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Chapter 18

Functional and structural brain asymmetries in language processing

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Abstract

The lateralization of language to the left hemisphere of the human brain constitutes one of the classic examples of asymmetry in biology. At the same time, it is also commonly understood that damage to the left hemisphere does not lead to a complete loss of all linguistic abilities. These seemingly contradictory findings indicate that neither our cognitive capacity for language nor its neural substrates are monolithic. This chapter reviews the functional and structural lateralization of the neural substrates of different aspects of language as revealed in the past decades by neuroimaging research. Most aspects of language processing indeed tend to be functionally lateralized to the left hemisphere in the adult human brain. Nevertheless, both hemispheres exhibit a certain equipotentiality with regard to some aspects of language processing, especially with regard to processing meaning and sound. In contrast, the so-called "core language network" in the left hemisphere constitutes a functional and structural asymmetry: This network (i) is crucial for a core aspect of language processing, namely syntax, which refers to the generation of hierarchically structured representations of utterances linking meaning and sound, (ii) matures in accordance with a genetically determined biologic matrix, and (iii) its emergence may have constituted a prerequisite for the evolution of the human language capacity.

INTRODUCTION

Humans are bilateria, a clade of animals whose body plans as embryos are essentially symmetric (i.e., the left and the right side of the body are largely mirror images of each other). This symmetric organization of our bodies is also reflected in a generally very high degree of symmetry in the brain, especially in sensorimotor regions. However, structural asymmetries, such as the imbalance of the left lung having fewer lobes to accommodate the heart, or functional dissymmetries, such as the preferential use of one hand over the other, emerge at different points in time during development. This emergence of asymmetries during development seems to be genetically determined (Corballis, 2020; Wan et al., 2022), though some research suggests that only the presence (or absence) of an asymmetry is genetically encoded and not its directionality (Arning et al., 2013). Importantly, asymmetries of body and brain emerge independently, as documented by patients with situs inversus totalis (i.e., a mirror-inversed organization of organs in the chest and abdomen) who nevertheless usually are right-handed (Matsumoto et al., 1997) and exhibit left-hemispheric dominance for language (Kennedy et al., 1999; Vingerhoets et al., 2018).

The insight that asymmetries in biology and human physiology are not limited to the abovementioned structural asymmetry of the left lung or the functional asymmetry of hand preference, but also extend to the human brain and cognitive functions such as language, dates back to the 19th century. The French physician Marc Dax was the first to link lesions to the left hemisphere of the adult human brain to both an impaired command of language and a disturbance of speech (Dax, 1863, 1865). A few decades later, in a usually much more widely known paper, fellow Frenchman and physician Paul Broca first claimed that lesions specifically to the third convolution of the left frontal cortex cause what he called aphemia, a permanent apraxia of speech (Broca, 1861). Yet, reexaminations of the conserved brains of some of Broca's patients using neuroimaging methods have since shown that their lesions actually extended far into neighboring regions of what is now called Broca's area, as well as into the white matter (Dronkers et al., 2007).

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In this chapter, we take Dax' and Broca's observations about the lateralization of language and speech as well as early work in neuropsychology, as a starting point for a review of the functional and structural lateralization of the neural substrates of language as revealed by the past decades of research using a variety of neuroimaging methods. Our focus will be on studies using (functional) magnetic resonance imaging ([f]MRI) but we include findings using other methods wherever relevant. We start by briefly considering the language–brain relationship as well as brain asymmetries in general. Next, we discuss the functional and structural properties of the language network in the left hemisphere as well as other regions and networks in both hemispheres that are frequently recruited in tandem with the language network—always in the context of lateralization. This description of language-related structures in the adult human brain is complemented by discussions of our current understanding of the development of the so-called "core language network" in the left hemisphere, which is crucial for hierarchical syntactic processing. Lastly, note that this review is primarily based on studies of spoken and written language processing (see Trettenbrein et al., 2025, this volume, for a review focusing on sign language).

What is "language"?

Modern linguistics distinguishes between individual *languages* as commonly understood, such as English, Swahili, or Japanese Sign Language; and *language* as a neurally implemented cognitive capacity that enables humans to produce and comprehend an, in principle, infinite amount of different hierarchically structured expressions (Chomsky, 1965, 1986, 1995; Everaert et al., 2015; Friederici et al., 2017). On this view, the language system uses individual lexical items (i.e., roughly "words"; but see Krauska and Lau, 2023 for a discussion of this notion) to generate structured representations of utterances, which are mapped to the sensorimotor system during production and perception and to the conceptual–intentional system for thought. *Language* in this technical sense then constitutes a structured mapping from meaning (i.e., semantics) to sound (phonetics/phonology) and vice versa; and the core functionality of the human language system is to generate representations that enable this mapping (Chomsky, 2011). Notice, however, that the mapping to the sensorimotor system is not fixed but develops during language acquisition. This explains why humans can readily acquire *languages* that differ with regard to their phonology, lexicon, grammar, and even in their modality, as in the case of sign languages (Klima et al., 1979; Emmorey, 2015; Trettenbrein et al., 2021).

A peculiarity of the human language system, to date not observed in other animals, appears to be that the representations it generates are structured hierarchically (Berwick et al., 2013; Everaert et al., 2015; Friederici et al., 2017). For example, the English sentence in Fig. 18.1 can be produced and perceived in different modalities (e.g., speech or writing), yet at the representational level, different signals rely on the same abstract hierarchically structed representation. Notice, however, that unlike speech or sign, the different writing systems for spoken languages constitute a relatively recent cultural invention (pictographic and ideographic systems emerged about 6000, alphabetic systems about 3000 years ago) and, unlike natural language acquisition, require explicit instruction (Friederici, 2017). This makes it unlikely that the human brain has adapted to reading and writing in the same way as it has for language. Instead, already existing neural circuitry appears to have been exapted for processing written language (Dehaene et al., 2005; Dehaene and Cohen, 2007). In this chapter, we equally consider studies carried out using spoken and written stimuli, as they have been shown to differentially recruit (primary) sensory cortex but not association cortex (Jobard et al., 2007; Vigneau et al., 2011; Walenski et al., 2019; Uddén et al., 2022).

Evidence for the hypothesis that representations of utterances are indeed structured hierarchically and do not simply constitute a flat concatenation of lexical items into a string can be observed when considering that certain elements of an utterance, such as "an apple," behave as functional units (i.e., constituents), whereas others does not. That is, in a more complex version of our example sentence such as (2) the unit "an apple" can be focused (i.e., moved to the more prominent position at the beginning of the sentence to express emphasis) in a so-called cleft construction, such as (3), whereas "apple in" cannot, as shown in (4):

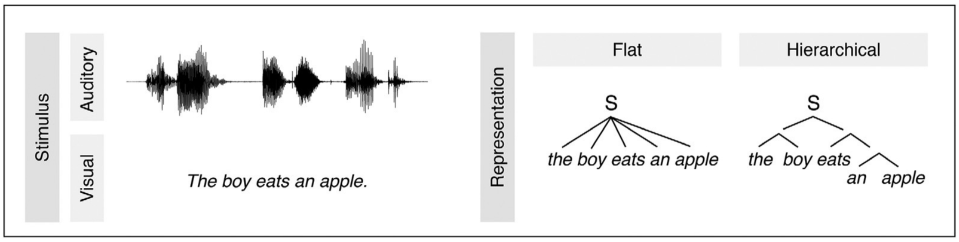

Fig. 18.1. Common linguistic signals and possible syntactic representations. The left panel shows two examples of linguistic signals frequently used as stimuli in experimental studies on language processing, a spectrogram of the recorded speech signal as well as the written version of the sentence *The boy eats an apple*. The right panel illustrates two possible ways of how the syntactic structure of either of these stimuli may be represented in linguistic analysis: Either as a flat structure in which all elements in the tree diagram are connected directly to the root, or as a hierarchical structure where elements form constituents which can be embedded in each other. Evidence from both linguistics and cognitive neuroscience strongly suggests that human brains automatically recover the hierarchical structure from linguistic signals, despite the fact that this structure is not contained in the strictly sequential signal in speech or writing. Illustration is loosely based on materials from Zaccarella and Trettenbrein (2021) and is subject to a Creative Commons (CC-BY 4.0) license.

(1) *The boy eats an apple.*
(2) *The boy eats an apple in the park.*
(3) *It is an apple that the boy eats __ in the park.*
(4) **It is apple in that the boy eats an __ the park.*

This indicates that "an apple" behaves as a functional unit in the examples above, whereas "apple in" does not. See Zaccarella and Trettenbrein (2021) for a more detailed discussion of hierarchy in language and its relevance to research in cognitive neuroscience.

The emerging picture in the cognitive sciences has been that the cognitive machinery that enables the generation of hierarchical syntactic structures linking meaning to a phonologic form is rooted in a universal computational mechanism that is biologically determined, implemented neurally, and specific to our species (Lenneberg, 1969; Hauser et al., 2002; Berwick et al., 2013; Friederici et al., 2017). Accordingly, the cognitive specifics of the language system are understood to be determined by a "biologic matrix" (Lenneberg, 1967) that enables and, at the same time, constrains the development of the language system from infancy into adulthood (Lenneberg, 1964, 1967, 1969; Crain et al., 2016; Yang et al., 2017). How such formal descriptions of the language system and its development relate to neurobiology remains, to an extent, an open question as there is no one-to-one mapping between the foundational elements of linguistic theory (e.g., phonemes, lexical items, etc.) and those of neuroscience (e.g., cell assemblies, brain regions, etc.; Poeppel and Embick, 2013; Embick and Poeppel, 2015). Consequently, it is important to keep in mind that the vast majority of studies in the cognitive neuroscience of language are correlational in nature and that their interpretation depends greatly on the operationalization of linguistic constructs in a particular experiment (van der Burght et al., 2023).

Asymmetries in the brain

Upon first look, the human brain may appear to be a rather symmetrically organized organ (Kandel and Hudspeth, 2013), yet asymmetries may manifest themselves in two major ways (Hervé et al., 2013): (i) An asymmetry is structural in nature when a certain part of the brain [e.g., a lobe, region, Brodmann area (BA), etc.] is more pronounced in one hemisphere than in the other with regard to its volume, size, surface, neuron density, predominant neurotransmitter, or a similar measure. (ii) An asymmetry is functional in nature when the activation observed with a method that indexes neural activity in a certain part of the brain [e.g., the blood oxygen level-dependent (BOLD) in functional magnetic resonance imaging (fMRI)] is more pronounced in one hemisphere than in the other. Intuitively, one may assume that structural and functional asymmetries are linked in a straightforward sense so that, for example, a bigger volume of one region implies also more activation in this region. However, there is no a priori reason for this assumption, and it is likely that structure–function correlations in the context of asymmetry are substantially influenced by the chosen task, measurement, and method. Indeed, structure–function correlations in speech- and language-related asymmetries seem ubiquitous (Toga and Thompson, 2003; Hervé et al., 2013; Bradshaw et al., 2017), but have not always been observed (Keller et al., 2011).

As already alluded to above, the neural substrates of speech and language have a long history of inspiring theories of hemispheric specialization and asymmetry which, to an extent, can be confirmed by contemporary large-scale meta-analyses of neuroimaging studies (Fig. 18.2) based on data from the BrainMap database (Fox and Lancaster, 2002; Laird et al., 2011). Both, speech production and language comprehension, are significantly left-lateralized and recruit regions in superior temporal cortex bilaterally, but differ in their involvement of frontal regions: Speech production recruits bilateral pre-motor and especially motor cortices, whereas spoken and written language comprehension always shows strong and lateralized recruitment of the entire left inferior frontal gyrus (including Broca's area), extending dorsally also into premotor regions. Notice, however, that these meta-analyses do not necessarily consider that there are actually two dichotomies involved here: (i) the difference between speech production and comprehension and (ii) the difference between speech and language (Friederici et al., 2017). The former refers to the production and perception of auditory signals, which form only one way in which language can be externalized (another possibility being the visuo-gestural modality of sign language; Trettenbrein et al., 2021). The latter refers to the processing of the abstract information reconstructed from and, in part, even imposed onto different linguistic signals with regard to, for example, their phonologic, semantic, and syntactic content.

Beyond the expected difference between production and comprehension, different subcomponents of the language system also recruit available neural resources differently during language processing, depending on the task (Bradshaw et al., 2017) and, even more importantly, the nature of the stimulus (i.e., the type of linguistic information being processed). This is evidenced by additional large-scale meta-analyses of studies that focused on the neural resources underlying phonologic, semantic, and syntactic processing in language also based on data from BrainMap (Fig. 18.2, central panels). Across hundreds of fMRI studies with several thousand participants, the general stark and significant left-lateralization of language processing is also confirmed for processing phonology, semantics, and syntax, essentially corroborating older meta-analytical work on lateralization of subcomponents of language (Vigneau et al., 2011). Among the three analyzed subcomponents, phonologic processing is the least left-lateralized. In contrast, syntactic processing (i.e., the neural substrates of the cognitive machinery that enables the generation of hierarchical syntactic representations linking sound to meaning) is almost completely left-lateralized and recruits large portions of the inferior frontal gyrus (including Broca's area) and the posterior temporal cortex. Notice, however, that this differentiation into phonology, semantics, and syntax constitutes a widely used classification highlighting the processing of these different types of linguistic information yet, at the same time, also disregards others (e.g., prosody, morphology, pragmatics, etc.; Everaert et al., 2015; Friederici, 2002, 2017; Hagoort, 2017).

From the meta-analyses of different linguistic domains summarized in Fig. 18.2 we can conclude that there generally is a clear

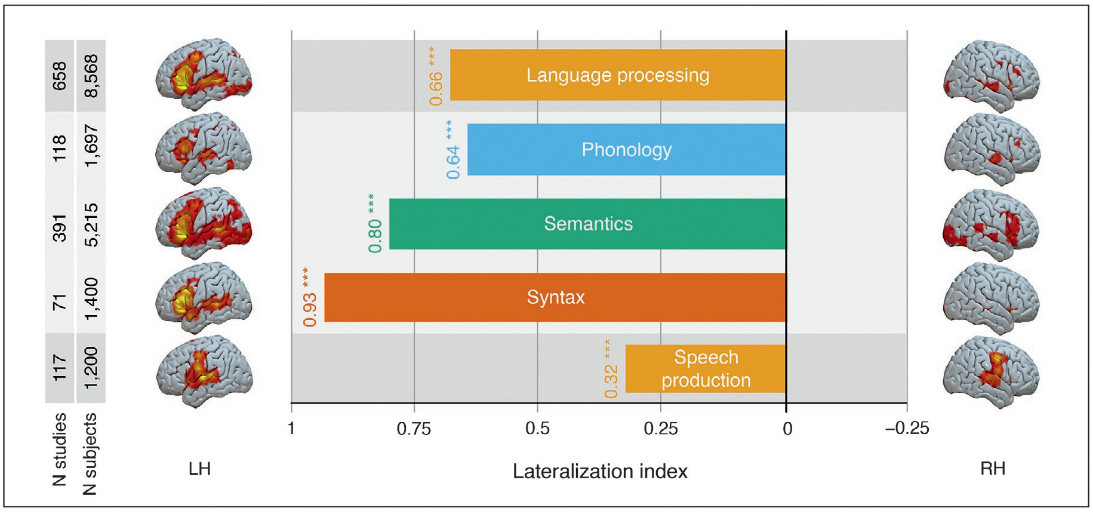

Fig. 18.2. Lateralization in meta-analyses of language processing and speech production. Five different meta-analyses of different aspects of language processing and speech production based on data from the BrainMap database (Fox and Lancaster, 2002; Laird et al., 2011) analyzed using Activation Likelihood Estimation (Eickhoff et al., 2009, 2012, 2017; Turkeltaub et al., 2012) and a weighted lateralization index (Matsuo et al., 2012). Each row contains the following data for one of the different meta-analyses: The number (N) of studies included in the analysis, the total number of study participants in the input data set, an illustration of the convergence across studies for the left hemisphere (LH), a plot of the lateralization index across hemispheres (ranging from 1 indicating complete left-lateralization to -1 indicating complete right-lateralization; significant differences from the mean was performed using permutation tests described in Trettenbrein et al. (2021) and are indicated using common significance levels: * for $P<0.05$, ** for $P<0.01$, and *** for $P<0.001$), and an illustration of the convergence across studies in the right hemisphere (RH). A short description of the data displayed in the five rows from top to bottom: The top row (color-coded in orange) displays information for a general meta-analysis of "language processing," that is all studies in the BrainMap database tagged as "Cognition.Language." The second to fourth row contain information for three different subcomponents of the language systems as identified in the taxonomy of the BrainMap database: Meta-analyses of phonologic ("Cognition.Language.Phonology"; color-coded in blue), semantic ("Cognition.Language.Semantics"; color-coded in green), and syntactic processing ("Cognition.Language.Syntax"; color-coded in brown). The last row (also color-coded in orange) contains another general meta-analysis of speech production including all studies tagged as "Action.Execution.Speech" in the BrainMap database. (The complete details as to how these data were retrieved and how the different analyses were performed are available as online supplementary material to this chapter via Figshare: https://10.6084/m9.figshare.21836079.) Illustration is subject to a Creative Commons (CC-BY 4.0) license.

functional leftward lateralization for language processing in the adult brain, with some involvement of the right hemisphere for semantics and phonology (i.e., meaning and sound) and only marginal involvement for syntax (i.e., grammatical structure). Such meta-analytic findings, generalizing about large sets of studies with different stimuli, can provide a useful general picture but should nevertheless be interpreted with some caution against the background of results from individual experiments: For example, in the domain of phonology, it has been shown that segmental aspects reflected in phonetic features are processed in the left hemisphere, whereas suprasegmental aspects reflected in prosodic features are processed in the right hemisphere (Meyer et al., 2002, 2004; Plante et al., 2002). That is, the hemispheres exhibit differential specializations for different types of phonologic information. Significantly, the functional activation associated with the processing of prosodic information shifts from the right to the left hemisphere as soon as this information is relevant for syntactic phrasing (van der Burght et al., 2019).

COMPONENTS OF THE FUNCTIONAL LANGUAGE NETWORK

Even though linguistic signals can be produced and perceived in different modalities (e.g., auditory or visual), the linguistic information (i.e., phonologic, semantic, or syntactic) recovered from or imposed on different signals is nevertheless processed predominantly in left-hemispheric networks in the perisylvian cortex in the adult brain (Fig. 18.3). Meta-analyses of functional studies on language processing using a variety of comprehension paradigms consistently implicate the left inferior frontal gyrus, especially the pars opercularis, superior and middle temporal gyrus, as well as posterior superior temporal sulcus as key regions subserving language processing (Vigneau et al., 2006, 2011; Price, 2010; Walenski et al., 2019; Stefaniak et al., 2021; see also Fig. 18.2, top panel). These regions identified in functional studies largely correspond to the two major canonical language regions first identified in the literature on aphasia: First, the so-called Broca's area, consisting of the cytoarchitectonic regions (i.e., Brodmann areas; Brodmann, 1909) BA 44 and BA 45 in the left inferior frontal gyrus, located ventrally and medially to the frontal operculum (Friederici, 2011; Tremblay and Dick, 2016). Second, the so-called Wernicke's area is in the left superior temporal gyrus, corresponding mostly to cytoarchitectonic BA 22 (though some researchers' definitions have also included BA 42 and BA 41, which are part of the primary auditory cortex or extended the region into BA 39 and BA 40 in the inferior parietal lobule; Bogen and Bogen, 1976; Tremblay and Dick, 2016; Wernicke, 1881).

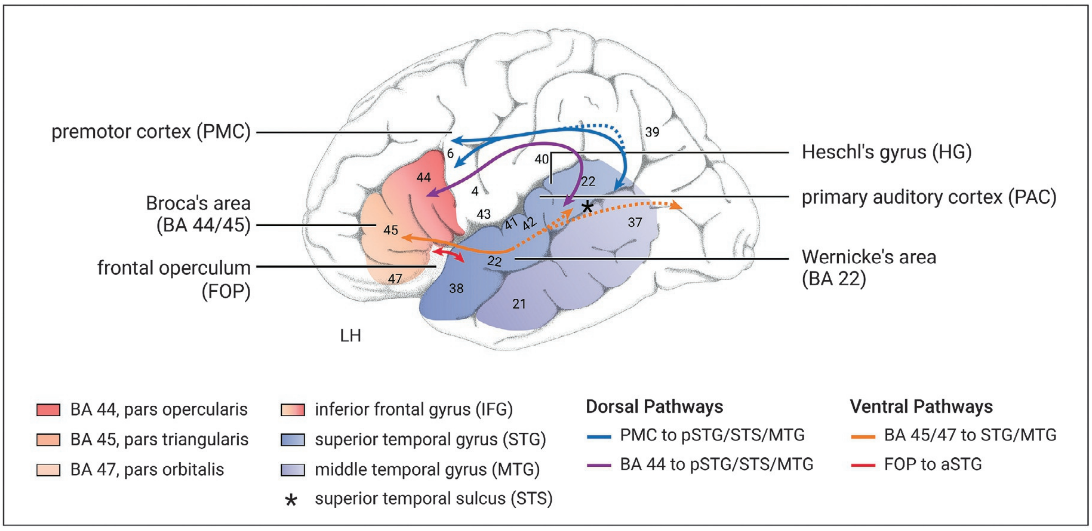

Fig. 18.3. Schematic of the language network. Schematic depiction of the left hemisphere (LH) showing anatomic landmarks and cytoarchitectonic details of language-relevant regions of the cortex. Major gyri that are part of the language network are color-coded: Inferior frontal gyrus (IFG) and its subregions Brodmann areas (BA) 44, BA 45, and BA 47 are depicted in shades of red; superior temporal gyrus (STG) and middle temporal gyrus (MTG) are shown in shades of blue. The location of the language-relevant portion of the superior temporal sulcus (STS) in between STG and MTG is indicated using an asterisk (*). Numbers on the schematic indicate the respective cytoarchitectonic label of a region (i.e., BA) as defined on the basis of histologic studies by Brodmann (1909). Together, BA 44 (pars opercularis) and BA 45 (pars triangularis) form Broca's area. The pars orbitalis (BA 47) is located anteriorly to Broca's area (BA 44 and BA 45) while the frontal operculum (FOP) is located ventrally and medially to it. Premotor cortex (PMC) is located in BA 6. Wernicke's area is located in BA 22, though some definitions also include BA 42 which is part of primary auditory cortex (PAC) together with Heschl's gyrus (HG). The main white-matter fiber tracts connecting these language-relevant regions of cortex dorsally and ventrally are indicated using color-coded arrows: Blue for the pathway connecting PMC to posterior STG (pSTG), STS, and MTG; purple for the pathway connecting BA 44 to pSTG, STS, and MTG; orange for the pathway connecting BA 45 and BA 47 to STG and MTG; and red for the pathway connecting FOP to aSTG. Adapted from Friederici AD (2011). The brain basis of language processing: from structure to function. Physiol Rev 91: 1357–1392. https://doi.org/10.1152/physrev.00006.2011.

In addition, the advent of functional neuroimaging has revealed that other left (perisylvian) regions besides the canonical Broca's area and Wernicke's area are also involved in different aspects of language processing. For example, the frontal operculum has frequently been implicated in studies of syntactic processing (Friederici et al., 2000). An extensive body of work by Pylkkänen and colleagues has demonstrated the involvement of the left anterior temporal lobe (i.e., BA 38) in different aspects of conceptual (i.e., semantic) combination (Bemis and Pylkkanen, 2011; Pylkkänen, 2019). In a synthesis of several fMRI studies, Kuhnke et al. (2023) have recently shown that the left angular gyrus may constitute a multimodal convergence zone for semantic processing. A meta-analysis of semantic processing by Binder et al. (2009) has revealed primarily left-lateralized effects located in posterior inferior parietal lobe, middle temporal gyrus, fusiform and parahippocampal gyri, dorsomedial prefrontal cortex, inferior frontal gyrus, ventromedial prefrontal cortex, and posterior cingulate gyrus. Lastly, large-scale study of sentence processing in the auditory and visual domain with more than 200 participants indicates that left inferior frontal cortex (i.e., BA 44 and 45), bilateral anterior temporal lobe, posterior middle temporal gyrus, and left inferior parietal lobule as major hubs for language processing (Uddén et al., 2022).

The observation that language processing recruits a wide set of regions primarily in the left perisylvian cortex is not surprising when considering that this notion is unlikely to capture a single monolithic cognitive operation. Instead, "language processing" involves several subcomponents, which have been shown to differentially recruit different parts of language-relevant networks. Accordingly, there is widespread agreement among researchers in the cognitive neuroscience of language that the primarily left-hemispheric frontotemporal networks in the human brain depicted in Fig. 18.3 are involved in, and, to an extent, specialized for processing linguistic information, whereas the exact details of functional associations within these regions and networks continue to be subject of extensive debate (Hickok, 2009; Fedorenko et al., 2011; Friederici, 2011; Friederici and Gierhan, 2013; Fedorenko and Thompson-Schill, 2014; Friederici et al., 2017; Hagoort, 2017, 2019; Matchin and Hickok, 2020). Such disagreements are not surprising because even a notion such as "syntax" is likely still too vague to be mapped to one particular cortical region or network, as syntactic processing at the very least entails the generation of a hierarchical representation and the mapping of this representation to the sensorimotor system during production and perception as well to the conceptual-intentional system for thought.

In our view, experiments using careful and well-controlled manipulations of linguistic constructs have the potential to reveal a more fine-grained picture of the functional correspondences of different parts of the brain, while we focus here on the cortex.

Traditionally, such experiments varied only one linguistic parameter between the experimental stimulus and the control stimulus, following the logic of "pure insertion" (but see Friston et al., 1996). Contemporary fMRI experiments frequently employ factorial experimental designs, which follow a similar basic logic but can also detect interactions between factors, whereas analyses of data from such experiments can be carried out using classic univariate or more recent multivariate methods. We will focus here on experiments that have investigated the processing of hierarchical structures in human language, because (i) the hierarchical nature of language is most evident in studies of sentence processing as a subsystem with the most pronounced pattern of functional lateralization to the left hemisphere (Fig. 18.2) and, as already discussed above, (ii) this hierarchical nature of linguistic representations also seems to be a property that is unique to our species (Berwick et al., 2013; Everaert et al., 2015; Friederici et al., 2017).

One strategy for identifying neural correlates of syntactic processing has been to systematically vary, step by step, the complexity of syntactic structures (but leaving the number of words identical) as done by Friederici et al. (2005). All example sentences from this study in (5)–(7) translate into English as *Today, the grandfather gifted the boy a lollipop.* Yet, the mandatory case marking of functional elements (i.e., determiners) in German allows elements of the sentence to be "scrambled," meaning that phrases can be moved from their canonical position, making their processing more complex and, presumably, more effortful with regard to cognitive resources.

(5) *Heute hat [der Opa]*$_1$ *[dem Jungen]*$_2$ *[den Lutscher]*$_3$ *geschenkt.*
(6) *Heute hat [dem Jungen]*$_2$ *[der Opa]*$_1$ ___$_2$ *[den Lutscher]*$_3$ *geschenkt.*
(7) *Heute hat [dem Jungen]*$_2$ *[den Lutscher]*$_3$ *[der Opa]*$_1$ ___$_2$ ___$_3$ *geschenkt.*

The authors found that the necessary reordering of non-canonical (i.e., scrambled) sentences activated BA 44. Interestingly, a look at the percent signal change in this region revealed that the activation systematically increased as a function of the number of scrambled elements, with sentences like (5) with the lowest and sentences like (7) with the highest activity. Other studies using similar designs have also observed activation of BA 44 (Meyer et al., 2012) or the inferior frontal gyrus (Röder et al., 2002; Grewe et al., 2005).

A possible confound in these studies is the increased working memory demand, which is why some researchers who have sought to investigate syntactic complexity turned to a related phenomenon, that is, sentences with hierarchically embedded structures. Makuuchi et al. (2009) systematically varied the amount of hierarchical embedding in German sentences as listed in (8)–(11). Example sentences (8) and (9) are high and (10) and (11) are low in syntactic complexity, whereas (8) and (10) are high and (9) and (11) are low in working memory requirements due to the differences in syntactic distance (illustrated by underlining the dependent elements).

(8) *Peter wusste, dass [Maria, [die Hans, [der gut aussah], liebte], Johann geküsst hatte].*
(Peter knew that Maria, who loved Hans, who was good looking, kissed Johann.)
(9) *Peter wusste, dass [Maria, [die weinte], Johann geküsst hatte] und zwar gestern Abend.*
(Peter knew that Maria, who cried kissed Johann and that was yesterday night.)
(10) *Peter wusste, dass [Achim den großen Mann gestern am späten Abend gesehen hatte].*
(Peter knew that Achim saw the tall man yesterday late at night.)
(11) *Peter wusste, dass [Achim den großen Mann gesehen hatte] und zwar am Abend.*
(Peter knew that Achim saw the tall man at night and that was late.

They found that the effect for processing syntactic hierarchy was located in left BA 44, and was distinct from the effect of sentence-related working memory processes, which was localized to the inferior frontal sulcus (Makuuchi et al., 2009). These findings have since been conceptually replicated with an adaptation of the basic experimental design to Japanese observing an effect for syntactic hierarchy in left BA 44 and left posterior middle temporal gyrus (Iwabuchi et al., 2019).

Because processing sentences usually entails the simultaneous constructing and processing of meaning (i.e., semantics) in addition to the hierarchical relations between lexical items, researchers have used experimental paradigms relying on the so-called artificial grammars (e.g., Bahlmann et al., 2008; Chen et al., 2021a,b). Usually, such artificial grammars use meaningless syllables (e.g., /de/, /bo/, etc.), which can be combined according to rules of varying grammatical complexity and participants are taught these associations prior to scanning. For example, a study by Friederici et al. (2006) taught participants two different types of artificial grammar: First, a so-called finite-state grammar where rules specify only the local linear relationship to other elements (i.e., category A is always followed by category B, resulting in ABABAB structures). Second, a so-called phrase-structure grammar where rules can entail long-distance dependencies (i.e., n elements from category A are always followed by n elements from category B, resulting in A^nB^n structures). The authors found that processing of finite-state grammars activated the left frontal operculum and right superior temporal sulcus, whereas processing of phrase-structure grammars activated left BA 44 and left middle temporal gyrus, in addition to the left frontal operculum and right superior temporal sulcus (Friederici et al., 2006). These results clearly implicate the core language network in the left hemisphere for processing grammars that rely on recursive rules (i.e., somewhat similar to natural language) and suggest that while both the frontal operculum and the posterior portion of Broca's area (i.e., BA 44) are involved in "syntactic" processing in the broader sense, processing hierarchical representations recruits also the latter in combination with posterior superior temporal gyrus and sulcus (Friederici et al., 2009; Goucha et al., 2017).

Lastly, yet another strategy adopted by many researchers to isolate the hierarchical relations of words processed in a sentential context has been to contrast grammatically correct sentences with mere word lists. In a meta-analysis reviewing studies that have employed such paradigms, Zaccarella et al. (2017) found that the meta-analytic convergence mass across studies was strongly influenced by the linguistic properties of the word lists that were used as part of the respective contrast analyses: When the word list conditions also included function words that enabled the build-up of local phrase structure (e.g., *money, the, [the, client], washed]*), the convergence mass was located in the anterior portion of Broca's area (i.e., left BA 45), the left posterior temporal gyrus and sulcus, as well as in left anterior temporal lobe. However, when the word list conditions used in the experiments contained only content words and thus did not enable the build-up of local phrase structure, the convergence mass was located in the posterior portion of Broca's area (i.e., left BA 44) as well as in the left posterior temporal gyrus und sulcus. Accordingly, the authors suggest that these two regions in the left hemisphere constitute the core system for the generation of hierarchical representations in language.

From the data reviewed here we can conclude that there is a strong left lateralization of the functional language network recruited for processing syntactic information in the typically developed mature brain.

COMPONENTS OF THE STRUCTURAL LANGUAGE NETWORK

The functional connectivity between the different perisylvian regions forming the core and extended language network in the left hemisphere described in the previous section is enabled structurally by myelinated fiber pathways in the white matter. A lot of work has focused on describing the direct connections between two regions, yet it should be mentioned that indirect tracts with a gray matter "relay station" in between are also feasible (Gierhan, 2013). For example, the posterior portion of Broca's area (i.e., BA 44) projects directly to cortical regions in the posterior temporal lobe via the arcuate fasciculus. At the same time, there also is an indirect connection from the premotor cortex and the dorsal portion of BA 44 to the inferior parietal cortex via the superior longitudinal fasciculus, which is then, in turn, connected to the posterior temporal cortex. Notice that structural imaging cannot detect the directions in which information flows in white-matter tracts, so that labeling a connection as "frontotemporal" does not imply any directionality. In general, the information flow in language-relevant networks is currently not well understood and will not be considered further here due to our focus on lateralization (but see Friederici, 2011, 2017 for discussion and a first model of information flow in language-relevant networks based on data from electroencephalography, magnetoencephalography, and fMRI connectivity analses).

For different aspects of language processing, at least four major pathways interconnecting inferior frontal and temporal regions dorsally and ventrally have been identified (Fig. 18.3). The already mentioned arcuate fasciculus and superior longitudinal fasciculus dorsally connect inferior and superior frontal regions to posterior temporal as well as inferior parietal regions. Due to methodological limitations in tracking the horizontal parts of both pathways, some researchers have sometimes grouped both pathways together (Friederici and Gierhan, 2013). However, both pathways show different functional associations, with the arcuate fasciculus having been shown to support the processing of complex syntax by connecting the posterior portion of Broca's area (i.e., BA 44) to the posterior temporal cortex, and the superior longitudinal fascicle supporting speech repetition by connecting premotor cortex to posterior temporal cortex via the inferior parietal cortex and can be subdivided into several substructures (Friederici and Gierhan, 2013; Gierhan, 2013; Janelle et al., 2022). In addition, at least two pathways connect the inferior frontal cortex to the temporal cortex ventrally: One pathway assumed to support basic syntactic processes connects the anterior inferior frontal cortex and the frontal operculum to the anterior temporal cortex via the uncinate fascicle. Another pathway hypothesized to support semantic processing connects the inferior frontal cortex including the anterior portion of Broca's area (i.e., BA 45) with the posterior temporal, occipital, and parietal cortex via what is either called the extreme capsule fiber system or the (inferior) fronto-occipital fasciculus (Friederici and Gierhan, 2013; Gierhan, 2013; Meola et al., 2015).

Among these four pathways, most studies have reported the arcuate fasciculus to show a clear left-lateralization in the majority of the population (Paus et al., 1999; Pujol et al., 2002; Glasser and Rilling, 2008), whereas the amount of lateralization observed seems to depend on the exact measurement and analysis method used. Some studies suggested that the arcuate fasciculus is strongly left-lateralized only in half of the population (e.g., Catani et al., 2007), yet recent studies with large samples of several hundred participants have found the arcuate fasciculus to be strongly left-lateralized in two-thirds of participants (Gallardo et al., 2020; Warrington et al., 2020). For example, in a sample of 600 subjects, Gallardo et al. (2020) found that 70% of participants had at least 1.5 times more streamlines for the arcuate fasciculus in the left hemisphere than in the right hemisphere. In contrast, the uncinate fasciculus and certain parts of the superior longitudinal fasciculus (i.e., the so-called SLF II and SLF III; Friederici and Gierhan, 2013; Janelle et al., 2022) have been shown to be strongly right-lateralized in most of the population (Gallardo et al., 2020; Warrington et al., 2020). The data and analyses of both groups are less clear for the (inferior) fronto-occipital fasciculus, which, however, also tends to be slightly right-lateralized.

Significantly, these patterns of lateralization of language-relevant fiber pathways, especially the left-lateralization of the arcuate fasciculus, seem to be independent of the modality of language use and have also been observed in deaf native signers who acquired a sign language early in life and use it as their primary means of communication (Cheng et al., 2019; Finkl et al., 2019). Despite the obvious modality differences between sign language and auditory language production and perception, which was evidenced in structural differences in production-related fiber tracts, Finkl et al. (2019) did not observe any differences between both groups with regard to the structural integrity of the arcuate fasciculus. This indicates that this pathway is relevant for processing linguistic information regardless of whether language is spoken or signed. Similarly, in another group comparison of different samples, Cheng et al. (2019) also found no differences in the structural integrity of the arcuate fasciculus between deaf signers and hearing controls, as well as a clear left-lateralization of this core language pathway. Interestingly, the authors also report data from three deaf individuals who grew up with severe language deprivation and only acquired a sign language late in life. These individuals showed altered white-matter microstructure in the arcuate fasciculus and presented with severe problems in comprehension of morphosyntax and complex sentences (Cheng and Mayberry, 2019; see Trettenbrein et al., 2025, this volume, for an in-depth discussion).

Structural differences between the left and the right hemisphere in language-related networks are not limited to the white matter but can also be observed using a number of other measures, such as cortical surface area derived using MRI data or the cytoarchitectonic structure of a region determined in ex vivo brains. Broca's area, as one of the canonical language regions and parts of the core language network, has repeatedly been described as an asymmetric region. However, studies using a variety of structural imaging approaches have not consistently reported a left-over-right asymmetry for Broca's area or its subregions (for extensive reviews see Keller et al., 2009; Sprung-Much et al., 2022). In contrast to these mixed findings from neuroimaging, studies investigating the microstructure of Broca's area post mortem paint the clearest picture and indicate a leftward asymmetry, especially for the cytoarchitecturally defined posterior portion of Broca's area (i.e., BA 44), over its right-hemispheric homolog (Amunts et al., 1999, 2003; Sprung-Much et al., 2022). These discrepancies between different kinds of data may either be related to methodological differences or, as some researchers have hypothesized, be related to the documented high individual variability in these regions (Sprung-Much and Petrides, 2020; Sprung-Much et al., 2022).

With regard to the posterior temporal cortex, which generally shows higher white-matter volume in the left hemisphere (Anderson et al., 1999), a number of structural asymmetries have been reported. A classic finding is that the upper portion of the superior temporal gyrus (i.e., the planum temporale) located within the Sylvian fissure is larger in the left hemisphere (Geschwind and Levitsky, 1968; Binder et al., 1996; Shapleske et al., 1999). Similarly, the superior temporal sulcus is deeper in the right hemisphere than in the left hemisphere close to the area of Heschl's gyrus (Leroy et al., 2015; Bodin et al., 2018), and generally exhibits a genetically constrained more chaotic morphology on the left side than on the right side (Le Guen et al., 2018). While the superior temporal sulcus has been shown to be involved in auditory language comprehension, establishing a structure–function correlation between these structural asymmetries and cognitive functions has not been met with success in experiments (Specht and Wigglesworth, 2018). Lastly, with regard to microstructure, Galuske et al. (2000) used postmortem neuronal tract tracing in posterior BA 22 to show that this region contained about 30% more distinct columnar subsystems in the left hemisphere than in the right hemisphere, suggesting increased processing capacity.

The data reviewed here suggests a structural lateralization of the arcuate fasciculus as one of the main fiber tracts connecting the temporal cortex to Broca's area in the inferior frontal cortex in the typically developed adult brain.

DEVELOPMENT OF THE LANGUAGE NETWORK

Spoken language acquisition starts before birth, because the auditory system is already functioning in the fetus in utero. However, the acoustic information perceivable in the uterus is filtered by the surrounding water and tissue. Therefore, the acoustic information that arrives at the auditory system of the fetus is filtered by about 400 Hz, leaving prosodic information of speech (i.e., the patterns of stress and intonation of a particular language) intact, but not its phonetic details (i.e., the actual speech sounds as such). The presumption that the prosody of a given language is processed even before birth is supported by newborns' behavior (for reviews see Gervain, 2018; Ghio et al., 2021), as it has been shown that newborns' first cries are already language-specific: For example, French babies and German babies cry with a different melody, each mirroring the speech melody of their respective prospective native language (i.e., the majority language spoken by the mother and used in her environment; Mampe et al., 2009). Moreover, newborns also react specifically and preferably when listening to their native language in comparison to a foreign language that is not familiar to them, even when these are filtered by 400 Hz to mimic the conditions previously experienced in utero (Mehler et al., 1988).

These are interesting observations given that it takes several months before children utter the first words in their native language, indicating that comprehension and production abilities and their neural basis do not necessarily develop in tandem despite their reliance on the development of linguistic competence as such. Over the past decades, systematic research in the field of language acquisition has advanced our knowledge not only concerning the language abilities of young infants and children but also concerning the neural networks supporting this process both with respect to its functional specifics and its structural basis. Here, we review the development of the core language network previously identified in adults and already discussed above, and particularly consider its hemispheric lateralization in the developing brain. The available literature on the development of the lateralization of language processing in the developing brain comes from studies that, at times, used very different methodological approaches and therefore allow us to draw a rather clear, converging picture: At birth, there is bilateral involvement for speech processing, then lateralization of language toward the left hemisphere increases during development leading to a dominance of the left hemisphere for language processing in the vast majority of the adult population.

Functional lateralization during development

Taking the language network in the newborn brain as a starting point, a seminal study by Perani et al. (2011) provided functional and structural data in the context of language lateralization in the developing brain. Functional brain data were acquired in a setting in which 2-day-old Italian newborns heard different acoustic sequences: Either normal Italian speech or speech with the intonational contour was taken out, leading to a flattened speech version, or the phonetic details were filtered out, leading to a hummed speech version. The functional brain activation in these newborns was mainly located in the posterior superior temporal gyrus in both hemispheres. A region-of-interest analysis of the activation in the auditory cortices revealed larger activation in the right compared to the left hemisphere for normal speech and no stimulus-specific activation for the altered speech conditions. This indicates that only normal speech triggers significant brain activity in newborns and that the right hemisphere shows a stronger involvement, possibly due to a perceptual preference for prosodic information, which in the adult brain is primarily processed in the right hemisphere.

Thus, the functional brain response to speech in newborns appears to be bilateral with a slight lateralization to the right, whereas a seeming left-hemispheric dominance has been reported as early as 3 months of age. Investigating the functional connectivity of language-relevant brain regions in these newborns studied by Perani et al. (2011) compared to adults revealed a clear difference: While the group of typically developed adults showed an intrahemispheric functional connectivity between Broca's area in the left frontal cortex and the left posterior superior temporal gyrus, healthy newborns displayed an interhemispheric functional connectivity between Broca's area and its right-hemispheric homolog as well as between left superior temporal gyrus and its right-hemispheric homolog (Lohmann et al., 2010; Perani et al., 2011; see Fig. 18.4). At the age of 3 months, infants already seem to show a somewhat different activity pattern related to speech: Two fMRI studies reported speech-related activation in the superior temporal cortex bilaterally, but with a dominance in the left hemisphere (Dehaene-Lambertz, 2002; Dehaene-Lambertz et al., 2006). However, when directly contrasting natural forward speech to speech played backward, the effect in the temporal cortex disappeared and activation was found in the left angular gyrus and the precuneus.

Functional neuroimaging studies on language processing and its lateralization in early childhood are rare due to the experimental constraint that the participant has to avoid movements in the scanner, which especially for young children has proven to be difficult. Alternative approaches to reduce scanning time often involve testing language function behaviorally outside the scanner and performing only structural scans, which allow for the analysis of the gray matter in language-relevant brain regions and the white matter connecting these regions and then correlating these structural data with behavioral data. One such study investigated the cortical thickness of the regions in the neural language network relevant in 5-year-old and 6-year-old children and found that an increase in language performance was associated with changes of cortical thickness asymmetry in the left inferior frontal gyrus, in particular in Broca's area (Qi et al., 2019). The cortical thinning of this region between the ages of 5 and 6 years observed in this study was larger in the left hemisphere than in its right-hemispheric homolog and furthermore associated with the observed language performance at the age of 7 years.

Another approach that aims to minimize scanning time and the requirement of children to comply with performing an experimental task in the scanner has been to use resting state MRI and behavioral language tests. With this approach, it was found that 5-year-old children displayed an interhemispheric correlation

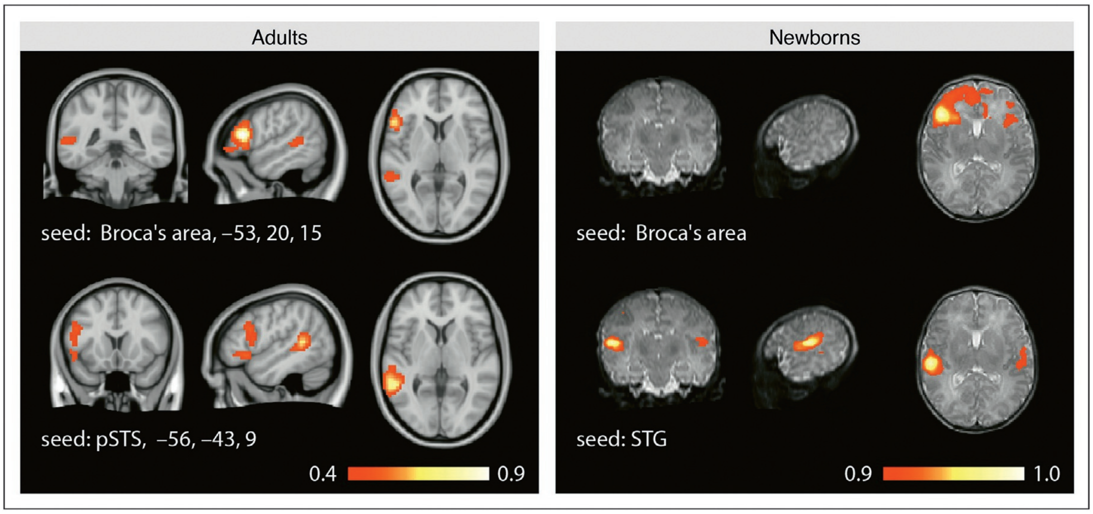

Fig. 18.4. Functional brain connectivity in adults and newborns. Functional connectivity results comparing the BOLD response to speech of adults and newborns. The left panel shows correlation values of low-pass–filtered residuals of language experiments in adults and the right panel shows corresponding data for newborns, in both cases with seeds in Broca's area (upper part of panels) and in the posterior superior temporal sulcus (pSTS) and superior temporal gyrus (STG) shown in the lower part of both panels. For adults in the left panel, coordinates are given in Talairach space (Talairach and Tournoux, 1988). As no such coordinates are available for newborns' brains, the neuroanatomic location of the seed is given instead in the right panel. In the upper and lower rows in both panels, slices are shown in the following order (from left to right): Coronal view, sagittal view, and axial view. Adapted from Perani D, Saccuman MC, Scifo P, et al. (2011). Neural language networks at birth. Proc Natl Acad Sci U S A 108: 16056–16061. https://doi.org/10.1073/pnas.1102991108.

of the left inferior frontal gyrus with its right homolog region. When relating resting state functional connectivity data to sentence processing, the local connectivity within the left inferior frontal gyrus was found to be associated with processing syntactically simple sentences, while the processing of syntactically complex sentences was associated with the long-range connectivity between the inferior frontal gyrus and the posterior superior temporal sulcus in the left hemisphere (Xiao et al., 2016). These data suggest that a selective left frontotemporal connectivity in the neural network is already in place at the age of 5 years when measured in a so-called “task-free” setting of resting state MRI.

However, it takes some more time before the neural language network in the left hemisphere reacts specifically to different aspects of the language input. An fMRI study that directly investigated syntactic processes during language comprehension demonstrated strong functional connectivity between left posterior superior temporal gyrus and left BA 44 in 6-year-olds, which was not observed in 3-year-olds, suggesting a clear development step (Vissiennon et al., 2017). These data, in combination with the infant data, suggest that the brain response to speech early in life differs from that in the adult brain, whereas the lateralization of speech and language processing seems to emerge during brain maturation. Hence, while the functional connectivity patterns observed during speech processing in newborns and adults shift from an initially bilateral to a mature left-hemispheric functional response, it should be considered that this developmental change does not merely reflect a change in the response to speech but instead evidences the emergence and functional segregation of a network that processes linguistic information (e.g., semantics, syntax, etc.) driven by the spoken input.

A number of developmental language studies used functional near-infrared spectroscopy (NIRS) to investigate speech and language processing in early life. This measurement does not provide the same spatial precision as fMRI, but allows to differentiate the involvement of the left and the right hemisphere. On the basis of a review of functional NIRS data, it was concluded that the lateralization for language emerges out of a bilateral left–right involvement for auditory processes to a left-hemispheric dominance during language learning (Minagawa-Kawai et al., 2011). Significantly, similar lateralization for processing linguistic input is also present in deaf children who acquire a sign language (Payne et al., 2019), again indicating that the observed left-hemispheric dominance relates to processing linguistic information and not just speech. This developmental pattern is confirmed by a recent study that analyzed fMRI language activation in children from 4 to 13 years and adults (Olulade et al., 2020): The study revealed language-related activation not only in the left-hemispheric language network but also in its right hemisphere homolog between the age of 4 and 6 years. During later childhood, a decrease in the involvement of the right hemisphere and an increase in the involvement of the left hemisphere were observed. This again suggests that language becomes more and more left-lateralized throughout life.

There are also several developmental language studies that only looked at functional activation in the left hemisphere and can therefore not speak directly to the asymmetry of language in the developing brain. Some of these studies, however, provide interesting information concerning the involvement of Broca’s area and the posterior temporal cortex during language development. A review of studies on the development of the cortical language network by Skeide and Friederici (2016) summarized the literature, including region-of-interest studies, and proposed that there are two development stages: a first stage from birth to 3 years and a second stage continuing into adolescence with a possible closure roughly at the age of puberty (Lenneberg, 1967; Friederici, 2017). During the first stage, language processing is mainly supported by the temporal cortex, whereas the second stage involves the inferior frontal cortex including Broca’s area and the dorsal fiber tract connection to the posterior temporal cortex (i.e., the core language network; also see Skeide and Friederici, 2016). It seems that phonologic, prosodic-, and word-based processes can be dealt with by both the left and right temporal cortices. Broca’s area in the left inferior frontal gyrus, in particular, comes into play later when the demands on processing syntax increase.

This raises the question as to how children process sentences and syntactic information at the age of 3 years before this developmental shift for language processing in the core language network occurs. One fMRI study investigated sentence processing in 3- to 10-year-old children and varied semantic plausibility and syntactic complexity of the sentences to answer this question (Skeide et al., 2014): Although activation in Broca’s area was observed in 3- to 4-year-old children, the main effects of activation for semantic and syntax were found only in the posterior temporal cortex, and similarly so in 6- to 7-year-olds. That is, main effects for syntax in Broca’s area were observed in 9- to 10-year-old children as well as adults. More recently, a combined gray matter and behavioral correlation study reported a regional shift in the correlation, indicating an involvement of the posterior STG in 3-year-olds and an involvement of Broca’s area in 4-year-old children (Klein et al., 2022). This suggests that, in addition to a developmental change in laterality of the language network from initially more bilateral involvement to a clear leftward preference, there appears to be an additional developmental shift within the left hemisphere, from the primary involvement of posterior temporal cortex to a preferential involvement of the inferior frontal cortex.

Lastly, a recent meta-analysis of functional fMRI studies on language comprehension, including 27 independent experiments involving children between the ages 4 and 12 years, with a mean age of 8.9 years, allows to further specify this assumed developmental shift in preschool children (Enge et al., 2020). As already discussed above, typically developed adults display activation in the left pars opercularis (BA 44) and the left temporal cortex during language and especially sentence comprehension. In contrast, the brain responses during language comprehension in children shift from bilateral temporal activation and the left pars triangularis (BA 45) toward the adult pattern involving the left posterior temporal cortex and the left pars opercularis (BA 44) during development (Fig. 18.5). Given that the maturation of the arcuate fasciculus as one of the main fiber pathways connecting these regions of the core language network has been linked to the performance during tasks involving processing complex sentences

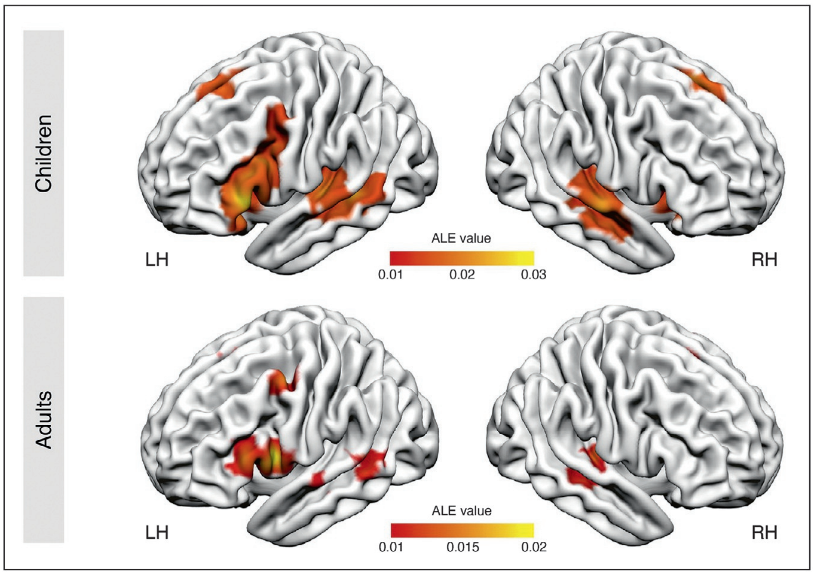

Fig. 18.5. Meta-analyses of language comprehension in children and adults. Results from meta-analyses of language comprehension in children and adults by Enge et al. (2020). The top panel shows an activation likelihood estimation (ALE) map of significant clusters associated with language comprehension in children, superimposed onto a standard cortical surface. Activations reported in 27 experiments that showed above-chance overlap ($P < 0.05$, cluster-wise family-wise error [FWE] corrected) are shown. The color bar represents the ALE value of any given voxel, that is, its degree of nonrandom convergence in activation between experiments. The bottom panel shows an ALE map of significant clusters associated with language comprehension in adults. These data were reproduced using the sample of studies reported in a previous meta-analysis by Rodd et al. (2015). Maps depict clusters with above-chance overlap ($P < 0.05$, cluster-wise FWE-corrected) and their associated ALE value (color bar), that is, the degree of nonrandom convergence in activation between experiments at any given voxel. Both panels show the left hemisphere (LH) as well as the right hemisphere (RH). Adapted from Enge A, Friederici AD, Skeide MA (2020). A meta-analysis of fMRI studies of language comprehension in children. Neuroimage 215: 116858. https://doi.org/10.1016/j.neuroimage.2020.116858.

(Skeide et al., 2014; Skeide and Friederici, 2016; Klein et al., 2022), it stands to reason that this developmental shift may be related to the increasing functional specialization of the brain for processing syntactic information.

Structural lateralization during development

The description of the lateralization of the structural language network in newborns and children has been of scientific interest for more than 50 years. Early research focused on the gray matter of the temporal cortex and found a larger left than right lateralization already in the fetus (Chi et al., 1977) and in the newborn (Witelson and Pallie, 1973). This is an important finding given that the asymmetry of the planum temporale in the posterior temporal gyrus has long been associated with the human lateralization of language (Binder et al., 1996); also see the discussion above. However, later studies showed that the leftward structural asymmetry of the planum temporale observed in many studies does not seem to relate systematically to language lateralization: One study examined the relation between the asymmetry of the planum temporale and language laterality in 287 healthy adults and concluded that the asymmetry of the planum temporale appears to be associated with local functional lateralization only in auditory areas, but is not a marker of interindividual variability of language lateralization (Tzourio-Mazoyer and Mazoyer, 2017). An earlier study by Dorsaint-Pierre et al. (2006) similarly found that it was not the planum temporale but rather the posterior part of the inferior frontal gyrus (i.e., Broca's area) for which a direct relationship to language lateralization was observed.

A structural analysis of Broca's area in the inferior frontal gyrus was performed using a cytoarchitectonic approach (Amunts et al., 2003). This approach quantifies the number of different types of neurons in the six layers of the cortex (Brodmann, 1909). It was discovered that the anterior part of Broca's area (BA 45) and the posterior part of Broca's area (BA 44) followed different development trajectories to achieve the asymmetry usually observed in the adult brain: BA 45, a region known to primarily support semantic processes, achieved a leftward asymmetry in its cytoarchitectonic profile by the age of 5 years, whereas BA 44, a region known to primarily support syntactic processes, achieved a leftward asymmetry in its cytoarchitectonic profile much later around the age of 10–11 years. This result indicates that different regions of the language network area show distinct lateralization patterns to the left hemisphere at different stages during development.

Another set of studies looked at the white-matter fiber tracts connecting the different regions of the language network and their lateralization. As discussed above, there are dorsally and ventrally located fiber tracts that connect the inferior frontal gyrus with the temporal cortex, among which the arcuate fasciculus has been shown to be stronger (e.g., in terms of the number of streamlines generated in diffusion MRI analyses, etc.) in the left hemisphere than in the right hemisphere in the adult brain (Paus et al., 1999;

Pujol et al., 2002; Glasser and Rilling, 2008; Gallardo et al., 2020; Warrington et al., 2020). The asymmetry of this fiber tract during development was investigated in 183 participants ranging from 5 to 30 years of age, including children from 5 to 13 years (Lebel and Beaulieu, 2009). This study reported that fractional anisotropy and the number of streamlines of the arcuate fascicle were higher in the left hemisphere than in the right hemisphere in most participants, independent of age. A subanalysis of the children revealed left lateralization of this fascicle for most children (N = 53) and right lateralization only for a few children (N = 15), suggesting that the usual left lateralization of the arcuate fascicle is already established in childhood, similar to the pattern observed in adults.

In a review of the functional and structural neural language network in the infant brain (Dehaene-Lambertz, 2017), it has been argued that during the maturation of the perisylvian regions, a relative delay of the dorsal pathway in comparison to the ventral pathway can be observed, but that this disparity begins to disappear after 3 months of age (Leroy et al., 2011; Dubois et al., 2016). The authors argue that this maturational step is related to the increase in vocalizations at this age. However, in the analysis of the dorsal pathway we have to consider that it may not constitute an indivisible entity: The arcuate fascicle is often taken to be a dorsally located fiber bundle that directly connects the inferior frontal gyrus with the temporal cortex. However, it has been demonstrated that in the adult brain, this dorsal pathway actually subdivides into two bundles: one targeting Broca's area and another targeting the premotor cortex (Perani et al., 2011). In the newborn brain, only the fiber bundle targeting the premotor cortex is myelinated, whereas the fiber bundle targeting Broca's area is not (Fig. 18.6). The fiber bundle targeting the premotor cortex supports auditory-to-motor mapping allowing early vocalization in infants and may well be detectable in 3-month-olds. In contrast, the bundle targeting Broca's area is only myelinated later (Skeide et al., 2016) and taken to support syntactic processing coming in later during development (Friederici, 2011).

Language development with only one hemisphere

Relatively rare cases where either the left or right hemisphere has been damaged or where one hemisphere had to be surgically removed for medical reasons early in life make it possible to study how language and its neural substrate develop in the absence of the typical functional and structural lateralization. Clinical findings from brain-injured individuals suggest that the left hemisphere and the right hemisphere, in principle, appear to be equipotential and therefore equally involved in speech and language processing early in life with a gradual increase of left hemisphere involvement

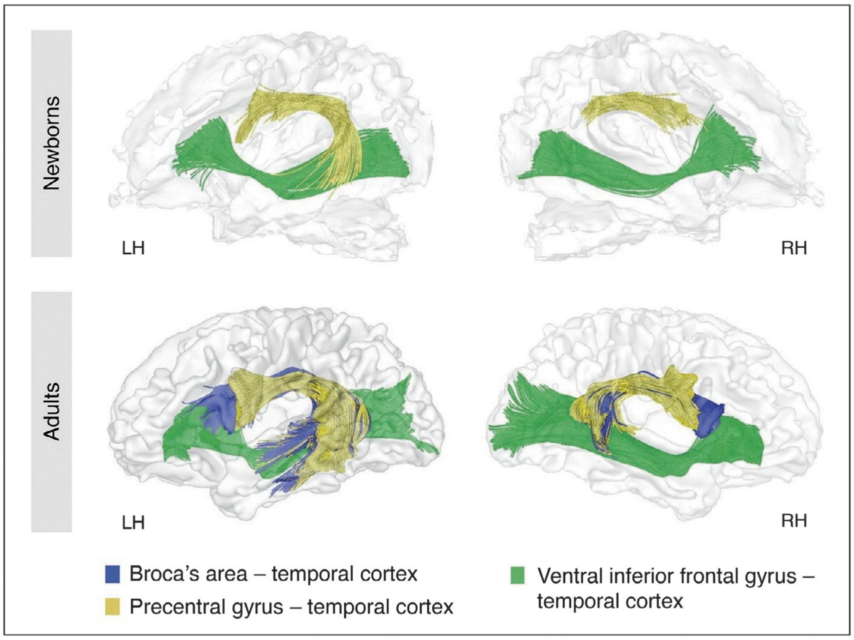

Fig. 18.6. Ontogeny of language-relevant white-matter tracts in the human brain. The top panel shows fiber tracking results of diffusion tensor imaging data seeding in Broca's area and the precentral gyrus/premotor cortex in the left hemisphere (LH) and right hemisphere (RH) of the brains of newborns (maximum age = 3 days). The bottom panel shows fiber tracking results with the same seed regions in a group of adults. In both newborns and adults, the pathway connecting the ventral inferior frontal gurus to the temporal cortex can be detected (color-coded in green). Only in adults, two dorsal pathways can be detected: The arcuate and superior longitudinal fasciculus connecting the temporal cortex to Broca's area (color-coded in blue) and the premotor cortex (color-coded in yellow). This indicates that the dorsal connection to Broca's area matures only later during development, whereas the ventral connection via the extreme capsule is present in both groups. A certain degree of structural asymmetry in the dorsal white-matter pathways is already visible early in life and becomes more pronounced in adulthood. Adapted from Perani D, Saccuman MC, Scifo P, et al. (2011). Neural language networks at birth. Proc Natl Acad Sci U S A 108: 16056–16061. https://doi.org/10.1073/pnas.1102991108.

during childhood (Basser, 1962; Bates et al., 2001). In a clinical study, 102 individuals with early unilateral brain lesions were examined (Basser, 1962): In children whose lesions occurred prior to speech onset (between 18 and 24 months), left hemisphere lesions and right hemisphere lesions equally resulted in delayed language development. Children who received a hemispherectomy before the age of 13 years only developed transitory aphasia in a few cases, whereas hemispherectomy in adults resulted in permanent aphasia when the left hemisphere was taken out. For those patients in whom the right hemisphere was surgically removed no aphasia was observed. This pattern has been confirmed by more recent studies, which show that adolescents and young adults who suffered a perinatal stroke to the left hemisphere nevertheless developed normal abilities for processing complex sentences in the right-hemispheric homolog of the language network (Newport et al., 2017, 2022).

The data reviewed here suggest a certain equipotentiality of the left and the right hemisphere for developing speech and language processing systems during the first months of life, as well as the increasing reliance of the language system on the left hemisphere during development, which usually results in the dominance of left hemisphere for language in the vast majority of typically developed adults.

DISCUSSION

Our review of functional and structural asymmetries in language-relevant regions of the cortex and the white matter has confirmed that the human language system in the typically developed adult brain exhibits a leftward asymmetry, whereas it remains an open question whether and how functional and structural asymmetries in the same regions and networks ultimately relate to each other (Keller et al., 2011). The core language network subserving the generation of hierarchically structured representations during syntactic processing is made up of the posterior portion of Broca's area (i.e., left BA 44) and the posterior superior temporal gyrus and sulcus. This network also showed the most pronounced functional leftward asymmetry in studies focusing on the processing of syntactic hierarchy even independent of meaning (e.g., in so-called artificial grammar studies). A left-hemispheric preference for processing linguistic information is already present early in life, however, the functional dissociation of semantic and syntactic processing on the cortical level emerges only gradually as part of brain maturation during childhood. The main fiber pathway connecting the regions of the core language network via the arcuate fascicle targeting BA 44 in Broca's area also shows a clear leftward asymmetry in the vast majority of the adult population and the maturation of this fiber pathway is correlated with the emergence of complex syntactic abilities.

Establishing consistent links between structure and function may have proven difficult to date because different definitions of "language" that confound language processing with speech production have sometimes been employed in the literature. For example, the widely cited number of more than 96% of right hander showing left-lateralized language functions is derived from studies using only production tasks (Rasmussen and Milner, 1977; Knecht, 2000). In contrast, meta-analyses of language processing, usually also showing strong left-lateralization, tend to rely on data stemming from studies using comprehension paradigms (Price, 2010; Vigneau et al., 2011; Walenski et al., 2019; see also Fig. 18.2). Hence, while both speech production and language comprehension necessarily access the same linguistic competence (Chomsky, 1965; van der Burght et al., 2023) and thus recruit the language network (Friederici, 2017; Friederici et al., 2017), this does not imply that all subcomponents of language always need to be lateralized to the same hemisphere.

Recent work investigating a large sample of 287 participants (Labache et al., 2020) has revealed a task-specific intra-individual differentiation of lateralization patterns in the core and extended language network: In this study, most participants showed a left-lateralized BOLD response in the core language network and its right-hemispheric homolog for speech production (92.34%), auditory (86.76%), and written (84.67%) sentence comprehension, whereas a small subgroup exhibited what the authors called a "crossed" pattern for different tasks (i.e., some of the tasks showed left lateralization and others right lateralization). This "crossed" pattern was observed in 5% of the participants for whom speech production was lateralized to the left hemisphere and auditory sentence comprehension to the right hemisphere in the same subject. The "crossed" pattern was most pronounced when the analysis was limited to the core language network and its right-hemispheric homolog. Participants exhibiting such a "crossed" activation pattern moreover showed a larger corpus callosum volume, indicating stronger inter-hemispheric connectivity and allowing for fast information transfer between the two hemispheres. The observed difference in lateralization for speech production in the left hemisphere and comprehension in the right hemisphere is interesting, since the right hemisphere is known to support prosodic processes, which appear to be most relevant for auditory language comprehension (Meyer et al., 2002; Sammler et al., 2010; van der Burght et al., 2019). The reported increased volume of the corpus callosum is crucial for the interaction of prosodic information and syntactic information during sentence comprehension (Friederici et al., 2007). Future work should examine whether these "crossed" individuals may have relied more on prosodic information during auditory sentence comprehension and therefore involved the right hemisphere.

From the point of view of evolutionary biology, both symmetry and asymmetry can constitute an advantage in fitness (Corballis, 2020). On the one hand, the natural world we live in does not have a systematic left–right bias, which is why sensorimotor systems can be symmetrically organized without any obvious negative consequences. By design, such a symmetric organization also allows for a certain degree of redundancy. On the other hand, an asymmetric organization, in the case of the brain, drastically increases the available neural resources (Rogers, 2021), as different regions or networks can be dedicated to distinct cognitive operations by means of differential functional specialization of the two hemispheres. At the same time, the typical strong left-lateralization of speech, language, and especially of the processing of complex syntax also illustrates that a high degree of asymmetry increases the probability of a design including a so-called "single point of failure" (i.e., a point of a system that, if it stops working, will stop the entire system or at least a major part of it from functioning). This is evidenced by the well-known aphasic syndromes that follow only left-hemispheric lesions but not right-hemispheric lesions to the perisylvian cortex and connecting white-matter tracts (for detailed discussions, see Raymer and Gonzalez Rothi, 2015).

Accordingly, while even semantic and phonologic processing tend to show left-lateralized patterns in functional neuroimaging studies (Vigneau et al., 2011; see also Fig. 18.2), the literature on development, as well as on aphasia and other neuropsychologic syndromes, makes it clear that the right hemisphere can also process these types of linguistic information, though maybe somewhat less efficiently or in a more restricted matter (Vigneau et al., 2011; Stefaniak et al., 2021; Wilson et al., 2023). For example, so-called "split-brain" patients, in which the left and right hemispheres have been surgically disconnected for medical reasons (Sperry, 1961), confirm such supposed limitations with regard to processing semantic and phonologic information, because their left hemisphere exhibits an advantage over the right hemisphere (Zaidel, 1978). In the only reported case of a split-brain patient with alleged right-hemispheric dominance for language, both hemispheres actually succeeded in oral naming, reading, and auditory comprehension tasks using single words, yet failed at a task testing passive voice syntax (Lutsep et al., 1995). Both hemispheres performed above chance in an active voice syntax task (i.e., the canonical word order of English). In the context of our discussion, such a pattern is difficult to interpret with regard to the impairment of syntactic abilities, but it provides evidence for both hemispheres' capabilities in semantics and phonology for comprehension and production.

The left-lateralization of language in typically developed persons is not merely an epiphenomenon of language acquisition, but reflects the maturation of a network dedicated to generating hierarchically structured representations in tandem with other language-relevant regions supporting the processing of semantics and phonology as well as speech production. However, relatively rare cases of so-called "crossed" lateralization patterns for sentence production and auditory sentence comprehension (Labache et al., 2020) confirm the theoretical stipulation that speech and language functions are principally independent also in terms of their neurobiologic implementation. At the same time, genetically determined biologic matrices of the core and extended language networks (Hervé et al., 2013; Kong et al., 2020; Sha et al., 2021; Wan et al., 2022) exhibit sufficient flexibility early in life for speech production and syntactic processing as usually highly left-lateralized processes to shift to the right hemisphere in cases of perinatal stroke (Newport et al., 2017, 2022). Significantly, this plasticity is highly constrained and has only been observed after injuries during the critical period for language acquisition early in life (Lenneberg, 1967; Friederici, 2017) and is always limited to the right-hemispheric regions homologous to the core and extended language network (Newport et al., 2022). Whether this reflects the plasticity and flexibility of the developing brain or a general equipotentiality of both hemispheres early in life for developing fully fledged language functions including syntactic processing and speech production remains an open question.

CONCLUSION

Our review of the neuroimaging literature in this chapter has confirmed the centuries-old assumption that the left hemisphere of the human brain is usually specialized for language processing in typically developed adults and, at the same time, has allowed us to draw the more nuanced conclusion that observed functional leftward asymmetries are most pronounced for components of the language system subserving syntactic processing. These functional asymmetries emerge during development and are, to an extent, paralleled in structural asymmetries, although with some individual variation. Both hemispheres display a weak equipotentiality with regard to processing meaning (i.e., semantics) and sound (i.e., phonetics/phonology), but even these processes tend to show a left-hemispheric dominance during most experimental tasks.

The processing of hierarchical syntactic structure is primarily supported by a left-hemispheric frontotemporal network connecting the posterior inferior frontal gyrus to the posterior temporal cortex via the arcuate fasciculus. This network constitutes both functional and structural asymmetries. It subserves the generation of hierarchically structured representations linking meaning and sound, develops in accordance with a genetically determined biologic matrix, and its emergence may have constituted a prerequisite for the evolution of the capacity for language in our species. In the future, studies that use linguistically informed experimental manipulations and consider individual variation will likely provide a more fine-grained picture of the lateralization of language and its different subsystems.

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CONFLICTS OF INTEREST

We have no known conflicts of interest to disclose.

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