

OPINION

The ontogeny of the cortical language network

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Abstract | Language-processing functions follow heterogeneous developmental trajectories. The human embryo can already distinguish vowels *in utero*, but grammatical complexity is usually not fully mastered until at least 7 years of age. Examining the current literature, we propose that the ontogeny of the cortical language network can be roughly subdivided into two main developmental stages. In the first stage extending over the first 3 years of life, the infant rapidly acquires bottom-up processing capacities, which are primarily implemented bilaterally in the temporal cortices. In the second stage continuing into adolescence, top-down processes emerge gradually with the increasing functional selectivity and structural connectivity of the left inferior frontal cortex.

Language is a unique evolutionary achievement considered to have decisively driven the sophistication of human cognition¹. Comprehending spoken language, which is the focus of this article, is the first challenge children have to master on their way towards becoming proficient language users, and it remains a fundamental cognitive ability throughout life. The complexity of this ability lies in the fact that it requires the brain to process multiple heterogeneous types of information. A well-orchestrated interplay of several cortical regions is needed to segment the incoming auditory stream into words that can be associated with meaning (semantics) and combined into sentences following certain rules (syntax).

Findings from electroencephalography (EEG), magnetoencephalography (MEG) and particularly functional MRI (fMRI) experiments in adults have recently made it possible to formulate novel neural models of language comprehension that now cover the entire processing cascade from audition to the interpretation of an utterance^{2–4}. Neural accounts of the developing language system are so far largely based on EEG data^{5–7}; however, in recent years, advances in adapting near-infrared spectroscopy (NIRS), MEG and fMRI settings for young

children have paved the way to start systematically investigating how the neural bases of specific language aspects emerge^{8–12} (see [Supplementary information S1](#) (box)). The knowledge gathered in these studies, which examine the relationships between language behaviour, brain function and brain structure, provides the basis for a first attempt to outline the ontogeny of the cortical language network.

In this article, we introduce a neural blueprint of language acquisition to explain where, when and how the maturing brain masters the language-processing steps that are finally carried out by the mature brain. We describe the processing capacities that represent the milestones to be reached in the course of ontogeny, and propose that the development of these capacities takes place during two developmental stages: a first one that mainly — but not exclusively — involves data-driven, bottom-up processes, and a second one that involves advanced, top-down processes. ‘Bottom-up processing’ here describes the low-level computation of mental representations from the sensory input, whereas ‘top-down processing’ denotes the further analysis of these representations under the influence of more-complex, higher-order mental representations.

The adult cortical language network

A description of the developing language system requires a description of the adult language system. Any neurocognitive model of language comprehension must be seen not only as an inventory of cognitive capacities that have to be acquired by a developing speaker, but also as an inventory of the neuronal circuits that have to mature in their specific and fully efficient functionality. The present description focuses on areas that have been repeatedly implicated as being functionally specialized for language using fMRI, NIRS, MEG and EEG. Domain-general areas (for example, underlying working memory or cognitive control) that contribute to language comprehension are not considered here (for a review, see REF. 13). An overview of the current findings on the neural basis of language production can be found in BOX 1.

Bottom-up comprehension processes.

Language comprehension as a process unfolds in time. Initially, it is driven by bottom-up processes that begin early (with onsets between 20 and 120 ms after the utterance is heard), are completed rapidly (with durations of 30–60 ms), are unconscious and run fully automatically. At the earliest stage of bottom-up processing, the acoustic-phonological features of the single sound segments (phonemes) of each word are determined. Such features are extracted in the bilateral superior temporal sulcus (STS) and, if the first syllable of a word provides an unambiguous cue for rapidly reconstructing the rest of the word, phonological word forms can be detected within a time window of 20–50 ms^{14–16}. Phonological word-form information undergoes morphosyntactic categorization — that is, the assigning of heard word forms to a syntactic group (such as noun, verb or preposition) — between 40 and 90 ms after the utterance¹⁷. In addition, lexical-semantic categorization — which is necessary to determine whether a heard word form can be semantically interpreted — occurs between 50 and 80 ms in the left anterior STS and superior temporal gyrus (STG)^{18,19}. Lexical-semantic categorization is necessary to identify, for example,

Box 1 | Language production in Broca's area

In 1865, Pierre Paul Broca, a French physician studying patients with brain lesions, suggested that the left inferior frontal cortex has a crucial role in producing language¹⁰⁴. This view is still widely accepted to this day, and Brodmann area 44 (BA44) and BA45 of the left inferior frontal gyrus are collectively named 'Broca's area' after its discoverer.

To initiate the action of speaking, a speaker has to select, access and retrieve a particular entry in the mental lexicon¹⁰⁵. The duration of the trajectory from the intention to speak to the selection of a lexical item cannot be measured directly, but lexical selection triggered by a visually presented word takes about 200 ms within the anterior BA45 (REF. 106). This was demonstrated in patients with epilepsy who, during presurgical preparation, had local field potentials recorded from depth electrodes implanted in Broca's area while they carried out a language production task. In this task, participants were asked to produce the plural form of the word 'horse', requiring them to retrieve the stem 'horse' and the plural suffix 's' to produce 'horses'. At around 320 ms after visual presentation of the word stem, a central portion of BA45 is recruited to extract the morphosyntactic features that are needed to inflect it (that is, to add the 's'). Then, phonological features of the word stem and all added inflectional morphemes are encoded in a posterior part of BA45 by approximately 450 ms after visual presentation¹⁰⁶. Finally, BA44 and BA45 of the inferior frontal gyrus together regulate the conversion of the mental representation of a phonological word form into an articulation code that can be propagated to the motor cortex to perform the actual articulation.

Importantly, although Broca's area has classically been implicated in speech production, it is not directly involved in the motor act of speaking but instead coordinates the transformation of phonological to articulatory information. Broca's area starts activating when a visually presented word that has to be repeated is still shown on a screen, but as soon as overt speech articulation commences, it deactivates, while activity in the motor cortex remains¹⁰⁷. Finally, given its relatively late activation onset (around 200 ms after visual presentation of a word), Broca's area does not appear to be directly involved in primary phonological access (which begins at about 20 ms) or lexical access (which begins at about 50–80 ms). Rather, Broca's area seems to regulate the further processing of lexical information and phonological inputs that it receives from the temporal cortex via long-distance white-matter fibre tracts^{2,106}.

pseudowords (that is, meaningless sound sequences resembling the acoustic features of a word) as being uninterpretable.

Once an interpretable word is identified, the corresponding lexicon entry — a mental representation associated with a phonological word form, carrying semantic and word category information — can be accessed and lexical items can be mentally 'retrieved' between 110 and 170 ms. This process is associated with neural activity in the left anterior STG and STS, and several other regions widely distributed over the cortex^{18,20,21}. In parallel, as soon as syntactic categories are identified, phrase structures can be built in the left anterior STG and STS, possibly together with the most ventral part of the inferior frontal cortex, between 120 and 150 ms after the utterance^{17,22,23}. As an example, recognizing the determiner "the" and the noun "boy" as elements of the phrase "the boy" requires phrase structure building.

Top-down comprehension processes.

Higher-level comprehension of language is characterized by top-down processes, which occur relatively late (with onsets usually between 200 and 600 ms following the utterance) and proceed relatively slowly (with durations of at least 150 ms) compared with lower-level comprehension,

are consciously controllable and do not run entirely automatically. Between 200 and 400 ms, lexical information is delivered from the left anterior STG and STS along the ventrally located inferior fronto-occipital fasciculus (IFOF) to Brodmann area 45 (BA45) and BA47 of the left inferior frontal gyrus (IFG; also known as Broca's area), where semantic ambiguity and semantic relations between lexical items are determined through interaction with the inferior parietal cortex^{21,24–28}. Between 300 and 500 ms, morphosyntactic information is transmitted ventrally from the left anterior STG and STS to the frontal opercular cortex and BA44, which support the rule-guided construction of phrases and sentences²⁹. It is assumed that this information is transferred along the uncinate fasciculus, but this hypothesis remains to be verified experimentally. BA44 also supports the ordering of phrases and, together with the left posterior STG and STS, enables the building up of sentence-level argument structure — that is, verb–noun arrays created in accordance with certain schemes to produce a meaningful sentence^{24,30–34}. Effective fMRI connectivity analyses modelling the causal interactions between brain areas during task performance have also revealed that top-down processing

of sentence-level syntax is driven by modulation of the left posterior superior temporal cortex by the left IFG^{35,36}.

Syntactic information is transferred dorsally from BA44 along the arcuate fasciculus (AF) to the posterior STG and STS, and semantic information is transferred ventrally from BA45 and BA47 along the IFOF to the left posterior STG^{2,24,27,32,37–39}. Note that the dorsal connection between BA44 and the left posterior STG and STS that is involved in syntactic processes⁴⁰ can be differentiated from a second dorsally located fibre bundle that connects the left posterior STG and STS to the premotor cortex and is involved in the repetition of speech³⁸.

Prosodic information — that is, intonation, tone, stress and rhythm information — is processed in a broad time window of 200–600 ms after the utterance, predominantly in the right STG and the right IFG^{32,41,42}. After at least 600 ms, all information is assumed to be integrated into a complex conceptual representation in the left posterior STG and STS, with a potential involvement of the left IFG^{2,3,23,32} (FIG. 1). Cross-domain interactions — for example, between prosody and syntax or between semantics and syntax — that occur before the final integration stage are not described here (for reviews, see REFS 2,3).

Developing bottom-up processes

In this section, we describe the ontological emergence of bottom-up language processing in approximately the first 3 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 ability, they can associate phonological word forms with semantic representations stored in memory (that is, lexicon entries) that can be semantically categorized. Moreover, the child acquires the ability to assign words to syntactic categories and to group words into phrase structures. Although the first years of life are dominated by the acquisition of bottom-up language-processing mechanisms, it is important to note that there is also evidence for the first manifestations of top-down-based integration of syntactic and semantic information occurring from the second year of life onwards.

Detection of phonological word forms.

Hearing is the first sense to be fully developed before birth. Accordingly, embryos gather their first experiences of speech *in utero*⁴³. A recent study examining preterm infants with NIRS — a technique

a Language comprehension in adults

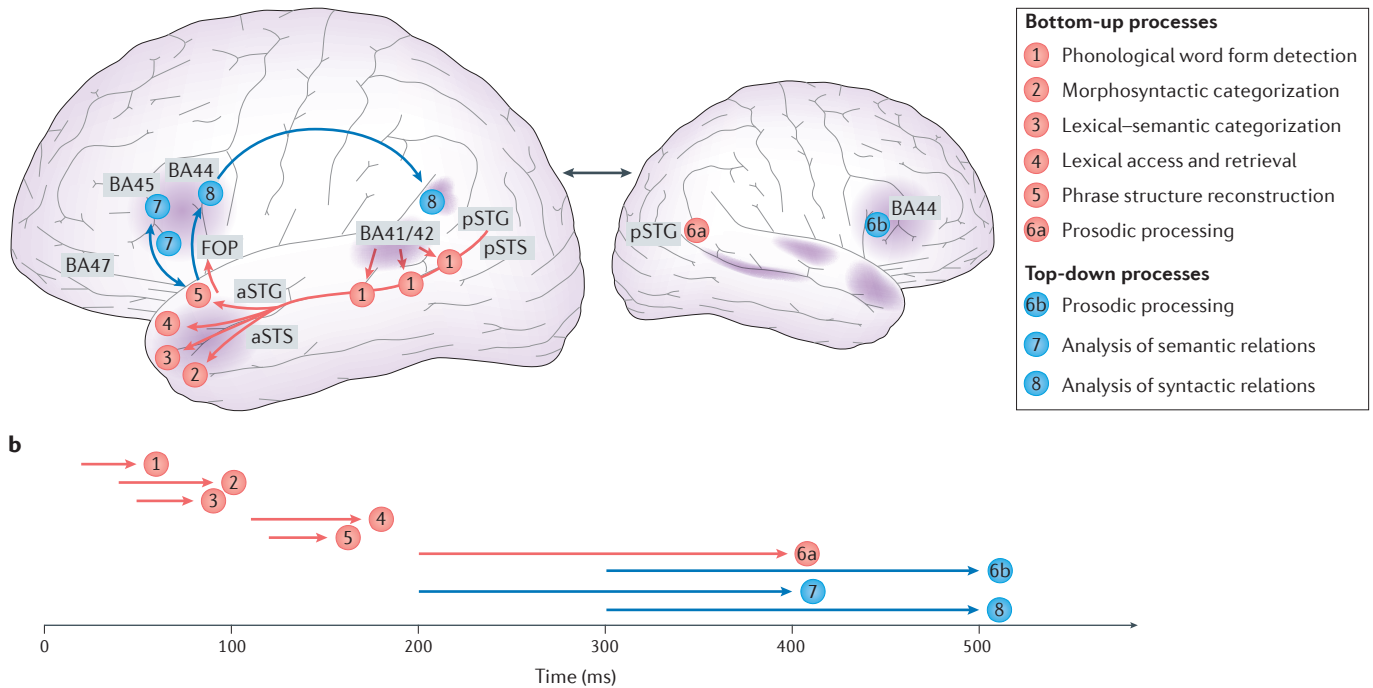


Figure 1 | The adult auditory language comprehension network. **a** | Grey-matter regions in the left perisylvian cortex (indicated by circles, shadows and black labelling) and their respective functional roles during eight central stages of auditory language comprehension (numbered 1–8). Arrows indicate the assumed flow of information along interconnecting white-matter fibre tracts. Bottom-up processes are coloured in red, and top-down processes are coloured in blue. **b** | Time windows (in milliseconds) during which the processing phases that underlie auditory language comprehension unfold. All values are approximate and subject to inter-individual variation. First, phonological word forms are detected within 20–50 ms after the utterance by extracting acoustic features from the auditory cortex^{14–16} (stage 1). Subsequently, phonological word forms are categorized at the morphosyntactic level between 40 and 90 ms¹⁷ (stage 2), and at the lexical-semantic level between 50 and 80 ms both in the left anterior superior temporal sulcus (aSTS) and left anterior superior temporal gyrus (aSTG)^{18,19} (stage 3). Lexical items associated with phonological word forms are retrieved at around 110–170 ms by the left aSTG and left aSTS^{18,20,21} (stage 4). In parallel, phrase structures are built at 120–150 ms in the same

areas^{17,22,23} (stage 5). Phrase-level prosody — that is, intonation, tone, stress and rhythm information — is processed in a time window of 200–400 ms after the utterance in the right posterior STG (pSTG)³² (stage 6a). Sentence-level prosody is processed in a time window of 300–500 ms after the utterance in the right inferior frontal gyrus (IFG)^{41,42} (stage 6b). Between 200 and 400 ms, lexical information is transferred from the left aSTG and left aSTS along the ventrally located inferior fronto-occipital fasciculus (IFOF) to Brodmann area 45 (BA45) and BA47 of the left IFG, where semantic relations between lexical items are determined^{21,24–28} (stage 7). At 300–500 ms after the utterance, phrase structure information is transmitted ventrally from the left aSTG and left aSTS, along the uncinate fasciculus (UF), to the frontal opercular cortex (FOP) and to BA44 in the left IFG²⁹ (stage 8). BA44 is involved not only in ordering phrases but also in building up argument structures together with the left pSTG and left pSTS, which are connected to BA44 via the left arcuate fasciculus (AF)^{24,30–34}. As soon as an utterance has gone through these processing steps, the left pSTG and left pSTS, potentially together with the left IFG, can start integrating all information into an interpretable conceptual representation^{2,3,23,32}.

in which 700–900 nm-wavelength light is used to measure activity-related changes in blood oxygenation — found that preterm infants born as early as after 28–33 weeks of gestation are able to detect a deviant phoneme in a sequence of otherwise identical phonemes (for example, ‘ga’ in a series of ‘ba’ sounds). Specifically, the NIRS technique revealed ‘mismatch’ responses in the bilateral posterior superior temporal cortex and the inferior frontal cortex in response to the deviant phoneme¹². Remarkably, this basal 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 week 32 of gestation. It is unlikely that early phonological skills are solely the result of prenatal environmental experience, as 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 that have lower frequency boundaries (around 200 Hz) but not between more subtly differing consonants, which in speech typically have higher frequencies, starting at around 300 Hz^{44,45}. 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^{46,47}. 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 towards 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^{48–51}. When listening passively to speech, (full-term) newborn babies show strong interhemispheric synchronization of haemodynamic activity in the bilateral posterior STG, but no such

intrahemispheric synchronization of haemodynamic activity in the left posterior STG and the left IFG⁸. However, by the age of 3 months, infants passively listening to speech show activity bilaterally in the mid and posterior STG during the first 3 seconds after stimulus onset, and in inferior frontal regions between 7 and 9 seconds⁵². These data are taken to suggest that the interaction between the inferior frontal motor system and the perceptual system functions before, and is required for, the infant's babbling stage: a phase in the first year of language acquisition in which infants produce articulate speech sounds, but not yet comprehensible words, through tuning in towards the phonology of their target language.

These findings from the newborn babies⁸ and from the 3-month-old infants⁵² can be reconciled when considering the structural connectivity pattern in adults, using diffusion-weighted MRI tractography. Specifically, adults exhibit two dorsal fibre tracts that start in the posterior temporal cortex: one that projects to the premotor cortex, and one that projects to BA44, which is part of Broca's area^{8,53}. In newborn babies⁸ and 2–5-month-old infants⁵³, the dorsal fibre 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 the integration of sensory and motor representations, as specifically evident, for example, during the babbling phase^{8,53}. Moreover, the information fed back from the premotor cortex to the temporal cortex may be crucial for establishing phoneme representations. This is suggested by the observation that 6-month-old infants cannot distinguish unfamiliar phonemes from one another when they are prevented from moving their tongue tips to articulate these phonemes⁵⁴. Similar work in adults corroborates the view that this auditory–motor link is not only important for language production but also for language comprehension⁵⁵. One could also hypothesize that the dorsal network connecting the posterior temporal and the premotor cortex underlies the remarkable ability of infants to implicitly learn relationships between non-adjacent syllables^{56–59}. These 'non-adjacent dependencies' usually follow a so-called AXB structure (for example, 'le ro bu'), in which, according to a predefined rule, syllable A ('le') predicts that syllable B ('bu') will follow the interspersed element X ('ro')⁵⁶. This type of rule

learning is considered to be crucial for the ability to memorize relations between non-neighbouring phonetic elements.

Importantly, when newborn babies hear a sentence, more activity is observed in the right mid STG than in the left mid STG⁸. Given that, in adults, the right mid STG is known to support prosodic processing^{41,42}, this finding indicates that newborn babies not only are sensitive to segmental (phonological) information but also are equally, or perhaps even more, sensitive to suprasegmental (prosodic) acoustic information in a sentence⁸. Interestingly, a similar lateralization effect was observed in the temporo-parietal cortex of sleeping 3-month-old infants⁶⁰.

The sensitivity of infants to prosody is not only vitally important for oxytocin-supported parental bonding⁶¹ but also forms the basis for learning how to segment the auditory stream into words, according to the specifics of the target language⁶². Event-related potential (ERP) work reveals that, at 6 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 forms⁶³. 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^{64–67}. The declining flexibility in recognizing phonemes is known as an instance of perceptual narrowing⁶⁸. For example, whereas before the age of 6 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 life⁴⁹. Crucially, losing this ability coincides with an increased sensitivity for acoustic differences between phonemes of the native language⁶⁹.

As described above, 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 haemodynamic 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 4-year-old children⁷⁰. 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 of acoustic information. Infants learn to discriminate the phonemes of their target language in the first half-year of life. From 6 months of age onwards, 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.

Lexical access and semantic categorization.

The refinement of speech segmentation skills in the first 6 months 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 6 months⁷¹. By the age of 9 months, infants can generalize the meanings of single words into lexical categories according to the visual features of the objects that they describe, such as their colour and shape. At this age, lexical–semantic learning is dependent on the consolidation of recent episodic memory traces during sleep after the awake encoding of experiences⁷². Support for this view comes from adult fMRI experiments that suggest that the retrieval of lexical items that were acquired early in life is controlled by the precuneus (a domain-general episodic memory area), whereas the retrieval of later-learned lexical items is controlled by BA45 and BA47 (that is, specialized language areas)⁷³. However, an adult-like semantic processing-associated N400 EEG response can be elicited at ~12 months in early talkers or ~18 months in normal talkers both in the EEG⁷⁴ and the MEG¹¹ in a lexical–semantic priming task (in which word recognition is facilitated if a target word is preceded by a congruous picture but not by an incongruous picture). The lexical–semantic processing abilities required to master this task are purely associative, and thus arguably reflect only bottom-up mechanisms. Importantly, source localization analyses reveal that the MEG signal corresponding to the N400 in this task originates mainly from mid and posterior portions of the left temporal cortex¹¹, similar to the pattern found in the adult brain²⁸.

Over the course of the second year of life, infants seem to recognize words not only in a bottom-up manner but also

in a top-down fashion. By 14 months of age, toddlers are already able to categorize nouns syntactically based on their knowledge that nouns are preceded by determiners: such toddlers spent less time listening to a phrase containing a determiner and a pseudoword than to a phrase containing a pronoun in combination with the same pseudoword^{75,76}. This effect was present regardless of which of the two stimulus types the children were familiarized with beforehand. At 18 months old, learning new words requires simultaneous evaluation of phonological features and conceptual-semantic and syntactic categories. Indeed, 18-month-old toddlers looked significantly longer at novel picture–word pairs if the words were from different syntactic and semantic categories from those of a phonologically similar word they had known before⁷⁷.

Syntactic categorization and reconstruction.

There is behavioural evidence that 6-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 is marked by lengthening of the final syllable and the pause that succeeds it⁷⁸. ERP work has shown that, by the age of 5 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 absent⁷⁹. 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 life⁸⁰. By 6 years of age, children have acquired more advanced syntactic phrase structure knowledge, enabling them to recognize phrases in sentences without the salient pause cues⁸¹.

One can hypothesize that an inter-hemispheric network comprising the left anterior STS and STG and the right STG, which are connected by posterior transcallosal fibres, underlies 6-month-old children’s skills in the prosody-enhanced detection of phrase structure. Low-frequency-fluctuation MRI analysis has revealed interhemispheric functional connectivity between the respective temporal regions in newborn babies⁸. Support for this functional role of the corpus callosum in adults comes from a study showing that an incongruity 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 callosum⁸².

Syntactic categorization ability can be observed by the age of 18 months: 18-month-old toddlers can already evaluate the compatibility of grammatical gender information between a case-marked article and a noun⁸³. 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 (associated with the recognition of syntactic anomalies) approximately 600 ms after stimulus onset when they encountered two grammatically incompatible phrase types, such as a prepositional and a verb phrase, in German⁸⁴. In addition, 32-month-old children showed an early left anterior negativity (ELAN) signal that originated from left anterior temporal sources¹⁷, similar to that observed during automatic reconstruction of phrases in adults⁸⁵.

It is clear that, at least by the age of 3 years, and often before, children are able to process sentences and take part in verbal communication. Within the present model, we assume that they do so by mainly involving the temporal cortex and its ventral connection to the IFG. This connection has been shown not only to support semantic processes at the sentence level⁸⁸ but also to support the processing of syntactically simple sentences^{37,86} in adults. MRI studies involving children below 3 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 3 years of life.

Developing top-down processes

The refinement of basic language skills and increases in working memory resources together drive the emergence of higher-order semantic and syntactic representations. These representations are specifically related to features relevant for combined phrases (that is, sentences). Top-down processing of semantic plausibility and phrase order is given special emphasis in the following section. Further top-down processes are currently only studied in adults (for a review, see REF. 2).

Analysis of semantic relations. The emergence of adult-like semantic processing at the sentence level occurs over a long developmental phase. ERP effects associated with the evaluation of semantic congruency at the word level have an adult-like appearance from 14 months of age onwards, and can be considered as prerequisites for semantic processing at the sentence level^{87,88}. N400 ERP components relating to the detection of sentence-level incongruity between a verb and a noun (for example, in the phrase “the cat drinks the ball”) can be detected in children before they are 2 years old, although, compared with the adult N400, these components have a later onset and last longer⁸⁹. As described above, 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; this occurs 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 between 7 and 9 years of age. Before this (ages 3–7 years), the haemodynamic activity associated with semantics and syntax largely overlaps^{90,91}. Moreover, there is a statistical interaction between the extent of processing of semantics and syntax in mid and posterior portions of the left STG, such that semantic plausibility reduces the haemodynamic resources needed to comprehend syntactically complex sentences. This was demonstrated in an experiment that presented either a semantically plausible proposition (in this case, a tall animal was the agent performing a certain action on a small animal — for example, “Where is the small beetle, whom the big fox carries?”) or, inversely, a semantically implausible proposition (for example, “Where is the big fox, whom the small beetle carries?”). The processing of the non-canonical but plausible sentences consumed less haemodynamic resources than did the non-canonical and implausible sentences; therefore, it is likely that young children use their conceptual semantic world knowledge to master syntactic complexity. By contrast, 9–10-year-old children are no longer biased towards conceptual semantic world knowledge to constrain syntactic processing. This is reflected at the neural level: haemodynamic activity indicating

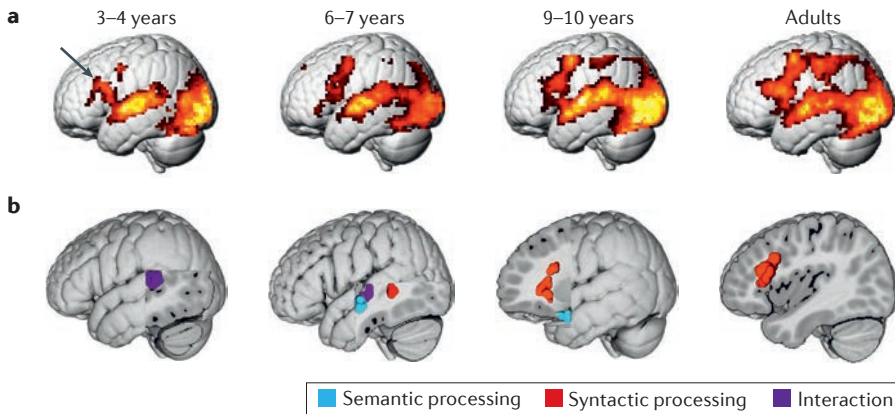


Figure 2 | The developmental segregation of syntax from semantics. a | Functional MRI (fMRI) responses in children and adults in a sentence comprehension task (thresholded at $P < 0.01$; Bonferroni- and cluster size-corrected). The haemodynamic patterns have a similar appearance across all age groups. Notably, unlike newborn babies and infants^{8,52,92} but like older children and adults, 3–4-year-old children recruit not only the left temporal cortex but also the left inferior frontal cortex when processing sentences (indicated by the arrow). Accordingly, it can be assumed that the brain has set the frame for top-down language processing at 3 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 acquisition¹⁰⁸. **b** | The development of cortical selectivity for syntactic and semantic information was followed in an fMRI experiment that used a sentence–picture matching task to investigate the functional effects of syntactic complexity and semantic plausibility. The effects of syntactic complexity were assessed by comparing responses to sentences with non-canonical word order with sentences with a canonical word order. The functional effects associated with semantic plausibility were investigated by comparing responses to sentences about conceptually plausible actions of an animal with those describing conceptually implausible actions. Depicted are main effects of syntactic complexity (red), semantic implausibility (blue) and the interaction of both factors (purple) ($P < 0.01$; Bonferroni- and cluster size-corrected). In the adult brain, syntax has a distinct spatial representation (left Brodmann area 44 (BA44)) to that of semantics, and children show slow development towards this segregation. In younger children, there is statistical interaction between the pattern of the semantics- and syntax-related haemodynamic responses in the mid and posterior portions of the left superior temporal gyrus (STG). Only 9–10-year-old children show selectivity for syntax in the left inferior frontal gyrus (IFG); however, unlike adults, they recruit not only BA44 but also BA45, which suggests that Broca’s area is not yet fully functionally specialized at this age⁹. Adapted with permission from REF. 9, Elsevier.

semantic processing is segregated from that indicating syntax, as in the adult brain⁹ (FIG. 2). Replication in follow-up studies is necessary to assess the generalizability of these data.

Analysis of syntactic relations. The growth of the ability to syntactically categorize heard words enables children in their third year of life to analyse syntactic relations between immediately neighbouring phrases. Moreover, unlike newborn babies and infants, 3–4-year-old children recruit not only the left temporal but also the left inferior frontal cortex when processing sentences^{9,10,52,92}, suggesting that the basic functional components for top-down syntax processing are established at this age. However, the neural and behavioural efficiency for computing the syntactic relationship between remote phrases in syntactically complex sentences arises gradually, and is only fully established in

young adulthood. The relationship between phrases is marked by morphological elements (for example, inflections and case markers) known as morphosyntactic elements. An ERP study that investigated the use of morphosyntactic information during online sentence comprehension showed that although 3-year-old children can detect grammatical case-marking cues, it takes until the age of 6 before children start to use this information to determine who is doing what to whom in a sentence^{93,94}. A combined fMRI–DTI study of 3 groups of children aged 3–4, 6–7 or 9–10 years, as well as an adult group, compared haemodynamic activity underlying the processing of spoken sentences with a canonical word order against sentences with a non-canonical (but owing to case marking, syntactically correct) word order. The effect of working memory was removed from the analysis, to allow specific investigation of syntactic computation. Children aged 3–7 years

exhibited no functional selectivity in BA44 or the left posterior STG for syntax. By contrast, although children aged 9–10 years, unlike the adults, did not show any such functional selectivity in the left BA44, they did show some functional selectivity for syntactic complexity in the left posterior STG: the haemodynamic response of these children and the adults in this region was markedly higher for non-canonical sentences than for canonical sentences. Remarkably, although 9–10-year-old children understand complex non-canonical sentences with an accuracy of more than 90%, adults still considerably outperform them with an accuracy of almost 100%, suggesting that the left BA44 has a decisive role in reaching full efficiency in processing syntax¹⁰. This view is corroborated by structural morphometric data of the brains of 5–8-year-old children and adults that indicate that increasing syntax skills are inversely correlated with the grey-matter volume of the left IFG and the left posterior STG (relative to the total grey-matter volume)⁹⁵. Accordingly, a maturational mechanism of cortical thinning in these areas, possibly driven by long-lasting synaptic pruning⁹⁶, 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 network³⁷. A recent study reconstructed the white-matter fibre tract that directly connects these areas — the left AF — and also the ventral language pathway along the left IFOF in the four age groups mentioned above¹⁰. From this, the individual fractional anisotropy (FA) values (reflecting structural connectivity) 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 are more strongly related to the FA of the AF than to that of the IFOF. Moreover, the correlational relationship between the FA of the AF and the behavioural response to syntactically more-complex non-canonical sentences was markedly stronger than the relationship between the FA of the AF and the behavioural response to canonical

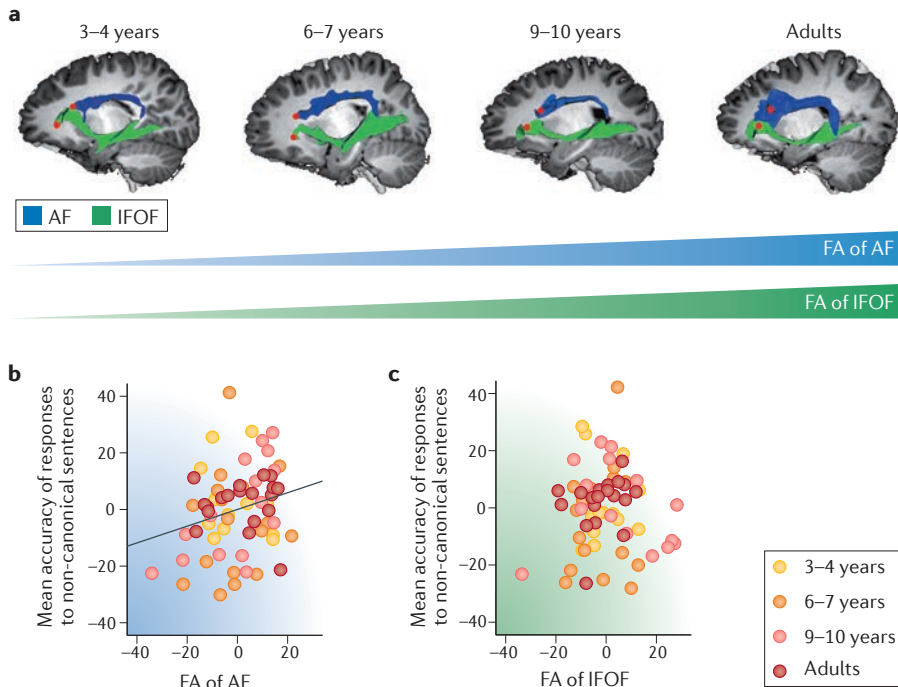


Figure 3 | The ontogenetic emergence of complex syntax. Processing syntactically complex sentences requires transfer of syntactic information from the left inferior frontal gyrus to the left superior temporal gyrus, where it can be integrated with semantic information². In adults, this information transfer depends on a dorsal pathway via the left arcuate fasciculus (AF; blue) but not on a ventral pathway via the left inferior fronto-occipital fasciculus (IFOF; green)³⁷. To track the emergence of this dissociation, the corresponding white-matter fibre tracts were recently reconstructed in four age groups and assessed for their fractional anisotropy (FA) using diffusion-weighted MRI (depicted by wedges; part **a**). The FA of the AF was more strongly correlated with accuracy in comprehending syntactically complex, non-canonical sentences (part **b**) than was the FA of the IFOF (part **c**). This effect generalized to comparisons between non-canonical and canonical sentences (not shown) and was robust to the unspecific effect of age and the domain-general influence of verbal working memory¹⁰. Adapted from Skeide, M. A., Brauer, J. & Friederici, A. D. Brain functional and structural predictors of language performance, *Cereb. Cortex*, 2015, <http://dx.doi.org/10.1093/cercor/bhv042>, by permission of Oxford University Press.

sentences (FIG. 3). Together, these first results indicate that several other maturational mechanisms, including myelination⁹⁷, axon growth⁹⁸ and increasing fibre density⁹⁹, 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 impairment¹⁰⁰ (see [Supplementary information S2](#) (box)).

Taken together, the studies discussed here suggest that top-down syntax processing develops by 3 years of age, when sentence comprehension is still inefficient. Increases in syntax performance continue into adulthood, and are related to the functional specialization of the left IFG and the left posterior STG, and to the maturation of their structural connection via the AF.

Conclusions

A neurodevelopmental blueprint of language. Considering the studies outlined above, we present a model of the ontogeny of the cortical language network. EEG studies on infants and toddlers have provided the main data basis for describing the acquisition of bottom-up language processing capacities. Owing to methodological challenges, complementary MRI and MEG data are currently rare, particularly for the second and third year of life. The exploration of the developmental dynamics of higher-order sentence-level mechanisms is still in its beginnings. Nevertheless, these first results allow us to draw a consistent picture that can be modified as new data become available (FIG. 4).

According to our model, at least 4 weeks before birth, the fetus is already equipped with bottom-up processing machinery

necessary for extracting basic segmental and suprasegmental features of speech, which is carried out in the bilateral superior temporal and inferior frontal cortices. Through refining their genetically predisposed acoustic skills, infants learn to segment the speech stream into phonological word forms in their first year of life. Well before their first birthday, infants also start associating phonological word forms with objects in their environment. By around 12 months, they can not only access and retrieve items from their lexicon but also begin to semantically categorize these items by recruiting central and posterior parts of the left middle and superior temporal cortex. 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.

The top-down processing of semantic and syntactic relations in the left inferior frontal cortex emerges in the fourth year of life but refines only gradually and slowly. Functional selectivity for sentence-level semantic information becomes neuroanatomically separable from functional selectivity for sentence-level syntactical information between the ages of 7 and 9, and it is only after the age of 10 that BA44 reaches its full specificity and ultimate efficiency in processing complex syntax. These maturational trajectories are assumed to be shaped by pruning of perisylvian neurons as well as myelination and growth of their interconnecting white-matter fibre tracts.

Implications. The present model might have implications for practitioners from several fields. It provides an empirical basis for the notion that children's progress in language acquisition is coupled to a relatively fixed time course of neurobiological maturation. Accordingly, it seems likely that the effectiveness of educational programmes can be maximized when adapting the complexity of the teaching language and educational media to the particular neurodevelopmental level of the corresponding age group.

Our model groups the brain maturation milestones for normal language acquisition along a timeline of cognitive development. Thus, it complements current behaviourally informed notions of the developmental trajectories underlying language acquisition. Speech and language therapists might consider it to be a useful additional source for determining faulty verbal communication skills potentially pointing to a language disorder.

a Developmental trajectories of language and comprehension

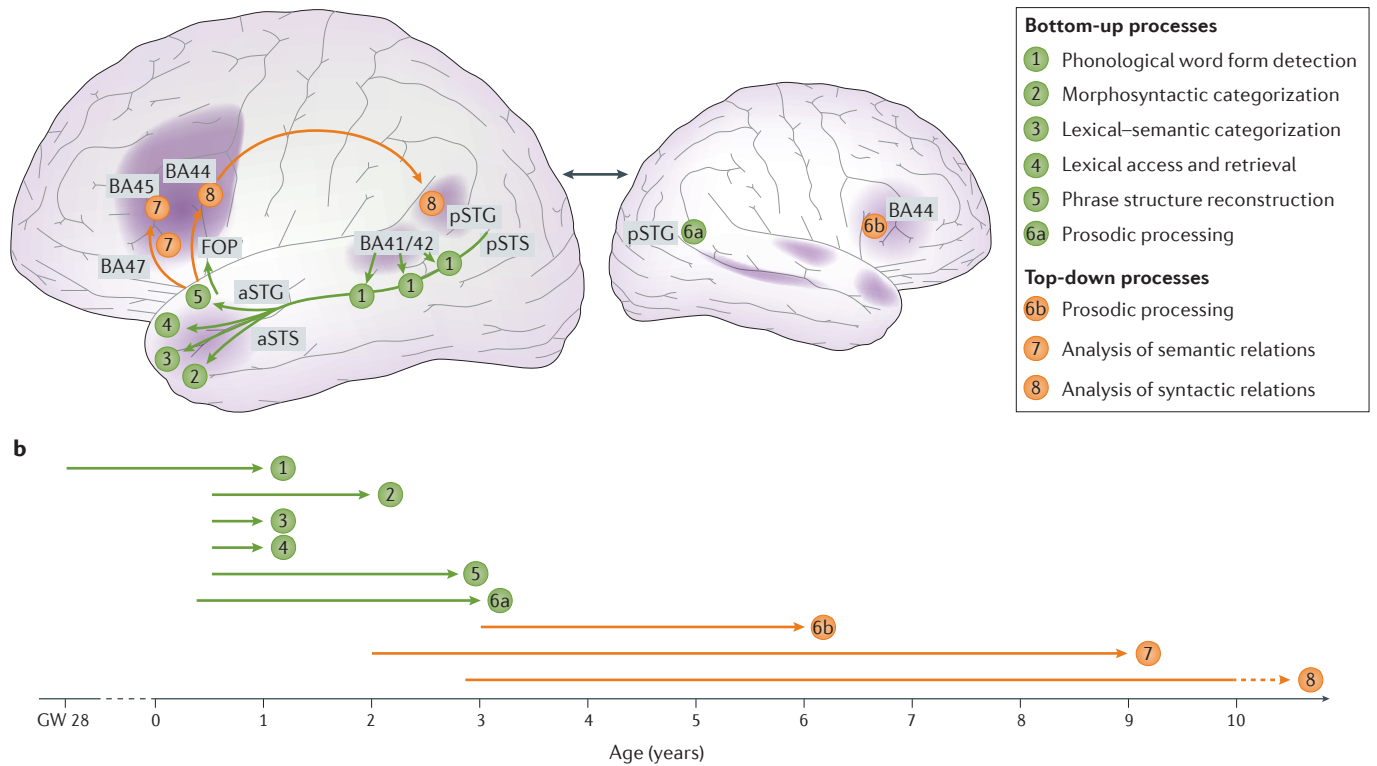


Figure 4 | The evolving cortical circuit underlying language comprehension. **a** | Neural implementation (indicated by circles, shadows, and black labelling) of the main processing stages (numbers 1–8) known from the adult brain. Arrows indicate the assumed flow of information along interconnecting white-matter fibre tracts. Bottom-up processes are coloured in green, and top-down processes are coloured in orange. **b** | A model of the language acquisition timeline (age in years). The earliest manifestations (starting points of the lines) and first appearance of adult-like functions (end points of the lines) of different neural processing milestones, at the group level, are shown. Note that these particular processes do not emerge and disappear abruptly, but do so gradually. Moreover, they are subject to inter-individual variation. From gestational week 28 (GW 28) onwards, at the latest, infants are able to extract basic segmental (phonological) and suprasegmental (prosodic) features of speech by recruiting the bilateral superior temporal sulcus (STS)¹². 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 by around 12 months of age⁶³ (stage 1). Prosodic cues also enable 6-month-old infants to categorize speech inputs according to morphosyntactic criteria; for example, into noun and verb phrases⁷⁸. However, by around the second birthday, prosodic information is no longer used for morphosyntactic categorization⁸⁴

(stages 2 and 6a). At around 32 months old, the reconstruction of phrase structures elicits adult-like electroencephalography (EEG) responses that are assumed to have sources in left anterior temporal regions⁸⁵ (stage 5). 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 its connection to the posterior superior temporal cortex via the arcuate fasciculus^{9,10} (stage 8). From 6 months onwards, children access and retrieve lexicon entries; that is, memorized associations between phonological word forms and objects in their environment. Around their first birthday, they sort lexical items into conceptual categories by recruiting central and posterior parts of the left middle and superior temporal cortex^{11,72} (stage 3). By 2 years of age, children can already evaluate the semantic compatibility of elements in a sentence⁷⁴ (stage 4), and this semantic information serves as a cue for understanding syntactically complex sentences until around 9 years of age⁹ (stage 7). Prosodic processing at the sentence level is documented in 3-year-old children, but it is only at around 6 years of age that children can recognize phrases in sentences without relying on pause information⁸¹ (stage 6b). aSTG, anterior superior temporal gyrus; aSTS, anterior superior temporal sulcus; BA, Brodmann area; FOP, frontal opercular cortex; pSTG, posterior superior temporal gyrus; pSTS, posterior superior temporal sulcus.

To date, neuropaediatricians have to rely largely on adult data when planning surgical operations in children. The current model could foster efforts to design better methods for localizing specific language functions in the individual developing brain. Novel diagnostic tools might make it possible to more accurately assess the risk of language impairment that follows a surgical procedure in young neurological patients.

Outstanding questions. Several important research questions remain to be answered in follow-up studies on the functional specialization and structural maturation of the language system. 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^{101,102}.

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 hardly anything is known about the neural basis of emerging pragmatic skills — that is, using contextual information for inferring the

meaning of utterances. This field could be explored by combining brain measures with behavioural paradigms that investigate how children disambiguate sentences such as “The window is open”, which can be a simple statement, an expression of being cold or a request to close the window, depending on the communicational situation.

Finally, extending the perspective from the neurobiology to the biology of language, there is now a consensus that both nature and nurture make us proficient language users. But whereas the environmental factors that shape the language-proficient brain have been studied extensively in the past few years¹⁰³, the genetic contributions to specific language skills remain largely unknown. Future work needs to specify systematically how genetic variation and environmental influences interact to give rise to the language-ready brain.

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Competing interests statement

The authors declare no competing interests.

SUPPLEMENTARY INFORMATION

See online article: [S1 \(box\)](#) | [S2 \(box\)](#)

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Supplementary Box 1 | Investigating the neural basis of language acquisition.

Owing to its ease of use, electroencephalography (EEG) is the most frequently employed neurophysiological technique in infants and children. As electric currents induced by neuronal activity are recorded directly on the scalp, children can move relatively freely during the measurements. Moreover, some paradigms applied in EEG experiments do not even require the participant's attention, making this method especially suitable for newborns and young infants^{1,2}. EEG has a high temporal resolution of the order of milliseconds, but its two-dimensional spatial resolution on the scalp is limited to around 5 cm when modeling 64 electrodes (REF 3). Additionally, non-invasive EEG recordings have a limited penetrance, making it hard to study subcortical structures with the exception of the auditory brain stem nuclei⁴. By contrast, magnetic resonance imaging (MRI) provides a spatial resolution of at least one 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 second⁵. MRI of healthy young adults has become a routine investigation in neuroscience, but it is difficult to acquire these data in children⁶. In order to reduce drop-out rates, young participants are prepared in a mock scanner prior to the actual measurement (see <http://www.cbs.mpg.de/depts/npsy/childlab> (in German only)). The rationale behind mock scanner training is to familiarize the child with the MR procedure and the experimental tasks it has to solve, thereby considering its current emotional, cognitive and motivational development. In practice, the experimenter embeds the training in a game, involving the parents if necessary. Crucially, young participants have to train lying still in the scanner and not to move their heads. This can be achieved by using motion sensors that stop the presentation in case of head movement. Thereby, the child should be accompanied with encouraging feedback to create a constructive awareness of head motion. All in all, 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 mock-up sessions are time-consuming, they markedly reduce drop-out rates to less than 40% in 3–4-year-old children and less than 10% in 6–7-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.

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Supplementary Box 2 | **Specific language impairments.**

Specific language impairment (SLI) is a heterogeneous disorder of language development and occurs with a prevalence of around 7%^{1,2}. SLI can manifest at all linguistic levels, including phonology, the lexicon, semantics, syntax and pragmatics. The majority of children with SLI, however, suffer from impaired syntax capacities. Grammatical-specific language impairment (G-SLI) is a particularly interesting subtype of syntactic SLI as it is primarily characterized by deficient processing of complex sentence-level syntax^{1,3}. Individuals affected by G-SLI have difficulties in comprehending and producing sentences such as “Who did Joe think hit the man?” Such questions require top-down ordering computations to identify all of the relevant syntactic relations between the phrases. In line with this, G-SLI participants consider syntactically incorrect sentences like “Who did Barbie push the clown into the wall?” as correct. When processing these sentences, individuals with G-SLI show not only a P600 response in the electroencephalogram (which is typically observed when two syntactically incompatible phrase types are detected) but, unexpectedly, also an N400 response (which is normally elicited by semantically incompatible words)^{4,5}. Thus, it was proposed that, during the processing of syntactically complex sentences, individuals with G-SLI might unsuccessfully try to ‘compensate’ for their dysfunctional higher-order syntax network (which includes the left Brodmann Area 44, the left posterior superior temporal gyrus and the interconnecting left arcuate fasciculus) by recruiting a neural network that is normally responsible for semantic processing (involving the left anterior temporal and the left ventral inferior frontal cortex, connected by the left inferior fronto-occipital fasciculus)³. The appeal of this hypothesis lies in the fact that both the fractional anisotropy of the arcuate fasciculus and SLI in general are known to be highly heritable^{6,7}. Accordingly, it could turn out that the syntactic deficits observed in G-SLI are at least partially related to a genetically driven maturational aberration of the arcuate fasciculus.

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