11 A Neural Blueprint of Language Acquisition

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Understanding language is a sophisticated cognitive ability requiring the brain to integrate multiple types of complex information. In the present chapter, I introduce a neural blueprint of language acquisition, to explain where, when, and how the maturing brain masters the language processing steps that are typical of adult processing. The development of these capacities can be roughly subdivided into two developmental stages: a first stage extending over the first three years of life that mainly involves low-level processes, and a second stage continuing into adolescence that involves high-level processes. *Low-level processing* describes the computation of language representations from the sensory input, whereas *high-level processing* denotes the further analysis of this information under the influence of more complex representations and mechanisms.

1. The Adult Cortical Language Network

A description of the neuroplastic changes of the developing language system requires a description of the neural processes involved in adult language processing. A neurocognitive model of language comprehension provides an inventory of cognitive capacities that have to be acquired by a developing speaker and, moreover, an inventory of the neuronal circuits that have to mature until they can serve their specific functions and reach their full processing efficiency. The present section will focus on areas that have been repeatedly implicated as being functionally specialized for language. An overview of domain-general areas that contribute to language comprehension (e.g., brain areas supporting working memory or cognitive control) will not be considered here (for a review, see Fedorenko & Thompson-Schill, 2014; see also part VI of this volume).

Two comprehensive neurolinguistic models of sentence comprehension covering the entire processing cascade, from perception to interpretation, have been recently proposed: the *dual-stream* model by Friederici (2012) and the *memory, unification, control* model by Hagoort (2013). Both models assume that acoustic, syntactic, and semantic processing levels are fundamental elements of the human language faculty. There is also a general agreement that the incoming speech signal initially undergoes spectrotemporal analyses in the auditory cortex and its vicinity (mid superior temporal gyrus [STG]/superior temporal sulcus [STS]). However, the two models differ in their categorization of the neural implementation of subsequent phonological, syntactic and semantic processes. Moreover, unlike the memory, unification, control model, Friederici's model comprises a suprasegmental acoustic processing level. The dual-stream model will be outlined first before turning to the memory, unification, control model. The dual-stream model will form the conceptual basis for the later perspective on language acquisition.

1.1. Language Comprehension as Dual-Level, Dual-Stream Processing

1.1.1. Low-level processes In Friederici's model, language comprehension is initially driven by low-level processes that are triggered early (with onsets between 20 and 120 ms after an utterance is heard) and completed rapidly (with durations of usually not more than 30–60 ms). At the earliest stage of low-level processing, the acoustic features of phonemes (single sound segments) of each word are extracted and analyzed in the bilateral STS (Hickok & Poeppel, 2007; Overath, McDermott, Zarate, & Poeppel, 2015). If syllables at salient positions within a word (i.e., at the beginning or at the end) provide an unambiguous cue for rapidly reconstructing the word as whole, phonological word forms can be detected within a time window of 20–50 ms (DeWitt & Rauschecker, 2012). Between 40 and 90 ms after utterance onset, phonological word forms undergo morphosyntactic categorization, that is, they are sorted into distinct syntactic groups (such as noun, verb, or preposition) (Herrmann, Maess, Hahne, Schröger, & Friederici, 2011). In parallel, lexical-semantic categorization, which is necessary to determine whether a wordlike acoustic form can be semantically interpreted, occurs between 50 and 80 ms (MacGregor, Pulvermüller, van Casteren, & Shtyrov, 2012) in the left anterior (a) STS and aSTG (MacGregor et al.; Visser, Jefferies, &

Lambon Ralph, 2010). Note that these early decoding and categorization processes run fully automatically and cannot be consciously controlled.

Once an interpretable word form is identified, the corresponding entry in the mental lexicon (carrying semantic and word category information) can be accessed and retrieved between 110 and 170 ms. This process is associated with neural activity in the left aSTG, left aSTS, the left middle temporal gyrus, and several other regions widely distributed over the cortex (Binder, Desai, Graves, & Conant, 2009; Huth, de Heer, Griffiths, Theunissen, & Gallant, 2016; MacGregor et al., 2012; Mitchell et al., 2008). In parallel, as soon as syntactic categories are identified, phrase structures can be built in the left aSTG and aSTS (Brennan et al., 2012), possibly together with the most ventral part of the inferior frontal cortex (Snijders et al., 2009), between 120 and 150 ms after the onset of the utterance (Herrmann et al., 2011).

1.1.2. High-level processes According to Friederici (2012), high-level language comprehension is characterized by processes that occur relatively late (with onsets usually between 200 and 600 ms after the utterance) and proceed relatively slowly (with durations of at least 150 ms) compared with low-level comprehension. Although often running automatically to ensure rapid communication, all of these processes are consciously controllable. Between 200 and 400 ms (Lau, Phillips, & Poeppel, 2008), lexical information is extracted from the left aSTG and aSTS and transferred along the ventrally located inferior fronto-occipital fasciculus (IFOF) (Weiller, Bormann, Saur, Musso, & Rijntjes, 2011) by Brodmann's area 45 (BA45) and BA47 of the left inferior frontal gyrus (IFG) (Binder et al., 2009; Newman, Ikuta, & Burns, 2010; Rodd, Davis, & Johnsrude, 2005), where semantic ambiguity and semantic relations between lexical items are determined in interaction with the inferior parietal cortex (Obleser, Wise, Dresner, & Scott, 2007). At 300 to 500 ms, morphosyntactic information is retrieved from the left aSTG and aSTS by the frontal opercular cortex and BA44, which support the rule-based construction and ordering of complex phrases and sentences (Friederici & Gierhan, 2013). It can be assumed that this information is transferred ventrally along the uncinate fasciculus (Friederici & Gierhan, 2013), but this hypothesis remains to be verified experimentally. BA44, together with the left posterior STG and STS, also supports the construction of a sentence-level argument structure, that is, verb-noun arrays created to produce a meaningful sentence (Dapretto & Bookheimer, 1999; Dick & Tremblay, 2012; Friederici, 2011; Makuuchi, Bahlmann, Anwander, &

Friederici, 2009; Meyer, Obleser, Anwander, & Friederici, 2012; Newman et al., 2010). Effective connectivity analyses modeling the causal functional interactions between brain areas during task performance have also revealed that the processing of sentence-level syntax is driven by the left IFG modulating the left posterior superior temporal cortex (den Ouden et al., 2012; Makuuchi & Friederici, 2013). Whether language information stays activated in the temporal cortex under the influence of the inferior frontal cortex remains to be directly tested by future studies (Snijders et al., 2009).

Prosodic information (e.g., intonation, tone, stress, and rhythm information) is processed in a time window of 200 and 500 ms after the utterance onset (Friederici, 2011), predominantly in the right STG and the right IFG (Ethofer et al., 2012; Frühholz, Ceravolo, & Grandjean, 2012; Sammler, Grosbras, Anwander, Bestelmeyer, & Belin, 2015).

After at least 600 ms (Friederici, 2012; Hagoort, 2013), all information is assumed to be integrated into an interpretable conceptual representation in the left posterior STG and STS (Friederici, 2011, 2012), with a potential involvement of the left IFG (Hagoort, 2013; Snijders et al., 2009). To achieve this, syntactic information is exchanged dorsally along the arcuate fasciculus (AF), between BA44 and the posterior (p) STG and STS, and semantic information is exchanged ventrally along the IFOF between BA45 and BA47 and the pSTG (Friederici, 2011, 2012; Newman et al., 2010; Saur et al., 2008; Weiller et al., 2011; Weiller, Musso, Rijntjes, & Saur, 2009; Wilson et al., 2011). Note that the dorsal connection between BA44 and the pSTG and STS that is involved in syntactic processes (Friederici, Bahlmann, Heim, Schubotz, & Anwander, 2006) can be anatomically separated from a second dorsally located fiber bundle that connects the pSTG and STS with the premotor cortex and is involved in the repetition of speech (Saur et al.) (figure 11.1).

1.2. LANGUAGE COMPREHENSION AS MEMORY, UNIFICATION, AND CONTROL PROCESSING CYCLES Hagoort (2013) assumed that auditory language comprehension is driven by multiple processing cycles that are repeated until an utterance can be interpreted. The starting point of the first stage of the first cycle is the arrival of the speech signal in the left primary auditory cortex. Subsequently, along a dorsal-to-ventral gradient in the left posterior temporal cortex, information about acoustic-phonological properties is retrieved from an area covering the left pSTG/STS, then information about syntactic properties is retrieved from a region spanning the left pSTS to the left posterior middle temporal sulcus. Finally, information about conceptual
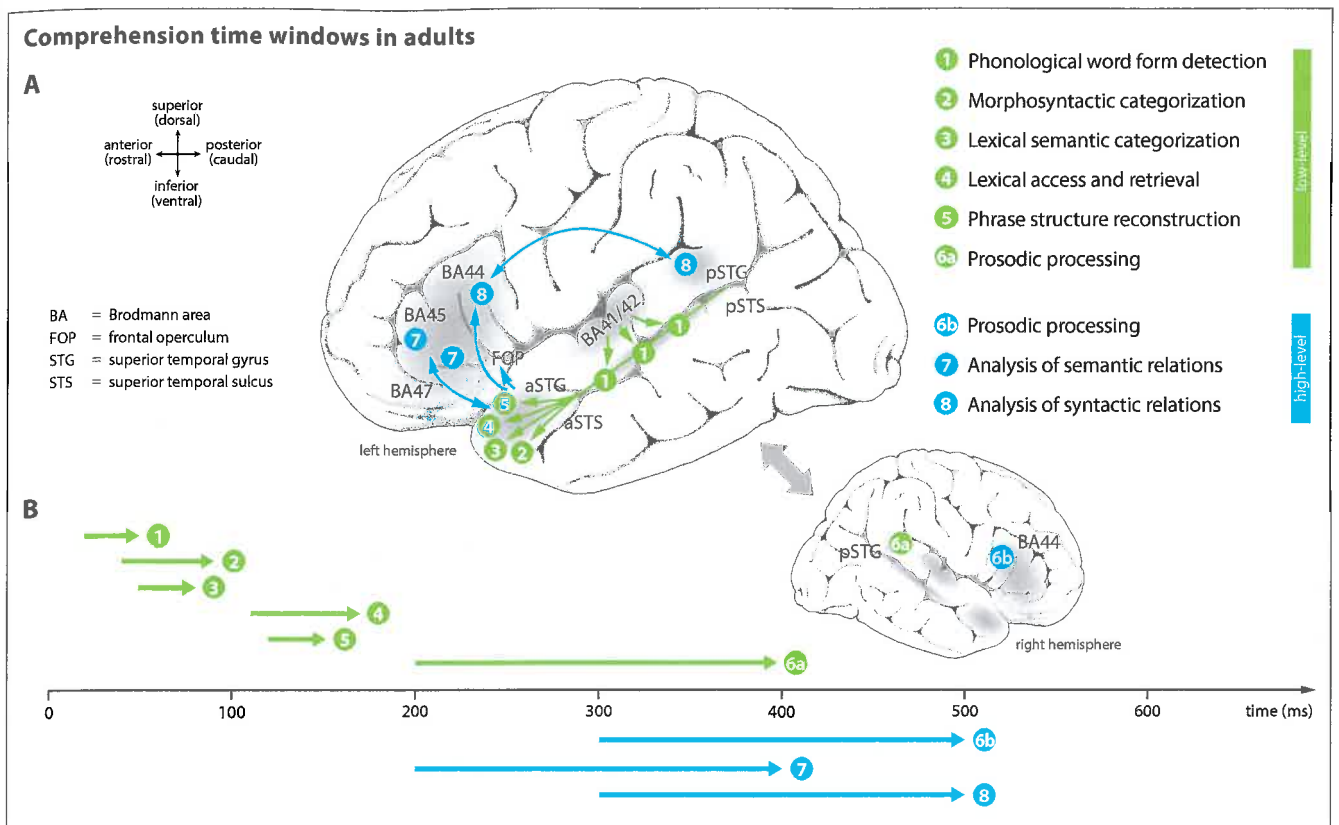
FIGURE 11.1   The auditory language comprehension network of the adult brain. (A) Gray matter areas in the left perisylvian cortex and their respective contributions to the main stages (1–8) of auditory language comprehension. Arrows indicate the assumed flow of information along the interconnecting white matter fiber tracts. "Low-level" processes are colored in green and "high-level" processes are colored in blue. (B) Typical time windows (in milliseconds) of the processing phases underlying auditory language comprehension. All values are approximate and subject to interindividual variation. (1) Phonological word forms are detected in the left STS within 20–50 ms after the utterance onset by extracting acoustic features of the raw signal delivered by the auditory cortex (DeWitt & Rauschecker, 2012; Hickok & Poeppel, 2007; Overath et al., 2015). (2) Subsequently, phonological word forms are categorized morphosyntactically between 40 and 90 ms (Herrmann et al., 2011) and (3) also categorized semantically between 50 and 80 ms in the left aSTS and aSTG (MacGregor et al., 2012; Visser et al., 2010). (4) Lexical items associated with the phonological word forms are retrieved at around 110–170 ms by the left aSTG and aSTS in an interplay with additional widespread cortical regions (Binder et al., 2009; Huth et al., 2016; MacGregor et al.; Mitchell et al., 2008). (5) In parallel, phrase structures are built at 120–150 ms in the left aSTG and aSTS (Brennan et al., 2012; Herrmann et al.; Snijders et al., 2009). (6a) Phrase-level prosody (e.g., phrasal intonation and word stress) is processed within 200–400 ms after the utterance in the right pSTG (Friederici, 2011). (6b) Sentence-level prosody is processed in a time window of 300–500 ms after the utterance in the right IFG (Ethofer et al., 2012; Frühholz et al., 2012; Sammler et al., 2015). (7) Between 200 and 400 ms, lexical information is transferred from the left aSTG and aSTS along the ventrally located IFOF to BA45 and BA47 of the left IFG, where semantic relations between lexical items are determined (Binder et al.; Lau et al., 2008; Newman et al., 2010; Rodd et al., 2005; Weiller et al., 2011). (8) At 300–500 ms after the utterance, phrase structure information is transmitted ventrally from the left aSTG and aSTS, along the uncinate fasciculus, to the frontal opercular cortex and to BA44 in the left IFG (Friederici & Gierhan, 2013). BA44 is involved not only in ordering phrases but also in building up argument structures together with the left pSTG and pSTS, which are connected to BA44 via the left AF (Dapretto & Bookheimer, 1999; Dick & Tremblay, 2012; Friederici, 2011; Makuuchi et al., 2009; Meyer et al., 2012; Newman et al.). As soon as an utterance has gone through these processing steps, the left pSTG and pSTS, potentially together with the left IFG, can start integrating all information into an interpretable conceptual representation (Friederici, 2011, 2012; Hagoort, 2013; Snijders et al., 2009).

semantic properties of the signal is retrieved from an area extending from the left posterior middle temporal gyrus to the left posterior inferior temporal gyrus. Depending on the type of linguistic information, another dorsal-to-ventral gradient activates in the left inferior parietal cortex, with phonological representations retrieved from the left supramarginal gyrus, syntactic representations retrieved from an area between the left supramarginal gyrus and the left angular gyrus, and semantic representations retrieved from the angular gyrus. These retrieval mechanisms, the core of the so-called memory component, operate sequentially at different but partially overlapping time scales until they are completed at around 250 ms. During the second stage of the first cycle, phonological, syntactic, and semantic information is relayed from the left posterior temporal and inferior parietal cortex to the left IFG over a feedforward pathway that includes the superior longitudinal fasciculus and the AF. The IFG in turn crucially supports the maintenance of the information due to its ability for self-sustained activity. Furthermore, it is involved in the rule-constrained combination of linguistic elements from all three domains along a posterior-dorsal to anterior-ventral gradient, with the posterior-dorsal BA44 and the neighboring ventral BA6 unifying phonological word forms into intonational phrases, the anterior-ventral BA44 and posterior-dorsal BA45 linking together syntactic phrases, and the anterior-ventral BA45 and BA47 integrating lexical items into the discourse context. This so-called unification component selects the optimal candidates out of multiple possible environments and optional alternative links. As soon as the selection procedure is over, the information is sent back from the left IFG to the left posterior temporal cortex along a slow feedback pathway comprising the uncinate fasciculus, the IFOF, and the inferior longitudinal fasciculus. This occurs until the first cycle is completed at around 400 ms. This pathway strengthens the role of the IFG for the maintenance of linguistic information. Usually, full comprehension requires additional recurrent feedforward and feedback signaling cycles between the posterior temporal and the inferior frontal cortex. The higher the competition among suitable candidate combinations, that is, the higher the unification load, the longer it takes to compute the final interpretation of an utterance. Finally, successful comprehension is guided by a so-called control system represented in the anterior cingulate cortex, the dorsolateral prefrontal cortex, and the inferior parietal cortex. The system subserves attentional and pragmatic operations such as attention allocation to a target language during language switching or turn taking in a conversation (see part VI for further details).

2. Methods for Studying the Neural Basis of Language Acquisition

Noninvasive electroencephalography (EEG) is the most frequently employed neurophysiological recording technique in infants and children. Electric currents induced by neuronal activity are recorded directly on the scalp, so that children can move relatively freely during the measurements. Moreover, some paradigms applied in EEG experiments do not even require the participant's attention. These factors make this method especially useful for experiments with newborns and young infants (Benasich et al., 2006; Guttorm et al., 2005). EEG has a high temporal resolution of the order of milliseconds, but its spatial resolution on the scalp is limited to around 5 cm when modeling 64 electrodes (Burle et al., 2015). Additionally, EEG recordings on the scalp have a limited penetrance, making it hard to study subcortical structures. However, successful examinations of childrens' auditory brain stem responses are documented in the literature (Johnson, Nicol, Zecker, & Kraus, 2008).

Depending on ethical regulations, newborns can undergo MRI and children as young as three years can solve simple tasks in the scanner (Skeide, Brauer, & Friederici, 2014). Functional MRI (fMRI) reveals information about the magnitude and the location of neural activity changes in response to external stimulation or intrinsic fluctuations at rest. These neural activity changes are quantified as blood-oxygen-level-dependent signal changes based on the effect of neurovascular coupling. Structural MRI provides morphometric and geometric features of the neural gray and white matter, such as its volume, density, thickness, and surface area. Finally, diffusion-weighted MRI is used to reconstruct the trajectory of white matter pathways interconnecting brain areas. Fractional anisotropy (FA), a measure of tissue diffusivity, can be combined with structural MRI to determine the degree of myelination or the density of fiber tracts, which is in turn related to their maturity. MRI provides a spatial resolution of at least 1 mm, which allows conclusions to be drawn about which brain areas are involved in a particular process. However, the temporal resolution of MRI is limited to about 1 s (Kim, Richter, & Ugurbil, 1997). MRI of healthy young adults has become a routine investigation in neuroscience, but it is difficult to acquire these data in children (Raschle et al., 2012). In order to reduce dropout rates, young participants are prepared in a mock scanner

prior to the actual measurement (see https://www.cbs.mpg.de/abteilungen/neuropsychologie/kindersprachlabor). Mock scanner training helps to familiarize the child with the MR procedure and the experimental tasks it has to solve. In practice, the experimenter embeds the training in a game, involving the parents if necessary. Motion sensors that stop the presentation on the screen in case of head movement have proved their worth when instilling in young participants the necessity of lying still in the scanner. Such familiarization should be accompanied by encouraging feedback to create a constructive awareness of the experimental setting. It is important to simulate the actual measurement session as precisely as possible so that the children do not get distracted or scared in the real MR environment. Although training sessions are time-consuming, they markedly reduce dropout rates to less than 40% in three- to four-year-old children and less than 10% in six- to seven-year-old children. An optimal result with respect to data quantity as well as data quality is achieved in a child-friendly, low-noise scanner with a wide tube.

Near-infrared spectroscopy is another method used to measure functional brain activity. The technique is based on 700- to 900-nm wavelength light that penetrates the scalp and is then absorbed differently by cortical areas as a function of their activity-related blood oxygenation. Like EEG, near-infrared spectroscopy allows for a more flexible recording of functional responses than MRI since the registration system is mounted directly on the participant's head. This advantage has made it an important method for language acquisition research in infants and young children. However, the spatial resolution of near infrared spectroscopy is lower than that of fMRI, while its temporal resolution is similarly poor.

3. The Developing Cortical Language Network

3.1. Developing Low-Level Processes of Language Comprehension In this section, we describe the ontological unfolding of low-level language processing in the first three years of life. The skills acquired during this developmental phase enable infants to segment the speech input into phonological word forms. On the basis of this capacity, they can associate phonological word forms with lexical representations that can be semantically categorized. Moreover, the child acquires the ability to sort words into syntactic categories and to group words into phrase structures. A mechanism for integrating syntactic and semantic information to interpret an utterance is established from the second year of life on, at the latest.

3.1.1. Detection of phonological word forms Embryos gather their first experiences with speech in utero (Schnupp, Nelken, & King, 2011). A recent near-infrared spectroscopy study found that preterm infants born between 28 and 32 weeks of gestation are able to detect a deviant phoneme in a sequence of otherwise identical phonemes. These individuals showed hemodynamic mismatch responses in the bilateral posterior superior temporal cortex and the inferior frontal cortex in response to the deviant phoneme (Mahmoudzadeh et al., 2013). Remarkably, it seems that this basic phoneme discrimination capacity is already present when most neurons are still located in the fetal subplate and have not yet migrated into their cortical target layers, as this maturational step is only completed after the 32nd week of gestation. It is unlikely that early phonological skills are solely the result of prenatal environmental experience, since sounds at frequencies above 300 Hz are strongly attenuated in utero. Given this level of acoustic degradation, fetuses in the womb can at best only discriminate between vowels (with lower frequency boundaries at around 200 Hz) but not between more subtly differing consonants, which in speech typically have higher frequencies starting at around 300 Hz (Gomez et al., 2014; Partanen et al., 2013). Further studies suggest that even though preterm infants experience an earlier and richer exposure to speech that is no longer degraded by maternal tissue, speech perception skills in preterm infants are not more advanced than those of age-matched full-term infants (Peña, Pittaluga, & Mehler, 2010; Peña, Werker, & Dehaene-Lambertz, 2012). These findings support the view that the primary, intrauterine speech perception skills are likely to be driven by genetic factors that bias the auditory processing system toward language-specific frequency spectra of the acoustic input. Nevertheless, active exposure to auditory stimuli is crucial for normal language acquisition, as it facilitates the differentiation of the sounds in the child's language environment (Benasich, Choudhury, Realpe-Bonilla, & Roesler, 2014; Kuhl, 2004; Werker & Hensch, 2015; Werker & Tees, 1984).

When listening passively to speech, full-term newborns show strong interhemispheric synchronization of hemodynamic activity in the bilateral posterior STG, but no intrahemispheric synchronization of hemodynamic activity in the left posterior STG and the left IFG, as has been documented in adults (Perani et al., 2011). However, left-hemispheric frontotemporal activity is documented by the age of three months. At this age, infants passively listening to speech show activity bilaterally in the mid and posterior STG during the first 3 s after stimulus onset, and in inferior frontal

premotor regions between 7 and 9 s (Dehaene-Lambertz et al., 2006).

These functional findings in newborns (Perani et al., 2011) and three-month-olds (Dehaene-Lambertz et al., 2006) can be reconciled when considering the structural connectivity pattern in adults derived by diffusion-weighted MRI tractography. Specifically, adults exhibit two dorsal fiber tracts that interconnect the posterior temporal cortex: one that projects to the premotor cortex, and one that projects to BA44 of Broca's area (Dubois et al., 2015; Perani et al., 2011). In newborns (Perani et al., 2011) and two- to five-month-old infants (Dubois et al., 2015), the dorsal fiber tract to the premotor cortex is already myelinated, but the one reaching into Broca's area is yet to be myelinated. The pathway that projects to the premotor cortex supports not only the integration of sensory and motor representations during the babbling phase (Dubois et al., 2015; Perani et al., 2011), but the information fed back from the premotor cortex to the temporal cortex may also be crucial for establishing phonemic representations. This is suggested by the observation that six-month-old infants cannot distinguish unfamiliar phonemes from one another when they are prevented from moving their tongue tips to articulate these phonemes (Bruderer, Danielson, Kandhadai, & Werker, 2015). Similar work in adults corroborates the view that this auditory–motor link is not only important for language production but also for language comprehension (Mottonen & Watkins, 2009).

Importantly, when newborns hear a sentence, more activity is observed in the right mid STG than in the left mid STG (Perani et al., 2011). A similar lateralization effect was observed in the temporoparietal cortex of sleeping three-month-old infants (Homae, Watanabe, Nakano, Asakawa, & Taga, 2006). Given that, in adults, the right mid STG is known to support prosodic processing (Ethofer et al., 2012; Frühholz et al., 2012), this finding indicates that newborns not only are sensitive to segmental (phonological) information, but also they are sensitive to suprasegmental (prosodic) information in a sentence (Perani et al., 2011).

The infant's sensitivity to prosody forms the basis for learning how to segment the auditory stream into words, according to the specifics of the target language (Friederici, Friedrich, & Christophe, 2007). Event-related potential (ERP) work reveals that at six months of age, infants only recognize words that have previously been accentuated (that is, marked as acoustically prominent by increasing sound pressure and frequency) but not if they have merely been repeated. It is only at 12 months of age that infants no longer rely on accentuation to detect phonological word forms

(Männel & Friederici, 2013). Interestingly, this trajectory coincides with the decrease in the infant's ability to discriminate phonemes that do not belong to the standard inventory of their native target language, as indicated by different patterns of neural oscillations (Bosseler et al., 2013; Gervain, 2015; Kuhl, Ramirez, Bosseler, Lin, & Imada, 2014; Ortiz-Mantilla, Hämäläinen, Musacchia, & Benasich, 2013). The declining flexibility in recognizing phonemes is known as an instance of perceptual narrowing (Pons, Lewkowicz, Soto-Faraco, & Sebastian-Galles, 2009). For example, whereas before the age of six months, English-learning infants can distinguish between not only English phonemes, but also Hindi phonemes, they lose the ability to discriminate Hindi phonemes in the second half year of life (Werker & Tees, 1984). Crucially, losing this ability goes hand-in-hand with an increased sensitivity for acoustic differences between phonemes of the native language (Kuhl et al., 2006).

In the mature brain, suprasegmental prosodic information is processed at the sentence level in the right STG and the right IFG. A similar pattern of dissociable hemodynamic responses in the right hemisphere (relating to prosodic information) and in the left superior temporal cortex (relating to segmental phonological processing) has been observed in four-year-old children (Wartenburger et al., 2007). It is likely, however, that this level of specialization is reached earlier during development. This hypothesis should be tested in follow-up experiments involving younger children.

In sum, language acquisition starts in utero, when the embryo gathers first experiences with acoustic information. Infants learn to discriminate the phonemes of their target language in the first half year of life. From six months of age onward, they are able to use prosodic information to segment speech into phonological word forms. These skills are assumed to be based on the interplay of the bilateral superior temporal auditory system and the inferior frontal motor system.

3.1.2. Lexical access and semantic categorization The refinement of speech segmentation skills in the first half of life provides the basis for associating phonological word forms with objects in the environment, an ability that has indeed been documented in infants as young as six months (Bergelson & Swingley, 2012). Nine-month-old infants can generalize the meanings of single words into lexical categories according to visual features of the objects they describe, such as their color and shape. At this age, lexical-semantic learning is dependent on the consolidation of recent episodic memory traces during sleep (Friedrich, Wilhelm, Born, &

Friederici, 2015). Support for this finding comes from adult fMRI experiments that suggest that the retrieval of lexical items that were acquired early in life is controlled by a domain-general episodic memory area (the precuneus), whereas the retrieval of later-learned lexical items is controlled by specialized language areas (BA45 and BA47) (Fiebach, Friederici, Müller, von Cramon, & Hernandez, 2003).

An adultlike N400 response that is associated with semantic congruency evaluation can be elicited at ~12 months in early talkers or ~18 months in normal talkers both in the EEG (Friedrich & Friederici, 2010) and the magnetoencephalography (MEG) (Travis et al., 2011) by employing a picture-word priming task. Source localization analyses have revealed that the MEG signal corresponding to the N400 in this task originates mainly from mid and posterior portions of the left temporal cortex (Travis et al., 2011), similar to the pattern found in the adult brain (Lau et al., 2008). Note that a precursor component of the N400 with a later onset at around 600 ms can already be observed at nine and even at six months of age (Friedrich & Friederici, 2011; Junge, Cutler, & Hagoort, 2012). Eighteen-month-old infants seem to learn new words by simultaneously evaluating phonological features and conceptual-semantic and syntactic categories. Indeed, at this age, toddlers looked significantly longer at novel picture–word pairs if the words were from different syntactic and semantic categories to those of a phonologically similar word they had known before (Dautriche, Swingley, & Christophe, 2015).

3.1.3. Syntactic categorization and phrase reconstruction

There is behavioral evidence that six-month-old infants are already able to recognize phrases if the speech input carries reliable prosodic cues. They detect noun phrases (for example, *new watches for men*) and verb phrases (for example, *buy the whole supply*) if the syntactic phrase boundary coincides with the prosodic phrase boundary, which in languages like English or German is marked by lengthening of the final syllable and the pause that succeeds it (Soderstrom, Seidl, Nelson, & Jusczyk, 2003). ERP work has shown that, by the age of five months, infants are able to "chunk" speech input into phonological phrases if the pause (a salient acoustic cue) is available, but not if the pause is absent (Männel & Friederici, 2009). An ERP component called the *closure positive shift*, which is associated with the detection of the phonological clause boundary, only emerges in the third year of life and reaches an adultlike appearance at six years of age when children have acquired more advanced syntactic knowledge (Männel & Friederici, 2011).

It is possible that an interhemispheric network comprising the left aSTS and aSTG and the right STG, which are connected by posterior transcallosal fibers, underlies six-months-olds' skills to detect phrase structures using prosodic cues. Low-frequency-fluctuation MRI analysis has revealed interhemispheric functional connectivity between the respective temporal regions in newborns (Perani et al., 2011). Support for this functional role of the corpus callosum in adults comes from a study showing that an incongruence between prosodic intonation and phrase structure, that is, a prosodic boundary occurring before all obligatory syntactic elements had occurred, elicited a mismatch response in healthy adults but not in patients with lesions in the posterior corpus callosum (Sammler, Kotz, Eckstein, Ott, & Friederici, 2010).

Fourteen-month-old toddlers are already able to categorize nouns syntactically based on their knowledge that nouns are preceded by determiners: such toddlers listened significantly shorter to a phrase containing a determiner and a pseudoword than to a phrase containing a pronoun in combination with the same pseudoword (Höhle, Weissenborn, Kiefer, Schulz, & Schmitz, 2004). More advanced syntactic categorization ability can be observed by the age of 18 months: 18-month-olds can already evaluate the compatibility of grammatical gender information between a case-marked article and a noun (van Heugten & Christophe, 2015). For example, French toddlers detected that the case-marked article *la* (which indexes the feminine gender), but not the case-marked article *le* (which indexes the masculine gender), was compatible with the feminine noun *poussette* 'pram'. Two-year-old children showed a P600 EEG response approximately 600 ms after stimulus onset when they encountered two grammatically incompatible phrase types, such as a prepositional and a verb phrase, in German (Oberecker & Friederici, 2006). Thirty-two-month-old children additionally showed an early left anterior negativity signal that originated from left anterior temporal sources (Herrmann et al., 2011), similar to that observed during automatic reconstruction of phrases in adults (Oberecker, Friedrich, & Friederici, 2005).

In children that are younger than three years of age, sentence comprehension is most likely grounded in the temporal cortex and possibly also its ventral connection to the IFG. This connection has been shown not only to support semantic processes at the sentence level (Saur et al., 2008), but also the processing of syntactically simple sentences (Tyler et al., 2011; Wilson et al., 2011) in adults. Nevertheless, very few data directly elucidate this phenomenon. MRI studies involving children below three years of age are needed to explore

how the dorsal and ventral connections between the temporal cortex and the IFG contribute to language comprehension in the first three years of life.

3.2. Developing High-Level Processes of Language Comprehension   The refinement of basic language skills and increasing working memory resources together drive the emergence of the higher-order semantic and syntactic representations at the sentence level. In the following section, special emphasis is given to studies that have focused on high-level processing of semantic plausibility and phrase order. Other high-level processes are currently only studied in adults (for a review, see Friederici, 2012).

3.2.1. Analysis of semantic relations   Neural mechanisms dedicated to extracting the semantic information of a sentence undergo extended refinement in the course of development. ERP effects associated with the evaluation of semantic congruency at the word level have an adultlike appearance from 14 months of age onward and can be considered as precursors for semantic processing at the sentence level (Friedrich & Friederici, 2005a, 2005b). An N400 marking the detection of an incongruence between a verb and a noun (for example, in the sentence *The cat drinks the ball*) can be detected in children before they are two years old, although, compared with the adult N400, this component has a later onset and duration (Friedrich & Friederici, 2005c). In the mature brain, the semantic and syntactic domains are dissociable both in terms of their neuroanatomical localization and in terms of the time windows during which their corresponding functions operate. They only interact at the final stage of sentence comprehension when both types of information have to be integrated into an interpretable conceptual whole in the left posterior STG and STS, and possibly also the left IFG. A recent fMRI study has revealed that this modular architecture of the syntax-semantics interface is implemented in the maturing brain only between seven and nine years of age. In children younger than seven years of age, the hemodynamic activity related to semantics and syntax largely overlaps (Brauer & Friederici, 2007; Nuñez et al., 2011). Moreover, semantic plausibility significantly reduces the hemodynamic resources needed to comprehend syntactically complex sentences and thus seems to provide a cue for sentence comprehension until high-level syntactic computations are fully available in adulthood. This was demonstrated in an experiment that presented either semantically plausible sentences (e.g., "Where is the small beetle, whom the big fox carries?"—in this case, a tall animal was the agent performing a certain action on a small animal)

or inversely, semantically implausible sentences (for example, "Where is the big fox, whom the small beetle carries?"). The processing of the noncanonical, but plausible sentences consumed fewer hemodynamic resources than did the noncanonical and implausible sentences. Accordingly, it is likely that young children use their conceptual semantic world knowledge to master syntactic complexity. By contrast, nine- to ten-year-old children who have acquired more advanced syntactic knowledge did not need to constrain their sentence processing by conceptual semantic world knowledge. This was reflected at the neural level where hemodynamic activity underlying semantic processing was anatomically separable from that activity underlying syntactic processing, as in the adult brain (Skeide et al., 2014) (figure 11.2). Follow-up studies are needed to replicate these data to determine whether they can be generalized to other languages.

3.2.2. Analysis of syntactic relations   In the third year of language acquisition, children have refined their ability to syntactically categorize words to such a degree that they become able to analyze syntactic relations between subsequent phrases. Moreover, three- to four-year-old children recruit not only the left temporal, but also the left inferior frontal cortex when processing sentences (Skeide et al., 2014; Skeide, Brauer, & Friederici, 2015), suggesting that the basic functional components for high-level syntax processing are established at this age. However, the full neural efficiency for computing syntactic relations between remote phrases in syntactically complex sentences arises gradually and is only established in young adulthood. An ERP study that investigated the use of morphosyntactic information during online sentence comprehension showed that although three-year-olds can detect grammatical case-marking cues, it takes until the age of six before children start to use this information to determine who is doing what to whom in a sentence (Schipke, Friederici, & Oberecker, 2011; Schipke, Knoll, Friederici, & Oberecker, 2012). A combined fMRI–diffusion tensor imaging study of three groups of children aged 3–4, 6–7, or 9–10 years, as well as an adult group, compared hemodynamic activity underlying the processing of well-formed spoken sentences with a canonical word order against sentences with a noncanonical word order. The effect of working memory was removed from the analysis, to allow for a domain-specific investigation of syntactic computation. Children aged three to seven years exhibited no functional selectivity of BA44 or the left posterior STG for syntax. By contrast although children aged nine to ten years, unlike the adults, did not show any such functional selectivity in the left
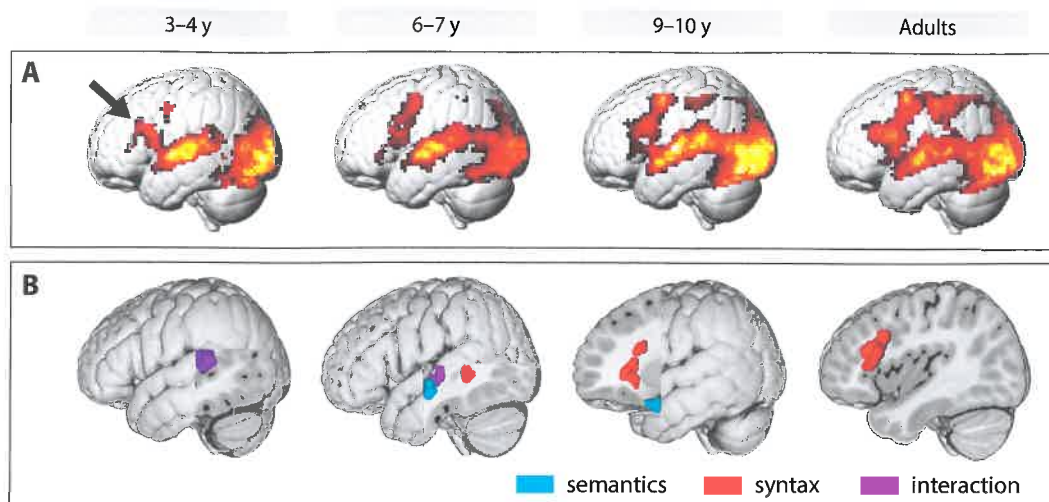
FIGURE 11.2 The functional neural segregation of syntax and semantics in the course of development. (A) Hemodynamic activity in children and adults during a sentence comprehension task (thresholded at $P < .01$; cluster size–and Bonferroni-corrected). The hemodynamic patterns cover similar cortical areas across all age groups. Like older children and adults, three- to four-year-old children recruit not only the left temporal cortex, but also the left inferior frontal cortex when processing sentences (see arrow). Accordingly, it can be assumed that the brain has set the frame for high-level language processing at three years of age. However, the full cortical selectivity for syntactic and semantic information emerges only gradually within this network. The increasing amount of activity in the left inferior parietal cortex could be related to literacy acquisition (Dehaene, Cohen, Morais, & Kolinsky, 2015). (B) The development of cortical selectivity for syntactic and semantic information is shown. Depicted are the results of a fMRI experiment employing a sentence–picture matching task to investigate the processing of syntactic complexity and semantic plausibility information. The effects of syntactic complexity were assessed by comparing responses to sentences with noncanonical word order with sentences with a canonical word order. The effects associated with semantic plausibility were investigated by comparing responses to sentences about conceptually plausible actions of an animal with sentences describing conceptually implausible actions. Depicted are main effects of syntactic complexity (red), semantic implausibility (blue), and the interaction of both factors (purple) ($P < .01$; cluster size- and Bonferroni-corrected). In young children (3–4 and 6–7 years), there is a statistical interaction between the semantics- and syntax-related hemodynamic responses in the mid and posterior portions of the left STG. Only 9- to 10-year-olds show a statistically independent effect of syntax in the left IFG, but, unlike adults, they recruit not only BA44, but also BA45, which might indicate that Broca's area is not yet fully functionally specialized at this age (Skeide et al., 2014).

BA44, they did show some functional selectivity for syntactic complexity in the left posterior STG. Remarkably, although nine- to ten-year-old children understand complex noncanonical sentences with an accuracy above 90%, adults still considerably outperform them with an accuracy of almost 100%, suggesting the left BA44 has a decisive role in reaching full efficiency in processing syntax (Skeide et al., 2015). This view is corroborated by structural morphometric data of five- to eight-year-old children and adults that indicate that increasing syntax skills are inversely correlated with the gray matter volume of the left IFG and the left posterior STG (relative to the total gray matter volume) (Fengler, Meyer, & Friederici, 2015). Accordingly, a maturational mechanism of cortical thinning in these areas, possibly driven by long-lasting synaptic pruning (Petanjek et al., 2011), has been proposed to underlie the sophistication of syntactic abilities. Future studies combining structural and functional imaging techniques are needed to corroborate this notion.

Ordering phrases and building up a sentence-level argument structure requires a common computational effort of the left IFG and the left posterior STG and STS within the dorsal language network (Wilson et al., 2011). A recent study reconstructed the left AF as the dorsal white matter fiber tract that directly connects these areas and also the ventral language pathway along the left IFOF in the four age groups mentioned (Skeide et al., 2015). Subsequently, the individual FA values for each tract of each participant were related to their individual sentence comprehension performance. When controlling for the unspecific effect of age and the domain-general influence of verbal working memory, both the increase in accuracy and the decrease in response times across development were more strongly related to the FA of the AF than to that of the IFOF (figure 11.3). Moreover, the correlational relationship between the FA of the AF and the behavioral response to syntactically more complex noncanonical sentences was markedly stronger than the relationship between the FA of the AF and the behavioral response to
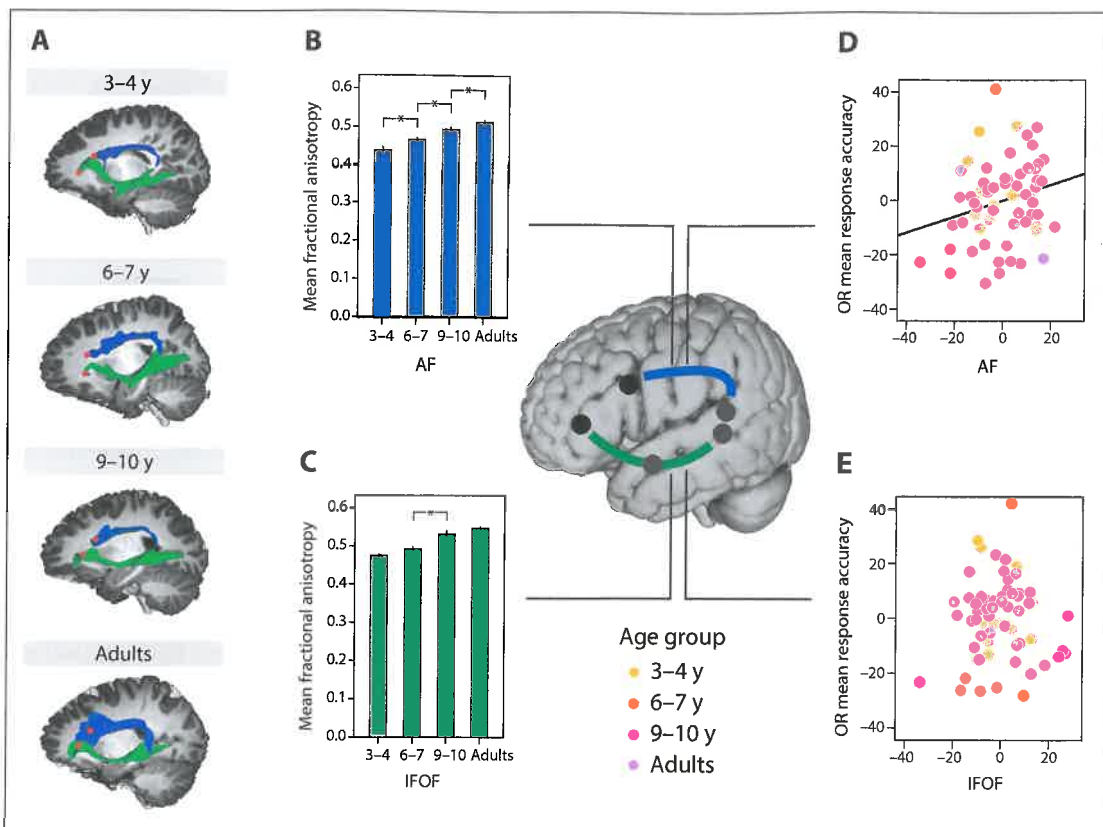
FIGURE 11.3 The ontogenetic emergence of structural networks for complex syntax. Interpreting syntactically complex sentences requires an exchange of syntactic and semantic information between the left IFG and the left STG (Friederici, 2012). In adults, this information transfer depends on a dorsal pathway via the left AF (blue) but not on a ventral pathway via the left IFOF (green) (Wilson et al., 2011). (A) To track the emergence of this dissociation, the corresponding white matter fiber tracts were reconstructed in four age groups and assessed for their FA using diffusion-weighted MRI (B: AF; C: IFOF). The FA of the AF was more strongly correlated with accuracy in comprehending syntactically complex, noncanonical sentences (D) than was the FA of the IFOF (E), whereas no such effect was found for canonical sentences (not shown). The unspecific contributions of age and the domain-general effect of verbal working memory are removed from these associations (Skeide et al., 2015). OR = object relative clauses (syntactically complex sentences).

canonical sentences. Together, these results derived from FA indicate that several other maturational mechanisms, including myelination (Gupta et al., 2012), axon growth (Paus, 2010) and increasing fiber density (Scholz, Klein, Behrens, & Johansen-Berg, 2009), are associated with the developmental refinement of the dorsal syntax network. The healthy maturation of the AF is a necessary precondition for normal language acquisition. Indeed, its disturbance might lead to faulty abstract grammatical representations and might manifest itself as specific language impairment (van der Lely & Pinker, 2014).

To conclude, the functional neural prerequisites for processing sentence-level syntax seem to be present already at three years of age when sentence comprehension is still inefficient. Sentence comprehension abilities improve into adulthood and are related to the functional specialization of the left IFG and the left posterior STG, and, moreover, to the maturation of their structural connection via the AF.

4. Summary

Taken together, at least four weeks before birth the embryo is already equipped with language processing machinery implemented in bilateral superior temporal and inferior frontal cortices, making it possible to analyze basic segmental and suprasegmental features of speech. Through refining their genetically predisposed acoustic skills, infants learn to segment the speech stream into phonological word forms in their first year of life. At the beginning of the second half of the first year of life, infants start associating phonological word forms with objects in their environment. By around 12 months, they not only can access and retrieve items from their lexicon, but they also begin to semantically
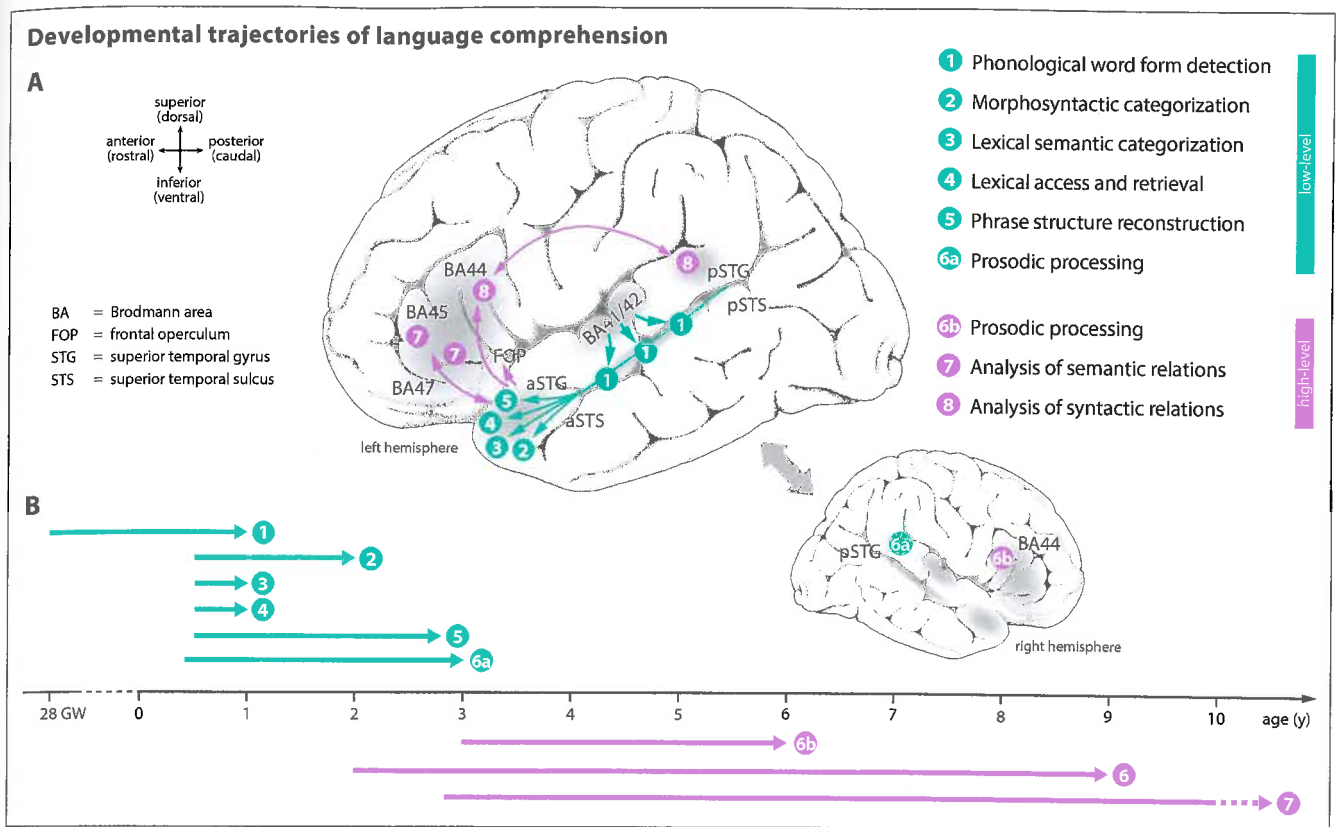
Figure 11.4 The developing cortical language comprehension circuit. (A) Neural implementation of the main processing steps (1–8) known from the adult brain. Arrows indicate the assumed flow of information along interconnecting white matter fiber tracts. Low-level processes are colored in turquoise green and high-level processes are colored in purple. (B) A schematic timeline of language acquisition (age in years). The starting points of the lines represent the earliest manifestations and the endpoints of the lines represent the first adultlike appearance of the different neural processing steps. All developmental trajectories are shown at the group level but it is important to note that they underlie interindividual variation. (1) From the 28th gestational week (GW) onward, at the latest, infants are able to extract basic segmental (phonological) and suprasegmental (prosodic) features of speech recruiting the bilateral STS (Mahmoudzadeh et al., 2013). In the first 9 months of life, they have to rely on prosodic cues (for example, accentuation) to detect phonological word forms, but this dependency is no longer present at 12 months of age (Männel & Friederici, 2013). (2, 6a) Prosodic cues enable six-month-old infants to categorize speech inputs according to morphosyntactic criteria, for example, into noun and verb phrases (Soderstrom et al., 2003), but around the second birthday, prosodic information is no longer needed for morphosyntactic categorization (Oberecker & Friederici, 2006). (5) At around 32 months of age, the reconstruction of phrase structures elicits adultlike ERPs marking automatic phrase structure reconstructions that are assumed to have sources in left anterior temporal regions (Oberecker et al., 2005). (8) Sentence-level processing of complex syntax develops gradually until young adulthood and is driven by the increasing selectivity of the left inferior frontal cortex and the maturation of its connection to the posterior superior temporal cortex via the AF (Skeide et al., 2014, 2015). (3) From six months onward, children access and retrieve lexical entries. Around their first birthday, they sort lexical items into conceptual categories and check their semantic compatibility by recruiting central and posterior parts of the left middle and superior temporal cortex (Friedrich et al., 2015; Travis et al., 2011). (4) Two-year-old children can already evaluate the semantic compatibility of elements in a sentence (Friedrich & Friederici, 2010), and this semantic information serves as a cue facilitating the understanding of syntactically complex sentences until around nine years of age (Skeide et al., 2014) (7). (6b) Prosodic processing at the sentence level is documented in three-year-old children, but only at six years of age do children recognize phrases in sentences without having to rely on pause information (Männel, Schipke, & Friederici, 2013).

categorize and compare these items, recruiting central and posterior parts of the left middle and superior temporal cortex to do so. Around their second birthday, children are able to apply their morphosyntactic knowledge to evaluate the grammatical compatibility of adjacent phrase categories in the left anterior superior temporal cortex (figure 11.4).

High-level computation of complex syntax in the left inferior frontal cortex emerges in the fourth year of life and is gradually and slowly refined from this point on. It is only after the age of 10 years that BA44 reaches its full specificity and ultimate efficiency in processing complex syntax. Functional responses to sentence-level semantic information become neuroanatomically separable from functional responses to sentence-level syntactical information around the age of seven years (figure 11.4). These maturational trajectories are assumed to be driven by general learning-related neuroplasticity, such as pruning and myelination of perisylvian nerve cell assemblies and their interconnecting white matter fiber tracts.

EEG studies on infants and toddlers have provided the main data basis for describing the acquisition of low-level language processing capacities and complementary MRI and MEG data are currently rare, particularly for the second and third year of life. Moreover, the exploration of the neurodevelopmental dynamics of higher-order sentence-level processing is still in its beginnings. Although these first results must await replication by follow-up studies, they currently reveal a consistent picture that can be adapted as new data become available.

Several important research questions remain to be answered. For example, subcortical structures, in particular the left caudate nucleus and the thalamus, are known to support the acquisition of a second language, presumably by regulating adaptation to increasing processing demands (Crinion et al., 2006; Friederici, 2006; Wartenburger et al., 2003). However, the role of these structures in the acquisition of the first language is not yet understood. Furthermore, considering the different linguistic levels of language processing, substantial progress has been made in uncovering the neural development of phonology, syntax, and semantics, but very little is known about the neural basis of emerging pragmatic skills.

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