1 Introduction

In a recent attempt to naturalise core features of phonological theory, Samuels (2015: 161) writes that the success of any biological approach to language is measured 'in terms of how much contact the study of language is able to make with the other cognitive sciences and other areas of biology more generally, and to what extent various components of language and the mind are more deeply understood as a result'. By making novel linking hypotheses between the formal study of semantics, pragmatics and monkey call systems, Schlenker et al. succeed on all counts. Given the apparent ability to formalise the semantics of nonhuman primate calls and explain their functionality in terms of general, universal pragmatic principles, a number of avenues open up regarding how to theorise about the evolution and implementation of such systems. In this commentary, I will focus my attention on questions (i), (ii) and (v) of Schlenker et al.'s article; namely, the syntax, semantics and evolution of monkey call systems.

Exploring the implementation of call comprehension in the primate brain not only has the potential to fruitfully employ pre-existing theoretical tools (as with formal monkey semantics), but could also generate insights into the evolutionary questions briefly discussed by Schlenker et al. Given the extraordinarily preserved nature of mammalian brain rhythms (Buszaki et al. 2013) and recent attempts to establish connecting hypotheses between them and language comprehension (Murphy 2015c), along with the similar structure of a number of primate calls, in what follows emerging models of neural oscillations will be used as a device to explore the similarly preserved structure of primate call systems. Schlenker et al.'s Evolutionary Monkey Linguistics will be discussed alongside a model of 'Evolutionary Monkey Oscillomics', using neural dynamics as a way of exploring the structure and development of primate call systems.
2 Labeling roots

Achieving a multi-disciplinary perspective on primate communication presupposes some understanding of the varying types of monkey computational systems, which generally seem limited to single-instance concatenation and a form of adjunction, itself a form of concatenation. Nonhuman primate communication systems appear to have a fully specified semantics related to basic, non-complex concepts.\(^1\) The primary reason for the richer levels of hierarchical representations in humans may lie in species-unique oscillatory properties of what is termed the ‘oscillome’ in Murphy (2016a), the level of brain dynamics – the ‘dynome’ (Kopell et al. 2014) – specific to oscillations, such as the globular brain-case context in which generic frequency-coupling operations apply. Even human focal stress (as in No, John went to PARIS in response to John went to London) seems to operate within hierarchical principles of c-command and precedence, such that the stress typically appears at the first available foci site (Büring 2015). Lacking certain oscillomic properties (discussed below) nonhumans are incapable of combining conceptual representations in an unbounded manner, being limited to the generation of ‘functionally referential signals’ (Townsend and Manser 2013). While human brains are considerably larger than those of nonhuman primates and a strong correlation exists between cranial size and cognitive capacities (Rushton and Ankey 2009, Benson-Amram et al. 2015), brain size alone cannot account for language evolution; rather, brain shape and organisation may be responsible. The wider cortical minicolumns seen in cytoarchitectonic sub-parts of Broca’s and Wernicke’s regions in humans (Schenker et al. 2008), along with the greater number of arcuate fasciculus projections connecting both regions with association cortex in the middle and inferior temporal cortex, suggests that the ‘memory buffer/stack’ available to humans during representation construction and maintenance is greater than in other primates. A number of scholars have drawn further, more far-reaching conclusions about these anatomical differences, attributing to them great explanatory power (Rilling 2014; Berwick and Chomsky 2016). In contrast, I will draw the more conservative conclusion that these structural changes, though necessary, were not sufficient for language evolution. The role of subcortical structures like the thalamus and basal ganglia has been argued to be pivotal in language comprehension (Tremblay et al. 2015), and so the interplay of these subcortical structures and species-specific neuronal dynamics may have played a more central role than the development of the traditional ‘language regions’.

\(^1\) Reboul (2015) presents convincing arguments against the common idea that human language is a ‘communication system’.
Schlenker et al. invoke pragmatic principles of call competition (of the kind found in scalar implicatures) and urgency (of the kind found in Relevance Theory), placing considerable explanatory burden on pragmatics. This not only appears to account for a wide range of ethological data, but is also compatible with evolutionary scenarios of language emergence (Murphy 2015a, 2015b, 2015c) which claim that the cyclic transfer of labeled hierarchical structures is the only species-specific feature of human language. Although they entertain a number of explanations, Schlenker et al. (2014) argue that the dialectal variation in krak calls across the Tai forest and Tiwai island may be the result of krak simply being a generalised alert call which could, optionally, be enriched into krak and not hok and not krakoo. This form of enrichment crucially implies merely the exclusion of one simplex call from other simplex calls, requiring only some form of (likely domain-general) processes of comparison, and not, for instance, theory of mind (which may causally and exclusively emerge from human language, as research into schizophrenia seems to show; Murphy and Benítez-Burraco 2016a).

Schlenker et al. review studies of Putty-nosed monkeys, Campbell’s monkeys, King Colobus monkeys and New World monkeys, and conclude that all are capable of morphologically simple calls, but that Campbell’s monkeys may be additionally capable of producing finite-state root-suffix structures (-oo) with an independent meaning generated by a simple conjunctivist semantics (contra Tallerman 2016). These call systems seem capable of concatenation (to what end, such as compositional semantics, remains open for debate), but not hierarchical phrase-building (Schlenker et al. 2014, Schlenker et al. 2016). This may be a consequence of their lack of a labeling mechanism, likely human-unique, which would also explain why basic call pairs do not appear to form even the most simple of labeled structures such as compounds like ‘apron string’ (subordinate), ‘sword fish’ (attributive) or ‘bitter sweet’ (coordinate), in which the following grammatical relationships appear to obtain (Guevera and Scalise 2009: 107):

\[ X \mathcal{R} Y \text{Z} \]

Where X, Y and Z represent the major lexical categories, and \( \mathcal{R} \) represents an implicit relationship between the constituents (a relationship not spelled out by any lexical item).

Monkeys appear unable to, firstly, construct nested and cross-serial dependencies, which are plausibly defined as dependencies between phrasal labels, not terminal strings (Fukui 2015). Secondly – and following directly from this – they are unable

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2 The role of pragmatics must indeed be substantial if Owren et al. (2010) are correct in claiming that many primate calls do not exist to primarily convey information. Instead, their main function is to ‘induce behaviors in the receiver that are advantageous to the communicator’ (Reboul 2015; see also Scott-Phillips 2015).
to construct a categorial identity of a multi-set object and maintain this object in memory. These two processes (property attribution and object permanence), though not species-specific, appear to function in humans in two unique ways: they are executed unboundedly, not being limited to $n$ applications, and they interface with a large number of other cognitive systems, not being confined to a small subset of representations. This system becomes more dynamic with the attribution of exocentric categorial labels which are distinct from either of the objects in a compound, such as the Brazilian Portuguese ‘quebra-quebra’ ('break-break', or ‘riot’), in which two verbs conjoin to be labeled N, not V. If the speculations reviewed by Schlenker et al. regarding the compositional nature of certain monkey calls is correct, this could be captured by invoking one of the above two operations. In the case of $krak$ conjoining with -oo, the root ($\sqrt[\cdot]{}$) would be modified by the adjoined morpheme, assuming that adjuncts do not provide labels:

$$[\sqrt[\cdot]{} \ [\sqrt[\cdot]{} k r a k \ - o o ] ]$$

This satisfies only one of the requirements for human language (labeling), the other being unboundedness (cyclicity). It is the interplay between labeling and cyclicity which gives rise to the human computational system. Cyclicity without labeling yields linear, birdsong-like structures (though ones lacking hierarchy and compositionality, contrary to the exaggerated claims in Suzuki et al. 2016), with songbirds likely being capable of the types of basic Search and Copy operations found in human phonology (Samuels 2015).³ Labeling without cyclicity yields categorised objects, but no hierarchical phrase structure. This ‘Labeling Hypothesis’ (Murphy 2015a) holds that labeling – and not Merge – amounts to the exclusive content of narrow syntax and hence should be the focus of any evolutionary scenario and ethological investigation.⁴ If primate calls are non-compositional, then it may be that the lexical atoms/roots used in human language are partly derived from such calls, since neither primate calls nor roots can be combined together to form new calls/words, being feature-less. Roots need to merge with categorial labels and

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³ Copy operations more generally are domain-independent operations; a perspective Abe (2016) claims is necessary to account for why a copy left behind by movement is invisible for labeling.

⁴ This goes against what we could call the standard ‘Merge-centric’ evolutionary hypotheses (Berwick and Chomsky 2016, Hauser et al. 2014, Mukherji 2010, Nóbrega and Miyagawa 2015, and much other work) as well as the gradualist theory of language evolution put forth by Progovac (2015) and others. It is also in line with Okanoya’s (2007) claim that human language is an emergent property arising out of several domain-general sub-faculties (which, from a brain’s-eye-view, is highly likely).
other morphological elements to enter the derivation (Panagiotidis 2014, 2015, Marantz 2013, Embick and Marantz 2008, Alexiadou and Lohndal in press); the reasons are ancillary, but this may be due to the presence of an unvalued edge feature ($uR$) (Nóbrega 2015).\footnote{It would be of interest to see if any primates have call systems involving multiple cases of conjunction, either involving whole units or morphemes, as in *interest-ing-ly* (though likely nothing as complex as *edit-or-ial-ize*).}

As we have seen, monkey calls have a highly constrained syntax, with Black-and-White Colobus monkey calls being limited to *snort-roar* patterns, and judging by the literature Schlenker et al. review the semantics of monkey calls may not encompass individual predators but simply their *location* at a given time. In addition, the generative power of concatenated -*oo* morphemes would not go beyond the finite-state, and would require only a concatenation operation and a memory buffer capable of maintaining two objects in memory (see Veselinović et al. 2014 analysis of Diana monkey calls and their ‘merged associations’). It follows that keeping to computational concerns, though necessary, will provide impoverished and biologically inadequate evolutionary scenarios.

### 3 Approaching monkey calls through dynamic cognomics

In a combinatorial system like human language, in which roots appear to be underspecified for meaning and need to be conjoined with grammatical feature complexes in order to be interpreted, ‘fewer elements are required to express the same number of possible messages, and so it allows for more efficient communication than a system in which each signal has a distinct form’

\footnote{If labeling is human-unique, then we would expect that a degree of variation in language change – indeed, perhaps a substantial degree – would result from labeling choices. This is precisely what van Gelderen (2015) found, with labeling failures in [XP YP] structures (typically leading to movement) accounting for a number of syntactic phenomena cross-linguistically.}

\footnote{I think the relationship between single-instance conjunction and unbounded conjunction should be thought of as analogous to the phase transition relationship between a gaseous state and plasma; that is, the change is brought about solely by external factors. In the case of a gas-plasma transition, temperature and pressure are responsible, whereas in the single-unbounded conjunction transition, the evidence increasingly points to braincase shape and novel rhythmic coupling interactions being responsible for our ‘plasmic minds’.}
It is quite possible that this combinatorial efficiency can be derived from lower-level connectomic and rhythmic efficiency. Recent work in systems neuroscience and human paleoneurology led to the suggestion in Murphy (2015c) that the reason nonhuman primates are restricted in their combinatorial capacities is due to their inefficiently structured braincase and neural wiring, with the former (partly) causing the latter. An approach termed Dynamic Cognomics was suggested to re-translate linguistic computational sub-operations into generic neural dynamics, against a background of evolutionary considerations. For example, a globular braincase (differing from the Neanderthal skull; Gunz et al. 2012) would have led to a decrease in ‘spatial inequalities’ (Salami et al. 2003) between brain regions, encouraging the forms of cross-modular conceptual combination exhibited by language. Attaheri et al. (2015) documented a P500 effect in macaques in response to mixed complexity grammars, homologous to the human P600, a late positivity relating to complex syntactic processing. The type of processing reflected in such late positivities in macaques may be a dormant faculty, not actively used by them but exposed in artificial circumstances, and when placed in a new domesticated environment and skull size may have adopted a novel function (see Murphy 2015a for a discussion of domestication in songbirds which seems to also result in the enhancement of computational competence). These interdisciplinary investigations of the structure and use of combinatorial systems have a strong likelihood of leading to explanations which make sense to all investigators across the cognitive and biological sciences, and not just to those who study formal semantics and philosophy of language.

Moreover, in human language the object resulting from the merger of a root and grammatical/categorial features is always labeled by the feature complex, not the root. Given these computational ‘instructions’, and the implementational properties of brain rhythms, the following linking hypothesis can be made: the slower rhythm which phase-modulates a higher coupled rhythm maintains the root in memory (after it is generated by a faster $\gamma$ rhythm) and forces the syntactic derivation (oscillatory phase cycle) down a particular path, just as how the grammatical features a root merges with determine its interpretation.

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7 Bonobos, our closest living primate relative, exhibit a degree of functional flexibility in their peep calls (Clay et al. 2015), and so presumably it did not take a particularly drastic neurological reorganisation to arrive at the flexibility of human language.

8 Recent evidence points to the precuneus (a central hub of brain organisation) as being prominently expanded in modern humans (Bruner et al. 2016), and given its role in visuospatial integration and consciousness it may also be involved in linguistic and non-linguistic combinatoric systems.
and subsequent combinatorial scope. It may be that the cell assemblies responsible for storing categorial feature-sets need to be synchronized with the assemblies responsible for storing the relevant root-based conceptual representations, and that human-specific oscillatory couplings achieve this (modulated by slight changes in myelination; Pajevic et al. 2014). Indeed, if Chomsky (2015) is correct in claiming that a full sentential CP structure is effectively a mirror of the vP embedded within it (sharing numerous, previously unrecognised properties, with the principles of ECP and EPP possibly being unified under simple principles of minimal search), then this would permit core features of linguistic theory to approach a tentative but coherent level of similarity to Ding et al. ’s (2016) findings that the rhythmic signatures of sentences effectively amount to those of an extended phrasal constituent. In an effort to develop these comparisons further, we can ask a basic question of human neural dynamics, (2), which is the implementational equivalent of (1), the foundation of much recent work in syntactic theory.

(1) Is there a unified labeling algorithm which applies to all syntactic configurations across all languages?

(2) Is there a unified oscillatory mechanism which labels all syntactic configurations across all languages?

In Murphy and Benítez-Burraco (2016b), it was suggested that there is such a general oscillatory mechanism responsible for labeling, involving θ-γ coupling and a number of other phase-locking patterns across cortical and

9 Going beyond the derivation, the different spatial and temporal scales seen in brain rhythms (from slow α to the multiple β bands to fast γ) and oscillatory operations like phase-locking and cycle skipping (Brandon et al. 2013) may also give rise to other linguistic properties such as the various ‘containment’ relations seen in the topology of functional projections, with events necessarily containing objects and so forth, just as how faster rhythms employed in memory retrieval operations must be contained/embedded within a slower rhythm for complex cognitive capacities like working memory to arise.

10 See López (2015) for suggestions that word formation is also syntactically complex and mirrors sentential derivations in a number of respects, such that ‘socialization’ (vsocialize vP ation) is effectively what we could think of as a ‘small sentence’. Such cases could act as interesting stimuli for the experimental design of Ding et al. (2016). Moreover, the principles of minimal search and computational efficiency documented in natural language syntax (via the Minimalist Program; Chomsky 1995) may arise from brain networks functioning through self-organised ‘connectome harmonics’ (Atasoy et al. 2016), with such harmonic principles being ubiquitous in nature and a possible ‘third factor’ in language design.
subcortical structures.\textsuperscript{11} Human-unique oscillatory couplings, modulated by distinctive myelinisation rates, may permit the combination of a cortically and subcortically widespread network of conceptual features, possibly stored either in (i) Hebbian clusters (Johansen et al. 2014) or (ii) single neurons (Fitch 2014). Murphy and Benítez-Burraco (2016b) and Benítez-Burraco and Murphy (2016) develop this proposal in detail and suggest that language deficits in schizophrenia and autism spectrum disorders can be explained by assuming that their abnormal cross-frequency coupling profiles impair (among other things) the domain-general ability to extract particular items from memory. For instance, hippocampal $\theta$ would embed a sequence of low to middle $\gamma$ rhythms within each cycle which would activate particular cell assemblies responsible for storing discrete language-relevant features, achieving the binding of feature-sets necessary for word-formation and phrase structure building. Call this the Pulse Model of Feature-Sets (PMF), represented in Figure 1. If, in contrast, primate call systems are restricted in their cross- and sub-cortical rhythmic coupling profile and PMF is limited to extracting a reduced sequence of features, this may explain why monkey calls convey limited information, not interfacing with conceptual systems responsible for actions, agents, patients and so forth (see also Lisman and Idiart 1995 for seminal proposals about related possible mechanisms for short-term memory constraints).\textsuperscript{12}

\textsuperscript{11} Boeckx and Theofanopolou (2015) argue that a strictly bottom-up reconstruction of the ‘cognome’ should instead be sought, but this is hopelessly optimistic. We are nowhere near the stage where neurobiology can impose direct constraints on higher-level theories of cognition. As Hochstein (2016) notes of neuroscientific history, ‘the assumption that there is a single ideally correct way of classifying or categorizing mental phenomena, and that neuroscience and psychology should adhere to this correct scheme, runs counter to productive scientific practices in these domains’. Distinct categorisational schemes require distinct goals and methodologies (hypothesis testing, design, pattern identification and prediction are just some of their uses), and so there is simply no way of showing a priori that linguistic concepts should be abandoned, to be replaced in full by implementational processes. Similarly, many generative linguists – call them ‘Marr Misreaders’ – have misinterpreted Marr (1982) through prioritising computational and algorithmic investigations over implementational research (see, for instance, Abels 2013) and believing that the three levels should be explored independently, despite the absence of anything in Marr which suggests this; indeed Marr’s program was geared towards bridging these levels of analysis, not segregating them.

\textsuperscript{12} An fMRI study by Gruber et al. (2016) explored the effects of reward motivation on memory encoding, which is known to rely on interactions between the substantia nigra/ventral tegmental area complex (SN/VTA) and the hippocampus. It was shown that post-learning increases in resting-state functional connectivity between the SN/VTA and hippocampus reflected the retention of objects learned in high-reward contexts. A similar design could be applied to nonhuman primates, investigating the functional and rhythmic dynamics of object retention during distinct reward contexts, which would indirectly enhance understanding of the retention mechanisms used in call sequence comprehension.
The finding that Campbell’s monkeys are limited to the deployment of the roots *boom*, *hok* and *krak* and a bound affix –oo would follow naturally from this oscillomic profile.

Schlenker et al. make the interesting claim that a certain degree of explanatory depth can be achieved when we assume that monkey call systems can be conceived of as the result of a dynamic interplay between simplex concepts and pragmatic processes (in particular the Informativity and Urgency principles). Having established this, further experimental work could present conditions of putative pragmatic ‘enrichment’ to cases in which the ape accesses a basic semantic representation to gauge which rhythmic coupling operations and neural ensembles appear to be implicated in pragmatic processes. Given that primate vocalisations exhibit only minor modifications throughout development (Hammerschmidt and Fischer 2008), monkeys of a wide range of ages would be viable for experimentation.\(^{13}\)

\(^{13}\)Indeed, due to the lack of evidence for cell specialization, the oscillome will likely be a considerably more fruitful domain of investigation than purely formal approaches.
Adding to Schlenker et al.’s rejection of using call data to reconstruct phylogenies and their proposal to instead employ phylogenies in the service of reconstructing call histories, I think that by now the primate electrophysiologival and oscillatory literature is comprehensive enough to permit a tentative reconstruction of call comprehension from the perspective of brain dynamics. Instead of attempting a synthesis of acoustic and genetic evidence, oscillatory data could serve as a useful intermediary level. In Murphy (2015c), the elementary syntactic sub-operations of syntax were proposed to arise from the well-preserved hierarchy of mammalian brain rhythms and their interactions. This idea is developed further in Murphy (2016a) through the construction of an ‘oscillomic tree’, complementing standard linguistic tree structures (Figure 2).

This oscillomic tree could also potentially be extended into a cognitive model in the sense of Love (2016), attempting to link behaviour with brain components. For instance, Brincat and Miller (2015) found functional differences and

14 This also disqualifies language from being a Fodorian module; instead, it is a cross-modular system arising from the interfacing of diverse neuronal devices performing low-level, generic functions.
frequency-specific interactions between the Rhesus hippocampus (HPC) and prefrontal cortex (PFC) when the monkeys were learning object pair associations, with $\theta$ synchrony being stronger after errors and decreasing with learning, while correct associations promoted $\beta$-$\alpha$ synchrony which was stronger in the HPC-PFC direction. These and other revelations about the pair-construction and pair-comparison mechanisms in Rhesus monkeys should point Schlenker et al.’s Evolutionary Monkey Linguistics in a possible direction for interdisciplinary linking hypotheses, of the kind proposed in Murphy (2015c, 2016a, 2016b) for human language and oscillomic studies of cognition.

Approaching monkey brain dynamics requires an understanding of brain structure. At perhaps the most general level, it is becoming increasingly possible to establish oscillatory homologues between species in which homologous calls have been proposed via the types of ‘call trees’ Schlenker et al. point to, potentially narrowing the candidate list of implementational mechanisms responsible for call comprehension. Interestingly, when the homologue of Broca’s region in the monkey brain is lesioned, call vocalisations are not impaired, suggesting other regions are involved, such as the limbic system and brainstem (Sage et al. 2006). On the interpretation side, macaques share similar call comprehension substrates with human language comprehension in the left posterior temporal gyrus (Heffner and Heffner 1986). The superior temporal gyrus is implicated in the interpretation of species-specific vocalisations in macaques (Hackett et al. 2001). However the density of white matter connections between Broca’s and Wernicke’s regions is also greater in humans than in monkeys (Petrides and Pandya 2009), and the human arcuate fasciculus connecting the two regions substantially projects to expanded temporal association cortex implicated in semantic processing. It is possible that these structural changes partly yielded the increased rate of information transfer between conceptual and articulatory systems in humans, restricting monkey calls to their limited hormone- and alarm-related content. Moreover, Wilson et al.’s (2015a) fMRI study of humans and macaques during nonsense word and rule-based sequence processing revealed that areas specified for sequence comprehension in the ventral frontal and opercular cortex, adjacent to BA44 and 45, have functional counterparts in the monkey brain. This leads to the possibility that ‘language-related processes in modern humans are functionally integrated with highly conserved, originally non-linguistic processes shared with our extant primate relatives’ (Wilson et al. 2015a: 10), the basis of which are likely oscillomic in nature.\(^\text{15}\)

\(^{15}\) Both humans and macaques also appear to use similar auditory sequence learning strategies when processing artificial grammars (Wilson et al. 2015b).
Given their role in cortical and subcortical information integration and segregation and involvement in systems like working memory and attention, \( \beta \), \( \alpha \) and \( \theta \) rhythms and their coupling interactions in the basal ganglia, thalamus and hippocampus may play a major role in linguistic computation – and also in the morphosyntactic comprehension of monkey calls. Esghaei et al. (2015) documented the phase-amplitude coupling of local field potentials from extra-striate area MT of macaque monkeys, a region specialising in processing visual motion. They discovered that directing spatial attention into the receptive field of MT neurons decreased the phase-amplitude coupling between the low frequency phase (1–8 Hz) and higher power (30–100 Hz) of local field potentials, suggesting that cross-frequency coupling is suppressed as a function of visual attention (see also Lowet et al. 2016). Esghaei et al. (2015) suggested that the macaque visual cortex uses phase-amplitude coupling to regulate inter-neuronal correlations, coding relevant stimuli more efficiently. Further investigations of phase-amplitude coupling during complex cognitive tasks in monkeys such as call interpretation and production would allow for comparative models of the functional role of dynamic brain activity to be constructed, fulfilling the goals of Computational Ethology (Murphy 2015a).

Adopting the model of the human oscillome in Murphy (2015c), we can make some preliminary predictions about what a monkey’s oscillomic profile might be. Since increased \( \gamma \) correlates with greater working memory load and maintenance and is primarily involved in local operations as a result of conduction delays, this rhythm may be involved in the generation of the roots which constitute morphologically basic call units (such as krak and boom). Upon the conjunction of an \(-oo\) unit (also generated by \( \gamma \)), a complex object such as krak-oo would be held by the \( \beta \) band, with this rhythm being implicated in maintaining existing cognitive sets. A recent study of Rhesus monkeys revealed that during the internally monitored continuation phase of a synchronisation-continuation task \( \beta \) increased relative to the amplitude found in reaction-time tasks, with the basal ganglia likely being responsible for generating the initiation signal before it spreads across portions of the striatum (Bartolo and Merchant 2015). These observations would speak to Honkanen et al.’s (2014) findings that more complex objects are represented with \( \beta \) rather than \( \gamma \). Koziol et al. (2009) present evidence suggesting that disinhibiting a basal ganglia loop leads to the maintenance of a particular representation to

16 It should be stressed that rhythms have distinct, non-overlapping roles varying by regional source, such that pulvinar \( \gamma \) can be involved both in feedforward processing for snake images and in cortico-pulvinar-cortical integration for face images (Le et al. 2016). Care should be taken to differentiate between distinct oscillatory roles in studies of monkey call systems.
the exclusion of others, while the dependence on inhibitory rebound documented in β1 (slow β) permits it to ‘continue in the absence of continuing input’ (Kopell et al. 2010: 3). In humans, this might allow a labeled object to be held in memory beyond the perception of its constituent elements, while in nonhuman primates it may allow the maintenance of a call pair.

Lewis et al. (2016) also reveal through an MEG study of Dutch subject- and object-relative clauses that β is an index of the maintenance/change of the ongoing sentential structure (or under the present model, the constructed feature-sets), and so an investigation into the role of β in primate call sequences may shed some much needed light on the mechanisms responsible for representation retrieval and maintenance. β additionally seems to be implicated in the maintenance of muscle synergy representations in the primary motor cortex (Aumann and Prut 2015), in contrast to Watanabe et al.’s (2015) findings that β is ‘related more to the attentive state and external cues as opposed to detailed muscle activities’ in Japanese monkeys (Macaca fuscata) and Hosaka et al.’s (2015) findings that β suppression reflects erroneous action sequence updating in the same species. These comparisons will lead to precisely the kind of explanatory granularity linguists and ethologists should be seeking in their investigations of the structure and evolution of cognitive combinatorics. For instance, the correct updating of action sequences in Japanese monkeys is achieved via increases in γ (Hosaka et al. 2015), an oscillomic profile similar to that involved in the ‘chunking’ of linguistic feature-sets, which also involves γ power increases (Lewis and Bastiaansen 2015, Murphy and Benítez-Burraco 2016a), though doubtless ones of distinct phasal properties. It appears that in humans and monkeys, then, construction of an internal sequence leads to β increases, maintenance failure/disruption leads to β decreases, and the execution (or in linguistic terms, the Spell- Out/Transfer) of the sequence is achieved via subsequent γ increases.17

Evolutionary Monkey Oscillomics will consequently permit an exploration of the mechanisms responsible for non-linguistic ‘proto combinatorics’ in the sense of Bornkessel-Schlesewsky et al. (2016), as a comparison between the human oscillome (Figure 2) and the suggested oscillomic tree for monkey calls in Figure 3 illustrates. As Backus et al. (2016) have demonstrated, the amplitude and coupling strength of θ oscillations in the hippocampus and medial prefrontal cortex (a region implicated in conceptual networks) is modulated by the degree of successful memory integration (see Roux and Uhlhaas 2014). Investigations of the monkey oscillome during call comprehension should proceed along a similar mechanistic basis, attempting to establish how memories (and not just percepts) are integrated in comparison to how this is achieved in humans. These approaches should not be

17 These findings about the role of β in language and motor control may speak to Llinás’s (2001) intuition that thinking amounts to a form of ‘internal movement’.
seen as intellectual exercises or examples of nebulous, metaphorical comparisons between neurobiology and computational competence. Schlenker et al.’s monkey linguistics system only has so much reach when it comes to biological adequacy, and so semantic formalisms need to be cashed out in terms which broach the more fundamental natural sciences.\(^{18}\)

\(^{18}\) As Samuels (2015: 164) notes of similar barriers in phonology: ‘[U]pon observing that a certain language has no consonant clusters, one posits that these facts are not random, but are due to a constraint like \(^{*}\)CC. But then, when one asks why the language has no consonant clusters, the answer is because \(^{*}\)CC bans them. While perhaps on some level all logic is ultimately circular, this is a very small circle’. Studies of brain dynamics are well placed between neurochemistry and genetics on the one side and perception and cognition on the other, potentially being able to break this small circle.

**Figure 3:** An oscillomic tree of the rhythms likely to be responsible for particular call sequences, pending further electrophysiological investigations. Along with the data discussed in the main text, additional support for this model comes from Ramirez-Villegas et al.’s (2015) study of sharp wave-ripples in the macaque hippocampal CA3-CA1 network, which attributed a role for these \(\gamma\) rhythms in memory reactivation, transfer and consolidation. The superscript next to each \(\gamma\) cycle denotes low, medium and high \(\gamma\) (sharp wave-ripples), with \(\gamma\) power scaling with the number of calls held in memory. Each \(\gamma\)-generated item would couple with hippocampal \(\theta\) (see Lee et al. 2005 and Jutras et al. 2013 for the role of this rhythm in monkey working memory) in order to achieve the binding of morphological elements (‘krak-oo’) before coupling with basal ganglia-initiated and striatal \(\beta\), which would in turn increase in amplitude until the event of either an erroneous action sequence (call production) or the termination of the call series. This hypothesis is supported by studies claiming that \(\beta\) activity operates as a general coupling mechanism of assembly activity across brain structures (Fujioka et al. 2012). Note that monkey oscillomic trees lack labels, being composed of call pair-combinations (‘krak hok’) and morphological elements (‘-oo’). A comparison with Figure 2 suggests that the richer levels of hierarchy seen in human language may result from the broader range of cross-frequency couplings available.
4 Conclusion

Evolutionary Monkey Oscillomics, in tandem with Dynamic Cognomics (with its globularization, PTF and other hypotheses) may allow for a natural extension of the explanatory scope of the brain sciences into the narrower domains of the language and ethological sciences, in particular syntactic theory and neuroethology. The different spatial and temporal scales seen in brain rhythms, from slow $\alpha$ to the multiple $\beta$ bands to fast $\gamma$, and diverse phase-relations and oscillomic operations like phase-locking and cycle skipping (van Ede et al. 2015, Murphy and Benítez-Burraco 2016a) may give rise to a number of linguistic and communicative properties. Upon its emergence, the human-specific oscillomic profile would have interfaced with more ancient systems shared with other primates, in turn influencing and modifying the internal organisation of such systems through a process of ‘reciprocal causation’ (Lewontin 1983, Walsh 2015), with the characteristics of an organism arising through interacting cascades of selection and construction. As a result, the emergence of the human oscillome, with its cyclic labeling mechanism, would likely have re-shaped the representations of the conceptual systems it interfaced with, while the reverse would also be expected – and indeed appears – to have occurred, with semantics imposing particular constraints on possible syntactic structures. This may explain why primate call units appear to be lacking in the diverse array of, for instance, Tense and $\phi$-features. Along with Schlenker et al.’s computational investigations, these perspectives may bear fruit in ways which would have seemed fanciful to the Marr Misreaders of past and present years.

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19 Exactly how this representational diversity emerged from the combination of the oscillomic mechanisms responsible for object permanence and property attribution (labeling) and cyclicity remains a mystery, and presupposes a neural model of representations, which, as the main text illustrates, currently only arises to various claims about synchronously activated call assemblies acting as informational sources. But regardless of the theory of neural representations one adopts, it is clear that the present model yields a serious degree of biological engagement not present in standard, somewhat mystical generative descriptions of ‘the rich expressive and open-ended power of human language, the creative aspect of normal language use in the Cartesian sense’ (Everaert et al. 2015: 740).
References

http://dx.doi.org/10.3765/salt.v25i0.3634.


In S. Scalise, A. Bisetto, & E. Magni (eds.), *Universals in language today*, 101–128. Amsterdam: Springer.


Murphy, Elliot & Antonio Benítez-Burraco. 2016b. Language deficits in schizophrenia and autism as related oscillatory connectopathies: an evolutionary account. Ms. University College London, University of Huelva.


van Ede, Freek, Stan van Pelt, Pascal Fries & Eric Maris. 2015. Both ongoing alpha and visually
induced gamma oscillations show reliable diversity in their across-site phase-relations. 
*Journal of Neurophysiology* 113. 1556–1563.

van Gelderen, Elly. 2015. Problems of projection: The role of language change in labeling

Veselinović, Dunja, Agnes Candiotti & Alban Lemasson. 2014. Female Diana monkeys
*Cercopithecus Diana* have complex calls. Ms. New York University.

University Press.

Watanabe, Hideroni, Kazutaka Takahashi & Tadashi Isa. 2015. Phase locking of β oscillation
in electrocorticography (ECoG) in the monkey motor cortex at the onset of EMGs
and 3D reaching movements. *Engineering in Medicine and Biology Society (EMBC)*,
37th Annual International Conference of the IEEE. 55–58.

Wilson, Benjamin, Yukiko Kikuchi, Li Sun, David Hunter, Frederic Dick, Kenny Smith, Alexander
Auditory sequence processing reveals evolutionarily conserved regions of frontal cortex in

Wilson, Benjamin, Kenny Smith & Christopher Petkov. 2015b. Mixed-complexity artificial
grammar learning in humans and macaque monkeys: Evaluating learning strategies.