**The Brain Dynamics of Linguistic Computation**

Elliot Murphy

Division of Psychology and Language Sciences

University College London

***Abstract***: Neural oscillations at distinct frequencies are increasingly being related to a number of basic and higher cognitive faculties. Oscillations enable the construction of coherently organised neuronal assemblies through establishing transitory temporal correlations. By exploring the elementary operations of the language faculty – labeling, concatenation, cyclic transfer – alongside neural dynamics, a new model of linguistic computation is proposed. It is argued that the universality of language, and the true biological source of Universal Grammar, is not to be found purely in the genome as has long been suggested, but rather within the extraordinarily preserved nature of mammalian brain rhythms employed in the computation of linguistic structures. Computational-representational theories are used as a guide in investigating the neurobiological foundations of the human ‘cognome’ – the set of computation performed by the human nervous system – and new directions are suggested for how the ‘dynome’ – the dynamics of the brain, specifically relating to oscillations – operates and executes linguistic operations. The extent to which brain rhythms are the suitable neuronal processes which can capture the computational properties of the human language faculty is considered against a backdrop of existing cartographic research into the localisation of linguistic interpretation. Particular focus is placed on labeling, the operation elsewhere argued to be species-specific. A Basic Label model of the human cognome-dynome is proposed, leading to clear, causally-addressable empirical predictions. In addition, a distinction between minimal and maximal degrees of explanation is introduced to differentiate between the depth of analysis provided by cartographic, rhythmic, neurochemical and other approaches to computation.

***Keywords***: Neural oscillations, syntax, biolinguistics, labeling effects, cognome, dynome, theta, alpha, gamma, cross-frequency coupling, RUNX2.

The argument for placing language at the centre of investigations into human cognition has by now been pushed on a number of fronts, from palaeoanthropology to philosophy (references). In contrast, attempts to place the brain at the centre of the language sciences have been met with suspicion and even ridicule, typically due to the observation that higher cognitive notions like *verb* and *phrase* cannot presently be made commensurable with lower-level neurophysiological structures like *dendrite* and *cortical column*. Substantial engagement with the biology literature remains lacking in departments of linguistics, despite the Minimalist Program’s narrowing of the boundaries between the computational and conceptual capacities of humans and non-humans (Chomsky 1995, 2012, 2015b).

One of the core motivations linguists have for leaving aside biology and keeping to computational investigations arises from Poeppel (2012) and Chomsky’s (2000) insightful discussions concerning philosophy of science, theoretical reduction and unification. These authors point out that, as with the reduction of physics to an unaltered chemistry in the early years of the twentieth century, it may well be that a new neurobiology yielded by a ‘Galilean’ revolution is required for commensurability with the computational theories of syntacticians to be achieved, rather than a revolutionised theory of language. But the common claim that linguistics is biology at a suitable level of abstraction (Berwick 2011) is also used to effectively get linguists ‘off the hook’ of directly exploring the biology of language, satisfied as many are with concluding that this is purely the job of neuroscience. Yet if neuroscientists are not guided by the concerns of computationalists across the cognitive sciences, and not just linguistics, then there is little reason to believe that this goal will ever be achieved. As Lenneberg (1964: 76) already noted, ‘[n]othing is gained by labeling the propensity for language as biological unless we can use this insight for new research directions – unless more specific correlates can be uncovered.’

1. **Dynamic Cognomics: Preliminary Remarks**

The central argument of this paper is that recent developments in brain dynamics and neurochemistry can provide the type of framework needed to meet Poeppel and Embick’s (2005) challenge of ‘granularity’ mismatch, or the problem of reconciling the primitives of neuroscience with the primitives of linguistics (observations going back to Poeppel 1996; see also Poeppel 2011, Fitch 2009). Already in 1996, Poeppel noted of cell assemblies and oscillations that ‘it is unclear whether these are the right biological categories to account for cognition’ (1996: 643), but by now oscillation literature has sufficiently expanded to incorporate numerous cognitive processes. Neurochemical precision is not sufficient in drawing up an account of neural computation, and a theory of brain dynamics will need to be constructed alongside physiological advances.

Linguistics can direct the brain sciences insofar as its insights into the universality of operations like concatenation (set-formation) inform the goals of neurobiology, while the brain sciences can direct linguistics insofar as they place constraints on what possible operations neuronal assemblies and their oscillations can perform. While linguists should focus on making their claims about language biologically feasible, neuroscientists should conversely ensure they do not sideline the notion of computation, as stressed by Gallistel and King (2009).

I will adopt the multidisciplinary approach promoted by Boeckx and Theofanopoulou (2014), embracing the set of computations performed by the human nervous system (the ‘cognome’; Poeppel 2012), brain dynamics (the ‘dynome’; Kopell et al. 2014), neural wiring (the ‘connectome’; Seung 2012) and the genome. This framework instantly reveals the misleading nature of common questions surrounding whether the brain’s wiring ‘makes us who we are’, which have been given an impetus by calls from Seung (2012) and others for a map of the connectome. The connectome constraints the *kinds* of operations performed by the nervous system, but it cannot reveal *what* operations in particular are performed. What is needed, as Seung himself has explained, is not just a comprehensive model of neural wiring, but also neural computation, which is what a theory of the cognome can contribute (see Reimann et al. 2015 for a proposed algorithm to predict the connectome of neural microcircuits).

Bridging the two domains, I will argue, is the dynome; or what physicists would term the mesoscale, and not the microscale. The dynome is the level of brain dynamics, encompassing electrophysiology and neural oscillations. It explores ‘not only *what* is connected, but *how* and in what directions regions of the brain are connected: what signals they convey and how those signals are acted upon as part of a neural computational process’ (Kopell et al. 2014: 1319). The cartographic literature (e.g. fMRI and DTI studies) typically displays theoretical and empirical satisfaction when discussing neural ‘activation’, ‘firing’ and ‘pathways’, keeping at a connectomic level of spatiotemporal brain nodes and edges (Bressler & Menon 2010). The dynome adds to such a ‘functional connectome’ an understanding of the regions involved in producing and processing brain signals. An understanding of the brain’s wiring needs to be accompanied by a theory of ‘the rules governing interactions among neurons and neuronal systems that give rise to overt and covert behaviors’, a major reason being because the neuron is ‘perhaps the most complicated cell type nature has created’ and so physiological accounts alone will not suffice (Buzsáki 2006: 29, 34). Although I will focus on brain rhythms, it should be noted that the dynome extends beyond neural oscillations and includes other temporal structures (Larson-Prior et al. 2013**).** This will also contribute to a solution to the granularity mismatch problem whilst also going beyond the classical Broca-Wernicke-Lichtheim model of neurolinguistics.

I would also like to propose that the universality of language, and the true biological source of Universal Grammar, is not to be found purely in the genome as has long been suggested (where there are surprising layers of variation; Benítez-Burraco & Boeckx 2014a, b), but rather within the extraordinarily preserved nature of mammalian brain rhythms (the oscillations of mice and rats have the same pharmacological profiles as humans) likely arising from the deployment of long-diameter axons of long-range neurons (Buzsáki et al. 2013, see also Calabrese & Woolley 2015). Such cortical and sub-cortical structures are ‘among the most sophisticated scalable architectures in nature’ (Buzsáki et al. 2013: 751), with scalability referring to the ability to perform the same operations with increasing efficiency despite increasing organisational complexity. Brain rhythms, yielded in part by such structures, would therefore be expected to be capable of complex forms of information-transmission and integration. The core of universality is therefore shifted from the genome to the dynome. More generally, as Grodzinsky (2010) shows, language comprehension exhibits a remarkable uniformity in brain structure correlates.

The model presented here will also be discussed within the framework outlined in Embick and Poeppel (2015), where a distinction is made between *correlational*, *integrated* and *explanatory* neurolinguistics. The first occurs when neurobiological (NB) computation is correlated with a computational/representational (CR) theory, the second when NB data provides a way of selecting between CR theories, and the third when properties of NB explain why a CR theory is the way it is. As the authors explain, ‘although cognitive theories and NB theories are advancing in their own terms, there are few (if any) substantive linking hypotheses connecting these domains’ (Embick & Poeppel 2015: 357).

A central question posed by this paper, then, is as follows: Why claim that neuroscience requires a Galilean revolution in order for it to be made commensurable with linguistics when the properties of syntax may be able to be translated into rhythmic brain processes? Russo and Treves (2011: 133) have already opened the way for this debate by pointing to ‘the mistaken expectation’ many linguists have that ‘a sudden discovery from the world of biology, like that of the structure of DNA, will at some point revolutionize the relation between language and the brain, and crack the neural codes for syntax’. The current paper will suggest a new research project, Dynamic Cognomics, to explore the neurobiology of language in a deeper and more electrophysiological explicit fashion than many existing cartographic neuroimaging studies, but some important background is needed before any concrete research goals can be drawn up.

1. **Syntactic Directions**

In Murphy (2015a) it was claimed that the ability to label linguistic structures with a categorical identity (e.g. determiner, verb and adjective) and transfer them in a cyclic fashion to the conceptual-intentional and sensorimotor interfaces is the defining property of the human computational system. This perspective will be maintained here. I will also follow Boeckx (2013) regard the relationship between single-instance set-formation (of the kind found in birdsong and primate cognition) and unbounded set-formation (of the kind found in labeling) as similar to that between water and ice (which simultaneously are and are not the same thing), resembling a phase transition. It will be argued that modifications in oscillatory couplings and the cell assemblies targeted by such dynomic operations are a viable candidate for what brought about such a transition. For instance, the phase/non-phase rhythm of syntactic computation ([C/T[*v*/V[D/N]]]), emphasised by Richards (2011), Uriagereka (2012) and Boeckx (2013), may translate well into the rhythmic processes of neural oscillations. Poeppel and Embick (2005: 112) note that ‘differently structured cortical areas are specialized for performing different types of computations, and … some of these computations are necessary for language but also for other cognitive functions’. Certain regions will be predicted to be implicated in labeling, then, while others will not be.

Following Poeppel and Embick (2005) and Embick and Poeppel (2015), the tools of linguistics and neuroscience need to be formulated at the right level of granularity if interdisciplinary exchange is to take place. The brain simply does not know what *syntax* or *phonology* are, and these concepts are much too coarse to be implemented neurally. I will suggest that once a finer-grained level of analysis is achieved by focusing on individual computations the possibilities for enhanced observations at both the computational and implementational level open up. I will consequently take *language* to be a set of representations (e.g. root) and computations (e.g. label), and will approach the study of this system as a natural sciences to be integrated with the biological and, in particular, neuropsychological sciences. The core insight of Fodor (2010), Pylyshyn (1984) and other cognitive scientists that the mind is a computational engine is sound. But distinguishing a human mind from that of a Bengalese finch requires more than an exploration of the cognome, as in Murphy (2015a), ultimately ‘descending’ to the implementational level.

Since the origins of modern cognitive neuroscience, linguistic processes have been claimed to elicit numerous event-related potentials (ERPs) by psycholinguists using magnetoencephalography (MEG) and electroencephalography (EEG) (see Swaab et al 2012 for a review). As time-frequency analysis and its Fourier transforms developed into a mainstay of ‘ERPology’ (Luck 2014) in the 1990s and 2000s, it became possible to test the involvement of distinct brain regions and the concomitant electrical activity in various linguistic processes, given the standard assumption that language is a cognitive system. The ERP community has spent a great deal of time decomposing the major components, such as the P600 and N400. It is taken for granted that the level of analysis provided by these ‘large’ components does not suffice at the electrophysiological level to describe typically generic linguistic sub-operations. The urge to seek a finer level of granularity, then, is clearly manifested in the ERP community through electroencephalography (EEG) and magnetoencephalography (MEG) investigations (Lau et al. 2008), but, as is shown below, this objective is not found in the vast majority of cartographic neuroimaging research. Consequently, methods are explored which would easily permit the neurophysiologists to follow the lead of the electrophysiologists. It is also worth bearing in mind that it was not until around 2000 that neurolinguists began to move beyond descriptions of ‘Broca’s area’ to more refined investigations of its sub-regions, such as Brodmann areas 44 and 45, and so it should be of little surprise if brain dynamics are not integrated swiftly into studies of linguistic computation.

1. **Cartographic Directions**

Inspired by the early work of Hippocrates and Descartes, scientists and philosophers since the time of the Enlightenment have attempted to investigate the physical basis of human language. In recent decades, neuroanatomical inquiry into the structures responsible for syntactic processing has led to a number of revelations concerning the biology of language. While the neuroimaging literature reveals fairly consistent findings regarding to the brain regions responsible for comprehending syntactic structures, the core neurolinguistic issues currently centre on theoretical, and not cartographic, controversies. A major limitation of neuroimaging studies, which numerous authors do not appear cognizant of, is that such research inadvertently focuses on the *externalisation* of language (morphophonology), and not its core computations (syntax-semantics), despite explicit claims to the contrary. Petersson et al. (2012) reveal the inadequacy of the classical Broca-Wernicke-Lichtheim language model of the brain by noting how the language network extends to substantial parts of superior and middle temporal cortex, inferior parietal cortex, along with subcortical areas such as the basal ganglia (Balari & Lorenzo 2013), the hippocampus and the thalamus (Theofanopoulou & Boeckx forthcoming). The network is also implicated in more general cognitive systems like the default-mode network and the multiple demand system.

Brodmann area (BA) 44 and the posterior superior temporal cortex appear to be involved in a pathway which supports core syntactic computations (Friederici et al. 2006, see also Santi & Grodzinsky 2010, Tettamanti & Weniger 2006), with the combinatorial network being identified by Poeppel (2014) as aMTG and aITS. Lieberman’s (2006) ‘Basal Ganglia Grammar’ model proposes the existence of a pattern generator whose excitation/inhibition mechanism is located in the basal ganglia. This interfaces with working memory space located in Broca’s area, whose role in syntactic movement processing has recently been shown to be directed by memory mechanisms influenced by agrammatically instantiated type-identity intervention, being significantly activated in fMRI studies when a noun phrase similar to the dependency head in a long-distance dependency intervenes in the dependency (Santi et al. 2015). Lieberman estimates that the dorsolateral prefrontal circuit is involved in sentence comprehension, projecting from the prefrontal cortex towards the lateral dorso-medial region of the globus pallidus, and the thalamus, which projects back to the prefrontal cortex. Balari and Lorenzo (2013: 100-2) have suggested that this may be the circuit used as language’s computational system operating within a structure of working memory networks (Balari et al. 2012). Though they do not characterise it in terms of labeling and concatenating, Balari and Lorenzo (2009: 45) note that the computational capacities concomitant with labeling effects (mildly-context sensitive grammars) would have granted Lieberman’s general sequencer ‘access to cognitive types of several modalities, essentially of the symbolic type’. Fitch and Friederici (2012) also detail how the use of AnBn grammar activates similar neuronal processing routines as natural language tasks (BA44), but different routines than (AB)n and other regular grammars.

1. **Evo-Devo Directions**

As the theory of evolution expands beyond the Modern Synthesis and into areas such as evolutionary-developmental (evo-devo) biology (Carroll 2006, Bolker 2008) there is in turn more space for linguists to find their place within in. I will consequently argue that the range of available biophysical discussion has by expanded sufficiently to permit the construction of a science of language which can exploit the full interdisciplinary range seen in the cognitive, biological and natural sciences, along the lines of the above cognome-dynome-connectome-genome framework.

In the evo-devo program, following the lead of traditional formalists such as Vicq-D’Azyr, Goethe and Owen (Amundson 1998), natural selection is ‘a constantly operating background condition, but the specificity of its phenotypic outcome is provided by the developmental systems’ (Pigliucci & Müller 2010: 13). Evo-devo departs from Neo-Darwinian adaptationism (NDA), or ‘phylogenetic empiricism’ (Chomsky 1968), in that it takes the saltationist view that species are the result of punctuated genetic changes. This flies against much of contemporary philosophy of biology, which denies ‘human nature’ since ‘species’ is not a natural kind term (indeed, perhaps only ‘physical’ qualifies, being ‘the ultimate natural-kind term’; Strawson 2010). I think it is instead likely that the emergence of language and of our particular human species were the same evolutionary event, with language being ‘virtually synonymous’ with the creative symbolic thought seen in Cro-Magnons (Tattersall 2008: 103). The reasons for the dominance of NDA during the 20th century are explored with great clarity in Amundson (2006). The functionalism of NDA should also be rejected, since functions do not pre-exist organic form (Müller 2008), which is determined by morphogenetic parameters such as the viscoelastic properties of cellular matrices and the kinetic activity of cellular diffusion (what Alberch termed ‘morphological evolution’), and which at best have what Balari and Lorenzo call a ‘functional potential’ (2013: 37). Contrary to ideas in Dawkins (2006: 202) and Lieberman (2015), laws governing the conservation of developmental pathways should be ‘acknowledged with a creative character similar – if not superior – to that of natural selection’ (Balari & Lorenzo 2013: 115). For all of Chomsky’s anti-adaptationist statements, Hauser et al. (2002) nevertheless assume the existence of a novel, diversified organic function which is manifested in different cross-species communication systems. Relatedly, philosophers of biology typically distinguish functions based purely on natural selection. For instance, Dennett (1987 – find reference) proposes that functions are in the mind of the beholder, but that natural selection is somehow one of those beholders, and acts for him with no restrictions on its scope upon the diversity found in populations yielded by genetic point mutations. Form precedes function, then, and natural selection acts as a ‘filtering condition on pre-existent variants’; thus ‘arrival of the fittest, instead of survival of the fittest, is the core issue in any evolutionary study’ (Narita & Fujita 2010: 364, see also Bertossa 2011).

In this connection, Rakic and Kornack (2001) observe that the phase of asymmetric cell division yielding neuronal cells differs in timing between humans and monkeys to the extent that human neuronal populations are thought to be between eight to sixteen times larger than those of monkeys. Human-specific neuronal traits include the protein ApoE4, providing stronger synaptic connections (Bufill & Carbonell 2004). Parker and McKinney (1999) also detail how the myelinisation of the neocortex occurs in humans until the age of 12, but lasts only 3.5 years in rhesus monkeys. Zhang et al. (2011) propose the existence of 1,241 primate-specific genes, 280 of which are human-specific. 54% of these human-specific genes are upregulated in a brain area implicated in higher cognition, the prefrontal cortex. These new genes are ‘much more likely to be involved in gene regulation’ (Diller & Cann 2013: 256).

Recent research in avian genomics suggests that the evolution of externalisation may also not be as difficult as typically considered in generative grammar. Pfenning et al. (2014: 1333) demonstrated that the profiles of transcription genes in vocal learners can be aligned, with 50 genes being shared between humans and birds which are ‘enriched in motor control and neural connectivity functions’. Both humans and birds appear to have converged on identical solutions to vocal learning. This is remarkable considering the 310 million year gap separating birds from humans. Crucial components of vocalisation may be yielded by the alteration of a small number of genes out of the 50 genes shared by humans and song-learning birds, implying that both labeling and (parts of) externalization emerged both rapidly and without considerable genetic alterations. In addition, the way humans and birds internalise their sensory experience of species-unique vocalisations and employ these internalisations in the service of manipulating vocal externalisation suggests that human articulation and birdsong may share similar neural substrates (Langus et al. 2013). In summary, a slight epigenetic change, termed the ‘Small Bang’ in Murphy (2015a), could have produced an alteration in the human computational system. While Murphy (2015a) explored how the species-specific aspects of the human computational system could have emerged, the next section will consider how these operations are implemented in the brain.

1. **Rhythmic Directions**

How much physiological detail is required to capture the operations of the language faculty? Ramirez et al. (2015) claim that studying neural dynamics only at the level of brain waves is sufficient, but as is demonstrated below, a more refined biophysical picture is not only possible but in fact necessary to adequately explain the origins of linguistic computations like concatenation, cyclic transfer and labeling. What is needed is not just a neuroscience of language, but a *neurophysiology* of language. For instance, at the most general mesoscopic physiological level of local neuronal groups, synchronized firing patterns result in synchronized input into other cortical areas, which gives rise to the large-amplitude oscillations of the local field potential. Inhibitory interneurons play an important role in producing neural ensemble synchrony by generating a narrow window for effective excitation and rhythmically modulating the firing rate of excitatory neurons. Interneurons place constraints on oscillations responsible, as argued here, for computation. Subthreshold membrane potential resonance may also contribute to oscillatory activity by facilitating synchronous activity of neighbouring neurons.

Shifting our focus from neuroimaging to more recent investigations of brain oscillations may provide a welcome (but as yet tenuous) way of translating into neural terms the operations of theoretical linguistics. Brain rhythms ‘have come of age’, as Buzsáki and Freeman (2015: v) put it. They reflect synchronised fluctuations in neuronal excitability and are grouped by frequency, with the most common rhythms being delta (*δ*: ~0.5-4Hz), theta (*θ*: ~4-10Hz), alpha (*α*: ~8-12Hz), beta (*β*: ~10-30Hz) and gamma (*γ*: ~30-100Hz). These are generated by various cortical and subcortical structures, and form a hierarchical structure since slow rhythms phase-modulate the power of faster rhythms.

It is by now well established that neural oscillations are related to a number of basic and higher cognitive functions, for example speech perception (Giraud & Poeppel 2012, Kayser et al. 2014). According to Giraud and Poeppel’s temporal linking hypothesis, oscillation-based decoding segments information into ‘units of the appropriate temporal granularity’ (2012: 511). Oscillations may consequently explain how the brain decodes continuous speech. Oscillations have also been linked to the timing of cortical information processing (Klimesch et al. 2007). As Vaas notes, ‘Intrinsic oscillatory electrical activities, resonance and coherence are at the root of cognition’ (2001: 86), with the condensing and dissolving of oscillatory bursts possibly explaining the ‘cinematic’ nature of subjective experience (Freeman 2015). As Poeppel has put it, the brain essentially ‘breathes’ through oscillations. Lower frequencies such as the *α* range are known to synchronise distant cortical regions; procedures which may represent the substrates of linguistic cross-modular transactions (Kinzler & Spelke 2007).

If such generic neural operations are also shown to be responsible for syntactic computations, and not just linguistic perception, this would lend weight to Hagoort’s (2014) interpretation of the cartographic literature that the establishment of an axis of language production and comprehension is not justifiable. Expanding on Giraud and Poeppel’s (2012: 511) goal of establishing a ‘principled relation between the time scales present in speech and the time constants underlying neuronal cortical oscillations’, one of the central challenges will therefore be to draw up relations between oscillatory time constants and the time scales of syntactic computation. This latter topic has yet to be explored in any serious detail, possibly due to a widespread prejudice that neurolinguistic investigations of syntax must analyse phrasal units, such as noun and verb phrases, rather than the underlying operations which construct them, such as set-formation and labeling (although see Ohta et al. 2013 for an innovative approach to localising Merge and Search operations).

* 1. **Oscillations as functional units**

It is somewhat surprising that although language has been shown to be at the core of major aspects of human cognition, investigations into the role of neural oscillations has focused on capacities like memory and attention (Lakatos et al. 2008). Even when language is studied using brain dynamics, only the ‘sound’ system has been extensively explored (Giraud & Poeppel 2012), while the ‘meaning’ system has been drastically overlooked.

Recent debates about the origins of ERP component generation have led some (Tass 2000, Makeig et al. 2002) to propose that components do not arise purely from latency-fixed polarity responses which are additive to continuing EEG responses, but rather arise through a superposition of oscillations which reset their phases in reaction to sensory input (although see Sauseng et al. 2007 for the methodological limitations of particular phase resetting claims). For our purposes, it is worth noting that this phase reset model was the first to propose a strong dependency between components and oscillations, introducing to brain dynamics a *functional* and not purely *electrophysiological* role. This immediately granted researchers the ability to transfer understanding of components (which are in turn linked to cognitive faculties) to brain rhythms whilst correspondingly inferring the nature of components from an emerging understanding of oscillations. While cognitive electrophysiologists have embraced this integrally reciprocal perspective (Klimesch et al. 2004), linguists generally remain hostile to the claim that the nature of mental computations – like components – could be explored explicitly through biophysics. Consequently, before the presenting further details about the dynome, I would like to propose the following generalisation for neurolinguistics, which assumes that linguistic computations are (somehow) neurally implemented:

1. *The Principle of Cognome-Dynome Reciprocation*:

Assume that knowledge of the cognome guides and delimits theories of the dynome, and that knowledge of the dynome guides and delimits theories of the cognome.

While the cognome resides at the Marrian computational level (Marr 1982), I would also like to propose that there is in fact no algorithmic level at syntax. At most there are algorithms at the interfaces. Psycholinguistic theories can of course algorithmically model language processing, as Neeleman (2013) discusses, but syntax itself (being composed of operations like Concatenate, Label and Transfer) has no need for this. Nevertheless, the dynome, with its operations of information segregation and spike timing organisation, can in some sense be seen as an algorithmic level, implemented by the cellular structures of the connectome. These Marrian concerns become even more vivid when we consider with Martins and Boeckx (2014) that syllables, which are unique to humans, evolved from primate lip-smacking. In terms of brain rhythms, they are both identical, yet one is human-specific and another is not. The implications for the study of labeling, not acknowledged in Murphy (2015a), are clear: only comparative investigations of domain-general neurophysiological mechanisms will lead to enhanced understanding of human-specific computations (see also Boeckx and Theofanopoulou 2015). We have already answered what Embick and Poeppel (2015: 363) term the second specialisation question: ‘Are there particular parts of the CR theory that are more likely to be candidates for explanatory neurolinguistic explanation than others?’ Labeling, concatenation and cyclic transfer have been suggested as candidates. But what about the opposite problem of neurobiological specificity? This is posed by the first specialisation question: ‘Are there particular levels of NB organisation that are to be privileged as candidates for CR specialisation?’ It will be suggested that brain dynamics, in particular neural oscillations, are likely candidates to be privileged in such a way.

There are ultimately only two possibilities for those concerned with these two specialisation questions: either neurobiology can be shown to be responsible for particular linguistic computations, or it cannot. There are also two central approaches to the cognome-dynome one could adopt: re-construct the cognome from the bottom-up, or import linguistic constructs into a model of the dynome. I will be primarily concerned with the latter methodology, though the material reviewed and the model outlined open up the possibilities of using neurophysiology to guide linguistic investigations.

* 1. **The Basic Label model of the cognome-dynome**

At the most general level of analysis, neural oscillations emerge from the tension between the brain’s two most central principles: segregation of function and dynamic integration (De Pasquale et al. 2012). Human brains are highly complex dynamical systems with principles of cellular and electro-chemical organisation which range across a hierarchy of scales. The brain cannot function purely through anatomical connections – the *locus classicus* of standard neuroimaging studies – but additionally requires dynamic functional connectivity, achieved through oscillatory synchronisation. Frequency bands alone are not sufficient for computation; rather, it is their interactions which are significant. Intuitive prejudices against studying complex systems in these dynamic terms abound: for instance, chemical dynamics are typically thought about in terms of reaction kinetics, being stipulated as pre-formed stable variables, ignoring the molecular composition/decomposition process.

A core feature of the brain’s functional complexity is created by the rhythms generated by different cortical and subcortical tissue. It is well established that neural oscillations denote distinct states of brain activity, while oscillatory activity reflects a dynamic interplay between the dissimilar cell types of discrete circuits (Buzsáki 2006). Brain rhythms, with their inter-wave hierarchies, provide ‘a syntactical structure for the spike traffic within and across circuits at multiple time scales’ (Buzsáki & Freeman 2015: viii). ‘Phase synchronisation’ will additionally be a central notion for our discussion, referring to a consistent phase coupling between two neuronal signals oscillating at a given frequency. *γ* band synchronisation (GBS) in particular has been intensively studied because of its apparent role in phase coding and perceptual integration (Fries 2009), and is thought to be a major process subserving a fundamental operation of cortical computation implicated in various cognitive functions. Which functions are involved depends ultimately on what neural circuits GBS is operating on. The follow sub-sections will present a way of exploring the operations of the cognome in terms of the dynome, leading to a form of what I will call Dynamic Cognomics.

* + 1. *Concatenation*

The central proposal of the model pursued here is that the interaction of brain rhythms yields linguistic computation. I will assume that the *α* band embeds *γ* rhythms generated cross-cortically, yielding a form of inter-modular conceptual combination, the electrophysiological equivalent of concatenation. This is consistent with recent claims that *α* is responsible for the binding of visuo-spatial features (Roux & Uhlhaas 2014) and is deployed in the service of determining successful lexical decisions, as a recent EEG study has shown (Strauss et al. 2015). Frequency coupling arises from a mathematically defined relationship between oscillations which form a hierarchy such that the speed of the slower rhythm controls the power of the faster rhythm. I will further assume with Ramirez et al. (2015) that the items concatenated are also initially ‘lexicalised’ by *α*-embedded cell assemblies oscillating at the *γ* range within supragranular layers of the default-mode network (Raichle et al. 2001).

* + 1. *Transfer*

Linguists take the above concatenation operation to occur cyclically (Chomsky 2008), and so I will additionally assume that this Spell-Out/Transfer process is realised through embedding the above *γ* rhythms inside the *θ* band, which finds its source in the hippocampus. I will adopt the claim of Ramirez et al. (2015) that *γ* must be decoupled from the *α* band for *γ*-*θ* embedding to take place.

* + 1. *Labeling*

Along with concatenation and transfer, there is also labeling. Two major observations have been made about this operation: (i) It is unique to humans (Murphy 2015a); (ii) It is a system of minimal computation (Chomsky 2015a). Labeling is also monotonic in that once a set has been labeled (as *v* or D, for instance) its identity is sustained when embedded inside another set. Since labeling must take place at the point of transfer to the interfaces (to prevent an XP being a VP at CI but a different phrase at SM), labeling must be seen as a core syntactic operation (Murphy 2015b, Piattelli-Palmarini & Vitiello 2015), and not emerging epiphenomenally at the interfaces, despite it having a less central role than unconstrained ‘Merge’ (concatenation) which operates independently from either CI or SM. We would consequently predict that labeling would more heavily implicative brain regions responsible for conceptual representations than the coordination of motor and articulatory actions.

As Boeckx and Theofanopoulou (2015) note, Murphy (2015a) did not formulate labeling at a fine enough level to avoid the granularity mismatch problem. In order to correct for this, I will define labeling as the attribution to a concatenated set some categorical specification created from the Labeling Assembly, which is composed of (i) general cognitive constraints, (ii) the CI system, (iii) the cognome and (iv) the precursor lexicon (*p*LEX). The final of these four constituents is taken to be the set of flat and atomic ‘root’ structures (Boeckx 2014a), from which morphology constructs internally hierarchical words (Nóbrega & Miyagawa 2015). When *John* is concatenated with *ran*, the labeling algorithm produces a Verb Phrase, not a Noun Phrase (see Adger 2013, Narita 2014 and Murphy 2015a for further algorithmic details). This covers the basic outline of labeling, but in order to achieve a higher level of granularity it will be necessary to descend to the dynomic level, and ultimately (in the final section) the cellular level.

In dynomic terms, I will take labeling to be the slowing down of *γ* to *β* followed by *β*-*α* coupling, involving a basal ganglia-thalamic-cortical loop, ‘likely crossing the dorsolateral striatum, disinhibiting the thalamic medio-dorsal nucleus, by means *β* of the rhythm, retaining in working memory one of the objects generated by [lexicalisation]’ (Ramirez et al. 2015: 8). The role of the thalamo-cortical network as a slow rhythm generator, and hence a single dynamic and functional unit of brain oscillations, has been recently supported by Crunelli et al.’s (2015) review of the EEG literature. Related to Balari and Lorenzo’s (2013) claim that the basal ganglia is the centre of their ‘Central Computational Complex’, Ramirez et al. propose that this region holds one of the *γ­*-supported items before slowing it down to the *β* frequency as a consequence of the conduction delays resulting from the surrounding neural regions. Thus the *β* band accomplishes the role of labels, a claim supported by findings that *β* activity maintains existing cognitive states (Engel & Fries 2010). More broadly, the basal ganglia and the striatum are implicated in sequencing and chunking, with striatal structures operating at the *β* range (Leventhal et al. 2012). The core position occupied by the basal ganglia in this labeling model also fits well with imaging studies which have revealed the region’s involvement in ‘syntactic complexity’, specifically the processing of type-identity intervention of matching labels (Santi et al. 2015). Basal ganglia nuclei in humans are also around twice as large as would be predicted for a primate of our size (Schoenemann 2012), and since humans do not appear to have substantially more sophisticated movements than apes, this increase may well have supported higher cognitive capacities like labeling.

* + 1. *Formal considerations*

Introducing new formalisms will permit a clearer explication of dynamic cognomics. First, we can notate *γ*-*θ* embedding as {*θ*(*γ*)}, with *γ* being embedded inside *θ* rhythms. If it is known how many *γ* cycles are to be embedded (for instance, 7), this can be notated as {*θ*(*γ*7)}. We can notate the decoupling process required to transfer concatenated structures as *γ*(•)*α*, where *γ* is decoupled from the *α* band. Frequency coupling can correspondingly be notated as *γ*•*α*. The decreasing of *γ* to *β* can be represented as *γ*<→*β*, where ‘→’ refers to a state change. Post-sentential wrap-up effects can be represented with ψ. Finally, the (hypothetical) cell assemblies responsible for particular lexical features, such as the [+singular] feature of *man*, can be represented as ζ[*man*(+singular)]. If it is known which regions (cytoarchitechtonic or otherwise) such assemblies are located, this can be represented as ζ:BA44[*man*(+singular)], while the rhythm band can be additionally represented as ζ[*man*]:*γ*.

We are now in a position to write a simple derivation using the Basic Label model. Take the sentence *The man is called John*. This can be represented in familiar syntactic terms as a Tense Phrase, ignoring superfluous details (e.g. morphological operations): [TP[DP *The man*][T *is*][VP *called John*]]. In the interests of clarity, I will put aside precise categorical concerns and denote labeled phrases with ‘l’, with multi-phrase labels being italicised. Even though sentences are parsed in a left-right fashion, generative linguistics holds that syntactic derivations proceed right-left. In order to deal with this perennial psycholinguistic problem, I suggest that structures are concatenated, labeled and transferred as and when they are heard, read or otherwise perceived, and after every lexical unit a ‘look back’ procedure is triggered to reanalyse the labels and features of each structure. In psycholinguistic terms, this may account for certain ‘wrap-up’ effects which occur when subjects reach the final word of a sentence during online processing (Field 2004). This approach is also consistent with the ‘one-system’ contention of Lewis and Phillips (2015) that grammatical theories and language processing models describe the same cognitive system, as evidenced by the fact that grammar-parser misalignments occur only as a consequence of limitations in domain-general systems such as memory access and control mechanisms. It follows that ‘online and offline representations are the product of a single structure-building system (the grammar) that is embedded in a general cognitive architecture, and misalignments between online (“fast”) and offline (“slow”) responses reflect the ways in which linguistic computations can fail to reflect the ideal performance of that system’ (Lewis & Phillips 2015: 39).

The derivation will proceed as follows. *The* is generated by distributed *γ* activity in the supragranular cell assemblies responsible for its long-term storage, ζ[*the*]. This rhythm would be embedded within *α* activity before being transferred to the interfaces through being decoupled from *α* and newly embedded within hippocampal *θ* activity. ζ[*man*], operating at the *γ* range, would then be embedded within *α* before being transferred. The two representations would then be labeled a Determiner Phrase. Continuing the line argument in Murphy (2015a), this would occur at the Labeling Assembly. To achieve labeling, the embedded cycles would be slowed to the *β* range (*γ*<→*β*) before being coupled to *β* (*β*•*α*). The labeled phrase [*the man*] would be maintained in memory via the *β* rhythm.The subsequent material [*is called John*] would then be concatenated in a similar fashion, leading to a complete formal derivation:

ζ[*the*]:*γ* → {*α*(ζ[*the*]:*γ*)} → *α*(•)ζ[*the*]:*γ* → {*θ*(ζ[*the*]:*γ*)}

ζ[*man*]:*γ* → {*α*(ζ[*man*]:*γ*)} → *α*(•)ζ[*man*]:*γ* → {*θ*(ζ[*man*]:*γ*)}

{*θ*(ζ[*the*]:*γ*)(ζ[*man*]:*γ*)}

*γ*<→*β*

*α*•((ζ[*the*]:*β*)(ζ[*man*]:*β*)) → *α*•(ζ[L *the man*]:*β*)

ζ[*is*]:*γ* → {*α*(ζ[*is*]:*γ*)} → *α*(•)ζ[*is*]:*γ* → {*θ*(ζ[*is*]:*γ*)}

*γ*<→*β*

*α*•((ζ[L *the man*]:*β*)(ζ[*is*]:*β*)) → *α*•(ζ[*L* [L *the man*][*L* *is*]]:*β*)

ζ[*called*]:*γ* → {*α*(ζ[*called*]:*γ*)} → *α*(•)ζ[*called*]:*γ* → {*θ*(ζ[*called*]:*γ*)}

*γ*<→*β*

*α*•((ζ[*L* [L *the man*][*L* *is*]]:*β*)(ζ[*called*]:*γ*)) → *α*•(ζ[*L* [L *the man*][*L* *is*][L *called*]:*β*)

ζ[*john*]:*γ* → {*α*(ζ[*john*]:*γ*)} → *α*(•)ζ[*john*]:*γ* → {*θ*(ζ[*john*]:*γ*)}

*γ*<→*β*

*α*•((ζ[*L* [L *the man*][*L* *is*][L *called*]]:*β*)(ζ[*john*]:*γ*)) → *α*•(ζ[*L* [L *the man*][*L* *is*][L *called* *john*]]:*β*)

ψ

Notice that, as with computational ethology (Murphy 2015a) and recent syntactic theories (Hornstein 2009, Adger 2013), labeling is here placed at the centre of the dynome’s linguistic operations. As a result, call the above cognome-dynome hypothesis the Basic Label model. What remains to be added to the derivation by empirical investigation are the factors of time-frequency domain and anatomical regions of cellular assemblies (e.g. ‘embed *γ* of region *r* within *α* of region *s* for time *t*’).

* 1. **Some empirical consequences of dynamic cognomics**

Given this rhythmic perspective of linguistic computation, the much-discussed fronto-temporal language network would consequently be purely an *output* system of the above operations, not a core syntax region. In addition, Friederici (2012) holds that distinct regions of the left inferior frontal gyrus are responsible for ‘different’ types of syntax, arguing, for instance, that the dorsal stream is only implicated in embedded structures or structures deviating from normal ordering. Yet, as the above model makes clear, the basic combinatorics are universal across syntactic structures, whether simple or complex; set-formation is still set-formation whether it is found in a small clause or a Shakespearean sonnet.

Among many other forms of imaging and behavioural data, the types of localisation neuroimaging studies mentioned above should be used as a guide for dynamic cognomic investigations. With respect to linguistic computation, the left anterior temporal lobe has been implicated in basic combinatorics (concatenation) and phrasal construction (labeling) (Bemis & Pylkkänen 2013, Westerlund & Pylkkänen 2014), while the posterior middle temporal gyrus is involved in lexical access (lexicalisation) and ambiguity resolution (Turken & Dronkers 2011). While I do not follow these authors in suggesting that these regions are exclusively the seat of core syntactic combinatorics, since the model above implicates numerous other regions, it nevertheless seems to me to be a suitable goal for neurolinguists to attempt to use cartographic research as a way of linking brain dynamics with, for instance, the BOLD responses monitored by fMRI studies.

While relatively little is known about how oscillations relate to cognitive operations, significant advances could come from direct empirical investigations teasing apart *γ* and *β* from other rhythms, demonstrating a correlation with a syntactic manipulation (and perhaps a dissociation with another operation which could be linked to slower rhythms and working memory or attention processes). In addition to the cartographic studies above, paradigms such as the one in Ohta et al. (2013), which differentiated the neural correlates of concatenation and search/agreement operations, could be employed. Despite having noted the limitations of cartographic studies, an area of ongoing neurolinguistic research is the spatial scales of brain rhythms. It could be explored, for instance, whether ongoing oscillations and generic computations share the same neuronal generators. Emerging technologies to experimentally test and refine the present Basic Label model include high-density electrode recordings and optogenetic tools (Chow et al. 2010), along with the more traditional EEG and MEG devices. Bemis and Pylkkänen (2013) showed that between 200 and 300ms after the presentation of a word which can be combined with a previous item, the left anterior temporal lobe is activated, implicating this region in semantic composition. This would consequently be a good estimate of when oscillation studies might detect labeling effects to arise, given the role of labels in semantic composition (Hornstein & Pietroski 2009, Murphy 2015b). At the most general level of lexical comprehension, EEG and MEG studies would also predictably find coherent oscillatory activation of large neuronal assemblies when processing words relative to processing pseudowords, as Pulvermüller et al. (1994) found.

Neural potentials have typically been analysed through frequency, time-frequency and wavelet representations (Kaiser 2010). Independent component analysis (ICA) has also been used successfully in estimating the sources of neural systems given multiple recording locations, since these systems generate independent and continuous activity and combine linearly and instantaneously (Hyvärine & Oja 2000). However, spatial ICA does not allow the interpretation of time-varying patterns, and in the case of EEG it also does not produce a model of ‘phasic events’ of rhythmic activity.

Given these shortcomings, I would like to introduce the possibility of analysing a continuous signal as a linear combination of reoccurring waveforms. This is achieved by combining overcomplete representations with adaptive signal models. If the goal is to extract waveforms from a single continuous channel, then it follows that we should adopt a generative model which summates impulse responses, being a multiple input, single output (MISO) model. Principe and Brockmeier (2015: 15) term this a *phasic event model*. This proceeds in two steps: learning a set of waveforms occuring repeatedly throughout a signal, and estimating an atomic decomposition of a signal in terms of timing, amplitude and waveform index (see Figure 1 for an example). The major advantages over other models is that the phasic event analysis learns the reoccurring waveform shape and allows the pinpointing of the amplitude and timing of phasic events. The model consequently captures the transitory nature of neural events.

<INSERT FIGURE 1 HERE>

**Figure 1**: Decomposition of a single local field potential (LFP) channel using the phasic event model. Data collected by Brandi Marsh in Joseph Francis’s laboratory at SUNY-Downstate. The original LFP signal is on top. In the middle are the component decompositions. The learned impulse response of the waveform is shown to the left of each component. The most significant amplitude atoms (timing, amplitude and waveform index) appear at the bottom as coloured bars. Colour intensity corresponds to amplitude (from Principe & Brockmeier 2015: 15).

Given the division of EEG patterns and local field potentials into rhythms (*α*, *β* etc.) and phasic events (sharp waves, *β* and *γ* ripples etc.), and given the nature of the Basic Label model, I think an approximate correlational (in the sense of Embick & Poeppel 2015) computational-representational division can be established between, respectively, phasic events (carried out in and between the cell assemblies of particular regions) and rhythms (necessarily localised at such regions).

Although oscillations are likely not all that is needed to provide a solution to the problem of linguistic computation, they nevertheless appear to be a vital part of the answer. Aside from language-centred obstacles, comparative dynamic cognomics will also face the notable challenge of the variation in oscillation presence across species, with the reasons for much rhythmic variation still unknown. For now, the Basic Label model presented above satisfies the cognome-dynome operational level, but we would ultimately want to write a full derivation satisfying the connectome and other lower levels. As a result, the next section will expand on the bare neurophysiological and mechanistic details outlined previously, leading to the broadening of multi-disciplinary concerns and perspectives.

1. **Biophysical Directions**

To adequately explore the neurochemical and biophysical details of the Basic Label model, it is useful to introduce a distinction between *minimal* and *maximal* degrees of explanation:

1. a. Minimal degree of explanation (MinDE): The use of brain dynamics to explain why the cognome performs the operations it does, and not some other imaginable operations.
2. Maximal degree of explanation (MaxDE): The use of brain dynamics in addition to causally relatable accounts of neurochemistry and its underlying biophysics to explain why the cognome performs the operations it does, and not some other imaginable operations.

Note that MinDE has minimal requirements, whereas MaxDE has no stipulated limits, embracing the full range and plurality of the natural sciences. Neuroimaging studies, for instance, do not even reach the level of MinDE, whereas a purely rhythmic approach to the dynome of the kind found in Ramirez et al. (2015) satisfies MinDE without reaching the neurochemical and biophysical precision of MaxDE. Kopell et al. (2014: 1319) stress that connectome-dynome linking hypotheses need to supplemented with ‘the biological details that relate this connectivity more directly to function’. This is where I will attempt to depart from analyses which remain at the connectome, dynome and cognome levels (e.g. Ramirez et al. 2015, Sporns 2013). For instance, Ramirez et al. (2015) only refer in passing to basic interneuron classes, and their model lacks any serious neurobiological detail. As Allen and Monyer (2015: 85) comment, ‘when considering interneurons, it would be important to investigate the role they play in the reactivation of cell ensembles occurring during sharp wave/ripples’. Mechanistic ventures beyond the dynome are, I think, in the proper spirit of Turing’s (other) thesis regarding morphogenesis, which was concerned not just with a description of an organism’s forms (similar to the computational level of modern linguistics) but also with a proto-evo-devo theory of the cellular mechanisms which give rise to such forms (Turing 1952, see also Maini 2004). As Kopell et al. (2014: 1324) astutely note, ‘an immersion in the physiology supporting temporal dynamics suggests mechanisms that would not be obvious if one were thinking abstractly about computation and rhythms’; a statement which carries urgent lessons for theoretical linguistics and neuroimaging.

Contrary to much of Koch’s (1999) ambitious work, it will be argued that the divide between biophysics and computation is in fact incommensurable, and that a different biolinguistic strategy will be required to resolve Poeppel’s granularity mismatch problem. This approach will use the Basic Label model alongside neurochemistry as tools to construct a neurobiologically feasible cognome, free of the technical baggage – though not the methodological naturalism (Chomsky 2000, Collins 2015) – of minimalist syntax and its lexico-centrism and ‘featuritis’ (Boeckx 2014a).

* 1. **Feeble currents and cognomic substrates**

Though much interdisciplinary work remains, dynamic cognomics has the potential to progress neurolinguistics beyond the situation described by Szathmáry in 1996: ‘Linguistics is at the stage at which genetics found itself immediately after Mendel. There are rules (of sentence production), but we do not yet know what mechanisms neural networks are responsible for each rule’ (1996: 764). So far I have only presented a model of how to embed the cognome within the dynome, but it is also vital to ground the dynome within the connectome and microlevel analyses, in turn addressing Szathmáry’s concern.

As has been well established, neuronal populations can synchronously discharge due to an internal or external event, and additionally as a result of dynamic interactions between reciprocally coupled networks, which serve to ‘tag the responses of neurones that need to be related to one another’, as König (1994: 31) put it in his seminal assessment of neural oscillations. This synchronous activity further tends to be oscillatory in nature. Cortical connectivity has been shown to be realised through this synchronous electrical oscillatory activity (Liu et al. 2010). Oscillations have also been linked to neurochemistry (Muthukumaraswamy et al. 2009). While oscillatory electrical activity in cell assemblies has been observed since the 1920s beginning with Berger’s (1929) ground-breaking work, inspired by the Liverpool surgeon Richard Caton’s (1875) studies of the ‘feeble currents’ generated by rabbit and monkey brains, its role in cognitive capacities has been intensively explored only since the new millennium (Jensen et al. 2002, Ossandón et al. 2011), largely down to theoretical, technological and optogenetic advances. Updating Caton’s imagery, McCormick et al. (2015: 133) summarise that brain rhythms are generated through ‘the interaction of stereotyped patterns of connectivity together with intrinsic membrane and synaptic properties’.

At the most common level of investigation, time-locked frequency analysis can decompose an EEG signal and identify changes in oscillations. But the widespread use of non-invasive and high-temporal resolution MEG, and recent advances in its source localisation power (Wipf et al. 2010), has led to enhanced understanding of the spatiotemporal dynamics of oscillations and how they operate within neural networks. Capitalising on these developments, Brookes et al. (2012) used pan-spectral independent component analysis (ICA) to analyse the results of task-modulated oscillation bands across networks. They discovered that frequency bands exhibit different contributions across networks, though the role of oscillations in network dynamics remains poorly understood. Recent work, however, has begun to deliver an increasingly precise account of how, for instance, different classes of GABAergic interneurons in the hippocampus coordinate activity giving rise to network oscillations (Allen & Monyer 2015), strengthening dynome-connectome correspondences. GABAB receptors also perform time integration of cell assemblies (classically defined as a set of neurons exhibiting stronger within-group connectivity than with other connected neurons; see Hebb 1949) from the subsecond to second scale (Deisz & Prince 1989), a vital function in computing conceptual and linguistic information representations. As Allen and Monyer (2015: 81) explain, due to ‘the convergence of excitatory inputs from multiple pyramidal cells onto single inhibitory interneurons and the divergence of interneuron outputs, interneurons are perfectly positioned to synchronize network activity’ (see Whittington & Traub 2003).

Going beyond this level of analysis will require mapping rhythms to the numerous interneuron classes, which are defined based on cell body location, expression of marker proteins, axonal arborisation and other properties (Klausberger et al. 2005, Somogyi & Klausberger 2005). Korotkova et al. (2010) attempted to reach such a goal by showing how the removal of NMDA receptors in parvalbumin-expressing (PV) interneurons reduced the power of *θ* oscillations in the CA1 hippocampal region, while also reducing the *γ*-power modulation by *θ* oscillations. PV interneurons and somatostatin-expressing (SOM) interneurons preferentially synapse, respectively, onto the cell bodies and proximal dendrites of pyramidal cells and the distal dendrites of pyramidal cells (Royer et al. 2012). The silencing of PV interneurons, but not SOM interneurons, altered the *θ* phase precession in the brains of mice running on a treadmill belt in the experiments conducted by Royer and colleagues, suggesting that PV interneurons are highly fit to control the firing phase of principal neurons during *θ* oscillations.

It should be noted, however, that PV and SOM expression is common to numerous hippocampal interneuron classes, and so further optogenetic work is needed in order to establish the role of individual interneuron classes in the generation of oscillations. I think fruitful prospects for such advances can be found in recent advances in juxtacellular recordings, permitting the monitoring of a single interneuron *in vivo*. To take a relevant case, Lapray et al. (2012) discovered that PV basket cells – providing inhibition to the pyramidal cell body and proximal dendrite – fire preferentially at the descending *θ* phase (findings reproduced by Varga et al. 2012), while ivy cells – providing inhibitory currents onto pyramidal cell dendrites – fire preferentially during ascension and at the trough. It has additionally been discovered that medial septal inactivation reduces *θ* oscillation power in the hippocampus (Brandon et al. 2014). In summary, these studies reveal that during a single *θ* cycle the inhibitory power onto distinct pyramidal cell sectors varies systematically.

Viewing cell assemblies as the fundamental unit of computation rather than single neurons can by now be justified in that assemblies can tolerate noise by not being redirected in their trajectory, unlike single or small clusters of neurons. Failures in spike transmission would also impact single neurons but not assembly partnerships, which have a high tolerance for spike rate variation. Given the information chunking and feature combination roles attributed to *γ* cycles, Buzsáki suggests that episodes of *γ* oscillations, which contain strings of cell assemblies, ‘may be regarded as a neural word’ (2010: 365); that is, a discrete unit of information, intensifying the role in computation attributed to cell assemblies here. If induced *γ* is also responsible for constructing coherent conceptual objects by synchronising neural discharges binding together distant brain regions, as proposed by Tallon-Baudry and Bertrand (1999), then oscillations may also be responsible for complex semantic phenomena like copredication, through which a single object or event can be conceptualised via simultaneously concatenated yet contradictory properties, e.g. *The newspaper I held this morning has gone bust* or *Lunch was delicious but took forever* (see Murphy forthcoming).

Topics in electrophysiology should also direct the concerns of those investigating the brain dynamics of linguistic computation. Certain areas of recent research appear to be more commensurable with elementary computational operations than other areas. To outline: Transfer of charges across membranes of all brain structures leads to a current giving rise to an extracellular field, which in turn influences the membranes. The transmembrane voltage (*Vm*) is defined as the difference between the intracellular (*Vi*) and extracellular voltage (*Ve*) at a time *t* and location *x*: *Vm*(*x*,*t*) = *Vi*(*x*,*t*) – *Ve*(*x*,*t*). A topic of contemporary debate is whether this endogenous field with its spatiotemporal *Ve*-fluctuations changes neuronal functions through ephaptic coupling (see Jeffreys 1995 for an overview). This process amounts to a feedback mechanism through which the neural structures producing a given field are in turn affected by them, yielding a self-generated cyclic loop. In terms of range, ephaptic coupling influences structures ranging from synapses to discrete neurons to neural networks.

At the microscale, a linear relationship is seen between a chemical synaptic current *Isyn*and *Vm*, with such current being able to be described as *Isyn*(*t*) = *gsyn*(*t*)(*Vm*(*t*) – *Erev*), where *gsyn* is the synaptic conductance and *Erev*is the reverse current. Following the above self-generated model, *Ve* changes alter synaptic currents. The electric field may also influence electrodiffusion of charged ions, since ‘ionic fluxes within the synaptic cleft (from presynaptic to postsynaptic neuron) via electrodiffusion induce electric fields locally, within the synapse’ (Anastassiou & Koch 2015: 96). Alternations in ionic flux can in turn be produced by presynaptic terminal membrane potential changes yielded by intrasynaptic electric fields. This can lead to the depolarisation of the presynaptic terminal and an increase of neurotransmitter release, as in the case of AMPA-mediated synaptic transmission in the cortex (Berretta et al. 2000). In addition, ephaptic coupling of *Vm*to electric fields influences spiking due to its effect on active cell conductances (Anastassiou et al. 2011). The explanatory force of ephaptic coupling becomes clearer with parallel plate whole-slice stimulation, which has shown that emergent properties of networks are more sensitive to electric fields than discrete neurons (Deans et al. 2007). As noted by Anastassiou and Koch (2015), the entrainment of spiking to field strengths as minimal as 0.5mV/mm suggests that ephaptic entrainment to endogenous fields contributes to brain rhythms. Stronger ephaptic feedback also occurs after slower (<8Hz) waves such as *θ* and *δ* compared to faster *γ* waves, suggesting that the non-synaptic electrical signals seen in ephaptic coupling contribute to neural computation. Nevertheless, such techniques, though instructive, are limited in virtue of their sidelining of other factors contributing to electrical field potentials.

As with ephaptic coupling, I would further like to propose cross-frequency coupling (CFC) as a core component of computation. It has been suggested that this generic operation coordinates spatiotemporal neural dynamics (Canolty & Knight 2013, Lisman & Jensen 2013), resolving a long-standing problem over how neural activity is synchronised. With larger neuronal populations oscillating at lower frequencies and smaller populations doing so at higher frequencies, CFC would enable their synchronisation. In particular, it has been shown that via ‘phase-amplitude’ CFC the phase of the lower frequency modulates the amplitude of the higher frequency component, a process claimed to be involved in information transfer for faculties such as memory (Tort et al. 2009, though see Aru et al. 2015 for current limitations of phase-amplitude modelling). But while much is known about the biophysical substrates of individual frequency components, the cellular mechanisms behind frequency *interactions* – what Basic Label proposes as the origin of linguistic computation – remains opaque. Initial research leading to such an account has already been mentioned: Recall Korotkova et al. (2010) and their findings regarding hippocampal *θ*-*γ* coupling and its reliance on NMDA receptor-mediated PV interneuron excitation (see also Bi & Poo 1998). Using laminar electrodes to measure activity in monkey primate visual cortex, Spaak et al. (2012) found that *α* phase in infragranular layers modulates *γ* amplitude in supergranular layers (see also Friston 2008); not dissimilar to how thalamic nuclei oscillating at the *α* band synchronise distant cortical regions oscillating at higher frequencies. As Aru et al. (2015) note, the most elegant theory to account for these findings is that periodic membrane potential fluctuations generate low frequency oscillations which subsequently gate the incidence of higher frequency activity in a phase-specific fashion. Phase synchronisation and cross-frequency coordination have also been shown to gate the flow of information across the brain (Canavier 2015). From a functional perspective, the above nested *γ* cycles could act as multiplexing mechanisms (Buzsáki 2006: 356) for sustaining working memory representations by sending multiple representations as a single complex message to be recovered and ‘unpacked’ downstream (see Hyafil et al. 2015 for empirical support, and Baddeley et al. 2014 for a review of working memory mechanisms), precisely as is seen in labeling.

Moving on to related topics of microcircuitry, certain figures have claimed that single dendrites contain all the sufficient mechanisms for performing complex computations such as temporal integration, coincidence detection and direction selectivity (London & Häusser 2005). Others such as Klampfl et al. (2009) argue that neuronal input is processed at the dendrite, soma and initial segment. But the forms of computations which concern us – set-formation and cyclic transfer – most probably require a form of neo-Hebbian distributed neural assembly (Lopes-dos-Santos et al. 2011) through which the collective spiking of the mobilised neurons leads to the discharge of a target assembly (Buzsáki 2010).

At a more general level, the cognome must operate within certain fundamental constraints on neuronal dynamics, such as the free-energy principle (following seminal insights from Friston 2010) through which the homeostatic brain minimises the dispersion (entropy) of interoceptic and exteroceptic states. If entropy is the average of ‘surprise’ over time, then the brain will choose appropriate sensations to minimise surprise, and in so doing ‘the brain is implicitly maximizing the evidence for its own existence’ (Bastos et al. 2012: 702); a notion not too far removed from Vaas’s assessment that the brain is ‘a self-referential, closed system, a functional reality emulator that constructs the world, rather than reconstruct it’ (Vaas 2001: 88). Yet the study of syntax invokes internal generative processes independent of sensory computations, and so predictive coding and other related matters will be of little use in drawing up an account of linguistic computations, despite the above biophysical limitations naturally extending to language. Studies of chaotic itinerancy (Tsuda 2013, 2015), many-body physics and thermodynamics (Vitiello 2015) may also prove indispensable in describing the high-dimensional state space of cortical activity implicated in computation. For instance, many-body formalisms can not only capture elementary particle physics but also the behaviour of macroscopic systems defined by ordered patterns, but this would take us too far afield (see Piattelli-Palmarini & Vitiello 2015 and the essays collected in Ohira & Uzawa 2015 for discussion).

An emerging consensus regarding the validity of the communication-through-coherence (CTC) hypothesis lends further impetus to the claim that rhythms bring about linguistic computations (Bastos et al. 2015). CTC claims that rhythmic synchronisation, especially in the *β* and *γ* bands, modulates the efficacy of anatomical connections, and that oscillations are necessary for long-distance assembly formation (König et al. 1995, Fries et al. 2008). CTC can be complemented with recent developments in the understanding of the functional role brain rhythms play, with assembly formation being the core operation at the connectome level necessary to establish the kinds of cross-modular representational structures seen in natural language. *γ* band activity, for instance, has been associated with numerous cognitive functions such as memory and selective attention (see Figure 2 for examples of connectome-cognition links). With *γ* bands arising from an interplay of inhibition (produced by GABAergic neurons) and excitation (produced by glutamergic neurons), Bosman et al. (2014) propose that these bands have their origin in basic functional motifs conferring an advantage for low-level system processing and multiple cognitive functions. Higher cognitive functions implicated in *γ* have their origin in ‘a limited set of circuit motifs which are found universally across species and brain structures’ (Bosman et al. 2014: 1982). Since inhibitory interneurons have been shown to target the perisomatic region of pyramidal neurons (Bartos et al. 2007), it has been suggested that this process imposes a *γ* rhythm and so controls the timing of relevant spike discharges (Buzsáki & Wang 2012).

<INSERT FIGURE 2 HERE>

**Figure 2**: The numerous roles attributed to gamma-band synchronisation (GBS) are represented by the higher tier, while their implementation in neural circuits is found in the lower tier (from Bosman et al. 2014: 1983).

The broad functionality of the *γ* band I think makes it an ideal candidate, along with the thalamus (discussed below), for being the conductor of language’s cross-modularity. The role of GBS in visual feature integration (Bosman et al. 2009), for instance, makes it a prime candidate for carrying out the forms of conceptual assimilation seen in any number of semantic phenomena. If linguistic computations are in fact responsible for this cross-modularity, then language can perhaps be more closely aligned to dominant descriptions of consciousness and working memory (Dehaene et al. 2014), even if we are forced to remain ‘virtually mute’ (Chomsky 1998: 440) about the nature of experiential content (Strawson 2008, 2010).

In addition, GBS has been shown to support certain low-level functions in the hippocampus which may be vital to particular cognitive functions attributed to this region, such as memory encoding and retrieval (Bosman et al. 2014). As mentioned, the hippocampus is the site of *γ*•*θ* coupling in that multiple *γ* waves are typically embedded within a single *θ* cycle (Bragin et al. 1995). The two rhythms are capable of being connected via a cross-frequency phase-amplitude mechanism through which *γ* is modulated by *θ* (Tort et al. 2008). Along with a phase locking operation through which higher waves occur at stable phases in cycles of lower waves (Belluscio et al. 2012), this allows spike coordination and may consequently be partly responsible for low-level dynome operations like phase coding (see Figure 3). As Lisman and Jensen (2013) review, the dual *γ* and *θ* oscillations form a code for representing multiple items in an ordered way. Since each *θ* cycle contains four to eight nested *γ* cycles, different forms of spatial information (such as a series of events from short-term memory, constituting an ‘episode’) can be represented and sequentially coordinated within a given cycle. The number of *γ* cycles able to be embedded within a *θ* cycle may also be the reason why working memory is limited to its classic constraint of 7 ± 2 (Kamiński et al. 2011). Roux and Uhlhaas (2014) make the related claim that oscillatory activity assures the maintenance of working memory information. This explanation is of precisely the kind of granularity linguists should seek to capture syntactic operations like labeling, which involves storing conceptual roots in memory. Through the coding scheme discussed by Lisman and Jensen (2013), the cell assembly that fires during a given *γ* cycle forms a topographic pattern representing a particular item from memory. If this oscillatory mechanism is also responsible for syntactic computation, this would lend weight to the strong connection drawn in Murphy (2015b) between phases and episodic memory, and it would also be a strong candidate for a neural substrate of the computational operation ‘Select’, which in syntactic terms takes items from the lexicon and inserts them into the derivation. In brief, and returning to issues outlined above, if intrinsic coupling across cortical oscillations is responsible for the hierarchical combination of computations at the syllabic and phonemic levels, ‘restoring the natural arrangement of phonemes within syllables’ (Hyafil et al. 2015), then this leads to the possibility that hierarchical syntactic computations result from similar mechanisms.

<INSERT FIGURE 3 HERE>

**Figure 3**: Schematic of the theta-gamma neural code. The ovals represent states of the same network during two gamma cycles. Active cells are in black and represent the cell assemblies which code for a particular item, i.e. memory units or, under the Basic Label model, conceptual representations and lexical features. Different assemblies are active in different cycles (from Lisman & Jensen 2013: 1003).

These operations, it should be stressed, are all conserved from early in mammalian evolution, with the above interplay between excitation and inhibition being found in crustaceans (Nusbaum & Beenhakker 2002) and major phyla dating back 350 million years (Katz & Harris-Warrick 1999). Bosman et al. (2014) draw on such considerations in claiming that the evolutionary acquisition of this excitation-inhibition interplay led to the selection of these *γ* waves as a principal element of computation. If this GBS mechanism was a ‘direct, inevitable consequence of early circuitry organization’ (Bosman et al. 2014: 1994), then it may be that it is an exaptation (being co-opted) in that is was later afforded a functional use in systems of memory and learning (see also Gould & Vrba 1982). Further, top-down neocortical processes implicated in particular higher cognitive faculties like working memory (Buschman, & Miller 2007) and free-choice reach (Pesaran et al. 2008) also appear to be carried by interareal synchrony in the *β* rhythm (Bressler & Richter 2015), increasing the electrophysiological validity of the functional roles attributed to this wave above. It is also worth noting in this connection that due to the frequent overlap between the functional roles attributed to *β* and *α* waves, Bressler and Richter (2015: 63) argue for a re-definition of neural oscillations based on functionality, not arbitrary clinical and frequency boundaries. Though this does not currently warrant a re-formulation of the cognome-dynome framework outlined here, the research of dynamic cognomics should bare this approach in mind, as a re-conceptualisation of the cognome may well simultaneously require a re-formulation of the dynome; much as how Poeppel (2012) and Chomsky (2000) originally suggested.

* 1. **Cognomic constraints and their neurobiological realisability**

In the same way that *γ* oscillations ‘arise simultaneously and inevitably with inhibitory-excitatory interplay, and are neither an epiphenomenon nor a separate cause of the functionality beyond the underlying circuits’ (Bosman et al. 2014: 1995), I would like to suggest that ‘linguistic’ ‘computations’ (which, as we have seen, are neither purely linguistic nor thoroughly computational) are to be seen as identical to the operations of the connectome, which can be described in electrophysiological terms at the dynome level and in still more abstract terms at the cognome level, in a similar way that *heat* and *energy* can be reduced to thermodynamics. While I hope to have shown that distinct oscillatory phases segregate discrete units of information (visual, olfactory, semantic, etc.), there remains the possibility that they also serve computations spanning multiple oscillatory cycles. Just as hippocampal sharp-wave ripples partition information into individual cycles, so too might multiple *β* or *θ* cycles represent distinct information from a continuous memory episode or lexical item; that is, oscillatory phases may be the means through which different lexical features (e.g. φ, tense) are processed or time-locked with other features, leading to agreement relations, the resolution of filler-gap dependencies, feature inheritance and other familiar syntactic operations. Multiple *β* or *θ* cycles could, for instance, employ dynomic operations like ‘cycle skipping’ (Brandon et al. 2013) to control which cell assemblies are activated upon subsequent cycles to trigger different aspects of lexical and conceptual representations.

These remarks cover some basic computations, but what of their *constraints*? Consider Wurmbrand’s (2014) Merge Condition, stated below:

1. *Merge Condition*:

Merge α and β if α can value a feature of β.

This condition ensures that set-formation via concatenation (and often labeling in addition) is licensed only under Agree, requiring also feature satisfaction. Leaving aside further details, the scientist concerned with establishing linking hypotheses between linguistics and neuroscience is faced here with a number of challenges but also some surprising possibilities. Assuming the Basic Label model, we can propose that the cell assemblies implicated via cycle skipping in the features of α and β can be phase-locked, leading to oscillatory synchronisation of two discrete units of information. When this occurs, feature valuation takes place and the derivation can converge. If this process is barred in virtue of rhythmic coupling restrictions and the limits of assembly synchronisation, feature valuation does not take place, in turn prohibiting merger of α and β. Notice that this model at once implies specific neurobiological limitations, in that the hypothetical coupling responsible for feature valuation should occur after the cross-cortical {α(γ)} embedding proposed to be the substrate of set-formation. This leads to clear, causally-addressable empirical predictions, to be investigated in future research.

We are now in a position to outline a concrete research project. The first phase of dynamic cognomics will involve the above ongoing research into translating the *operations* of syntax into oscillation terms. The second phase should centre on translating the *constraints* of syntax, such as those concerning agreement, movement and anti-locality. For instance, Richard’s (2010) Distinctness Condition, prohibiting the presence of multiple lexical units within a single phase, may be the consequence of how many distinct rhythms it is possible to couple in specific actions (Boeckx 2013). What is needed is consequently a re-conceptualisation of language as not just a system of thought, planning and interpretation (as many generativists, operating at the most basic psychological level, have long proposed), but also a system of oscillatory and electrophysiological information synchronisation. Following the principle of cognome-dynome reciprocation, the computational constraints explored by Wurmbrand and others will direct inquiry into the possibilities of dynomic operations, although this process may require further elaboration of the nature of the role of oscillations in cognition.

* 1. **Globularity and cortico-centrism**

Recent developments in systems neuroscience have identified large scale distributed brain networks, typically explored through fMRI and MEG using ICA (Brookes et al. 2012). Data from fMRI suggests that the implication of a functionally specific set of neurons in any given computation is assisted by a backdrop of large-scale neural assembly inter-communication. These networks are composed of sub-networks with correlating and anti-correlating patterns, leading to a situation in which a single large-scale network may operate through overlapping but distinct neural sub-networks. Relatedly, the evolution of cognitive sub-systems (vision, olfaction, etc.) builds on its neurocomputational ancestors, leading to direct expectations of finding neural homologies in computations which echo this influence. This permits the extension of the concerns of computational ethology outlined in Murphy (2015a) into the domain of computational neuroscience, specifically neuroethology. Figure 4 highlights the major operations at the level of the cognome, dynome and connectome, along with general laws influencing such operations.

<INSERT FIGURE 4 HERE>

**Figure 4**: The central operations implicated by the Basic Label model of the cognome, dynome and connectome, along with more general laws.

As the cognome-dynome-connectome linking hypotheses expand, it is important not to ignore the fundamental role of the genome. Consider briefly the genes *RUNX2*, the *DLX* suite and the *BMP* family, involved in skull and brain development (Perdomo-Sabotal et al. 2014). In a series of ongoing research, Boeckx and Benítez-Burraco (2014a, b, Benítez-Burraco & Boeckx 2015) hypothesise that a modification in this gene network gave rise to a more globular head shape (relative to Neanderthals/Denisovans; Gunz et al. 2012, Bruner 2004) and the consequent re-wiring of cortical and sub-cortical structures, permitting the construction of the forms of cross-modular representations well established in psychological, philosophical and semantic theories of concepts (Spelke 2010, Pietroski forthcoming). Globularity may also have contributed, as some have suggested, to an increase in wiring efficiency across the brain (Chklovskii et al. 2002). It is of outstanding interest for biolinguistics and dynamic cognomics that functional links are beginning to be drawn between genes and their cellular consequences for the human cognitive phenotype.

An evaluation of these observations can also be made alongside a consideration of what Piatelli-Palmarini and Uriagereka (2008) see as the optimising role language has in building syntactic and phonological structures, which proceeds via minimal search and related principles of computational efficiency (Larson 2015). This minimalist perspective leads to a separation of optimality from language’s proposed ‘function’ of mapping structures to the interfaces, since similar optimising principles are found elsewhere in the natural world, leading Piatelli-Palmarini and Uriagereka (2008: 209) to ‘suspect that the process behind the abstract form follow[s] from physico-chemical invariants’. But lacking a theory of brain dynamics (or even basic connectomics), the authors are unable to go ground these general proposals within any neurobiological framework. I suggest that the microcellular level and the dynome, operating within some general physical laws of neural organisation such as free-energy, can provide a potential substrate of such optimising ‘physico-chemical invariants’. The only human-unique aspect of the model pursued here, then, is the *context* in which the conserved and universal rhythms discussed above perform their operations of coupling and decoupling; namely, a globular context. A more globular brain would have led to a decrease in ‘spatial inequalities’ (Salami et al. 2003) between cortical and subcortical regions which prohibits long-distance coupling. This would imply that the numerous centuries-long approaches to human-uniqueness, ranging from philosophy to medicine, have approaching the matter from the wrong perspective. Instead of asking ‘What is it about humans which allows us to form complex systems of symbolic interpretation?’ we should instead ask ‘What is it about other animals which *prohibits* them from doing so?’

Globularity may also have led to the expansion of the neo-cortex and the pulvinar, spurred on by the reduction of the large Neanderthal visual system (Pearce et al. 2013). As Benítez-Burraco and Boeckx (2015) point out, cross-modular concepts likely employ thalamic nuclei such as the pulvinar and the medio-dorsal nucleus, not least because of the thalamus’s role in modulating fronto-parietal activity, regulating cortical oscillations (Saalmann et al. 2012) and enhancing the rhythmic range of different frequency bands (Singer 2013). Controlling rhythmic behaviour is also a function attributed to *RUNX2* (Reale et al. 2013, see also van der Lely & Pinker 2014 for genetic discussion relating to phonological computations). A literature review leads Theofanopoulou and Boeckx (2015) to claim that the thalamus is ‘the part of the brain assigned to tune the oscillations of the other subcortical structures’, while there is accumulating evidence that ‘cognitive disorders that are routinely associated with language and the distinctive mode of thought it entails such as schizophrenia, autism, dementia, major depression, verbal working memory impairments, etc. crucially involve thalamic disorders’. The relation between thalamic shape and these cognitive disorders is so close that Vila-Rodriguez et al. (2008) regard the shape of the thalamus as ‘a possible endophenotype’. Boeckx (2014b) argues that ‘if a key function of language is to link units from different cognitive domains’, the thalamus is ‘well placed for it’, possibly being ‘the conductor in a large orchestra’.

Relatedly, due to the few protein differences between humans and chimpanzees, the individuating computational factors may be attributed to cis-regulatory and trans-regulatory genes (Somel et al. 2013). Hominid-unique features which may have led to the higher mental faculties of humans include novel neuronal cell types and the duplication of developmental proteins such as SRGAP2 leading to unique dendritic spine density and form (Geschwind & Rakic 2013); examples of what we could dub ‘formalist neuroscience’, applying the formalist concern for natural morphological constraints to the study of the connectome. Synaptic and dendritic maturation also occurs in humans for a considerably longer time than in non-humans (Bianchi et al. 2013).

If we also consider the conclusions of Harris’s review of cortical computation in mammals and birds, that the ‘human cortex appears to contain the same cell types, and their patterns of wiring and gene expression appear basically similar to well-studied model systems’ (2015: 3184), the importance of subcortical investigations into linguistic computation become even clearer. While subcortical structures have often been derided as the ‘reptilian brain’, responsible for only primitive drives, far removed from the higher echelons of thought supposedly brought about by the neocortex, the perspective of dynamic cognomics re-situates subcortical regions like the thalamus and the basal ganglia into the core areas responsible for linguistic phrase structure building (see also Johnson & Knight 2015 for a strong case that the thalamus plays a key role in neocortical oscillations involved in memory processes, and Saalmann & Kastner 2011 for an argument against the classical view that the thalamus is confined to passively relaying cortical information). These tensions and complexities become particularly vivid when we acknowledge that the basal ganglia’s *β* rhythm, proposed here to be vital for labeling, is also crucially involved in attention tasks and muscular contraction (Khanna & Carmena 2015). The importance of the thalamus for higher cognition was also speculated in work by Campion and Elliott-Smith (1934), rejecting the dominant cortico-centrism and suggesting that cortico-thalamic impulse circulation was responsible for ‘thought’.

Summarising these findings, it appears that the developed interneurons and dendritic spinal strength proposed by Geschwind and Rakic (2013) fortified long-distance assembly connections and, in turn, the mechanisms of ephaptic coupling, CFC and other neuronal processes (operating within the confines of the CTC hypothesis) necessary for the rhythmic interactions claimed above to be the source of computations like labeling and cyclic transfer. Though many intervening neurochemical processes need to be accounted for and explained, it seems that such processes, along with novel *Ve*-fluctuations, are the reason why we find the cyclic short-term memory storage capacities seen in labeling; that is, they are (part of) the reason why a *red box* is an object and not a special kind of property. Updating Darwin’s claim of ‘He who understands baboon would do more towards metaphysics than Locke’, we can conclude that he who understands brain rhythms would do more towards biolinguistics than Lenneberg.

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**REFERENCES**

Allen, K., Monyer, H. (2015). Interneuron control of hippocampal oscillations. *Current Opinion in Neurobiology*, 31: 81-87.

Amundson, R. (1998). Typology reconsidered: Two doctrines on the history of evolutionary biology. *Biology and Philosophy*, 13: 153-77.

Amundson, R. (2006). EvoDevo as cognitive psychology. *Biological Theory* 1(1), 10-11.

Anastassiou, C. A., & Koch, C. (2015). Ephaptic coupling to endogenous electric field activity: why bother? *Current Opinion in Neurobiology* 31, 95-103.

Anastassiou, C. A., Perin, R., Markram, H., & Koch, C. (2011). Ephaptic coupling of cortical neurons. *Nature Neuroscience* 14(2), 217-223.

Aru, J., Aru, J., Priesemann, V., Wibral, M., Lana, L., Pipa, G., Singer, W., & Vicente, R. (2015). Untangling cross-frequency coupling in neuroscience. *Current Opinion in Neurobiology* 31, 51-61.

Baddeley, A., Eysenck, M. W., & Anderson, A. C. (2014). *Memory*. 2nd ed. Abingdon, Oxon: Psychology Press.

Balari, S., Boeckx, C., & Lorenzo, G. (2012). On the feasibility of biolinguistics: Koster’s word-based challenge and our ‘natural computation’ alternative. *Biolinguistics* 6(2), 205-21.

Balari, S., & Lorenzo, G. (2013). *Computational Phenotypes: Towards an Evolutionary Developmental Biolinguistics*. Oxford: Oxford University Press.

Bartos, M., Vida, I., & Jonas, P. (2007). Synaptic mechanisms of synchronized gamma oscillations in inhibitory interneuron networks. *Nature Reviews Neuroscience*, 8, 45-56.

Bastos, A. M., Martin Usrey, W., Adams, R. A., Mangun, G. R., Fries, P., Friston, K. J. (2012). Canonical microcircuits for predictive coding. *Neuron* 76, 695-711.

Bastos, A. M., Vezoli, J., & Fries, P. (2015). Communication through coherence with inter-areal delays. *Current Opinion in Neurobiology* 31, 173-180.

Belluscio, M. A., Mizuseki, K., Schmidt, R., Kempter, R., & Buzsáki, G. (2012). Cross-frequency phase-phase coupling between θ and γ oscillations in the hippocampus. *Journal of Neuroscience* 32, 423-435.

Bemis, D. K., & Pylkkänen, L. (2013). Basic linguistic composition recruits the left anterior temporal lobe and left angular gyrus during both listening and reading. *Cerebral Cortex* 23, 1859-1873.

Benítez-Burraco, A., & Boeckx, C. (2013). Language disorders and language evolution: Constraints on hypotheses. *Biological Theory* 1-6.

Benítez-Burraco, A., & Boeckx, C. (2014a). FOXP2, retinoic acid, and language: a promising direction. *Frontiers in Cellular Neuroscience* 8: 387. doi: 10.3389/fncel.2014.00387.

Benítez-Burraco, A., & Boeckx, C. (2014b). Universal grammar and biological variation: an evo-devo agenda for comparative biolinguistics. *Biological Theory* 9, 122-134. doi: 10.1007/s13752-014-0164-0.

Benítez-Burraco, A., & Boeckx, C. (2015). Possible functional links among brain- and skull-related genes selected in modern humans. *Frontiers in Psychology* 6: 794. doi:10.3389/fpsyg.2015.00794.

Berger, H. (1929). Uber das elektrenephalogramm des menschen. *Archiv für Psychiatrie und Nervenkrankheiten* 87, 527-570.

Berretta, N., Rossokhin, A. G., Kasyanov, A. M., Sokolov, M. V., Cherubini, E., & Voronin, L. L. (2000). Postsynaptic hyperpolarization increases the strength of AMPA-mediated synaptic transmission at large synapses between mossy fibers and CA3 pyramidal cells. *Neuropharmacology*, 39, 2288-2301.

Bertossa, R. (2011). Morphology and behaviour: functional links in development and evolution. *Philosophical Transactions of the Royal Society B* 366: 2056-68.

Bi, G. Q., & Poo, M. M. (1998). Synaptic modifications in cultured hippocampal neurons: dependence on spike timing, synaptic strength, and postsynaptic cell type. *Journal of Neuroscience* 18, 10464-10472.

Bianchi, S., Stimpson, C.D., Duka, T., Larsen, M.D., Janssen, W.G., Collins, Z., Bauernfeind, A.L., Schapiro, S.J., Baze, W.B., McArthur, M.J., Hopkins, W.D., Wildman, D.E., Lipovich, L., Kazuwa, C.W., Jacobs, B., Hof, P.R., & Sherwood, C.C. (2013). Synaptogenesis and development of pyramidal neuron dendritic morphology in the chimpanzee neocortex resembles humans. *Proceedings of the National Academy of Sciences of the United States of America* 110(Supplement 2): 10395-10401.

Boeckx, C. (2013). Merge: biolinguistic considerations. *English Linguistics* 30(2), 463-484.

Boeckx, C. (2014a). *Elementary Syntactic Structures: Prospects of a Feature-Free Syntax*. Cambridge: Cambridge University Press.

Boeckx, C. (2014b). Our brain’s language-readiness. *El País*. 7 February.

Boeckx, C., & Benítez -Burraco, A. (2014a). The shape of the human language-ready brain. *Frontiers in Psychology* 5, 282.

Boeckx, C., & Benítez-Burraco, A. (2014b). Globularity and language-readiness: generating new predictions by expanding the set of genes of interest. *Frontiers in Psychology* 5, 1324.

Boeckx, C., & Theofanopoulou, C. (2014). A multidimensional interdisciplinary framework for linguistics: The lexicon as a case study. *Journal of Cognitive Science* 15, 403-420.

Boeckx, C., & Theofanopoulou, C. (2015). Language, cognomes, and the challenges of building cognitive phylogenies. *Frontiers in Psychology* 6:784. doi:10.3389/fpsyg.2015.00784.

Bolker, J. A. (2008). Developing a history of evo‐devo. *BioScience* 58: 461-463.

Bosman, C. A., Lansink, C. S., & Pennartz, C. M. A. (2014). Functions of gamma-band synchronization in cognition: from single circuits to functional diversity across cortical and subcortical systems. *European Journal of Neuroscience* 39, 1982-1999. doi:10.1111/ejn.12606.

Bosman, C. A., Womelsdorf, T., Desimone, R., & Fries, P. (2009). A microsaccadic rhythm modulates gamma-band synchronization and behavior. *Journal of Neuroscience* 29, 9471-9480.

Bragin, A., Jando, G., Nadasdy, Z., Hetke, J., Wise, K., & Buzsáki, G. (1995). Gamma (40–100 Hz) oscillation in the hippocampus of the behaving rat. *Journal of Neuroscience* 15, 47-60.

Brandon, M. P., Bogaard, A. R., Schultheiss, N. W., Hasselmo, M. E. (2013). Segregation of cortical head direction cell assemblies on alternating θ cycles. *Nature Neuroscience*, 16, 739-748.

Brandon, M. P., Koenig, J., Leutgeb, J. K., Leutgeb, S. (2014). New and distinct hippocampal place codes are generated in a new environment during septal inactivation. *Neuron*, 82, 789-796.

Bressler, S. L., & Menon, V. (2010). Large-scale brain networks in cognition: emerging methods and principles. *Trends in Cognitive Sciences* 14, 277-290.

Bressler, S. L., & Richter, C. G. (2015). Interareal oscillatory synchronization in top-down neocortical processing. *Current Opinion in Neurobiology* 31, 62-66.

Brookes, M. J., Liddle, E. B., Hale, J. R., Woolrich, M. W., Luckhoo, H., Liddle, P. F., & Morris, P. G. (2012). Task induced modulation of neural oscillations in electrophysiological brain networks. *NeuroImage* 63, 1918-1930.

Bruner, E. (2004). Geometric morphometrics and paleoneurology: brain shape evolution in the genus homo. *Journal of Human Evolution* 47(5), 279-303. doi: 10.1016/j.jhevol.2004.03.009.

Bufill, E., & Carbonell, E. (2004). Are symbolic behavior and neuroplasticity an example of gene-culture evolution? *Revista de Neurologia* 39, 48-55.

Buschman, T. J., & Miller, E. K. (2007). Top-down versus bottom-up control of attention in the prefrontal and posterior parietal cortices. *Science*, 315, 1860-1862.

Buzsáki, G. (2006). *Rhythms of the Brain*. Oxford: Oxford University Press.

Buzsáki, G. (2010). Neural syntax: Cell sssemblies, synapsembles, and readers. *Neuron* 68, 362-385.

Buzsáki, G., & Freeman, W. (2015). Editorial overview: Brain rhythms and dynamic coordination. *Current Opinion in Neurobiology* 31, v-ix.

Buzsáki, G., Logothetis, N., & Singer, W. (2013). Scaling brain size, keeping timing: evolutionary preservation of brain rhythms. *Neuron* 80, 751-764.

Buzsáki, G., & Wang, W.-J. (2012). Mechanisms of gamma oscillations. *Annual Review of Neuroscience.* 35, 203-225.

Calabrese, A., & Woolley, S. M. N. (2015). Coding principles of the canonical cortical microcircuit in the avian brain. *Proceedings of the National Academy of Sciences of the United States of America* 112(11), 3517-3522.

Campion, G., & Elliot-Smith, G. (1934). *The Neural Basis of Thought*. New York: Harcourt Brace Jovanovich.

Canavier, C. C. (2015). Phase-resetting as a tool of information transmission. *Current Opinion in Neurobiology* 31, 206-213.

Canolty, R. T., & Knight, R. T. (2010). The functional role of cross-frequency coupling. *Trends in Cognitive Sciences*, 14(11), 506-515.

Carroll, S. B. (2006). *The Making of the Fittest: DNA and the Ultimate Forensic Record of Evolution*. New York: W.W. Norton.

Caton, R. (1875). The electric currents of the brain. *British Medical Journal* 2, 278.

Chklovskii, D. B., Schikorski, T., & Stevens, C. F. (2002). Wiring optimization in cortical circuits. *Neuron* 34, 341-347. doi:10.1016/S0896-6273(02)00679-7.

Chomsky, N. (1968). Quine’s empirical assumptions. *Synthese* 19(1), 53-68.

Chomsky, N. (1995). *The Minimalist Program*. Cambridge, MA: MIT Press.

Chomsky, N. (1998). Comments: Galen Strawson, *Mental Reality*. *Philosophy and Phenomenological Research* 58(2), 437-441.

Chomsky, N. (2000). *New Horizons in the Study of Language and Mind*. Cambridge: Cambridge University Press.

Chomsky, N. (2008). On phases. Freidin, R., Otero, C. P., & Zubizarreta, M. L. (eds). *Foundational Issues in Linguistic Theory: Essays in Honor of Jean-Roger Vergnaud*. Cambridge, MA: MIT Press. 133-166.

Chomsky, N. (2012). *The Science of Language: Interviews with James McGilvray*. Cambridge: Cambridge University Press.

Chomsky, N. (2015a). Problems of projection: extensions. Di Domenico, E., Hamann, C., & Matteini, S. (eds.). *Structures, Strategies and Beyond: Studies in Honour of Adriana Belletti*. Amsterdam: John Benjamins. 1-16.

Chomsky, N. (2015b). Some core contested concepts. *Journal of Psycholinguistic Research* 44(1), 91-104.

Chow, B. Y., Han, X., Dobry, A. S., Qian, X., Chuong, A. S., Li, M., Henninger, M. A., Belfort, G. M., Lin, Y., Monahan, P. E., & Boyden, E. S. (2010). High-performance genetically targetable optical neural silencing by light-driven proton pumps. *Nature* 463, 98-102.

Collins, J. (2015). Naturalism without metaphysics. In Fischer, E., & Collins, J. (eds.). *Experimental Philosophy, Rationalism, and Naturalism*. London: Routledge. 85-109.

Crunelli, V., David, F., Lőrincz, M. L., & Hughes, S. W. (2015). *Current Opinion in Neurobiology* 31, 72-80.

Dawkins, R. (2006). *Climbing Mount Improbable*. Oxford: Oxford University Press.

De Pasquale, F., Della Penna, S., Snyder, A. Z., Marzetti, L., Pizzella, V., Luca Romani, G., Corbetta, M. (2012). A cortical core for dynamic integration of functional networks in the resting human brain. *Neuron* 74, 753-764.

Deans, J. K., Powell, A. D., Jefferys, J. G. R. (2007). Sensitivity of coherent oscillations in rat hippocampus to AC electric fields. *The Journal of Physiology*, 583(2), 555-565.

Dehaene, S., Charles, L., King, J-R., & Marti, S. (2014). Toward a computational theory of conscious processing. *Current Opinion in Neurobiology* 25, 76-84.

Deisz, R. A., & Prince, D. A. (1989). Frequency-dependent depression of inhibition in guinea-pig neocortex in vitro by GABAB receptor feed-back on GABA release. *Journal of Physiology* 412, 513-541.

Diller, K.C., & Cann, R.L. (2013). “Genetics, evolution, and the innateness of language,” in *The Evolutionary Emergence of Language: Evidence and Inference*, eds. R. Botha & M. Everaert (Oxford: Oxford University Press), 244-258.

Embick, D., & Poeppel, D. (2015). Towards a computational(ist) neurobiology of language: correlational, integrated and explanatory neurolinguistics. *Language, Cognition and Neuroscience* 30(4), 357-366.

Engel, A. K., & Fries, P. (2010). Beta-band oscillations - signalling the status quo? *Current Opinion in Neurobiology* 20, 156-165.

Fodor, J. (2010). *LOT2: The Language of Thought Revisited*. Oxford: Oxford University Press.

Field, J. (2004). *Psycholinguistics: The Key Concepts*. London: Routledge.

Fitch, W. T. (2009). Prolegomena to a future science of biolinguistics. *Biolinguistics* 3, 283-320.

Fitch, W.T., & Friederici, A.D. (2012). Artificial grammar learning meets formal language theory: an overview. *Philosophical Transactions of the Royal Society B* 367(1598), 1933-1955.

Freeman, W. J. (2015). Mechanism and significance of global coherence in scalp EEG. *Current Opinion in Neurobiology* 31, 199-205.

Friederici, A. D. (2012). The cortical language circuit: from auditory perception to sentence comprehension. *Trends in Cognitive Sciences* 5, 262-268.

Friederici, A. D., Bahlmann, J., Heim, S., Schubotz, R. I., & Anwander, A. (2006). The brain differentiates human and non-human grammars: functional localization and structural connectivity. *Proceedings of the National Academy of Sciences of the United States of America* 103: 2458-63.

Fries, P. (2009). Neuronal gamma-band synchronization as a fundamental process in cortical computation. *Annual Review of Neuroscience* 32, 209-224. doi: 10.1146/annurev.neuro.051508.135603.

Fries, P., Womelsdorf, T., Oostenveld, R., & Desimone, R. (2008). The effects of visual stimulation and selective visual attention on rhythmic neuronal synchronization in macaque area V4. *Journal of Neuroscience*, 28, 4823-4835.

Friston, K. (2008). Hierarchical models in the brain. *PLoS Computational Biology* 4(11), e1000211. doi:10.1371/journal.pcbi.1000211.

Friston, K. (2010). The free-energy principle: a unified brain theory? *Nature Reviews Neuroscience* 11, 127-138. doi:10.1038/nrn2787.

Gallistel, C. R., & King, A. P. (2009). *Memory and the computational brain: Why cognitive science will transform neuroscience*. Wiley-Blackwell, Malden.

Geschwind, D.H., & Rakic, P. (2013). Cortical evolution: Judge the brain by its cover. *Neuron* 80, 633-47.

Giraud, A.-L., & Poeppel, D. (2012). Cortical oscillations and speech processing: emerging computational principles and operations. *Nature Neuroscience* 15(4), 511-517.

Gould, S. J,. &, Vrba, E. S. (1982). Exaptation-a missing term in the science of form. *Paleobiology* 8, 4-15.

Grodzinsky, Y. (2010). The picture of the linguistic brain: how sharp can it be? Reply to Fedorenko & Kanwisher. *Language and Linguistics Compass* 4, 605-622.

Gunz, P., Neubauer, S., Golovanova, L., Doronichev, V., Maureille, B., & Hublin, J.-J. (2012). A uniquely modern human pattern of endocranial development: insights from a new cranial reconstruction of the Neandertal newborn from Mezmaiskaya. *Journal of Human Evolution* 62(2), 300-313.

Hagoort, P. (2014). Nodes and networks in the neural architecture for language: Broca’s region and beyond. *Current Opinion in Neurobiology* 28, 136-141.

Harris, K. D. (2015). Cortical computation in mammals and birds. *PNAS* 112(11), 3184-3185.

Hauser, M., Chomsky, N., & Fitch, W.T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science* 298(5598), 1569-79.

Hebb, D. O. (1949). *The Organization of Behavior*.New York: John Wiley & Sons.

Hornstein, N., & Pietroski, P. (2009). Basic operations: minimal syntax-semantics. *Catalan Journal of Linguistics* 8, 113-139.

Hyafil, A., Fontolan, L., Kabdebon, C., Gutkin, B., & Giraud, A.-L. (2015). Speech encoding by coupled cortical theta and gamma oscillations. *eLife* 10: 7554. doi: http://dx.doi.org/10.7554/eLife.06213.

Hyvärinen, A., & Oja, E. (2000). Independent component analysis: algorithms and applications. *Neural Networks* 13, 411-430.

Jefferys, J. G. (1995). Nonsynaptic modulation of neuronal activity in the brain: electric currents and extracellular ions. *Physiological Reviews*, 75(4), 689-723.

Jensen, O., Gelfand, J., Kounios, J., Lisman, J.E. (2002). Oscillations in the alpha band (9-12 Hz) increase with memory load during retention in a short-term memory task. *Cerebral Cortex* 12, 877-882.

Johnson, E. J., & Knight, R. T. (2015). Intracranial recordings and human memory. *Current Opinion in Neurobiology* 31, 18-25.

Kaiser, G. (2010). *A Friendly Guide to Wavelets*. New York: Springer.

Kamiński, J., Brzezicka, A., & Wróbel, A. (2011). Short-term memory capacity (7 ± 2) predicted by theta to gamma cycle length ratio. Neurobiol. Learn. Mem. 95, 19-23.

Katahira, K., Suzuki, K., Kagawa, H., & Okanoya, K. (2013). A simple explanation for the evolution of complex song syntax in Bengalese finches. *Biology Letters* 9(6): 20130842.

Katz, P. S., & Harris-Warrick, R. M. (1999). The evolution of neuronal circuits underlying species-specific behavior. *Current Opinion in Neurobiology* 9, 628-633.

Kayser, C., Wilson, C., Safaai, H., Sakata, S., & Panzeri, S. (2014). Rhythmic auditory cortex activity at multiple timescales. *Journal of Neuroscience* 35(20), 7750-7762.

Khanna, P., & Carmena, J. M. (2015). Neural oscillations: beta band activity across motor networks. *Current Opinion in Neurobiology* 32, 60-67.

Kinzler, K. & Spelke, E. (2007). Core systems in human cognition. *Progress in Brain Research* 164, 257-64.

Klausberger, T., Marton, L. F., O’Neill, J., Huck, J. H., Dalezios, Y., Fuentealba, P., Suen, W. Y., Papp, E., Kaneko, T., Watanabe, M., Csicsvari, J., Somogyi, P. (2005). Complementary roles of cholecystokinin- and parvalbumin-expressing GABAergic neurons in hippocampal network oscillations. *Journal of Neuroscience*, 25(42), 9782-9793.

Klampfl, S., Legenstein, R., & Maass, W. (2009). Spiking neurons can learn to solve information bottleneck problems and extract independent components. *Neural Computation* 21, 911-959.

Klimesch, W., Schack, B., Schabus, M., Doppelmayr, M., Gruber, W., & Sauseng, P. (2004). Phase-locked alpha and theta oscillations generate the P1-N1 complex and are related to memory performance. *Cognitive Brain Research* 19, 302-316.

Klimesch, W., Sauseng, P., & Hanslmayr, S. (2007). EEG alpha oscillations: the inhibition/timing hypothesis. *Brain Research Reviews* 53, 63-88.

Kopell, N. J., Gritton, H. J., Whittington, M. A., & Kramer, M. A. (2014). Beyond the connectome: the dynome. *Neuron* 83, 1319-1328.

Korotkova, T., Fuchs, E. C., Ponomarenko, A., von Engelhardt, J., & Monyer, H. (2010). NMDA receptor ablation on parvalbumin-positive interneurons impairs hippocampal synchrony, spatial representations, and working memory. *Neuron*, 68(3), 557-569.

König, P. (1994). A method for the quantification of synchrony and oscillatory properties of neuronal. *Journal of Neuroscience Methods* 54, 31-37.

König, P., Engel, A. K., & Singer, W. (1995). Relation between oscillatory activity and long-range synchronization in cat visual cortex. *Proceedings of the National Academy of Sciences of the United States of America* 92, 290-294.

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.

Langus, A., Petri, J., Nespor, M., & Scharff, C. (2013). “FoxP2 and deep homology in the evolution of birdsong and human language,” in *The Evolutionary Emergence of Language: Evidence and Inference*, eds. R. Botha & M. Everaert (Oxford: Oxford University Press), 223-243.

Lapray, D., Lasztoczi, B., Lagler, M., Viney, T. J., Katona, L., Valenti, O., Hartwich, K., Borhegyi, Z., Somogyi, P., Klausberger, T. (2012). Behavior-dependent specialization of identified hippocampal interneurons. *Nature Neuroscience* 15, 1265-1271.

Larson, B. (2015). Minimal search as a restriction on merge. *Lingua* 156, 57-69.

Larson-Prior, L. J., Oostenveld, R., Della Penna, S., Michalareas, G., Prior, F., Babajani-Feremi, A., Schoffelen, J. M., Marzetti, L., de Pasquale, F., Di Pompeo, F. et al. (2013). Adding dynamics to the human connectome project with MEG. *NeuroImage* 80, 190-201.

Lau, E., Phillips, C., & Poeppel, D. (2008). A cortical network for semantics: (de)constructing the N400. *Nature Reviews Neuroscience* 9, 920-933. doi:10.1038/nrn2532.

Lenneberg, E. H. (1964). A biological perspective of language. In Lenneberg, E. H. (ed). *New Directions in the Study of Language*. Cambridge, MA: MIT Press. 65-88.

Leventhal, D. K., Gage, G. J., Schmidt, R., Pettibone, J. R., Case, A. C., & Berke, J. D. (2012). Basal ganglia beta oscillations accompany cue utilization. *Neuron* 73, 523-536.

Lewis, S., & Phillips, C. (2015). Aligning grammatical theories and language processing models. *Journal of Psycholinguistic Research* 44, 27-46.

Lieberman, P. (2006). *Toward an Evolutionary Biology of Language*. Cambridge, MA: Harvard University Press.

Lieberman, P. (2015). Language did not spring forth 100,000 years ago. *PLoS Biology* 13(2): e1002064.

Lisman, J. E., & Jensen, O. (2013). The theta–gamma neural code. *Neuron*, 77: 1002-1016.

Liu, Z., Fukunaga, M., de Zwart, J. A., Duyn, J. H. (2010). Large-scale spontaneous fluctuations and correlations in brain electrical activity observed with magnetoencephalography. *NeuroImage* 51(1) 102-111.

London, M., & Häusser, M. (2005). Dendritic computation. *Annual Review of Neuroscience* 28, 503-532.

Lopes-dos-Santos, V., Conde-Ocazionez, S., Nicolelis, M. A. L., Ribeiro, S. T., & Tort, A. B. L. (2011). Neuronal assembly detection and cell membership specification by principal component analysis. *PLoS ONE* 6(6), e20996. doi: 10.1371/journal.pone.0020996.

Maini, P. K. (2004). The impact of Turing’s work on pattern formation in biology. *Mathematics Today* 40(4), 140-141.

Makeig, S., Westerfield, M., Jung, T. P., Enghoff, S., Townsend, J., Courchesne, E., Sejnowski, T. J. (2002). Dynamic brain sources of visual evoked responses. *Science* 295, 690-694.

Marr, D. (1982). *Vision: A Computational Investigation into the Human Representation and Processing of Visual Information*. New York: Freeman.

Martins, P. T., & Boeckx, C. (2014). Attention mechanisms and the mosaic evolution of speech. *Frontiers in Psychology* 5: 1463. doi:10.3389/fpsyg.2014.01463.

McCormick, D. A., McGinley, M. J., & Salkoff, D. B. (2015). Brain state dependent activity in the cortex and thalamus. *Current Opinion in Neurobiology* 31: 133-140.

Müller, G. B. (2008). “EvoDevo as a discipline,” *Evolving Pathways: Key Themes in Evolutionary Developmental Biology*, eds. A. Minelli & Fusco, G. (Cambridge: Cambridge University Press), 3-29.

Murphy, E. (2015a). Labels, cognomes and cyclic computation: An ethological perspective. *Frontiers in Psychology* 6: 715. doi: 10.3389/fpsyg.2015.00715.

Murphy, E. (2015b). Reference, phases and individuation: Topics at the labeling-interpretive interface. *Opticon1826* 17, 1-13. doi:10.5334/opt.cn.

Murphy, E. (Forthcoming). Neural substrates of copredication: when an unstoppable scan meets an impossible object. *York Papers in Linguistics*.

Muthukumaraswamy, S. D., Edden, R. A. E., Jones, D. K., Swettenham, J. B., Singh, K. D. (2009). Resting GABA concentration predicts peak gamma frequency and fMRI amplitude in response to visual stimulation in humans. *Proceedings of the National Academy of Sciences of the United States of America* 106, 8356-8361.

Narita, H. (2014). *Endocentric Structuring of Projection-free Syntax*. Amsterdam: John Benjamins.

Narita, H., & Fujita, K. (2010). A naturalist reconstruction of minimalist and evolutionary biolinguistics. *Biolinguistics* 4(4), 356-76.

Neeleman, A. (2013). Comments on Pullum. *Mind & Language*, 28(4), 522-531.

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. doi:10.3389/fpsyg.2015.00271.

Nusbaum, M. P., & Beenhakker, M. P. (2002). A small-systems approach to motor pattern generation. *Nature* 417(6886), 343-350.

Ohira, T., & Uzawa, T. (eds.) (2015). *Mathematical Approaches to Biological Systems: Networks, Oscillations, and Collective Motions.* New York: Springer.

Ohta, S., Fukui, N., & Sakai, K. (2013). Syntactic computation in the human brain: the degree of merger as a key factor. *PLoS ONE* 8(2): e56230.

Ossandón, T., Jerbi, K., Vidal, J. R., Bayle, D. J., Henaff, M. A., Jung, J., Minotti, L., Bertrand, O., Kahane, P., Lachaux, J. P. (2011). Transient suppression of broadband gamma power in the default-mode network is correlated with task complexity and subject performance. *Journal of Neuroscience* 31, 14521-14530.

Parker, S.T., & McKinney, M.L. (1999). *Origins of Intelligence: The Evolution of Cognitive Development in Monkeys, Apes, and Humans*. Baltimore, MD: Johns Hopkins University Press.

Pearce, E., Stringer, C., & Dunbar, R. I. M. (2013). New insights into differences in brain organization between Neanderthals and anatomically modern humans. *Proceedings of the Royal Society B* 280, 20130168.

Perdomo-Sabotal, A., Kanton, S., Walter, M. B., & Nowick, K. (2014). The role of gene regulatory factors in the evolutionary history of humans. *Current Opinion in Genetics & Development* 29C, 60-67.

Pesaran, B., Nelson, M. J., & Andersen, R. A. (2008). Free choice activates a decision circuit between frontal and parietal cortex. *Nature* 453, 406-409.

Petersson, K. M., Folia, V., & Hagoort, P. (2012). What artificial grammar learning reveals about the neurobiology of syntax. *Brain & Language* 120(2), 83-95

Pfenning, A.R., Hara, E., Whitney, O., Rivas, M.V., Wang, R., Roulhac, P.L., Howard, J.T., Wirthlin, M., Lovell, P.V., Ganapathy, G., Mountcastle, J., Moseley, M.A., Thompson, J.W., Soderblom, E.J., Iriki, A., Kato, M., Gilbert, M.T.P., Zhang, G., Bakken, T., Bongaarts, A., ernard, A., Lein, E., Mello, C.V., Hartemink, A.J., Jarvis, E.D. (2014). Convergent transcriptional specializations in the brains of humans and song-learning birds. *Science* 346(6215), 1333, 1256846.

Piattelli-Palmarini, M., & Vitiello, G. (2015). Linguistics and some aspects of its underlying dynamics. arXiv:1506.08663.

Pietroski, P. (Forthcoming). *Conjoining Meanings: Semantics without Truth Values*. Oxford: Oxford University Press.

Pigliucci, M., & Müller, G.B. (2010). “Elements of an extended evolutionary synthesis,” in *Evolution – The Extended Synthesis*, eds. M. Pigliucci & G.B. Müller (Cambridge, MA: MIT Press), 3-17.

Poeppel, D. (1996). Neurobiology and linguistics are not yet unifiable. *Behavioral and Brain Sciences* 19, 642-643.

Poeppel, D. (2011). Genetics and language: a neurobiological perspective on the missing link (-ing hypothesis). *Journal of Neurodevelopmental Disorders* 3(4), 381-387.

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. doi: 10.1080/02643294.2012.710600.

Poeppel, D. (2014). The neuroanatomic and neurophysiological infrastructure for speech and language. *Current Opinion in Neurobiology*. 28C, 142-149.

Poeppel, D., & Embick, D. (2005). “Defining the relation between linguistics and neuroscience,” in *Twenty-First Century Psycholinguistics: Four Cornerstones*, ed. A. Cutler (New Jersey: Lawrence Erlbaum), 103-18.

Principe, J. C., & Brockmeier, A. J. (2015). Representing and decomposing neural potential signals. *Current Opinion in Neurobiology* 31, 13-17.

Pulvermüller, F., Preissl, H., Eulitz, C., Pantev, C., Lutzenberger, W., Elbert, T., & Birbaumer, N. (1994). Brain rhythms, cell assemblies and cognition: evidence from the processing of words and pseudowords. *Psycoloquy* 5(48), 1-30.

Pylyshyn, Z. (1984). *Computation and Cognition: Towards a Foundation for Cognitive Science*. Cambridge, MA: MIT Press.

Raichle, M. E, MacLeod, A. M., Snyder, A. Z., Powers, W. J., Gusnard, D. A., & Shulman, G. L. (2001). A default mode of brain function. *Proceedings of the National Academy of Sciences* 98, 676-682.

Rakic, P., & Kornack, D.R. (2001). “Neocortical expansion and elaboration during primate evolution,” in *Evolutionary Anatomy of the Primate Cerebral Cortex*, eds. D. Falk & K.R. Gibson (Cambridge: Cambridge University Press), 30-56.

Reale, M. E., Webb, I. C., Wang, X., Baltazar, R. M., Coolen, L. M., & Lehman, M. N. (2013). The transcription factor Runx2 is under circadian control in the suprachiasmatic nucleus and functions in the control of rhythmic behavior. *PLoS ONE* 8: e54317. doi:10.1371/journal.pone.0054317.

Reimann, M. W., Muller, E. B., Ramaswamy, S., & Markram, H. (2015). An algorithm to predict the connectome of neural microcircuits. *Frontiers in Neural Circuits* 9: 28. doi:10.3389/fncir.2015.00028.

Richards, M. (2011). Deriving the edge: what’s in a phase? *Syntax* 14: 74-95.

Richards, N. (2010). *Uttering Trees*. Cambridge, MA: MIT Press.

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.

Royer, S., Zemelman, B. V., Losonczy, A., Kim, J., Chance, F., Magee, J. C., Buzsáki, G. (2012). Control of timing, rate and bursts of hippocampal place cells by dendritic and somatic inhibition. *Nature Neuroscience*, 15, 769-775.

Russo, E., & Treves, A. (2011). An uncouth approach to language recursivity. *Biolinguistics* 5(1-2), 133-150.

Saalmann, Y. B., & Kastner, S. (2011). Cognitive and perceptual functions of the visual thalamus. *Neuron* 71, 209-223.

Saalmann, Y. B., Pinsk, M. A., Wang, L., Li, X., & Kastner, S. (2012). The pulvinar regulates information transmission between cortical areas based on attention demands. *Science* 337, 753-756. doi:10.1126/science.1223082.

Santi, A., & Grodzinsky, Y. (2010). fMRI adaptation dissociates syntactic complexity dimensions. *NeuroImage* 51(4), 1285-1293.

Santi, A., Friederici, A. D., Makuuchi, M., & Grodzinsky, Y. (2015). An fMRI study dissociating distance measures computed by Broca’s area in movement processing: clause boundary vs. identity. *Frontiers in Psychology* 6: 654. doi: 10.3389/fpsyg.2015.00654.

Sauseng, P., Klimesch, W., Gruber, W.R., Hanslmayr, S., Freunberger, R., & Doppelmayr, M. (2007). Are event-related potential components generated by phase resetting of brain oscillations? A critical discussion. *Neuroscience* 146, 1435-1444.

Seung, S. (2012). *Connectome: How the brain’s wiring makes us who we are*. Boston: Houghton, Mifflin, Harcourt.

Schoenemann, P. T. (2012). Evolution of brain and language. *Progress in Brain Research* 195, 443-459.

Singer, W. (2013). Cortical dynamics revisited. *Trends in Cognitive Sciences* 17, 616-626. doi: 10.1016/j.tics.2013.09.006.

Somogyi, P., & Klausberger, T. (2005). Defined types of cortical interneurone structure space and spike timing in the hippocampus. *The Journal of Physiology*, 562(1), 9-26.

Spaak, E., Bonnefond, M., Maier, A., Leopold, D. A., Jensen, O. (2012). Layer-specific entrainment of gamma-band neural activity by the alpha rhythm in monkey visual cortex. *Current Biology*, 22, 2313-2318.

Spelke, E. 2010. Innateness, choice, and language. In Bricmont, J., & Franck, J. (eds.). *Chomsky Notebook*. New York: Columbia University Press. 203-210.

Sporns, E. (2013). The human connectome: origins and challenges. *NeuroImage* 80, 53-61.

Strauss, A., Henry, M. J., Scharinger, M., & Obleser, J. (2015). Alpha phase determines successful lexical decision in noise. *Journal of Neuroscience* 35(7), 3256-3262.

Strawson, G. (2008). *Real Materialism and Other Essays*. Oxford: Oxford University Press.

Strawson, G. (2010). *Mental Reality*. 2nd ed. Cambridge, MA: MIT Press.

Szathmáry, E. (1996). From RNA to language. *Current Biology* 6(7), 764.

Tallon-Baudry, C., & Bertrand, O. (1999). Oscillatory gamma activity in humans and its role in object representation. *Trends in Cognitive Sciences* 3(4), 151-162.

Tass, P. A. (2000). Stochastic phase resetting: a theory for deep brain stimulation. *Progress of Theoretical Physics Supplement* 139, 301-313.

Tattersall, I. (2008). *The World from Beginnings to 4000BCE*. Oxford: Oxford University Press.

Tettamanti, M., & Weniger, D. (2006). Broca’s area: A supramodel hierarchical processor? *Cortex* 42(4), 491-494.

Theofanopoulou, C., & Boeckx, C. (Forthcoming). The central role of the thalamus in language and cognition. In Boeckx, C., & Fujita, K. (eds.). *Advances in Biolinguistics: The Human Language Faculty and its Biological Basis*. London: Routledge.

Tort, A. B., Kramer, M. A., Thorn, C., Gibson, D. J., Kubota, Y., Graybiel, A. M., & Kopell, N. J. (2008). Dynamic cross-frequency couplings of local field potential oscillations in rat striatum and hippocampus during performance of a T-maze task. *Proceedings of the National Academy of Sciences of the United States of America* 105, 20517-20522.

Tort, A. B., Komorowski, R. W., Manns, J. R., Kopell, N. J., Eichenbaum, H. (2009). Theta–gamma coupling increases during the learning of item-context associations. *Proceedings of the National Academy of Sciences of the United States of America* 106: 20942-20947.

Tsuda, I. (2013). Chaotic itinerancy. *Scholarpedia* 8, 4459.

Tsuda, I. (2015). Chaotic itinerancy and its roles in cognitive neurodynamics. *Current Opinion in Neurobiology* 31, 67-71.

Turing, A. M. (1952). The chemical basis of morphogenesis. *Philosophical Transactions of the Royal Society of London B* 237, 37-73.

Turken, A. U., Dronkers, N. F. (2011). The neural architecture of the language comprehension network: converging evidence from lesion and connectivity analyses. *Frontiers in Systems Neuroscience* 5:1. doi: 10.3389/fnsys.2011.00001.

Uriagereka, J. (2012). *Spell-Out and the Minimalist Program*. Oxford: Oxford University Press.

Vaas, R. (2001). It binds, therefore I am! Review of Rodolfo Llinás’s *I of the Vortex*. *Journal of Consciousness Studies* 8(4), 85-88.

van der Lely, H. K., & Pinker, S. (2014). The biological basis of language: insight from developmental grammatical impairments. *Trends in Cognitive Sciences* 18(11), 586-595.

Varga, C., Golshani, P., Soltesz, I. (2012). Frequency-invariant temporal ordering of interneuronal discharges during hippocampal oscillations in awake mice. *Proceedings of the National Academy of Sciences of the United States of America* 109, E2726-E2734.

Vila-Rodriguez, F., French, L., Barakauskas, V., Mead, C-L., & Khorram, B. (2008). Thalamic shape: a possible endophenotype. *Journal of Neuroscience* 28, 3533-3534.

Vitiello, G. (2015). The use of many-body physics and thermodynamics to describe the dynamics of rhythmic generators in sensory cortices engaged in memory and learning. *Current Opinion in Neurobiology* 31, 7-12.

Viventi, J., Kim, D. H., Vigeland, L., Frechette, E. S., Blanco, J. A., Kim, Y. S., Avrin, A. E., Tiruvadi, V. R., Hwang, S. W., Vanleer, A. C., et al. (2011). Flexible, foldable, actively multiplexed, high-density electrode array for mapping brain activity in vivo. *Nature Neuroscience* 14, 1599-1605.

Westerlund, M., & Pylkkänen, L. (2014). The role of the left anterior temporal lobe in semantic composition vs. semantic memory. *Neuropsychologia* 57: 59-70.

Whittington, M. A., & Traub, R. D. (2003). Interneuron diversity series: inhibitory interneurons and network oscillations in vitro. *Trends in Neuroscience* 26: 676-682.

Wipf, D. P., Owen, J. P., Attias, H. T., Sekihara, K., Nagarajan, S. S. (2010). Robust Bayesian estimation of the location, orientation, and time course of multiple correlated neural sources using MEG. *NeuroImage* 49, 641-655.

Wurmbrand, S. (2014). The Merge condition: a syntactic approach to selection. Franks, L., Radeva-Bork, T., & Schürcks, L. (eds). *Minimalism and Beyond: Radicalizing the Interfaces*. Amsterdam: John Benjamins. 130-166.

Zhang, Y.E., Landback, P., Vibranovski, M.D., & Long, M. (2011). Accelerated recruitment of new brain development genes into the human genome. *PLoS Biology* 9(10), e1001179. doi: 10.1371/journal.pbio.1001179.

Zipf, G.K. (1965/1949). *Human Behavior and the Principle of Least Effort: An Introduction to Human Ecology*. New York: Hafner.