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Chapter 21

Functional and structural brain asymmetries in sign language processing

PATRICK C. TRETTENBREIN[1,2,3*], EMILIANO ZACCARELLA[1], AND ANGELA D. FRIEDERICI[1]

[1]*Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Leipzig, Germany*

[2]*International Max Planck Research School on Neuroscience of Communication: Structure, Function, and Plasticity (IMPRS NeuroCom), Leipzig, Germany*

[3]*Experimental Sign Language Laboratory (SignLab), Department of German Philology, University of Göttingen, Göttingen, Germany*

Abstract

The capacity for language constitutes a cornerstone of human cognition and distinguishes our species from other animals. Research in the cognitive sciences has demonstrated that this capacity is not bound to speech but can also be externalized in the form of sign language. Sign languages are the naturally occurring languages of the deaf and rely on movements and configurations of hands, arms, face, and torso in space. This chapter reviews the functional and structural organization of the neural substrates of sign language, as identified by neuroimaging research over the past decades. Most aspects of sign language processing in adult deaf signers markedly mirror the well-known, functional left-lateralization of spoken and written language. However, both hemispheres exhibit a certain equipotentiality for processing linguistic information and the right hemisphere seems to specifically support processing of some constructions unique to the signed modality. Crucially, the so-called "core language network" in the left hemisphere constitutes a functional and structural asymmetry in typically developed deaf and hearing populations alike: This network is (i) pivotal for processing complex syntax independent of the modality of language use, (ii) matures in accordance with a genetically determined biologic matrix, and (iii) may have constituted an evolutionary prerequisite for the emergence of the human capacity for language.

INTRODUCTION

The capacity for language serves as a cornerstone of human cognition and is one of the key properties that distinguishes our species from other animals. The first known attempts to establish a possible neural basis for this capacity date back to the 19th century and were based on the observations of Marc Dax, who determined that damage to the left hemisphere of the brain would lead to either a disturbance of speech or impaired language abilities (Dax, 1863, 1865). This was later followed by the often much more widely known work of Broca (1861) suggesting that especially lesions to the left inferior frontal gyrus of the cortex affected expressive language. This cortical region is nowadays known as Broca's area, even though a reexamination of the conserved brains of some of Broca's patients using modern neuroimaging has shown that their lesions extended into neighboring regions and the white matter tracts originating from them (Dronkers et al., 2007). Ample lesion studies in combination with the advent of neuroimaging have since confirmed Dax' and Broca's very first notions that certain aspects of speech and language processing are asymmetrically organized in the adult human brain (see Trettenbrein and Friederici, 2025, for a review based primarily on studies of spoken and written language).

Since the 1960s, research in the cognitive sciences has accumulated evidence which strongly suggests that the human-specific language capacity (Hauser et al., 2002; Bolhuis et al., 2014) is not bound to speech but may be perceived and externalized in different modalities (Stokoe, 1960; Klima et al., 1979; Chomsky, 1986a): auditory-oral for spoken language, visuospatial for sign language, and tactuo-spatial for tactile sign language. Sign languages are the natural languages of the deaf and, just like spoken languages, exhibit complex linguistic organization on different levels such as phonology or syntax (Sandler and Lillo-Martin, 2008; Mathur and Rathmann, 2014; Cecchetto, 2017). (Note: In English, uppercase "Deaf" is sometimes used to refer to people, who identify as members of a linguistic and cultural

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[*]Correspondence to: Patrick C. Trettenbrein, Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany. Tel: +49-341-99402625, E-mail: trettenbrein@cbs.mpg.de

minority, lowercase “deaf” is then seen to refer to people’s audiologic status. Following Caselli et al. (2017), we use lowercase “deaf” throughout here because we discuss studies with diverse groups of participants from laboratories around the world, who may differ in whether and how they identify with the respective community.) Intriguingly, emerging research on tactile sign languages of the deafblind has revealed a similarly complex linguistic organization (Checchetto et al., 2018; Edwards and Brentari, 2020). In contrast to speech, sign, and tacticle sign, the different writing systems for spoken languages constitute cultural inventions that have to be acquired by explicit instruction. Written language only emerged relatively recently (about 6000 years for pictographic and ideographic systems and about 3000 years for alphabetic systems), which makes it unlikely that the human brain has evolutionarily adapted to reading and writing as it has for language processing as such (Dehaene et al., 2005; Dehaene and Cohen, 2007; Friederici, 2017).

First neuropsychologic evidence for a left-lateralization of sign language, similar to spoken language, came from case studies of deaf signers, who exhibited a variety of aphasic symptoms in their signing following lesions to the left but not the right hemisphere (Klima et al., 1979; Poizner et al., 1987; Bellugi et al., 1989; Hickok et al., 1996a, 1998; Corina, 1998). For example, Poizner et al. (1987) documented case studies of two deaf signers with agrammatic and paragrammatic behavioral profiles following left-hemispheric lesions to the perisylvian cortex. Similarly, mirroring the picture of Broca’s classic cases for speech production, Hickok et al. (1996b) report a deaf signer with a lesion to the left inferior frontal gyrus extending into neighboring regions and white matter, who exhibited acute expressive aphasia. These data are complemented by a case study of a hearing bimodal bilingual that underwent presurgical Wada testing (i.e., left intracarotid injection of Amytal to render left-hemispheric language areas inoperative), which led to a temporary aphasia in both American Sign Language (ASL) and spoken English (Damasio et al., 1986). Collectively, these studies provided the first, suggestive evidence that the left hemisphere of the human brain may not be specialized for processing the fast temporal structure of speech (Zatorre et al., 2002; Schönwiesner et al., 2005), but is specialized for processing language independent of modality.

In this chapter, we take these early neuropsychologic observations about the lateralization of language across different modalities as a starting point for a review of the functional and structural lateralization of the neural substrates of sign language as revealed by the past decades of research using a range of neuroimaging methods. Throughout the discussion, we will assume that readers are already familiar with the fundamentals of the functional and structural neuroanatomy of spoken and written language processing (for an overview see, e.g., Friederici, 2017; Hagoort, 2017). While we aim to incorporate findings using a variety of neuroimaging methods, our focus here will be on studies using (functional) magnetic resonance imaging ([f]MRI). We start by briefly considering the nature of language and its relation to the brain in general, including a primer on the linguistic analysis of sign languages, as well as sign language acquisition. Next, we review case studies of sign language aphasia before laying out the functional and structural neural basis for processing sign language in the brains of adult deaf signers (i.e., individuals with congenital or early onset hearing loss, who primarily use a sign language to communicate). We end with a summarizing discussion as well as an attempt to sketch a model of the functional neuroanatomy of sign language processing.

What is “language”?

Different from everyday use, modern linguistics distinguishes between *language* as a neurally implemented cognitive capacity and individual *languages* such as, for example, English, Japanese Sign Language (JSL), and Nahuatl. *Language* as a cognitive capacity enables humans to assemble individual lexical items (i.e., a technical notion from linguistics roughly corresponding to “words” that also includes signs) into structured representations of utterances, which are mapped to the sensorimotor system for production and comprehension and the conceptual-intentional system for thought (Chomsky, 1965, 1986b, 1995; Everaert et al., 2015; Friederici et al., 2017). In a technical sense, the human language system therefore enables a structured mapping from meaning to a physical signal (i.e., signs or sound) and vice versa (Chomsky, 2011). This architecture of *language* enables humans to flexibly produce and comprehend an in principle infinite number of different utterances, which they have never encountered before. At the same time, this cognitive architecture also accounts for why *language* can readily be externalized in different modalities and why individual *languages*, regardless of whether they are spoken or signed, differ in their phonology, lexicon, and grammar: The specifics of the mapping to the sensorimotor system appear not to be fixed in human biology but instead develop during language acquisition (Lenneberg, 1964; Crain et al., 2016; Yang et al., 2017).

The representations generated by the human language system are evolutionarily distinctive because they are not merely sequences of lexical items but instead specify the relations between individual lexical items hierarchically, a property that seems to be shared across modalities (spoken, signed, etc.) but has not yet been observed in the communication systems of other animals (Berwick et al., 2013; Everaert et al., 2015; Friederici et al., 2017). The German Sign Language (DGS) sentence schematically depicted in Fig. 21.1 (top panel) can be used to illustrate two different ways in which the grammatical relationship between the individual signs making up a sentence can be analyzed linguistically: We might assume that the signs are merely a sequence of lexical items, which can be represented as a flat structure in which all elements in the diagram are connected directly to the root (Fig. 21.1, bottom-left panel). Alternatively, we may assume that lexical items are grouped into constituents, which are embedded in each other hierarchically (Fig. 21.1, bottom-right panel). Significantly, despite the fact that spoken languages and sign languages are perceived and produced in radically different modalities, linguistic analysis has demonstrated that they exhibit deep structural similarities on several levels of description, including the hierarchical syntactic

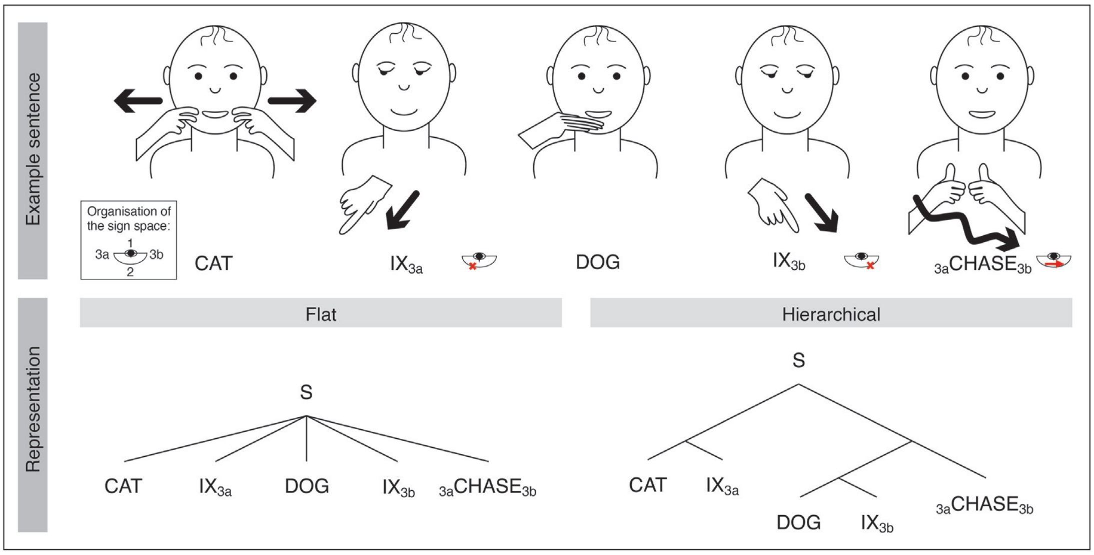

Fig. 21.1. Example sentence in German sign language (DGS) and possible syntactic representations. The top panel shows a schematic depiction of an example sentence in German Sign Language (DGS), which roughly translates into English as "The cat chased the dog." The schematics indicate handshape, location, and movement of manual signs, known nonmanual components, as well as mouthings and are accompanied by English glosses. Glossing amounts to writing one language (i.e., DGS) using another (i.e., English) and is therefore necessarily an imprecise yet widely used tool in sign language linguistics (see Pfau et al., 2012 for an in-depth explanation of notational conventions). Index signs are glossed using the abbreviation IX and locations in sign space are given as subscripts for the respective signs, indicating start (and endpoint) of a syntax-relevant movement in sign space. Notice that the sentence in this example primarily serves illustrative purposes; in natural conversations, indexing can also occur by producing a sign in the respective location in sign space and is also frequently at least partially or even completely omitted if relying only on word order patterns [the default word order for DGS is subject-object-verb (SOV)] may be sufficient for expressing a proposition (Mathur and Rathmann, 2012; Pfau et al., 2018). The bottom panel illustrates two possible ways in which the syntactic structure of this example sentence may be represented in linguistic analysis: The bottom-left panel depicts an analysis of the sentence of a flat structure in which all elements in the tree diagram are directly connected to the root. In contrast, the bottom-right panel shows an analysis of the sentence highlighting its hierarchical structure, where lexical items combine to form constituents, which can be embedded in each other. While research on spoken and written language has, by now, established that human brains automatically attribute hierarchical structure to a linguistic signal despite the fact that this structure is not contained in the signal itself (see, e.g., Friederici et al., 2017; Zaccarella and Trettenbrein, 2021), only a handful of studies have investigated syntactic processing in sign language so far (e.g., MacSweeney et al., 2006; Stroh et al., 2019; Matchin et al., 2021), which is why the relevance of hierarchical structure during sign language processing requires further psycho- and neurolinguistic research. However, formal linguistic analyses strongly suggests that sign languages, just like spoken languages, rely on such hierarchical representations (Sandler and Lillo-Martin, 2001, 2008; Tang and Lau, 2012; Mathur and Rathmann, 2014; Cecchetto, 2017). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

structure of grammatical representations (Sandler and Lillo-Martin, 2001, 2008; Tang and Lau, 2012; Mathur and Rathmann, 2014; Cecchetto, 2017).

The, at least, more than 200 different sign languages of the deaf around the world (Hammarström et al., 2022) as well as various tactile sign languages of the deafblind, are testament to the contemporary understanding among cognitive scientists that the capacity for language is not bound to speech, but that the neurocognitive machinery for language flexibly interfaces with the sensorimotor system depending on individual developmental circumstances. Accordingly, the emerging picture in the cognitive sciences has been that the language system essentially enables the generation of hierarchically structured syntactic representations linking meaning (i.e., semantics) to a physical signal (i.e., sign or sound; respectively, representations thereof) and vice versa, whereas this capacity is rooted in a universal computational mechanism that is biologically determined, implemented neurally, and specific to humans (Lenneberg, 1969; Hauser et al., 2002; Berwick et al., 2013; Friederici et al., 2017). That is, the "biologic matrix" (Lenneberg, 1967), which determines and, at the same time, also constrains the cognitive specifics and development of the language system from infancy into adulthood (Lenneberg, 1964, 1967, 1969; Crain et al., 2016; Yang et al., 2017) appears not to specify the modality in which linguistic information can be perceived and externalized (Lenneberg, 1970; Klima et al., 1979; Poizner et al., 1987; Meier, 2016).

Once this perspective on the language system is adopted, it is not surprising that sign languages and spoken languages share deep similarities on the level of formal description but, at the same time, also exhibit features, which specifically reflect the different constraints (or lack thereof) imposed by the respective modality in which language is externalized and perceived (i.e., visuospatial for sign language and auditory-oral for spoken language). For example, the hierarchical grouping of lexical items into constituents is motivated by the formal analysis of the structure of both sign and spoken languages (Sandler and Lillo-Martin, 2001, 2008; Tang and Lau, 2012; Mathur and Rathmann, 2014; Cecchetto, 2017; Friederici et al., 2017; Zaccarella and Trettenbrein, 2021). However, while the auditory-oral modality imposes a strictly sequential organization of lexical items as well as morphologic elements (i.e., the minimal meaning-bearing elements that make up a word, e.g., *eat* and *-s* in *eats*), these constrains seem to be relaxed for the visuospatial modality where several articulators (i.e., hands, face, and body) can be used simultaneously to a certain extent. For example, the sign CHASE in the example sentence in Fig. 21.1 (top panel) expresses lexical information (i.e., handshape) and grammatical information (i.e., movement path marking thematic roles) at the same time (while in English *eat* and the third-person marker *-s* can only be produced sequentially).

The way in which such formal descriptions of the language system and its development as outlined here ultimately relate to neurobiology generally still remains an unresolved issue in cognitive neuroscience, whereas researchers working on sign language face some additional challenges. Like other areas of cognitive neuroscience, the neuroscience of sign language faces the issue that there is no established linking theory for mapping the basic elements of linguistic theory (e.g., lexical items, syntactic operations, etc.) to the basic elements of neuroscience (e.g., cell assemblies, brain regions, etc.; Poeppel and Embick, 2013; Embick and Poeppel, 2015). Accordingly, the vast majority of studies in the cognitive neuroscience of language in any modality are correlational in nature and their interpretation depends greatly on the way in which formal constructs from linguistics have been operationalized in an experiment (van der Burght et al., 2023). In addition, because sign languages are minority languages primarily used by the respective deaf communities, they are frequently understudied in comparison to the primarily Western spoken languages commonly used in experiments (Henrich et al., 2010). As a consequence, relatively little previous research and formal analyses of many phenomena may be available (Baker et al., 2016; Quer and Steinbach, 2019) and resources that are routinely used in research on spoken languages (e.g., corpus data) are currently not available for the vast majority of sign languages.

A PRIMER ON SIGN LANGUAGE LINGUISTICS

As already alluded to above, the study of sign language over the past decades and the therefrom emerging understanding that sign languages are fully fledged natural languages with complex organization on all levels of linguistic analysis have revolutionized how cognitive scientists attempt to understand the human capacity for language. Pioneering work carried out from the 1960s of the past century onward (e.g., Stokoe, 1960; Klima et al., 1979) demonstrated that sign languages such as, for example, ASL are not in any way "translations" of the spoken majority language in a region (i.e., English in case of the United States) into a gestural system but instead have their own and independent grammar as well as lexicon. This is best demonstrated by the fact that ASL and British Sign Language (BSL) are not mutually intelligible, even though the spoken majority language in both countries is English. When an ASL signer and a BSL signer, who do not know the other's language meet, they may, however, still be able to make basic communication work by resorting to what is sometimes called International Sign. This ad hoc sign system used in international settings heavily relies on signs from the signers' respective sign languages that can be considered to have a strong iconic motivation as well as grammatical features (e.g., modifications of path movement overtly marking the agreement of verbs; see below) shared among many sign languages (Mesch, 2010).

A unique affordance of the visuospatial modality appears to be that it lends itself to the use of iconic strategies of depiction (i.e., a certain similarity between the form of the respective sign and its actual lexical meaning). Accordingly, approximately one-third of all lexical signs in the lexicon of a particular sign language are estimated to be iconic (Boyes-Braem, 1986), but more recent work has questioned this estimate (Caselli et al., 2017; Sehyr et al., 2021). For example, in their so-called citation form (i.e., the way in which a sign is produced in isolation as opposed to a sentence or discourse context), the DGS signs in Fig. 21.2 (top-right panel) are clearly iconic: The sign TREE depicts the ground as well as stem and crown of a tree, whereas the sign for SLEEP depicts the head of the signer being laid down on a cushion. Because the latter sign overlaps with a similar-looking gesture for "sleeping," its meaning is rather transparent also to nonsigners (Trettenbrein et al., 2021b). Despite its clear iconic motivation this is not true for the sign TREE, because comprehending the sign requires knowledge of the structured mapping from the strategy of iconic depiction to the lexical meaning (Emmorey, 2014; McGarry et al., 2023). Importantly, iconic strategies differ between sign languages: Whereas the DGS sign iconically depicts a tree with stem and crown using the arm and hand, Chinese Sign Language depicts only the outline of the stem (Bellugi and Klima, 1976).

While sign language relies on a set of articulators that is radically different from those used for spoken language, signs and spoken words nevertheless exhibit familiar internal organizational principles. The visuospatial modality allows for the simultaneous use of different articulators (i.e., hands, face, and body), which can combine in different ways to articulate a sign and convey linguistic information: Usually, a distinction between manual and nonmanual components of signs is made, which can be accompanied by so-called mouthings or mouth gestures (Fig. 21.2, left panel). Just like lexical items and morphemes in spoken languages can be broken down into individual phonemes (i.e., speech sounds), the manual components of individual signs are also not holistic units but consist of sub-lexical parameters (i.e., phonemes; Stokoe, 1960; Brentari, 2012; Baker et al., 2016; Fenlon et al., 2017): These parameters include hand form, hand position, contact area, and movement (from the starting point to end point). Sign languages differ with regard to the phonemes they use. The relevance of sub-lexical parameters for sign formation is evidenced by the existence of minimal pairs (i.e., words, which differ only in one phonologic parameter such as *grammar* and *glamour* in English) in sign languages. For example, the DGS signs TEACHER and LECTURER differ in one

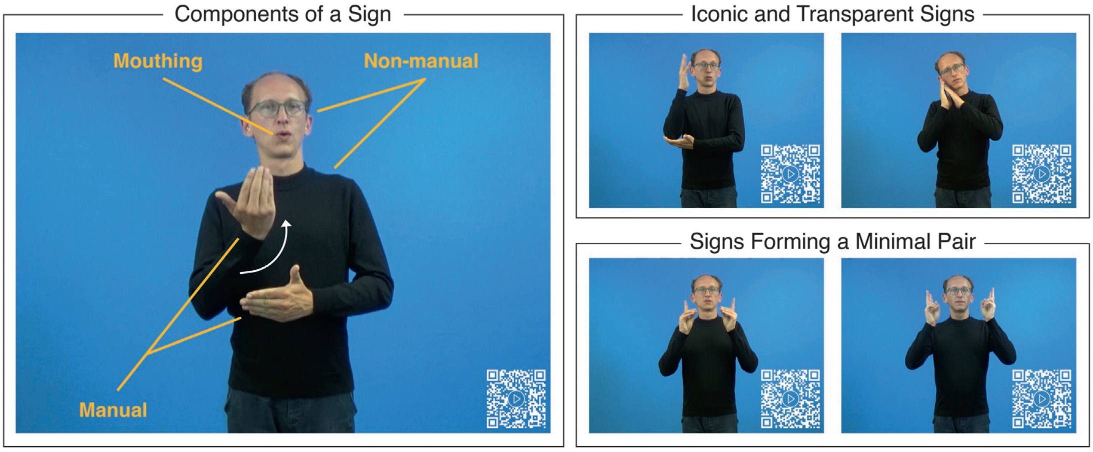

Fig. 21.2. Linguistic analysis of individual signs. The left panel shows the different manual, and nonmanual components of a sign. In general, nonmanual components include the direction of gaze, movement of eyebrows, movement of head and torso, facial expression, mouthings [i.e., forming (part of) a spoken word with the lips], and mouth gestures. Manual components include the hand form, hand position, contact area, and movement (starting point to end point). The example shown here is the DGS sign NEW (video: https://doi.org/10.6084/m9.figshare.21711794), which is signed with flat hands with the nondominant (left) hand steady in front of the body, whereas the dominant (right) performs an upward movement behind the nondominant hand. These manual components are accompanied by a mouthing roughly corresponding to the spoken German nɔɪ̯ as well as momentarily raised eyebrows. The right top panel shows the DGS signs TREE (left; video https://doi.org/10.6084/m9.figshare.21712619) and SLEEP (right; video: https://doi.org/10.6084/m9.figshare.21713123), which are both iconic signs yet have different levels of transparency. While the iconic motivation of the sign TREE (i.e., the dominant right hand depicting the stem whereas the fingers represent the treetop) is obvious once the meaning of the sign is revealed; the meaning of the sign is, nevertheless, accurately identified by only 10% of non-signing participants in a guessing task (Trettenbrein et al., 2021b), rendering the sign nontransparent to nonsigners despite its iconic motivation. In contrast, the iconic motivation for the lexical sign SLEEP overlaps with a gesture also frequently used by nonsigners to indicate "sleep," "sleeping," or "being tired," thereby rendering the sign highly transparent also to nonsigners. The right-bottom panel shows the DGS signs LECTURER (left; video https://doi.org/10.6084/m9.figshare.21711575) and TEACHER (right; https://doi.org/10.6084/m9.figshare.21708107), which form a so-called minimal pair, as their manual components differ only in hand form but share the hand position, and movement from the starting to the end point. In addition, the lexical distinction may be emphasized when both signs are accompanied by different mouthings. Representative frames of signs in this illustration and the accompanying videos available online via a QR code or DOI have been adapted from a publicly available dataset by Trettenbrein et al. (2021b) under a Creative Commons (CC-BY 4.0) license to which this illustration is also subject.

manual parameter, namely hand form (Fig. 21.2, bottom-right panel; notice though that, in many cases, these DGS signs will also be accompanied by different mouthings).

Besides phonology, sign languages also exhibit a rich morphologic structure, which closely interacts with syntax (i.e., the grammatical structure of the entire sentence). In the visuospatial modality, morphologic processes can be realized in two ways: First, one or more phonemes of a sign may be altered (e.g., the DGS sign TREE depicted in Fig. 21.2 may be produced with a slight left-to-right movement to mark plurality and change the meaning to TREES or FOREST). Such alterations of the movement path, in combination with repetitions of (part) of a sign, yield complex and language-specific systems of derivational morphology (Bellugi and Klima, 1976; Bellugi et al., 1989). Second, an affix may be added to a sign to derive a related, yet different meaning (e.g., in the DGS sign SCIENCE + PERSON a lexicalized person marker is suffixed to the sign SCIENCE to derive the meaning "scientist"). Yet, because producing signs sequentially generally takes longer than producing speech sounds (Klima et al., 1979), affixation appears to be relatively rare in sign languages. That is, the signing rate is generally lower than the speaking rate when only sequentially produced manual signs are considered. However, the simultaneous morphology and articulation of signs ultimately results in an overall similar information density for sign and speech (Klima et al., 1979).

Moving to the level of sentences, many sign languages including DGS can express grammatical relations using a combination of two different syntactic strategies: The relation of lexical elements in a sentence may either be marked by relying on word order [subject-object-verb (SOV) being the default word order for DGS, different from the subject-verb-object (SVO) order of German] or via the grammatical use of sign space. For example, the proposition "the cat is chasing the dog" can be expressed by signing CAT DOG CHASE. In this case, the order in which signs are produced indicates their grammatical role in the sentence (i.e., CAT is the subject and DOG is the object). Alternatively, the same proposition can be expressed using the spatial grammar that is unique to the visuospatial modality (Fig. 21.1, top panel): In the example sentence, subject and object are first assigned positions in sign space (the sign CAT location 3a and the sign DOG location 3b) and the sign CHASE is then produced in morphologically modified form (glossed as ${}_{3a}$CHASE$_{3b}$) where the start and end of the altered movement path indicate the position of the subject and object in sign space (Mathur and Rathmann, 2012;

Pfau et al., 2018). Inverting the path movement (i.e., by signing the inflected form $_{3b}$CHASE$_{3a}$) would also invert the meaning of the sentence (i.e., the dog would then chase the cat). Sign languages therefore provide suggestive evidence for the view that lexical processes are inherently syntactic (Krauska and Lau, 2023).

Lastly, besides the grammatical use of space, which is unique to the visuospatial modality, signers can also use space to iconically depict scenes and spatial relations using so-called classifier constructions. Classifiers are morphemes with a nonspecific meaning expressed using the hands, are attested in almost all sign languages that have been studied, and use a particular configuration of the hand to represent a specific category of entities by depicting a salient property shared by all entities belonging to that category (Zwitserlood, 2012). For example, when referring to a car slowly driving along a road, in a classifier construction a deaf signer using DGS would use a flat handshape (i.e., ) with the palm pointing downward. This is a classifier for vehicles with four wheels that can then be used to iconically depict the slow movement in sign space (i.e., the hand would be moving forward slowly). However, if the signer was referring to a motorcycle they would use the same handshape but with the palm pointing sideways, a classifier that is used in DGS for all vehicles, which have only two wheels. Classifiers are lexicalized and differ between sign languages (e.g., ASL uses the  handshape for vehicles regardless of the number of wheels; Zwitserlood, 2012; Baker et al., 2016).

Interim summary

Sign languages are natural languages with complex organization on all levels of linguistic analysis (e.g., phonology, morphology, and syntax) which are externalized in the visuospatial modality. This indicates that the mapping of the hierarchically structured representations of the language system to the sensorimotor system is not biologically specified but emerges during development. The principally iconic motivation of many signs, grammatical use of space, as well as flexible use of classifiers in sign space are affordances specific to the visuospatial modality.

SIGN LANGUAGE ACQUISITION AND DEVELOPMENT

The language experience of deaf children is highly variable and this developmental variability is also reflected both behaviorally and neurally. Language acquisition in the deaf population depends on several factors: (i) the degree and age of onset of hearing loss (i.e., either congenital, during early childhood, or later), (ii) the use of aided technology (if desired and suitable), and (iii) the language primarily used by a child's caregivers. It has been estimated that 90%–95% of infants with profound hearing loss are born to hearing parents, who do not know any sign language (Mitchell and Karchmer, 2004; Meier, 2016). Consequently, the number of deaf children, who naturally acquire the sign language used by their parents, is remarkably small with the vast majority of the deaf population exhibiting heavily varying language acquisition profiles. Indeed, in large parts of the world, including most so-called developed countries, deaf children's exposure to a sign language is still frequently delayed—a situation that is completely preventable (Mayberry, 2002). Crucially, such a lack of early access to a linguistic system has lasting developmental consequences: Deaf individuals who were only exposed to an established sign language in late childhood or adolescence show considerable limitations in grammatical knowledge and performance but not nonlinguistic abilities (Emmorey et al., 1995a; Mayberry, 2002; Mayberry and Squires, 2006; Meier, 2016).

Typically developing children of deaf parents, regardless of whether they are deaf or hearing, undergo the same developmental milestones during sign language acquisition that have previously been identified based on studies of hearing children acquiring spoken language (Mayberry, 2002; Mayberry and Squires, 2006; Meier, 2016). This similarity is evidenced by the near-identical growth curves observed during early development of the productive vocabulary of a group of deaf children acquiring BSL and a larger cohort of hearing children acquiring British English (Fig. 21.3, left panel). The development of deaf children's syntactic abilities also proceeds in similar stages and at a similar pace like that of their hearing peers (Fig. 21.3, right panel), despite the fact that common measures like the mean length of utterance are prone to underestimate the complexity of signed utterances (Terrace et al., 1979). While recent research suggests that lexical development during the early phase of sign language acquisition of a deaf child born to hearing parents can be aided by the parent's rudimentary learning and usage of the local sign language (Berger et al., 2023), early exposure to a sign language in its full form is, nevertheless, crucial for the typical development of the language system (Mayberry, 2002; Meier, 2016).

The deep similarities between the development of the language system in deaf children acquiring a sign language and hearing children acquiring a spoken language indicate that language constitutes a modality-independent capacity for manipulating abstract units and rules, but this does not imply that there are no effects of modality. A widely known example is the observation that deaf children, on average, seem to produce their first signs several months before their hearing peers produce their first words (Newport and Meier, 1985; Meier, 2016). This is predicted by the fact that motoric systems relevant for producing signs mature before those for controlling speech, in combination with the greater perspicuity and recognizability of signs to caretakers (Newport and Meier, 1985). However, even in cases where one might expect an impact of modality, for example, due to an overlap between sign and gesture, the independent maturation of the language system can be observed: Even though the ASL signs for the pronouns ME and YOU superficially resemble paralinguistic gestures (i.e., pointing with the index finger at oneself or a second person), which are commonly used prelinguistically by deaf and hearing children already at 9 months of age, deaf children undergo a later developmental phase during language acquisition in which they systematically confuse these pronominal signs at the same age when hearing children acquiring a spoken language make similar pronoun-reversal errors (Petitto, 1987).

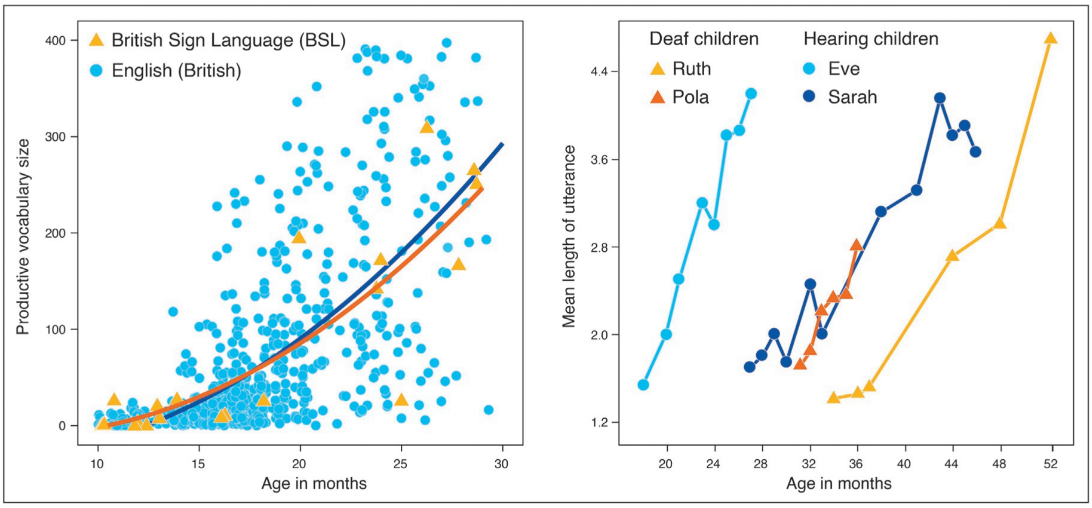

Fig. 21.3. Lexical and syntactic development in deaf children acquiring a sign language. Two plots showing growth curves for the lexical (left panel) and syntactic (right panel) development of deaf children acquiring a sign language in comparison to hearing peers acquiring a spoken language, both measured by analyzing produced utterances. The graph in the left panel shows the development of the productive vocabulary size for a group of typically developing deaf children acquiring British Sign Language (BSL) (color-coded in orange) in comparison to a group of typically developing hearing children acquiring British English (color-coded in blue). The figure clearly indicates that the size of the productive vocabulary grows at a similar speed in both groups. The illustration is based upon data freely available from the Wordbank database as of June 20, 2023 (Frank et al., 2017); specifically the graph shows quadratic regression models fit to the BSL data (Wordbank identifier "WG") by Woolfe et al. (2010) as well as the data for British English (Wordbank identifier "Oxford CDI") by Floccia (2017), which includes data from Hamilton et al. (2000). The right panel shows the development of mean length of utterance (MLU) of two deaf children acquiring American Sign Language (ASL) in comparison to two hearing children acquiring American English. These data are reproduced here from Terrace et al. (1979) in an adapted form and should be treated with some caution because MLU was measured here based on definitions developed for research on spoken languages, as the authors of the original paper also remark in a footnote. While spoken utterances are often broken down not just into words but also sequentially produced morphemes (e.g., *drive there* vs *drive-ing*), many sign languages (e.g., ASL or DGS) will rely on simultaneity to express the same propositions using a single morphologically modified sign (see section "A Primer on Sign Language Linguistics"). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

Additional evidence for the notion that humans are born with a modality-independent propensity for symbolic communication (Lenneberg, 1964) comes from studies uncovering the generative and rule-based nature of so-called homesign systems developed by deaf children, whose hearing parents have not exposed them to a sign language (Goldin-Meadow, 2003, 2017; Goldin-Meadow and Yang, 2017; Flaherty et al., 2021). Deaf children, who do not have access to a conventionalized sign language, have been found to develop such homesign systems derived ad hoc from iconic gestures. That is, these children develop individual homesign systems, which exhibit many of the properties of natural languages (e.g., morphologic patterns, basic syntactic structure of utterances, etc.), despite the fact that these properties are not contained in the gestural input they receive from caretakers (Goldin-Meadow, 2003, 2017; Flaherty et al., 2021). Analyzing the statistical profile of observed grammatical patterns in homesign confirms that, while homesign systems fall short of the conventionalized lexical and syntactic complexity of natural languages, they are nevertheless based on productive grammars (Goldin-Meadow and Yang, 2017). This strongly suggests that children bring a structural bias to the process of language acquisition, which determines them to impose discrete units that are combined in a rule-based fashion onto any kind of potentially linguistic input.

Whereas the cognitive prerequisites and developmental milestones of sign language acquisition in deaf children have, as of now, been studied for decades and with veritable success, the neural basis of sign language during infancy and childhood and its development remain severely understudied. A relatively recent study by Payne et al. (2019) is an interesting exception to this general lack of neural data: The authors used functional transcranial Doppler sonography (fTCD), a method that measures cerebral perfusion changes in response to neural activation, in a sample of 19 typically developing deaf children, who were on average 8 years old, and found that language production was significantly left-lateralized, independent of the modality of language use (i.e., whether the children were producing BSL, spoken English, or a combination of the two). The authors conclude that the lateralization of language in the tested sample reflects a left-hemispheric specialization for processing linguistic representations. While this interpretation is in line with the data of typically developed deaf adults, as we will discuss below, studies of how this usually left-lateralized pattern for (sign) language processing emerges in deaf signers during (sign) language acquisition are missing, especially when considered in comparison to the neural data available for spoken language acquisition (Trettenbrein and Friederici, 2025).

Interim summary

Most deaf children are born to hearing parents and their language experience is highly variable. The developmental milestones during sign language acquisition mirror those familiar from studies of spoken language acquisition in hearing children and suggest that the maturation of the language system is input-dependent but modality-independent.

SIGN LANGUAGE APHASIA

While reports of patients, who had suffered lesions, provided the first evidence for the specialization of the left hemisphere of the human brain for spoken language processing already more than 150 years ago (Broca, 1861; Dax, 1863, 1865), the first detailed reports of deaf signers with aphasia following left-hemispheric brain damage surfaced only in the 1980s of the past century (e.g., Poizner et al., 1987; Bellugi et al., 1989). Until then, it was still commonly assumed that the left hemisphere and especially the posterior portion of the left inferior frontal gyrus (i.e., Broca's area) are specialized for processing speech. A case report by Damasio et al. (1986) about a hearing, bimodal, bilingual patient provided the first evidence for a left-hemispheric specialization for language and not just speech: The patient was a native speaker of English but had acquired ASL for professional reasons, when she was 18 years of age, and used ASL daily for her work. An examination of the patient's linguistic performance, while undergoing a so-called Wada test (i.e., the injection of barbiturate into the left carotis), revealed that the patient exhibited a marked aphasia in both English and ASL when left-hemispheric, language-relevant areas of the cortex were rendered inoperative by the procedure.

This first suggestive evidence for a general specialization of the left hemisphere for language independent of modality, based on data from a hearing late signer, was soon complemented by detailed and linguistically sophisticated case studies of deaf signers with left-hemispheric damage, who exhibited different impairments in their signing depending on the location of the lesion within the perisylvian regions of the left hemisphere (Poizner et al., 1987; Bellugi et al., 1989; Hickok et al., 1996b). For example, Bellugi et al. (1989) reported data from a deaf patient (GD), who had suffered a left frontal lesion comprising most of the frontal lobe, including Broca's area, in the inferior frontal gyrus. After the stroke, the patient's signing exhibited clear signs of agrammatism as it was generally slow and effortful, consisted mostly of one-sign utterances, and lacked the grammaticalized morphologic and syntactic markings of ASL. Generally speaking, the aphasic syndromes observed in deaf signers with left-hemispheric damage mirror those known from research with hearing users of a spoken language insofar as lesions affecting frontal perisylvian regions and white matter cause non-fluent aphasia, whereas lesions to posterior perisylvian regions lead to fluent aphasias (see Goldberg and Hillis, 2022, for an in-depth treatment of sign language aphasia).

Despite the importance of space in sign language as, for example, in the grammatical use of sign space (Fig. 21.1) or in classifier constructions (see section "A Primer on Sign Language Linguistics"), damage to the RH, which is widely assumed to be dominant for visuospatial processing (Corballis, 2003), has not been found to cause aphasia in deaf signers. Bellugi et al. (1989) also report data from three deaf signers with right-hemispheric lesions, which all exhibited fluent, grammatical, and practically error-free signing without any indication of agrammatism. However, it seems not to be the case that right-hemispheric damage has no effect on signing abilities: Several case studies suggest that the processing of topographic sentences and classifier constructions (in which space is not used in a grammatically conventionalized way but instead iconically depicts spatial relations and movement patterns) is impaired in deaf signers following right-hemispheric lesions (Hickok et al., 1996c; Atkinson et al., 2005). These observations are in line with data from so-called split-brain patients indicating that the left hemisphere retains relatively sophisticated visuospatial abilities (Corballis, 2003), which can support the processing of spatial aspects of sign language in the context of generating syntactic representations (i.e., grammatical use of sign space) but not the generation of spatial representations iconically depicting spatial relations (Bellugi et al., 1989; Emmorey et al., 1995b; Hickok et al., 1996c; Atkinson et al., 2005).

In contrast to sign language aphasias following damage to left but not right perisylvian regions, two independent case studies have documented a unique pattern of sign language aphasia following lesions to the left occipital cortex. Hickok et al. (1995) documented a case of a deaf signer with a lesion spanning the left medial temporal and occipital lobe, the left occipital pole, and the white matter giving rise to the splenium of the corpus callosum. Behaviorally, the patient presented with right hemianopia (i.e., loss of half of the visual field), alexia (i.e., inability to recognize written words), and a severe inability to comprehend signs in spite of seemingly intact sign production with the exception of occasional paraphasic errors (i.e., incorrect substitution of a sign or a part of it). The authors interpreted this as a case of so-called "sign blindness" where the spared visual areas of the RH were disconnected from the spared left perisylvian language regions by the lesion. Saito et al. (2007) describe a similar case of a deaf signer with a lesion to the left occipital lobe, medial temporal lobe and hippocampus, as well as the corpus callosum. Interestingly, this patient presented also with severely impaired sign production abilities in addition to impaired comprehension. In sum, these cases (i) show that the RH is unable to fully support sign language comprehension and (ii) suggest that posterior regions of the left hemisphere may undergo some plastic changes, which make them more language-relevant as the result of deafness and/or sign language acquisition.

Given that both hands are usually used as the primary articulators during sign language production, the observed lateralization patterns for sign language aphasia seem to confirm the dissociation between the primarily left-hemispheric processing of linguistic representations generated by the language system as opposed to the respective modality-specific (i.e., speech or sign) processing of the bilateral production system during externalization. That is, even though sign language imposes articulatory demands that are radically different from those of spoken language, processing sign language seems to primarily involve the left hemisphere for processing linguistic representations independent of whether the left or right hand is being used as the primary articulator during sign production (Corina et al., 2003). In this context, it is also interesting to note that Gutiérrez-Sigut et al. (2015) compared spoken and sign language production in a group of hearing, native, bimodal bilingual users of English and BSL and found that the left-hemispheric lateralization was actually more pronounced for producing signs in comparison to producing speech. Because the lateralization was not primarily driven by motor (i.e., production) factors, the authors argue that the visuospatial modality imposes increased processing demands with regard to somatosensory feedback and the simultaneous processing of phonologic parameters (i.e., handshape, location, and path movement; Gutiérrez-Sigut et al., 2015).

Additional evidence for a dissociation of the language system from the sensorimotor system as well as other cognitive systems used during the externalization of language and communication stems from the observation that the production of signs and the production of gestures can be differentially impaired in aphasic signers despite both being produced in the same modality. A suggestive case study by Corina et al. (1992) describes a deaf signer with a marked aphasia disrupting comprehension and production of ASL following left-hemispheric damage, while their ability to communicate using nonlinguistic gestures was mostly preserved. The patient would substitute lexical signs with pantomimic gestures iconically related to the object such as, for example, miming the bouncing of a ball instead of using the lexical ASL sign, BALL. Interestingly, these substitutions were produced regardless of the iconicity of the target sign, hinting at the lexicalized status even of highly iconic signs (also see Marshall et al., 2004, for a similar case report). Likewise, Bellugi et al. (1989) found that all three aphasic deaf signers with left-hemispheric damage showed strong dissociations between their linguistic, nonlinguistic gestural, and general motoric capacities. As of now, there is also neuroimaging evidence indicating that the processing of gestures as opposed to lexicalized signs differentially engages perisylvian regions (Newman et al., 2015), thereby supporting the idea that sign and gesture rely on distinct representations.

Lastly, independent of the interesting data from the variety of case studies discussed here it must also be mentioned that researchers and clinicians working with deaf patients with aphasic symptoms frequently face the problem that suitable diagnostic tools may simply not be available for the particular sign language under study, a subsisting issue that also has serious consequences for the quality of care that deaf patients may receive. In such cases, researchers have to create a suitable test either by adapting an existing standardized aphasia test battery for a spoken language to the sign language under study (e.g., the adaptation of the Boston Diagnostic Aphasia Examination to ASL available from the Salk Institute; https://lcn.salk.edu/ASLNew/SAT.htm) or by creating a suitable test battery de novo (e.g., the BSL Aphasia Assessment Battery developed by the Deafness Cognition and Language Research Centre; https://dcalportal.org/tests/aab). For nonlinguistic assessment, researchers or clinicians, who are not proficient in the respective sign language used by the participant, may opt to work closely with interpreters and rely on available tests standardized using data from the hearing, nonsigning population. However, tests that depend on knowledge of the spoken majority language used in the respective environment are likely not appropriate (Miranda et al., 2022).

Interim summary

In adult signers, the left hemisphere is usually dominant for sign language processing. The patterns of documented aphasic syndromes in deaf signers with damage to different left perisylvian regions align with those known from studies of hearing aphasics. In contrast, lesions to the left occipital cortex that also affect the splenium of the corpus callosum may cause primarily receptive aphasia in deaf signers by disconnecting left perisylvian regions from the visual system. Moreover, deaf signers' difficulties with processing classifier constructions following right-hemispheric lesions constitute a modality-specific syndrome.

FUNCTIONAL NEUROIMAGING STUDIES OF SIGN LANGUAGE

While case studies of deaf signers with aphasia provided important, first insights into the neural basis of sign language, the advent of neuroimaging in the 1990s of the past century brought about the first, functional neuroimaging studies of sign language processing in deaf signers using noninvasive methods such as electroencephalography (EEG), positron emission tomography (PET), and functional magnetic resonance imaging (fMRI). Whereas the methodological foundations and respective limitations of these research methods apply to sign language research in the same way as they apply to research on spoken and written language, the specifics of the visuospatial modality nevertheless require adaptations such as, for example, the reliance on videos for presenting stimulus materials and a variety of associated potential issues for presentation as well as analysis (Capek and Neville, 2015). We will begin by briefly reviewing EEG studies of sign language processing in deaf signers in comparison to insights from similar studies in hearing users of spoken languages, but will then focus on studies of the neural basis of sign language processing using PET and fMRI as these are potentially more informative in the context of lateralization. Studies carried out with different functional methods [e.g., magnetoencephalography (MEG)] or different populations (e.g., hearing signers) will be considered wherever relevant.

Electrophysiologic studies

The major event-related potentials (ERPs) observed during sign language comprehension parallel those reported for auditory language comprehension (Fig. 21.4, top panel). Early ERPs peaking

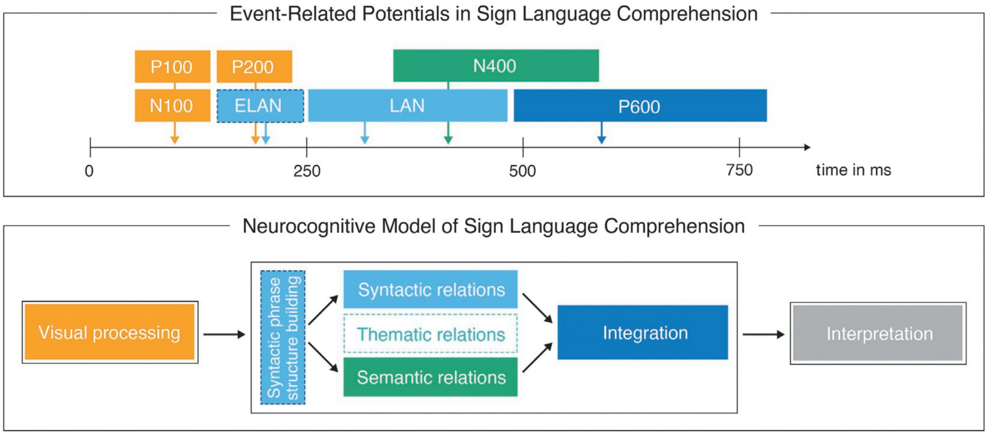

Fig. 21.4. Event-related potentials and a neurocognitive model of sign language comprehension. The top panel depicts the time course of ERPs that have been observed in studies of sign language comprehension. The colored boxes indicate different ERPs, whereas the width of boxes roughly indicates associated time-windows reported for different components in the literature. Arrows for each box indicate the canonical peak of a component in milliseconds (ms). Notice that part of the reported variability with regard to the timing of peaks reported for different components may reflect researchers' degrees of freedom (Luck and Gaspelin, 2017) with regard to the time-locking of their analyses: ERPs can be time-locked to the onset of stimulus videos, the actual onset of the first sign (Emmorey et al., 2022), or the so-called recognition or uniqueness point. However, determining the recognition or uniqueness point is complicated by the fact that signers use transitional movements between signs as cues during comprehension (Hosemann et al., 2013). Abbreviations used in the top panel: positivity (P), negativity (N), early left anterior negativity (ELAN), and left anterior negativity (LAN). The bottom panel describes the major consecutive processing steps of a tentative neurocognitive model of sign language comprehension. Different processing stages are indicated by different boxes. Arrows depict the temporal relationship between processing stages. The color coding is consistent between the two panels and links the different ERPs to their assumed processing stage: Visual processing is depicted in orange, syntax-related processing in light blue, semantic processing in green, and integration and repair processes in dark blue. The diagram in the bottom panel is loosely based on the neurocognitive model for auditory language comprehension depicted in Friederici (2017). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

at around 100 ms (i.e., P100 and N100) and 200 ms (i.e., N200) have been attributed to visual processing (Emmorey et al., 2022). Yet, some studies report differential topographic distributions of ERPs related to open and closed class signs (e.g., nouns vs pronouns) already as early as 100 ms (Neville et al., 1997). During the processing of sign language sentences, an early left anterior negativity (ELAN) peaking at 140–200 ms assumed to reflect syntactic phrase structure building (Capek et al., 2009; Friederici, 2011) and (left) anterior negativities in the time-window of 250–600 ms related to the manipulation of syntactic information (Capek et al., 2009; Hänel-Faulhaber et al., 2014) have been reported. Following semantic manipulations on the sentence- and single-sign level, negativities peaking at approximately 400 ms (i.e., N400) have been observed (Gutiérrez et al., 2012b; Hosemann et al., 2013; Hänel-Faulhaber et al., 2014), whereas their amplitude and latency can be modulated by priming (Gutiérrez et al., 2012a; Emmorey et al., 2022) and psycholinguistic variables such as lexical frequency (Emmorey et al., 2020). Lastly, late positivities assumed to reflect integration and repair processes occur after 500 ms (i.e., the so-called post-N400 positivities or P600s; Neville et al., 1997; Capek et al., 2009; Hänel-Faulhaber et al., 2014).

Interpreting the topographic distribution of ERPs observed during sign language processing has proven difficult because (i) EEG generally allows only coarse and approximate estimation of lateralization due to the so-called "inverse problem" (Grech et al., 2008), and (ii) some language-related components and their corresponding canonical topographies have actually not consistently been observed. In their study of violations of so-called agreement verbs (see Fig. 21.1) in ASL, Capek et al. (2009) found an ELAN when the agreement between subject and object was reversed (a manipulation possible due to the SVO word order of ASL) and a more right-lateralized anterior negativity when the agreement relation was unspecified (i.e., the verb agreed with a locus in space that had not previously been assigned). Hänel-Faulhaber et al. (2014) employed another violation of verb agreement where signs did not agree with either the subject or the object but moved from a neutral point in sign space toward the signer. Interestingly, they did not observe an ELAN but a relatively late LAN (400–600 ms). Lastly, using unspecified agreement violations in DGS, Hosemann et al. (2018) observed neither an ELAN, nor a LAN, nor a P600, but two independent effects (one mostly right posterior positivity at 220–570 ms, followed by a left anterior effect at 300–600 ms).

This diversity of ERP findings related to sign language comprehension indicates that a first model of the time course of differ rent processing steps sketched in Fig. 21.4 (bottom panel) will require refinement in the future, including adjustments reflecting possible modality-specific aspects (Gutiérrez et al., 2012b). A possible explanation for the observed variation is that all sign language studies relating to ELAN and LAN to date have used manipulations of agreement verbs: This likely constitutes a confound because the spatial nature of sign language agreement requires the recruitment of additional cognitive resources. Moreover, almost all paradigms mentioned above using agreement manipulations relied on morphologic alteration of the verb sign's movement parameter (e.g., moving in sign space from point 3a to 2 instead of from 3a to 3b; see Fig. 21.1). Recall, however, that the ELAN in auditory language comprehension is elicited by word category violations (Friederici, 2011, 2017). For example, the words *he butterfly* cannot be integrated into a phrase but *her butterfly* can (Maran et al., 2022a,b). Yet, verb agreement violations in sign language do not necessarily always also constitute word category violations, which block local phrase structure building, because alternative and less likely yet nevertheless grammatical interpretations of an utterance may be possible (for extended discussion, also see Hosemann et al., 2018).

Magnetic resonance and radionuclide imaging studies

The first fMRI and PET studies of sign language were carried out in the late 1990s of the past century and yielded conflicting results which, on the one hand, confirmed the stronger involvement of the left hemisphere and left perisylvian regions during sign language processing similar to spoken language but, on the other hand, also implicated right-hemispheric perisylvian regions as well as regions not typically reported in studies of spoken language processing. One of the first direct comparisons between hearing non-signers, deaf signers, and hearing signers processing videos in ASL revealed that both deaf and hearing signers showed activation in left perisylvian regions as well as their right-hemispheric homologs (Bavelier et al., 1998; Neville et al., 1998). This pattern was absent in all groups when processing written English. A study by Söderfeldt et al. (1997) was among the first to report the largest response to sign language in the bilateral visual association cortex (BA 37 and BA 19) in a sample of so-called children of deaf adults (CODAs), who were native signers, regions that are not usually observed in studies of spoken language processing. Lastly, studies by McGuire et al. (1997) and Petitto et al. (2000) suggested the primary involvement of left perisylvian regions in sign language processing, overlapping with frontal and temporal sites previously identified in studies of spoken and written language processing.

A recent meta-analysis of PET and fMRI studies of sign language comprehension in deaf signers confirmed the larger left-hemispheric involvement especially in left frontal regions, but also found extensive right-hemispheric convergence across all 23 neuroimaging studies in their dataset (Trettenbrein et al., 2021a; Fig. 21.5). Specifically, the authors observed seven clusters of convergence mass across studies in (1) Broca's area in the left inferior frontal gyrus (IFG) with peaks in both anatomic subregions, the anterior Brodmann area (BA) 45 and the more posterior BA 44; (2) left precentral and middle frontal gyrus (with peaks in BA 6 and BA 8); (3) left anterior insula; (4) left middle occipital gyrus (BA 19) bordering middle temporal gyrus; (5) right pars triangularis (i.e., BA 45); (6) right superior temporal gyrus (STG; BA 22); and (7) posterior portions of right middle- and inferior temporal gyrus spanning into the occipital gyrus (BA 37). Notice that the studies included in the dataset varied with regard to the experimental paradigms (e.g., semantic judgments, etc.), baseline conditions (e.g., fixation cross, videos of reversed signing, etc.), and stimulus complexity (e.g., single signs, sentences, etc.). Accordingly, while this analysis identified brain regions that are engaged by deaf signers during sign language comprehension, the functional characteristics of these regions remain underspecified.

To better characterize the observed pattern of convergence across studies of sign language processing, Trettenbrein et al. (2021a) performed two additional analyses which revealed that (i) the convergence mass was generally left-lateralized and especially so within Broca's area and (ii) part of the convergence mass

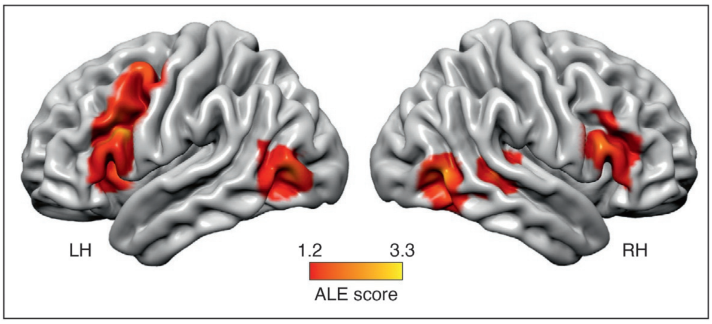

Fig. 21.5. Meta-analysis of sign language comprehension. Meta-analytical convergence across different fMRI and PET studies of significant clusters for sign language comprehension over baseline contrasts from 23 different neuroimaging studies with deaf signers and (total number of participants = 316). Color bar at the bottom indicates the Activation Likelihood Estimation (ALE; Eickhoff et al., 2009, 2012, 2017; Turkeltaub et al., 2012) score of any given voxel, which represents the degree of nonrandom convergence in activation between contrasts in the dataset. In the left hemisphere (LH), convergence was observed in the inferior frontal gyrus, middle occipital gyrus, precentral gyrus, middle frontal gyrus, and insula (ordered by descending size of clusters). In the RH, convergence was observed in middle and inferior temporal gyrus extending into occipital cortex, inferior frontal gyrus, and superior temporal gyrus. Based on data from Trettenbrein PC, Papitto G, Friederici AD, et al. (2021a). Functional neuroanatomy of language without speech: an ALE meta-analysis of sign language. Hum Brain Mapp 42: 699–712. https://doi.org/10.1002/hbm.25254. This illustration is subject to a Creative Commons (CC-BY 4.0) license.

in Broca's area but not its right-hemispheric homolog was specific to sign language processing in deaf signers and overlapped with spoken and written language processing in hearing non-signers. In a first step, the authors computed weighted lateralization indices using hemispheric and anatomic masks of Broca's area, which revealed a slight global left-lateralization [lateralization index (LI): 0.24, P 0.001] as well as a strong left-lateralization in Broca's area and it's right-hemispheric homolog (LI: 0.68, P 0.001). The left lateralization was especially pronounced in the posterior portion of Broca's area (BA 44, LI: 0.78, P 0.001). In a second step, the authors contrasted their meta-analysis of sign language comprehension studies with an independent meta-analysis of studies in which hearing participants observed sign-like actions. This revealed that only a cluster in Broca's area (peak in BA 44), the right superior temporal gyrus (peaks in BA 22) and left middle frontal and precentral gyrus (peaks in BA 6, BA 44, and BA 8) were uniquely involved in sign language processing but not in processing sign-like actions.

Based on the three clusters in IFG, right STG, and left middle frontal and precentral gyrus identified as sign-language specific by the contrast analysis with an independent meta-analysis of the processing of sign-like actions, Trettenbrein et al. (2021a) used the BrainMap database to characterize the functional associations of these clusters using a purely data-driven approach. This analysis revealed that voxels within the sign-language specific cluster in Broca's area were associated with studies that investigated cognition and, more specifically, with studies of language processing in hearing nonsigners across the several thousand studies listed in the database (Fig. 21.6). Broca's area can, therefore, be considered a modality-independent hub for language processing that is involved in processing linguistic information both in deaf signers as well as in hearing users of a spoken language. The sign-language-specific right STG cluster as well as left middle frontal and precentral cluster were also mostly associated with different aspects of language and speech processing in hearing nonsigners in the BrainMap database, though to a lesser extent and with larger variation in functional attributions. These regions, therefore, appear to be some of the key regions that deaf signers recruit for processing visual stimuli showing manual, facial, and bodily gestures that carry conventionalized linguistic structure and meaning in their respective sign language.

Because an overlap between sign and spoken language processing in the left inferior frontal and right posterior temporal regions is expected on the basis of the literature for spoken language processing as well as the literature on sign language aphasia, it is surprising that the meta-analysis by Trettenbrein et al. (2021a) did not observe convergence across studies in the left posterior temporal cortex, which houses Wernicke's area as another major hub for language processing. The involvement of posterior STG, posterior superior temporal sulcus (STS), and posterior middle temporal gyrus (MTG) in sign language processing is well documented by individual studies (Bavelier et al., 1998; Neville et al., 1998; San José-Robertson et al., 2004; MacSweeney et al., 2006; Moreno et al., 2018; Matchin et al., 2021). A possible explanation for this lack of convergence in the meta-analysis is that the different articulators (Fig. 21.2, left panel) were not used uniformly across studies in the data set: Stimuli including mouthings or mouth gestures have been found to activate the middle portion of the superior temporal cortex, whereas stimulus videos using only manual actions activate more posterior and inferior parts of lateral temporal lobe (Capek et al., 2008). The left and right posterior temporal cortex may, therefore, not subserve the same functional role during sign language processing, similar to the usually left-hemispheric linguistic advantage in spoken language processing (Vigneau et al., 2011; Wilson et al., 2023).

Similarly, given the important role of space in most sign languages, it is also surprising that Trettenbrein et al. (2021a) did not observe any convergence in either the left or right parietal cortex, after all a region, which is known to generally support spatial processing and has been found relevant for encoding phonologic information in sign languages (Cardin et al., 2013, 2016). The most likely explanation for this lack of convergence across studies in the meta-analysis is that involvement of parietal regions in sign language processing is, in many cases, only observed when the experimental paradigm explicitly taps into a property of sign language that requires the kind of information processing for which parietal regions seem to be specialized (Söderfeldt et al., 1997). For example, in a study of ASL locative classifier constructions, Emmorey et al. (2021) found bilateral involvement of the superior parietal lobule. Additional studies have found involvement of the left parietal cortex in processing topographic sentences (MacSweeney et al., 2002a), as well as bilateral involvement of the supramarginal gyrus and right superior parietal lobule for the processing of classifier constructions that use space iconically (Emmorey et al., 2002; Jednoróg et al., 2015). Thus, the neuroimaging literature as well as lesion studies (Bellugi et al., 1989; Emmorey et al., 1995b; Hickok et al., 1996c; Atkinson et al., 2005) demonstrate the relevance of parietal regions for sign language processing.

While a meta-analytic approach has the potential to reveal the commonalities of different studies, it is evident that carefully designed, individual experiments that pay close attention to linguistic details and insights from sign language linguistics are indispensable for gaining a closer understanding of the functional specifics of regions involved in sign language processing. In such studies, Broca's area has been implicated in processing mouthing and mouth gestures (Capek et al., 2008), as well as sign language morphology (Newman et al., 2010). Anterior and posterior portions of the left superior temporal cortex and sulcus have been linked to processing semantic as well as syntactic information in sign language (Blanco-Elorrieta et al., 2018; Moreno et al., 2018; Matchin et al., 2021). The left posterior middle temporal gyrus, which houses the motion-sensitive area MT/V5 and borders on the extrastriate regions of the occipital cortex has been found to be involved in processing movement in signed stimuli (Levanen, 2001; McCullough et al., 2012) and in lexical processing (Capek et al., 2008). Processing mouth gestures involves the fusiform face area located bilaterally at the bottom of the inferior temporal cortex in the fusiform gyrus (Capek et al., 2008). The left supramarginal gyrus has been linked to processing sign language

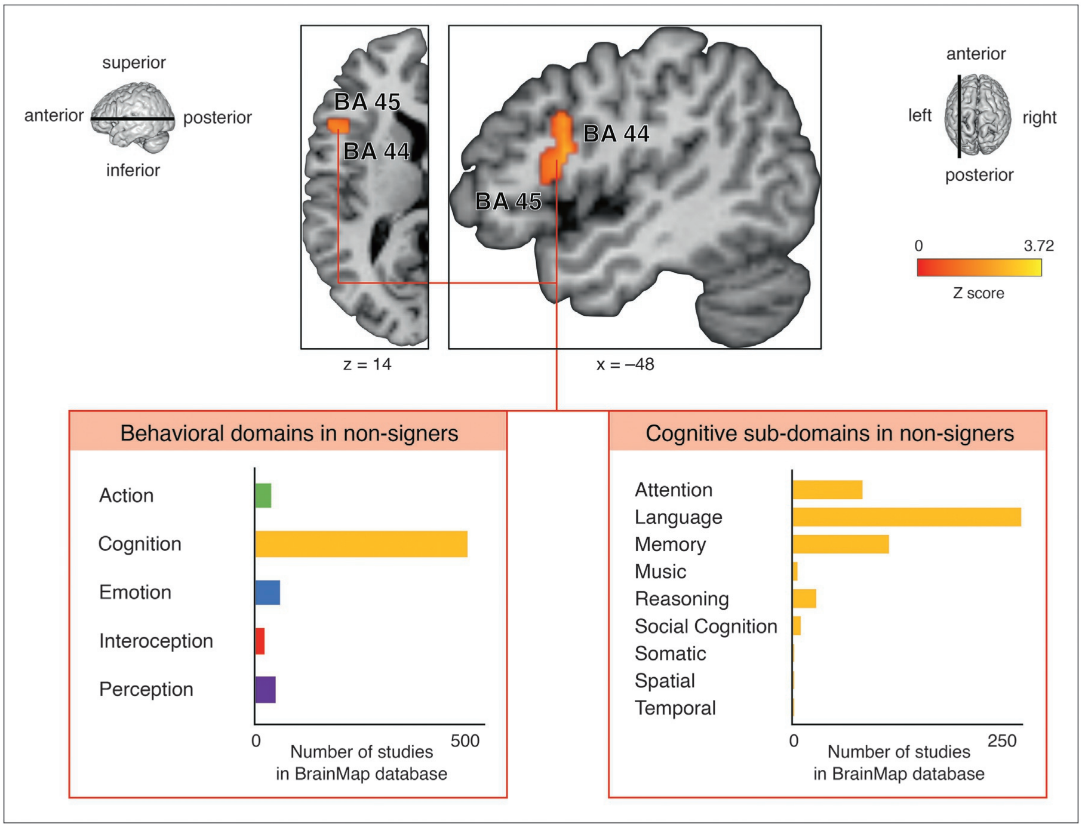

Fig. 21.6. Sign language-specific voxels in Broca's area and their function in non-signers. Functional attributions according to the BrainMap database (Fox and Lancaster, 2002) for sign language-specific voxels in Broca's area resulting from a contrast analysis comparing a meta-analysis of sign language comprehension in deaf signers and an independent meta-analysis of the observation of sign-like actions by hearing non-signers. The top panel shows a transverse and sagittal plane of the left hemisphere with the significant cluster in Broca's area [spanning Brodmann areas (BA) 44 and 45] surviving the contrast analysis of sign language comprehension and sign-like actions. The left box shows the number of studies with nonsigners in the BrainMap database that report peaks in voxels of the cluster specific to sign language comprehension in the left inferior frontal gyrus (Broca's area) organized by behavioral domain. Most studies in the database clearly have associated voxels in this cluster with cognitive processing. The right box shows the number of studies with nonsigners in the BrainMap database that reported peaks in voxels of the sign language-specific cluster in Broca's area organized by behavioral subdomains within the domain of cognition, according to the BrainMap taxonomy. Most studies in the database clearly associated voxels in the sign-language specific cluster with language processing in hearing non-signers, as well as to a lesser extent with attention and well as memory-related processes according to the BrainMap taxonomy. This meta-analytic overlap suggest that Broca's area constitutes a modality-independent hub in the (core) language network that processes linguistic information regardless of whether it was originally perceived as sign, speech, or writing. Adapted from Trettenbrein PC, Papitto G, Friederici AD, et al. (2021a). Functional neuroanatomy of language without speech: an ALE meta-analysis of sign language. Hum Brain Mapp 42: 699–712. doi:https://doi.org/10.1002/hbm.25254. This illustration is subject to a Creative Commons (CC-BY 4.0) license.

phonology as well as classifier constructions (Emmorey et al., 2002, 2021; MacSweeney et al., 2002a; Jednoróg et al., 2015; Cardin et al., 2016).

Given that the generation of hierarchically structured representations of phrases and sentences is a key function of the language network, it is somewhat unsatisfying to observe that syntactic processing remains one of the relatively understudied areas of neurocognitive research on sign language (Emmorey, 2021). An early study by MacSweeney et al. (2006) used a contrast of sentences and mere lists of unconnected signs in BSL and found that the presence of syntactic structure reliably recruited posterior portions of the left middle and superior temporal gyrus and left inferior frontal cortex. A more recent study used a semantic and syntactic violation paradigm in DGS and found that semantic processing recruited the posterior portion of Broca's area (i.e., BA 45), whereas syntactic processing of DGS sentences using spatial syntax increased activation in the right supramarginal gyrus (Stroh et al., 2019). Two independent studies in French Sign Language (LSF) and ASL attempted to implement a parametric design similar to Pallier et al. (2011), where the neural response is thought to increase systematically as a function of constituent size: Moreno et al. (2018) found main effects for this manipulation in subcortical structures such as the basal ganglia and only a smaller effect was found in the left perisylvian regions—possibly due to the manner in which stimuli were constructed. Matchin et al. (2021) used a similar design in ASL but only observed a left-lateralized parametric response in the anterior and posterior superior temporal sulcus in the syntactically most complex condition.

Lastly, directly reflecting insights from behavioral studies of sign language acquisition, neuroimaging data also suggests that the observed activations during sign language processing in deaf signers are modulated as a factor of the age at which a sign language was acquired by individual participants. In a seminal fMRI study, Mayberry et al. (2011) found that the percent of signal change of the blood oxygen level dependent (BOLD) response in left perisylvian language-related regions (BA 9, insula, BA 44, BA 6, and BA 22) was negatively correlated with the age at which participants had acquired sign language (with the onset of acquisition ranging from 0 to 14 years). At the same time, the age of sign language acquisition was also positively correlated with the percent signal change of the BOLD response in the occipital cortex (BA 18 and BA 19). The authors employed two different tasks, a phonemic as well as a grammatical judgment task in ASL, the latter of which consistently showed bilateral activations with a clear leftward asymmetry in the left IFG—specifically, the posterior portion of Broca's area (i.e., BA 44)—and the frontal operculum. Mayberry et al. (2011) hypothesized that these findings could be reflective of a modality-independent developmental shift during language acquisition, where more posterior and sensory/signal-based processing shifts to a more anterior adult pattern of automatic and abstract linguistic processing (Trettenbrein and Friederici, 2025).

Interim summary

The deep formal similarities between sign and spoken language are mirrored on the neural level. Major ERP components observed during sign language processing parallel those reported for spoken language. Studies with PET and fMRI have shown that sign language processing primarily recruits left perisylvian regions, which have previously been identified as relevant for spoken language processing. In particular, Broca's area has been identified as a modality-independent hub for language processing. Bilateral visual association areas as well as parietal regions subserve modality-specific aspects of sign language processing. Several brain regions including Broca's area show modulations in their response to sign language, according to the age of onset of sign language acquisition.

STRUCTURAL NEUROIMAGING OF SIGN LANGUAGE

A primary interest in the context of structural imaging has been to identify whether and where structural changes in the brain's gray and white matter can be observed as the result of deafness or sign language acquisition, whereas it is not clear whether these factors can actually be disentangled. In a systematic review and meta-analysis, Grégoire et al. (2022) identified a volumetric decrease in gray matter around the auditory cortex in deaf signers. This is not surprising, even though it is understood that auditory cortices show plasticity related changes and seem to participate in visual or sign language processing in deaf signers (Finney et al., 2001; Sadato et al., 2004; Ding et al., 2015; MacSweeney and Cardin, 2015). Beyond this, Grégoire et al. (2022) also identified a volumetric decrease in the gray and white matter in the visual cortex and a gray matter increase in the right cerebellum as consistent findings in structural imaging studies with profoundly deaf participants. The general decrease in gray and white matter volume in visual areas is unexpected given the visuospatial nature of sign language, but it may reflect the varied and delayed language experience of the majority of deaf children. Indeed, studies of deaf signers, who acquired a sign language early in life, actually show an increase in gray matter in the occipital cortex (Pénicaud et al., 2013) and there is evidence that sign language experience leads to lateralized changes in surface area and cortical thickness in the occipital cortex (McCullough and Emmorey, 2021).

More relevant to our interest in this chapter are structural changes or asymmetries that are likely to be the consequence of sign language acquisition, though the evidence for such changes has been scarce and somewhat conflicting. For example, some studies have reported an increase in gray matter volume in the left insula as the result of sign language acquisition (Allen et al., 2008), whereas others have reported a bilateral decrease in gray matter in comparison to hearing controls and a decrease in the right insula linked to the acquisition of sign language (Olulade et al., 2014). Another approach has been to specifically investigate the structural properties of regions, which have already been identified as relevant for spoken language processing: In a recent paper, Cheng et al. (2023) attempted to link age of acquisition to differences in structural data for the group of participants for which they previously reported an effect of age of sign language acquisition on the BOLD response (Mayberry et al., 2011). Significantly, delayed language exposure in early childhood was associated with negative changes in gray matter volume and cortical thickness in bilaterial perisylvian regions. No such differences were observed in deaf signers with early exposure to ASL (Cheng et al., 2023).

With regard to the white matter pathways connecting the inferior frontal and posterior temporal perisylvian language regions, no differences between deaf signers and hearing users of a spoken language have been observed in the pathways that have been studied to date. Cheng et al. (2019) studied the arcuate fasciculus connecting the inferior frontal to posterior temporal regions, inferior fronto-occipital fasciculus, inferior longitudinal fasciculus connecting the anterior temporal to extrastriate cortex and occipital lobe, and the uncinate fasciculus connecting the anterior inferior frontal cortex and the frontal operculum to the anterior temporal cortex in a group of native deaf signers using ASL and a control group of hearing nonsigners using English and observed no group differences. Significantly, the arcuate and inferior longitudinal fascicles constituted structural asymmetries and were left-lateralized in both groups, thereby reproducing a pattern already reported in hearing speakers (Gallardo et al., 2020; Warrington et al., 2020). The inferior fronto-occipital fasciculus as well as the uncinate fasciculus have been reported to be right-lateralized in the literature (Gallardo et al., 2020; Warrington et al., 2020), but this pattern was not observed by Cheng et al. (2019) for either group. A possible reason could be that this pattern has been reported in studies with very large samples with several hundred participants so that the analysis of a necessarily smaller sample of deaf signers may not have sufficient power to detect these effects.

Due to its role as a part of the core language network, Finkl et al. (2019) specifically investigated the arcuate fasciculus using diffusion tensor imaging (DTI) and probabilistic tractography and observed no difference in the connectivity profiles of this pathway between a group of deaf signers, who had acquired DGS early in life, and matched controls. However, some differences between groups were observed depending on the respective seed region: When seeding in the posterior portion of Broca's area (i.e., BA 44), the authors found differences in the pathways connecting this region to the pre-supplementary motor area as well as to the thalamus (Fig. 21.7, left panel). When seeding in the posterior superior temporal gyrus (i.e., BA 22), the authors observed a difference in the pathway connecting this region to the ipsilateral parietal cortex and the precuneus (Fig. 21.7, right panel). Lastly, the transcallosal connection between the auditory cortices was lower in the deaf group. The lack of a difference between groups indicates that a typically developed arcuate fascicle does not require auditory language input. Furthermore, the authors interpret the remaining observed group differences as relating to different requirements of the mapping to the sensorimotor system imposed by the visuospatial modality.

While the arcuate fasciculus exhibits no difference between typically developed early deaf signers and hearing users of a spoken language, the development of this pathway is nevertheless shaped by language experience early in life. Cheng et al. (2019) reported data from three deaf individuals, who experienced only minimal language during childhood and acquired a conventionalized sign language only later in life after the onset of puberty and thus outside the so-called critical period for language acquisition (Lenneberg, 1967, 1969). Significantly, when compared to a control group of deaf early signers, all three deaf late signers showed alterations of white matter microstructure in all four fiber pathways investigated in this study; yet, the difference was most pronounced for the arcuate fasciculus. The authors argued that the decreased values in fractional anisotropy in the left doral pathway that they observed when comparing each of the three participants, who were deaf late signers to a group of deaf controls, who were early signers, are due to the reduced laterality of the pathway (Cheng et al., 2019). These data suggest that adequate early language exposure is required for the emergence of the usually left-lateralized structural pattern of the dorsal pathway that is part of the core language network in typically developed adults.

In this context, it is suggestive to note that the behavioral linguistic profiles for all three deaf late signers in the study by Cheng et al. (2019) reported in independent publications indicate limited syntactic abilities in ASL (Ramírez et al., 2013; Ferjan Ramirez et al., 2014; Mayberry et al., 2018). Moreover, all three participants also exhibited atypical neural response patterns to ASL signs that primarily recruited the bilateral dorsolateral superior parietal and occipital cortex and minimally involved perisylvian language regions (Ferjan Ramirez et al., 2014; Mayberry et al., 2018). A follow-up study conducted 15 months after data collection for two of the three deaf late signers showed an altered response to highly familiar ASL signs, which was more concentrated in left perisylvian language regions (Ferjan Ramirez et al., 2016). Notice that these case studies provide only indirect

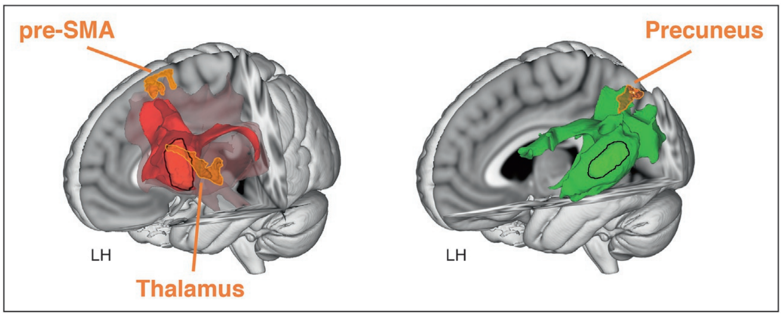

Fig. 21.7. Fiber-tracking of the core language network in the deaf brain. Visualization of fiber-tracking results with two hubs of the so-called "core" language network in the left hemisphere (LH) as seed regions in a sample of deaf signers. Both illustrations show results based on a group comparison of deaf signers compared to a sample of matched hearing controls without any knowledge of sign language. Parts shown in orange indicate regions where connectivity was weaker in the group of deaf signers compared to the hearing controls. Left panel: Using the posterior portion of Broca's area, left Brodmann area 44 (BA 44; shown in red and indicated using a black outline), as a seed region demonstrates the strong frontal connectivity of this core language region, as well as its connection to the posterior temporal cortex via the arcuate fasciculus. The group of deaf signers shows weaker connectivity to pre-supplementary motor area (pre-SMA) as well as the thalamus (both indicated in orange). Right panel: Using the left posterior temporal gyrus (pSTG; shown in green and indicated using a black outline) as a seed region confirms the connection of this core language region to other parts of temporal as well as parietal cortex, including also the canonical connection to frontal language-relevant regions via the arcuate fasciculus. The connection of pSTG to the precuneus is weaker in the LH for the deaf group when compared to hearing controls (indicated in orange). Adapted from Finkl T, Hahne A, Friederici AD, et al. (2019). Language without speech: Segregating distinct circuits in the human brain, Cereb Cortex 30: 812–823. doi:https://doi.org/10.1093/cercor/bhz128, under a Creative Commons (CC-BY 4.0) license.

evidence for the relevance of a typically developed dorsal pathway for processing complex syntactic structures in sign language. However, as studies of spoken language processing have shown that the structural integrity of the arcuate fasciculus during maturation correlates with the ability for processing syntactically complex sentences (Friederici and Gierhan, 2013; Skeide and Friederici, 2016), it seems reasonable to take these case studies as indicative of the important role that the arcuate fasciculus and its development may play in the deaf brain during sign language acquisition.

Interim summary

The core language network connecting the left posterior inferior frontal and posterior temporal regions shows no differences between deaf signers, who acquired a sign language early in life, and hearing speakers, pointing at its potentially modality-independent nature. Observed structural brain differences between deaf signers and hearing controls all pertain to the modality of language use as they seem to either be the consequence of deafness or sign language acquisition. Several studies have observed an effect of the age of sign language acquisition on the structural properties of the brains of deaf signers, thereby underlining the importance of an early exposure to a sign language for the typical development of the language system.

DISCUSSION

Our review of the functional and structural asymmetries in cortical regions and the white matter relevant for sign language processing has confirmed that the human language system in the typically developed adult deaf brain is functionally and, with regard to the core language network also structurally left-lateralized, though the RH appears to be more engaged during sign language processing due to the nature of the stimulus (i.e., sign language stimuli are always presented as videos showing a person signing) as well as due to constructions unique to the visuospatial modality (e.g., classifier constructions). While prevalent in the deaf, hearing, and even deafblind (Obretenova, 2010) population, this functional left-lateralization is not absolute and cases of reversed cerebral dominance for sign language have been reported in the literature (e.g., Pickell et al., 2005), similar to what has previously been observed for studies of spoken and written language processing (Labache et al., 2020). In direct comparison, sign and spoken language processing both engage left perisylvian regions, yet rely on different mappings to the sensorimotor system determined by the modality of language use. In addition, the spatial nature of sign language is also reflected in the engagement of bilateral parietal regions, though it seems that the left and right parietal cortex differentially support either the construction of grammatical or spatial representations (Hickok et al., 1996c).

The neural substrates of sign, spoken, and written language processing in the left perisylvian cortex show significant overlap in the inferior frontal and posterior temporal regions (MacSweeney et al., 2002b; Sakai et al., 2005; Inubushi and Sakai, 2013; Trettenbrein et al., 2021a; Uddén et al., 2022), though the exact activation patterns in the (posterior) temporal regions appear to be modulated by modality-specific properties (Evans et al., 2019), including the use of different articulators (Capek et al., 2008) but not iconicity (Emmorey et al., 2004; Klann et al., 2005). These data are compatible with the notion that the language network primarily processes linguistic information in a modality-independent fashion and interacts with modality-specific regions and networks depending on the requirements of the modality of language use as well as task demands. For example, the greater self-monitoring demands of the visuospatial modality lead to a more pronounced left-lateralization during sign than speech production (Gutiérrez-Sigut et al., 2015, 2016). Moreover, comprehension and production tasks may induce different activation patterns (Emmorey, 2021); but, while many studies have treated Broca's area as a primarily production-related brain region (Braun, 2001; Horwitz et al., 2003; Emmorey, 2006), the identification of Broca's area as a modality-independent hub for language comprehension speaks against a clear dichotomy between production and comprehension (Trettenbrein et al., 2021a).

The engagement of the bilateral occipital cortex in sign language is, of course, expected because sign language is perceived visually (Fig. 21.5) and due to the neuroanatomic properties of the visual system, however, it seems that sign language acquisition does not simply lead to a differential recruit of the visual system but instead triggers lasting structural (Pénicaud et al., 2013) and possibly also functional adaptions within the visual system (Brookshire et al., 2017; Stroh et al., 2022). While the bilateral clusters located on the border of the posterior middle temporal and extrastriate cortex observed in the meta-analysis of sign language comprehension in deaf signers by Trettenbrein et al. (2021a) did not survive the comparison with an independent meta-analysis of sign-like actions in hearing non-signers, this does not imply that these regions do not show any adaptation to language modality in (early) deaf signers. In fact, lesion studies suggest that, in rare cases, occipital lesions can lead to sign language aphasias (see section "Sign Language Aphasia"). Moreover, a study by Brookshire et al. (2017) looked at cortical entrainment to oscillations (i.e., rhythmic modulation) of ASL stimuli in a group of deaf signers and hearing nonsigners and found that, while both groups showed phase-locking to visual changes in ASL, only deaf signers showed strong coherence in frontal areas. The authors take this as evidence for top-down sensory predictions occurring as the result of knowledge of ASL.

A number of different explanations for the seemingly larger right-hemispheric involvement observed in neuroimaging studies of sign language processing in deaf signers have been put forward in the literature, with most researchers arguing for either a modality-specific or stimulus-specific difference (Peperkamp and Mehler, 1999). That is, if the greater right-hemispheric involvement was due to specific requirements or properties of the signed modality, then some regions in the RH should show a stronger response to modality-specific constructions. This is actually the case for the seemingly right-hemispheric specialization for processing classifier constructions, which can also be selectively impaired by lesions (Hickok et al., 1996c; Atkinson, 2005). Similarly, if the greater right-hemispheric involvement was due to specific properties of stimuli used in sign language experiments (i.e., videos showing a person signing) as well as their linguistic properties, then we should expect that processing this additional (social) information about the signer performing manual actions, which is part of the sign language stimuli but not necessarily of auditory or written stimuli will recruit more right-hemispheric networks in signers and nonsigners alike (Campbell et al., 2011). The meta-analysis by Trettenbrein et al. (2021a) seems to confirm this in line with studies attempting to disentangle sentence processing from processing prosody and discourse-level information (Atkinson et al., 2004; Inubushi and Sakai, 2013; Newman et al., 2015). Hence, larger involvement of the RH during signing than during auditory or written language processing appears to be driven by both modality and stimulus-specific properties.

The role that left perisylvian language regions, including Broca's area, take on in language processing appears to be dependent on exposure to adequate linguistic input already early in life, independent of the modality of language use. That is, delayed exposure to a sign language has a severe and lasting impact on the development of the core and extended language network in the LH of deaf signers, which is evidenced in structural properties of the brain, functional neural correlates, as well as on the behavioral level (see sections "Structural Neuroimaging of Sign Language" and "Sign Language Acquisition and Development"). The different studies of the effects that delayed exposure to a sign language has on neural and linguistic development reviewed here provide strong support for the notion that the growth of language in the individual is determined and also constrained by a biologic matrix, whereas this matrix does not specify the modality in which language can or should be perceived or externalized. Similarly, the limited syntactic abilities of individuals who were exposed to a conventionalized sign language only later in life after the onset of puberty supports the notion of a critical period for language acquisition (Lenneberg, 1967, 1969), independent of the modality in which language is acquired. In sum, these observations underpin the importance of providing early access to a sign language to deaf children to foster the typical development of the language system.

Lastly, it should be mentioned that the studies reviewed here suggest that the usual left-lateralization of language processing in the typically developed adult brain does not merely reflect a specialization for processing the fast temporal structure of speech (Zatorre et al., 2002; Schönwiesner et al., 2005); instead, we take this pattern to indicate that the LH is usually specialized for the processing of linguistic information and, specifically, the generation of the hierarchically structured representations underlying sentences independent of the modality of language use. Ursula Bellugi and colleagues had already reached a similar conclusion based on their extensive studies of deaf aphasics (Poizner et al., 1987; Emmorey et al., 1995b; Hickok et al., 1996a, 1998), though it has been questioned whether sign language processing indeed does not impose similar temporal processing demands like speech because it is not clear that a greater reliance on space in the signed signal does not impose demands on temporal processing (Corina, 1999). A middle ground between both views may be supplied by the literature on so-called split-brain patients who were hearing and non-signers: Based on his work with these patients, especially in the domain of visual processing, Zaidel (1978) proposed that, while the RH can recognize units (e.g., spoken or printed words) as whole patterns, the LH always decomposes words and by extension signs as well as sentences into smaller units by feature analysis.

TOWARD A FUNCTIONAL NEUROANATOMY OF SIGN LANGUAGE

Against the background of the data discussed in this chapter, we can attempt a sketch of the neural basis of sign language processing including relevant cortical regions and white-matter pathways (Fig. 21.8). It seems clear now that the so-called "classical" model of language processing consisting only of Broca's and Wernicke's area familiar from text books was severely underspecified not just in the context of spoken language but even more so when we consider sign language processing (Poeppel et al., 2012; Emmorey, 2015, 2021). While sign language and spoken language processing overlap in their recruitment of the bilateral posterior temporal cortex and a strong left-lateralization in the IFG, sign language processing additionally recruits higher parts of the bilateral visual system as well as bilateral parietal cortices for the processing of modality-specific phenomena such as classifier constructions in which space is used iconically. We take this to indicate that the core language system exhibits similar functional and structural asymmetries, independent of the modality of language use, yet interfaces with different networks depending on modality-specific processing demands. This is also reflected in overall similar electrophysiologic response patterns and processing stages (Fig. 21.4). The white-matter pathways connecting regions implicated in sign language processing are best understood for the perisylvian cortex and remain to be explored in future studies in the context of regions recruited specifically during sign language processing.

In direct comparison to models of spoken and written language processing (e.g., Friederici, 2011, 2017; Hagoort, 2017), our current understanding of exact functional attributions of regions or possible functional dissociations of different linguistic subsystems (e.g., semantics vs syntax) for sign language processing remains somewhat limited and requires further research. Broca's area has been identified as a modality-independent hub for language processing and has also been implicated in studies of grammatical processing in ASL, in processing mouthing and mouth gestures, as well as processing sign morphology. Both the anterior and posterior portions of the left superior temporal cortex and sulcus have been linked to semantic and syntactic processing. The left posterior middle temporal gyrus (i.e., area V5/MT) bordering on occiptial cortical regions such as the extrastriate body area has been found to be involved in lexical processing, sentence comprehension, and motion processing. Regions on the underside of the temporal cortex such as the fusiform face area are involved in processing mouth gestures. The bilateral parietal cortex has been linked to processing phonologic and

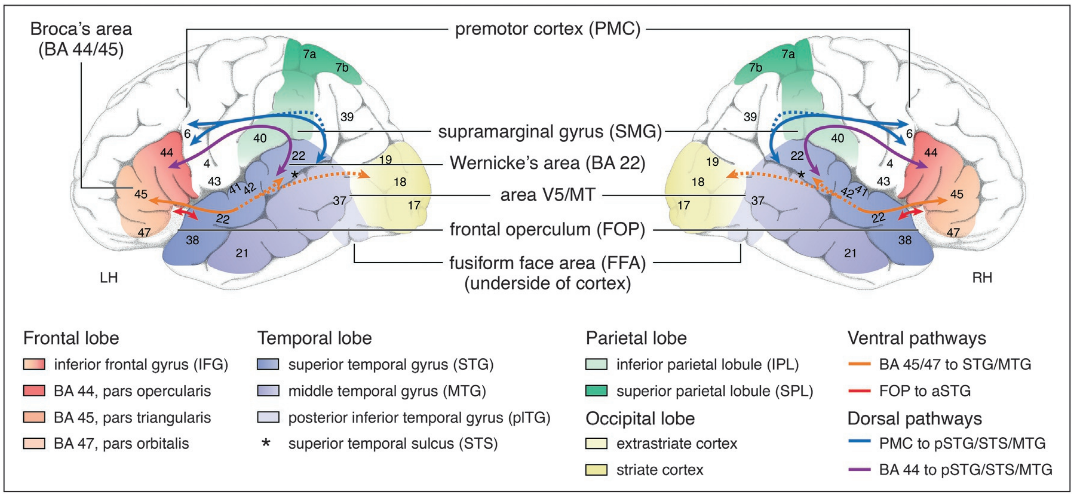

Fig. 21.8. Schematic of the neural basis of sign language. Schematic depiction of the LH and RH displaying anatomic landmarks and cytoarchitectonic details of cortical regions relevant for processing sign language. Major gyri that are involved in sign language processing are color-coded: The IFG and its subregions, Brodmann areas (BA) 44, BA 45, and BA 47, are depicted in shades of red; superior temporal gyrus (STG), middle temporal gyrus (MTG), and posterior inferior temporal gyrus (pITG) are shown in shades of blue. The location of the superior temporal sulcus (STS) in between STG and MTG is indicated using an asterisk (*). Inferior parietal lobule (IPL) and superior parietal lobule (SPL) are depicted in shades of green. Extrastriate and striate portions of the visual cortex are indicated in shades of yellow. The different numbers on the schematic indicate the respective cytoarchitectonic label of a region (i.e., BA), as defined by Brodmann (1909), on the basis of histologic studies. BA 44 (pars opercularis) and BA 45 (pars triangularis) in the LH jointly form Broca's area. BA 47 (pars orbitalis) in the LH is located anteriorly to Broca's area, whereas the frontal operculum (FOP) is located ventrally and medially to it. The premotor cortex (PMC) is located in BA 6. Wernicke's area is located in BA 22 in the LH, though definitions based on studies of spoken language sometimes also include BA 42, which is part of primary auditory cortex and adjacent to Heschel's gyrus (BA 41). The supramarginal gyrus is located dorsally in the IPL in BA 40. The extrastriate body area (EBA) is located in BA 19. The fusiform face area (FFA) is not shown in the diagram as it is located at the bottom of the inferior temporal cortex in the fusiform gyrus (BA 37). The main white matter fiber tracts connecting regions of the cortex relevant for processing sign language are located dorsally and ventrally and indicated using color-coded arrows: Blue for the pathway connecting PMC to the posterior STG (pSTG), STS, and MTG; purple for the pathway connecting BA 44 to pSTG, STS, and MTG; orange for the pathway connecting BA 45 and BA 47 to STG and MTG; and red for the pathway connecting FOP to aSTG. Based on a similar schematic based on studies of spoken and written language processing by Friederici AD (2011). The brain basis of language processing: from structure to function. Physiol Rev 91: 1357–1392. https://doi.org/10.1152/physrev.00006.2011. This illustration is subject to a Creative Commons (CC-BY 4.0) license.

spatial information in sign language: The left supramarginal gyrus has been linked to lexical phonologic processing, whereas its right-hemispheric counterpart has been linked to form-based phonologic processing. The right superior parietal lobule may be functionally more relevant for processing classifier constructions.

CONCLUSION

Our review of the neuroimaging literature on sign language in this chapter has confirmed the general insight that the LH of the typically developed adult human brain is specialized for processing language independent of the modality of language use. This functionally asymmetric organization emerges during development and is, to an extent, paralleled in structural asymmetries. Both functional and structural asymmetries are subject to individual variation and directly impacted by delays in sign language acquisition. Generally speaking, both hemispheres display a certain equipotentiality and are involved in processing sign language, especially with regard to processing visual and spatial information in the occipital and the parietal cortex as well as linguistic information in the posterior temporal cortex. The RH seems to specifically support processing of some constructions unique to the signed modality (i.e., classifier constructions that use space iconically and not grammatically). A key difference between our current state of knowledge about sign and spoken language processing concerns our lack of understanding of syntactic processing in the visuospatial modality.

The studies reviewed in this chapter support the speculative notion that the processing of sentences in both spoken and sign language in typically developed adults is supported by a primarily left-hemispheric fronto-temporal network connecting the IFG to the posterior temporal cortex. This network appears to subserve the generation of hierarchically structured representations linking meaning to the representations of a physical signal (i.e., sign or sound) independent of the modality of language use and develops in accordance with a genetically determined biologic matrix, suggesting that its emergence may have constituted a prerequisite for the evolution of the human language capacity. However, the precise functional roles of the major frontal and temporal hubs in this network during sign language processing remain underspecified, at least in comparison to work on spoken and written language processing. Future work using linguistically informed experimental manipulations and methodologic advances will likely provide a more fine-grained picture of the functional specialization and lateralization of sign language and its subsystems.

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CONFLICTS OF INTEREST

We have no known conflicts of interest to disclose.

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