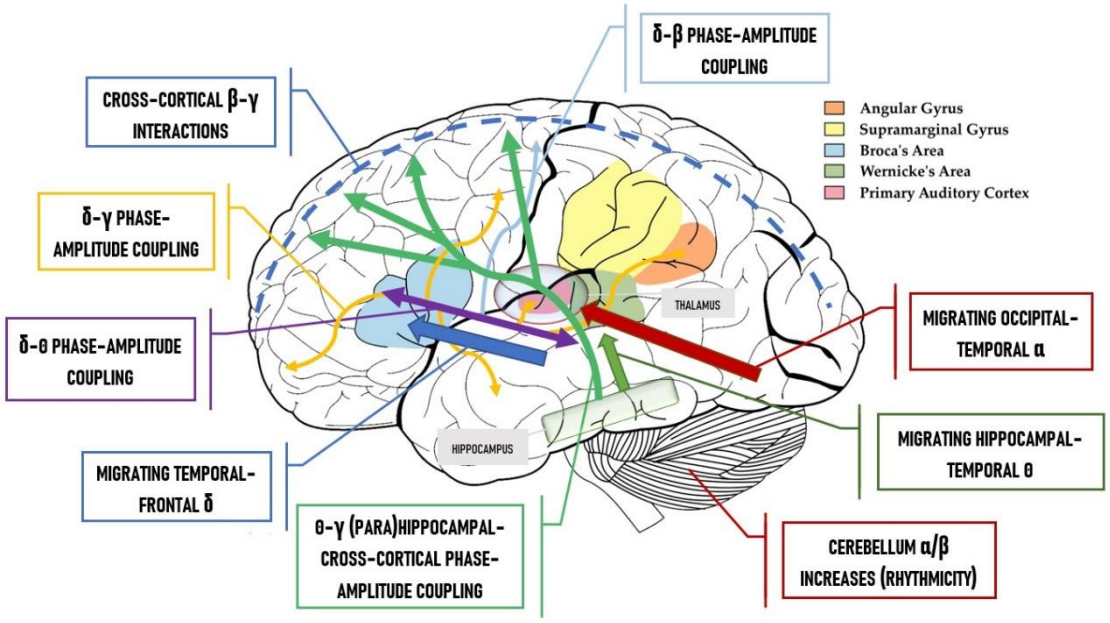

Figure 3: The 'Where' Question: A cartographic map of where the neural code for language is hypothesized to be implemented. Additional features not discussed in the main text: Prefrontal predictions facilitate δ-entrained speech tracking in anterior superior temporal gyrus, while the cerebellum contributes to rhythmic perceptions and hence aids phrasal processing in frontotemporal regions.

Although we refer the reader to Murphy (2018) for the further discussion of the empirical details, we should briefly mention that there is increasing support for this model. For instance, Brennan and Martin (2019) analysed a naturalistic story-listening EEG dataset and showed that δ-γ coupling increases with the number of predicates bound on a given word (the authors only analysed the central Cz electrode, so further analysis is required to flesh out the picture). They also discovered an increasing scale of δ-θ coupling beginning at the point of a word completing a single phrase, through to words completing two and three phrases. As such, δ-γ and δ-θ coupling increases with predication. Overall, these observations illustrate how the presently defended analysis of travelling waves can help explain how such a complex thing as a fragment of discourse, which entails both linguistic and extralinguistic (i.e. encyclopaedic) knowledge, is processed by the brain.

3. Brain Oscillations and a Systems-Biology Approach to Language

Mastering a language and being able to use it, in the way we have sketched in the previous section, depends on having received the proper triggering environmental stimuli during development. But this is only possible because of complex biological processes, which are assembled mostly under genetic guidance. Thousands of biological factors interact to regulate language development and processing. Nevertheless, for many years it was not clear where the specificity of language resides – and if there is much biologically specific at all. Accordingly, although language seems to be a very specialized, human-specific faculty, it undoubtedly relies on biological components, such as its genetic basis, which may not be specific to language since 'language genes' contribute to a range of biological functions.

Brain oscillations are highly heritable traits (van Beijsterveldt et al. 1996; Linkenkaer-Hansen et al. 2007, Müller et al. 2017), including oscillations related to language (Araki et al. 2016). Oscillations are both more proximal to gene function (in particular, regulatory function) and less complex than standard cognitive labels. Accordingly, we should expect that gene-oscillations-language links are more robust and explanatory than genes-neuroanatomy-language links (Figure 4). As we have shown in a recent paper (Murphy and Benítez-Burraco 2018), the basic aspects of the language oscillome (that is, the particular phasal and cross-frequency coupling properties of neural oscillations involved in, and accounting for, language) result from genetic guidance, and a confident list of candidate genes for this guidance can be posited. Moreover, a number of linking hypotheses between particular genes and particular oscillatory brain activity implicated in language processing can be posited, suggesting that much of the oscillome is likely genetically-directed; the set of genes implicated here is termed the *oscillogenome.* Importantly, these candidate genes map on to specific aspects of brain function, particularly on to neurotransmitter function, and particularly through dopaminergic, GABAergic and glutamatergic synapses.

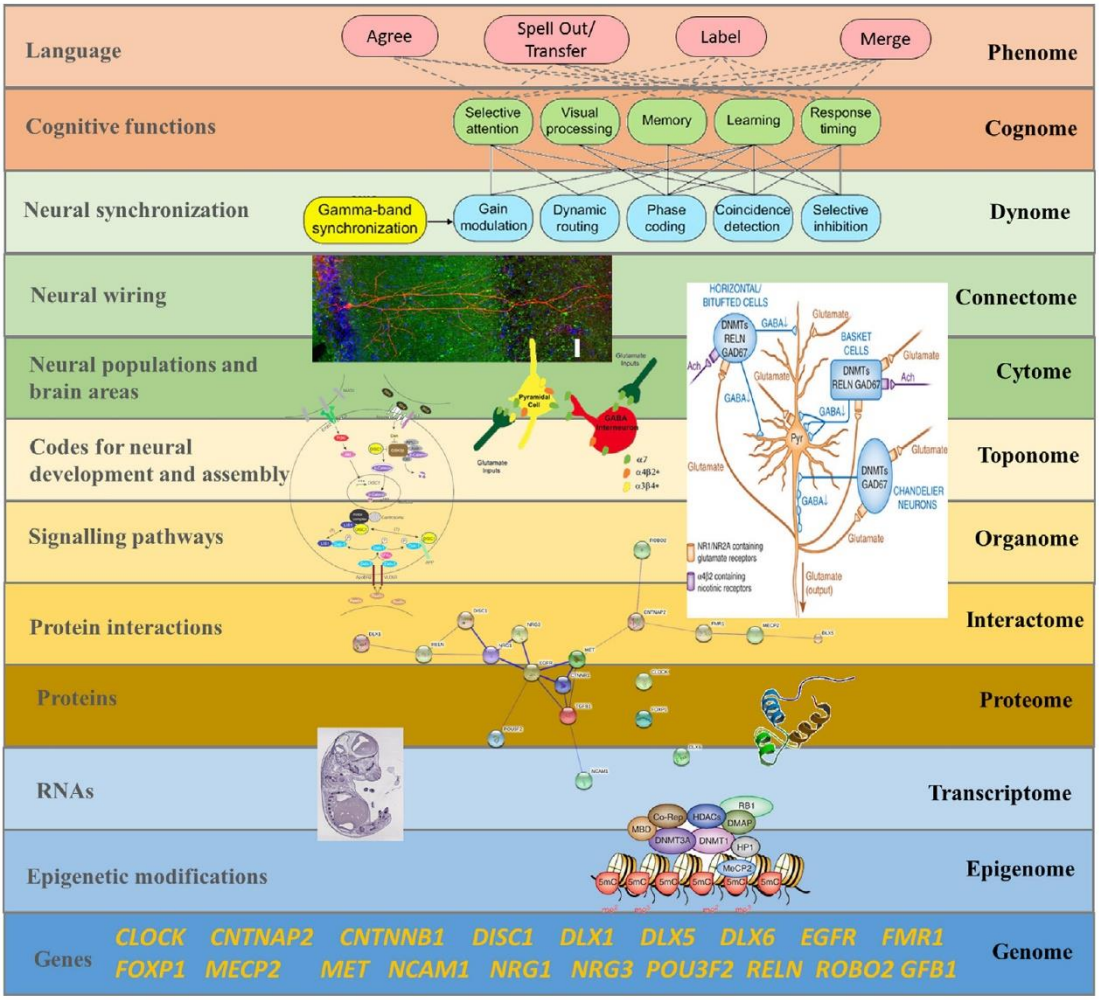

Figure 4. The 'Who' Question. A systems biology approach to language, focused on the dynamics of cellular and organismal function and on the (emergent) properties of the whole system, is compulsory if one wants to understand how language emerges from these complex interactions (Benítez-Burraco, 2019). It seems that the biological specificity of language may emerge at the oscillomic level (reproduced from Murphy and Benítez-Burraco, 2017; Figure 8)

4. Brain Oscillations and Language Disorders

Most cognitive disorders entail problems with language. Whereas each disorder can be said to exhibit a disorder-specific abnormal language profile (with deficits in the domains of phonology, grammar, semantics, or language use), each particular deficit are commonly found in several disorders, to the extent that most of them are shared by different disorders with different symptomatology and aetiology. This accounts for the frequent comorbidity of disorders. Moreover, these deficits are only indirectly related to (broad) cognitive deficits at the bottom. Finally, although most of these conditions have a genetic basis, the same gene can contribute to more than one cognitive disorder (see Benítez-Burraco, 2019 for an ample discussion of these problems for clinical linguistics). This circumstance seemingly explains why the divide between the genetics and pathophysiology of prevalent cognitive/language disorders like autism spectrum disorder (ASD), schizophrenia (SZ) or developmental dyslexia (DD) remains open. In recent years, a number of promising directions have opened up for investigating the neural and

genetic basis of these disorders. Due to an emerging body of work concerning the oscillatory dynamics of language processing, it has become possible to associate certain features of the ASD, SZ or the DD neurobiological profile, particularly, language deficits, to abnormal patterns of brain oscillations. Likewise, contemporary developments have allowed researchers to explore the genetic basis of particular oscillatory rhythms in distinct brain regions (e.g. Hancock et al. 2017), as well as the genetic signature of these disorders. All of these developments have allowed us to make promising and insightful linking hypotheses between seemingly unrelated domains in the life and cognitive sciences, to the extent that we can begin to map particular gene mutations to specific abnormal oscillatory profiles which can in turn be used to explain the existence of impairments in language processing in selected cognitive conditions.

In a series of related papers (Benítez-Burraco and Murphy 2016; Murphy and Benítez-Burraco 2016; Jiménez-Bravo et al., 2017; Murphy and Benítez-Burraco, 2018a, Wilkinson and Murphy, 2016) we have shown that the distinctive language deficits found in clinical conditions like ASD, SZ, and DD can be satisfactorily construed in terms of an abnormal, disorder-specific pattern of brain rhythmicity. Interestingly, we have also shown that selected candidate genes for the language oscillogenome exhibit a distinctive, disorder-specific pattern of up- and downregulation in the brain of patients. In other words, the molecular signature of each disorder from this oscillogenomic perspective mostly relies not on the set of genes involved, which are essentially the same, but on their expression patterns in each brain region, which is different in each condition (Figure 5). This contributes to bridging genes (with their disorder-specific expression profile) and oscillations (with their disorder-specific profile too) and language (which is also impaired in a disorder-specific way).

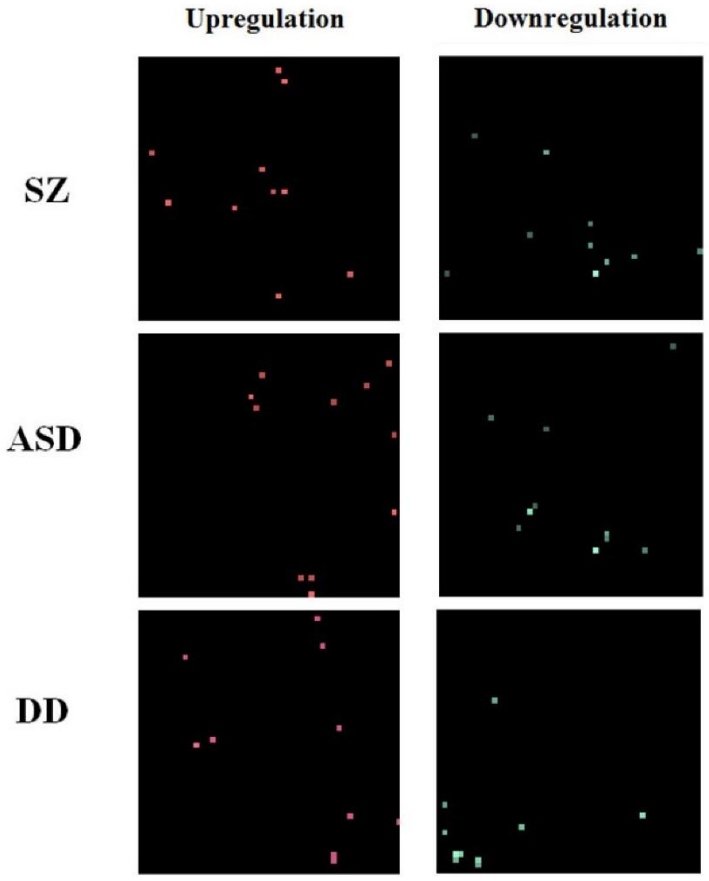

Figure 5. The 'Why' Question. Genes involved in brain rhythmicity exhibit a disorder-specific expression profile in the brain of affected people. The figure shows the expression grids generated with Enrichr (amp.pharm.mssm.edu/enrichr). Brain regions where genes of interest are most upregulated are displayed in red, whereas regions in which genes are most downregulated are shown in green (the lighter the colour, the more up- or downregulated a gene is) (adapted from Murphy and Benítez-Burraco, 2018; Figure 2).

Just to give a flavour of this systems-biology approach to language disorders that heavily relying on brain oscillations, we discuss the case of ASD. Both structural and functional aspects of language are impaired in ASD. Approximately one third of children with ASD exhibit difficulties with morphosyntax (Tager-Flusberg and Joseph 2003) and both adults and children with ASD typically use a low number of functional words (Tager-Flusberg et al. 1990). This population also integrates and consolidates semantic information differently from neurotypicals when processing sentences (Eigsti et al. 2011). More specific impairments include problems with relative clauses, *wh*-questions, raising and passives (Perovic and Janke 2013). These difficulties all speak to a more general deficit in procedural memory. Concerning the oscillatory basis of these deficits, increased γ power has been documented for individuals with ASD (e.g. Kikuchi et al. 2013), and since this rhythm is involved in the binding of semantic features this finding can likely contribute to a causal-explanatory oscillatory model of language deficits. Kikuchi et al. (2013) additionally found reduced cross-cortical θ, α and β in the ASD brain, while Bangel et al. (2014) documented lower β power during a number estimation task. Given the role of these slower rhythms in cross-cortical information integration, and the major role β likely plays in syntactic processing (Murphy 2018), problems with executing complex syntactic operations like passivization and interpreting *wh*-dependencies seems not too surprising. At the same time, many of the differences in cognition and behaviour found in ASD are seemingly explained by differences in oscillatory activity resulting from pathogenic genetic diversity, mostly in genes indirectly or directly related to GABAergic activity, like *MECP2* (Liao et al., 2012), the genes encoding some of the GABAA-receptor subunits (particularly of β2 and β3) (Porjesz et al., 2002; Heistek et al., 2010), or *PDGFRB* (Nguyen et al., 2011; Nakmura et al., 2015).

Eventually, these oscillatory anomalies found in cognitive disorders in tandem with an increasingly sophisticated oscillatory model of language (see Section 2 above) can yield predictions about the cortical profile of an individual exhibiting them. Specifically, considering language disorders as 'oscillopathic' traits (that is, involving abnormal patterns of brain rhythmicity) is a productive way to generate endophenotypes of the disorders and ultimately, achieving earlier and more accurate diagnoses.

5. Brain Oscillations and Language Evolution

As discussed above, language is a complex system. Accordingly, we should expect that specific evolutionary changes in specific components of this complex system prompted the transition from an ape-like cognition to human-cognition, and ultimately resulted in our language-readiness. At present, we have precise characterizations of the recent evolutionary changes in our brain and in our genomic endowment that seemingly account for our language-readiness (see Boeckx and Benítez-Burraco, 2014; Neubauer et al., 2018; Gunz et al., 2019). Nonetheless, as we noted earlier, brain anatomy and brain maps can only provide indirect and rough accounts of how the brain process language.

Moreover, because, as we also noted earlier, the specificity of language is seemingly born at the oscillomic level, and because each species-specific pattern of brain coupling builds on a shared set of basic rhythms, we should expect as well that the human-specific pattern of coupling accounting for our language-readiness resulted from selected changes in the oscillatory signature of the hominin brain. These modifications can be traced via comparative studies, with humans exhibiting a species-specific richness in possible cross-frequency couplings (see Murphy 2018 for references and discussion). Regarding extinct hominins, such as Neanderthals or Denisovans, it is evident that we cannot track the oscillatory activity of their brains. However, it is possible to rely on available (although still scarce) information from genes encompassing the language oscillogenome – as characterised above – to infer the particular changes in phasal and cross-frequency coupling properties of neural oscillations that resulted in the emergence of core features of language. Accordingly, several candidates for the language oscillogenome show differences in their methylation patterns (and hence, in their expression levels) between Neanderthals and anatomically-modern humans (Table 1). These differences can be informative of differences in cognitive functions important for language (Murphy and Benítez-Burraco 2018a); for instance, we can infer that the working memory capacity of Neanderthals likely differed from that of modern humans due to the differences in θ and γ expression.

GENE	FIXED AA CHANGE IN AMHS	POSITIVELY SELECTED IN AMHS	DIFFERENTIALLY METHYLATED IN AMH SKELETAL SAMPLES	ENRICHED IN AMH DMRS	OSCILLOMIC/OSCILLOPATHIC FEATURES
AUTS2		✓	↑(body gene)		Epilepsy
CACNA1C			↑ (body gene)		β, γ
CNTNAP2	✓				α
COL4A2			↑(body gene)		Epilepsy
COMT			↑(downstream the gene)		α
DYRK1A		✓			Inhibition of neural activity
EGR1				✓	Epilepsy
ELP4		✓			High amplitude centrotemporal sharp waves
FMR1	✓				θ, γ
FOXP1		✓	↑(body gene)		Epileptiform discharges
ROBO1		✓			Epilepsy

Table 1. The 'When' Question. Selected genes encompassing the language oscillogenome exhibit fixed derived changes in modern humans compared to extinct Neanderthals, either in their regulatory or coding regions, or in their methylation patterns (suggestive of differences in their expression levels) (reproduced from Murphy and Benítez-Burraco, 2018b; Table 1).

6. Brain Oscillations and an Eco-Evo-Devo Approach to Language

A growing body of evidence suggests that genomic regions showing signals of positive selection in our species are enriched in candidates for cognitive conditions entailing

problems with language, like ASD (Polimanti and Gelernter, 2017) or SZ (Srinivasan et al., 2016; 2017). These findings are suggestive that these conditions may have mainly developed recently in our evolutionary history. This is seemingly due to the circumstance that the most recently evolved components of human cognition are more sensitive to the deleterious effect of developmental perturbations resulting from factors either internal to the organism or external to it, because of the lack of robust compensatory mechanisms to damage, which are typically found in more ancient biological functions which have been shaped by stronger selective pressures (see Toro et al., 2010 for discussion). In a similar vein, when searching for the basis for genomic trade-offs potentially involved in the evolution of the human brain, Sikela and Searles Quick (2018) have concluded that changes in the genome producing beneficial results might persist despite their ability to also produce diseases and that "the same genes that were responsible for the evolution of the human brain are also a significant cause of autism and schizophrenia" (2018: 2). This is in line with current views of complex diseases as the consequence of the uncovering of cryptic variation resulting from the assorted changes (genomic, demographic, behavioural) promoting the transition from an ape-like biology to a human-specific biology (see Gibson 2009 for details).

As noted in Section 3 above, a systems biology approach to language is compulsory in order to understand how it emerges from the complex interactions among thousands of biological factors, most notably brain oscillations. It is now clear that because language evolved mostly as a result of specific changes in the developmental path of the hominin brain in response to changes in the environment in which our ancestors lived (the latter encompassing both physical and cultural factors), we need to pay attention to developmental, evolutionary, and ecological aspects. Putting it differently, an eco-evo-devo approach to language is compulsory. This approach should enable us to understand better how language is implemented in the brain, how it evolved, and how it is disrupted in language disorders. What's more, the evidence we have reviewed suggests that this can be ideally achieved if we focus on brain rhythms. Specifically, brain rhythms might be a better (or perhaps, the optimum) candidate for properly defining the morphospace or adaptive landscape of language growth in the species, either pathological or neurotypical; that is, defining the limited set of language faculties available during development.

7. Conclusions

Overall, the evidence reviewed in this paper suggests that brain oscillations can be the most fruitful approach for understanding how language is implemented in our brain as a result of our evolutionary history. This is not just because they are both domain-general and domain-specific, but because they help explain why and how *processing*, *evolution* and *development* are closely interwoven. Still, although new avenues for research are rapidly opening up, there remain a large number of unanswered questions: Which sub-domains of linguistics have the potential to make greater contact with the life sciences (e.g. pragmatics)? What are the anatomical similarities and differences regarding human and nonhuman temporal processing networks? How does the notion of a travelling oscillator tie in with existing findings concerning the supposedly fixed, regionalised oscillatory activity found in existing EEG and MEG experiments of language processing? How might one test the hypothesis that nonhuman primates exhibit a differently organised array of cortical cross-frequency couplings? Solving these and others complex questions will help refine our oscillatory view of human language.

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