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 biological matrix, and (iii) its emergence may have constituted a prerequisite for the evolution of the human language capacity.

Keywords: neurobiology of language; language network; lateralization; syntax; sentence processing; brain development; neurolinguistics

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Humans are bilateria, a clade of animals whose body plans as embryos are essentially symmetrical (i.e., the left and right side of the body are largely mirror images of each other). This symmetrical organisation 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, for example, 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 organisation 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 above-mentioned 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 as well as a disturbance of speech (G. Dax, 1863; M. Dax, 1836/1865). About 25 years later, in a usually much more widely known paper, fellow Frenchman and physician Paul Broca then 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, re-examinations of the conserved brains of some of Broca's patients using neuroimaging methods have since shown that their lesions actually extended far into neighbouring regions of what is now called Broca's area, as well as into the white matter (Dronkers et al., 2007).

In the present 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., this volume, for a review focusing on sign language).

What is "language"?

Modern linguistics distinguishes between individual *languages* as commonly understood such as, for example, 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 & 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 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 which 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 (Emmorey, 2015; Klima et al., 1979; 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 Figure 20.1 can be produced and perceived in different modalities (e.g., speech or writing), yet still 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 6,000, alphabetic systems about 3,000 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 & 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; Uddén et al., 2022; Vigneau et al., 2011; Walenski et al., 2019).

< Figure 20.1 here >

Evidence for the hypothesis that representations of utterances are indeed structured hierarchically and 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):

(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 & Trettenbrein (2021) for a more detailed discussion of hierarchy in language and its relevant to research in cognitive neuroscience.

The emerging picture in the cognitive sciences has been that the cognitive machinery which enables the generation of hierarchical syntactic structures linking meaning to a phonological form is rooted in a universal computational mechanism that is biologically determined, implemented neurally, and specific to our species (Berwick et al., 2013; Friederici et al., 2017; Hauser et al., 2002; Lenneberg, 1969). Accordingly, the cognitive specifics of the language system are understood to be determined by a “biological matrix” (Lenneberg, 1967) which enables and, at the same time, constrains the development of the language system from infancy into adulthood (Crain et al., 2016; Lenneberg, 1964, 1967, 1969; 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.) to those of neuroscience (e.g., cell assemblies, brain regions, etc.; Embick & Poeppel, 2015; Poeppel & Embick, 2013). 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., 2022).

Asymmetries in the brain

Upon first look the human brain may appear to be a rather symmetrically organised organ (Kandel & 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 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 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 (Bradshaw et al., 2017; Hervé et al., 2013; Toga & Thompson, 2003), but have not always been observed (Keller et al., 2011).

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 (Figure 20.2) based on data from the BrainMap database (Fox & 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), dorsally extending also into pre-motor 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 phonological, semantic, and syntactic content.

Beyond the expected difference between production and comprehension, different sub-components 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 which focused on the neural resources underlying either phonological, semantic, and syntactic processing in language also based on data from BrainMap (Figure 20.2, 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 sub-components of language (Vigneau et al., 2011). Amongst the three analysed sub-components, phonological processing is the least left-lateralized. In contrast, syntactic processing (i.e., the neural substrates of the cognitive machinery which 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).

< **Figure 20.2 here** >

From the meta-analyses of different linguistic domains summarized in Figure 20.2 we can conclude that there generally is a clear 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 (M. Meyer et al., 2002, 2004; Plante et al., 2002). That is, the hemispheres exhibit differential specializations for different types of phonological 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., phonological, semantic, or syntactic) recovered from, respectively imposed on different signals is nevertheless being processed predominantly in left-hemispheric networks in perisylvian cortex in the adult brain (Figure 20.3). Meta-analyses of functional studies on language processing using a variety of comprehension paradigms consistently implicate the left inferior frontal gyrus and especially the pars opercularis, superior and middle temporal gyrus, as well as posterior superior temporal sulcus as key regions subserving language processing (Price, 2010; Stefaniak et al., 2021; Vigneau et al., 2006, 2011; Walenski et al., 2019; see also Figure 20.2, top panel). These regions identified in functional studies largely correspond to the two major canonical language regions first identified in the literature on aphasia: Firstly, 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 & Dick, 2016). Secondly, so-called Wernicke's area 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 primary auditory cortex or extended the region into BA 39 and BA 40 in inferior parietal lobule; Bogen & Bogen, 1976; Tremblay & Dick, 2016; Wernicke, 1881).

< **Figure 20.3 here** >

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 & 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 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 sub-components which, in turn, have been shown to differentially recruit different parts of language-relevant networks. Accordingly, by now there is widespread agreement amongst researchers in cognitive neuroscience of language that the primarily left-hemispheric fronto-temporal networks in the human brain depicted in Figure 20.3 are involved in and, to an extent, specialised for processing linguistic information, whereas the exact details of functional associations within these regions and networks continue to be subject to extensive debate (Fedorenko et al., 2011; Fedorenko & Thompson-Schill, 2014; Friederici, 2011; Friederici et al., 2017; Friederici & Gierhan, 2013; Hagoort, 2017, 2019; Hickok, 2009; Matchin & 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 classical univariate or more recent multivariate methods. We will focus here on such 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 sub-system with the most pronounced pattern of functional lateralization to the left hemisphere (Figure 20.2) 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 for syntactic processing has been to systematically vary, step by step, the complexity of the syntactic structures (but leaving the number of words identical) such 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, 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 (L. Meyer et al., 2012) or the inferior frontal gyrus (Grewe et al., 2005; Röder et al., 2002)

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 so-called artificial grammars (e.g., Bahlmann et al., 2008; Chen, Goucha, et al., 2021; Chen, Wu, et al., 2021). 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: Firstly, 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). Secondly, 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-strutcure 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 which 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 fibre pathways in the white matter. A lot of work has focused on describing so-called direct connections between two regions, yet it should be mentioned that indirect tracts with a so-called grey 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 labelling a connection as “fronto-temporal” 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 upon 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 (Figure 20.3). 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 & 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 sub-divided into several sub-structures (Friederici & 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 fibre system or the (inferior) fronto-occipital fasciculus (Friederici & Gierhan, 2013; Gierhan, 2013; Meola et al., 2015).

Amongst these four pathways, most studies have reported the arcuate fasciculus to show a clear left-lateralization in the majority of the population (Glasser & Rilling, 2008; Paus et al., 1999; Pujol et al., 2002), 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-lateralised 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 in their sample had at least 1.5 times more streamlines for the arcuate fasciculus in the left than in the right hemisphere. In contrast, the uncinate fasciculus and sup-parts of the superior longitudinal fasciculus (i.e., the so-called SLF II and SLF III; Friederici & Gierhan, 2013; Janelle et al., 2022) have been shown to be strongly right-lateralised 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 fibre pathways and 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 as such 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 & Mayberry, 2019; see Trettenbrein et al., this volume, for in-depth discussion).

Structural differences between the left and 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, for example, 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 asymmetrical region. However, studies using a variety of structural imaging approaches have not consistently reported such a left-over-right asymmetry for Broca's area, respectively its sub-regions (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 seem to indicate a leftward asymmetry, especially for the cytoarchitecturally defined posterior portion of Broca's area (i.e., BA 44) over its right-hemispheric homologue (Amunts et al., 1999, 2003; Sprung-Much et al., 2022). These discrepancies between the 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 et al., 2022; Sprung-Much & Petrides, 2020).

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 classical 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 (Binder et al., 1996; Geschwind & Levitsky, 1968; Shapleske et al., 1999). Similarly, the superior temporal sulcus is deeper in the right than in the left hemisphere close to the area of Heschl's gyrus (Bodin et al., 2018; Leroy et al., 2015), and generally exhibits a genetically-constrained more chaotic morphology on the left 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 & Wigglesworth, 2018). Lastly, with regard to microstructure, Galuske et al. (2000) have used post-mortem neuronal tract tracing in posterior BA 22 to show that this region contained about 30 % more distinct columnar sub-systems in the left than 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 which 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, Cara, & Tettamanti, 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, moreover, 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 which, at times, used very different methodological approaches and therefore allow to draw a rather clear, converging picture: At birth, there is bilateral involvement for speech processing, then lateralization of language towards the left hemisphere increases during development leading to a dominance of the left hemisphere for language processing in adults in the vast majority of the 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 two-day-old Italian newborns heard different acoustic sequences: Either normal Italian speech or speech in which either 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 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-hemipsheric dominance has been reported as early as at three 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 left frontal cortex and left posterior superior temporal gyrus, healthy newborns displayed an interhemispheric functional connectivity between Broca's area and its right-hemipsheric homologue as well as between left superior temporal gyrus and its right-hemispheric homologue (Lohmann et al., 2010; Perani et al., 2011; see Figure 20.4). At the age of three 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.

< Figure 20.4 here >

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 tried to reduce scanning time often testing language function behaviorally outside the scanner and only performing structural scans which allow to analyze the gray matter of language-relevant brain regions and the white matter connecting these and to then correlate these structural data with behavioral data. One such study investigated the cortical thickness of the regions in the neural language network relevant in five-year-old children and six-year-old children and found that an increase of 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 age of five and six years observed in this study was larger in the left hemisphere than in the right hemispheric homologue and furthermore associated with the observed language performance at the age of seven 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 five-year-old children displayed an interhemispheric correlation of left inferior frontal gyrus with its right homologue 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 fronto-temporal connectivity in the neural network is already in place at the age of five years when measured in a so-called “task-free” setting of resting state MRI.

However, it needs some more time before the neural language network in the left hemisphere directly reacts specifically to different aspects of the language input. An fMRI study which directly investigated syntactic processes during language comprehension demonstrated a strong functional connectivity between left posterior superior temporal gyrus and left BA 44 in 6-year-olds that 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 the brain response to speech 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, a 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 four to 13 years and adults (Olulade et al., 2020): The study revealed language-related activation in the left-hemispheric language network but also in its right hemisphere homologue between the age of four to six years. During later childhood, a decrease of the involvmenet of the right hemisphere and an increase of the involvement of the left hemisphere was 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 such region-of-interest studies and proposed that there are two development stages: A first stage from birth to three years and a second stage continuing into adolescence with a possible closure roughly at the age of puberty (Friederici, 2017; Lenneberg, 1967). 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 & Friederici, 2016). It seems that phonological, prosodic and word-based processes can be dealt with by 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 three years before this developmental shift for language processing in the core language network occurs? One fMRI study investigated sentence processing in three- to ten-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 3-4-year-old children, main effects of activation for semantic and syntax were found only in the posteriorly temporal cortex and similarly so even in six-to-seven-year-olds. That is, main effects for syntax in Broca's area were only observed in nine to ten year old children as well as adults. More recently, a combined gray matter and behavioral correlation study reported a regional shift of the correlation indicating an involvement of the posterior STG in three-year-olds to 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 age 4 and 12 years with a mean age of 8.9 years allows to furher 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) towards the adult pattern involving left posterior temporal cortex and the left pars opercularis (BA 44) during development (Figure 20.5). 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 (Klein et al., 2022; Skeide et al., 2014; Skeide & Friederici, 2016), it stands to reason that this developmental shift may be related to the increasing functional specialization of the brain for processing syntactic information.

< Figure 20.5 here >

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 & 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 & 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 as such 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 five 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 ten-to-eleven 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 amongst 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 than in the right hemisphere in the adult brain (Gallardo et al., 2020; Glasser & Rilling, 2008; Paus et al., 1999; Pujol et al., 2002; Warrington et al., 2020). The asymmetry of this fiber tract during development was investigated in 183 participants ranging from five to 30 years of age including children from five to thirteen years (Lebel & Beaulieu, 2009). This study reported that fractional anisotropy and number of streamlines of the arcuate fascicle was higher in the left than the right hemisphere in most participants, independent of age. A sub-analysis of the children revealed a left lateralization of this fascicle for most children (N=53) and a 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 on 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 three months of age (Dubois et al., 2016; Leroy et al., 2011). 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 one 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 (Figure 20.6). The fiber bundle targeting the premotor cortex supports auditory-to-motor mapping allowing early vocalization in infants and may well be detectable in three-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).

< **Figure 20.6 here** >

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 develops in 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 a left hemisphere involvement 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 18-24 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 a 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 homologue 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 the 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 by 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 clear functional dissociation of semantic and syntactic processing on the cortical level emerges only gradually as part of brain maturation during childhood. The main fibre 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 fibre 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-handers showing left-lateralised language functions is derived from studies using only production tasks (Knecht, 2000; Rasmussen & Milner, 1977). In contrast, meta-analyses of language processing, usually also showing strong left-lateralisation, tend to rely on data stemming from studies using comprehension paradigms (Price, 2010; Vigneau et al., 2011; Walenski et al., 2019; see also Figure 20.2). Hence, while both speech production and language comprehension necessarily access the same linguistic competence (Chomsky, 1965; van der Burght et al., 2022) and thus recruit the language network (Friederici, 2017; Friederici et al., 2017), this does not imply that all sub-components 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 tasks-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 homologue 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 a left lateralization and others a 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 homologue. Participants exhibiting such a “crossed” activation pattern moreover showed a larger corpus callosum volume indicating stronger inter-hemispheric connectivity, allowing 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 (M. Meyer et al., 2002; Sammler et al., 2010; van der Burght et al., 2019). The reported increase 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). One the one hand, the natural world we live 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 symmetrical organization also allows for a certain degree of redundancy. On the other hand, an asymmetrical organization, in 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 to include 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 different well-known aphasic syndromes following only left but not right-hemispheric lesions to perisylvian cortex and the connecting white-matter tracts (for detailed discussions, see Raymer & Gonzalez Rothi, 2015).

Accordingly, while even semantic and phonological processing tend to show left-lateralized patterns in functional neuroimaging studies (Vigneau et al., 2011; see also Figure

20.2), the literature on development, as well as on aphasia and other neuropsychological syndromes make 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 phonological 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 hemisphere’s capabilities for semantics and phonology in comprehension and production.

The left-lateralization of language in typically developed persons then 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 neurobiological implementation. At the same time, the genetically determined biological 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 (Friederici, 2017; Lenneberg, 1967) 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 specialised 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 certain 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 fronto-temporal network connecting the posterior inferior frontal gyrus to the posterior temporal cortex via the arcuate fasciculus. This network constitutes a functional and structural asymmetry: It subserves the generation of hierarchically structured representations linking meaning and sound, develops in accordance with a genetically determined biological 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 be able to provide a more fine-grained picture of the lateralization of language and its different sub-systems.

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Figures

Figure 20.1

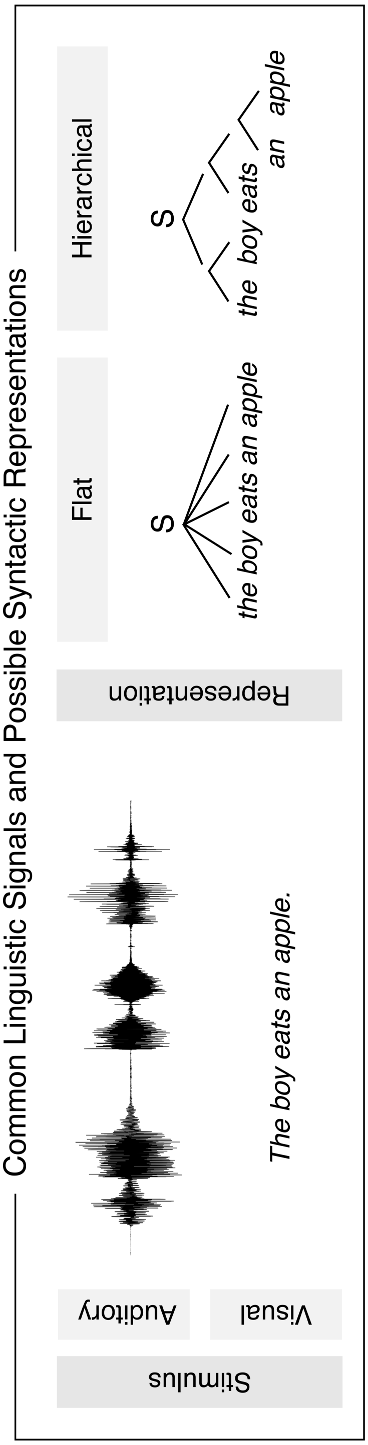

Figure 20.2

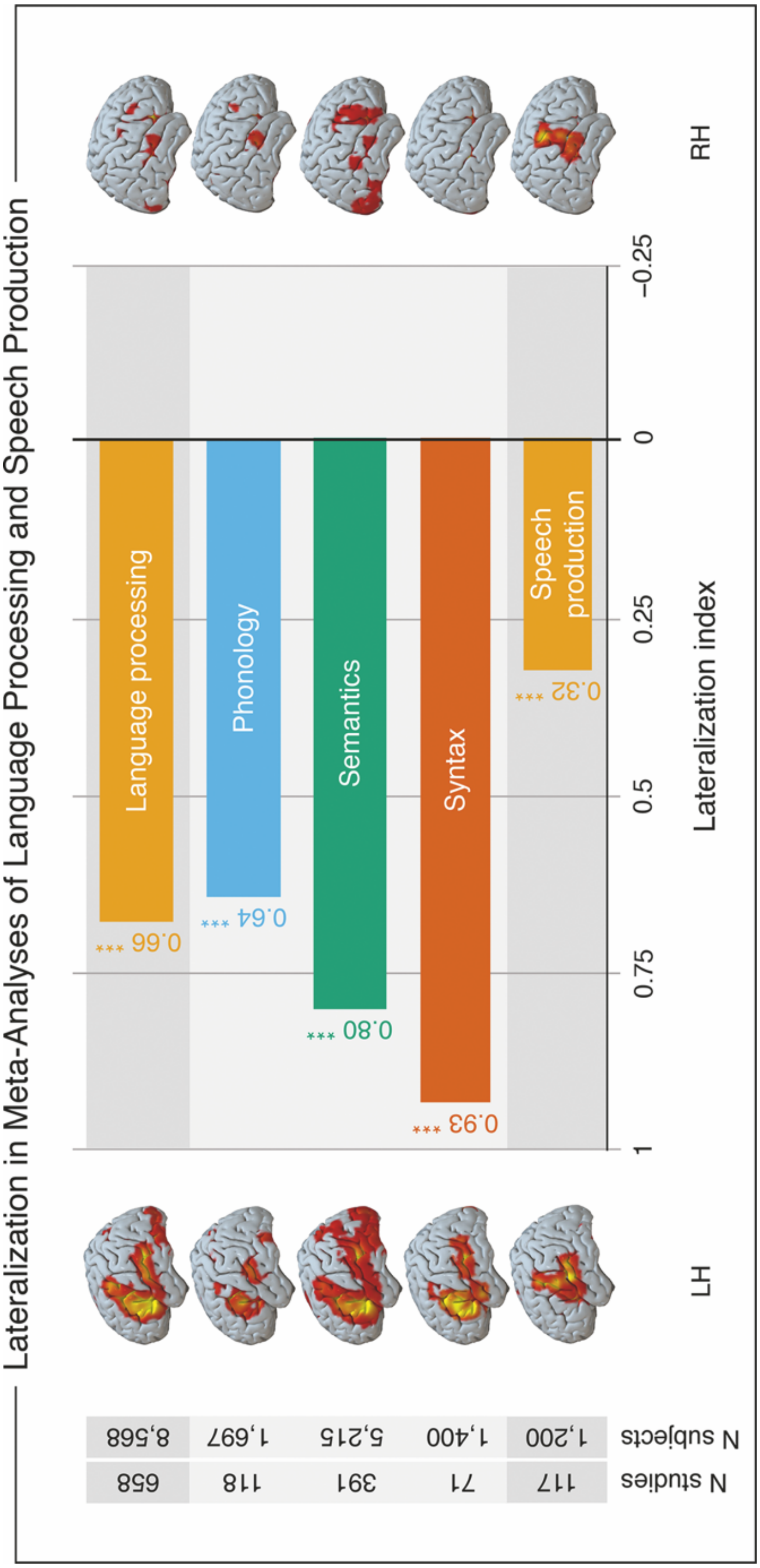
Lateralization in Meta-Analyses of Language Processing and Speech Production
LH
RH
Language processing
Phonology
Semantics
Syntax
Speech production
0.66 ***
0.64 ***
0.80 ***
0.93 ***
0.32 ***
1
0.75
0.5
0.25
0
−0.25
Lateralization index
N studies
N subjects
658
8,568
118
1,697
391
5,215
71
1,400
117
1,200

Figure 20.3

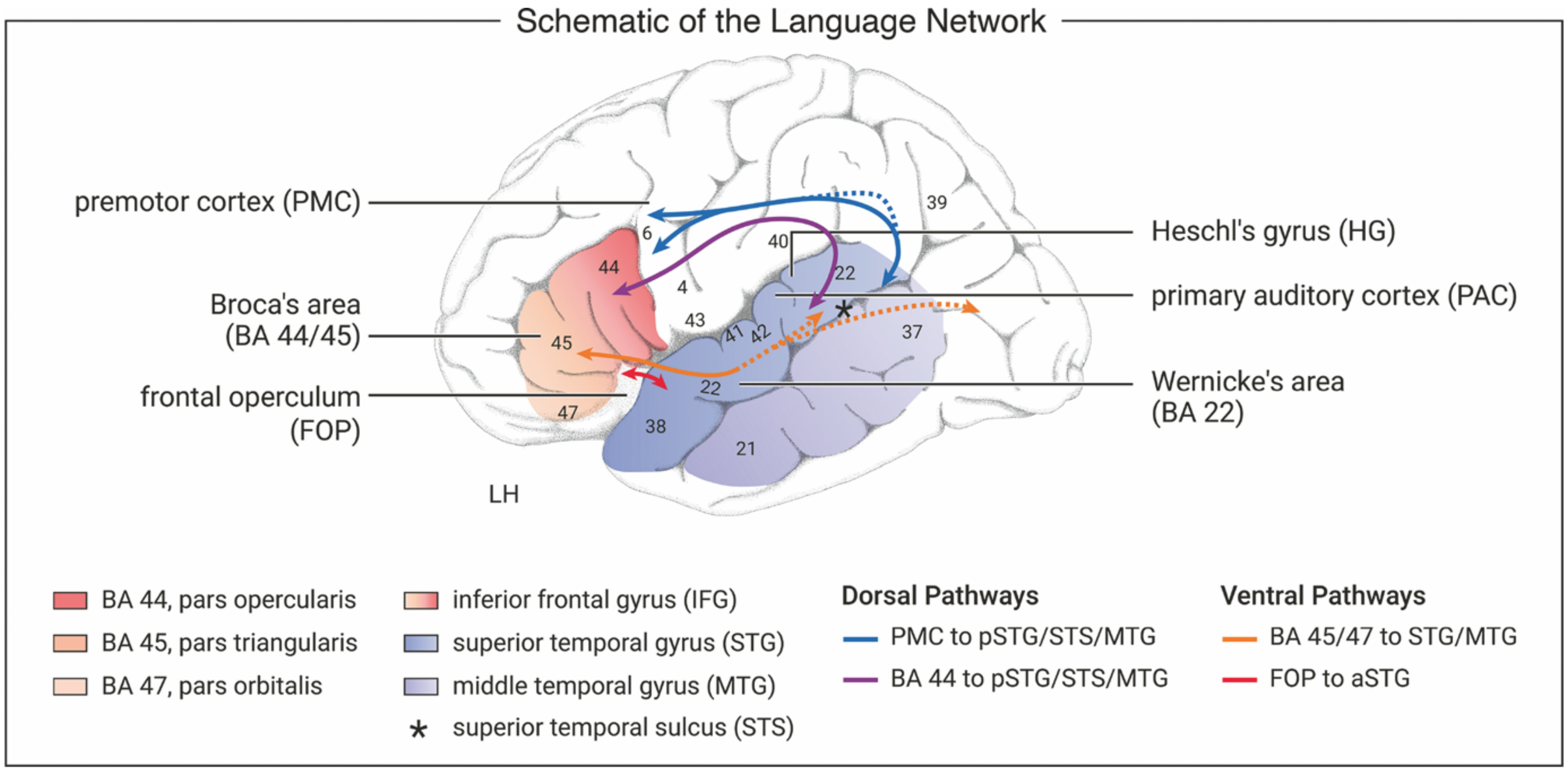
Schematic of the Language Network
premotor cortex (PMC)
Broca's area
(BA 44/45)
frontal operculum
(FOP)
Heschl's gyrus (HG)
primary auditory cortex (PAC)
Wernicke's area
(BA 22)
LH
6
44
4
43
45
47
38
40
22
41
42
22
21
37
39
*
BA 44, pars opercularis
BA 45, pars triangularis
BA 47, pars orbitalis
inferior frontal gyrus (IFG)
superior temporal gyrus (STG)
middle temporal gyrus (MTG)
* superior temporal sulcus (STS)
Dorsal Pathways
PMC to pSTG/STS/MTG
BA 44 to pSTG/STS/MTG
Ventral Pathways
BA 45/47 to STG/MTG
FOP to aSTG

Figure 20.4

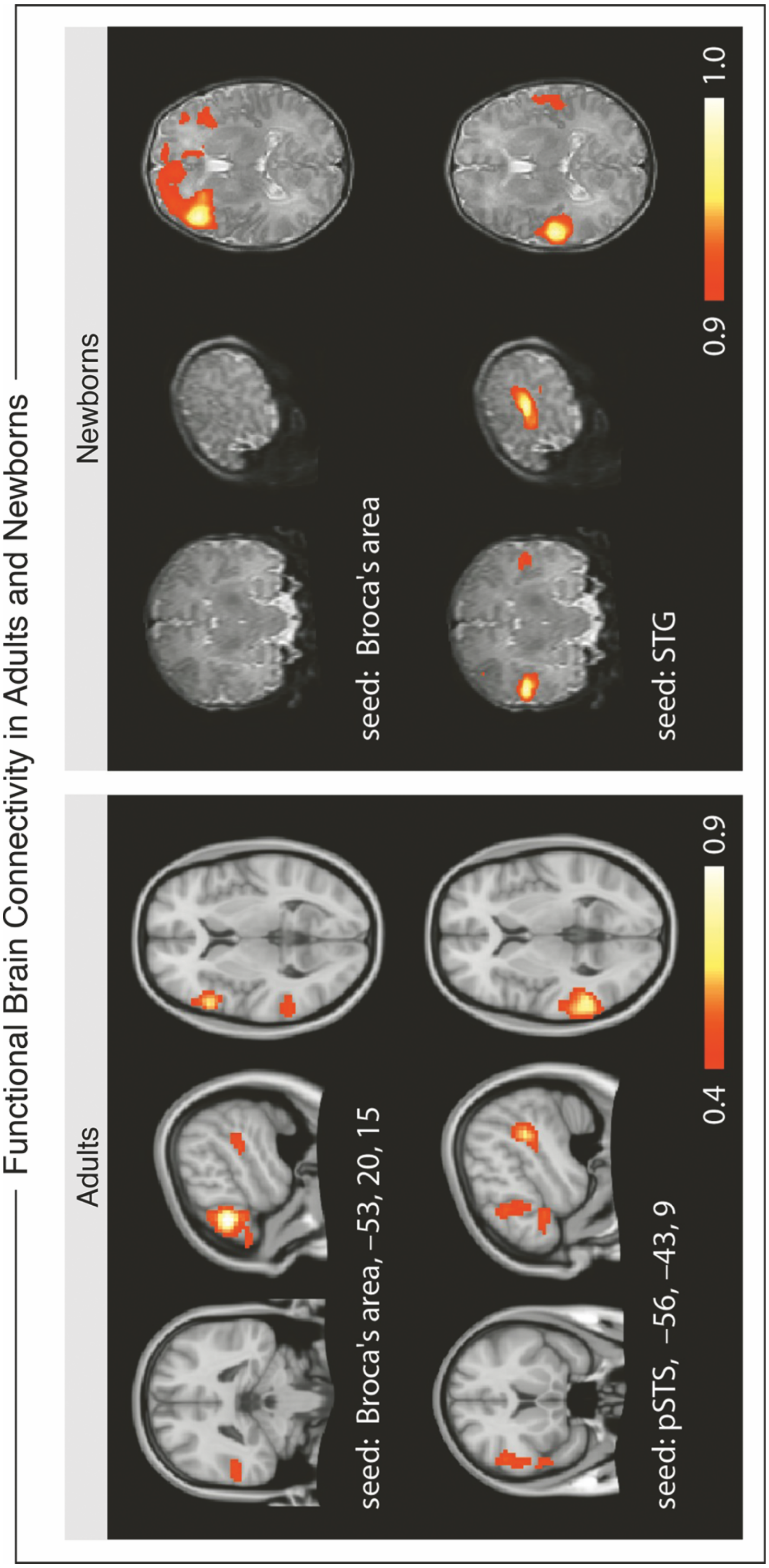
Functional Brain Connectivity in Adults and Newborns
Adults
seed: Broca's area, −53, 20, 15
seed: pSTS, −56, −43, 9
0.4
0.9
Newborns
seed: Broca's area
seed: STG
0.9
1.0

Figure 20.5

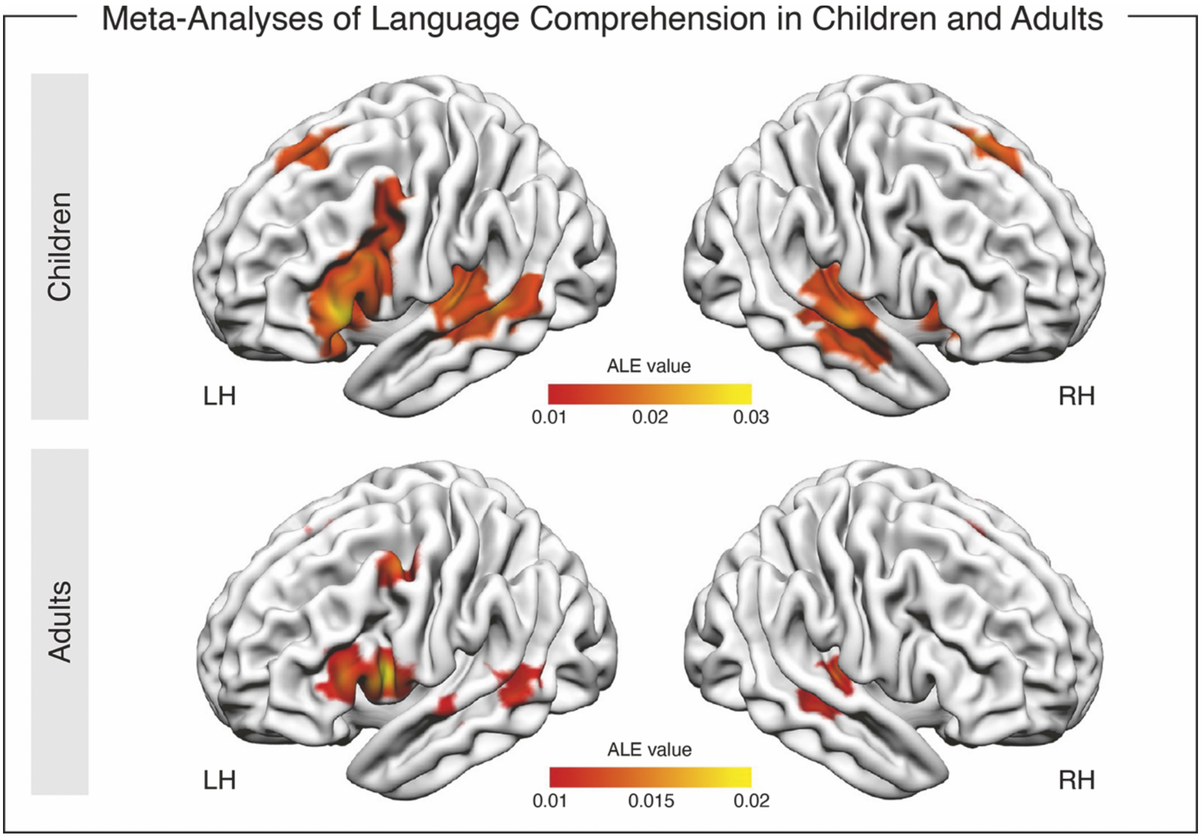
Meta-Analyses of Language Comprehension in Children and Adults
Children
LH
ALE value
0.01
0.02
0.03
RH
Adults
LH
ALE value
0.01
0.015
0.02
RH

Figure 20.6

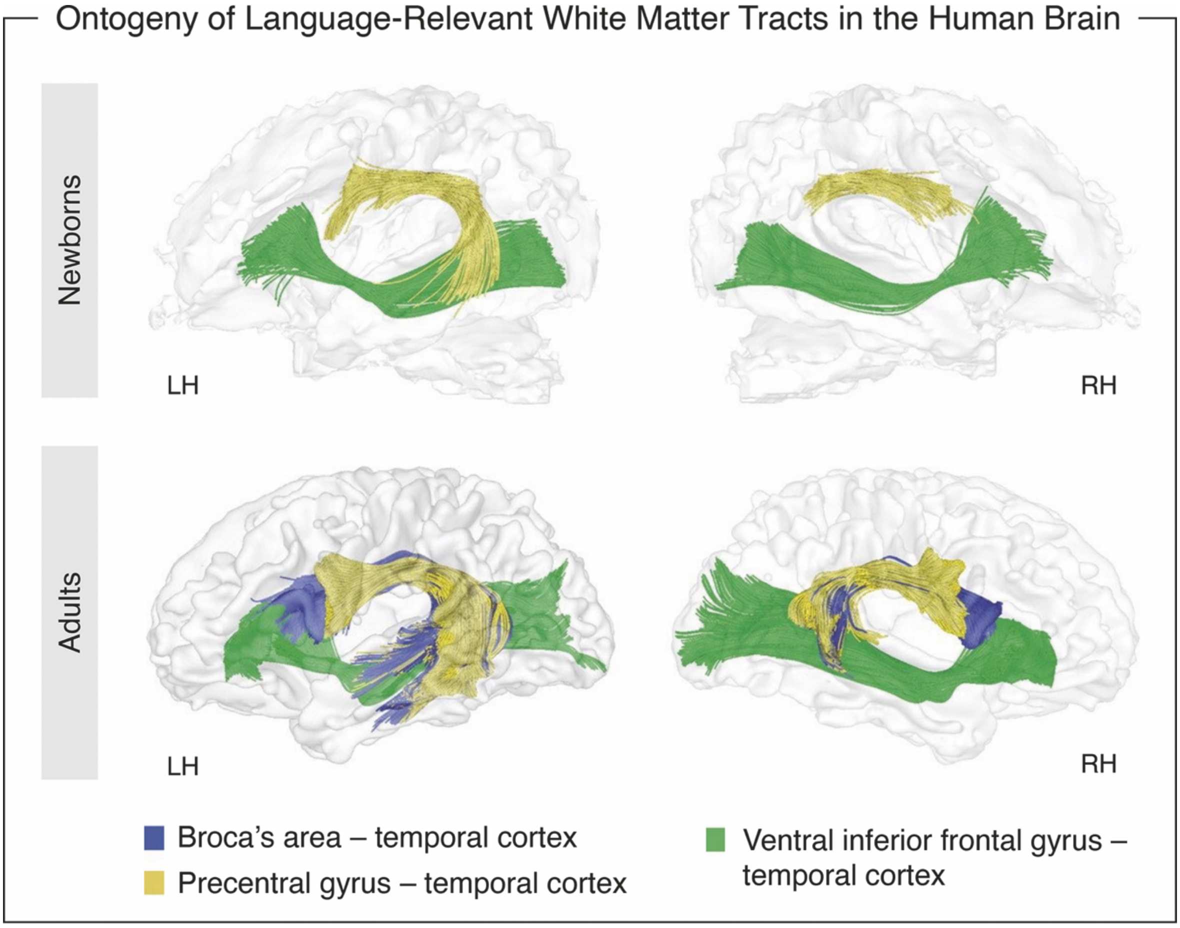
Ontogeny of Language-Relevant White Matter Tracts in the Human Brain
Newborns
LH
RH
Adults
LH
RH
Broca's area – temporal cortex
Precentral gyrus – temporal cortex
Ventral inferior frontal gyrus – temporal cortex

Figure Legends

Figure 20.1

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 & Trettenbrein (2021) and is subject to a Creative Commons (CC-BY 4.0) license.

Figure 20.2

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 & Lancaster, 2002; Laird et al., 2011) analysed 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 < .05, ** for p < .01, and *** for p < .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 (colour-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 sub-components of the language systems as identified in the taxonomy of the BrainMap database: Meta-analyses of phonological ("Cognition.Language.Phonology"; colour-coded in blue), semantic ("Cognition.Language.Semantics"; colour-coded in green), and syntactic processing ("Cognition.Language.Syntax"; colour-coded in brown). The last row (also colour-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.

Figure 20.3

Schematic of the Language Network

Schematic depiction of the left hemisphere (LH) showing anatomical landmarks and cytoarchitectonic details of language-relevant regions of cortex. Major gyri that are part of the language network are colour-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 histological 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 fibre tracts connecting these language-relevant regions of cortex dorsally and ventrally are indicated using colour-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. Illustration adapted from Friederici (2011).

Figure 20.4

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 & Tournoux, 1988). As no such coordinates are available for newborns' brains, the neuroanatomical location of the seed is given instead in the right panel. In the upper and lower row in both panels, slices are shown in the following order (from left to right): Coronal view, sagittal view, and axial view. Illustration adapted from Perani et al. (2011).

Figure 20.5

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 ($p < .05$, cluster-wise family-wise error [FWE] corrected) are shown. The colour bar represents the ALE value of any given voxel, that is, its degree of non-random 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 ($p < .05$, cluster-wise FWE-corrected) and their associated ALE value (colour bar), that is, the degree of non-random convergence in activation between experiments at any given voxel. Both panels show the left hemisphere (LH) as well as the right hemisphere (RH). Illustration adapted from Enge et al. (2020).

Figure 20.6

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 in 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 (colour-coded in green). Only in adults two dorsal pathways can be detected: The arcuate and superior longitudinal fasciculus connecting temporal cortex to Broca’s area (colour-coded in blue) and premotor cortex (colour-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. Illustration adapted from Perani et al. (2011).