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The brain circuitry of syntactic comprehension

Edith Kaan and Tamara Y. Swaab

Syntactic comprehension is a fundamental aspect of human language, and has distinct properties from other aspects of language (e.g. semantics). In this article, we aim to identify if there is a specific locus of syntax in the brain by reviewing imaging studies on syntactic processing. We conclude that results from neuroimaging support evidence from neuropsychology that syntactic processing does not recruit one specific area. Instead a network of areas including Broca's area and anterior, middle and superior areas of the temporal lobes is involved. However, none of these areas appears to be syntax specific.

Reading or hearing a sentence such as '*The little old man knocked out the giant wrestler*' demonstrates the crucial role of syntax in normal language understanding. Identifying who did what to whom enables humans to understand the unlikely scenario that is described here. Thus, syntactic information helps us combine the words we hear or read in a particular way such that we can extract the meaning of sentences (see Box 1). Many regard syntax as a cognitive module that is separable from other more general cognitive processes such as memory and attention [1] and whose properties can be distinguished from semantic-conceptual information ('meaning') [2]. In this tradition, some theories of sentence processing propose a separate syntactic processing mechanism that is insensitive to nonsyntactic information [3]. However, alternative views exist [4,5]. Given these competing views of syntax, one can ask whether there is neurological evidence in favor of a syntactic processing module [1]; that is, is there a specific area in the brain that is specialized for syntax alone?

Evidence from brain lesions

Research on the relationship between brain and language dates back to the mid- to late-1800s when Paul Broca and Karl Wernicke linked specific lesions in the brain to specific language deficits known as aphasia. Broca identified patients with problems in

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Box 1. Syntactic processes and information

When reading or listening to sentences, we use syntactic information, among other types of information [a], to determine the meaning of a sentence ('Who did what to whom?'). Syntactic processes and information used in sentence comprehension include the following:

- **Structure building:** combining words into larger units (phrases, clauses) on the basis of word category information (e.g. *the* is a determiner, *cat* a noun) and grammar rules ('*the cat*' is a legal phrase in English whereas '*cat the*' is not);
- **Checking agreement:** for instance, in English the verb needs to agree in number and person with the subject; in German, noun phrases need to be marked for case. To illustrate the importance of these inflectional features in comprehension, a phrase such as '*the daughters of the colonel who were killed*' means something different from '*the daughters of the colonel who was killed*'.
- **Mapping thematic roles:** such as agent ('doer') and patient ('do-ee') onto certain positions in the sentence. For instance, '*John loves Mary*' means something different from '*Mary loves John*'. This mapping of roles is not always straightforward: the agent does not always come before the patient. For instance, in '*the dog was chased by the cat*', the agent ('chaser') is the cat and the patient ('chasee') is the dog.
- **Complexity:** in this article we take the view that a sentence is more complex if the order of the noun phrases that receive the thematic roles (or, simply put, word order) is non-canonical, that is, deviates from the agent-before-patient order. Sentences such as '*the dog was chased by the cat*' are more complex in this view than '*the cat chased the dog*', and clauses such as '*the reporter who the senator attacked*' are more complex than '*the senator who attacked the reporter*'. A common assumption is that the sentence processor reconstructs the original agent-before-patient order in clauses with non-canonical order by postulating an empty element in the original position of the patient. Hence, patient-before-agent sentences involve an additional syntactic operation. In addition, patient-before-agent sentences impose a larger burden on working memory, because the first noun phrase (corresponding to the eventual patient) cannot be syntactically and thematically integrated until the verb is encountered, and must be retained in working memory until that point [a]. However, for alternative views of complexity and working memory involvement, see Ref. [b].

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speech production, linking this to damage in the left ventral lateral frontal cortex. Wernicke identified patients with comprehension problems associated with damage in the left posterior temporal cortex. A century later, studies in these types of patients provided evidence in favor of the idea that there is a specialized brain system for syntax. Broca's aphasics typically produce halted speech, omitting inflections and words with syntactic functions such as '*the*', '*of*', or '*is*'. In addition, they are impaired when comprehending so-called reversible passives such as '*The dog was chased by the cat*', which can only be interpreted correctly by relying on syntactic information [6]. Broca's patients are therefore said to have syntactic deficits. Wernicke's aphasics typically show a complementary pattern of deficits: they produce fluent and grammatical, although contentless, speech. In addition, it has been shown that they make use of syntactic information in comprehension [7]. This double dissociation has been taken as evidence for the idea that brain damage can affect syntax selectively, indicating that certain brain regions are specialized for syntactic processing. But which brain regions are specific for syntactic processing? Because Broca's aphasia has been typically associated with damage involving Broca's area [left inferior frontal cortex, Brodmann areas (BA) 44/45; see Fig. 1], an area that is generally spared in Wernicke's aphasia, it was thought that Broca's area was the seat of syntax.

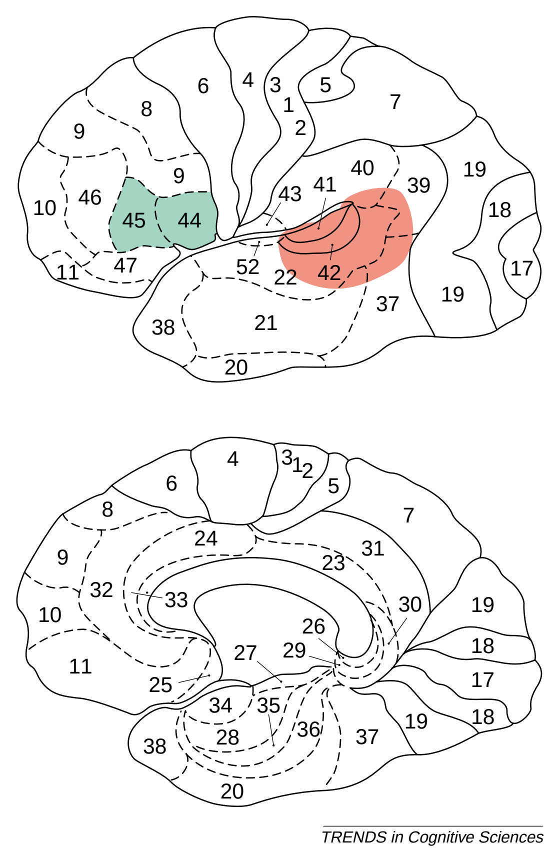

Fig. 1. Brodmann's areas. Schematic overview of the left lateral and medial surface of the brain, with Brodmann's areas indicated. Broca's area is shown in green, Wernicke's area in red. Reprinted with permission from Ref. [55].

However, recent insights from aphasia research lead to different conclusions. First, lesions in Broca's area are neither sufficient nor necessary to induce syntactic deficits. Dronkers *et al.* [8] reported that patients who scored low on morphosyntactic tests did not have a common lesion in Broca's area but rather in the left anterior temporal lobe (anterior BA 22). This area was spared for patients who did not show severe morphosyntactic deficits. Moreover, some patients with damage in Broca's area did not show severe morphosyntactic deficits [8]. Second, Broca's aphasics do not completely lack knowledge of syntax. They are able to judge correctly the grammaticality of certain sentence structures [9]. However, complex sentence structures that involve non-canonical word order such as '*Which dog did the*

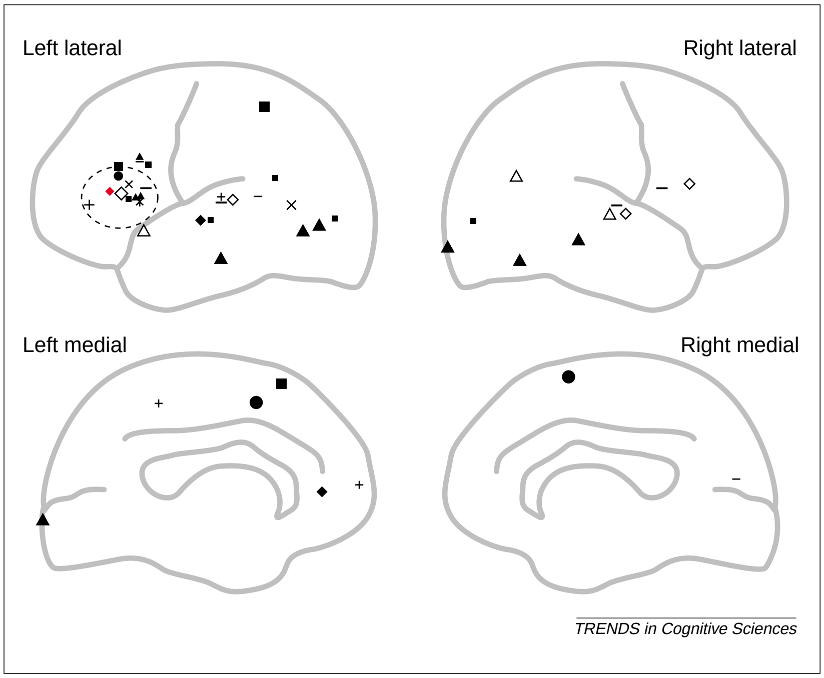

Fig. 2. Complex versus simple sentences. Centers of activation for reading or listening to complex versus simple sentences (black symbols); for making a same/different judgment for syntactically different sentences (red symbol); and for processing sentences with long versus short dependencies (white symbols). In this and following figures, the dotted circle includes activations in Broca's area. Centers of activation are projected on the left lateral, left medial, right lateral, and right medial surface of the brain, using Talairach coordinates [56]. Centers of activation are considered lateral if the absolute value of the *x*-coordinate is larger than 12 mm, and medial for *x* equal to or smaller than 12 mm. When the *x*-value is 0 mm, the center of activation is projected on the left medial surface. When no coordinates are provided in the report, the coordinates are estimated on the basis of the information available ('est.'). Studies using a region of interest analysis are indicated with 'roi'. Key to symbols: ● [57] exp. 1; ■ [58]; + [59]; ◆, ◇ [22]; × [19]; * [24]; ▲, △ [21]; - [53] (roi); – [42] (roi, est.); ▪ [20] (roi, est.); ▴ [60] (est.); ◆ [26]. Both complexity and length manipulations systematically lead to increased activation in the left inferior frontal cortex (BA 44,45), suggesting that this area is involved in increased memory or processing load during sentence processing.

cat chase?' often do provide a challenge (see Box 1). Although controversial [10], these observations suggest that if Broca's aphasics have a syntactic deficit, it is restricted to this type of complex sentence structure [11]. Third, Broca's aphasics also exhibit semantic deficits [12], which suggests that the damaged areas are not unique for syntax. Finally, aphasia need not be a knowledge deficit but can also be interpreted as a processing deficit [13,14]. In this view, the problems of Broca's aphasics with syntax are a result of a temporal processing deficit in activating or integrating information, or a shortage of resources needed for these processes. The brain areas that are damaged in Broca's aphasics therefore need not be the areas where syntactic knowledge is stored.

The view that Broca's area is not the seat of syntax is further supported by recent studies that have used functional imaging techniques with healthy volunteers to investigate the neural substrates of syntax. In the following, we review PET and fMRI studies [15] aimed at isolating areas involved in syntactic processing during sentence comprehension. For sentence production studies see Refs [16,17].

Neuroimaging studies of syntactic processing

To date, almost all neuroimaging studies of syntax have relied on the assumption of 'pure insertion'. That is, researchers have tried to identify the optimal contrast between a set of two or more conditions that are designed to differ only with respect to the process(es) of interest. There are some inherent problems with this logic [18] but nevertheless such research has led to some interesting results that can point to the brain areas involved in syntactic processing. The brain imaging studies that are reviewed in this article have tried to isolate syntactic aspects of language using four types of contrast: (1) by comparing syntactically complex sentences to simple sentences; (2) by comparing sentences to lists of unrelated words; (3) by comparing sentences containing pseudowords (e.g. 'Jabberwocky') or senseless sentences ('syntactic prose') to rest conditions or normal sentences; and (4) by comparing sentences with a syntactic violation versus sentences without. It is important to bear in mind that often not all active areas in the brain can be detected. First, fMRI is limited by artifacts caused by air in the sinuses and ear cavities, which can make it difficult to detect activation, especially in the anterior and medial temporal areas and orbitofrontal cortex. Second, some studies restrict their analyses to predefined regions of interest (ROIs) to test a priori predictions. This precludes the detection of activity in other areas of the brain that might be involved in the process of interest.

Complex versus simple sentences

The first approach to isolate syntactic processing is to compare complex with simple sentences (Box 1). A comparison that has often been used is that between (complex) object relatives, such as '*The reporter who the senator attacked admitted the error*', and (simple) subject relatives, such as '*The reporter who attacked the senator admitted the error*'. The assumption is that the complex conditions involve additional syntactic operations (reconstruction of the canonical word order), hence the areas that are activated to a higher extent in the complex compared with the simple condition are probably the sites where syntactic processing takes place. Figure 2 shows the results for the complex versus simple contrast (black symbols) and for a study in which volunteers were asked to say whether two syntactically different sentences had the same meaning, a task that can be assumed to involve a reconstruction of the canonical word order (red symbol). In most studies, enhanced activity is found in Broca's area (left BA 44/45), sometimes extending to BA 47, 6 and 9. Additional activation is occasionally found in the left or bilateral superior and middle temporal gyri (BA 21,22), left angular/supramarginal gyri (BA 39,40), and cingulate gyrus (BA 23,24,31,32).

Although left BA 44 and 45 are consistently activated for complex versus easy sentences, this does

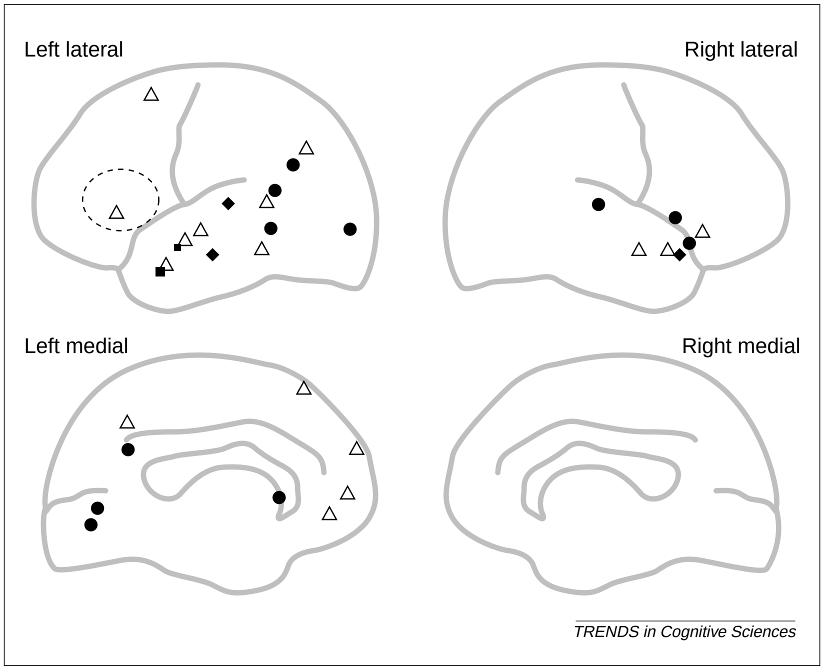

Fig. 3. Sentences versus words. Activation for reading or listening to sentences versus word lists. ■ [19] passive reading; ▪ [27] passive reading; ● [36] acceptability judgment; ◆ [34] Jabberwocky and normal speech, structure judgment task (roi, est. – see Fig. 2 legend); △ [25] sentence plausibility task versus lexical decision in word lists. Compared with word lists, processing sentences does not lead to an increase in the left inferior frontal cortex, except in one study that used different tasks for the two conditions [25]. In general, processing sentences versus words leads to an increased activation in the anterior, superior, and middle areas of the temporal lobe (BA 38,21,22).

not mean that syntactic processing resides in Broca's area. As mentioned in Box 1, complex conditions differ from simple not only in terms of syntactic operations (reconstructing the canonical word order) but also in terms of memory load (keeping nonintegrated material active while processing other words). Support for the view that Broca's area is implicated in increasing memory or processing load rather than in reconstructing the canonical word order is the finding that Broca's area becomes increasingly active when sentences contain ambiguous words [19], when sentences with non-canonical order contain low-frequency words [20], or when some words need to be retained in working memory before they can be syntactically and semantically integrated in the structure [21,22] (white symbols in Fig. 2), even though the word order is the same as in the comparison condition. This suggests that Broca's area is not unique for syntactic processing but is additionally activated when processing load increases because of lexical or other factors [23,24].

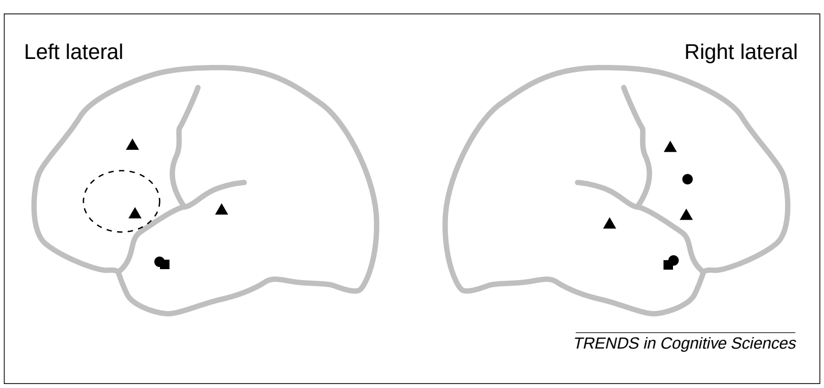

Fig. 4. Jabberwocky and syntactic prose. Activation listening to grammatical Jabberwocky/syntactic prose. ▲ [34], areas where processing Jabberwocky versus a pseudo-word list shows greater activation than processing normal speech versus a word list (roi, est. – see Fig. 2 legend); ● [28] Jabberwocky versus rest (roi, est.); ■ [28] syntactic prose versus rest (roi, est.). Processing Jabberwocky/syntactic prose activates anterior and posterior temporal areas. The activation in the inferior frontal cortex could be due to task demands (see text).

Sentences versus word lists

The contrast between complex and simple sentences is an attractive one, because it is well controlled in many respects. However, this particular feature might also mask the activation of brain areas involved in syntactic processing, because both conditions share a large number of syntactic operations. Hence, areas that are commonly involved might be canceled out in this comparison. Comparing sentences (containing a syntactic structure) with lists of unrelated words (no syntactic structure) is a contrast that does not share many syntactic operations, and might therefore reveal more of the brain areas implied in the syntactic processes mentioned in Box 1. Figure 3 shows the results for this contrast. Unlike the complex versus simple contrast, Broca's area is not significantly activated in most studies. One exception is the frontal activation found in the Bottini *et al.* study [25] (indicated in Fig. 3 by white triangles). However, this activation might be due partly to the different tasks used for the sentence and the word-list conditions in this study, and to the inclusion of implausible sentences [26,27]. Note that in most studies the sentences were fairly simple in structure. The absence of a strong activation in Broca's area therefore supports the view that this area is not necessarily involved in syntactic operations but only comes into play when the processing load increases.

An increased activation for sentences versus word lists is found in the anterior parts of the temporal lobe, including the temporal pole (BA 38), often bilaterally. This brain region has also been found to be active when sentences are compared with a rest condition [27–30] or a non-word control [30–33]. This area corresponds roughly to the area that is damaged in patients with morphosyntactic problems [8]. In addition, activation for sentences versus words is found in the superior and middle temporal gyri (BA 22 and 21).

Jabberwocky and syntactic prose

The contrast reviewed earlier is not optimal because sentences differ from word lists not only with respect to syntactic structure but also concerning semantic operations, among other things. A third approach is to reduce semantic processing by using 'Jabberwocky' or 'syntactic prose' (see Fig. 4 for results). Jabberwocky (based on the poem by Lewis Carroll) consists of grammatically correct sentences in which nouns, verbs and adjectives are replaced by pseudowords,

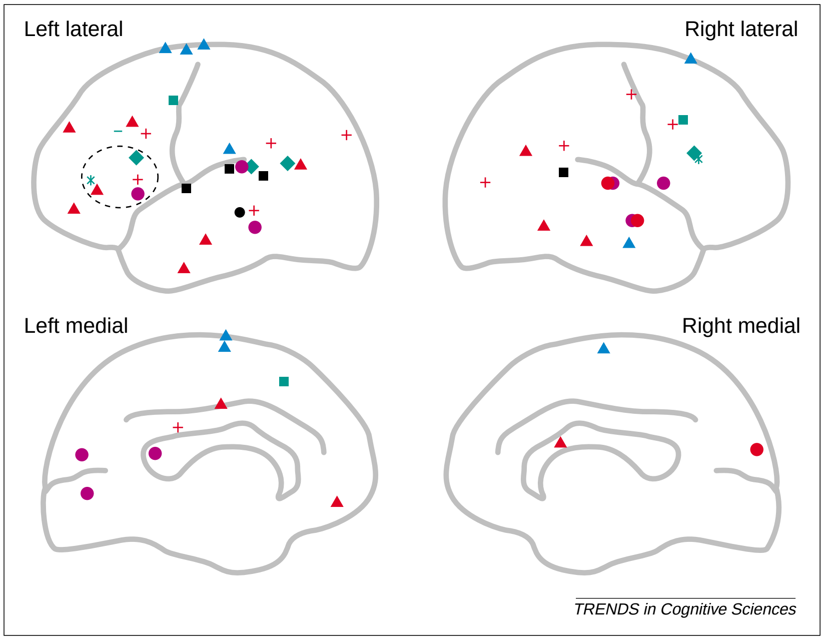

Fig. 5. Syntactic and semantic violations. Activation for reading or listening to sentences containing syntactic violations versus correct sentences (black symbols), versus sentences containing semantic violations (blue symbols), and versus other violations (green symbols). Also depicted are activations to sentences containing semantic or pragmatic violation versus correct sentences (pink symbols), and versus sentences containing syntactic violations (red symbols). Circles [36]; Squares [43] (roi – see Fig. 2 legend); Triangles [37]; Diamonds [38]; Small squares [40] (roi); Plus signs [35] exp. 1 (roi, est. – see Fig. 2 legend); Asterisks [41] using Jabberwocky; Dashes [17] using Jabberwocky in a production task. Syntactic violations activate parts of the frontal and temporal cortex. However, comparable and more widespread activation is found for semantic violations.

that is letter strings that are phonologically and orthographically legal in the language under investigation but do not have any meaning, such as '*The mumphy folofel fonged the apole trecon*' [34]. In syntactic prose, existing words are used to construct grammatically correct but nonsensical sentences, such as '*The infuriated water grabbed the justified dream*'. The areas that would be commonly activated for Jabberwocky/syntactic prose and normal sentences compared with a word list can thus be said to subserve syntax. In addition, Jabberwocky/syntactic prose might activate some of those areas more than normal prose because Jabberwocky and syntactic prose lack semantic cues and, hence, might engage the syntactic system to a greater extent, especially those processes dealing with word order and inflection (Box 1). Friederici *et al.* [34] found such an activation pattern in the posterior superior temporal sulcus (posterior BA 22,41/42) when comparing Jabberwocky with normal prose. In addition, some activation was found in the anterior superior temporal sulcus (anterior BA 38,22). This latter area was also activated in a different study that contrasted Jabberwocky and syntactic prose with a rest condition [28]. Furthermore, a medial part of Broca's area was bilaterally activated for Jabberwocky compared with normal sentences, lists of real words, and lists of pseudowords [34]. However, because there was no difference between the latter three conditions in this area, and no left frontal activation was found for either Jabberwocky or syntactic prose compared with a rest condition in the study by Mazoyer *et al.* [28], it might be that the activation of Broca's area in the Friederici *et al.* study is due to task demands rather than to syntactic processing *per se*.

Syntactic violations

A fourth approach to isolate syntactic processes is to compare sentences containing syntactic violations (e.g. '*Trees can grew*' [35]) with correct sentences and with sentences containing different kinds of violation (e.g. semantic violations such as '*Trees can eat*' [35–37] or spelling errors [38]). The assumption is that syntactic violations will additionally activate areas that are involved in syntactic processing because normal operations such as structure building and agreement checking (Box 1) are disrupted, and extra attention is drawn to these aspects of syntax. In addition, this approach is highly validated by research using event-related potentials (ERPs), in which different brain responses have been found for semantic and syntactic violations [5,39].

Results from studies using syntactic violations are shown in Fig. 5 (black, blue, and green symbols). With only one exception [38], syntactically anomalous sentences generally do not activate Broca's area compared with correct sentences or sentences containing other violations. Occasionally, more superior frontal activity (BA 6,8) is found for syntactic than for other errors [35,37,40], but an increased activation in these areas has been reported for semantic violations as well [35,37]. As one can also see in Fig. 5, semantic violations lead to a more widespread activation (pink and red symbols). However, syntactic errors activate frontal areas to a larger extent than posterior (temporal) areas, whereas no such frontal-posterior difference, or a greater involvement of posterior areas, is seen for semantic or spelling errors [35,37,38].

One problem with these studies is that syntactic violations often also have consequences for the semantic interpretation of the sentence. The similarity in activation between semantic and syntactic errors is therefore not surprising. One way to avoid this problem is to use Jabberwocky. In one study volunteers were asked to detect syntactic versus other (phonotactic, orthographic) violations in Jabberwocky [41]. In this study, activity was seen in right BA 44 and syntactic errors in left BA 45. However, in another study in which people were asked to repeat or correct ungrammatical Jabberwocky sentences [17], only the left middle frontal gyrus (BA 9) was activated. The right BA 44 was active for all conditions involving (syntactic or nonsyntactic) error detection, suggesting that this area is not uniquely involved in syntactic processing.

Where is syntax in the brain?

Is there a specific area in the brain that is specialized for syntax alone? The neuroimaging

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Questions for future research

- How can we further specify the relationship between specific syntactic operations and certain areas of the brain and the connections between those brain areas?
- What is the connection of syntax with non-linguistic processes (e.g. general working memory)?
- Are there individual differences in the brain circuitry of syntax?

results described earlier correspond with recent insights from aphasia suggesting that Broca's area (BA 44/45) is not necessarily involved in syntactic processing. Broca's area is only systematically activated when processing demands increase due to working memory demands or task requirements. Broca's area is also not the only area involved in syntax: other areas include the anterior temporal lobe (BA 38, and anterior parts of BA 21 and 22) and the middle and posterior parts of the superior and middle temporal gyri (BA 22,21). Interestingly, activations are not restricted to the left hemisphere [28,37,41–43].

Are these areas uniquely activated for syntactic processing? The answer is no. Each of these areas has been shown to be activated for tasks involving lists of syntactically unconnected words and, in some cases even for tasks using non-linguistic materials. Broca's area (BA 44/45) is involved in a wide variety of tasks using lists of words or syllables, including semantic tasks [44], phonological tasks [44], and memory tasks [23], and is also active during music perception [45]. Similarly, the anterior temporal lobe has shown sensitivity to semantic priming [46], categorization [47], and recall [48] of individual words, but has also been implicated in processing multisentence stories versus unconnected sentences [49]. The middle and posterior temporal lobe has been systematically implicated in single word processing, with the upper parts being more involved in acoustic and phonological processing, and the lower lateral and medial parts in verbal and nonverbal conceptual processing [50]. However, the posterior temporal cortex has also been found to be involved in nonverbal temporal predictability [51]. The areas that were activated for syntactic manipulations are therefore not uniquely involved in syntactic aspects of language processing.

Conclusion

Syntactic processing, as investigated by the contrasts reviewed here, recruits not one brain region but multiple areas that are not each uniquely involved in syntactic tasks. This is inconsistent with a strict modular view of syntactic processing. However, it remains unclear how modularity might be instantiated in the brain. One possibility is that there is a dissociation at the level of cellular networks within these areas that cannot currently be differentiated with functional imaging techniques. Another possibility is that although the brain areas reviewed here are not uniquely involved in syntax, the interaction among the areas might be uniquely tied to the nature of the materials and the tasks employed. Taking the latter stance, we propose that the different parts of the network are recruited for different aspects of syntactic processing. The middle and superior temporal lobes might be involved in lexical processing and activating the syntactic, semantic and phonological information associated with the incoming words [20]; the anterior temporal lobe might be involved in combining the activated information or encoding the information for later use [52]; and Broca's area might be involved in storing non-integrated material when processing load increases [19,23,24]. In addition, an increase in processing load might feed back to the processing of lexical information, causing an increase in activation in the middle and posterior temporal areas [19,20,42] or even recruitment of visual working memory areas in the occipital lobe to store information [52,53]. The right hemisphere has a role in prosody [5], maintenance of multiple analyses in the case of ambiguity [14], discourse processing [54], and error detection [17].

Unraveling the exact function of the various parts and connections of the network and the relation between linguistic and non-linguistic processes will clearly remain a challenge for cognitive neuroscience in the foreseeable future.

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