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Neuroimaging of syntax and syntactic processing

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Recent results challenge and refine the prevailing view of the way language is represented in the human brain. Syntactic knowledge and processing mechanisms that implement syntax in use are mapped onto neural tissue in experiments that harness both syntactic concepts and imaging technologies to the study of brain mechanisms in healthy and impaired populations. In the emerging picture, syntax is neurologically segregated, and its component parts are housed in several distinct cerebral loci that extend beyond the traditional ones — Broca's and Wernicke's regions in the left hemisphere. In particular, the new brain map for syntax implicates portions of the right cerebral hemisphere.

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Introduction

Language is usually thought of as a left hemispheric, peri-sylvian affair. Here, we present results that challenge this view. Our research, which aims to uncover the neurological underpinnings of the human language faculty, suggests a revision: once decomposed along lines that current theory dictates, language seems to involve brain parts that go beyond the traditional language regions.

The effort to map language in the brain has taken many forms since Broca's pioneering attempt 145 years ago. The first brain maps, mostly largely as a result of Wernicke and his students, located expressive language mechanisms in Broca's region, and receptive ones in Wernicke's. In addition, devices for reading and writing were attributed to the left temporal lobe [1•]. Since then, new experimental methods to probe behavior and its cerebral correlates have been devised, and new ways to think about language have been proposed. Although initially language was taken to be a collection of activities (such as speaking, listening, reading and writing), it was

later understood that neurological reflexes can be detected not only for linguistic activities but also for linguistic knowledge. This approach led to attempts to map syntax and semantics onto Broca's and Wernicke's regions, respectively. The original hypothesis — that the brain map for language comprises communicative activities — was then refined by making reference to linguistic levels of representation [2–4].

However, as time went by new results indicated that the linguistic refinement was insufficient. Intensified cross-linguistic research on language deficits subsequent to focal brain damage (aphasia), in addition to EEG (electroencephalography), MEG (magnetoencephalography) and fMRI (functional magnetic resonance imaging) in the intact brain, revealed inconsistencies; it was gradually realized that the areas involved in syntax processing are not all in Broca's region, nor are all of those that deal with semantics in Wernicke's. These results paved the way to a neurolinguistic approach to brain–language relationships [5–7]. The conjecture that this new research program seeks to explore is that each subpart of the linguistic system — whether it is phonology, syntax or semantics — can be neurologically decomposed into subcomponents. This idea leads to the generation of new types of experiments, which carry hope for new discoveries that would result in theoretically motivated, detailed maps of linguistic ability.

A central part of this research program is the brain map for syntax. This map, and recent results relevant to its construction, is the topic of our review. Approaches to this effort harness various theoretical considerations and experimental methods towards the construction of a precise and detailed syntax map. We describe two instantiations of this approach that are constructed largely on the basis of lesion studies and studies using EEG, MEG and fMRI.

The first approach concerns the cerebral localization of syntactic knowledge. Call it the quest for a formal syntax map (FSM), which one of us (Y Grodzinsky) has been investigating for some time now. The working hypothesis behind the FSM posits that there is a regular relationship between subcomponents of syntactic theory and brain loci. The theory of syntactic knowledge defines natural classes of operations that assign structural descriptions to sentences (i.e., syntactic rules). These complex, universal data structures (designed to accommodate cross-linguistic differences) encode what we know about our language. The theory behind the FSM maintains that distinct pieces of this knowledge base are neurologically

Glossary
Broca's aphasia: A selective language impairment subsequent to focal damage to the inferior frontal gyrus of the left cerebral hemisphere (commonly occurring after stroke). Traditionally thought to be a language production deficit, it is now also recognized as a deficit in linguistic reception, in which the patient's abilities in sentence grammar are partially impaired.
Category information: DET, determiner; N, noun; NP, noun phrase; OG, orbital gyrus; PP, prepositional phrase; S, sentence; V, verb; VP, verb phrase.
Wernicke's aphasia: Another type of selective impairment to language after focal brain damage to left peri-sylvian regions (left superior temporal sulcus and gyrus). It has long been thought that the semantic receptive skills are the primary deficit in these patients. In recent years, a growing body of evidence has suggested a selective impairment in syntax, although the precise nature of this deficit has largely remained elusive.

individuated, and localizable. That is to say, components of the human syntactic knowledge reside in distinct brain loci. As such, they can be mapped, which is what we present below.

The second approach focuses on the processes involved in the real-time analysis of language. Call it the search for a language processing map (LPM), which is the research topic for the other one of us (A Friederici). The working hypothesis of the LPM is that mechanisms dealing with different knowledge sources on-line during sentence analysis (in particular, the knowledge that is implicit from the FSM) separate neurological units. Informed by psycholinguistic theory, the LPM posits a view complementary to that of FSM: it suggests that subcomponents of the language processing system are neurologically distinguishable and localizable.

Below, we review the current state of affairs in each of these two domains.

A sketch of a formal syntax map
The most explicit guise of the FSM is embodied in the following statement: ''Syntacto-Topic Conjecture: [8] (a) Major syntactic operations are neurologically individuated. (b) The organization of these operations in brain space is linguistically significant''.

The first part of the syntacto-topic conjecture relates pieces of syntax to brain parts. It suggests that formal properties of the linguistic signal reside in distinct brain loci, and align with anatomically defined borders (or at a minimum, exhibit different spatial patterns). The second part imputes syntax-theoretic significance to spatial properties of the neural organization of syntax. Here, we focus on efforts to map major components of syntactic knowledge onto brain loci, namely the first part of the conjecture.

The search for a syntax brain map presupposes a clear conception of the nature of syntactic representation,

forcing a combined neurolinguistic approach. Linguistically, this search has centered around major, universally accepted components of syntax; neurologically, various imaging and lesion-based approaches have been used. Below, we describe an emerging brain map of basic building blocks of the syntactic knowledge that humans possess, which is based on the results of recent neurolinguistic tests of several classes of syntactic operations.

To date, two groups of syntactic entities have been studied: the first consists of rules and relationships that determine basic sentence structure, whereas the second regulates dependency relationships within a sentence (Table 1).

Basic syntactic structure is determined by the lexical properties of words, and by the rules that combine words into phrases and eventually sentences. The mental lexicon contains words, listed as sound-meaning pairs, but also annotated for certain properties relevant to syntax (*LEX*). The *MERGE* component contains rules that analyze sentences into hierarchical, tree-like structures or graphs (see Table 1), the units of which are phrases and lexical categories, and the *LEX* properties of words in the sentence are taken into account. The structure created by *MERGE* and the lexical information encoded by the format dictated by *LEX* make semantic interpretation of basic sentences possible. Thus, *MERGE* would combine a verb such as 'run' or 'sleep' with a subject to create a coherent and well-formed sentence (e.g. John ran, Mary slept). The fact that these verbs are intransitive and take no object would exclude a *MERGE* operation resulting in ungrammatical strings such as 'John ran Mary', or 'Mary slept a bed'. Congruence between these two knowledge sources works to ensure the well-formedness of sentences at a basic, 'canonical' level.

Natural language consists of syntactically more complex phenomena. Elements in a sentence are not always found in their canonical positions. As the bottom part of Table 1 indicates, certain elements might be displaced (*MOVE*), or referentially dependent (*BIND*). In both instances, a dependency relationship between positions in a sentence is encoded. As Table 1 indicates, there are cross-linguistic differences.

These are basic components of syntax that are universally assumed (although their implementation might vary, depending on approach) [9]. Their knowledge of these components has been tested in health and in focal brain disease. Investigations into the receptive syntactic abilities of Broca's aphasic (see glossary) patients have long documented a remarkably selective deficit; patients' receptive abilities distinguish between types of movement operations: they are deficient in $MOVE_{XP}$, which changes the position of (mostly) noun phrases in a sentence, but not in $MOVE_V$, which changes the position of

Table 1

The building blocks of syntactic knowledge

Operation	Description	Examples
Basic relationships among words and phrases		
LEX	Lexical relations that have syntactic relevance. For example, an argument structure of a verb — the type and number of arguments that natural language predicates require.	1 argument: *He* ran/slept/died 2 arguments: *He* saw/hit/followed *Mary* 3 arguments: *He* gave/sent/mailed *Sue presents*
MERGE	A class of highly constrained structure-building operations, which analyze sentences into hierarchical structures. This example shows how syntactic *MERGE* rules build a sentence from the set of lexical categories ('numeration'). *MERGE* creates phrasal nodes (NP = noun phrase, VP = verb phrase, PP = prepositional phrase) out of merged categories (DETerminer, Noun, Verb, Preposition), which are in turn merged into a 'root', sentence node.	Numeration: {DET=*a, the*; N=*man, woman, tree*; V=*saw*; P=*near*} Result of iterated MERGE:
Dependency relations within a sentence		
MOVE$_{XP}$	A central syntactic operation on trees (created by *MERGE*). It links an audible phrase XP (=NP,VP,PP) to one or more silent, yet syntactically active, position(s) '■' in the representation of the same sentence.	Sam knows that he saw the ballet dancer on Monday $\Rightarrow$ Which dancer does Sam know that he saw ■ on Monday?
MOVE$_V$	A movement relationship that links distinct positions a verb might occupy. Only one is audible; the rest are silent ('♦').This relation is shown in English yes/no questions, and in German, in which the verb 'sah' (saw) and its participle 'gesehen' (seen) occupy different positions.	English: John is tall $\Rightarrow$ Is John ♦ tall? German: Hans hat Maria gesehen $\Rightarrow$ Hans sah Maria ♦ $\Rightarrow$ Gestern Sah Hans ♦ Maria ♦
BIND	A relationship that determines how reflexives and pronouns link to other NPs, on which they depend for reference, in the same sentence.	<u>John</u> looked at <u>himself</u> <u>Mary</u> asked John to help <u>her</u>

verbs (see Table 1) [7]. Thus, they fail to understand sentences such as '...which dancer did John touch?'; they also fail to detect violations of grammaticality that implicate *MOVE$_{XP}$*. At the same time, the patients exhibit intact abilities with sentences that contain a moved verb, and hence are governed by the *MOVE$_V$* relation. For example, they are unable to detect the ill-formedness of questions such as 'who what saw?', which are ruled out by *MOVE$_{XP}$*; at the same time, they are sensitive to *MOVE$_V$*-determined violations of grammaticality, quickly detecting the ungrammaticality of questions such as 'have they would left the city?' (compare with the well-formed counterpart 'would they have left the city?') [10–12].

Finally, the patients have unimpaired abilities with basic relations, such as those governed by *LEX* [13,14] and *MERGE* [6,7], and with dependency relations governed by *BIND* [15,16••].

It should be noted that intriguing variability in the abilities of individuals with Broca's aphasia has been documented, both between individuals [17], and across

Table 2

The neurological distribution of formal syntactic operations

Syntactic operation	Impaired in Broca's aphasia?	Main loci of activation in fMRI
LEX	No	?
MERGE	No	?
$MOVE_{XP}$	Yes	L-IFG, R-STS, L-STS
$MOVE_V$	No	L-SFG, L-MFG
BIND	No	R-MFG, L-SFG, L-OG

patients who speak different languages [18,19]. However, recent large-scale quantitative analyses (n > 100) have demonstrated the robustness of the highly-selective $MOVE_{XP}$ deficit in receptive language that is associated with this syndrome [20••,21].

These results carry implications for clinical methods of rehabilitation [22•], and for the way syntax is represented in the healthy brain. Indeed, exemplars drawn from most syntactic classes have been tested in the intact brain using fMRI and positron emission tomography (PET). Below some current research highlights are discussed (Table 2).

$MOVE_{XP}$
The use of this rule system, which as we have seen is impaired in Broca's aphasia, activates Broca's region in health. This has been shown repeatedly with PET and fMRI during cross-linguistic experiments in which subjects are asked to judge the grammaticality of sentences, or to decide whether the sentences they hear or read are semantically and pragmatically plausible. These experiments have been conducted in English [23–25], German [26,27] and Hebrew [28,29••]. Not all of these studies contain truly minimal $\pm MOVE_{XP}$ contrasts (e.g., object-relative clauses versus embedded complement clauses [28]); some contain potential confounds that have arisen from complexity and discourse factors. Still, results consistently implicate the left inferior frontal gyrus (IFG), in keeping with the data from Broca's aphasia. Other brain regions are also involved; $MOVE_{XP}$ has activated the superior temporal gyrus (STG) bilaterally in several studies, although independent evidence (see the LPM section) seems to suggest that these effects might not be purely syntactic, but are instead due to processes that implement syntax in use.

$MOVE_V$
The use of this rule system, which is intact in Broca's aphasia, also keeps the left IFG silent, although it is a movement relation. It does, however, activate other left frontal structures. For example, an fMRI experiment contrasting $\pm MOVE_V$ in Dutch revealed that $+MOVE_V$ activated the left superior and middle frontal gyri (SFG, MFG), despite a frequency-of-occurrence bias in the

opposite direction ($f [+MOVE_V] = 2x f[−MOVE_V]$) [30]. Thus, the effect seems purely structural, and is consistent with the aphasia results. Neurological dissociation between different types of movement hint at the feasibility of a detailed syntax brain map.

BIND
BIND modulates the MFG of the right hemisphere, the MTG of the left hemisphere and the left orbital gyrus (OG) [25]. A direct comparison shows that the OG is anterior to, and not overlapping with, the MOVE activated region, in keeping with the intact BIND function in Broca's aphasia.

Thus, a bi-hemispheric, lesion- and fMRI-based map of syntactic ability is emerging, as summarized in Table 2. More studies that will be brought to bear on the syntacto–topic conjecture are underway, with the hope of making further theoretically relevant discoveries regarding cerebral loci for components of syntax.

Language processing map
The aim of the LPM is to map psycholinguistically defined processing components onto brain space (as measured by PET and fMRI) and time (as revealed by EEG and MEG). Here, we focus on syntactic processes, modeled to be separable from phonology and semantics [31,32•,33]. This model assumes three processing phases: an initial phase, during which local phrase structure on the basis of lexical category information is built, a second phase, during which dependency relationships (syntactic and thematic) between constituents are established, and a third phase, during which the final integration of all information takes place.

Phase 1: computing local phrase structures
During phase 1, the processing systems first identify word category information (determiner [DET], noun [N], verb [V] etc.; see glossary) upon which a local phrase structure is built. For example, when perceiving a determiner (DET: the), the system starts to build a noun phrase (NP), which can be completed by a noun (N: man), resulting in a noun phrase [[the][man]].

Results from recent fMRI studies suggest that the frontal operculum, that is an area in the left IFG adjacent to the inferior portion of Broca's area, but located more medially, is involved in the computation of phrase structures [34,35••]. Although phrase structure building is considered to be part of MERGE (compare Table 1, basic relations), the available data suggest an involvement of the frontal operculum in structure building up to the phrase level (noun phrases [NPs], verb phrases [VPs], prepositional phrases [PPs]).

To date, an increase in activation in the frontal operculum has been reported in a few syntax fMRI studies for an

unpredicted word given the grammar in use [34,35••,36]. Others, however, also reported activation in response to unexpected, but rule-based, word order in the left IFG outside Broca's area, namely in the ventral premotor cortex which is in close vicinity to the frontal operculum [29••,37]. It has yet to be determined whether the frontal operculum and the ventral premotor cortex are functionally distinct areas.

A second area that is active when processing local phrase structure violations [34,38] is the anterior STG. This area is also activated when processing sentences requiring syntactic processes, as compared with processing random word lists [39–41]. Therefore, the anterior STG appears to be recruited for on-line local structure building during normal sentence processing or, in the case of local violations, for fast identification of a mismatch between the input and the expected local structure.

The view that the anterior STG together with inferior frontal structures is involved in local phrase structure building is supported by a MEG study revealing two dipoles for the activation during the phase of phrase structure building, the largest of which is located in the left anterior STG and the smaller one in the inferior frontal cortex [41].

Phase 2: computing dependency relations

The comparison of dependency relationships between different constituents in a sentence is necessary in order to figure out who is doing what to whom. The reconstruction of the interpretation of a sentence becomes increasingly difficult for non-canonical sentences (e.g., object-first sentences) in which the order of the arguments (word order) does not enable direct mapping to the underlying syntactic structure. In such cases, hierarchical syntactic structures must be constructed from sequential input. These computations are supported by Broca's areas (BA 44/45). Activation in this area is determined by the degree of deviance from canonicity of a sentence, defined as the number of operations necessary to reconstruct the basic structure of the sentence. Such deviations mostly amount to 'movement' (compare Table 1, dependency relations).

Broca's area (BA 44/45) is activated when syntactically simple and complex sentences are contrasted [23,26,28,42••]. Complexity in these studies can be defined as the number of moved elements [42••], but in the some of the studies, the variation of complexity goes hand in hand with an increase in memory demands [23], it could even be the case that syntactic working memory demands are the main factor for BA 44/45 activation [43].

Many processing perspectives [44–46] maintain that during the processing of non-canonical sentences, a displaced element must be held in syntactic memory until a possible empty position (indicated as "■" in Table 1), to which the filler is linked, is found. This processing assumption is supported by electrophysiological data; a sustained negativity over left anterior recording sites is reported for object-first sentences, starting when the displayed element is encountered and ending at the position from which it was moved [47].

Keeping the factor of working memory constant, increased activation of BA 44/45 is observed when the processing of dependency relationships in non-canonical sentences depends on movement operations [28,29••] but also when interpretation is governed by 'linearization principles' [27]. This is evident from the differential activation of this region by sentences containing different verb classes (action versus experiencer verbs).

### Phase 3: syntactic integration

Processes of syntactic integration are subserved by the left posterior STG. This area is activated when the parser encounters ungrammatical strings for which syntactic integration of the violating element into the prior structure is impossible [33], when processing syntactically complex object-first compared with subject-first sentences [48,49], and when processing scrambled compared with normal word-order sentences [27].

However, because the left and the right posterior STG have also been involved when processing the selectional restriction information of a verb [34], as a function of verb complexity [28] and of verb-based argument hierarchies [27], it appears that the posterior STG supports the integration of lexical and syntactic information.

Additional support for this view comes from event-related brain potential work. Studies using this tool have identified a late centro-parietal positivity around 600 ms after the onset of the critical word (labeled P600) in correlation with processes of syntactic integration [50]. This positivity is observable at the position of a syntactic violation [51], at the position at which it becomes obvious that the initially built syntactic structure needs revision (so-called 'garden path' sentences) [52], and at a position at which a wh-phrase (wh-phrase meaning all phrases that are headed by words that begin with wh-, e.g. 'which' and 'what', but 'how' is also considered a wh-phrase) is integrated with the verb [49]. Patients with lesions in the posterior portion of the left temporal lobe including posterior STG demonstrate a selective absence of the P600 [53], indicating an involvement of the posterior STG in processes of syntactic integration (as reflected by the P600).

Thus, separable syntactic subnetworks can be described: one consisting of Broca's area recruited for the construction of dependency relationships and the posterior STG

Figure 1
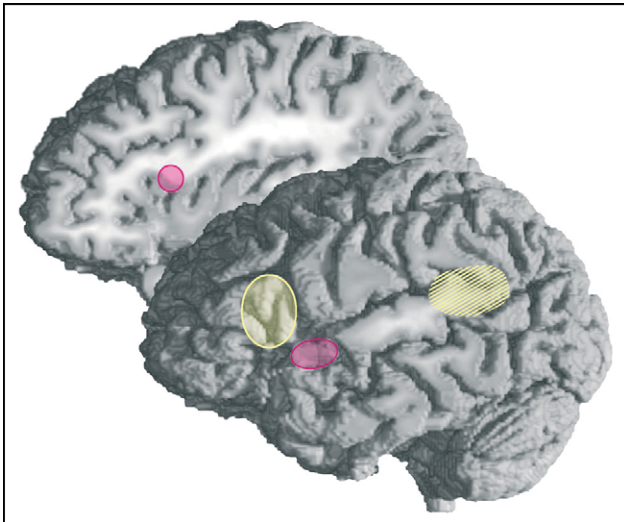
A schematic view of the main areas activated during syntactic processing. Pink areas (frontal operculum and anterior STG) are involved in the build-up of local phrase structures, the yellow area (Broca's area, BA 44/45) supports the computation of dependency relations between constituents of a sentence, and the striped area (posterior STG/STS) is involved in integration processes, possibly involving syntactic and syntax-relevant lexical information.

responsible for processes of final syntactic integration, and one consisting of the frontal operculum and the anterior STG, which appears to subserve local phrase structure building (see Figure 1). Interestingly, structural connectivity data based on diffusion tensor imaging reflect these two fronto-temporal networks as separable structural circuits. Broca's area is connected to the posterior STG through the fasciculus longitudinalis superior, whereas the frontal operculum is connected to the anterior STG through the fasciculus uncinatus [35••].

Conclusions

We have presented the results of two complementary approaches to the localization of syntax in neural tissue — FSM and LPM. Although knowledge recruited for grammatical analysis (FSM) does not necessarily reside in the same anatomical loci as the processes that implement it in use (LPM), the two approaches do converge on at least two important conclusions. First, they underscore the central role played by Broca's region in the syntactic analysis of incoming strings (Table 2, Figure 1). Second, they bring to the fore additional regions in both hemispheres that have thus far not been known as syntactic loci. As these regions are beginning to be identified with new functional roles, we can see how, as preliminary as it is, a sketch of a brain map for syntax and syntactic processing is beginning to emerge, calling for more neurolinguistic research that would make it clearer and more precise.

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