

Implications of Travelling Weakly Coupled Oscillators for the Cortical Language Circuit*

Elliot Murphy

Abstract

The search for the neural code across a range of cognitive domains has seen a marked transition from the analysis of individual spike timings to larger patterns of synchronisation. It is argued that the study of language should readily embrace these systems-level developments. In particular, recent findings concerning the scope of possible oscillatory synchronisation in the human brain have revealed the existence of travelling/migrating oscillations, adding further impetus to reject the typical stasis found in cartographic neurolinguistics models. After exploring empirically-motivated revisions to the neural code for hierarchical phrase structure, it is discussed how this code could provide a new perspective on language disorders.

Keywords: Neural oscillations, weakly coupled oscillators, delta, gamma, language deficits

1 Introduction

I will here be assuming the framework for phrase structure generation in Murphy (2016a-c, Forthcoming) involving, at a minimum, δ - θ phase-amplitude coupling to construct multiple sets of linguistic representations, 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 hierarchical phrase structure, with α being involved in the early stages of binding to synchronise distant cross-cortical γ sites needed for the ' θ - γ code' of working memory and to modulate attentional resources. Grimaldi (2017, p. 17) summarises that 'Murphy [(2016b)] proposes a revolutionary theory of neurolinguistics ... that nested oscillations execute elementary linguistic computations', adding that this theory 'goes considerably beyond existing models'. Although there is accumulating empirical support for this model and its computational basis (see discussion in Segaert et al., 2018; Zaccarella et al., 2017), recent research opens up the possibility for expansion and refinement.

2 Travelling Oscillations

Zhang et al. (2017) present novel insights into a relatively new mechanism for large-scale neural coordination in the form of travelling oscillations which cycle cross-cortically at a speed of ~ 0.27 - 0.75 metres per second. These form spatially coherent waves that move across the cortex. The propagation of these waves was found in 96% of neurosurgical patients (through electrocorticography, ECoG) and was consistent with good performance on the Sternberg working memory task. Zhang et al. (2017) conclude that 'human behaviour is supported by ... traveling waves'. What precisely constitutes the range and influence of travelling waves over cognition is a topic for future study, but we can begin to sketch possible directions and explanations for these discoveries.

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The authors discovered what they define as travelling ‘theta and alpha oscillations’, yet their analysis reveals that the full range of migrating waves stretched from 2-15Hz, therefore implicating mid- δ . Mid- δ is involved in phrasal chunking, though not sentential chunking (which low- δ seems responsible for). This could potentially lead to a refined neural code for language processing: δ waves cycle across the cortex, building up the syntactic representation phrase-by-phrase and being endogenously reset by a newly constructed phrase, either traveling to parts of the cortex responsible for storing the required semantic representations or being coupled to travelling θ waves which perform the same function. The limitations of semantic processing could be derived either from the physical limitations placed on the speed of traveling cycles as they move from station to station (~ 0.25 - 0.75 m/s) or the width of the propagating waves (median: ~ 2.4 - 4.8 cm) which might limit the range of conceptual structures manipulated.

As discussed elsewhere (Murphy & Benítez-Burraco, 2017; Murphy Forthcoming), the brain was re-shaped in our lineage via globularisation and the development of the Torque, and so I would like to hypothesise that this granted oscillations the ability to travel across new areas of the cortex and subcortex whilst also being coupled to a number of other regions. Further, Zhang et al.’s findings support a model of travelling waves as a network of weakly coupled oscillators (WCO), according to which the travelling wave is a result of phase coupling. According to the WCO model, oscillators are arranged in a linear array and are weakly coupled with their neighbours. The model also assumes that there is a spatial gradient in intrinsic frequency across the oscillators. Since the travelling wave is assumed to be the result of phase coupling, these assumptions conspire to yield the prediction – fulfilled by Zhang et al.’s (2017) data – that faster waves would travel in the direction of slower waves. The language model assumed here complements these findings, since Zhang et al. found that waves typically travelled in a posterior-to-anterior direction, and it is assumed here that elementary syntactic combinatorics involve a parahippocampal and cortico-basal ganglia-thalamo-cortical loop (concatenation and semantic conjunction) which is later coupled with left inferior frontal regions such as BA 44 and BA 45 which act as crucial memory buffers for the maintenance of hierarchically organised syntactic objects. Both this model and the WCO travelling wave model predict poster-to-anterior directionality as the language system proceeds from selecting linguistic features (parahippocampal, thalamic and basal ganglia regions), to combining them (anterior temporal regions), to attributing to them a labelled identity (cortico-basal ganglia-thalamo-cortical loop), and finally to storing them in working memory (left inferior frontal regions, in particular pars opercularis). This directionality also notably correlates with the rhythms hypothesised to be responsible for these operations, with faster γ and β rhythms in posterior and central regions being coupled with slower central θ and α rhythms, which in turn travel towards slow left inferior frontal δ regions they are coupled with. While faster γ and β rhythms have currently not been shown to migrate, we can assume that this simply reinforces the neuroanatomically fixed nature of conceptual representations as being stored in typically resilient neural clusters (*=representations*), which can nevertheless be coupled to slower, travelling rhythms (*=computations*).

More pertinently, Zhang et al. (2017) conclude that ‘[w]hen phase coupling is absent, there are no traveling waves because intrinsic oscillation frequencies differ between electrodes’. This suggests a strong degree of co-dependence between the phenomenon of cross-frequency coupling and travelling waves. If certain findings reviewed in Murphy (2016c, Forthcoming) are accurate – in particular, the finding of human-specific phase coupling diversity, hypothesised here to have occurred due to cranial reshaping – then the language system likely evolved as a direct outcome of a broader range of oscillatory migration routes which resulted from new inter-regional phase couplings. One of language’s hallmark characteristics, of breaking modular boundaries and combining representations from distinct

domains to be stored cyclically in an expanded memory buffer (or phonological loop; Aboitiz, 2017), would arise immediately from this. Though it has been explored elsewhere how the core oscillatory architecture of δ - θ - γ interactions can generate phrase structure building, the work of deriving the mechanism of syntactic combinatorics was previously left simply to phase-amplitude coupling. We can now add to this basic mechanism the understanding that language-relevant representations can be accessed cross-cortically through a process of posterior-to-anterior wave propagation.

Concerning the topic of what type of grammatical representations are manipulated by the brain, Greenhill et al. (2017) used a Dirichlet process mixture model to explore the rates of change in lexical and grammatical data from 81 Austronesian languages, showing that while many features change rapidly there exists ‘a core of grammatical and lexical features that are highly stable’ (2017, E8822), and hence are strong candidates for being central components in the dynamics of language evolution. These stable features include inclusive vs. exclusive distinctions, gender distinctions, the existence of tense auxiliaries, prepositions, clause chaining, and the presence of animacy features on the noun/class gender system (see Dataset S2 in Greenhill et al., 2017).

Since the poster-to-anterior propagations documented in the literature are involved in feedforward processes, it is possible that instances of anterior-to-posterior migration (a phenomenon documented in Zhang et al. (2017) and which was extremely rare compared to the reverse migration pattern) have a distinct functional role such as supporting feedback or top-down processes. It would be of interest to explore in future work whether δ waves propagate in an anterior-to-posterior direction at particular points of syntactic processing, perhaps accessing distinct loops of a memory buffer stretching from pars opercularis to posterior regions of Broca’s area as the number of syntactic labels increases over the course of phrase structure building. Moreover, these findings should encourage neurolinguists to reconsider some core assumptions considering event-related potentials, which might (under the present framework) result from travelling waves transiently organising at a given timepoint and phase (see also Murphy, 2015 for connections between oscillations and event-related potentials).

These observations speak against the idea that linguistic computation is based on *regional stasis* (e.g. the claim in Friederici et al., 2017 that BA 44 and its temporal dorsal pathway – and this pathway only – constitutes the basis of natural language syntax) and is rather implemented via a cortical circuit even more dynamic than previously assumed (for perspective: Zhang et al., 2015 discovered for the first time travelling θ waves, but only throughout the human hippocampus; see also Patten et al., 2012).

It may not simply be oscillations, then, but more specifically travelling oscillations that could provide the optimal way to bridge neuroanatomy and brain dynamics, fulfilling the goal articulated succinctly in Friederici et al. (2017, p. 719) of ‘finding the explanatory link between the neuroanatomical data, the electrophysiological data, and the formal properties of human syntax’. As Zhang et al. (2017) conclude, ‘individual traveling-wave cycles represent spatially discrete pulses of neural activity that correspond to distinct behavioral states’. The task now for the language sciences is to investigate how travelling waves might serve as a general mechanism for transmitting discrete pockets of neural activity in ways which map onto the functions of semantic, phonological and syntactic combinatorics. Indeed, in their original discovery of travelling waves, Patten et al. (2012, p. 7) speculate that ‘the thalamus may exert an important influence on cortico-cortical propagation via thalamocortical reentrant loops’, and since travelling waves appear to propagate along corticocortical fibers the role of the thalamus may be crucial (see Murphy, 2015 for the role of the thalamus in language).

3 Rethinking Language Disorders, Fluid Intelligence and Language Acquisition

Travelling oscillations may also be able to account for certain language disorders and aphasias, since in the literature there are often cases documenting damage to brain areas not typically seen as ‘language areas’ and yet which negatively impact language processing. It is possible that these damaged regions serve to ‘block’ the migration of travelling oscillations. Likewise, there are an even greater number of documented cases regarding the survival of key language skills after a supposedly core language region is damaged. Under the present perspective, this could simply imply that only part of the migration route was taken, impairing some representations from being accessed but nevertheless leaving much intact, or indeed that only part of the migration route was damaged. Disruption of the anterior head of the caudate and putamen results in verbal aphasias (Lieberman, 2000), which may be due not to damage to white-matter fibers projecting from the cortex to the striatum (*à la* Nadeau & Crosson, 1997) but because oscillations responsible for constructing necessary speech signals are blocked from travelling across the full network responsible for vocal production (extending far beyond the thalamus). A similar explanation might account for the various verbal communication deficits resulting from lesions to the globus pallidus (Strub, 1989).

Turning briefly to another area where travelling oscillations may provide novel insights, Gągol et al. (2018) discovered that fluid intelligence level (*gf*), or the ability to solve novel problems via abstract reasoning regardless of prior knowledge, depends on the precise synchronization of fast rhythms to the phase of slow rhythms. In particular, $\{\delta(\gamma)\}$ phase-amplitude coupling was found to be indicative of *gf* (more precisely, low γ at $\sim 36\text{Hz}$ and δ at $\sim 3\text{Hz}$), suggesting under the model in Murphy (2016a-c, Forthcoming) that δ coordinates the extraction of various cortical representations. No ‘intervening’ rhythms are involved in this form of phase-amplitude coupling, unlike in linguistic computation, which involves hierarchical structures and hence coupling between δ , θ , β and γ of differing combinations. Buzsáki et al. (2013) discuss that the propagation of low frequency oscillations across the cortex is considerably faster in the human brain than in the smaller rat brain, likely explaining the origins of *gf*. Further, the close rhythmic similarities between the oscillatory basis of fluid intelligence and language processing seem to support the notion that the computational basis of memory and certain language processes – *Load*, *Maintain*, *Spell-Out*, *Concatenate* and so forth – is essentially shared (with the exception of labeling and cyclicity). Billeke et al. (2017) provide related evidence from EEG that the coupling of the amplitude of slow γ ripples (90-110Hz) to the phase of cortical δ differs as a function of cognitive task, ranging from memory recall to directed attention; supporting the role of δ - γ interactions in fluid intelligence.

Duncan (2013) discusses his frontoparietal Multiple Demand system and regards it as the basis of fluid intelligence, with this system more broadly implicating subcortical structures like the thalamus and basal ganglia. It seems to follow from this model and the findings in Gągol et al. (2018) that $\{\delta(\gamma)\}$ coupling ranges over this frontoparietal circuit, with the general processes of fluid intelligence possibly being enhanced by elementary forms of linguistic computation involving *Search* and *Concatenate* processes. While general forms of intelligence are coordinated by $\{\delta(\gamma)\}$ coupling, more complex, hierarchical syntax arrives only through a broader range of cross-frequency couplings. This likely explains why fluid intelligence is also at risk of impairment in the event of brain lesions, with either the paths of the travelling δ waves across the frontoparietal Multiple Demand circuit either being limited, or the cortical γ clusters they are typically coupled with being unable to synchronise.

Lastly, according to Wexler’s (1998) Unique Checking Constraint (UCC), a child’s linguistic system is limited to checking only one syntactic property per linguistic environment. For instance, in the clausal domain AGReement and Tense features cannot both be checked, and so only one is eliminated (producing the Optional Infinite stage of language acquisition).

Since we are beginning to understand the oscillatory differences between child and adult language comprehension (Leong & Goswami, 2015), this constraint may be due to particular limitations on travelling θ oscillations across cortical areas responsible for coupling with γ pockets storing AGR-relevant and Tense-relevant features, with maturity likely providing the brain with a broader and more extensive travelling path. Since this area of neurobiological research is a recent development, further studies of child language processing within these frameworks will be needed to elaborate on these hypotheses any further. The psycholinguistic possibilities of testing the morphology of travelling oscillations using magnetoencephalography (MEG) seem highly promising. Lastly, an interesting question for future research concerns the relevance of travelling subcortical oscillations (e.g. parahippocampal migrations) and the morphology of travelling waves in nonhuman primates.

References

- Aboitiz, F. (2017). *A Brain for Speech: A View from Evolutionary Neuroanatomy*. London: Palgrave Macmillan.
- Billeke, P., Ossandon, T., Stockle, M., Perrone-Bertolotti, M., Kahane, P., Lachaux, J.-P., & Fuentetaja, P. (2017). Brain state-dependent recruitment of high-frequency oscillations in the human hippocampus. *Cortex*, *94*, 87-99.
- Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron*, *80*, 751-764.
- Duncan, J. (2013). The structure of cognition: attentional episodes in mind and brain. *Neuron*, *80*, 35-50.
- Gągól, A., Magnuski, M., Kroczyk, B., Kałamała, P., Ociepka, M., Santarnecchi E., & Chuderski, A. (2018). Delta-gamma coupling as a potential neurophysiological mechanism of fluid intelligence. *Intelligence*, *66*, 54-63.
- Greenhill, S.J., Wu, C.-H., Hua, X., Dunn, M., Levinson, S.C., & Gray, R.D. (2017). Evolutionary dynamics of language systems. *PNAS*, *114*(42), E8822-E8829.
- Grimaldi, M. (2017). The phonetics-phonology relationship in the neurobiology of language. *bioRxiv* <http://dx.doi.org/10.1101/204156>.
- Lieberman, P. (2000). *Human Language and Our Reptilian Brain: The Subcortical Bases of Speech, Syntax, and Thought*. Cambridge, MA: Harvard University Press.
- Leong, V., Goswami, U. (2015). Acoustic-emergent phonology in the amplitude envelope of child-directed speech. *PLoS ONE*, *10*(12), 1-37.
- Murphy, E. (2015). The brain dynamics of linguistic computation. *Frontiers in Psychology*, *6*, 1515.
- Murphy, E. (2016a). Evolutionary monkey oscillomics: generating linking hypotheses from preserved brain rhythms. *Theoretical Linguistics*, *42*(1-2), 117-137.
- Murphy, E. (2016b). The human oscillome and its explanatory potential. *Biolinguistics*, *10*, 6-20.
- Murphy, E. (2016c). A theta-gamma neural code for feature set composition with phase-entrained delta nestings. *UCL Working Papers in Linguistics*, *28*, 1-23.
- Murphy, E. (Forthcoming). *Principles of Language Evolution*. London: UCL Press.
- Murphy, E., & Benítez-Burraco, A. (2017). Language deficits in schizophrenia and autism as related oscillatory connectomopathies: an evolutionary account. *Neuroscience & Biobehavioral Reviews*, *83*, 742-764.
- Nadeau, S.E., & Crosson, B. (1997). Subcortical aphasia. *Brain and Language*, *58*, 355-402, discussion 418-423.
- Patten, T.M., Rennie, C.J., Robinson, P.A., & Gong, P. (2012). Human cortical traveling waves: dynamical properties and correlations with responses. *PLoS ONE*, *7*(6), e38392.
- Segaert, K., Mazaheri, A., & Hagoort, P. (2018). Binding language: structuring sentences through precisely timed oscillatory mechanisms. *European Journal of Neuroscience* doi:10.1111/ejn.13816.
- Strub, R.L. (1989). Frontal lobe syndrome in a patient with bilateral globus pallidus lesions. *Archives of Neurology*, *46*, 1024-1027.
- Wexler, K. (1998). Very early parameter setting and the unique checking constraint: a new explanation of the optional infinitive stage. *Lingua*, *106*, 23-79.
- Zaccarella, E., Meyer, L., Makuuchi, M., & Friederici, A.D. (2017). Building by syntax: the neural basis of minimal linguistic structures. *Cerebral Cortex*, *27*(1), 411-421.
- Zhang, H., Watrous, A.J., Patel, A., & Jacobs, J. (2017). Theta and alpha oscillations are travelling waves in the human neocortex. *bioRxiv* <http://dx.doi.org/10.1101/218198>.
- Zhang, H., & Jacobs, J. (2015). Traveling theta waves in the human hippocampus. *Journal of Neuroscience*, *35*(36), 12477-12487.