

A Theta-Gamma Neural Code for Feature Set Composition with Phase-Entrained Delta Nestings*

Elliot Murphy

Abstract

Continuing a recent line of research into the functional role of neural oscillations in language and cognition, I propose that a central computational system (implemented via gamma, theta and delta interactions) interfaces with external interpretive and attentional systems (implemented via beta and alpha modulations) to derive certain core features of phrasal construction. These interactions are achieved through the coupling of the phase and amplitude of distinct rhythms. A theta-gamma code generates the initial feature-set while thalamic and occipital alpha is used to inhibit irrelevant information sources. This code is itself embedded within left-cortical delta rhythms while an increasing beta rhythm, which finds its source within a cortico-basal ganglia-thalamo-cortical loop, is used to maintain the existing cognitive set in memory. Neuroethological arguments are presented in favour of the species-specific nature of this neural code, and it is argued that the unique hierarchies exhibited in natural language emerge from this human-specific rhythmic profile.

Keywords: Neural oscillations, theta, gamma, delta, labeling hypothesis, oscillome

1 Introduction

In what follows I will adopt the Labeling Hypothesis put forward in Murphy (2015a), that labeling – and not Merge – constitutes the exclusive content of ‘narrow syntax’ and hence should be the focus of any evolutionary scenario and neuroethological investigation. This is in contrast to standard ‘Merge-centric’ evolutionary hypotheses (Berwick & Chomsky, 2016; Hauser, Yang, Berwick, Tattersall, Ryan, Watumull, Chomsky, & Lewontin 2014; Mukherji, 2010; Nóbrega & Miyagawa, 2015, and much other work). Boeckx and Theofanopoulou (2015) noted that the concept of labeling in Murphy (2015a) was not formulated at a fine enough level of granularity to permit linking hypotheses to be drawn up between linguistic theory and neurobiology. This was later achieved in Murphy (2015b), in which the elementary syntactic sub-operations of set-formation, labeling, and cyclic transfer were proposed to arise from the well-preserved hierarchy of mammalian brain rhythms and their interactions, following seminal work by Giraud and Poeppel (2012) on the dynamics of phonological computation. Through outlining a program of Dynamic Cognomics, a number of hypotheses were presented concerning the neurobiological basis of phrase structure building, feature valuation, and other properties of language. In brief, this research program attempts to attribute to neural oscillations (at the level of the ‘oscillome’, or oscillatory brain activity ascribed certain computational roles) particular computational and representational properties which were previously attributed only at the level of the ‘cognome’, the set of computational operations the human nervous system could execute (Poeppel, 2012).

Oscillations enable the construction of coherently organised neuronal assemblies through establishing transitory temporal correlations, and are increasingly being implicated in

*My thanks go to Daniel Bush, Karl Friston, John O’Keefe, Andrea E. Martin and the participants of the Eighth Annual Meeting of the Society for the Neurobiology of Language at the UCL Institute of Education and the Cell Symposia: Big Questions in Neuroscience conference in San Diego for helpful discussion in developing the ideas presented here. This work was supported by an ESRC scholarship (1474910).

numerous cognitive processes (see, for instance, Kaplan, Adhikari, Hindriks, Mantini, Murayama, Logothetis, & Deco (2016)). They are typically measured through electroencephalography (EEG) and magnetoencephalography (MEG) and reflect synchronised fluctuations in neuronal excitability and are grouped by frequency, and include delta (δ : ~0.5-4Hz), theta (θ : ~4-8Hz), alpha (α : ~8-12Hz), beta (β : ~12-30Hz) and gamma (γ : ~30-100Hz). These are generated by cortical and subcortical structures and form hierarchical, nested relationships such that slower rhythms can modulate the amplitude of faster rhythms.

Contrary to what might be expected from a program declaring interest in mind-brain commensurability, Dynamic Cognomics (which I will here refer to simply as oscillomics) is purely an oscillation-based methodology set against a backdrop of Marrian and evo-devo assumptions, with no stipulations about what form linguistics-neuroscience linking hypotheses should necessarily take. Oscillomics has the potential to reduce what Tomalin (2006, p. 188) calls the ‘attendant logico-philosophico-mathematical baggage’ of generative grammar by re-embedding linguistic combinatorics within a framework of brain dynamics.

Language itself is argued by some to be the origin of complex thought and imagination. Tattersall (2016) writes:

This symbolic capacity of ours resonates in every realm of our experience, and in combination with the complex ancestral foundation of intuitive intelligence and association-making on which it is superimposed ... it is the fount not only of our imagination and creativity, but of all those other cognitive peculiarities that set us apart from even our closest living relatives in nature.

Throughout the 20th century and into the 21st, artificial intelligence research has repeatedly moved in and out of synch with biology, at one point being closely aligned with current developments only to diverge slightly at another. Linguistics, on the other hand, has often claimed to be in synch with biology, but has never in fact achieved this goal. The relative lack of interest in biology exhibited by many linguists becomes even more curious when we see how interested in language many biologists are: While perhaps novel to linguists and cognitive scientists, the potential existence of a relationship between language and neural oscillations was discussed as early as 1978 in O’Keefe and Nadal’s monumental work *The Hippocampus as a Cognitive Map* (O’Keefe & Nadal, 1978). Here, the authors discuss Chomsky and Jackendoff’s work on syntax and the semantic representation of space, attempting to draw links between how the hippocampus appears to represent vectors and how the language system appears to represent space. O’Keefe and Nadal attempted to show how their theory of cognitive maps could account for certain properties of linguistic ‘deep structure’ and semantic long term memory. In effect, the present contribution is an attempt to do the opposite of O’Keefe and Nadal, broadening both the neurophysiological and computational landscape that these authors set down and discussing a wide number of cortical and subcortical structures and how they might implement elementary linguistic operations.

Computational models of syntactic, semantic and phonological knowledge are likely not going to be reduced fully to neural tissue, but George Box’s famous saying that ‘all models are wrong but some are useful’ should remind us that the ultimately ‘incorrect’ nature of neurocomputational models can at least provide a useful function in directing future research. The study of language should take advantage of whatever sciences could enhance its hypotheses and methodologies. In the Enlightenment period, developments in what would today be termed philosophy of mind contributed to an understanding of some fundamental linguistic concepts like personhood. In the 1950s, developments in meta-mathematics contributed to an understanding of language’s grammatical architecture. Today, with the

proliferation of the brain sciences, it is likely that other features of language can now be explored.

Yet this proliferation can come with certain risks, often not acknowledged by researchers. Jonas and Kording (2016) used the methods of neuroscience to try and understand the MOS 6502 microchip (the processor in, amongst other things, the Commodore 64), which contains 3510 transistors as is able to run only the most primitive, vintage video games. Their results should generate a fair degree of humility: They discovered only that the chip has a clock and is able to read and write to memory. Nothing else was uncovered about it via the standard methods of neuroscience ('lesioning' transistors, analysing individual transistors and local field potentials, performing Granger causality analysis, and so forth). Jonas and Kording discovered general-purpose operations which transistors could perform, but they found no 'Donkey Kong transistor' or 'Space Invaders transistor', i.e. transistors essential and exclusive to a given game. And while the chip is purely deterministic, neurons can exhibit random behaviour. The neurolinguistic lessons are clear, with Jonas and Kording's work serving as a further motivation for abandoning classical 'cartographic' models of language comprehension, which propose one-to-one mappings between brain regions and (often fairly complex) cognitive operations, fixating on Broca's and Wernicke's areas. We are often told by neurolinguists that certain linguistic operations 'take place' at a given region, or are 'interpreted' along a particular pathway, yet the story of what exactly the brain is doing to derive these localised interpretations is left unanswered.

Even a cursory look at the regions implicated in recent oscillatory studies of language comprehension (see Lam, Schoffelen, Udden, Hulten and Hagoort (2016) for a review) indicates that the classical Broca-Wernicke model is far from adequate. Language comprehension generates multiple, large-scale oscillatory changes in a number of distant regions, and so limiting the 'language regions' to Broca's and Wernicke's areas is unjustified, and the dynamic functioning of the brain at once suggests that a simple mapping between a given region and a particular linguistic representation or operation is not going to be forthcoming. The fact that certain regions implicated in syntactic, semantic and phonological processes are spatially overlapping suggests that a different system of segregation will be required than standard cartographic approaches; namely, frequency-based segregation.

The same criticisms apply to Boeckx's (2016) hypothesis that since both the fronto-parietal and fronto-temporal networks process sequences, the strengthened connections between them found in the human brain 'could allow for the processing of sequences of sequences, of the sort attested in grammatical constructions'. How exactly these strengthened connections could lead to recursion is not explained, and no further details – algorithmic or implementational – are presented.

In what follows I will consequently approach the problem of implementing language in the brain with a number of crucial caveats. The models and hypotheses put forward may not ultimately produce a degree of understanding that Marr or Lazbnick would appreciate, but scientific inquiry needs to have its limits, and being able to recognize these limits does not as a result invalidate a given neuroscientific enterprise. Neurolinguistics has been flooded with data over recent years but it has also seen a remarkable lack of conceptual or theoretical innovation to account for this data. So severe has the flooding been that major neurolinguists continue to apply the intuitive cartographic mindset to newly emerging modes of analysis, with Bastiaansen and Hagoort (2015) coming to the neurobiologically implausible conclusion that γ rhythms are responsible for something as complex as 'semantic unification' simply because they detected γ increases during semantically well-formed structures. Notice that this 'theory' is in fact purely a re-description of the data, and an explanation for why we see γ increases is absent. Brown (2014) summarizes the current situation well in a brief report:

If we really care about the question of how the brain works, we must not delude ourselves into thinking that simply collecting more empirical results will automatically tell us how the brain works any more than measuring the heat coming from computer parts will tell us how the computer works. Instead, our experiments should address the questions of what mechanisms might account for an effect, and how to test and falsify specific mechanistic hypotheses.

The physical sciences place a great deal of emphasis on the importance of theoretical physics, and not just, for instance, experimental particle physics. There is no reason why neuroscientists should not afford the same respect to theoretical neurobiology, yet the drive for experimental innovation is currently by far the dominant force in the field. Filling the gap between the flood of data and neurobiological theory, I will argue, is a particular neurocomputational multiplexing algorithm supported by an understanding of how the brain dynamically operates in real time.

2 Beyond Functional Mapping: A Neural Code for Language

As Jackendoff presciently noted, ‘even if we know *where* a structure is localized in the brain – the sort of information that neural imaging can provide – we do not know *how* the brain initiates the structure’ (2007, p. 13). A neurolinguistic theory is ‘incomplete if it does not offer genuine solutions to the problems of combinatoriality, structural hierarchy, and binding among structures’ (2007, p. 15). An understanding of how the brain operates – and not simply what it looks like under a scanner – is provided by brain dynamics and the study of oscillatory neural activity. These are produced by cortical and subcortical structures and form a hierarchy such that slow rhythms phase-modulate the power of faster rhythms (a relationship explained in Figure 2, below). Slower rhythms synchronize distant brain regions while faster rhythms activate local neuronal assemblies (Yan & Li, 2013; Murphy, 2015b).

Brain dynamics and neurochemistry can constrain the types of operations performed by the nervous system, but they cannot easily reveal *what* operations are performed (Seung, 2012). For this, we need to turn to linguistic theory. In what follows I will present some basic operations required for phrasal construction and interpretation and attempt to re-embed them within a particular oscillomic framework.

2.1 Merge

The set-forming operation Merge constructs a new syntactic object out of two already formed (Chomsky, 1995). Merge(*the,book*) would form {*the, book*}. We can define the operation as follows:

- (1) *Merge*
 Select two lexical items α and β and form the set $\{\alpha,\beta\}$:
 $\mathbf{M}(\alpha,\beta) = \{\alpha,\beta\}$

In Murphy (2015b) it was suggested that since lower frequencies are known to synchronise distant cortical regions, this may represent the oscillomic implementation of Merge. I assumed that thalamic and occipital α embeds cross-cortical γ to generate, or ‘lexicalize’, individual representations before these γ -individuated units were themselves embedded within parahippocampal θ . The decoupling of γ from α would be achieved through the activity of the thalamic reticular nucleus.

Maintaining mentally constructed visual objects in memory (i.e. combining a small number of basic shapes into a larger unit), in contrast to ‘whole’ objects, leads to greater fronto-

parietal θ synchronisation (Ewerdwalbesloh, Palva, Rösler, & Khader 2016), and so this rhythm seems well-suited to the maintenance of complex objects generated in fronto-parietal circuits. In addition, θ is involved in engaging functionally distinct sub-regions of the medial prefrontal cortex, integrating information from the output of different cognitive operations (Mas-Herrero & Marco-Pallarés, 2016); a capacity presumably well-suited to transferring representational information from distinct linguistic sub-systems (e.g. phonology, semantics).

2.2 Labeling

Labeling is the operation selecting which lexical features determine the phrasal category, ensuring that $\{A, N\}$ forms an NP, not an AP. This process leads to the asymmetric hierarchies found in phrase structures and appears to be human-specific. Labeling is also monotonic since the identity of a labeled set is sustained when embedded inside another set. Tomalin (2007, p. 1784) notes in his account of the development of the theory of recursive functions that ‘even if a label-free system is proposed, the essential constructional process remains the same’; procedures of set-formation, property attribution and maintenance are required for the construction of ‘a potentially infinite set of hierarchical structures’. Labeling permits the brain to generate items which can be freely deployed (i.e. maintained, retrieved and recombined with other structures), partly independent of perception.

I will now briefly outline some existing proposals, refining and expanding on some of the central ideas. It was suggested in Murphy (2015b) that labeling arises from the slowing down of the above γ -itemized clusters to β followed by $\{\alpha(\beta)\}$ coupling, involving a cortico-basal ganglia-thalamo-cortical loop. The involvement of this loop would be a result of it being a major source of the brain’s core timing system, with a feature of labeling being rhythmicity (Bartolo, Prado, & Merchant, 2014; Bartolo & Merchant, 2015). However, for reasons expanded on below, it now seems that β more likely nests within left-cortical δ while remaining coupled with parahippocampal θ . This is partly due to δ being implicated in phrasal processing in recent experimental work (e.g. Ding, Melloni, Zhang, Tian, & Poeppel, 2016), but there are other reasons to suppose the importance of $\{\delta\{\theta(\beta)\}\}$ coupling, returned to in Section 2.5. For now, I will assume that the $\{\theta(\gamma)\}$ feature-sets ultimately shift to $\{\delta\{\theta(\beta)\}\}$ phrasal/labeled units. An important question, which must be addressed in future experimental work, is how this shift occurs. There appear to be two options: Either the γ -itemized clusters first slow to β before the $\{\theta(\beta)\}$ complex is nested within δ , or the multiplexed $\{\theta(\gamma)\}$ units are embedded first and the items slow to β at a later point. Fewer β -itemized clusters would be able to phase-lock to θ due to the size of each β cycle (around three β cycles per θ cycle), potentially accounting for the unequal ratio between feature-sets responsible for determining phrasal status and feature-sets which perform other roles with respect to syntactic function (e.g. tense features) and content (e.g. lexical features).

Regardless of which route the language system takes to achieve phrasal nesting, the above model seems to be a particularly robust one, from both conceptual and empirical standpoints.¹ For instance, accruing evidence suggests that β holds objects while γ simply generates them (Martin & Ravel, 2014). Dean, Hagan and Pesaran (2012) demonstrate that β is capable of comparing old and new information from distinct modalities due to its wide temporal windows; in a linguistic context, it would compare recently generated but stored phrasal structures with newly-merged non-phrasal elements such as complements.

¹ Indeed, both routes may be taken under different scenarios. In the case of an ambiguously labeled phrase which could constitute either a DP or an NP, it may be that γ is not slowed to β until after phase-entrainment to δ has taken place when the precise interpretation is fixed.

Alternatively, it may be that only some γ -itemized clusters slow to β , namely those clusters responsible for storing the features determining the phrasal/labeled status of a given δ -entrained set. Generative grammar has long suggested that what determines the label of a given set of lexical items is only a subset of the entire feature complex, and so it is possible that the language system is composed of two simultaneously entrained δ and θ complexes; β labeling features and γ non-labeling features:

LABELING FEATURES: $\{\delta\{\theta(\beta)\}\}$
 NON-LABELING FEATURES: $\{\delta\{\theta(\gamma)\}\}$

The cortico-basal ganglia-thalamo-cortical loop is especially appealing with respect to its potential role in labeling given the findings that different ‘stations’ on the loop can be responsible for information integration from distinct cortical sources: convergence appears to occur at the pallidum (Yelnik, Percheron, & Francois, 1984), subthalamic nucleus (Haynes & Haber, 2013) and thalamus (Theyel, Llano, & Sherman, 2010). These stations also display a degree of functional specificity, and it is likely that different features of linguistic representations (phonological, semantic, and so forth) are integrated into the phrase structure-building process in a procedural manner. The anterior thalamus, for instance, is already being considered a major site of memory formation (Sweeney-Reed, Zaehle, Voges, Schmitt, Buentjen, Kopitzki, Hinrichs, Heinze, Rugg, Knight, & Richardson-Klavehn, 2015), going against standard cortico-centric and hippocampal-centric models. The fact that lesions to Broca’s area do not always result in syntactic impairments or modulations in sentential processing competence (Mohr, Pessin, Finkelstein, Funkenstein, Duncan, & Davis, 1978) also suggests that other, possibly non-cortical circuits are (or at least can be) implicated in phrase structure building.²

2.3 A Multiplexing Algorithm for Feature-Set Composition

In Murphy (2016a) the above model for Merge and labeling was significantly expanded in an attempt to explore the algorithmic properties of the oscillatory interactions invoked to explain the human capacity for phrasal construction and interpretation.³ Phase-aligned oscillatory activity permits multiplexing, or the encoding and decoding of multiple information streams (Akam & Kullmann, 2014) – precisely what is required to bind the representationally distinct syntactic, semantic and phonological streams of information which constitute any given lexical item. Multiplexing allows the reconfiguration of connectivity and information types stored and extracted from a given neural network, and this was applied in Murphy (2016a) to phrasal construction.

Under the present model, parahippocampal regions are the site of initial $\{\theta(\gamma)\}$ coupling. The hippocampus seems particularly suited to facilitate these cross-modular interactions since

² Friederici’s (2016) claim that BA 44 and its dorsal fiber connections to the temporal cortex ‘support the processing of structural hierarchy in humans’ is therefore not incorrect, but is rather simply a piece of a larger system found in the language-ready brain. Indeed, neurolinguists should acknowledge more readily that functional, structural hypotheses regarding language comprehension and production are necessarily limited by technology: fMRI may (and in fact appears to) implicate distinct structures from, for instance, MEG. Relying solely on fMRI to build a cartographic model of the language system will lead to hypotheses ignoring the dynamical nature of the brain’s activity.

³ The model in Murphy (2015b) was referred to as the ‘Basic Label’ model. The expanded version in Murphy (2016a) was termed a multiplexing algorithm and here I will subsume the Basic Label model under this more general term, part of the broader ‘oscillomic’ approach to language advocated throughout.

it has been argued to play a role in integrating ‘what’ and ‘where’ information in the perirhinal cortex through the lateral entorhinal cortex and the postrhinal cortex through the medial entorhinal cortex (Fernández-Ruiz & Oliva, 2016). Lisman and Jensen (2013) suggested that these γ and θ rhythms form a code for representing multiple, ordered items. Since each θ cycle contains four to eight nested γ cycles, different representations (e.g. a series of short-term memory sequences) can be sequentially coordinated. This also fits the revision of working memory from the classic five-nine items to four items (Cowan, 2001). This may constrain the number of lexical features able to be transferred in a given derivational cycle, with this idea being implemented in Murphy (2016a) through the algorithm in Figure 1.

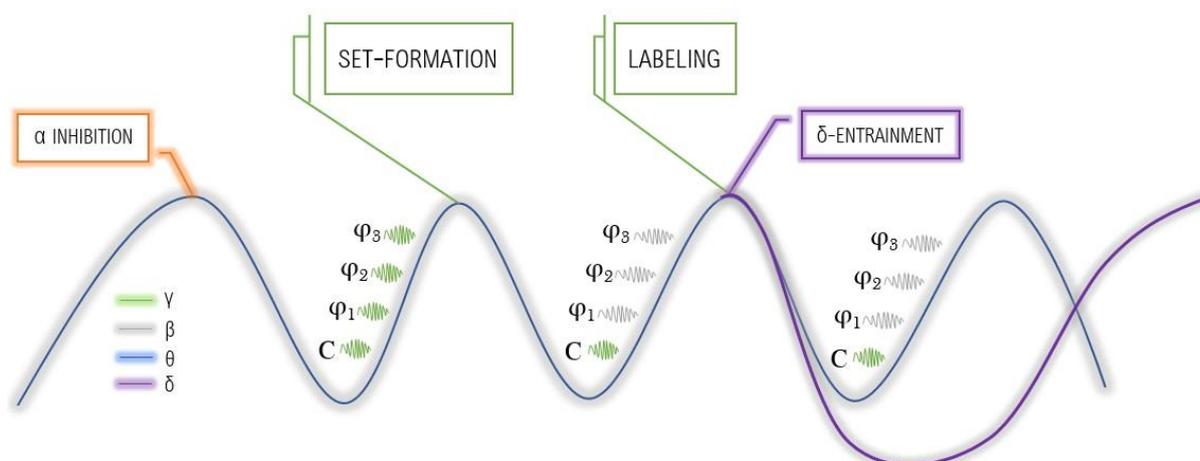


Figure 1: A multiplexing algorithm for feature-set construction. ‘C’ denotes Case feature, ‘ ϕ ’ refers to ϕ -features (Person, Number, Gender). During the encoding of the feature-set, the initial features are represented at the most preferred phase of θ (the trough), resulting in cross-frequency coupling.

In Figure 1, after inhibition reduces over the θ cycle the most excitable representation would be itemized through low-middle γ , followed sequentially by other, less excitable clusters (the right-hand side of the figure detailing the role of δ will be returned to below).⁴ Certain of these γ clusters would then slow to β to be maintained as the ongoing structure’s phrasal identity. After the feature-sets are constructed, phase resetting θ would induce a pause in γ and β activity and, as a result, a γ and β phase reset (Teschke & Karhu, 2000). This would determine the composition of the feature-set, completed after θ phase resetting. The process of phase resetting involves the re-alignment of ongoing oscillatory phases in relation to a reference point. This reference is either endogenous or exogenous (Voloh & Womelsdorf, 2016), and so in the case of generating (sets of) feature-sets during, for instance, internal monologue, the ‘cue’ itself would be endogenous (see also Murphy 2016c for a similar proposal applied to the domain of pragmatics).

During the construction of each set, a ‘check list’ of items would be sent downstream to regions oscillating at slower rhythms to be interpreted in a strict, linear sequence. This model presupposes that a given cluster (or indeed a given neuron within a cluster) will only fire once during the slow cycle, something which at least approximates neurobiological plausibility in that spikes and bursts are followed by strong after-hyperpolarization currents which are

⁴ I should stress that there will certainly still be a need to invoke processes such as cultural evolution to account for the ultimate complexity of the grammatical system acquired by speakers, but this algorithmic model can at least act as the foundation of this linguistic knowledge.

normally a consequence of Ca-activated K currents which last ~ 100 ms, hence reducing the chances of multiple within-cycle firings (Storm, 1990).

As mentioned above, certain of these γ clusters would slow to β to determine how the feature-set is stored in the existing 'cognitive set'. Reconciling any cartographic neurolinguistic model with the present oscillomic algorithm could take a number of forms, but perhaps the most parsimonious and empirically adequate direction would be to assume that after a phrase has been constructed via cross-frequency coupling feature-set construction (implicating temporal regions of the ventral stream like the medial temporal lobe), regions along the dorsal stream firing at β (likely regions closer towards the inferior frontal gyrus) would be able to synchronise with the cortico-basal ganglia-thalamic loop via phase-phase coupling and transfer the categorised set to be maintained through an increasing β rhythm. Regions in the left inferior frontal cortex typically seen as the 'seat of syntax' would consequently become buffering zones where particular multiplexed cycles are interpreted, hence their increased activity during fMRI scanning in response to hierarchical linguistic structures.

With the exception of this claim about β - β coupling, the present oscillomic model, and the views expressed in the neurolinguistics literature more generally, do not make any empirical claims about the function of phase coupling between identical rhythms. For instance, Kaplan, Bush, Bonnefond, Bandettini, Barnes, Doeller and Burgess (2014) discovered θ phase coupling between medial prefrontal cortex and medial temporal lobe during spatial memory recall, and θ - θ phase coupling would also be a possibility, for instance, between parahippocampal regions and the prefrontal cortex, although the precise functional role of this form of coupling remains an open question.

The property-attribution feature of labeling (i.e. attributing to a constructed set a particular computational identity, such as a DP or VP) can be explained through the above $\{\delta\{\theta(\gamma/\beta)\}\}$ code. But what about the other core feature, cyclicity? I suggest that this is achieved through β increases as phrases are constructed and labeled, with each 'old', already-constructed phrase being maintained by β as the newer phrases are constructed by the θ - γ code and selective γ decreases to β .

The particular kind of coupling relationship which could most effectively implement the above model is found in Figure 2: Phase-frequency cross-frequency coupling (D in Figure 2) ensures that the number of cycles of the faster rhythm correlates with the specific phase of the slower rhythm, while phase-power coupling ensures a correlation between the amplitude of the faster rhythm and the phase of the slower rhythm. Both of these coupling types could implement the current oscillomic model. As claimed above, cross-frequency coupling could coordinate activity across distant cortical areas as a way of integrating information from different representational domains, giving rise to the combinatoric power of linguistic generativity.

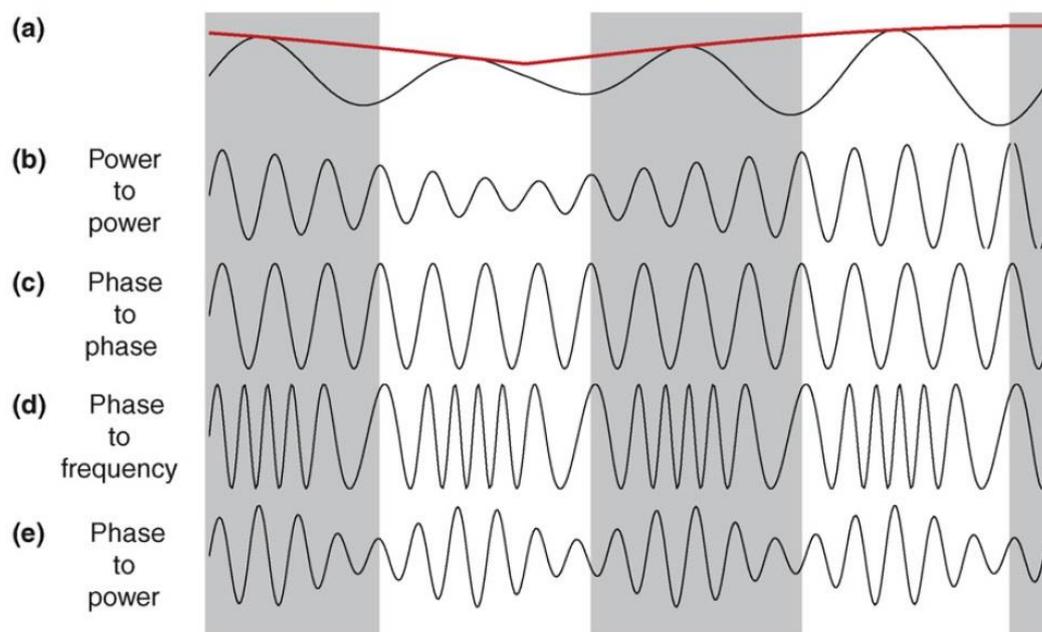


Figure 2: A representation of the different types of interplay slower and faster rhythms exhibit. (A) A theta oscillation and its power denoted by the red line. (B) Power-power: The amplitude of the slower and faster rhythms correlates. (C) Phase-phase: A set number of faster cycles within a given slower phase. (D) Phase-frequency: The faster rhythms correlate with the specific phase of the slower rhythm. (E) Phase-power: The power of the faster rhythm correlates with the phase of the slower rhythm. Reproduced from Jensen and Colgin (2007).

Early research by Sternberg (1966) suggested that short-term memory items are recalled at a rate of one per 30ms, and this appears to be the approximate temporal separation of γ cycles – possibly placing constraints on the number of linguistic features able to be retrieved. Given that top-down, higher-level processes involved in language comprehension begin to occur around 200-600ms post-utterance (Skeide & Friederici, 2016), this presumably presents these γ rhythms with enough time to extract a number of features before top-down processes (such as lexical-semantic categorisation and phrase structure reconstruction, coordinated by slower rhythms) end and bind them into feature-sets. This permits a natural transition to the well-established findings of the cartographic literature, which have shown that 200-400ms post-stimulus lexical information is sent from the left anterior superior temporal gyrus and superior temporal sulcus to BA 45 and BA 47 via the fronto-occipital fasciculus, at which point semantic relations between lexical feature-sets is determined via interactions with the inferior parietal cortex (Binder, Desai, Graves, & Conant, 2009).

A potentially interesting topic for research surrounds whether each stored γ item/representation within the slower rhythm is maintained with equal accuracy, or whether a degree of decay occurs depending on the circuits involved, and indeed whether this would influence the retrievability and interpretability of a given feature in comparison with its neighbours. Increases in γ , nested within θ , have been found across working memory maintenance tasks, including visual (Roux & Uhlhaas, 2014), auditory (Kaiser, Rahm, & Lutzenberger, 2009) and somatosensory (Haegens, Osipova, Oostenveld, & Jensen, 2010), suggesting that this general mechanism can be implemented via distinct neural codes triggering domain-specific representations.

The next issue which needs to be addressed concerns the regions involved in γ -itemisation during feature retrieval. Motivations for assuming that the stored γ -individuated features are widely distributed across the cortex come, most recently, from Keene, Bladon,

McKenzie, Liu, O'Keefe, and Eichenbaum (2016). This study of object-context associations in rats showed that all task dimensions (object position, identity and context) were encoded in every parahippocampal processing stream they investigated: the medial entorhinal cortex, the lateral entorhinal cortex and the perirhinal cortex. This degree of representational diversity across the hippocampus was present even at the single-cell level; neurons traditionally assumed to be 'spatial' cells (e.g. grid cells) were often involved in object identity, in the same way that the perhaps ill-named 'place cells' can also be involved in object encoding. It is therefore likely that semantic features triggered during sentence comprehension are also widely distributed and not specified to a particular language-relevant cortical or subcortical region. The subcellular format of the γ -itemisation process remains to be explored, however recent work by Kastellakis, Silva, and Poirazi (2016) provides something of a first step in developing an algorithmic model of associative memory formation by probing into the mechanisms underlying the linking of memories of different strengths. Such memories appear to exhibit synaptic co-clustering within the dendrites of neurons common to each memory.

$\{\theta(\gamma)\}$ coupling in entorhino-hippocampal regions has been shown to be crucial for memory recall (Schomburg, Fernandez-Ruiz, Mizuseki, Berenyi, Anastassiou, Koch, & Buzsaki, 2014), but reasons to believe that the $\{\theta(\gamma)\}$ code is causally implicated in memory retrieval and maintenance (and does not simply correlate with some experimental manipulation) come from Vosskuhl, Huster, and Herrmann's (2015) use of transcranial alternating current stimulation (tACS) to decrease participant's θ such that the $\theta:\gamma$ ratio changed and an abnormally large number of γ cycles could be nested within θ . This resulted in enhanced short-term memory performance (i.e. the storage of information, but not the manipulation of a memorised set of items), however working memory operations themselves (i.e. manipulation of items) were not affected, neither during nor after stimulation (see Figure 3).

This suggests that the cross-frequency coupling documented in memory tasks is not epiphenomenal but is rather representative of a coding scheme and the physical limitations of cognition. Given what has been reviewed above, the reason why working memory operations were not affected by θ modulation in Vosskuhl et al. (2015) may be a result of the fact that this process does not influence the structure of γ -itemization nor does it change the topology of the derived feature-set, it merely expands it.

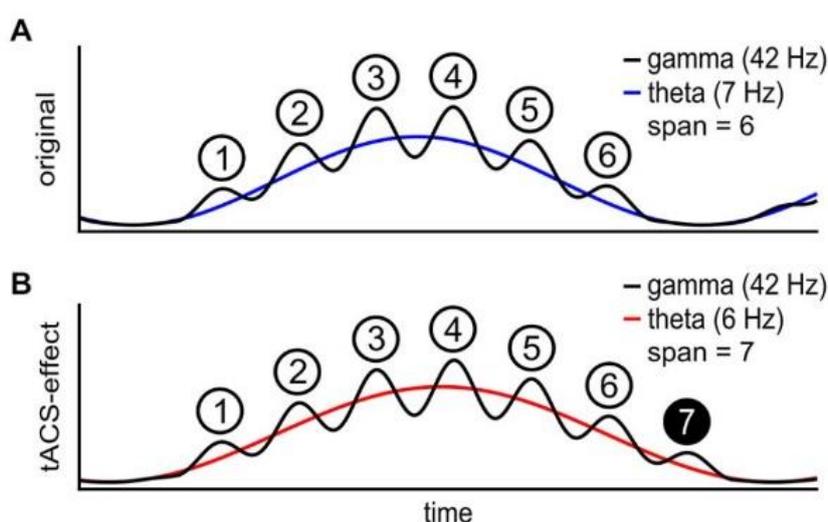


Figure 3: The theta-gamma neural code for working memory (A) and the slowing of theta via transcranial alternating current stimulation (tACS) permitting the maintenance of an additional item (B). Reproduced from Vosskuhl et al. (2015).

Finally, a recent study concerning episodic memory also made a small step towards the types of goals for neurolinguistics outlined here. Heusser, Poeppel, Ezzyat, and Davachi (2016) showed that episodic sequence memory is supported by a θ - γ phase code, such that ‘elements within an experience are represented by neural cell assemblies firing at higher frequencies (gamma) and sequential order is encoded by the specific timing of firing with respect to a lower frequency oscillation (theta)’. This should surely boost the confidence of language scientists trying to show that some form of phase-amplitude coupling is responsible for basic aspects of syntactic and semantic feature-set composition. Given that baboons have recently been shown to be capable of accurately storing the linear position of single episodes (Noser & Byrne, 2015), a comparative oscillomic approach to episodic memory could easily be adopted (for instance, of the kind proposed in Murphy 2016b).

2.4 α -Inhibition

The roles of δ , θ , β and γ in language have been discussed so far. But what of α ? Due to the inherently inhibitory nature of this rhythm (generated, for instance, via pulvinar connectivity with early/visual parietal cortex), it is also likely that it inhibits a given region permitting only the most excitable representations to be triggered. Along with the role attributed to it above of ‘generating’ the initial γ -itemization process, the inhibition and information gating capacities of α could contribute to the efficient coordination of the $\{\theta(\gamma)\}$ coupling model. The α band would therefore act to shield the ongoing concatenation of features from irrelevant information, otherwise excitable (a form of ‘protection’, for Roux and Uhlhaas (2014)). This would constitute a particular implementation of the ‘inhibition-timing hypothesis’ of Klimesch, Sauseng, and Hanslmayr (2007), according to which α can inhibit task-irrelevant neural circuits, increasing in amplitude over irrelevant regions. For instance, Friese, Köster, Hassler, Martens, Trujillo-Barreto, and Gruber (2013) discovered that successful memory encoding not only yielded enhanced $\{\theta(\gamma)\}$ cross-frequency coupling, but also decreased prefrontal and occipital α .⁵ Likewise, Michelmann, Bowman, and Hanslmayr (2016) found that when subjects mentally replayed a short sound or video clip, α decreases were found in sensory-specific regions. Using simulated neural networks, Gips, van der Eerden, and Jensen (2016) also showed that inhibitory α modulations coupled to γ serve to temporally segment visual information, preventing an overload of information. Finally, α decreases at right fronto-temporal sites were found when clear syllables were temporally expected, with a longer foreperiod duration (Wilsch, Henry, Herrmann, Maess, & Obleser, 2015). These expectancy effects also appear in language, with increased semantic predictability leading to reduced parieto-occipital α (Wöstmann, Herrmann, Wilsch, & Obleser 2015).

The finding that α is also generated in the thalamus and hippocampus (Buffalo, Fries, Landman, Buschman, & Desimone, 2011) lends further support to the role of subcortical structures in language comprehension, and the spatial proximity of thalamic and hippocampal α to θ and β sources suggests that the present oscillomic model could be implemented highly efficiently, with minimal conduction delays (see also Kleen, Testorf, Roberts, Scott, Jobst, Holmes, & Lenck-Santini (2016)). The susceptibility of particular circuits to synchronise with α is modulated by cholinergic and serotonergic mechanisms alongside glutamatergic afferents acting via metabotropic receptors (Uhlhaas, Haenschel, Nikolic, & Singer, 2008). Both metabotropic glutamate receptors (mGluR) and muscarinic acetylcholin receptors (mAChR)

⁵ See also Kaplan et al. (2014) for evidence of the role of $\{\theta(\gamma)\}$ cross-frequency coupling in spatial memory retrieval, with their θ source being the medial temporal lobe.

generate thalamo-cortical α , with this distinction being of particular functional relevance: Vijayan and Kopell (2012) tested a conductance-based thalamic model of awake α which demonstrated that mAChR-generated α supports information processing during tasks, while mGluR-generated α performs the above discussed role of shutting out interfering information.

Thalamic α has also been implicated in modulating cortical γ power, and is also suited to synchronize distinct cortical regions oscillating at α (Gips et al., 2016), increasing the likelihood that it plays an important role in phrase structure building and semantic composition. Finally, a recent verbal generation task by Wojtecki, Elben, Vesper and Schnitzler (2016) using EEG found θ - α power increases (i.e. 6-12Hz) and enhanced θ - α coherence between the subthalamic nucleus and frontal sites, with power increasing with performance on the task.

Thalamic, hippocampal and frontal α and θ rhythms may consequently act as, respectively, inhibitory and control processes which modulate γ -related processes involved in the retrieval and activation of language-relevant features, with β then being employed in the maintenance of existing feature-sets in memory. Altogether, this suggests that linguistic communication and the interpretation of speech/gesture/sign results in multiple brains effectively being coupled together, their oscillatory activity in some degree of synchrony.

Other studies can shed further light on the oscillatory dynamics employed by the language system. Hanslmayr, Staresina, and Bowman (2016) review the experimental literature from rodents and humans and suggest a general trend. While hippocampal $\{\theta(\gamma)\}$ synchronisation mediates the binding of distinct episodic memory representations, the desynchronisation of slower neocortical rhythms (α and β) also appears to mediate the encoding of episodic memories. Once again, we find the potentially inhibitory role of α in aiding successful memory encoding and retrieval by other regions of the brain. The hippocampal synchronisation system therefore appears to bind information, while the neocortical desynchronisation system stores the representational content.

2.5 Recursively Nesting Feature-Sets

One of the human-unique aspects of language is its featurally rich lexical representations, which cannot be reduced to simplex or binary structures but are rather composed of a cluster of distinct syntactic, semantic and phonological features. This level of representational complexity could possibly and feasibly be generated by more widespread cross-frequency coupling yielding greater levels of representational information than that permitted in the brains of other primates. Moreover, there appear to be human-unique levels of cross-frequency coupling diversity in the neocortex (Maris, Fries, & van Ede, 2016), with both phase and frequency being modulated to transfer information stored in local ensembles across distributed networks. In this sense, the computational properties of brain rhythms appear able to implement some (perhaps all) of the core syntactic and semantic operations of language.

Although phase-amplitude coupling is most commonly found between θ and γ , recent work suggests that θ can also entrain to δ in the human brain (Miller, Hermes, Honey, Sharma, Rao, den Nijs, Fetz, Sejnowski, Hebb, Ojemann, Makeig, & Leuthardt, 2010; Maris, van Vugt, & Kahana, 2011). Given experimental findings that δ can entrain to the full range of hierarchical linguistic structures from syllables to phrases and sentences (Ding et al., 2016), the discovery of human-specific $\{\delta(\theta)\}$ phase-amplitude coupling is potentially of great significance. I would like to suggest that the above $\{\theta(\gamma)\}$ feature-set multiplexing algorithm can itself be embedded within δ cycles originating within regions shown to entrain to hierarchical linguistic structures and which can also oscillate at slow δ frequencies; namely, the superior temporal gyrus and left inferior frontal cortex (see Figure 1). This additional layer of nesting would then give rise to the additional layer of hierarchy seen in human syntax, which

goes beyond both the phonological syntax of birdsong and the semantically atomic structures of primate calls and gestures:

LINGUISTIC HIERARCHY: {PHRASE{LEXICAL ITEM(FEATURES)}}
 OSCILLOMIC HIERARCHY: { δ { θ (γ)}}

Indeed, phase-amplitude coupling is itself not unique to language, let alone humans, being involved in perception, decision-making and navigation (Lakatos, Karmos, Mehta, Ulbert, & Schroeder, 2005; Kepecs, Uchida, & Mainen, 2006), and so the interactions between distinct types of cross-frequency couplings and the representations they manipulate are instead the likely source of language-specific combinatorial capacities. There is a growing consensus that phase-amplitude coupling can support the phase coding of neural representations through, for instance, the categorisation of visual objects (Watrous, Deuker, Fell, & Axmacher, 2015), and given the inherently semantic nature of the categorisation processes documented by Watrous et al. – faces, tools, houses and scenes – it would be somewhat surprising if this form of cross-frequency coupling is not also involved in the interpretation of linguistic structures. As the authors of the study put it, exploring cross-frequency coupling ‘may provide new avenues for decoding the human representational system’.

The emergence of these species-specific oscillatory nestings would constitute the exclusive content of the ‘Small Bang’, as it was termed in Murphy (2015a); the neural alterations required to bring about modern *homo sapiens* and what linguists refer to as narrow syntax, the basis of Tattersall’s (2016) ‘symbolic’ capacity. The Labeling Hypothesis is therefore given renewed support.

A topic for future research concerns the physiological properties of { δ (θ)} and { θ (γ)} coupling, their developmental profile, and whether their emergence can be explained within certain evolutionary frameworks, such as the ‘globularity’ hypothesis (Benítez-Burraco & Murphy, 2016; Murphy & Benítez-Burraco, 2016) or perspectives oriented around human-specific myelination rates (Murphy, 2015b). Parsing research by Momma (2016) investigating the time course of syntactic priming effects has even suggested that structure-building units during production are very small, going against much of the production literature which claims that pre-formed templates are large. The above basic oscillomic schema (accounting as it does only for labeled units) may therefore carry considerable explanatory reach both in terms of production and comprehension.

To detail the oscillomic process of hierarchical phrase structure building in a more familiar way, consider Figure 4. In the four-step procedure outlined here, a determiner and noun are encountered and their respective feature-sets are triggered by the above α -supported and θ -coupled algorithm. The γ -itemized clusters responsible for identifying the phrase as a DP then slow to β , and the entire complex is nested within δ . The phrase is then maintained in memory (a necessary feature for labeling for occur) via an increasing β rhythm. The same procedure occurs for the next phrase, ν P, and the two β -maintained identities are stored together and interpreted in anterior portions of Broca’s area as the larger multi-phrasal unit, TP.

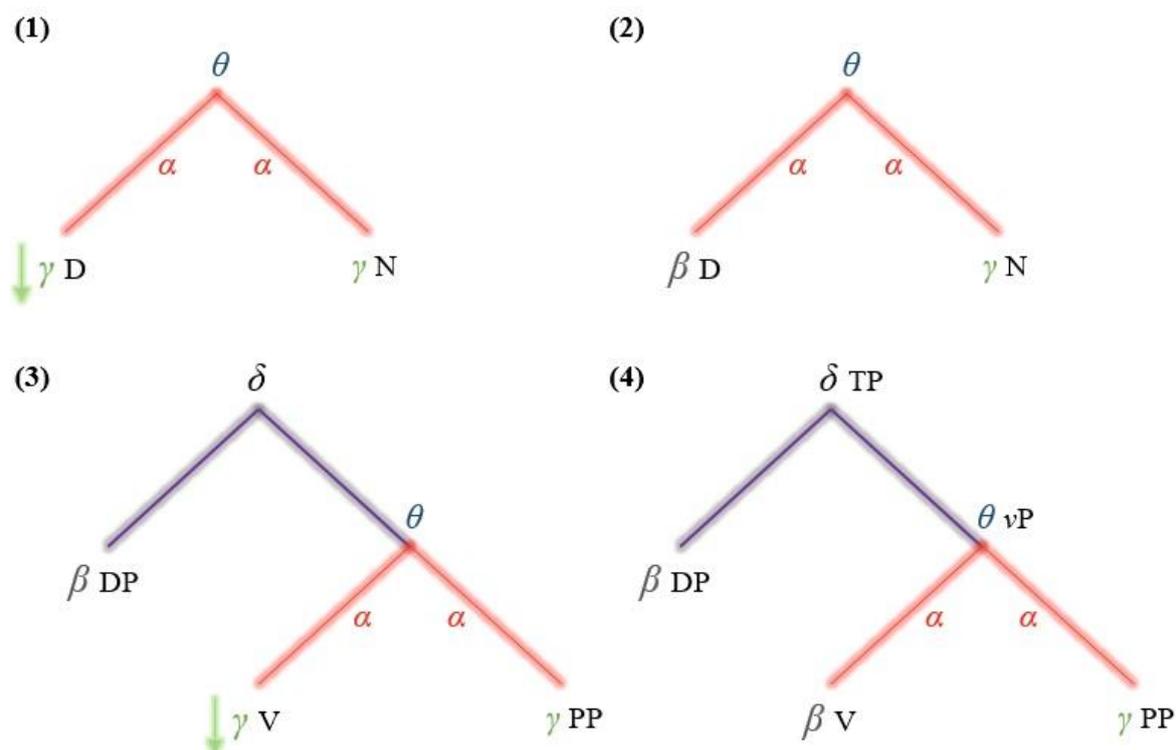


Figure 4: An oscillomic tree representing the putative rhythms responsible for particular lexical and phrasal structures according to the present multiplexing algorithm. ‘TP’ denotes Tense Phrase, ‘vP’ denotes Verb Phrase (e.g. ‘swam in the river’), ‘DP’ denotes Determiner Phrase (e.g. ‘the man’), and ‘PP’ denotes Prepositional Phrase (e.g. ‘in the river’). Regions of generation: Delta = left inferior frontal regions, anterior and middle temporal regions. Theta = parahippocampal regions. Alpha = thalamic and occipital regions. Beta = anterior regions of Broca’s area and the basal ganglia. Gamma = cross-cortical sites storing features in long-term memory. Following the findings in Ding et al. (2016), it is likely that the delta peak in (3) is at 2Hz due to it being a simple phrase, whereas the peak in (4) would shift to 1Hz due to its sentential nature.

If coupling across cortical and subcortical oscillations is responsible for the hierarchical combination of computations at the syllabic and phonemic levels, ‘restoring the natural arrangement of phonemes within syllables’ (Hyafil, Fontolan, Kabdebon, Gutkin, & Giraud, 2015), and if the present multiplexing algorithm is an accurate representation of syntactic and semantic feature composition, then we can conclude that oscillations are also responsible for restoring the natural arrangement of features within words.⁶

As discussed, I am assuming that α plays an important inhibitory role, but I additionally want to suggest that it is functionally closely related to θ cycles such that α can coordinate feature-sets organized by θ . Since α is a crucial part of domain-general attentional mechanisms, I will adopt the claim in Jensen, Gips, Bergmann and Bonnefond (2014) that direct attention is allocated only to the first items in a given θ - or α -constructed sequence, and that the final (and hence least excitable) items are processed pre-attentively. Along with explaining a number of visual phenomena (see Jensen et al., 2014), it is possible that this mechanism is responsible for

⁶ Oscillomic research into the development of attentional mechanisms will be crucial here, with recent work showing a direct correlation between the emergence of endogenous attentional mechanisms (mind-internal directed attention, in contrast to exogenous attention, directed at the environment) and the ability to track non-adjacent morphosyntactic dependencies, both emerging at around 12-15 months (de Diego-Balaguer, Martinez-Alvarez, & Pons, 2016).

certain facts about language, such that, quite often, only certain features of a given word or phrase come to attention during sentence comprehension and are made ‘prominent’. The firing of particular neural clusters representing a given feature X could also engage fast GABAergic inhibition (a result of γ activity) and inhibit the firing of clusters representing feature Y . Indeed, it has been found that patients with attention deficit hyperactivity disorder exhibit impaired control of posterior α (Mazaheri, Coffey-Corina, Mangun, Bekker, Berry, & Corbett, 2010), and it is possible that these sorts of oscillatory connectopathies could explain deficits in cognitive functions reliant to some extent on attention.

These assumptions are supported by a recent self-paced reading study which monitored oscillatory dynamics. Vignali, Himmelstoss, Hawelka, Richlan, and Hutzler (2016) had participants read syntactically and semantically well-formed sentences, sentences containing a semantic violation, and word lists. Fixations at semantically unrelated words elicited lower β desynchronisation, while γ power increased as well-formed sentences were processed. This γ effect was not found with word lists. In addition, θ power increased in the 300-800ms window after sentence onset in well-formed sentences, but not during word lists, lending support to the present hypothesized role of θ in memory retrieval and syntactic ‘chunking’ operations.⁷

If the present hypothesis about human-specific forms of δ -entrainment is correct, then non-human primates should exhibit markedly distinct oscillatory profiles. As reviewed in Murphy (2016b), the current experimental literature suggests that in both humans and monkeys, the construction of an internal sequence leads to β increases, maintenance failure/disruption leads to β decreases, and sequence execution results in subsequent γ increases. Yet as Figure 5 indicates, there also appears to be a less broad range of oscillatory couplings available in monkeys with respect to the crucial representational properties implicated in the forms of cognitive operations required for interpreting and producing call sequences.

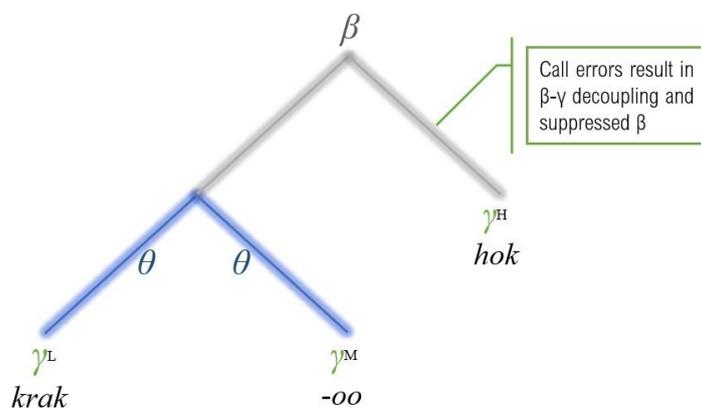


Figure 5: An oscillomic tree of the rhythms responsible for monkey call sequences (from Murphy 2016b). The superscript next to each γ cycle denotes low, medium and high γ (sharp wave-ripples), with γ power scaling with the number of calls held in memory. Each γ -generated item would couple with hippocampal θ (see Lee, Simpson, Logothetis and Rainer (2005) and Jutras, Fries and Buffalo (2013) for the role of this rhythm in monkey working memory) in order to achieve the binding of morphological elements ('krak-oo') before coupling with basal ganglia-

⁷ A further advantage of the present model is that it points to the compatibility between dynamical systems approaches to the brain and more traditional computational models which treat the brain as a digital computer. These perspectives are not incommensurable if we assume that particular discrete computational operations are executed via dynamical properties of neural oscillations.

initiated and striatal β , which would in turn increase in amplitude until the event of either an erroneous action sequence (call production) or the termination of the call series. This hypothesis is supported by studies claiming that β activity operates as a general coupling mechanism of assembly activity across brain structures (Fujioka, Trainor, Large, & Ross, 2012). Note that monkey oscillomic trees lack labels, being composed of call pair-combinations ('krak hok') and morphological elements ('-oo').

Notable support for the model in Figure 5 comes from Ramirez-Villegas, Logothetis, and Besserve's (2015) study of sharp wave-ripples in the macaque hippocampal CA3-CA1 network, which credited a role for γ rhythms in memory reactivation, transfer and consolidation (findings echoed in Kaplan et al., 2016). As mentioned, it seems that language-relevant δ -entrainment is not easily achieved in non-humans. For instance, while the rat globus pallidus can nest β and γ rhythms within a slower δ rhythm, Dejean, Arbuthnott, Wickens, Le Moine, Boraud, and Hyland's (2011) electrode recordings of local field potentials indicated that when such nesting did occur β and γ were negatively correlated and at anti-phase, with the phase positions of both the β and γ clusters being significantly different. The rat oscillome and its intrinsic rhythmic hierarchies may exhibit reduced nesting capabilities relative to the human oscillome – and, indeed, relative to the primate oscillome more generally, given Charvet, Hof, Raghanti, van der Kouwe, Sherwood, and Takahashi's (2016) findings of expanded anterior to posterior cortico-cortical tracts in primates relative to other mammals. These species-specific oscillomic interactions may lay the foundations of what Hauser and Watumull (2016) term the 'Universal Generative Faculty' common to language, mathematics, morality and music; a combinatorial system constructing a potentially infinite array of hierarchically organised sequences interfacing with distinct representational domains.

Connectivity issues would also be crucial to this account. It may ultimately be found that the $\{\delta\{\theta(\gamma)\}\}$ code is not strictly human-specific, but rather that the regions involved in long-range cross- and sub-cortical nesting are unique in their rich, cross-modular connections. Since frequency bands themselves fulfil various functional roles depending on their region of generation, it is possible that the present neural code can be found in some form or another across a range of mammalian species but that the particular regions involved in humans are widespread enough to produce the forms of rich cross-modularity exhibited by language.

In any event, these findings lead to direct predictions for the monkey oscillome given what is known about the combinatorial capacities of monkeys. Schlenker, Chemla, Schel, Fuller, Gautier, Kuhn, Veselinović, Arnold, Căsar, Keenan, Lemasson, Ouattara, Ryder, and Zuberbühler (2016), for instance, show that monkeys can combine two word-like elements, but cannot then combine this set with another atomic element. This would require a concatenation operation, a representational base ('lexicon'), and finally a temporary workspace where the combined set can be stored in memory. Rizzi (2016) calls this a 2-merge system (word-phrase merger), while monkeys seem limited to 1-merge systems (word-word) – although they may be capable of 2-merge systems if one defines a *krak-oo* conjunction followed by another distinct call as a type of phrase-word combination. Human language, in contrast, is a 3-merge system, permitting not just word-phrase merger, but phrase-phrase merger, requiring a secondary workspace in addition to the temporary workspace required by 2-merge systems. Nested rhythmic activity of the kind discussed here might act as the foundation of this secondary workspace, with a greater number of nested couplings seemingly available to the human oscillome yielding the greater number of stored representations in memory, although the precise details of this dual memory buffer (both with respect to anatomic connectivity and oscillatory dynamics) currently remain elusive.

interaction between these two layers. Displacement and agreement, for instance, connect items from across the two layers:

(5) What did you eat ___?

In this instance, a lexical item has been displaced to the functional layer, facilitating novel conceptual combinations and hierarchical relations. Cross-frequency interactions between the structures responsible for storing representations from each layer may give rise to this L-F-L-F pattern.

There does, however, seem to be a certain degree of disagreement concerning this oscillomic approach to language. Goucha, Zaccarella and Friederici (2016), for instance, make the following claim:

Alternative mechanisms based on brain oscillations have been proposed as a crucial element for the emergence of language (Murphy, 2015b) ... However, those mechanisms seem to already be in place in other species. For example, despite the crucial brain expansion that took place in primates and especially humans compared to other mammals, the rhythmical hierarchy of oscillations is mainly kept unchanged (Buzsáki et al., 2013). As Friederici and Singer (2015) pinpoint, the basic neural mechanisms behind cognition through the hierarchical embedding of oscillations are transversal across animals.

This is a perhaps unwarranted criticism since in the paper they discuss I cite the same authors as Goucha, Zaccarella and Friederici, pointing out that while the hierarchy of brain rhythms themselves may be preserved, it is crucially their cross-frequency coupling relations which are human-specific. The authors also make no attempt to explore the various functional roles of the ‘rhythmical hierarchy of oscillations’ in human and animal cognition, and it seems as if simply noting that Friederici and Singer (2015) ‘pinpoint’ something which is in fact well-known within neuroethology is a sufficient reason to reject any forthcoming linking hypotheses concerning linguistic computation and neural oscillations. Notice how in their claim that ‘the rhythmical hierarchy of oscillations is mainly kept unchanged’, one particular word is operative: *mainly*. No attempt is made by Goucha et al. to explore oscillatory features which are in fact human-specific, and what their functional implications may be for language and cognition.

Lastly, there are various ways to experimentally test the present model. Along with using MEG to compare word lists to acceptable phrases and comparing phrases of legal words to phrases of non-words (which would probe into the neural correlates of labeling), there are also particular stimuli types involving semantic rather than syntactic manipulations which could be of use. For instance, there are certain sentences permitting copredication which involve nouns being modified by multiple, semantically distinct adjectives (e.g. a *man* can be tall [PHYSICAL] but also happy [MENTAL STATE], and a *book* can be interesting [INFORMATION] but also blue [PHYSICAL]):

- (5) Distinct senses; legal noun: The tall and happy **man** left the building.
- (6) Related senses; legal noun: The tall and skinny **man** left the building.
- (7) Distinct senses; illegal noun: The tall and happy **mulg** left the building.
- (8) Related senses; illegal noun: The tall and skinny **mulg** left the building.

This stimuli set would reveal the oscillatory dynamics behind two major processes: (i) The maintenance in working memory of an ongoing sentential structure, and (ii) the attribution

of distinct semantic representations to a single nominal. Performing an analysis at the point of the word *left* will also be revealing, since this is the point when subjects will need to syntactically ‘reanalyse’ or ‘re-label’ the ongoing construction from a simple DP to a more complex TP.

3 Conclusion

Accruing evidence from independent domains in neuroscience and broader areas of biology converge on the suggestion that human-specific hierarchical interactions between brain rhythms may have brought about the emergence of language. Overall, the computational roles ascribed here are supported by a range of experimental findings, such as the general claims in Ketz, Jensen, and O’Reilly (2015) that θ is related to recollective/episodic memory processes, β is related to familiarity and executive control, and α is related to the gating of sensory information into higher order systems. Even something seemingly as simple as Merge or semantic composition requires complex interactions between a range of oscillations and regions. A number of research directions open up at this point, taking either the route of theoretical neurobiology or experimental linguistics, through which the neurocomputational basis of language may well reveal itself.

References

- Akam, T., & Kullmann, D.M. (2014). Oscillatory multiplexing of population codes for selective communication in the mammalian brain. *Nature Reviews Neuroscience*, *15*, 111-122.
- Bartolo, R., & Merchant, H. (2015). β oscillations are linked to the initiation of sensory-cued movement sequences and the internal guidance of regular tapping in the monkey. *Journal of Neuroscience*, *35*(11), 4635-4640.
- Bartolo, R., Prado, L., & Merchant, H. (2014). Information processing in the primate basal ganglia during sensory-guided and internally driven rhythmic tapping. *Journal of Neuroscience*, *34*, 3910-3923.
- Bastiaansen, M., & Hagoort, P. (2015). Frequency-based segregation of syntactic and semantic unification during online sentence level language comprehension. *Journal of Cognitive Neuroscience*, *27*(1), 2095-2107.
- Benítez-Burraco, A., & Murphy, E. (2016). The oscillopathic nature of language deficits in autism: from genes to language evolution. *Frontiers in Human Neuroscience*, *10*, 120.
- Berwick, R., & Chomsky, N. (2016). *Why Only Us: Language and Evolution*. Cambridge, MA: MIT Press.
- Binder, J.R., Desai, R.H., Graves, W.W., & Conant, L.L. (2009). Where is the semantic system? A critical review and meta-analysis of 120 functional neuroimaging studies. *Cerebral Cortex*, *19*, 2767-2796.
- Boeckx, C. (2016). A conjecture about the neural basis of recursion in light of descent with modification. *Journal of Neurolinguistics* <http://dx.doi.org/10.1016/j.jneuroling.2016.08.003>.
- Boeckx, C., & Theofanopoulou, C. (2015). Commentary on: Labels, cognomes, and cyclic computation: an ethological perspective. *Frontiers in Psychology*, *6*, 784.
- Brown, J.W. (2014). The tale of the neuroscientists and the computer: why mechanistic theory matters. *Frontiers in Neuroscience*, *8*, 349.
- Buffalo, E.A., Fries, P., Landman, R., Buschman, T.J., & Desimone, R. (2011). Laminar differences in gamma and alpha coherence in the ventral stream. *PNAS*, *108*, 11262-11267.
- Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron*, *80*(3), 751-764.
- Charvet, C.J., Hof, P.R., Raghanti, M.A., van der Kouwe, A.J., Sherwood, C.C., & Takahashi, E. (2016). Combining diffusion MR tractography with stereology highlights increased cross-cortical integration in primates. *Journal of Comparative Neurology* doi:10.1002/cne.24115.
- Chomsky, N. (1995). *The Minimalist Program*. Cambridge, MA: MIT Press.
- Chomsky, N. (2000). *New Horizons in the Study of Language and Mind*. Cambridge: Cambridge University Press.
- Cowan, N. (2001). The magical number 4 in short-term memory: a reconsideration of mental storage capacity. *Behavioral and Brain Sciences*, *24*(1), 87-114.
- De Diego-Balaguer, R., Martinez-Alvarez, A., & Pons, F. (2016). Temporal attention as a scaffold for language development. *Frontiers in Psychology*, *7*, 44.

- Dean, H.L., Hagan, M.A., & Pesaran, B. (2012). Only coherent spiking in posterior parietal cortex coordinates looking and reaching. *Neuron*, *73*(4), 829-841.
- Dejean, C., Arbutnot, G., Wickens, J.R., Le Moine, C., Boraud, T. & Hyland, B.I. (2011). Power fluctuations in beta and gamma frequencies in rat globus pallidus: association with specific phases of slow oscillations and differential modulation by dopamine D1 and D2 receptors. *Journal of Neuroscience*, *31*, 6098-6107.
- Ding, N., Melloni, L., Zhang, H., Tian, X., & Poeppel, D. (2016). Cortical tracking of hierarchical linguistic structures in connected speech. *Nature Neuroscience*, *19*, 158-164.
- Ewerdtwalbesloh, J.A., Palva, S., Rösler, F., & Khader, P.H. (2016). Neural correlates of maintaining generated images in visual working memory. *Human Brain Mapping* doi:10.1002/hbm.23313.
- Fernández-Ruiz, A., & Oliva, A. (2016). Distributed representation of 'what' and 'where' information in the parahippocampal region. *Journal of Neuroscience*, *36*(32), 8286-8288.
- Friederici, A.D. (2016). Evolution of the neural language network. *Psychonomic Bulletin & Review* doi: 10.3758/s13423-016-1090-x.
- Friederici, A. D., & Singer, W. (2015). Grounding language processing on basic neurophysiological principles. *Trends in Cognitive Sciences*, *19*(6), 329-338.
- Friese, U., Köster, M., Hassler, U., Martens, U., Trujillo-Barreto, N., & Gruber, T. (2013). Successful memory encoding is associated with increased cross-frequency coupling between frontal theta and posterior gamma oscillations in human scalp-recorded EEG. *NeuroImage*, *66*, 642-647.
- Fujioka, T., Trainor, L.J., Large, E.W., & Ross, B. (2012). Internalized timing of isochronous sounds is represented in neuromagnetic beta oscillations. *Journal of Neuroscience*, *32*, 1791-1802.
- Gips, B., van der Eerden, J.P.J.M., & Jensen, O. (2016). A biologically plausible mechanism for neuronal coding organized by the phase of alpha oscillations. *European Journal of Neuroscience* doi:10.1111/ejn.13318.
- Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience*, *15*(4), 511-517.
- Goucha, T., Zaccarella, E., & Friederici, A.D. (2016). A revival of the *homo loquens* as a builder of labeled structures: neurocognitive considerations. Ms. Max Planck Institute for Human Cognitive and Brain Sciences, Germany.
- Hanslmayr, S., Staresina, B.P., & Bowman, H. (2016). Oscillations and episodic memory: addressing the synchronization/desynchronization conundrum. *Trends in Neurosciences*, *39*(1), 16-25.
- Haegens, S., Osipova, D., Oostenveld, R., & Jensen, O. (2010). Somatosensory working memory performance in humans depends on both engagement and disengagement of regions in a distributed network. *Human Brain Mapping*, *31*(1), 26-35.
- Hauser, M., & Watumull, G. (2016). The universal generative faculty: the source of our expressive power in language, mathematics, morality, and music. *Journal of Neurolinguistics* <http://dx.doi.org/10.1016/j.jneuroling.2016.10.005>.
- Hauser, M., Yang, C., Berwick, R. C., Tattersall, I., Ryan, M. J., Watumull, J., Chomsky, N., & Lewontin, R. C. (2014). The mystery of language evolution. *Frontiers in Psychology*, *5*, 401.
- Haynes, W.I.A., & Haber, S.N. (2013). The organization of prefrontal-subthalamic inputs in primates provides an anatomical substrate for both functional specificity and integration: implications for basal ganglia models and deep brain stimulation. *Journal of Neuroscience*, *33*(11), 4804-4814.
- Heusser, A.C., Poeppel, D., Ezzyat, Y., & Davachi, L. (2016). Episodic sequence memory is supported by a theta-gamma phase code. *Nature Neuroscience* doi:10.1038/nn.4374.
- Hyafil, A., Fontolan, L., Kabdebon, C., Gutkin, B., & Giraud, A.-L. (2015). Speech encoding by coupled cortical theta and gamma oscillations. *eLife*, *10*, 7554.
- Jackendoff, R. (2007). *Language, Consciousness, Culture: Essays on Mental Structure*. Cambridge, MA: MIT Press.
- Jensen, O., & Colgin, L.L. (2007). Cross-frequency coupling between neuronal oscillations. *Trends in Cognitive Sciences*, *11*, 267-269
- Jensen, O., Gips, B., Bergmann, T.O., & Bonnefond, M. (2014). Temporal coding organized by coupled alpha and gamma oscillations prioritize visual processing. *Trends in Neurosciences*, *37*(7), 357-369.
- Jonas, E., & Kording, K. (2016). Could a neuroscientist understand a microprocessor? *bioRxiv* <http://dx.doi.org/10.1101/055624>.
- Jutras, M.J., Fries, P., & Buffalo, E.A. (2013). Oscillatory activity in the monkey hippocampus during visual exploration and memory formation. *PNAS*, *110*(32), 13144-13149.
- Kaiser, J., Rahm, B., & Lutzenberger, W. (2009). Temporal dynamics of stimulus-specific gamma-band activity components during auditory short-term memory. *NeuroImage*, *44*(1), 257-264.
- Kaplan, R., Adhikari, M.H., Hindriks, R., Mantini, D., Murayama, Y., Logothetis, N.K., & Deco, G. (2016). Hippocampal sharp-wave ripples influence selective activation of the default mode network. *Current Biology*, *26*, 1-6.

- Kaplan, R., Bush, D., Bonnefond, M., Bandettini, P.A., Barnes, G.R., Doeller, C.F., & Burgess, N. (2014). Medial prefrontal theta phase coupling during spatial memory retrieval. *Hippocampus*, *24*(6), 656-665.
- Kastellakis, G., Silva, A.J., & Poirazi, P. (2016). Linking memories across time via neuronal and dendritic overlaps in model neurons with active dendrites. *Cell Reports*, *17*, 1491-1504.
- Keene, C.S., Bladon, J., McKenzie, S., Liu, C.D., O'Keefe, J., Eichenbaum, H. (2016). Complementary functional organization of neuronal activity patterns in the perirhinal, lateral entorhinal, and medial entorhinal cortices. *Journal of Neuroscience*, *36*, 3660-3675.
- Kepecs, A., Uchida, N., & Mainen, Z.F. (2006). The sniff as a unit of olfactory processing. *Chemical Senses*, *31*, 167-179.
- Ketz, N.A., Jensen, O., & O'Reilly, R.C. (2015). Thalamic pathways underlying prefrontal cortex–medial temporal lobe oscillatory interactions. *Trends in Neurosciences*, *38*(1), 3-12.
- Kleen, J.K., Testorf, M.E., Roberts, D.W., Scott, R.C., Jobst, B.J., Holmes, G.L., & Lenck-Santini, P-P. (2016). Oscillation phase locking and late ERP components of intracranial hippocampal recordings correlate to patient performance in a working memory task. *Frontiers in Human Neuroscience*, *10*, 287.
- Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition-timing hypothesis. *Brain Research Reviews*, *53*, 63-88.
- Lakatos, P., Karmos, G., Mehta, A. D., Ulbert, I., & Schroeder, C.E. (2008). Entrainment of neuronal oscillations as a mechanism of attentional selection. *Science*, *320*(5872), 110-113.
- Lam, N.H.L., Schoffelen, J.-M., Udden, J., Hulst, A., & Hagoort, P. (2016). Neural activity during sentence processing as reflected in theta, alpha, beta, and gamma oscillations. *NeuroImage* <http://dx.doi.org/10.1016/j.neuroimage.2016.03.007>.
- Lee, H., Simpson, G.V., Logothetis, N.K., & Rainer, G. (2005). Phase locking of single neuron activity to theta oscillations during working memory in monkey extrastriate visual cortex. *Neuron*, *45*, 147-156.
- Lisman, J.E., & Jensen, O. (2013). The theta–gamma neural code. *Neuron*, *77*, 1002-1016.
- Maris, E., Fries, P., & van Ede, F. (2016). Diverse phase relations among neuronal rhythms and their potential function. *Trends in Neurosciences*, *39*(2), 86-99.
- Maris, E., van Vugt, M., & Kahana, M. (2011). Spatially distributed patterns of oscillatory coupling between high-frequency amplitudes and low-frequency phases in human iEEG. *NeuroImage*, *54*, 836-850.
- Martin, C., & Ravel, N. (2014). Beta and gamma oscillatory activities associated with olfactory memory tasks: Different rhythms for different functional networks? *Frontiers in Behavioral Neuroscience*, *8*, 218.
- Mas-Herrero, E., & Marco-Pallarés, J. (2016). Theta oscillations integrate functionally segregated sub-regions of the medial prefrontal cortex. *NeuroImage* doi:10.1016/j.neuroimage.2016.08.024.
- Mazaheri, A., Coffey-Corina, S., Mangun, G.R., Bekker, E.M., Berry, A.S., & Corbett, B.A. (2010). Functional disconnection of frontal cortex and visual cortex in attention-deficit/hyperactivity disorder. *Biological Psychiatry*, *67*, 617-623.
- Michelmann, S., Bowman, H., & Hanslmayr, S. (2016). The temporal signature of memories: identification of a general mechanism for dynamic memory replay in humans. *PLoS Biology*, *14*(8), e1002528.
- Miller, K.J., Hermes, D., Honey, C.J., Sharma, M., Rao, R.P., den Nijs, M., Fetz, E.E., Sejnowski, T.J., Hebb, A.O., Ojemann, J.G., Makeig, S., & Leuthardt, E.C. (2010). Dynamic modulation of local population activity by rhythm phase in human occipital cortex during a visual search task. *Frontiers in Human Neuroscience*, *4*, 197.
- Miyagawa, S., Berwick, R.C., & Okanoya, K. (2013). The emergence of hierarchical structure in human language. *Frontiers in Psychology*, *4*, 71.
- Mohr, J.P., Pessin, M.S., Finkelstein, S., Funkenstein, H.H., Duncan, G.W., & Davis, K.R. (1978). Broca aphasia: pathologic and clinical. *Neurology* *28*: 311-324.
- Momma, S. (2016). Parsing, generation, and grammar. PhD dissertation. University of Maryland.
- Moro, A. (2006). Copular sentences. In M. Everaert & H. van Riemsdijk (Eds), *The Blackwell Companion to Syntax II* (pp. 1-23). Oxford: Blackwell.
- Mukherji, N. (2010). *The Primacy of Grammar*. Cambridge, MA: MIT Press.
- Murphy, E. (2015a). Labels, cognomes and cyclic computation: An ethological perspective. *Frontiers in Psychology* *6*: 715.
- Murphy, E. (2015b). The brain dynamics of linguistic computation. *Frontiers in Psychology*, *6*, 1515.
- Murphy, E. (2016a). The human oscillome and its explanatory potential. *Biolinguistics*, *10*, 6-20.
- Murphy, E. (2016b). Evolutionary monkey oscillomics: Generating linking hypotheses from preserved brain rhythms. *Theoretical Linguistics*, *42*(1-2), 117-137.
- Murphy, E. (2016c). A pragmatic oscillome: aligning visual attentional mechanisms with language comprehension. *Frontiers in Systems Neuroscience*, *10*, 72.
- Murphy, E., & Benítez-Burraco, A. (2016). Language deficits in schizophrenia and autism as related oscillatory connectopathies: an evolutionary account. *Neuroscience & Biobehavioral Reviews* <http://dx.doi.org/10.1016/j.neubiorev.2016.07.029>.

- Narita, H. (2014). $\ast\{t,t\}$. Poster presented at the 32nd West-Coast Conference on Formal Linguistics (WCCFL 32), University of Southern California.
- Nóbrega, V., & Miyagawa, S. (2015). The precedence of syntax in the rapid emergence of human language in evolution as defined by the integration hypothesis. *Frontiers in Psychology*, 6, 271.
- Noser, R., & Byrne, R.W. (2015). Wild chacma baboons (*Papio ursinus*) remember single foraging episodes. *Animal Cognition*, 18(4), 921-929.
- O'Keefe, J., & Nadal, L. (1978). *The Hippocampus as a Cognitive Map*. Oxford: Oxford University Press.
- Poeppel, D. (2012). The maps problem and the mapping problem: two challenges for a cognitive neuroscience of speech and language. *Cognitive Neuropsychology*, 29, 34-55.
- Ramirez-Villegas, J.F., Logothetis, N.K., & Besserve, M. (2015). Sharp wave-ripple complexes in a reduced model of the hippocampal CA3-CA1 network of the macaque monkey. *BMC Neuroscience*, 16(Suppl 1), P15.
- Reuland, E. (2011). *Anaphora and Language Design*. Cambridge, MA: MIT Press.
- Richards, N. (2010). *Uttering Trees*. Cambridge, MA: MIT Press.
- Rizzi, L. (2016). Monkey morpho-syntax and merge-based systems. *Theoretical Linguistics*, 42(1-2), 139-145.
- Roux, F., & Uhlhaas, P.J. (2014). Working memory and neural oscillations: alpha-gamma versus theta-gamma codes for distinct WM information? *Trends in Cognitive Sciences*, 18, 16-25.
- Schlenker, P., Chemla, E., Schel, A.M., Fuller, J., Gautier, J.-P., Kuhn, J., Veselinović, D., Arnold, K., Căsar, C., Keenan, S., Lemasson, A., Ouattara, K., Ryder, R., & Zuberbühler, K. (2016). Formal monkey linguistics. *Theoretical Linguistics*, 42(1-2), 1-90.
- Schomburg, E.W., Fernandez-Ruiz, A., Mizuseki, K., Berenyi, A., Anastassiou, C.A., Koch, C., Buzsaki, G. (2014). Theta phase segregation of input-specific gamma patterns in entorhinal-hippocampal networks. *Neuron*, 84, 470-485.
- Seung, S. (2012). *Connectome: How the brain's wiring makes us who we are*. Boston: Houghton, Mifflin, Harcourt.
- Skeide, M.A., & Friederici, A.D. (2016). The ontogeny of the cortical language network. *Nature Reviews Neuroscience*, 17, 323-332.
- Sternberg S. (1966). High-speed scanning in human memory. *Science*, 153(736), 652-654.
- Storm, J.F. (1990). Potassium currents in hippocampal pyramidal cells. *Progress in Brain Research*, 83, 161-187.
- Sweeney-Reed, C.M., Zaehle, T., Voges, J., Schmitt, F.C., Buentjen, L., Kopitzki, K., Hinrichs, H., Heinze, H.-J., Rugg, M.D., Knight, R.T., & Richardson-Klavehn, A. (2015). Thalamic theta phase alignment predicts human memory formation and anterior thalamic cross-frequency coupling. *eLife*, 4, e07578.
- Tattersall, I. (2016). How can we detect when language emerged? *Psychonomic Bulletin & Review* doi:10.3758/s13423-016-1075-9.
- Tesche, C.D., & Karhu, J., (2000). Theta oscillations index human hippocampal activation during a working memory task. *PNAS USA*, 97, 919-924.
- Theyel, B.B., Llano, D.A., & Sherman, S.M. (2010). The corticothalamocortical circuit drives higher-order cortex in the mouse. *Nature Neuroscience*, 13(1), 84-88.
- Tomalin, M. (2006). *Linguistics and the Formal Sciences: The Origins of Generative Grammar*. Cambridge: Cambridge University Press.
- Tomalin, M. (2007). Reconsidering recursion in syntactic theory. *Lingua*, 117, 1784-800
- Uhlhaas, P.J., Haenschel, C., Nikolic, D., & Singer, W. (2008). The role of oscillations and synchrony in cortical networks and their putative relevance for the pathophysiology of schizophrenia. *Schizophrenia Bulletin*, 34, 927-943.
- Vignali, L., Himmelstoss, N.A., Hawelka, S., Richlan, F., & Hutzler, F. (2016). Oscillatory brain dynamics during sentence reading: a fixation-related spectral perturbation analysis. *Frontiers in Human Neuroscience*, 10, 191.
- Vijayan, S., & Kopell, N.J. (2012). Thalamic model of awake alpha oscillations and implications for stimulus processing. *PNAS U.S.A.*, 109(45), 18553-18558.
- Voloh, B., & Womelsdorf, T. (2016). A role of phase-resetting in coordinating large scale neural networks during attention and goal-directed behavior. *Frontiers in Systems Neuroscience*, 10, 18. <http://dx.doi.org/10.3389/fnsys.2016.00018>
- Voskuhl, J., Huster, R.J., & Herrmann, C.S. (2015). Increase in short-term memory capacity induced by down-regulating individual theta frequency via transcranial alternating current stimulation. *Frontiers Human Neuroscience* 9, 257. doi: 10.3389/fnhum.2015.00257.
- Watrous, A.J., Deuker, L., Fell, J., & Axmacher, N. (2015). Phase-amplitude coupling supports phase coding in human ECoG. *eLife*, 4, e07886.
- Wilsch, A., Henry, M.J., Herrmann, B., Maess, B., & Obleser, J. (2015). Alpha oscillatory dynamics index temporal expectation benefits in working memory. *Cerebral Cortex*, 25(7), 1938-1946.
- Wojtecki, L., Elben, S., Vesper, J., & Schnitzler, A. (2016). The rhythm of the executive gate of speech: subthalamic low-frequency oscillations increase during verbal generation. *European Journal of Neuroscience* doi: 10.1111/ejn.13429.

- Wöstmann, M., Herrmann, B., Wilsch, A., & Obleser, J. (2015). Neural alpha dynamics in younger and older listeners reflect acoustic challenges and predictive benefits. *Journal of Neuroscience*, *35*(4), 1458-1467.
- Yan, B., & Li, P. (2013). The emergence of abnormal hypersynchronization in the anatomical structural network of human brain. *NeuroImage*, *65*, 34-51.
- Yelnik, J., Percheron, G., & Francois, C. (1984). A Golgi analysis of the primate globus pallidus. II. Quantitative morphology and spatial orientation of dendritic arborizations. *Journal of Comparative Neurology*, *227*(2), 200-213.