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Subcortical syntax: Reconsidering the neural dynamics of language

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ABSTRACT

Subcortical contributions to core linguistic computations pertaining to syntax-semantics remain drastically under-studied. We critique the cortico-centric focus which has largely accompanied research into these higher-order linguistic functions and suggest that, while much remains unknown, there is nevertheless a rich body of research concerning the possible roles of subcortex in natural language. Although much current evidence emerges from distinct domains of cognitive neuroscience, in this review article we attempt to show that there is a clear place for subcortex in models of natural language syntax-semantics, including a role in binary set-formation, categorized object maintenance, lexico-semantic processing, conceptual-to-lexical transformations, morphosyntactic linearization, semantic feature-binding, and cross-cortical representational integration. In particular, we consult models of language processing relying on oscillatory brain dynamics in order to investigate both the apparent and possible functional roles of subcortex in language.

1. Introduction

Investigating the neural basis of natural language syntax and semantics (i.e., the generative, interpretive component of language) is one of the most important issues in modern cognitive neuroscience. It has also proven to be one of the most intractable directions of inquiry. Of those neurophysiological models which have succeeded in developing a considerable degree of descriptive scope (Friederici, 2017; Griffiths et al., 2013; Wilson et al., 2011), these appear “cortico-centric” (Parvizi 2009), sidelining contributions from subcortex, despite Lenneberg’s (1967) caveat about the likely importance of subcortex. In the past, and given the overwhelming focus of most neuroimaging research and the spatiotemporal resolution of traditional imaging techniques, this was justifiable and empirically motivated. We will here argue that this is no longer the case, and that there is increasing evidence from a broad range of domains suggesting that certain subcortical structures play important roles in natural language processing.

While subcortical structures have often been labeled as part the *reptilian brain*, responsible for only primitive drives, far removed from the higher echelons of thought, there is renewed motivation to re-situate subcortical regions like the thalamus and basal ganglia

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at the heart of language processing. The classical physician Galen held that the seat of the mind was in the ventricles, since donkeys also had highly convoluted brains. Through examining the crucial role of subcortical structures like the thalamus and basal ganglia in language, the Broca-Wernicke-Lichtheim model may go the way of the ventricular doctrine and the reptilian brain model, paving the way for more comprehensive accounts. And while neocortical expansion is the major focus in studies concerning the evolution of human intelligence, it is notable that the basal ganglia, cerebellum and hippocampus are two-to-three times larger in humans than in great apes (Gibson & Jessee, 1999). During the process of domestication, limbic structures are typically reduced, yet in humans limbic structures appear larger, not smaller (Bruner & Gleeson, 2019), rendering it unwarranted to sideline them when discussing human-specific higher cognitive capacities (Benítez-Burraco, 2021).

We are not the first to discuss the possible involvement of subcortex in language. In 1959, Penfield and Roberts reported a case of thalamic aphasia and hypothesized that the thalamus might play an integrative role in language (Penfield & Roberts 1959). Going considerably further back, the ancient Greek physician Erasistratus (c. 304 – c. 250 BC) believed that cerebellar size related to intelligence. He is sometimes thought to be founder of neuroscience due to his exploration of nerves and their involvement in motor control through the brain and skeletal muscles. During his time in Alexandria, Erasistratus conducted a large number of controversial vivisections on criminals to study their anatomy and the physiology of human organs, later being condemned by Roman authors such as Celsus and Tertullian (Ferngren, 2017). In contrast, our own methodology will appear somewhat more subdued: We aim to comprehensively review the current state of the art in subcortical contributions to natural language syntax, synthesizing recent empirical work to survey what we see as relatively underappreciated components of the language network.

Framing this discussion, we will be assuming a particular approach to natural language phrase structure processing that we have developed in recent years, based on the central importance of neural oscillations and their interactions (Murphy, 2016, 2018; Murphy & Benítez-Burraco, 2016, 2017, 2018, 2016; Benítez-Burraco et al., 2017, 2018; Benítez-Burraco & Murphy, 2016, 2019; Hoshi & Miyazato, 2016; Progovac & Benítez-Burraco 2019; Wilkinson & Murphy 2016). Our goal is to explore the role of subcortical brain regions in this framework and to consult more recent developments in the field, marshalling further theoretical and empirical work which might expand and refine our understanding of language with respect to subcortical contributions. Our intention is not to provide a comprehensive review of subcortical contributions to all studied components of language; rather, we aim to provide a focused discussion of syntax-semantics. We also do not aim to make any particularly strong claims about the causal-explanatory role of subcortical structures in elementary linguistic computations, since we still lack the necessary empirical work to evaluate this. Yet, we nevertheless believe there to be ample evidence that conspires to suggest potential causal involvement of subcortical structures in a number of core components of natural language.

Lastly, we wish to present our discussion within the context of the following remark: Few neurolinguistic models of language seem to be exclusively committed to cortico-centrism, and the current absence of subcortex from many models does not necessitate the conclusion that the authors of these models wish to intentionally exclude subcortical structures, or otherwise deny their importance. Indeed, a number of authors who have developed influential cortico-centric models of language have *also* conducted seminal studies of subcortical language function, e.g., Angela Friederici (Jeon et al., 2014; Kotz et al., 2002, 2003; Mestres-Misse et al., 2012; Wahl et al., 2008) and Peter Hagoort (Snijders et al., 2010). While the notion that subcortical structures contribute to language remains, in our view, a minority position, there are nevertheless a range of researchers who appear to be converging on the view that subcortex is recruited for language; for instance, in bilingualism (Bice et al., 2020; Burgaleta et al., 2016; Cargnelutti et al., 2019; Hervais-Adelman et al., 2018, Stocco et al., 2012), phonological processing (Booth et al., 2007), syntax (Lieberman 2006, 2015), reading (Braun et al., 2019; Yeatman & White 2021), word learning (Takashima et al. (2014) and lexical access (Crinion et al., 2013; Hernandez & Li, 2007; Meinzer et al., 2006). Our aim is not to label various models as subcortical-inclusive or subcortical-exclusive, but to evaluate the apparent roles of subcortical structures in higher-order language processing, with particular emphasis on brain dynamics (Hoshi, 2017).

2. Subcortical dynamics of language: Basal ganglia as syntactic generator

Far from being isolated to inferior frontal regions or posterior temporal regions, subcortical grey matter structures such as the striatum, caudate nucleus and thalamus appear to be implicated in the processing of syntactic operations (Moro et al., 2001; Teichmann et al., 2015; Wahl et al., 2008). We will begin by reviewing the basal ganglia, before turning to other subcortical structures such as the thalamus, hippocampus and cerebellum.

2.1. Basal Ganglia Grammar

As we noted above, the idea that subcortex plays a role – potentially a crucial role – in higher language functions is not a new one. Petersson et al. (2012) critique the classical Broca-Wernicke-Lichtheim language model of the brain by observing that 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) and hippocampus (Kepinska et al., 2018). Going beyond this, the potential *interplay* between subcortex and certain cortical structures involved in language has been noted, with language being a clear example of a network phenomenon, rather than a “localizationist” process (Li et al., 2020). BA 44 and the posterior superior temporal cortex seem to be implicated in a pathway which supports core syntactic computations (Friederici et al., 2006; Poeppel 2014), but the precise role of any subcortical connectivity has been studied much less than these discrete centers of cortical activity during language processing.

One of the first modern models of language processing that proposed a central role for subcortical structures was Ullman’s declarative/procedural model of the lexicon and grammar (Ullman 2001, 2004). In brief, the lexicon and grammar are hypothesized to rely on two different memory systems: associative memory, with distributed representations subserved by medial temporal lobe circuits, and procedural memory, subserved by frontal/basal ganglia circuits and specialized for computing hierarchical structures. A more elaborate example of how subcortex has been implicated in language is Lieberman's (2006) Basal Ganglia Grammar model, which proposes the existence of a pattern generator whose excitation/inhibition mechanism is in the basal ganglia. Recent work suggests that this might interface with working memory resources located in Broca's area and other portions of middle frontal gyrus (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, projecting back to the prefrontal cortex. Balari and Lorenzo (2013: 100–102) have gone somewhat beyond this and suggest that the basal ganglia-thalamic-cortical loop may be the circuit used as language's computational system operating within a structure of working memory networks. Most recently, Copland et al. (2021) have suggested that the striatum contributes only to domain-general processes that pertain to higher-order language; corticostriatal loops serve to respond to uncertainty and conflict which requires selection, sequencing, and cognitive control (e.g., syntactic processing involving high computational demands, competition and ambiguity).

2.2. Low frequency dynamics

As mentioned, we aim here to discuss the role of subcortex within the context of brain dynamics, not just local cortical activation profiles. Neural oscillations are thought to reflect synchronized fluctuations in neuronal excitability and are grouped by frequency, with the most common rhythms seemingly relevant to cognition being delta (δ: ~0.5–4 Hz), theta (θ: ~4–8 Hz), alpha (α: ~8–12 Hz), beta (β: ~12–30 Hz) and high gamma (γ: ~60–150 Hz). These are generated by various cortical and subcortical structures, and form a hierarchical structure since slow rhythms phase-modulate the power of faster rhythms. In terms of electrophysiological dynamics, we will assume the model in Murphy (2020) in which elementary syntactic combinatorics recruits a parahippocampal and cortico-basal ganglia-thalamo-cortical loop (i.e., some version of linguistic feature conjunction) coupled with posterior superior temporal gyrus/sulcus (syntactic categorization, or "labeling"), which is later coupled with left inferior frontal regions such as BA 44 and BA 45 which act as crucial memory buffers for the maintenance of hierarchically organized objects. For example, and following on from some of the empirical work mentioned above, this model proposes that when γ-itemised linguistic representations (referring to mid- and broadband high-gamma neural activity) are coupled to parahippocampal θ, some of them ultimately slow to β to be maintained in short-term memory as the existing cognitive set (see Engel & Fries, 2010 for evidence that β is responsible for such maintenance operations, and also Armeni et al., 2019 for evidence that unexpected words lead to β decreases, disrupting the "status quo" and the maintenance of the set). Evidence that this process is neurophysiologically plausible comes from Gollo et al. (2017), who showed that after cortical regions are coupled together, their frequency changes as a result of network interactions, such that "slower hub regions speed up, and faster peripheral regions slow down their activity". Moreover, the hippocampus is highly effective at "generating ordinal cell assembly sequences relevant to the particular situation", be that a spatial, temporal, auditory or memory-related function (Buzsáki & Llinás, 2017: 484). The domain-generality of its computational power indicates a likely crucial role in linguistic feature-set combinatorics, even if current empirical work concerning language and hippocampus seems to be limited to hierarchical structure processing (Blank et al., 2016) and semantics (Piai et al., 2016). Lastly, Murphy (2020) proposes that α is involved in the early stages of binding (Pina et al., 2018) to synchronize distant cross-cortical γ sites required for the θ-γ code of working memory and to modulate attentional resources, likely coordinated by thalamocortical regulation.

Keeping with these low frequency dynamics, findings reported in Gehrig et al. (2019) suggest a role for β rhythms in phrasal categorization. These authors investigated speech memory representations using direct, intracranial cortical recordings in the left perisylvian cortex during delayed sentence reproduction in patients undergoing awake tumor surgery. Based on patient memory performance, the phase of fronto-temporal β appears to represent sentence identity in working memory. The notion of sentential identity presupposes a labeled structure (e.g., Complementizer Phrase, Tense Phrase, Verb Phrase), seemingly represented (at least partially) by fronto-temporal β. Since subcortex is known to modulate fronto-temporal connectivity, this opens up future inquiry into how this process impacts language. More generally, accumulating evidence suggests that β holds objects, whereas γ generates them (Martin & Ravel 2014). Dean et al. (2012) relatedly show how β is a good candidate for comparing old and new information from distinct modalities due to its wider temporal windows, likely drawing on different conceptual representations.

Low frequency dynamics are clearly relevant to syntactic-semantic computations – but how does this relate to subcortex? We will review below how basal ganglia is a primary generator of cortical β waves, and how portions of the thalamus regulate cortico-cortical high frequency activity. These dynamical considerations were already suggested in early work: For instance, in Kotz et al. (2003) it was reported that during the processing of sentences with verb-argument structure violations the resulting N400 (marking some form of late semantic-thematic integration process) was partially modulated by the basal ganglia. Friederici et al. (2003) also reported that syntactic violations in sentence processing not only resulted in greater activation levels in left anterior superior temporal gyrus and posterior frontal operculum, but also the putamen in the left basal ganglia. The idea that a frontal-basal ganglia network is recruited for rule-governed language use is supported by a report of increased activation within the left inferior frontal gyrus, anterior insula and the putamen when healthy adults listened to a story (Bhattasali et al., 2019). Recall here Wernicke's (1874) belief that lesions to the left putamen and globus pallidus cause aphasia due to convergence of frontal projections.

2.3. Rules and computations

The core position occupied by the basal ganglia in these explorations of natural language also fits well with imaging studies which have revealed the involvement of this region in 'syntactic complexity' (or, at least, one measure of it, given the polysemous nature of this concept), specifically the processing of type-identity intervention of matching labels, being activated in an fMRI study when a noun phrase similar to the dependency head in a long-distance dependency intervenes in said dependency (Santi et al., 2015). Specifically, Santi et al. (2015) document these effects in the caudate nucleus, and other studies have also found effects of syntactic complexity in the basal ganglia (Prat & Just 2011). This calls back to the notion of sentential identity. Indeed, the cortico-basal ganglia-thalamo--cortical loop is especially appealing with respect to its potential role in phrase structure building given the finding that different 'stations' on the loop can be responsible for information integration from distinct cortical sources: convergence appears to occur at the pallidum (Yelnik et al., 1984), subthalamic nucleus (Haynes & Haber, 2013) and thalamus (Theyel et al., 2010). These stations also display a degree of functional specificity, and it is possible that different features of linguistic representations are integrated into the phrase structure building process in a procedural manner. The real-time dynamics of this 'relaying' process are yet to be tapped into by any direct, intracranial monitoring, to the best of our knowledge.

Reviewing related literature, Klostermann et al. (2013) conclude that "malfunction of the [basal ganglia] leads to deficits in applying combinatorial rules to linguistic messages, compatible with proposed superordinate [basal ganglia] functions, such as the sequencing or time-critical selection of input signals in general". Damage to thalamic relay stations of basal ganglia loops may also result in the typical constellation of monopitch, reduced stress and imprecise consonants (Ackermann & Ziegler, 2013; Duffy, 2005), again indicating a role for these structures in aspects of temporality. Even though dorsal path connections may be implicated in constructing hierarchical phrase structures (Friederici, 2017), other work suggests that the basal ganglia and thalamus act as network hubs forming a circuit supporting large-scale integration (Acsády, 2017; Bell & Shine, 2016). Large-scale information integration is "a key computational priority" of the subcortex, for Bell and Shine, presumably essential for a language network that is spatially distributed. This model lends further credence to the idea that dorsal stream circuits can extend into subcortical regions to participate in maintenance/memory and syntactic categorization processes which are coordinated and structured by low frequency bands. While information segregation and storage is a clear priority for anterior temporal and posterior temporal regions, information integration appears to additionally recruit a complex system of subcortical structures – approximating closer the generative power of natural language.

In addition, deficits in syntactic rule application in Huntington's disease are connected to basal ganglia damage (Teichmann 2005). Huntington's disease patients exhibit normal performance in phoneme discrimination in the context of isolated words, but display a deficit in phrasal (syntactic) contexts (Teichmann et al., 2009), linking phrase-level computations to basal ganglia degeneration. Sambin et al. (2012) revealed that Huntington's disease patients with basal ganglia damage specifically exhibit syntactic deficits when processing Principle C (Binding Theory) pronoun violations, and not working memory deficits. Basal ganglia damage also leads to difficulties in selecting appropriate verb tense (Teichmann et al., 2015).

Testing Parkinson's disease patients, García et al. (2017) documented impaired performance on two sentence comprehension tests: (1) An embedded sentence test (e.g., "The woman who is tall is kissing her husband"); (2) A touching A-with-B test (e.g., "Touching the scissors with the comb"). The authors found that syntactic deficits extended beyond Parkinson's disease patients and included asymptomatic carriers of a gene mutation associated with nigral degeneration. While the asymptomatic group performed well on task (1), they displayed impairments during task (2) – even though (2) had a relatively low working memory load relative to task (1). This helps to isolate specific syntactic operations to portions of the basal ganglia (in this instance, the substantia nigra); namely, the assignment of particular functional roles within predicates.

A related study (García et al., 2018) focusing on Huntington's disease patients found that performance on both tasks (1) and (2) was impaired relative to healthy controls. Interestingly, the asymptomatic Huntington's disease gene mutation carriers showed deficits in task (1) but not task (2) – the opposite profile from the asymptomatic Parkinson's disease relatives. Putting these two studies together, it appears that the telencephalic (caudate and putamen) basal ganglia contributes to hierarchical syntactic processing, but the mesencephalic (substantia nigra) basal ganglia contributes to functional role assignment.

Alongside these grammatical processes, amongst others we have reviewed, the basal ganglia has been implicated in a number of processes that support natural language syntax: working memory (Kemmerer, 1999), attention and/or information processing speed (Lee et al., 2003), and linear sequencing during syntactic processing (Chan et al., 2013). To illustrate, using fMRI in young healthy adults Ye et al. (2012) compared responses to 'before' sentences (e.g., "Before the female dancer canceled the show, the director fired the conductor") relative to 'after' sentences (e.g., "After the magician removed the bunny, the cameraman changed the film"). 'Before' sentences require additional computational resources pertaining to temporal rearrangement, and the authors found greater activity within the caudate nucleus and left middle frontal gyrus for these sentences. In addition, 'before' sentences resulted in greater functional connectivity between the bilateral caudate nucleus, right middle frontal gyrus, left precentral gyrus, bilateral parietal lobule and inferior temporal gyrus. It may therefore be the case that frontal-basal ganglia connectivity supports a number of syntactic functions.

The implementation of rule-based computations seems clear from much of the above literature, and it remains an open question whether language's rule-based grammatical processes recruit other subcortical structures. Current evidence at least points towards basal ganglia, but here another question arises: What 'rules' are engaged here? Recent work (Johari et al., 2019) suggests that, in Farsi-speaking Parkinson's disease patients, basal ganglia damage may not in fact be implicated in complex sentence comprehension, but rather executive functioning and, as the authors suggest, more minimal forms of syntactic computation involving "simpler rule-governed grammatical forms" (Johari et al., 2019: 232), as opposed to complex multi-phrasal working memory processing. A range of other work points to the role of the frontostriatal loop and basal ganglia in syntactic deficits in Parkinson's disease (for a review, see Smith & Caplan 2018). As such, basal ganglia is recruited for minimal compositional schemes, although the full scope and format of these schemes remains an open area for research. In line with the executive functioning view, Giavazzi et al. (2018) propose that the basal ganglia participates in selecting between grammatical alternatives (what they consider "linguistic selection").

2.4. The origins of MERGE: Thalamo-cortico-basal ganglia connectivity

Moving beyond rule-based processes, are there any other related levels of linguistic computation seemingly relevant to subcortical activity? Consider that syntax involves the construction of binary-branching hierarchically organized sets via the operation MERGE, taking objects from the lexicon or objects already part of the workspace to form a set; i.e., MERGE takes X and Y and forms the unordered set {X, Y}. Further structural complexity can be added – simply by applying the *same* operation again. For example, given the set {X, Y}, we can either select a new lexical object and MERGE it, to form {Z, {X, Y}}, or we can select an existing object and MERGE it to the same workspace, to form {X, {X, Y}}. These would then be labeled, respectively, as ZP and XP, given that Z and X provide the most structurally prominent features to serve the demands of categorization. In light of the fact that the cognitive process of categorization is shared across vertebrates (Corballis, 2002; Denenberg, 1981; Mareschal et al., 2010; Rogers et al., 2013; Vallortigara et al., 1999), and the observation that the syntactic combinatorial process of MERGE and categorization share the property of recursive set-formation, Hoshi (2018, 2019) hypothesizes that MERGE as an unbounded recursive set-formation operation was phylogenetically derived from the cognitive process of categorization in our pre-linguistic hominin ancestors. If categorization and syntactic combinatoriality are phylogentically related, it is possible that there are neural underpinnings common to both. In fact, as summarized in Lieberman (2006), categorization implicates interactions between the pre-frontal cortex and the striatum, as demonstrated in Huettel et al. (2002); see also Monchi et al. (2001). There is in addition evidence for increased effective connectivity between the left inferior frontal gyrus, posterior middle temporal gyrus and striatum during lexical-syntactic processing (Snijders et al., 2010). Seger and Miller (2010) note that categorization crucially implicates cortico-striatal loops, which may mediate interactions between fast reward-gated plasticity in the basal ganglia and slow plasticity in the cortex, enabling a balance between experiential learning and generalization.

Continuing with the theme of global coordination, top-down induced shifts in α phase between two cortical areas has been shown to strongly effect interregional γ coherence (Quax et al., 2017). In turn, it has been shown that this higher γ coherence between cortical regions also results in more efficient transmissions of spiking information. These findings point to "the feasibility of a … realistic mechanism for routing information in the brain based on coupled oscillations" (Quax et al., 2017). Its prominent interareal α and connectivity point to the pulvinar (the posterior portion of the thalamus) as being a possible locus where combinatorial processes might take place, or are coordinated, given its rich connectivity with perisylvian language areas (Jones, 2007), allowing the brain to "enhance processing of uncued stimuli" (Quax et al., 2017), with the importance of "uncued stimuli" for neurolinguistics being clear given the inherent creativity of grammar. In addition, the human pulvinar occupies a proportionately larger part of the thalamus than in other primates (Chalfin et al., 2007), which we believe may form part of the story for its involvement in the species-unique faculty of natural language syntax-semantics. With respect to which sub-portion of the pulvinar is most likely to be critical for language, we note that stimulation of the anterior superior lateral pulvinar disrupts object naming (Ojemann 1977), although the midline surface is more richly connected with cortical language regions; as such, we remain agnostic about the precise roles of sub-portions of the pulvinar.

Further, optogenetic approaches suggest that subgroups of the thalamic reticular nucleus facilitate attention switching from external stimuli to internal monitoring (Halassa et al., 2014), a dynamic process required, for instance, in the mapping of language-relevant sensory information to endogenous inferences. Saalman (2014) demonstrated that the envelope of cortical γ power in areas V4 and inferior temporal area TEO (cytoarchitectonic "area TEO" in posterior inferior temporal cortex) of the visual pathway was coupled to the phase of cortical α generated in higher-order thalamic nuclei, suggesting that the thalamus plays a major role in the creation of cortical γ rhythms known to be implicated in a variety of cognitive processes (via local ensemble activation). Since they have been shown to be involved in both local and global oscillatory control (Fogerson & Huguemard, 2016), the apparent flexibility of thalamic cellular and synaptic mechanisms could be readily exploited by language.

Moves towards direct intracranial monitoring of thalamic or subthalamic activity in humans during language processing (already a feasible goal, as demonstrated by Chrabaszcz et al., 2021) could further confirm or repudiate these ideas. While previous work has implicated subthalamic nucleus in speech production (Lipski et al., 2018), only recently has this region been implicated in lexical processing (Chrabaszcz et al., 2021), suggesting that the representational and computational scope of this and neighboring regions should be explored further.

Deepening our understanding of these regions, Deco et al. (2017) show that the reason why certain regions can oscillate at very low frequencies and sustain these rhythms is due to internal connectivity along with external thalamo-cortical connectivity, seemingly strengthening the ties between the thalamus and cortical language-relevant regions. Subcortex appears to play a causal role in coordinating the oscillatory behavior of cortical regions generating linguistic inferences. The kinds of low frequency entrainment and endogenous synchronicity in left fronto-temporal structures that is being connected to syntactic representations in recent literature (for review, see Meyer et al., 2020) are clearly a crucial part of any model of language, yet it may also be the case that without subcortex these fronto-temporal dynamics would not be possible. While we note that there are no cases of authors directly denying this possibility, there is also currently no direct evidence to support these dynamical systems-level proposals, with further empirical work jointly addressing neural dynamics and subcortical connectivity profiles being needed.

An additional reason for expecting research into subcortical language processing to be illuminating comes from the recent finding that human prefrontal cortex has the same relative volume of grey and white matter neurons as other primates, challenging any claims that uniquely human cognitive capacities arose due to an expansion of the prefrontal cortex (Gabi et al., 2016). Martin (2016) documents evidence suggesting that the classical view of the cortex as being exclusive to mammals is outdated, and that a number of vertebrates have cortex-like features.

How can we relate these ideas to more well-established findings of cortical involvement in syntax-semantics? Research by Matchin et al. (2017) considers the finding that damage to the inferior frontal gyrus does not impair basic structure-building processes and suggests that increased activity in this area during phrase structure building reflects the generation of top-down structural predictions.

The inferior frontal gyrus and posterior superior temporal sulcus did not show increased activity for simple phrases in their fMRI experiment, in contrast for sentences, most likely because the simple phrases used did not trigger structural predictions. Frontal regions seem key to aspects of active inference needed to generate accurate syntax-relevant information – yet they may not be causally implicated in basic syntax-semantics. Mayberry et al. (2018) also investigated the brain of an individual who experienced minimal linguistic input until young adulthood, showing that during language processing the dorsal pathway in the right hemisphere was primarily active rather than the classical perisylvian network. In this connection, Martins and Villringer (2018) discuss how structured sequences that are difficult to process appear to implicate left inferior frontal gyrus, and not hierarchical structures specifically.

These results seem compatible with the claim that parts of the inferior frontal gyrus do not provide "the seat of syntax", but rather something of a footstool – a memory buffer and system of control interfacing with a construction memory stack in superior posterior temporal regions (Leivada & Murphy 2021). The fact that the inferior frontal gyrus is active during the processing of unexpected stimuli suggests that its role is memory/control-related, not specifically hierarchy-related.

Going even further, Young et al. (2021) reviewed a range of existing results from intracranial cortical stimulating mapping and showed how left inferior frontal regions do indeed play a role in syntax-semantics, but likely in complex sentence processing, rather than in elementary structure building. Cortical stimulation mapping has also shown that action naming (involving verbs), which is more pertinent for basic syntactic structure than nominal information, recruits posterior temporal lobe sites, while common object naming (involving nouns) recruits more anterior temporal sites (Corina et al., 2005); in accord with what we have briefly reviewed about posterior temporal involvement in syntax (Murphy et al., Forthcoming); see also Flick et al. (2018) and Flick and Pylkkänen (2020) for careful analysis and evidence for posterior temporal involvement in minimal phrase binding.

With respect to any apparent human-specific computational properties of Broca's area and its memory buffer and externalization control system (i.e., its apparent involvement in processing linear morphosyntactic relations, complex phonology, and its use as an additional syntactic workspace), Palomero-Gallagher and Zilles (2019) provide a tentative answer as to its cytoarchitectonic and microstructural uniqueness. These authors quantitively studied the cytoarchitecture of areas 44 and 45 using layer-specific grey level indices (volume proportion of neuropil and cell bodies) in serially sectioned and cell body stained human, bonobo, chimpanzee, gorilla, orangutan and macaque brains (studying homologues to areas 44 and 45 in non-human primates). Humans were found to have the largest neuropil volume, indicating greater space for local and interregional connectivity. This may play a causal role in the additional workspace demands needed by natural language syntax, but likely not in more elementary computations. Additional cortical stimulation mapping of elementary syntactic structures could speak to this hypothesis. In addition, we note that much of the processes pertaining to complex (workspace-demanding) syntax and semantic memory implicates pars triangularis, while elementary phrase structure-building implicates pars orbitalis (Friederici, 2017; Zaccarella & Friederici 2015). We highlight in this connection, as a possible substrate, the absent (agranular) or rudimentary (dysgranular) layer 4 in certain frontal cortices. For example, pars triangularis is deemed eulaminate cortex (with all layers fully represented), whereas pars opercularis is considered dysgranular (Schenker et al., 2008).

Other recent evidence points away from traditional cortico-centric models. Moreno et al. (2018) used fMRI to scan the brain of congenitally deaf adults who had acquired French sign language as their first language and written French as a second language while watching a list of signs which corresponded to syntactic constituents of varying sizes. They discovered an effect of constituent structure in the basal ganglia (including the head of the caudate and putamen) and a much smaller effect on temporal and frontal regions known to be involved in written language. When the same participants read sentences versus word lists, the processing of sentences resulted in activation in the basal ganglia. This study highlights the importance of the basal ganglia in modality-independent syntactic processing. Tagarelli et al. (2019) conducted a meta-analysis of language learning and documented engagement of the anterior caudate/putamen in grammatical learning, and the authors note that the basal ganglia may contribute to lexical learning only under certain conditions involving cognitive control. Relatedly, Takashima et al. (2014) reported selective pallidum/putamen/caudate activity on the first day of a new word learning task that significantly decreased after 24 h, pointing to subcortical involvement with increased learning demands which are then relaxed after initial success and consolidation. In a different learning paradigm, Jeon et al. (2014) report how corticostriatal involvement in language learning varies as a function of task demands. Presenting subjects with grammaticality judgements of varying complexity and with differing memory demands, the authors show that the most demanding form of judgements that involved branching and episodic conditions and required temporal integration of events engaged the head of the caudate nucleus, ventro-anterior prefrontal cortex and ventral anterior thalamus. In contrast, less demanding judgements engaged the body of the caudate, the medial dorsal nucleus of the thalamus, and the posterior prefrontal cortex. A similar anterior-posterior effect in the caudate was documented by Mestres-Misse et al. (2012). These authors contrasted the processing of ambiguous, unambiguous and ungrammatical sentences. Dorsal aspects of the caudate head were active for ambiguous and ungrammatical sentences, but only the ambiguous sentences (yielding the greatest computational effort) activated the most anterior and ventral aspects of the caudate head.

A core part of natural language syntax (i.e., phrase categorization, labeling) may therefore take part in subcortical structures involving, and close to, the basal ganglia. In Murphy (2020), the categorization aspect of labeling was claimed to involve a network of posterior temporal regions and certain forms of cross-frequency coupling, while the maintenance/workspace aspects of labeling (which are necessary for any form of multi-phrasal construction; i.e., maintaining a category in memory), along with feature concatenation, more directly implicate subcortex. Supporting the centrality of the labeling computation in natural language processing (as predicted in Hornstein, 2009; Hornstein & Pietroski, 2009; Murphy & Shim 2020), there is recent evidence for the role of a category-sensitive phrase-building (labeling) mechanism driving the cortical tracking of hierarchical linguistic structures (Burroughs et al., 2021). We again return here to the possible role of subcortex in regulating and generating these forms of cortical oscillatory tracking mechanisms – a clear project for future research.

Pursuing this line of inquiry, left inferior frontal regions are regulated by the basal ganglia and thalamus via a cortico-basal ganglia-thalamic loop (Haber & Calzavara, 2009), an integrative system which is much more likely to be involved in structure-building operations than purely Broca's area alone. If anything, Broca's area seems specialized for executing retrieval operations which operate over constructed sets of linguistic features, hence why after a lesion to this area individuals retain the ability to comprehend and produce such feature-sets, albeit with reduced cognitive control over them. Contrary to standard models implicating the basal ganglia purely in physical movement, Haber and Calzavara (2009: 70) explore how it is also involved in "the processes that lead to movement" such as motivation and planning.

In connection with the important role of subcortical structures such as the basal ganglia and hippocampus in language processing, consider also Landau-Kleffner syndrome (LKS). This is a rare childhood neurological condition accompanied by loss of language skills and abnormal EEG signatures. Murugesan et al. (2020) demonstrated that the language delay in a patient with LKS is caused by pathology in the left side of the "language area" involving the basal ganglia and the hippocampus (and the temporal cortex). In particular, they discovered that the basal ganglia shows asymmetric diminished activity in the left hemisphere. While this study provides no means to causally separate the contributions of subcortical and cortical structures, basal ganglia and hippocampus at least appear implicated in language delay.

2.5. *Status quo*

Other work suggests that disinhibiting a basal ganglia loop leads to the maintenance of a particular representation to the exclusion of others (Koziol et al., 2009), 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, maintaining representations after "continuing input" over extended durations of discourse may allow a labeled object to be held in memory beyond the perception of its inference-initializing elements. More generally, human β activity has been linked to top-down control of information processing (Lundqvist et al., 2018).

What do these disparate findings about subcortex ultimately amount to, when faced with the much more robust, replicated findings about, say, the sensitivity of Broca's area and posterior temporal regions to various linguistic structures? We are not aiming to throw the baby out with the bathwater – on the contrary, we are interested in potential forms of reconciliation and providing further causal-explanatory details to the full range of brain dynamics of natural language, rather than isolating some sub-region generally sensitive to linguistic structure. Alongside its putative role in feature concatenation and object maintenance, we propose that the basal ganglia could also be involved in the sequencing of syntactic information, likely a very early stage of externalization or the interface mapping from narrow syntax to external performance systems. Some linguists have proposed that aspects of syntactic computation could in principle relate to notions of linearity (e.g., Mathieu 2016; but see; Chomsky, 2020; Chomsky et al., 2019), such that morphophonological factors may play a direct role in syntax. For instance, metrical requirements of affixes and other sensorimotor constraints are said to impact how syntactic computation is carried out. These stages of computation could potentially be encoded via the presently proposed neural dynamics of subcortex alongside functional connectivity with inferior frontal regions and its sensitivity to linear morphosyntactic relations. Whether or not interface conditions impact the application of syntax would determine the degree of interactivity between subcortical and temporal structures on the one hand (responsible for narrow syntactic computations) and inferior frontal regions on the other hand (responsible for these linearity-related and control-related sub-processes). It remains purely a question for theoretical linguistics as to whether certain aspects of linearity are part of syntax proper or are instead simply 'close' to syntax (in terms of derivational stage and, presumably, processing timing) and remote from other performance systems, but we believe our proposals here can more readily situate linguistic sub-domains in a neurobiologically feasible context. The involvement of cortico-basal ganglia-thalamo-cortical loops would be due to this complex being a major source of the brain's core timing system, with a feature of phrase structure building being rhythmicity (e.g., compare Bartolo et al., 2014 with Chomsky, 2008, who both stress the importance of cyclicity).

Given the likelihood that the left inferior frontal gyrus is not in fact crucial to elementary linguistic combinatorics, recent work by Wilson et al. (2017) can be more easily integrated into this framework. These authors synthesized current research into sequence processing in primate frontal cortex and propose a ventrodorsal gradient model of frontal cortical function in sequencing operations. Reviewing comparative fMRI studies led them to propose the existence of a "conserved, bilateral, ventral frontal and opercular subsystem within frontal cortex that supports the evaluation of adjacent sequencing dependencies". The literature suggests that in both monkeys and humans, ventral regions of frontal cortex conduct processing of adjacent sequence dependencies. This leaves open the possibility that temporal regions (e.g., posterior superior temporal sulcus), alongside subcortical regions (e.g., basal ganglia, thalamus), are responsible for language-specific computational processes, as suggested here, and as we will describe in more detail in the next section. We have discussed elsewhere why we should prioritize inquiry into minimal syntactic computations to posterior temporal areas and subcortical areas over fronto-parietal areas (Murphy 2020; see also; Matchin & Hickok 2020), but for further lines of inquiry in this direction, consider the finding that chronic Broca's aphasia is associated with damage to *both* Broca's and Wernicke's areas (Fridriksson et al., 2015; see also Volkmer et al., 2015, 2020).

2.6. *Rethinking the "seat of syntax"*

To close our discussion of the basal ganglia, we will briefly discuss this issue of the role of Broca's area and its basal ganglia connectivity in further detail. Relevant here is Lieberman's (2006) review of Broca's aphasia. Damage to Broca's area alone does not cause the full, permanent syndrome of Broca's aphasia, but damage deep into subcortex, including the basal ganglia, is also implicated (see Dronkers et al., 1992; D'Esposito & Alexander, 1995; Stuss & Benson 1986). Subcortical damage with Broca's area intact can also produce speech production and language deficits (see Alexander et al., 1987; Benson & Geschwind, 1985; Mega & Alexander 1994;

Naeser et al., 1982). A similar, well-established and developed model of language is found in Dominey and Inui (2009). These authors suggest that cortico-striatal connections deliver a mechanism binding cortical representations of syntactic context in BA 47 to grammatical representations in BA 44. This permits the retrieval of appropriate grammatical constructions to be read-out at BA 44 via thalamo-cortical connections. The authors claim that these connections subserve forms of rule-based processing not unique to language, but which are likely recruited by the language system for regularized, overlearned grammatical computations (see also van Schouwenburg et al., 2010).

Progressing further with these concerns, Teichmann et al. (2015) discovered a "Broca-caudate pathway" which is functionally involved in natural language syntax. They found a Broca-striatum tract linking BA 45 with the left caudate head that overlapped with voxel-based lesion-symptom mapping clusters related to complex syntax. The lesion load values for this Broca-striatum tract were correlated with the complex syntax scores of their subjects. Patients with frontal/striatal damage displayed impairments in processing phrasal syntax and verbal morphosyntax, with this impairment being most clear for noncanonical sentences, though crucially independent of semantic factors pertaining to plausibility or structural factors (relative vs. non-relative). This points to issues with transformational operations of structural reorganization. These results again speak to the idea that portions of basal ganglia are implicated in externalization-related properties of syntactic information processing, and the results pertaining to phrasal syntax even indicate an earlier role in minimal phrase categorization or maintenance processes. Further, assessing the patients' forward and backward digit scans, the authors showed that there was no correlation between general working memory deficits and performance on these language tasks, pointing to a more specific syntactic deficit. These ideas chime with separate findings. While the thalamus is often discussed in relation to attention – e.g., rich thalamocortical connections give rise to cortical dynamics that appear to be associated with consciousness (Mofakham et al., 2021) – basal ganglia loops have been found to be crucial for *intention* (Heilman et al., 2003), being involved in enhancing signal-to-noise in action-related processes; in contrast to layer 6 corticothalamic feedback mechanisms, which have been argued to be involved with improving signal-to-noise in sensory and perceptual processes (Crosson, 2013).

We note that a necessary feature of language is that its structure-building processes (elementary syntax) need to have direct access to the categories of the items being combined and stored together as a larger unit. We believe it is likely that the posterior inferior frontal gyrus and the temporal lobe (being implicated in categorization processes in phonology, semantics and conceptual storage), in particular the posterior middle temporal gyrus and superior temporal sulcus, dynamically interact during the construction and maintenance of linguistic representations, generating the human-specific trait of phrase structure building (Murphy et al., Forthcoming), with this interactivity crucially modulated by subcortex. We have defended this position in detail elsewhere (Murphy 2020), where we also call upon certain measures of functional connectivity and travelling oscillatory components, which are now known to be present not just over the cortical mantle, but over deep structures such as the insula (Das et al., 2021). We refer the reader to recent publications outlining the details of this travelling wave framework for higher-order language (Benítez-Burraco & Murphy, 2019; Murphy 2018, 2020), but we note here that more recent work has provided insight into the implementation of this model with respect to subcortical contributions. Bhattacharya et al. (2021) developed a computational model of a two-dimensional thalamocortical network which produces travelling waves similar to those that have been experimentally observed. They show that intracortical and thalamocortical network connectivity, cortical excitation/inhibition balance, and thalamocortical or corticothalamic delay can independently or jointly modify the spatiotemporal patterns (radial, planar and rotating waves) and characteristics (speed, direction and frequency) of cortical and thalamic travelling waves. The author's simulations predict that increased thalamic inhibition induces slower cortical frequencies. This work presents promising directions for models of language that not only invoke thalamocortical connectivity, but more specifically thalamic regulation of cross-cortical travelling waves (i.e., Murphy 2020).

This discussion brings us to our next topic: thalamic contributions to language.

3. Thalamus, hippocampus and cerebellum: Dynamic connectivity modulation, lexico-semantics and rhythmicity

What other evidence is there for a role of subcortex in higher-order language functions? We address this question by now focusing on the thalamus, hippocampus and cerebellum.

3.1. *Thalamus: Lexical memory and global coordination*

At the outset, we wish to stress that while the thalamus is often discussed in the neuroimaging literature as having a monolithic role in perception and cognition, this generalization obscures the rich and intricate connectivity profile of sub-nuclei and their apparent functional roles. While we will indeed explore general roles of the thalamus, we will ultimately be specifying which sub-portions.

Beginning first with a theme introduced above concerning connectivity profiles, Schmitt et al. (2017) demonstrated that mediodorsal thalamic input can modulate prefrontal cortical connectivity, "enabling rule-specific neural sequences to emerge and thereby maintain rule representations". The authors explain that these findings expose "a previously unknown principle in neuroscience; thalamic control of functional cortical connectivity", indicating that the role of the thalamus in cognition is much wider than has typically been assumed (see also Ashby et al., 2005; Stocco et al., 2010). As noted in Sherman and Guillery (2006), not only do thalamic nuclei serve as first-order gated relays to the brain from the periphery, but they also serve as higher-order gated relays with respect to one cortical area to another. For instance, Llano and Sherman (2008) discovered circuitry that can provide the mechanisms for a higher-order cortico-thalamo-cortical relay from primary to secondary auditory cortices via the dorsal and ventral medial geniculate body (the auditory thalamic regions), primary auditory cortex, and layers 1, 4 and 6 of secondary auditory cortices (see Asilador & Llano, 2021). More generally, "thalamo-cortical contact makes information conveyed by the thalamic relay neurons available to cortical computational machinery" (Crosson, 2021a: 518).

We have previously argued (Benítez-Burraco & Murphy, 2016; Murphy 2020) that the thalamus plays a role in lexicalizing conceptual representations through coordinating γ-oscillating ensembles seemingly responsible for conceptual-to-lexical transformations, and we maintain that the role of this region in syntax-semantics is much more crucial than typically assumed. While the centromedian nucleus of the thalamus is often touted as being most readily capable of coordinating topologically disparate cortico-cortical interactions, in principle any thalamic nuclei could drive selective engagement of portions of cortex most relevant for a given cognitive process. Indeed, the centromedian nucleus seems to be mostly connected to motor and premotor cortex (Sadikot & Rymar 2009), rendering its involvement in higher-order semantics (e.g., posterior association cortices) less likely. More broadly, the thalamus is strategically placed to interface with a range of cortical regions and is impaired in cognitive disorders associated with language (Boeckx & Benítez-Burraco, 2014). It has been implicated more directly in lexico-semantic processing (Assaf et al., 2006). As mentioned, the cellular and synaptic mechanisms that regulate thalamic oscillations appear to have a role in controlling local and global brain rhythms (Acsády, 2017; Fogerson & Huguemard, 2016). While the "outputs" of this system are detected in fronto-temporal dynamics (e.g., low frequency phase synchronization, cross-frequency coupling), it appears that subcortex forms a crucial part of the generative system which constructs, maintains, and regulates linguistic structures (see Fig. 1 for a brief summary of apparent and proposed subcortical contributions to higher-order language functions).

Changes in thalamic neuronal activity between tonic (Henning Proske et al., 2011) and bursting (Llinas and Jahnsen 1982) modes have been argued to generate oscillations that spread through intrathalamic and thalamo-cortical connections, permitting the modulation of cortical activity. The thalamus serves as an output station from the basal ganglia (Goldberg et al., 2013), and posterior portions such as the pulvinar are richly connected with visual cortex and exhibit retinotopic organization (Leh et al., 2008). For instance, the medial pulvinar receives fibers from and projects fibers to inferior parietal cortex and the ventral visual stream (Jones, 2007), and it projects to the majority of frontal cortices and also superior and inferior temporal regions (Goldman-Rakic & Porrino, 1985). Hence, compared to lateral and inferior divisions of the pulvinar (which are connected to early visual cortices and "area MT" of the occipital-temporal-parietal junction), the medial divisions of the pulvinar are more likely to be implicated in language. These long-range Broca's-pulvinar-parietal connections may be involved in refining the search space during lexical access, in particular during the transformations from lexical search to phonological planning. This would permit Broca's area to engage distant cortical areas, such as the inferior parietal lobe, during semantically complex sentence processing; e.g., complex event representations, which are known to engage inferior parietal cortex (Van Ettinger-Veenstra et al., 2016). As mentioned, stimulation of the pulvinar also evokes object naming failures, in line with this framework (Ojemann 1977; Ojemann et al., 1968).

At the representational level, cross-modular concepts widely deployed by natural language (Pietroski 2018) likely recruit thalamic nuclei such as the pulvinar and the mediodorsal nucleus, not least because of the role of the thalamus in modulating fronto-parietal activity, regulating cortical oscillations (Saalmann et al., 2012) and enhancing the rhythmic range of different frequency bands (Singer 2013). The anterior thalamus, for instance, is recently being considered a major site for predicting memory formation (Sweeney-Reed et al., 2015). It is possible that this thalamic activity relates to lexical memory (see Johnson & Knight, 2015 for evidence that the thalamus plays a key role in cortical oscillations involved in memory processes). Supporting this memory-related framework, Crosson (2021b) discusses the possibility that the thalamus, via its involvement in basal ganglia loops, participates in linguistic procedural memory processes that pertain to syntactic procedures and lexical search procedures.

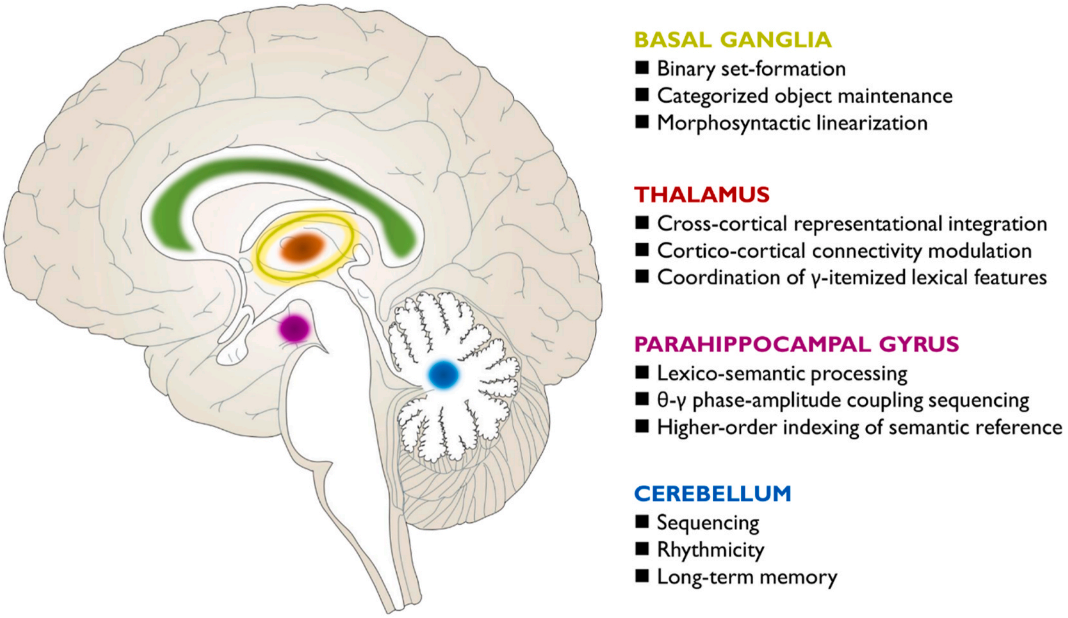

Fig. 1. General schema for subcortical contributions to language. For reference, corpus callosum is marked in green. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

Related research points to three thalamic sub-regions responsible for coordinating oscillatory activity and facilitating memory-related processes (potentially involved in accessing lexical representations), each of which is modulated by frontal cognitive control: the medial dorsal nucleus is implicated in β synchrony (generated by connectivity with parahippocampal/rhinal cortex), the pulvinar in α synchrony (generated by connectivity with early/visual parietal cortex), and the anterior thalamus in θ synchrony (generated by connectivity with the hippocampus; see the 'three circuit model' in Ketz et al., 2015). Thalamo-cortical interactions are increasingly being seen as central to facilitating higher cognitive processes (Pratt et al., 2017), and evidence for pulvinar expansion in humans (Pearce et al., 2013) also resonates with its presently purported role in language. Instead of viewing the thalamus as functioning as the brain's central rhythm generator (Theofanopoulou & Boeckx 2016), the evidence instead suggests that cortical rhythms are generated by an *interaction* between cortico-thalamic and thalamo-cortical behavior (Crosson, 2021a; Steriade 2006). Thalamic α has been implicated in modulating cortical γ power, and is also suited to synchronize distinct cortical regions oscillating at α (Gips et al., 2016), increasing the likelihood that it plays an important role in phrase structure building and semantic composition given the role of α in lexicality judgements (Strauss et al., 2015) and minimal syntactic binding (Segaert et al., 2018). Nevertheless, we stress that direct causal evidence for these dynamics with respect to language remain absent, and intracranial thalamic recordings in humans are required to probe these issues further. β coherence has also been reported between the prefrontal cortex and thalamus during working memory maintenance (Parnaudeau et al., 2013), while optogenetic suppression of the mediodorsal thalamus suppresses cortical delay activity (Schmitt et al., 2017); indicating a crucial role for thalamocortical connections in cognition.

At the level of functional connectivity, a recent model developed by Asano et al. (2021) marshals a range of evidence to suggest that the basal ganglia and thalamus exhibit functional connectivity with Broca's area to engage hierarchical control in both language and music. It appears that subcortex is involved in controlled syntactic processing, while BA 44 is independently recruited for more automatic (e.g., canonical, non-complex) syntactic processing. For instance, focal basal ganglia patients show abnormality in controlled linguistic syntax processing (Kotz et al., 2002, 2003), and a case report of an aphasic patient details how improved language performance post-therapy was mirrored by increased fronto-thalamic activation (Meinzer et al., 2006). Indeed, basal ganglia lesions tend to lead to executive language deficits, rather than, say, lexico-semantic search difficulties, as in thalamic aphasia. Still, further empirical work is needed to explore the real-time functional connectivity profiles of subcortex and cortex during automatic and overlearned versus controlled syntactic processing, in particular given the possible sensitivity of subcortex to forms of non-complex, minimal grammatical rules. Furthermore, there is a range of evidence that seems to account for a variety of syntactic priming effects using only declarative representations (Ivanova et al., 2017; Reitter et al., 2011), explicitly avoiding procedural ones; although, at the same time, more recently cognitive control of declarative memory processes has been associated with the striatum (Copland et al., 2021). Further research is needed to properly tease apart the reliance of grammatical processing on particular sub-networks of the brain responsible for priming, attention and control.

Nevertheless, there seems to be little doubt that connectivity between frontal cortex and subcortex is a core regulator of cognition. Bohsali et al. (2015) document substantial structural connectivity between Broca's area and the thalamus, in particular the pulvinar and ventral anterior nucleus. Fibers from Broca's area pierce the thalamus via the ventral anterior nucleus, before connecting to the pulvinar. Even though Bohsali et al. (2015) did not explore other frontal regions and their thalamic connectivity profile, following what it known from macaques it is likely that the vast majority of frontal sites will have some form of connection to the pulvinar and ventral anterior thalamus (Goldman-Rakic & Porrino, 1985). It is highly probable that the well-documented expansion of Broca's area in humans resulted in thalamic expansions, likely enhancing its ability to act as the (spatially) central oscillatory modulator in the binding of distant cortical representations via cortico-cortical and cortico-thalamic regulation. Indeed, the only sensory system which does not include a thalamic nucleus receiving sensory signals and transferring them to primary cortical regions is the olfactory system, and unless it is discovered that the sense of smell plays an unprecedentedly important role in language processing it seems safe to assume that the thalamus is central to the coordination and integration of cross-modular representations, required for typical sentence comprehension involving distinct conceptual domains. Hence, we assume a role for thalamus in aspects of lexicality, and further experimental work could test whether certain thalamic structures (e.g., anterior thalamus) are sensitive to distinct levels of linguistic structure.

Recent work also implicates the subthalamic nucleus in lexicality, with pseudoword processing resulting in greater γ activity in intracranial recordings than for word processing in a large cohort of Parkinson's disease patients undergoing awake deep brain stimulation (Chrabaszcz et al., 2021). Also using intracranial recordings from the subthalamic nucleus in Parkinson's disease patients, De Letter et al. (2020) found early (0–100 ms) differences in the processing of body-related action verbs (e.g., sew) relative to mental action verbs (e.g., hope). The authors note that it remains unclear whether these differences are due to phonological, semantic or syntactic cues. Given that the subthalamic nucleus has been proposed to inhibit temporal cortex output from the thalamus which enables controlled word selection (hypothetically, from the posterior temporal lexicon), these effects appear to implicate this structure in controlled aspects of lexical search (perhaps along the lines of set-reduction over an initially searched space). Wojtecki et al. (2017) also demonstrated a significant α and θ power increase and enhanced α-θ coherence between the subthalamic nucleus and frontal EEG sites during a verbal generation task.

Subcortex is consequently at the centre (both spatially an operationally) of coordinating the dynamic brain activity which gives rise to the constellation of cognitive processes required for natural language syntax. Thalamic pathways contribute to oscillatory interactions between the prefrontal cortex and medial temporal lobe, two structures widely implicated in language comprehension. Connectivity between prefrontal cortex, the caudate nucleus and the ventral anterior nucleus in the thalamus also appears to be functionally involved in higher-order sentence processing (Jeon et al., 2014); perhaps not due to *structural* sensitivity, but possibly due to *representational* richness of a monotonically increasing memory load (although thalamus may be involved in certain structural properties of language, as reviewed below). Cortico-subcortical circuits have been implicated in a range of cognitive and motor functions (Bell & Shine, 2016; McCarty & Brumback 2021). If Klostermann et al. (2013) are correct to suggest that the major thalamic functions with respect to language are "the control and adaptation of corticocortical connectivity and bandwidth for informational exchange" (a process termed "transthalamic network orchestration" by the authors), then it is likely that this region plays a crucial role in regulating other regions which are responsible for constructing and interpreting syntactic structures, through a fine-tuning of subcortical oscillations.

Highlighting again the apparent involvement of the thalamus in issues of linguistic *representation*, lesions in the left ventral anterior thalamus (typically ischemic) lead to aphasia characterized by semantic paraphasias, often accompanied by semantic jargon (Crosson, 1992). Meanwhile, lesions involving the left pulvinar (typically hemorrhagic) also result in semantic paraphasias and comprehension levels that are less impaired than what would be expected for cortical lesions. The most persistent symptom of thalamic aphasia is difficulty with lexical search; as such, thalamic deficits most clearly reside at the interface of semantic/conceptual and lexical transformations, during the transition from selecting a concept to searching for an appropriate lexical item. Language deficits in thalamic aphasia more generally indicate that the thalamus plays a role in lexico-semantic selection during word comprehension, with Raymer et al. (1997) reporting patients that made more errors in naming than neurotypical subjects by several standard deviations, regardless of the input modality or mode of externalization. Interestingly, these patients had greater difficulty with low frequency English words than high frequency words, which suggests that the transformation difficulties were indeed from conceptual (basic core knowledge systems) to lexical rather than the reverse.

Due to thalamic connectivity extending to relatively discrete portions of cortex, it also seems to be the case that the thalamus may be involved more critically in certain types of lexico-semantic processing than for others, being more crucial for a sub-type of possible objects that can be entered by MERGE into an active workspace – presumably similar to how, as we reviewed above, subthalamic activity differs between body-related action verbs (e.g., sew) and mental action verbs (e.g., hope). Moreaud et al. (1995) report a case of category-specific naming deficits for proper nouns in the dominant polar artery territory. Crosson et al. (1997) report a case of category-specific naming deficits for medical objects and conditions with a small hemorrhagic lesion of the pulvinar and posterior limb of the internal capsule. It is likely that these proper noun deficits are a reflection of the role of the frontal cortices that certain thalamic nuclei communicate with.

In this connection, Crosson (2013) highlights four major thalamic mechanisms that are seemingly relevant for language: (1) cortico-thalamo-cortical circuitry passes information between cortical areas via the thalamus; (2) cortico-thalamic circuitry changes the mode of information transfer for thalamo-cortical relay neurons; (3) cortico-striato-pallido-thalamo-cortical circuitry enhances the efficiency of action selection; and (4) cortico-thalamic feedback mechanisms sharpen the focus on specific cognition-relevant information. This last mechanism in (4) speaks to the role of the thalamus in reducing the search space for lexical selection.

A range of work suggests that terminal processes of layer 5 cortico-thalamic connections exhibit commonalities with fibers passing information from the periphery to cortex via the thalamus. Through their firing patterns these cortico-thalamic terminals pass information to thalamic relay neurons that then pass that information to the next cortical region in a processing chain (Crosson, 2021a; Usrey & Sherman 2019). While cortico-thalamic circuitry seems geared toward maintaining information encoding in firing patterns (i.e., these neurons change their firing pattern slowly), cortico-cortical circuitry seems geared toward (rapid) changes in information processing (Kawaguchi, 2017). Crosson (2021a) proposes that this property of cortico-cortical cells in layer 5 is useful when neural code from lower-order cortex is translated in higher-order cortices, since this involves considerable modifications in neural code, such as translating information stored in elementary lexical roots to higher-order conceptual code.

Is there any indication that the human thalamus might be implicated not just in generating conceptual representations, but also in constructing them into larger structures? Alongside the model we briefly reviewed above (Murphy 2020), which posits that α power increases that seem to be regulated by thalamo-cortical connectivity are involved in lexical memory and the early stages of binding/MERGE (i.e., selecting and bundling sub-lexical features into a coherent lexical item), there is suggestive empirical work in this domain. We highlight here the work of Kraut et al. (2002a, b, 2003). These authors developed an innovative semantic feature binding paradigm paired with fMRI, through which they presented pairs of semantic features (either via words or pictures) and participants had to judge whether the features could be combined into a coherent object or not (e.g., "desert + humps" could make a camel). For features that could be combined into an object, dorsal and posterior thalamus is active, but not for features that cannot be combined (e.g., "milk + bullet" does not yield a possible object). Kraut et al. (2003) considered the two foci of thalamic activity for combinatorial object pairs: the dorsal medial nucleus, and the pulvinar. Activity in the former preceded activity in the latter, and the authors hypothesized that the early dorsal medial activity indexed semantic search for a matching candidate, and the later pulvinar activity indexed feature-binding during object recognition. In addition, when the stimulus pairs are words and not pictures, thalamic activity is mostly limited to the left hemisphere.

Using the same paradigm in a larger cohort, Assaf et al. (2006) also found greater activity in the left thalamus for combinatorial pairs than for non-combinatorial pairs. Slotnick et al. (2002) also used the same paradigm, and found that combinatorial pairs resulted in a decrease in α (7–8 Hz) power in the thalamus and multiple cortical sites 1–2 s after stimulus onset (average reaction time was 1.57 s). This was followed by an increase in β activity (21–34 Hz) at thalamic and cortical locations 2–3 s post-stimulus onset (what the authors characterize as "gamma" activity). These thalamic and cortical responses were also phase-locked, indicating that the thalamus may have been driving cortical rhythms in the service of conceptual feature-binding. This provides tentative evidence that thalamus may indeed be involved in aspects of combinatorial processing, although it is also possible that the thalamic activity the authors document is purely due to successful lexical feature bundling, or a kind of lexicon-internal MERGE (i.e., taking "desert" and "hump" and using them to search, and construct, "camel").

With respect to how this potential feature-binding mechanism is realized, we point to the work of Malekmohammadi et al. (2015). These authors report simultaneous invasive recordings of cortical and thalamic electrophysiological activity in two awake and spontaneously behaving human subjects. They found that cortical phase-amplitude coupling between θ phase and β amplitude is spatially dependent on, and time-variant with, the magnitude of thalamocortical θ coherence. Causality analysis and MR diffusion tractography provided evidence that thalamic θ activity drives cortical θ oscillations and phase-amplitude coupling across structures, with these thalamocortical relationships being structurally constrained by anatomical connectivity. Malekmohammadi et al. (2015) do not specify which sub-portions of thalamus their analyses were driven from, and so further intracranial work could provide a more precise picture. Thalamocortical phase-amplitude coupling could therefore contribute to the implementation of feature-binding and MERGE, as we have hypothesized.

We discussed above Raymer et al.'s (1997) report of object naming errors in thalamic aphasia, which indicated a deficit in conceptual to lexical transformations, but without any clear syntactic deficits. However, Raymer et al.'s (1997) patient assessments were conducted 4–5 months after stroke, raising the question of whether other syntax-related deficits may have been detected earlier, before reorganization. De Witte et al. (2006) report a grammatical comprehension assessment of a patient with a bilateral paramedian thalamic infarction. They performed this assessment only one month after stroke. Like Raymer et al. (1997), they report semantic errors in spoken language – but they additionally report a clear simplification in syntax (the patient used only a single subordinate clause throughout assessment), few conjugated verbs, and a reduced number of lexical verbs. The patient performed well on grammaticality judgements, but had an impairment in verb and sentence comprehension. When tasked with describing a large number of pictures in a single sentence, the patient made a range of errors: omitting function words, failing to conjugate verbs, and semantic errors. The patient also made some errors during sentence anagrams (i.e., putting a collection of words into the right order to describe a picture) that involved *wh*-expressions. Given that the patient's lesions were primarily in the dorsal medial nucleus, which exhibits rich frontal connectivity, this may explain the syntactic deficits.

With respect to precise syntactic computations, much else remains unexplored. For example, we have here discussed some aspects of hierarchical processing and linearity, but what of the notion of unordered set-formation, which is core to models of theoretical syntax (Chomsky et al., 2019)? What of the process of reading basic lexical items (Forseth et al., 2021)? We have proposed that the timing of linguistic features is, broadly speaking, organized by forms of cross-frequency coupling, through which an ordered set of features can be read off from a series of fast γ cycles embedded inside the phase of low frequency rhythms (Benítez-Burraco & Murphy, 2019; Murphy 2015, 2020). But it has recently been discovered via human intracerebral recordings that high-frequency γ oscillations (70–200Hz) can also exhibit long-range phase synchronization, which appears behaviorally-relevant in a response-inhibition task (Arnulfo et al., 2020). This broadens the scope for simultaneously active (bound) linguistic features to be organized into a unit of cross-cortical manipulation and computation (likely coordinated via low frequency activity in the service of workspace construction; Murphy 2020), approximating closer the formal notion of unordered binary set-formation (Chomsky et al., 2019) than the linear feature-clocking of phase-amplitude coupling suggested in our previous work. The joint coordination and activation of cross-cortical linguistic features (free from any serialization constrained via phase-amplitude coupling) may constitute one of the earliest stages of phrase structure building, with these coordinated high-frequency γ cycles being then phase-coupled to the familiar lower frequency bands seemingly responsible for generating structural inferences. Again, we point to the thalamus as a strong candidate for modulating and constraining cross-cortical activity, synchronizing distant cortical areas.

3.2. *Hippocampus: Representational binding*

There are recent indications that left hippocampus is involved in hierarchical linguistic interpretation (Blank et al., 2016), linguistic semantics and referential processing (Piai et al., 2016) and auditory language comprehension (Wilson et al., 2008). Vanier et al. (2019) discovered that, relative to apes and monkeys, the human hippocampal formation shows an increase in size in the CA3, subiculum and rhinal cortex regions, and also an increase in the neocortex; expansions which might underlie our unique episodic memory capacity, as the authors speculate, but also our unique ability to string together large clusters of cortical linguistic features into coherent lexical items and phrases (see also Benítez-Burraco, 2021). The hippocampus also seems particularly suited to facilitate cross-modular interactions, since it has been argued to play a role in integrating 'what' and 'where' information in the perirhinal cortex through the lateral entorhinal cortex and the postrhinal cortex through the medial entorhinal cortex (Fernández-Ruiz & Oliva, 2016). Henin et al. (2021), using intracranial recordings in humans, exposed patients to auditory and visual sequences containing temporal regularities. Early on, both lower-level features, such as syllables, and learned units, such as words, were tracked neurally, while in later periods of the experiment only learned units were tracked. In particular, associative regions and hippocampus encoded the ordinal position and identity of hierarchical units.

Moreover, as Covington and Duff (2016) review, it is increasingly being shown that "the same hippocampal computations used in support of memory are also used for language processing", pointing to a shared neural code for particular computations. θ-γ phase-phase coupling in the human hippocampus has also been shown to be involved in multi-item working memory maintenance (Chaieb et al., 2015), and we have previously argued that different cognitive domains may construct representational stacks via different types of couplings (Murphy 2020). In essence, it is possible that some domain-general stack-construction algorithms implemented via forms of oscillatory coupling are exploited by certain sub-components of the language system (Benítez-Burraco & Murphy, 2019), from sub-lexical feature concatenation to more abstract representations denoting aspects of linguistically-constructed situation models (Horner et al., 2015). Again speaking to the sub-lexical level, the hippocampus, globus pallidus and caudate nucleus have been recently implicated in orthographic single-word processing (Braun et al., 2019), seemingly being involved in certain aspects of mapping orthographic forms onto long-term memory representations, potentially via the basal ganglia maintaining orthographic forms in working memory and hippocampal activity indexing the mapping to stored representations.

Nevertheless, the role of hippocampus appears to be somewhat specific: Binder et al. (2020) found that in epilepsy patients picture naming performance decline was unrelated to hippocampal resections, but was rather linked to fusiform gyrus resections (see also Forseth et al., 2018); indeed, resections to mid-fusiform gyrus are significantly associated with a decline in confrontation naming (Snyder et al., 2021). Hippocampus may be recruited for specific language functions pertaining to representational binding, but seems not to be causally implicated in visual object naming abilities. The possibility of post-resection reorganization is a possibility here, and indeed pre-resection reorganization, given that the presence of epileptic tissue may trigger reorganization years before surgery, possibly to contralateral hippocampal sites (Trimmel et al., 2019; see also Trebuchon-Da Fonseca et al., 2009 for discussion of how temporal lobe epilepsy may induce functional deafferentation between non-local structures). In this connection, given the lack of hippocampal resection impact on naming, it seems unlikely that this formation is causally involved in semantic memory, but is instead involved in aspects of episodic memory. We note that hippocampus has recently been argued to enable organisms to *bridge spatial and temporal experiential gaps*, and is thereby implicated in spatial cognition, event segmentation, and memory (Nadel 2021). Lexical items themselves are therefore unlikely to be encoded in the hippocampus, and instead it appears that this structure is involved in event-related conceptual processing that lexical items may provide instructions for.

While the causal role of hippocampus in language seems unclear (and also the parahippocampal gyrus, which seems implicated in episodic memory and context processing; Aminoff et al., 2013), the real-time dynamical engagement of this region has been explored extensively. Reviewing experimental literature investigating rodents and humans, Hanslmayr et al. (2016) propose a general trend: While hippocampal θ-γ phase-amplitude coupling mediates the binding of distinct episodic memory representations, the desynchronization of slower neocortical rhythms (α and β) also appears to mediate the encoding of episodic memories; exposing the inhibitory role of α in aiding successful memory encoding and retrieval by other brain regions. The hippocampal synchronization system therefore appears to *bind* information, while the neocortical desynchronization system *stores* the representational content. Both episodic memory and language involve the binding of discontiguous representations such as distinct memories and unrelated semantic features; with the latter being most clearly demonstrated in complex forms of polysemy involving the association of semantic features of distinct categories Murphy (2012, 2017, 2021). This crucial computational similarity may imply that both systems recruit the same hippocampal-neocortical system for aspects of their representational triggering and storage (see Piai et al., 2016 for hippocampal theta dynamics in natural language lexico-semantics). To emphasize a point already made: Certain fronto-temporal cortical clusters may be sensitive to the output of natural language syntactic computations (and can hence be readily detected via functional neuroimaging), but the early stages of initial generation are likely reliant on subcortex to a much greater degree than typically acknowledged.

The role of hippocampus in language may go even beyond this. Recent work (Ellamil et al., 2016) has demonstrated the central role of the hippocampus in spontaneous thought generation (or 'mind-wandering', which seemingly occupies 20–50% of daily life; Killingsworth & Gilbert, 2010), with a large portion of cells in this region being involved in short-distance and long-distance connections. This may contribute to an explanation for the existence of some of the qualities of spontaneous thought, such as the fact that it often contains semantic representations "of wild diversity and content" (Ellamil et al., 2016), since hippocampal long-range connections interface with numerous cortical regions which store a variety of representations. Likewise, much of spontaneous linguistic thought of the kind seen in mind-wandering crosses modular boundaries, in the sense of encapsulated "core knowledge systems" (Spelke 2016) such as place, number, social relations, intuitive geometry and physics. The creative expression of cross-modular concepts is paramount to ordinary linguistic productivity, in both interpretation and production, and these hippocampal dynamics appear to be part of the basis for such behavior. As such, the hippocampus might not only explain features of "the restless nature of our minds" (Ellamil et al., 2016: 195), but could also more specifically shed light on lexico-semantics (relatedly, Mišić et al., 2014 provide evidence that the hippocampus is a crucial convergence zone for information flow).

3.3. Cerebellum: The syntactic time Keeper

Lastly, there are recent indications that the cerebellum may play a role in certain aspects of language. Portions of cerebellum (lobule VIIb/VIIIa) hold objects from visual working memory (Brissenden et al., 2021), crucial for semantic categorization. As we have previously reviewed (Murphy 2019), the cerebellum also plays a role in long-term memory, while Nozaradan et al. (2017) reveal how the cerebellum and basal ganglia are involved in the neural representations of rhythmic sequences. Cerebellar lesions can lead to non-motor language deficits impacting syntax, semantics and sentence formation (for review, see Moberget & Ivry 2019), with the cerebellum having been implicated in linguistic syntax (Adamaszek & Kirkby, 2016) and the maintenance of phrase structure in working memory (Mariën et al., 2001). Patients with cerebellar lesions have displayed reduced abilities to discriminate between grammatical and ungrammatical sentences (Justus, 2004). Cerebellar contributions to language appear to be structured by major pathways comprising the cerebrocortico-ponto-cerebellocortico-dentato-thalamocerebrocortical and cerebrocortico-rubro-olivo-neodentato-cerebrocortical loops (Adamaszek & Kirkby, 2016; Schmahmann & Pandya 1997). Typically, right-hemispheric cerebellum activity is coordinated with dominant left-hemispheric activity, forming part of the extended language network (Justus 2014), although ipsilateral activity has also been documented (Adamaszek & Kirkby, 2016). Right and left cerebellum, in isolation but also together, have been claimed to be essential for certain linguistic tasks, although a common generalization is that right cerebellum responds greater for high-frequency information and language, while left cerebellum responds greater for low-frequency information and singing (Callan et al., 2007).

Cerebellar interfacing via cerebrocerebellar pathways with the left temporal and prefrontal gyrus also appears involved in language perception and production, such as in verbal fluency, word stem completion, word and letter generation, and semantic processing (Murdoch 2010). Along with the pre-SMA, SMA and basal ganglia, the cerebellum has been implicated in the coordination of temporal structure (Kotz & Schwartze, 2010). Based on event-related potential responses to morphosyntactically correct versus incorrect sentence processing, other authors suggest that the cerebellum offers "a preattentive support role", being involved in "forwarding results of syntactic analysis to frontotemporal pathways" via the thalamus (Adamaszek & Kirkby, 2016: 89).

Turning to more detailed anatomical dissociations, Stipdonk et al. (2021) investigated children born very preterm (VTP), who quite typically have language deficits. They explored whether total cerebellar volume, or specific posterior lobule structures, are associated with language abilities in school-aged VPT children. They found that specific cerebellar lobules (right Crus I + II) are positively associated with semantic language functions, whereas whole cerebellar volume was not. Syntactic language functions are positively associated with grey matter volume of Crus I + II in right-handed children only.

In a recent editorial commentary, Mariën and Manto (2018) claim that the cerebellum is "a masterpiece for linguistic predictability", reviewing its extensive involvement in both motor and non-motor predictions, and providing clear directions for integrating it into models of higher cognition. While this optimistic assessment arguably constitutes a form of propaganda given its appearance in the journal *Cerebellum*, the authors provide convincing arguments and citations, with cerebellar predictions likely being implemented via extensive connectivity with the spinal cord, brainstem and the supra-tentorial structures – including cerebellar-basal ganglia loops (Caligiore et al., 2017).

The cerebellum also appears to regulate the temporal integration of items in working memory relevant to morphosyntactic information, handling the temporal coordination of grammatically-relevant memory items. Cerebellum-related deficits are often performance-related aspects of language (e.g., monitoring and timing of sequences, and the detection of violations of predicted grammatical rules; Booth et al., 2007; Mariën & Borgatti 2018), though given the small number of direct recordings of the human cerebellum during tasks manipulating some component of syntax-semantics, it also seems too early to make strong conclusions here.

4. Conclusion

The potential for empirical assessments of the architectural claims we have made here is rapidly increasing. For instance, intracranial electrocorticographic research during deep brain stimulation surgery has recently been shown to not significantly alter complication rates (Sisterson et al., 2021), suggesting that academic research into the assessment of basal ganglia-thalamocortical circuit physiology is a safe procedure, opening up new avenues for investigating subcortical involvement in natural language syntax-semantics.

The common thread that we wish to summarize here is that the major subcortical structures we have reviewed appear to be living double lives. They are implicated in generic syntax-external processes but also syntax-internal processes. For instance, thalamic coordination of cross-cortical lexicalization seemingly occurs in parallel with thalamic cortico-cortical connectivity modulation necessary for apportioning various attentional demands. Meanwhile, the basal ganglia's potential role in labeled object maintenance ("interpretation", "internalization") can be seen alongside its role in morphosyntactic linearization ("externalization"). We also wish to stress that while the language-relevant roles for subcortex we have presented have often been motivated via direct experimental or neuropsychological findings, we have motivated other roles primarily through inductive reasoning, and we encourage others to explore the empirical implications of these and related hypotheses, and to further theorize about subcortical contributions to higher cognition. We also encourage groups investigating subcortical aphasias (in particular, thalamic and basal ganglia aphasias) to undertake syntactic-semantic assessments, given their relative scarcity in current literature.

Since subcortex has readily been acknowledged to be essential for a range of higher cognitive functions, it seems reasonable to expect important contributions from these regions with respect to language processing. The small number of subcortical structures we have reviewed here are something of a motley crew, each contributing quite distinct computational roles and exhibiting widely different connectivity profiles, and we expect future research will expand the list of subcortical structures known to be recruited for language. In brief, we have here tried to marshall a range of evidence suggesting that subcortex plays an essential role in natural language syntax-semantics – a suggestion which, if further validated in future work, would demand a considerable revision to major neurolinguistic models.

Declaration of competing interest

The authors declare no competing interests.

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