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NEUROBIOLOGICAL INSIGHTS INTO THE FACULTY OF LANGUAGE WITHIN BIOLINGUISTICS

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Abstract: In the field of biolinguistics, theoretical models treating language as a biological system have advanced rapidly, yet the neurobiological evidence underpinning these models has lagged behind, creating a significant gap between theory and data. This study bridges the theoretical framework of biolinguistics with empirical neurobiological evidence to examine the neural foundations of the faculty of language, both in its broad (FLB) and narrow (FLN) senses. Drawing on recent neurobiological findings, the study demonstrates that the modular architecture of FLB—comprising phonological-phonetic, syntactic, semantic, and pragmatic modules—is instantiated in distinct yet dynamically interacting neural circuits. Notably, the left inferior frontal gyrus (IFG) and the posterior superior temporal gyrus (pSTG) play central roles in syntactic computation, while the left superior and middle temporal gyri are primarily involved in semantic computation. Evidence from comprehension studies further highlights that syntactic computations may continue beyond the point of initial phrase construction, indicating that syntactic computations are not necessarily complete once their outputs are transmitted to other modules (semantic, pragmatic, phonological-phonetic modules). Regarding FLN, the core syntactic operation merge is shown to be implemented in the BA 44 of the left IFG as the neural locus of external merge. While some cross-species studies suggest merge-like abilities in non-humans, the neurobiological specificity of merge remains uniquely human. Internal merge, responsible for syntactic movement, has not yet been systematically investigated in terms of its neural underpinnings; however, a review of neuroimaging studies involving syntactic displacement suggests that internal merge engages overlapping regions in the IFG, indicating a shared but functionally distinct neural basis. This study affirms the biological grounding of the faculty of language and argues for a more integrative empirical agenda in biolinguistics—one that combines theoretical precision with neuroscientific rigor to uncover the architecture of language.

Keywords: Biolinguistics; Neurobiology of language; The faculty of language; Modularity

1 INTRODUCTION

Biolinguistics highlights the commitment of the generative enterprise to the biological foundations of language, and emphasizes the necessarily interdisciplinary character of such enterprise [1]. It emerged in the late 1950s from early collaborations between linguists and biologists (Chomsky, Lenneberg, and Salvador Luria), and was formally established as a scientific framework with Lenneberg's seminal work *Biological Foundations of Language* [2-3], which laid the groundwork for subsequent theoretical and empirical developments. As a research program, Biolinguistics addresses five fundamental issues in the field: what the knowledge of language is; how that knowledge develops in individuals; how it is used; how it is represented in the brain; and how it evolved in our species [4]. In answering the first three questions, scholars in the field typically conceive knowledge as a specific neurophysiological state of the brain: genetically specified and shaped by environmental input through neurodevelopmental processes, culminating in a mature language organ that enables thought, speech, and comprehension. By contrast, the latter two questions—neural representations and evolutionary origin—cannot be resolved solely through abstract theorizing or behavioral observation; they demand interdisciplinary neurobiological investigations and diachronic, cross-species research. Indeed, the generative tradition has often remained at a highly abstract level, rendering concrete biological inquiry challenging [5]. To move beyond this abstraction and fully articulate the biological foundations of language, rigorous neurobiological inquiry is both necessary and long overdue.

Central to biolinguistics is to identify the property of the faculty of language, which Hauser, Chomsky, Fitch divided into the faculty of language in the broad sense (FLB) and the faculty of language in the narrow sense (FLN) [6]. FLB encompasses the sensory–motor system (the phonological–phonetic module) responsible for externalization and the conceptual–intentional system (the semantic and pragmatic modules) responsible for thought and action planning [7], and the computational capacity for recursive merge—FLN [i.e., syntactic module (including lexicon)]—which alone underlies our uniquely human ability to generate an infinite array of expressions from a finite set of elements. In this framework, language is generated by first retrieving lexical items from the lexicon and then assembling them into hierarchical structures through syntactic computation. These candidates (i.e., syntactic representations) are subsequently mapped onto the phonological-phonetic module for auditory processing, and onto the semantic and pragmatic modules for interpretation. Moreover, these modules do not operate in isolation; rather, they interact dynamically, allowing for continuous exchange and integration of information across various modules of the faculty of language. To illustrate this, before we utter "the river runs," we extract the (syntactic, semantic, phonological, and phonetic) representations of "the", "river" and "runs," generate and evaluate possible syntactic representations (e.g., *"river runs the," *"the runs river," "the river runs"), and only those that satisfy the interfaces between syntactic module and other modules (e.g., semantic, phonological-phonetic modules) are ultimately phonologically realized and interpreted as "the river runs".

This naturally leads us to ask: what neurobiological evidence currently supports such an architecture of the faculty of language? Or is this framework still largely confined to the realm of theoretical speculation? To date, much of biolinguistic research has remained predominantly theoretical, relying on inductive and deductive reasoning to formulate hypotheses [8], which are subsequently tested through behavioral experiments. In contrast, empirical evidence from neuroimaging studies remains relatively limited—particularly within biolinguistics, a field historically grounded in theoretical innovation, despite the originality and far-reaching implications of its proposals. Against this backdrop, the present study aims to help bridge the gap between biolinguistic theory and empirical inquiry by systematically evaluating the neurobiological substrates of the faculty of language—both in its broad (FLB) and narrow (FLN) senses—through a critical and integrative synthesis of existing neural evidence.

2 NEURAL FOUNDATIONS OF THE FACULTY OF LANGUAGE IN THE BROAD SENSE

The neural underpinnings of the FLB reside in the precisely coordinated activity of distinct cortical and subcortical regions in our brain, as well as in the dynamic exchange of information among these regions, often via functional connectivity or long-range white matter tracts. Biolinguistics, by conceptualizing language as a biological organ, tends to assume that these neural systems correspond to theoretically motivated modules—phonological-phonetic, syntactic, semantic, and pragmatic modules—each of which is instantiated in specific, functionally or anatomically specialized, and reproducible neural circuits that can be studied across individuals and populations.

To date, the majority of empirical support for this modular architecture of FLB has come from neurobiological investigations from Friederici and colleagues [9-10]. They have provided perhaps the most comprehensive neuroanatomical model of language comprehension, delineating successive yet interactive processing stages. In their framework, an initial acoustic–phonological analysis is reflected by the N100 component (occurring around 100 ms post-stimulus) and arises in primary auditory cortex. From there, signals bifurcate: a posterior pathway toward the planum temporale and posterior superior temporal gyrus (pSTG) specializes in segmental, phonemic detail, while an anterior route toward the planum polare and anterior superior temporal gyrus (aSTG) processes prosodic, suprasegmental cues. Crucially, these pathways operate in parallel and engage both hemispheres, with the left hemisphere preferentially supporting fine-grained, time-sensitive analyses and the right hemisphere more sensitive to contour and rhythmic structure. Within the left hemisphere, processed auditory representations are further parsed into three interleaved stages. First, ventral Brodmann area 44 (BA 44) in the inferior frontal cortex instantiates rapid, automatic initial phrase-structure building—indexed by the ELAN (early left-anterior negativity) between 120 and 250 ms. This stage aligns neatly with the biolinguistic notion of a syntactic module in FLB that generates hierarchical structure from lexical items. Second, between 300 and 500 ms, the LAN and N400 components reflect parallel semantic and thematic integration processes, recruiting left superior and middle temporal gyri along with BA 45/47 in the inferior frontal cortex. These activations correspond to the semantic module of FLB, demonstrating how meaning is computed in real time. Third, syntactic relations that involve long-distance dependencies—such as in center-embedded or subordinate clauses—further re-engage BA 44 and pSTG, illustrating the sustained role of the syntactic module in handling complex structures. Finally, the P600 component (approximately 600 ms) indexes the integration of syntactic and semantic representations in the posterior superior temporal sulcus (pSTS) and adjacent pSTG, indicating the convergence of multiple pathways into a unified interpretation. Right-hemisphere mechanisms complement these left-lateralized processes by parsing prosodic phrase boundaries. Specifically, right superior temporal and inferior frontal regions are engaged in prosodic processing, with interhemispheric coordination mediated by the corpus callosum. This bilateral division of labor underscores FLB's design that the sensory–motor and conceptual–intentional systems operate in concert, yet with specialized subcomponents tuned to distinct informational streams. Taken together, this neuroanatomical evidence offers compelling support for the modular and interactive nature of FLB, bridging abstract theoretical constructs with temporally and spatially specific brain mechanisms.

Although these findings illustrate a modular decomposition of language comprehension processes, it is important to emphasize that neural evidence also indicates a high degree of parallel processing among the modules of FLB. Contrary to a strictly linear biolinguistic pipeline—in which lexical retrieval feeds into syntactic assembly, which then sequentially sends outputs to the semantic, pragmatic, and phonological–phonetic modules—time-resolved neural recordings reveal that outputs from early phrase-structure building rapidly cascade into semantic networks, even as syntactic computations, such as the processing of long-distance dependencies, continue to unfold. This dynamic temporal profile suggests that multiple components of the language system may partially operate in parallel rather than being activated in a strictly sequential manner. Moreover, the evidence strongly indicates that these modules are densely interconnected—for instance, through the flow of information between syntactic and semantic processors in the left hemisphere, and through the integration of phonological processing via white matter tracts connecting to the right hemisphere. Such a highly interactive and temporally flexible architecture aligns closely with the central claim of biolinguistics: that the modules jointly constitute a human language system (FLB) that is both flexible and biologically constrained.

It is also important to realize that biolinguistic models maintain a fundamental interdependence between language comprehension and production (i.e., generation), positing that both domains rely on shared core computational mechanisms that collectively support linguistic competence. Demonstrating converging evidence across these domains is therefore crucial not only to substantiate the integrative architecture of the FLB, but also to establish a robust neurobiological foundation for biolinguistic theory. To fully validate the design principles underlying FLB, empirical inquiry must extend beyond aforementioned comprehension to include language production paradigms, which remain comparatively underexplored in the existing literature [11-13]. Three principal methodologies offer complementary insights into the neural bases of production. First, lesion studies involving aphasic patients—particularly those with focal damage to Broca's or Wernicke's areas—have shown that impairments in the production of phonological, syntactic, or semantic components can be selectively traced to specific cortical regions. Although interindividual variability present methodological challenges [14], the recurrence of similar deficits across patients provides compelling support for modular specialization. Second, elicitation of speech errors in neurologically intact individuals—through techniques such as tongue twisters or speeded naming tasks—can reveal breakdowns in specific processing stages, illustrating, for instance, that phonological encoding errors may occur independently of semantic selection. Third, experimental paradigms that prompt target utterances via picture naming, word fluency tasks, or scripted dialogues allow researchers to systematically investigate production subroutines under controlled conditions. While such tasks often involve some engagement of comprehension circuits (e.g., reading prompts), careful task design in combination with neuroimaging techniques enables researchers to isolate neural activity specific to production processes. By integrating evidence from lesion studies, behavioral experiments, and neuroimaging research, we may map the neural representations for language production—evidence that may offer a more decisive evaluation of the biological foundations of FLB within the biolinguistic framework.

Moreover, the pragmatic dimension of language—often marginalized in comprehension-focused research—is rarely treated as a core component in Friederici's model. Yet this aspect of language use may constitute a fundamental part of the FLB. Mao compellingly argues for the inclusion of a dedicated pragmatic module within the FLB architecture [15]. Drawing on evidence from autism spectrum disorders, he demonstrates that individuals with impaired pragmatic inference do not rely on mind-reading when processing linguistic and communicative demands; instead, they resort to self-sufficient mental computations among organism-internal submodules (e.g., semantic, syntactic modules) or rely on nearly intact grammatical systems. This suggests that there is a strong theoretical rationale for incorporating a pragmatic module into the FLB. In addition, neuroimaging studies of pragmatic inference have implicated bilateral inferior frontal gyri and middle temporal gyri [16], regions that overlap with core semantic networks. This anatomical overlap indicates that pragmatic computation may be closely integrated with semantic computation, rather than residing at the periphery. Incorporating pragmatics into the neurobiological study of core linguistic capacities would not only extend the explanatory power of the FLB but also align with biolinguistics' broader aim of accounting for the full range of human linguistic capabilities.

In summary, current neurobiological evidence on language comprehension largely supports the architecture of the FLB as proposed within the biolinguistic framework, particularly in demonstrating the neural substrates of syntactic and semantic computations and the interactive flow of information among modules. However, complementary findings suggest that syntactic computations may continue beyond the point of initial phrase construction indicating that such operations are not necessarily complete once their outputs are transmitted to other modules. These observations may contribute to refining and extending the FLB model. Moreover, the inclusion of a pragmatic module within the FLB architecture appears theoretically justified, and future neurobiological research on language could further substantiate the validity of this modularization.

3 NEURAL FOUNDATIONS OF THE FACULTY OF LANGUAGE IN THE NARROW SENSE

The concept of merge, introduced by Noam Chomsky, constitutes the core syntactic operation common to all human languages, reflecting a universal property of human cognition. Defined as an unbounded binary set-formation operation, merge applies recursively to generate hierarchical structures. In the case of external merge, two syntactic objects, α and β, are combined to form a new set $\{\alpha, \beta\}$. For instance, merging the lexical items *the* and *river* yields {*the*, *river*}; further merging with a third item, such as *runs*, results in the structure {{*the*, *river*}, *runs*}. Note that the syntactic objects generated by external merge are unordered and must be interpreted by the conceptual-intentional system and externalized by the sensory-motor system.

Beyond external merge, the operation of merge also includes internal merge, which accounts for displacement phenomena observed in natural language. For instance, suppose we begin with the representations such as *Mary is seeing who*, constructed via external merge. To form a *wh*-question like *tell me who Mary is seeing ~~who~~*, the *wh*-phrase *who* must move to the edge of the clause via internal merge, yielding a derived structure where the fronted *who* indicates interrogative force, while the unpronounced lower copy *who* retains semantic content for interpretation. This derivational process highlights the core property of internal merge: it repositions existing elements within a syntactic structure rather than introducing new ones, allowing for complex hierarchical configurations to emerge through minimal operations. Notably, this movement-driven operation underlies a wide range of syntactic phenomena across languages—such as question formation, topicalization, and relativization—further illustrating its central role in the generative system.

Crucially, both external and internal merge constitute the core of the FLN—a capacity widely considered unique to humans and central to our species' linguistic competence. It is hypothesized that this capacity emerged in modern humans who first appeared in southern Africa around 200,000 years ago, but before the last major migration out of Africa approximately 60,000 (or possibly 80,000) years ago [17]. This period likely marks a species-specific biological mutation that endowed humans—with no comparable capacity observed in other primates such as gorillas—with this uniquely human linguistic computation. In what follows, we examine the neural basis of this fundamental property of language, focusing on how recent advances in neuroimaging and comparative research contribute to our understanding of merge as a biologically grounded and potentially uniquely human computational operation.

Neuroscientific evidence bolsters the claim that external merge is a universal human attribute by identifying its biological basis in the brain. Most of this evidence derives from studies of both complex sentence structures and two-word compositions. For the former, Goucha & Friederici employed a multi-level syntax–semantics dissociation paradigm to reveal that the BA 44/45 network in Broca's area operates in concert during full sentence processing [18]; as semantic and derivational morphological cues are incrementally stripped away—leaving only pure syntactic markers—posterior BA 44 alone emerges as the neural "engine" of external-merge operations. This fine-grained functional segregation provides direct and robust support for external merge as a core computational mechanism. Complementing these findings, one MEG study demonstrates that cortical ensembles track hierarchical linguistic units at distinct temporal rates—4 Hz for words, 2 Hz for phrases, and 1 Hz for sentences—across typologically diverse languages, reflecting a merge-driven computation of structure independent of language-specific content [19].

Because complex sentences inherently introduce confounds—such as propositional meaning, increased processing demands, and contextual effects [20]—investigators have turned to the paradigm of two-word phrases to isolate pure syntactic composition. In this domain, Zaccarella & Friederici found that the ventral-anterior subcluster (C3) of left BA 44 exhibits significantly greater activation for externally merged two-word phrases than for unstructured word lists [21], and Schell et al. showed that determiner–noun pairs, which engage basic syntactic computation merge [22], selectively recruit inferior-ventral BA 44 along with the frontal operculum and anterior insula, underscoring BA 44's sensitivity to function-word–driven combinatory operations. An ALE (activation likelihood estimation) meta-analysis also confirmed that merge [23]—the core syntactic mechanism combining words into hierarchies—consistently engages the left BA44 and the posterior STG/STS. BA44 was identified as a pure syntactic processor, while posterior STG/STS integrates syntactic and semantic information. Together, these data define the neural mechanism of external merge as a hierarchical computation powered by BA 44 within a fronto-temporal network specialized for syntactic composition, firmly grounding this mechanism as a universal attribute of human language.

However, behavioral evidence from both human and animal studies might be against the notion that external merge is a uniquely human attribute with a specific biological basis. Research involving monkeys, children, U.S. adults, and native Amazonians demonstrates that recursive sequence generation [24], a fundamental component of merge, is not exclusive to humans and can be observed across different species and cultures, suggesting a broader cognitive capacity rather than a human-specific trait. Furthermore, research on songbirds reveal their ability to learn recursive syntactic patterns [25], indicating that the cognitive mechanisms supporting merge-like processes are present in non-human species as well. While these findings imply a broader cognitive substrate, they do not directly challenge the neurobiological specificity of external merge in humans. To mount a decisive critique, comparable neuroscientific investigations—ideally employing fMRI, MEG, EEG, or invasive recordings—in species such as non-human primates and songbirds are needed to determine whether analogous fronto-temporal circuits underlie their merge-like abilities, and how these circuits diverge from the human blueprint.

Although previous studies have provided neural evidence for the operation of external merge, no research to date has clearly distinguished the neural correlates of internal merge versus external merge. Theoretically, internal merge involves movement of elements within a structure—such as the fronting of a *wh*-word in interrogatives—while external merge introduces new elements into the structure, as in the initial combination of lexical items (see earlier discussions of external merge). Most existing neuroimaging studies have treated the two as functionally equivalent or have overlooked internal merge altogether, with no direct neural comparisons available to dissociate their activation patterns. Nevertheless, we may attempt to infer the neural basis of internal merge by examining well-attested syntactic phenomena that are canonically analyzed as involving this operation. These can include *wh*-movement (e.g., *What did you buy?*, where the *wh*-word is fronted from its base position [26-28]), topicalization (e.g., *This book, I really like.*, with fronting for emphasis; cf. Maki et al. [29]), passivization (e.g., *This book was read by John.*, involving NP movement; cf. Collins [30]), and scrambling (e.g., in Japanese *Sono hon-o Taroo-ga yonda* 'That book, Taro read', where the object precedes the subject without topicalization or focus marking ; cf. Miyagawa [31]). Identifying common activation patterns across these constructions may shed light on the neural substrates of internal merge.

Findings from several neuroimaging studies may support this approach. Ben-Shachar et al. found that syntactic movement [32]—examined through Hebrew topicalization and *wh*-questions—consistently activated the left IFG, left ventral precentral sulcus (vPCS), and bilateral posterior STS, regions that were selectively sensitive to movement-based syntactic contrasts. This supports a stable neural signature for syntactic movement consistent with internal merge. Ohta et al. further demonstrated that scrambling [33], which involves structure-internal displacement, elicited significant activation in the left IFG and lateral premotor cortex—both associated with core syntactic computation—using stimuli from Kaqchikel Maya, a language with flexible word order. Crucially, when controlling for semantic and phonological confounds such as topicalization, the scrambling effect persisted. Similarly, Mack et al. showed that passive sentences [34], which involve NP-movement, triggered stronger activation in the left IFG, as well as bilateral IFG and the left temporo-occipital cortex, compared to active counterparts. The authors interpreted the left IFG activation as reflecting the processing of syntactic displacement, again consistent with the computational role of internal merge. In sum, these studies may converge on the left IFG as key neural substrates for the implementation of internal merge in natural language.

An important consideration is that although existing evidence points to the left IFG as supporting the neural basis of internal merge, it is crucial to recognize that sentence types involving syntactic movement often entail semantic changes as well. For example, *wh*-movement contributes to interrogative force, while topicalization shifts a constituent to the left periphery to mark it as a topic—both operations associated with the CP layer. These constructions are not purely syntactic but carry discourse-pragmatic or interpretive functions that may confound attempts to isolate movement-related activation. While semantic interpretation typically involves left posterior temporal regions, it also engages the left frontal cortex, especially the IFG. This overlap raises the possibility that observed IFG activity reflects a confluence of syntactic computation and semantic integration. Therefore, future efforts to isolate the neural correlates of internal merge must carefully control for semantic factors—ideally by using syntactic contrasts that hold semantic content constant—in order to determine the specific contribution of syntactic movement. Carefully designed paradigms, possibly incorporating artificial grammar learning or minimalist pairwise contrasts, will be essential to teasing apart these intertwined processes and clarifying the precise role of internal merge in our brain. Further, although the left IFG may be the primary candidate region responsible for internal merge, its subregions—such as pars opercularis (BA 44), pars triangularis (BA 55), and pars orbitalis (BA 47)—are likely to support distinct and functionally specialized aspects of linguitistic computation [35]. This implies that internal merge may not be uniformly distributed across the IFG, but rather localized to specific subcomponents depending on the syntactic operation involved. Consequently, future research will need to investigate the left IFG with greater anatomical and functional precision, employing high-resolution neuroimaging and fine-grained task designs to disentangle these subregional contributions.

In sum, merge—the core syntactic operation of the FLN—has garnered growing neuroscientific support as a biologically grounded mechanism. External merge, which combines discrete syntactic objects, is consistently associated with a fronto-temporal network, particularly the left IFG, notably BA 44, selectively supporting the hierarchical computation essential for syntactic composition. MEG findings further corroborate this by revealing frequency-specific cortical tracking of linguistic hierarchies, consistent with merge-based structure building. Although these findings support the neural specificity of external merge, its status as a uniquely human capacity remains contested, as some recursive abilities have also been observed in non-human primates and songbirds, albeit without comparable neural evidence. In contrast, internal merge—responsible for syntactic movement—has received relatively less attention. Evidence from constructions involving displacement (e.g., *wh*-movement, topicalization, passivization, and scrambling) indicates consistent activation in the left IFG. These findings suggest a partially overlapping but functionally differentiated neural basis for internal merge. Importantly, many of these constructions also entail semantic changes, making it essential to control for such confounds in future work.

4 CONCLUSION

This study has sought to bridge the theoretical framework of biolinguistics with empirical neurobiological evidence, systematically evaluating the neural foundations of the FLB and the FLN. Through a critical synthesis of existing neural data, we have demonstrated that the modular architecture of the FLB—encompassing phonological-phonetic, syntactic, semantic, and pragmatic modules—is instantiated in distinct yet interactively coordinated neural circuits. Neuroimaging evidence, particularly from language comprehension studies, reveals a dynamic interplay among these modules, with parallel processing reflecting the flexible yet biologically constrained nature of the human language system. To fully substantiate the integrative design of the FLB, future research must extend beyond comprehension to encompass language production, leveraging lesion studies, behavioral paradigms, and neuroimaging to map the neural correlates of generative processes.

Regarding the FLN, our analysis underscores the neural grounding of merge, the core syntactic operation, centered on the left IFG. This region, particularly BA 44 of left IFG, emerges as a universal neural signature for external merge across languages, while phenomena involving internal merge (e.g., *wh*-movement, topicalization, passivization, and scrambling) similarly engage the left IFG. These findings affirm the biological foundations of hierarchical structure-building as a uniquely human cognitive capacity. Nevertheless, further neurobiological inquiry is warranted to disentangle the precise neural distinctions between external and internal merge. By integrating these insights, this study not only advances our understanding of the neurobiological underpinnings of language but also reinforces the interdisciplinary promise of biolinguistics in unraveling the complexities of human cognition.

Looking ahead, the continued progress of biolinguistics might depend on its ability to incorporate a broader range of interdisciplinary methodologies to rigorously test and refine its core theoretical constructs. Advances in neuroimaging, computational modeling, genetic analysis, and cross-species comparisons offer powerful tools for probing the biological substrates of language with increasing precision. By embracing these approaches, biolinguistics can move beyond abstract theories toward a more evidence-based paradigm, where theoretical insights are continually informed, constrained, and enriched by empirical data. Such integrative efforts will not only clarify the architecture of the faculty of language but also enhance the field's capacity to generate robust, falsifiable models of uniquely human linguistic competence.

COMPETING INTERESTS

The authors have no relevant financial or non-financial interests to disclose.

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