

Functional and Structural Brain Asymmetries in Sign Language Processing

Patrick C. Trettenbrein^{1,2,3}, Emiliano Zaccarella¹, and Angela D. Friederici¹

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 SignLab, Department of German Philology, University of Göttingen, Göttingen, Germany

Invited chapter to appear in the *Handbook of Clinical Neurology*
(Corballis, P. & Papagno, C., eds.) in the volume on “Cerebral Asymmetries”

Author Note

Patrick C. Trettenbrein  <https://orcid.org/0000-0003-2233-6720>

Emiliano Zaccarella  <https://orcid.org/0000-0002-5703-1778>

Angela D. Friederici  <https://orcid.org/0000-0002-6328-865X>

We have no known conflicts of interest to disclose.

Correspondence should be addressed to Patrick C. Trettenbrein, Department of Neuropsychology, Max Planck Institute for Human Cognitive and Brain Sciences, Stephanstraße 1a, 04103 Leipzig, Germany. E-mail: trettenbrein@cbs.mpg.de

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 organisation 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 biological matrix, and (iii) may have constituted an evolutionary prerequisite for the emergence of the human capacity for language.

Keywords: sign language; neurobiology of language; language network; lateralization; sign language processing; modality of language use; modality-independence

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. 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 (G. Dax, 1863; M. Dax, 1865). This was later followed by the often much more widely known work of Paul 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 re-examination 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 & Friederici, this volume, for a review based primarily on studies of spoken and written language).

Since the 60s of the past century, research in the cognitive sciences has accumulated evidence which strongly suggests that the human-specific language capacity (Bolhuis et al., 2014; Hauser et al., 2002) is not bound to speech but may be perceived and externalized in different modalities (C. Chomsky, 1986; Klima et al., 1979; Stokoe, 1960): Auditory-oral for spoken language, visuo-spatial for sign language, and tactuo-spatial for tactile sign language. Sign languages are the natural languages of the deaf¹ and, just like spoken languages, exhibit

¹ In English, uppercase "Deaf" is sometimes used to refer to people who identify as members of a linguistic and cultural minority, lowercase "deaf" is then seen to refer to people's audiological status. Following Caselli et al. (2017), we use lowercase "deaf" throughout here because we discuss studies with diverse groups of participants from labs around the world who may differ in whether and how they identify with the respective community.

complex linguistic organization on different levels such as phonology or syntax (Cecchetto, 2017; Mathur & Rathmann, 2014; Sandler & Lillo-Martin, 2008). Intriguingly, emerging research on tactile sign languages of the deafblind has revealed a similarly complex linguistic organization (Checchetto et al., 2018; Edwards & Brentari, 2020). In contrast to speech, sign, and tactile 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 6,000 years for pictographic and ideographic systems and about 3,000 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 & Cohen, 2007; Friederici, 2017).

First neuropsychological 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 (Bellugi et al., 1989; Corina, 1998; Hickok, Bellugi, et al., 1996; Hickok et al., 1998; Klima et al., 1979; Poizner et al., 1987). For example, Poizner et al. (1987) documented case studies of two deaf signers with agrammatic and paragrammatic behavioral profiles following left-hemispheric lesions to perisylvian cortex. Similarly, mirroring the picture of Broca's classic cases for speech production, Hickok, Kritchevsky et al. (1996) report a deaf signer with a lesion to the left inferior frontal gyrus extending into neighboring regions and the white matter who exhibited acute expressive aphasia. These data are complemented by a case study of a hearing bimodal bilingual that underwent pre-surgical 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 first suggestive evidence that the left hemisphere of the human brain may not be specialized for processing the fast temporal

structure of speech (Schönwiesner et al., 2005; Zatorre et al., 2002), but for processing language independent of modality.

In the present chapter, we take these early neuropsychological 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

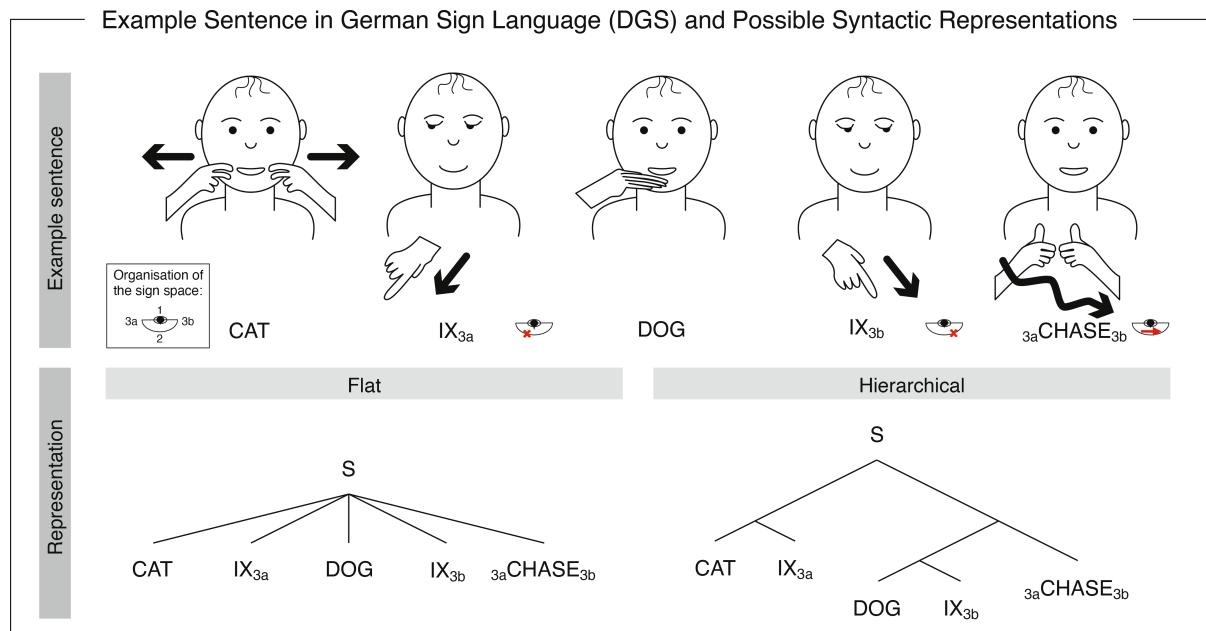
and the conceptual-intentional system for thought (N. Chomsky, 1965, 1986, 1995; Everaert et al., 2015; Friederici et al., 2017). In a technical sense, the human language system therefore enables a structured mapping from meaning to a physical signal (i.e., signs or sound) and vice versa (N. Chomsky, 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 (Crain et al., 2016; Lenneberg, 1964; 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 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 Figure 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 connect directly to the root (Figure 1, bottom-left panel). Alternatively, we may assume that lexical items are grouped into constituents which are embedded in each other hierarchically (Figure 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 structure of grammatical representations (Cecchetto, 2017; Mathur & Rathmann, 2014; Sandler & Lillo-Martin, 2001, 2008; Tang & Lau, 2012).

Figure 1

Example Sentence in German Sign Language (DGS) and Possible Syntactic Representations



Note. 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 non-manual 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 & 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 & Trettenbrein, 2021), only a handful of studies have investigated syntactic processing in sign language so far (e.g., MacSweeney et al., 2006; Matchin et al., 2021; Stroh et al., 2019) 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 (Cecchetto, 2017; Mathur & Rathmann, 2014; Sandler & Lillo-Martin, 2001, 2008; Tang & Lau, 2012). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

The at least more than 200 different sign languages of the deaf around the world (Hammarström et al., 2022) as well as the various tactile sign languages of the deafblind are testament to the contemporary understanding amongst 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 (Berwick et al., 2013; Friederici et al., 2017; Hauser et al., 2002; Lenneberg, 1969). That is, the “biological 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 (Crain et al., 2016; Lenneberg, 1964, 1967, 1969; Yang et al., 2017) appears not to specify the modality in which linguistic information can be perceived and externalized (Klima et al., 1979; Lenneberg, 1970; Meier, 2016; Poizner et al., 1987).

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., visuo-spatial 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 (Cecchetto, 2017; Friederici et al., 2017; Mathur & Rathmann, 2014; Sandler & Lillo-Martin, 2001, 2008; Tang & Lau, 2012; Zaccarella & Trettenbrein, 2021). However, while the auditory-oral modality imposes a strictly sequential organization of lexical items as well as morphological elements (i.e., the minimal meaning-bearing elements that make up a word, e.g., *eat* and *-s* in *eats*), these constraints seem to be relaxed for the visuo-spatial 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 Figure 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.; Embick & Poeppel, 2015; Poeppel & Embick, 2013). 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 & 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

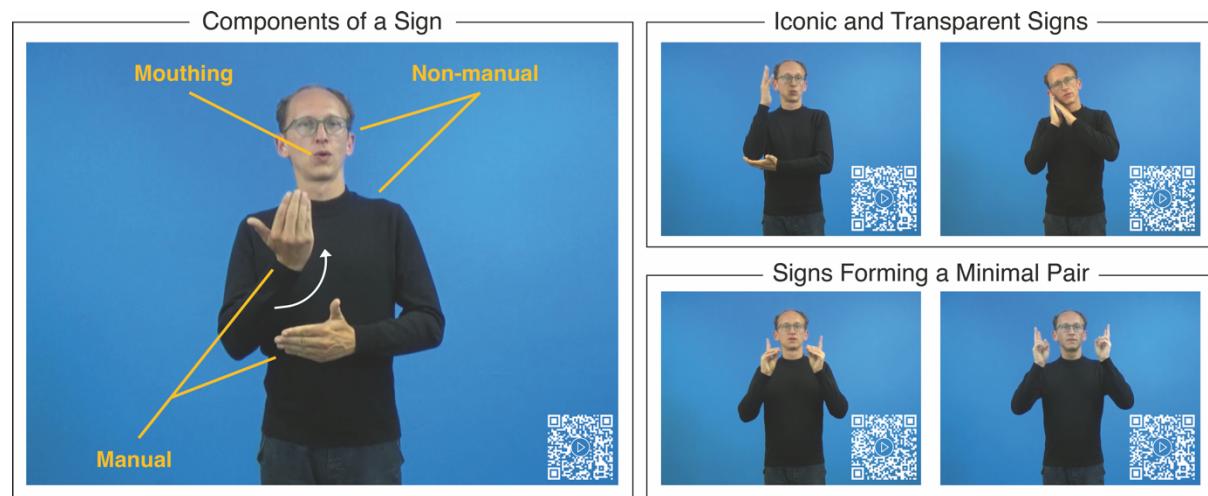
carried out from the 60s of the past century onwards (e.g., Klima et al., 1979; Stokoe, 1960) demonstrated that sign languages such as, for example, American Sign Language (ASL) are not in any way “translations” of the spoken majority language in a region (i.e., English in case of the United States) 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 others 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 amongst many sign languages (Mesch, 2010).

A unique affordance of the visuo-spatial 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 respective the 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 Figure 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 non-signers (Trettenbrein, Pendzich, et al., 2021). 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 & Klima, 1976).

Figure 2

Linguistic Analysis of Individual Signs



Note. The left panel shows the different manual, and non-manual components of a sign. In general, non-manual 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), as well as 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 non-dominant (left) hand steady in front of the body, whereas the dominant (right) performs an upwards movement behind the non-dominant hand. These manual components are accompanied by a mouthing roughly corresponding to the spoken German /noɪ/ 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 10 % of non-signing participants in a guessing task (Trettenbrein, Pendzich, et al., 2021) rendering the sign non-transparent to non-signers despite its iconic motivation. In contrast, the iconic motivation for the lexical sign SLEEP overlaps with a gesture also frequently used by non-signers to indicate “sleep,” “sleeping,” or “being tired”, thereby rendering the sign highly transparent also to non-signers. 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 starting to 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 QR code or DOI have been adapted from a publicly available data set by Trettenbrein, Pendzich, et al. (2021) under a Creative Commons (CC-BY 4.0) license to which this illustration is also subject.

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 visuo-spatial 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 non-manual components of signs is made which can be accompanied by so-called mouthings or mouth gestures (Figure 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; Baker et al., 2016; Brentari, 2012; Fenlon et al., 2017; Stokoe, 1960): These parameters include the hand form, hand position, contact area, and movement (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 phonological parameter such as *grammar* and *glamour* in English) in sign languages. For example, the DGS signs TEACHER and LECTURER differ in one manual parameter, namely hand form (Figure 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 morphological structure which closely interacts with syntax (i.e., the grammatical structure of the entire sentence). In the visuo-spatial modality morphological processes can be realized in two ways: Firstly, one or more phonemes of a sign may be altered (e.g., the DGS sign TREE depicted in Figure 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 et al., 1989; Bellugi & Klima, 1976). Secondly, 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 visuo-spatial modality (Figure 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 $_{3a}\text{CHASE}_{3b}$) where the start and end of the altered movement path indicate the position of the subject and object in sign space (Mathur & Rathmann, 2012; Pfau et al., 2018). Inverting the path movement (i.e., by signing the inflected form $_{3b}\text{CHASE}_{3a}$) 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 & Lau, 2023).

Lastly, besides the grammatical use of space which is unique to the visuo-spatial modality, signers can also use space to iconically depict scenes and spatial relations using so-called classifier constructions. Classifiers are morphemes with a non-specific 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 downwards. This is a classifier for vehicles with four wheels that can then be used to ironically 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; Baker et al., 2016; Zwitserlood, 2012).

Interim Summary

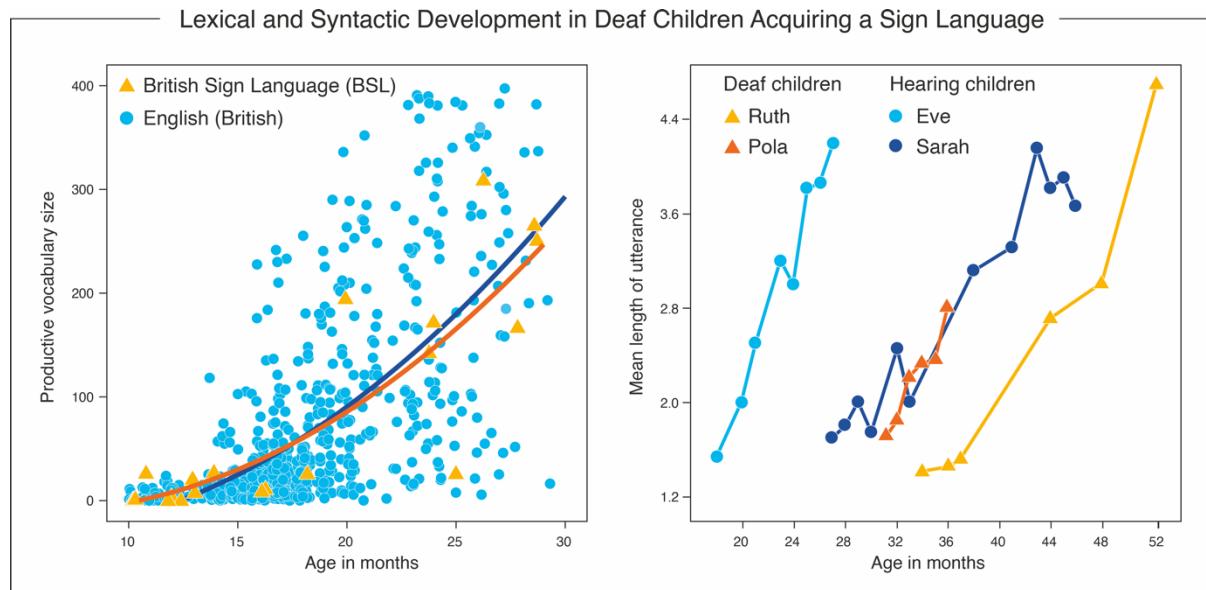
Sign languages are natural languages with complex organization on all levels of linguistic analysis (e.g., phonology, morphology, and syntax) which are externalized in the visuo-spatial modality. This indicates that the mapping of the hierarchically structured representations of the language system to 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 visuo-spatial 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 (Meier, 2016; Mitchell & Karchmer, 2004). 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 non-linguistic abilities (Emmorey, Bellugi, et al., 1995; Mayberry, 2002; Mayberry & 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 & 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 (Figure 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 (Figure 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).

Figure 3*Lexical and Syntactic Development in Deaf Children Acquiring a Sign Language*

Note. 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” above). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

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 (Meier, 2016; Newport & Meier, 1985). 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 & 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 nine 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).

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 (Flaherty et al., 2021; Goldin-Meadow, 2003, 2017; Goldin-Meadow & Yang, 2017). 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., morphological patterns, basic syntactic structure of utterances, etc.), despite the fact that these properties are not contained in the gestural input they receive from caretakers (Flaherty et al., 2021; Goldin-Meadow, 2003, 2017). 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 & 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 & Friederici, this volume).

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 first evidence for the specialization of the left hemispheres of the human brain for spoken language processing already more than 150 years ago (Broca, 1861; G. Dax, 1863; M. Dax, 1865), the first detailed reports of deaf signers with aphasia following left-hemispheric brain damage surfaced only in the 80s of the past century (e.g., Bellugi et al., 1989; Poizner et al., 1987). 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 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 (Bellugi et al., 1989; Hickok, Kritchevsky, et al., 1996; Poizner et al., 1987). 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 morphological and syntactic markings of ASL. Generally speaking, the aphasic syndromes observed in deaf signers with left-hemispheric damage mirrors those known from research with hearing user 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 & 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 (Figure 1) or in classifier constructions (see section "A Primer on Sign Language Linguistics" above), damage to the right hemisphere which is widely assumed to be dominant for visuo-spatial 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 (Atkinson et al., 2005; Hickok, Say, et al., 1996). These observations are in line with data from so-called split-brain patients indicating that the left hemisphere retains relatively sophisticated visuo-spatial 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 (Atkinson et al., 2005; Bellugi et al., 1989; Emmorey, Corina, et al., 1995; Hickok, Say, et al., 1996).

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 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, 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 right hemisphere 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 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 show that (i) the right hemisphere 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 seems 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 sign in comparison to producing speech. Because the lateralization was not primarily driven by motor (i.e., production) factors, the authors argue that the visuo-spatial modality imposes increased processing demands with regard to somatosensory feedback and the simultaneous processing of phonological 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 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 non-linguistic gesture 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, non-linguistic 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 non-linguistic 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 non-signing 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 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.

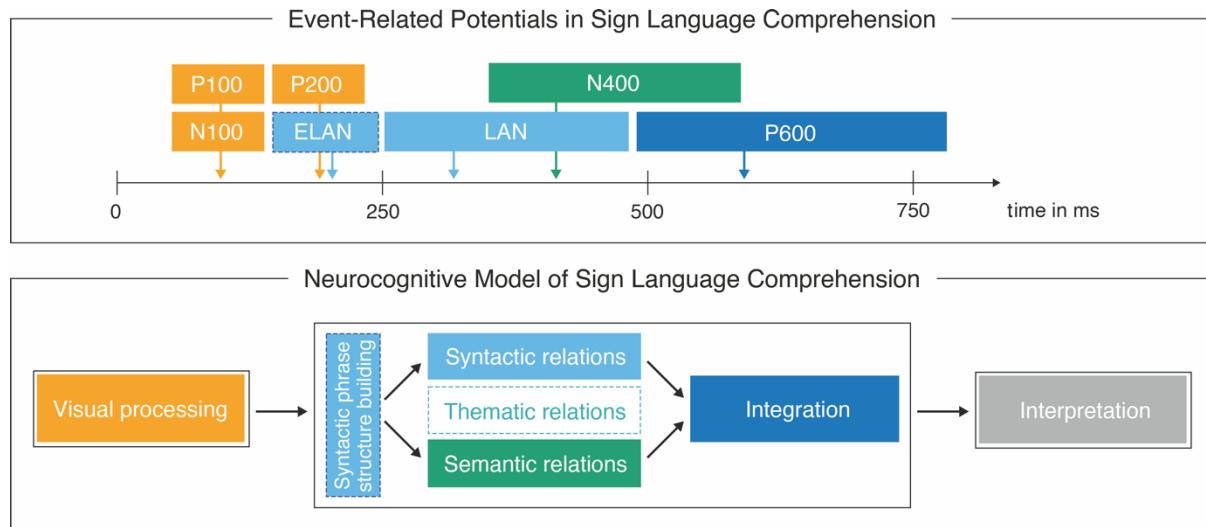
Functional Neuroimaging Studies of Sign Language

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 90s of the past century brought about the first functional neuroimaging studies of sign language processing in deaf signers using non-invasive 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 visuo-spatial 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 & 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.

Electrophysiological Studies

The major event-related potentials (ERPs) observed during sign language comprehension parallel those reported for auditory language comprehension (Figure 4, top panel). Early ERPs peaking 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 around 400 ms (i.e., an N400) have been observed (Gutiérrez, Williams, et al., 2012; Hänel-Faulhaber et al., 2014; Hosemann et al., 2013), whereas their amplitude and latency can be modulated by priming (Emmorey et al., 2022; Gutiérrez, Müller, et al., 2012) 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., so-called post-N400 positivities or P600s; Capek et al., 2009; Hänel-Faulhaber et al., 2014; Neville et al., 1997).

Figure 4*Event-Related Potentials and a Neurocognitive Model of Sign Language Comprehension*

Note. The top panel depicts the time course of even-related potentials (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 & 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.

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 Figure 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 subject or object but moved from a neutral point in sign space towards 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, 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 ERPs findings related to sign language comprehension indicates that a first model of the time-course of different processing steps sketched in Figure 4 (bottom panel) will require refinement in the future, including adjustments reflecting possible modality-specific aspects (Gutiérrez, Williams, et al., 2012). A possible explanation for the

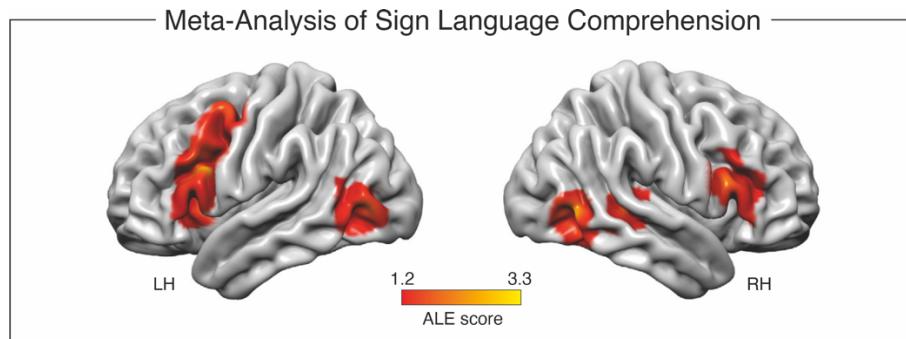
observed variation is that all sign language studies relating to ELAN and LAN to date have used manipulations of agreement verbs: This likely constitutes a confound because the spatial nature of sign language agreements requires the recruitment of additional cognitive resources. Moreover, almost all paradigms mentioned above using agreement manipulations relied on morphological 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 Figure 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, Friederici, et al., 2022; Maran, Numssen, et al., 2022). 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 90s 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 homologues (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 amongst the first to report the largest response to sign language in bilateral visual association cortex (BA 37 and

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 data set (Trettenbrein, Papitto, et al., 2021; Figure 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 anatomical 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 occipital gyrus (BA 37). Notice that the studies included in the data set 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.

Figure 5*Meta-Analysis of Sign Language Comprehension*

Note. 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 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 data set. In the left hemisphere (LH), convergence was observed in inferior frontal gyrus, middle occipital gyrus, precentral gyrus, middle frontal gyrus, and insula (ordered by descending size of clusters). In the right hemisphere (RH), convergence was observed in middle and inferior temporal gyrus extending into occipital cortex, inferior frontal gyrus, and superior temporal gyrus. Illustration based on data from Trettenbrein, Papitto, et al. (2021). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

To better characterize the observed pattern of convergence across studies of sign language processing, Trettenbrein, Papitto, et al. (2021) 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 in Broca's area but not its right-hemispheric homologue was specific to sign language processing in deaf signers and overlapped with spoken and written language processing in hearing non-signers. In a first

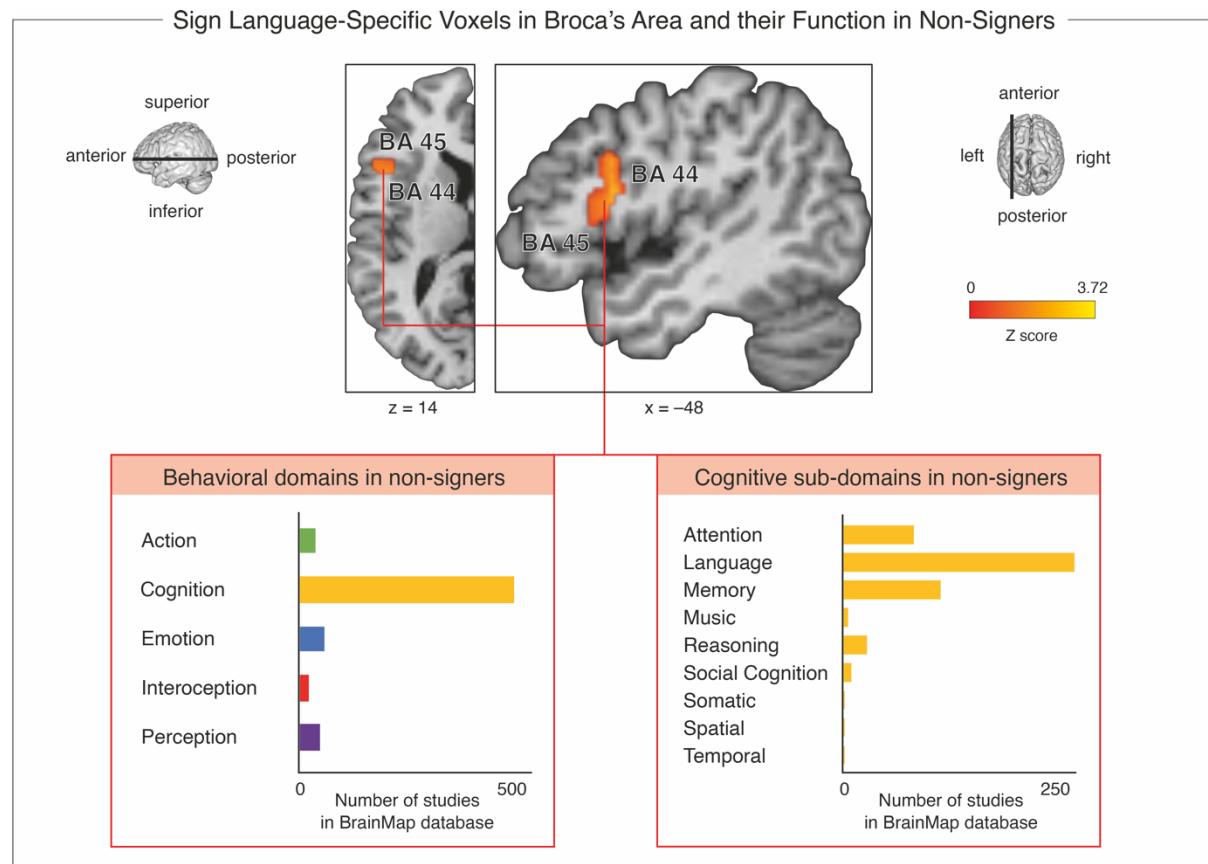
step the authors computed weighted lateralization indices using hemispheric and anatomical masks of Broca's area which revealed a slight global left-lateralization (lateralization index [LI]: 0.24, $p < .001$) as well as a strong left-lateralization in Broca's area and its right-hemispheric homologue (LI: 0.68, $p < .001$). The left-lateralization was especially pronounced in the posterior portion of Broca's area (BA 44, LI: 0.78, $p < .001$). 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, Papitto, et al. (2021) 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 non-signers across the several thousand studies listed in the database (Figure 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 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 non-signers 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.

Figure 6

Sign Language-Specific Voxels in Broca's Area and their Function in Non-Signers



Note. Functional attributions according to the BrainMap database (Fox & 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 non-signers 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 non-signers 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. Illustration adapted from Trettenbrein, Papitto, et al. (2021). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

Because an overlap between sign and spoken language processing in 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, Papitto, et al. (2021) did not observe convergence across studies in 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; MacSweeney et al., 2006; Matchin et al., 2021; Moreno et al., 2018; Neville et al., 1998; San José-Robertson et al., 2004). A possible explanation for this lack of convergence in the meta-analysis is that the different articulators (Figure 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 superior temporal cortex, whereas stimulus videos using only manual

actions activate more posterior and inferior parts of lateral temporal lobe (Capek et al., 2008). 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, Papitto, et al. (2021) did not observe any convergence in either left or right parietal cortex, after all a region which is known to generally support spatial processing and has been found relevant for encoding phonological 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 superior parietal lobule. Additional studies have found involvement of left parietal cortex in processing topographic sentences (MacSweeney, Woll, Campbell, Calvert, et al., 2002), as well as bilateral involvement of 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 (Atkinson et al., 2005; Bellugi et al., 1989; Emmorey, Corina, et al., 1995; Hickok, Say, et al., 1996) 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 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; Matchin et al., 2021; Moreno et al., 2018). The left posterior middle temporal gyrus which houses motion-sensitive area MT/V5 and borders on extrastriate regions of occipital cortex has been found to be involved processing movement in signed stimuli (Levanen, 2001; McCullough et al., 2012) and 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). Left supramarginal gyrus has been linked to processing sign language phonology as well as classifier constructions (Cardin et al., 2016; Emmorey et al., 2002, 2021; Jednorög et al., 2015; MacSweeney, Woll, Campbell, Calvert, et al., 2002).

Given that the generation of hierarchical syntactic representations 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 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 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 left perisylvian regions—possible due to the nature in which stimuli were constructed. Matchin et al. (2021) used a similar design in ASL but only observed a left-lateralized parametric response in anterior and posterior superior temporal sulcus in the syntactically most complex condition.

Lastly, directly reflecting the insight of 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 0–14 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 occipital cortex (BA 18 and BA 19). The authors employed two different tasks, a phonemic as well as a grammaticality judgement 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) hypothesize 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 more anterior adult pattern of automatic and abstract linguistic processing (Trettenbrein & Friederici, this volume).

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 grey 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 grey matter around auditory cortex in deaf signers. This is not surprising, even though it is understood that auditory cortices show plasticity-related changes and seems to participate in visual or sign language processing in deaf signers (Ding et al., 2015; Finney et al., 2001; MacSweeney & Cardin, 2015; Sadato et al., 2004). Beyond this, Grégoire et al. (2022) also identified a volumetric decrease in grey and white matter in visual cortex and a grey matter increase in the right cerebellum as consistent findings in structural imaging studies with profoundly deaf participants. The general decrease in grey and white matter volume in visual areas is unexpected given the visuo-spatial nature of sign language, but 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

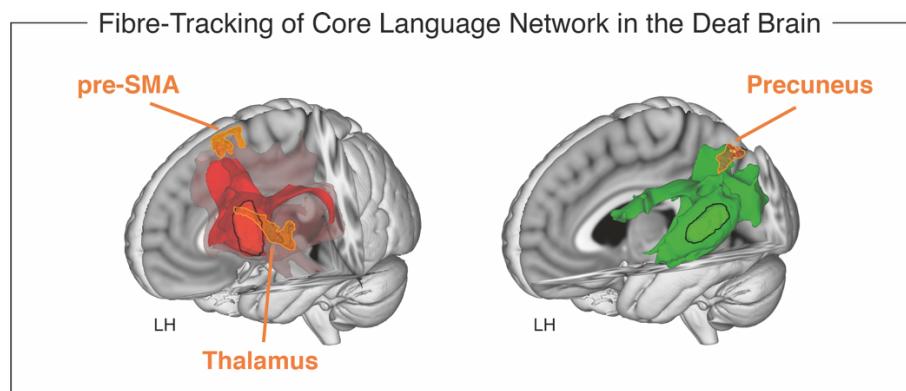
show an increase in grey matter in occipital cortex (Pénicaud et al., 2013) and there is evidence that sign language experience leads to lateralized changes in surface area and cortical thickness in occipital cortex (McCullough & Emmorey, 2021).

More relevant to our interest in the present 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 grey matter volume in left insula as the result of sign language acquisition (Allen et al., 2008), whereas others have reported a bilateral decrease in grey matter in comparison to hearing controls and a decrease in 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 grey matter volume and cortical thickness in bilateral 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 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 inferior frontal to posterior temporal regions, inferior fronto-occipital fasciculus, inferior longitudinal fasciculus connecting anterior temporal to extrastriate cortex and occipital lobe, and uncinate fasciculus connecting 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 non-signers using English and observed no group differences. Significantly, the arcuate and inferior longitudinal fascicles constituted a 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 pre-supplementary motor area as well as to the thalamus (Figure 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 ipsilateral parietal cortex and the precuneus (Figure 7, right panel). Lastly, the transcallosal connection between 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 visuo-spatial modality.

Figure 7*Fibre-Tracking of Core Language Network in the Deaf Brain*

Note. Visualization of fibre-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 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 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 left hemisphere for the deaf group when compared to hearing controls (indicated in orange). Illustration adapted from Finkl et al. (2019) under a Creative Commons (CC-BY 4.0) license.

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) report 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 fibre pathways investigated in this study, yet the difference was most pronounced for the arcuate fasciculus. The authors argue 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 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 (Ferjan Ramirez et al., 2014; Mayberry et al., 2018; Ramírez et al., 2013). Moreover, all three participants also exhibited atypical neural responses patterns to ASL signs that primarily recruited 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 15 month of the data collection for two of the three deaf late signers showed an altered response to highly familiar ASL signs that was more concentrated in left perisylvian language regions (Ferjan Ramirez et al., 2016). Notice that these case studies provide only indirect 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 & Gierhan, 2013; Skeide & 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 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 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 right hemisphere 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 visuo-spatial 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 left and right parietal cortex differentially support either the construction of grammatical or spatial representations (Hickok, Say, et al., 1996).

The neural substrates of sign, spoken, and written language processing in left perisylvian cortex show significant overlap in inferior frontal and posterior temporal regions (Inubushi & Sakai, 2013; MacSweeney, Woll, Campbell, McGuire, et al., 2002; Sakai et al., 2005; Trettenbrein, Papitto, et al., 2021; Uddén et al., 2022), though the exact activation patterns in (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 visuo-spatial 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; Emmorey, 2006; Horwitz et al., 2003) the identification of Broca's area as a modality-independent hub for language comprehension

speaks against a clear dichotomy between production and comprehension (Trettenbrein, Papitto, et al., 2021).

The engagement of bilateral occipital cortex in sign language is of course expected because sign language is perceived visually (Figure 5) and due to the neuroanatomical 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 posterior middle temporal and extrastriate cortex observed in the meta-analysis of sign language comprehension in deaf signers by Trettenbrein, Papitto, et al. (2021) 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” above). 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 non-signers 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 & 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 right hemisphere 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 (Atkinson, 2005; Hickok, Say, et al., 1996). 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 that is part of the sign language stimuli but not necessarily of auditory or written stimuli will recruit more right-hemispheric networks in signers and non-signers alike (Campbell et al., 2011). The meta-analysis by Trettenbrein, Papitto, et al. (2021) 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 & Sakai, 2013; Newman et al., 2015). Hence, larger involvement of the right hemisphere during sign than during auditory or written language processing appears to be driven by both modality and stimulus-specific properties.

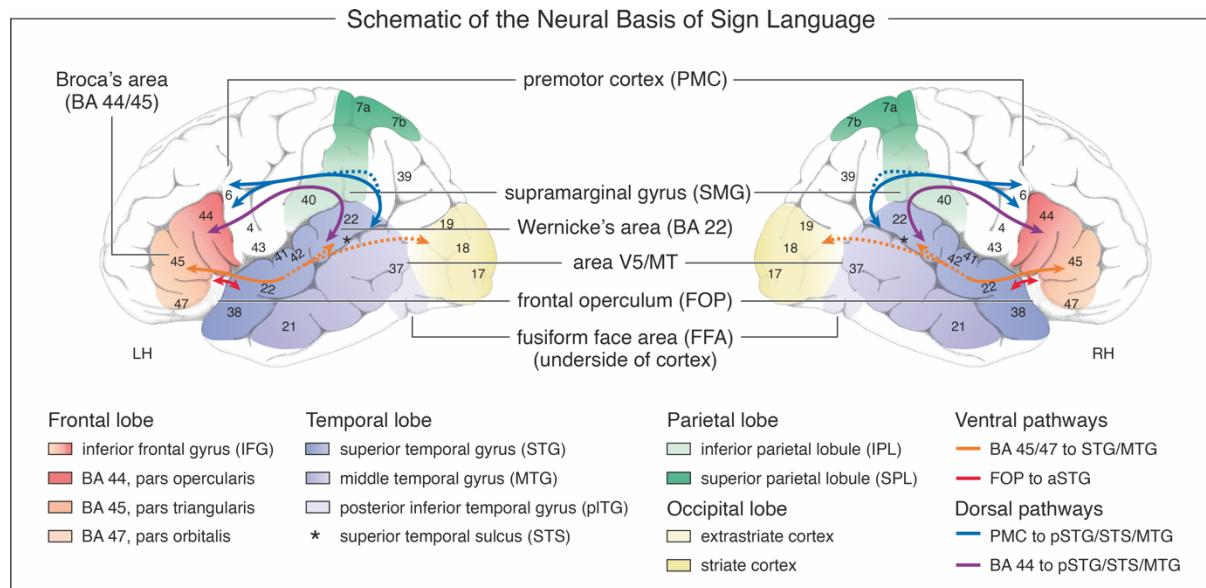
The role that left perisylvian language regions including Broca's area take on in language processing appears to be dependent on exposure to adequate linguistic input already early in life independent of the modality of language use. That is, delayed exposure to a sign language has a severe and lasting impact on the development of the core and extended language network in the left hemisphere 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" above). 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 biological 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 (Schönwiesner et al., 2005; Zatorre et al., 2002), instead we take this pattern to indicate that the left hemisphere 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 (Emmorey, Corina, et al., 1995; Hickok, Bellugi, et al., 1996; Hickok et al., 1998; Poizner et al., 1987), 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: Based on his work with these patients especially in the domain of visual processing Zaidel (1978) proposes that while the right hemisphere can recognize units (e.g., spoken or printed words) as whole patterns, the left hemisphere always decomposes words and by extension signs as well as sentences by feature analysis.

Towards 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 (Figure 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 (Emmorey, 2015, 2021; Poeppel et al., 2012). While sign language and spoken language processing overlap in their recruitment of bilateral posterior temporal cortex and a strong left-lateralization in the inferior frontal gyrus, 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 electrophysiological responses patterns and processing stages (Figure 4). The white-matter pathways connecting regions implicated in sign language processing are best understood for perisylvian cortex and remain to be explored in future studies in the context of regions recruited specifically during sign language processing.

Figure 8*Schematic of the Neural Basis of Sign Language*

Note. Schematic depiction of the left hemisphere (LH) and right hemisphere (RH) displaying anatomical landmarks and cytoarchitectonic details of cortical regions relevant for processing sign language. Major gyri that are involved in sign language processing are colour-coded: The inferior frontal gyrus (IFG) and its subregions Brodmann areas (BA) 44, BA 45 and BA 47 are depicted in shades of red; superior temporal gyrus (STG), 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 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 histological 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). 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 fibre tracts connecting regions of cortex relevant for processing sign language are located dorsally and ventrally and indicated using colour-coded arrows: Blue for the pathway connecting PMC to posterior STG (pSTG), STS, and MTG; purple for the pathway connecting BA 44 to pSTG, STS, and MTG; orange for the pathway connecting BA 45 and BA 47 to STG and MTG; and red for the pathway connecting FOP to aSTG. Illustration based on a similar schematic based on studies of spoken and written language processing by Friederici (2011). This illustration is subject to a Creative Commons (CC-BY 4.0) license.

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 sub-systems (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 portion of left superior temporal cortex and sulcus have been linked to semantic and syntactic processing. Left posterior middle temporal gyrus (i.e., area V5/MT) bordering on occipital 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 temporal cortex such as the fusiform face area are involved in processing mouth gestures. Bilateral parietal cortex has been linked to processing

phonological and spatial information in sign language: Left supramarginal gyrus has been linked to lexical phonological-processing, whereas its right-hemispheric counterpart has been linked to form-based phonological processing. 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 left hemisphere of the typically developed adult human brain is specialized for processing language independent of the modality of language use. This functionally asymmetrical 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 occipital and parietal cortex as well as linguistic information in posterior temporal cortex. The right hemisphere 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 visuo-spatial 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 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 biological 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 methodological advances will likely provide a more fine-grained picture of the functional specialization and lateralization of sign language and its sub-systems.

Acknowledgements

The authors would like to thank (in alphabetical order by last name) Thomas A. Finkbeiner, Cheslie C. Klein, Nina-Kristin Meister, Joëlle A. M. Schroën, and Markus Steinbach for consultation, discussion, and/or feedback on a first draft of this manuscript. We are grateful to Heike Schmidt-Duderstedt and Andrea Gast-Sandmann for their artistic assistance with creating illustrations, to Jens-Michael Cramer for recording the original set of videos from which the stills and videos in Figure 2 are derived, as well as to Alfred Anwander and Theresa Finkl for providing materials for Figure 7. This work was funded by the Max Planck Society. While completing revisions of this chapter Patrick C. Trettenbrein was funded by the Deutsche Forschungsgemeinschaft (DFG, German Research Foundation) – 501984557 which is part of the DFG SPP 2392 “Visual Communication” (ViCom).

References

- Allen, J. S., Emmorey, K., Bruss, J., & Damasio, H. (2008). Morphology of the insula in relation to hearing status and sign language experience. *The Journal of Neuroscience*, 28(46), 11900–11905. <https://doi.org/10.1523/JNEUROSCI.3141-08.2008>
- Atkinson, J. R. (2005). The Perceptual Characteristics of Voice-Hallucinations in Deaf People: Insights into the Nature of Subvocal Thought and Sensory Feedback Loops. *Schizophrenia Bulletin*, 32(4), 701–708. <https://doi.org/10.1093/schbul/sbj063>
- Atkinson, J. R., Campbell, R., Marshall, J., Thacker, A., & Woll, B. (2004). Understanding “not”: Neuropsychological dissociations between hand and head markers of negation in BSL. *Neuropsychologia*, 42(2), 214–229. [https://doi.org/10.1016/S0028-3932\(03\)00186-6](https://doi.org/10.1016/S0028-3932(03)00186-6)
- Atkinson, J. R., Marshall, J., Woll, B., & Thacker, A. (2005). Testing comprehension abilities in users of British Sign Language following CVA. *Brain and Language*, 94(2), 233–248. <https://doi.org/10.1016/j.bandl.2004.12.008>
- Baker, A., van den Bogaerde, B., Pfau, R., & Schermer, T. (2016). *The linguistics of sign language*. John Benjamins.
- Bavelier, D., Corina, D., Jezzard, P., Clar, V., Karni, A., Lalwani, A., Rauschecker, J. P., Braun, A., Turner, R., & Neville, H. J. (1998). Hemispheric specialization for English and ASL: Left invariance-right variability. *NeuroReport*, 9, 1537–1542.
- Bellugi, U., & Klima, E. S. (1976). Two faces of sign: Iconic and abstract. *Annals of the New York Academy of Sciences*, 280(1 Origins and E), 514–538. <https://doi.org/10.1111/j.1749-6632.1976.tb25514.x>

Bellugi, U., Poizner, H., & Klima, E. S. (1989). Language, modality and the brain. *Trends in Neurosciences*, 12(10), 380–388. [https://doi.org/10.1016/0166-2236\(89\)90076-3](https://doi.org/10.1016/0166-2236(89)90076-3)

Berger, L., Pyers, J., Lieberman, A., & Caselli, N. (2023). Parent American Sign Language skills correlate with child—but not toddler—ASL vocabulary size. *Language Acquisition*, 1–15. <https://doi.org/10.1080/10489223.2023.2178312>

Berwick, R. C., Friederici, A. D., Chomsky, N., & Bolhuis, J. J. (2013). Evolution, brain, and the nature of language. *Trends in Cognitive Sciences*, 17(2), 89–98. <https://doi.org/10.1016/j.tics.2012.12.002>

Blanco-Elorrieta, E., Kastner, I., Emmorey, K., & Pylkkänen, L. (2018). Shared neural correlates for building phrases in signed and spoken language. *Scientific Reports*, 8(1). <https://doi.org/10.1038/s41598-018-23915-0>

Bolhuis, J. J., Tattersall, I., Chomsky, N., & Berwick, R. C. (2014). How could language have evolved? *PLoS Biology*, 12(8), e1001934. <https://doi.org/10.1371/journal.pbio.1001934>

Boyes-Braem, P. (1986). Two aspects of psycholinguistic research: Iconicity and temporal structure. In *Proceedings of the Second European Congress on Sign Language Research; Signs of Life*. University of Amsterdam.

Brentari, D. (2012). Phonology. In R. Pfau, M. Steinbach, & B. Woll (Eds.), *Sign language: An international handbook* (pp. 21–54). de Gruyter.

Broca, P. (1861). Remarques sur le siège de la faculté du langage articulé, suivies d'une obsevation d'aphémie (perte de la parole). *Bulletin de La Société Anatomique*, 6, 330–357.

Brodmann, K. (1909). Beiträge zur histologischen Lokalisation der Grosshirnrinde: VI. Die Cortexgliederung des Menschen. *Journal Für Psychologie Und Neurologie*, 10, 231–246.

Brookshire, G., Lu, J., Nusbaum, H. C., Goldin-Meadow, S., & Casasanto, D. (2017). Visual cortex entrains to sign language. *Proceedings of the National Academy of Sciences*, 114(24), 6352–6357. <https://doi.org/10.1073/pnas.1620350114>

Campbell, R., Capek, C. M., Gazarian, K., MacSweeney, M., Woll, B., David, A. S., McGuire, P. K., & Brammer, M. J. (2011). The signer and the sign: Cortical correlates of person identity and language processing from point-light displays. *Neuropsychologia*, 49(11), 3018–3026.
<https://doi.org/10.1016/j.neuropsychologia.2011.06.029>

Capek, C. M., Grossi, G., Newman, A. J., McBurney, S. L., Corina, D., Roeder, B., & Neville, H. J. (2009). Brain systems mediating semantic and syntactic processing in deaf native signers: Biological invariance and modality specificity. *Proceedings of the National Academy of Sciences*, 106(21), 8784–8789.
<https://doi.org/10.1073/pnas.0809609106>

Capek, C. M., & Neville, H. J. (2015). Studying sign language processing using functional neuroimaging techniques: fMRI, ERP, MEG and TMS. In E. Orfanidou, B. Woll, & G. Morgan (Eds.), *Research methods in sign language studies: A practical guide* (pp. 321–335). Wiley-Blackwell.

Capek, C. M., Waters, D., Woll, B., MacSweeney, M., Brammer, M. J., McGuire, P. K., David, A. S., & Campbell, R. (2008). Hand and mouth: Cortical correlates of lexical

processing in British Sign Language and speechreading English. *Journal of Cognitive Neuroscience*, 20(7), 1220–1234. <https://doi.org/10.1162/jocn.2008.20084>

Cardin, V., Orfanidou, E., Kästner, L., Rönnberg, J., Woll, B., Capek, C. M., & Rudner, M. (2016). Monitoring different phonological parameters of sign language engages the same cortical language network but distinctive perceptual ones. *Journal of Cognitive Neuroscience*, 28(1), 20–40. https://doi.org/10.1162/jocn_a_00872

Cardin, V., Orfanidou, E., Rönnberg, J., Capek, C. M., Rudner, M., & Woll, B. (2013). Dissociating cognitive and sensory neural plasticity in human superior temporal cortex. *Nature Communications*, 4(1). <https://doi.org/10.1038/ncomms2463>

Caselli, N. K., Sehyr, Z. S., Cohen-Goldberg, A. M., & Emmorey, K. (2017). ASL-LEX: A lexical database of American Sign Language. *Behavior Research Methods*, 49(2), 784–801. <https://doi.org/10.3758/s13428-016-0742-0>

Cecchetto, C. (2017). The syntax of sign language and Universal Grammar. In I. Roberts (Ed.), *The Oxford handbook of Universal Grammar*. Oxford UP.

Cecchetto, A., Geraci, C., Cecchetto, C., & Zucchi, S. (2018). The language instinct in extreme circumstances: The transition to tactile Italian Sign Language (LIS) by Deafblind signers. *Glossa: A Journal of General Linguistics*, 3(1), 65. <https://doi.org/10.5334/gjgl.357>

Cheng, Q., Roth, A., Halgren, E., Klein, D., Chen, J.-K., & Mayberry, R. I. (2023). Restricted language access during childhood affects adult brain structure in selective language regions. *Proceedings of the National Academy of Sciences*, 120(7), e2215423120. <https://doi.org/10.1073/pnas.2215423120>

- Cheng, Q., Roth, A., Halgren, E., & Mayberry, R. I. (2019). Effects of Early Language Deprivation on Brain Connectivity: Language Pathways in Deaf Native and Late First-Language Learners of American Sign Language. *Frontiers in Human Neuroscience*, 13, 320. <https://doi.org/10.3389/fnhum.2019.00320>
- Chomsky, C. (1986). Analytic study of the Tadoma method: Language abilities of three deaf-blind subjects. *Journal of Speech Language and Hearing Research*, 29(3), 332. <https://doi.org/10.1044/jshr.2903.347>
- Chomsky, N. (1965). *Aspects of the Theory of Syntax*. The MIT Press.
- Chomsky, N. (1986). *Knowledge of language: Its nature, origins, and use* (R. N. Anshen, Ed.). Praeger.
- Chomsky, N. (1995). *The minimalist program*. MIT Press.
- Chomsky, N. (2011). Language and other cognitive systems: What is special about language? *Language Learning and Development*, 7(4), 263–278. <https://doi.org/10.1080/15475441.2011.584041>
- Corballis, P. M. (2003). Visuospatial processing and the right-hemisphere interpreter. *Brain and Cognition*, 53(2), 171–176. [https://doi.org/10.1016/S0278-2626\(03\)00103-9](https://doi.org/10.1016/S0278-2626(03)00103-9)
- Corina, D. P. (1998). The processing of sign language: Evidence from aphasia. In B. Stemmer & H. A. Whitaker (Eds.), *Handbook of Neurolinguistics* (pp. 313–329). Academic Press.
- Corina, D. P. (1999). On the Nature of Left Hemisphere Specialization for Signed Language. *Brain and Language*, 69(2), 230–240. <https://doi.org/10.1006/brln.1999.2062>

Corina, D. P., Poizner, H., Bellugi, U., Feinberg, T., Dowd, D., & O'Grady-Batch, L. (1992).

Dissociation between linguistic and nonlinguistic gestural systems: A case for compositionality*1. *Brain and Language*, 43(3), 414–447.

[https://doi.org/10.1016/0093-934X\(92\)90110-Z](https://doi.org/10.1016/0093-934X(92)90110-Z)

Corina, D. P., San Jose-Robertson, L., Guillemin, A., High, J., & Braun, A. R. (2003).

Language lateralization in a bimanual language. *Journal of Cognitive Neuroscience*, 15(5), 718–730. <https://doi.org/10.1162/089892903322307438>

Crain, S., Koring, L., & Thornton, R. (2016). Language acquisition from a biolinguistic

perspective. *Neuroscience & Biobehavioral Reviews*.

<https://doi.org/10.1016/j.neubiorev.2016.09.004>

Damasio, A., Bellugi, U., Damasio, H., Poizner, H., & Gilder, J. V. (1986). Sign language

aphasia during left-hemisphere Amytal injection. *Nature*, 322(6077), 363–365.

<https://doi.org/10.1038/322363a0>

Dax, G. (1863). M. Dax Soumet Au Jugement de l'Académie Un Mémoire Intitulé:

‘Observations Tendant à Prouver La Coïncidence Constante Des Dérangements de La Parole Avec Une Lésion de l'hémisphère Gauche Du Cerveau.’

Compt.Rend.Hebdom.Séan.l'Acad Scien, 56, 536.

Dax, M. (1865). Lésions de La Moitié Gauche de l'encéphale Coïncident Avec l'oubli Des

Signes de La Pensée (Lu à Montpellier En 1836). *Bulletin Hebdomadaire de Médecine et de Chirurgie*, 2, 259–262.

Dehaene, S., & Cohen, L. (2007). Cultural recycling of cortical maps. *Neuron*, 56(2), 384–

398. <https://doi.org/10.1016/j.neuron.2007.10.004>

Dehaene, S., Cohen, L., Sigman, M., & Vinckier, F. (2005). The neural code for written words: A proposal. *Trends in Cognitive Sciences*, 9(7), 335–341.
<https://doi.org/10.1016/j.tics.2005.05.004>

Ding, H., Qin, W., Liang, M., Ming, D., Wan, B., Li, Q., & Yu, C. (2015). Cross-modal activation of auditory regions during visuo-spatial working memory in early deafness. *Brain*, 138(9), 2750–2765. <https://doi.org/10.1093/brain/awv165>

Dronkers, N. F., Plaisant, O., Iba-Zizen, M. T., & Cabanis, E. A. (2007). Paul Broca's historic cases: High resolution MR imaging of the brains of Leborgne and Lelong. *Brain*, 130(5), 1432–1441. <https://doi.org/10.1093/brain/awm042>

Edwards, T., & Brentari, D. (2020). Feeling phonology: The conventionalization of phonology in protactile communities in the United States. *Language*.
<https://doi.org/10.1353/lan.0.0248>

Eickhoff, S. B., Bzdok, D., Laird, A. R., Kurth, F., & Fox, P. T. (2012). Activation likelihood estimation meta-analysis revisited. *NeuroImage*, 59(3), 2349–2361.
<https://doi.org/10.1016/j.neuroimage.2011.09.017>

Eickhoff, S. B., Laird, A. R., Fox, P. M., Lancaster, J. L., & Fox, P. T. (2017). Implementation errors in the GingerALE Software: Description and recommendations: Errors in the GingerALE Software. *Human Brain Mapping*, 38(1), 7–11. <https://doi.org/10.1002/hbm.23342>

Eickhoff, S. B., Laird, A. R., Grefkes, C., Wang, L. E., Zilles, K., & Fox, P. T. (2009). Coordinate-based activation likelihood estimation meta-analysis of neuroimaging

data: A random-effects approach based on empirical estimates of spatial uncertainty.

Human Brain Mapping, 30(9), 2907–2926. <https://doi.org/10.1002/hbm.20718>

Embick, D., & Poeppel, D. (2015). Towards a computational(ist) neurobiology of language:

Correlational, integrated and explanatory neurolinguistics. *Language, Cognition and Neuroscience*, 30(4), 357–366. <https://doi.org/10.1080/23273798.2014.980750>

Emmorey, K. (2014). Iconicity as structure mapping. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 369(1651), 20130301–20130301.

<https://doi.org/10.1098/rstb.2013.0301>

Emmorey, K. (2015). The neurobiology of sign language. In A. W. Toga, P. Bandettini, P. Thompson, & K. Friston (Eds.), *Brain mapping: An encyclopedic reference* (Vol. 3, pp. 475–479). Academic Press.

Emmorey, K. (2021). New perspectives on the neurobiology of sign languages. *Frontiers in Communication*, 6, 748430. <https://doi.org/10.3389/fcomm.2021.748430>

Emmorey, K., Bellugi, U., Friederici, A., & Horn, P. (1995). Effects of age of acquisition on grammatical sensitivity: Evidence from on-line and off-line tasks. *Applied Psycholinguistics*, 16(1), 1–23. <https://doi.org/10.1017/S0142716400006391>

Emmorey, K., Brozdzowski, C., & McCullough, S. (2021). The neural correlates for spatial language: Perspective-dependent and -independent relationships in American Sign Language and spoken English. *Brain and Language*, 223, 105044.

<https://doi.org/10.1016/j.bandl.2021.105044>

Emmorey, K., Corina, D. P., & Bellugi, U. (1995). Differential processing of topographic and referential functions of space. In *Language, gesture, and space* (pp. 43–62). Lawrence Erlbaum Associates.

Emmorey, K., Damasio, H., McCullough, S., Grabowski, T., Ponto, L. L. B., Hichwa, R. D., & Bellugi, U. (2002). Neural Systems Underlying Spatial Language in American Sign Language. *NeuroImage*, 17(2), 812–824. <https://doi.org/10.1006/nimg.2002.1187>

Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L., Hichwa, R., & Bellugi, U. (2004). Motor-iconicity of sign language does not alter the neural systems underlying tool and action naming. *Brain and Language*, 89(1), 27–37.
[https://doi.org/10.1016/S0093-934X\(03\)00309-2](https://doi.org/10.1016/S0093-934X(03)00309-2)

Emmorey, K., Midgley, K. J., & Holcomb, P. J. (2022). Tracking the time course of sign recognition using ERP repetition priming. *Psychophysiology*, 59(3).
<https://doi.org/10.1111/psyp.13975>

Emmorey, K., Winsler, K., Midgley, K. J., Grainger, J., & Holcomb, P. J. (2020). Neurophysiological Correlates of Frequency, Concreteness, and Iconicity in American Sign Language. *Neurobiology of Language*, 1(2), 249–267.
https://doi.org/10.1162/nol_a_00012

Evans, S., Price, C. J., Diedrichsen, J., Gutierrez-Sigut, E., & MacSweeney, M. (2019). Sign and Speech Share Partially Overlapping Conceptual Representations. *Current Biology*, S0960982219311583. <https://doi.org/10.1016/j.cub.2019.08.075>

- Everaert, M. B. H., Huybregts, M. A. C., Chomsky, N., Berwick, R. C., & Bolhuis, J. J. (2015). Structures, not strings: Linguistics as part of the cognitive sciences. *Trends in Cognitive Sciences*, 19(12), 729–743. <https://doi.org/10.1016/j.tics.2015.09.008>
- Fenlon, J., Cormier, K., & Brentari, D. (2017). The phonology of sign languages. In S. J. Hannahs & A. Bosch (Eds.), *The Routledge Handbook of Phonological Theory*. Routledge.
- Ferjan Ramirez, N., Leonard, M. K., Davenport, T. S., Torres, C., Halgren, E., & Mayberry, R. I. (2016). Neural Language Processing in Adolescent First-Language Learners: Longitudinal Case Studies in American Sign Language. *Cerebral Cortex*, 26(3), 1015–1026. <https://doi.org/10.1093/cercor/bhu273>
- Ferjan Ramirez, N., Leonard, M. K., Torres, C., Hatrak, M., Halgren, E., & Mayberry, R. I. (2014). Neural Language Processing in Adolescent First-Language Learners. *Cerebral Cortex*, 24(10), 2772–2783. <https://doi.org/10.1093/cercor/bht137>
- Finkl, T., Hahne, A., Friederici, A. D., Gerber, J., Mürbe, D., & Anwander, A. (2019). *Language without speech: Segregating distinct circuits in the human brain*. <https://doi.org/10.1093/cercor/bhz128>
- Finney, E. M., Fine, I., & Dobkins, K. R. (2001). Visual stimuli activate auditory cortex in the deaf. *Nature Neuroscience*, 4(12), 1171–1173. <https://doi.org/10.1038/nn763>
- Flaherty, M., Hunsicker, D., & Goldin-Meadow, S. (2021). Structural biases that children bring to language learning: A cross-cultural look at gestural input to homesign. *Cognition*, 211, 104608. <https://doi.org/10.1016/j.cognition.2021.104608>

Floccia, C. (2017). *Data collected with the Oxford CDI over a course of 5 years in Plymouth Babylab, UK*. [dataset]. <https://wordbank.stanford.edu>

Fox, P. T., & Lancaster, J. L. (2002). Mapping context and content: The BrainMap model. *Nature Reviews Neuroscience*, 3(4), 319–321. <https://doi.org/10.1038/nrn789>

Frank, M. C., Braginsky, M., Yurovsky, D., & Marchman, V. A. (2017). Wordbank: An open repository for developmental vocabulary data. *Journal of Child Language*, 44(3), 677–694. <https://doi.org/10.1017/S0305000916000209>

Friederici, A. D. (2011). The brain basis of language processing: From structure to function. *Physiological Reviews*, 91(4), 1357–1392.
<https://doi.org/10.1152/physrev.00006.2011>

Friederici, A. D. (2017). *Language in our brain: The origins of a uniquely human capacity*. MIT Press.

Friederici, A. D., Chomsky, N., Berwick, R. C., Moro, A., & Bolhuis, J. J. (2017). Language, mind and brain. *Nature Human Behaviour*. <https://doi.org/10.1038/s41562-017-0184-4>

Friederici, A. D., & Gierhan, S. M. E. (2013). The language network. *Current Opinion in Neurobiology*, 23(2), 250–254. <https://doi.org/10.1016/j.conb.2012.10.002>

Gallardo, G., Wassermann, D., & Anwander, A. (2020). *Bridging the Gap: From Neuroanatomical Knowledge to Tractography of Brain Pathways* [Preprint]. Neuroscience. <https://doi.org/10.1101/2020.08.01.232116>

Goldberg, E. B., & Hillis, A. E. (2022). Sign language aphasia. In *Handbook of Clinical Neurology* (Vol. 185, pp. 297–315). Elsevier. <https://doi.org/10.1016/B978-0-12-823384-9.00019-0>

Goldin-Meadow, S. (2003). *The resilience of language: What gesture creation in deaf children can tell us about how all children learn language*. Psychology Press.

Goldin-Meadow, S. (2017). What the hands can tell us about language emergence. *Psychonomic Bulletin & Review*, 24(1), 213–218. <https://doi.org/10.3758/s13423-016-1074-x>

Goldin-Meadow, S., & Yang, C. (2017). Statistical evidence that a child can create a combinatorial linguistic system without external linguistic input: Implications for language evolution. *Neuroscience & Biobehavioral Reviews*, 81, 150–157. <https://doi.org/10.1016/j.neubiorev.2016.12.016>

Grech, R., Cassar, T., Muscat, J., Camilleri, K. P., Fabri, S. G., Zervakis, M., Xanthopoulos, P., Sakkalis, V., & Vanrumste, B. (2008). Review on solving the inverse problem in EEG source analysis. *Journal of NeuroEngineering and Rehabilitation*, 5(1), 25. <https://doi.org/10.1186/1743-0003-5-25>

Grégoire, A., Deggouj, N., Dricot, L., Decat, M., & Kupers, R. (2022). Brain Morphological Modifications in Congenital and Acquired Auditory Deprivation: A Systematic Review and Coordinate-Based Meta-Analysis. *Frontiers in Neuroscience*, 16, 850245. <https://doi.org/10.3389/fnins.2022.850245>

- Gutiérrez, E., Müller, O., Baus, C., & Carreiras, M. (2012). Electrophysiological evidence for phonological priming in Spanish Sign Language lexical access. *Neuropsychologia*, 50(7), 1335–1346. <https://doi.org/10.1016/j.neuropsychologia.2012.02.018>
- Gutiérrez, E., Williams, D., Grosvald, M., & Corina, D. (2012). Lexical access in American Sign Language: An ERP investigation of effects of semantics and phonology. *Brain Research*, 1468, 63–83. <https://doi.org/10.1016/j.brainres.2012.04.029>
- Gutiérrez-Sigut, E., Daws, R., Payne, H., Blott, J., Marshall, C., & MacSweeney, M. (2015). Language lateralization of hearing native signers: A functional transcranial Doppler sonography (fTCD) study of speech and sign production. *Brain and Language*, 151, 23–34. <https://doi.org/10.1016/j.bandl.2015.10.006>
- Hagoort, P. (2017). The core and beyond in the language-ready brain. *Neuroscience & Biobehavioral Reviews*. <https://doi.org/10.1016/j.neubiorev.2017.01.048>
- Hamilton, A., Plunkett, K., & Schafer, G. (2000). Infant vocabulary development assessed with a British communicative development inventory. *Journal of Child Language*, 27(3), 689–705. <https://doi.org/10.1017/S0305000900004414>
- Hammarström, H., Forkel, R., Haspelmath, M., & Bank, S. (2022). *Glottolog database* (v4.7) [dataset]. Zenodo. <https://doi.org/10.5281/ZENODO.7398962>
- Hänel-Faulhaber, B., Skotara, N., Kügow, M., Salden, U., Bottari, D., & Röder, B. (2014). ERP correlates of German Sign Language processing in deaf native signers. *BMC Neuroscience*, 15(1), 62. <https://doi.org/10.1186/1471-2202-15-62>

Hauser, M. D., Chomsky, N., & Fitch, W. T. (2002). The faculty of language: What is it, who has it, and how did it evolve? *Science*, 298(5598), 1569–1579.
<https://doi.org/10.1126/science.298.5598.1569>

Henrich, J., Heine, S. J., & Norenzayan, A. (2010). The weirdest people in the world? *Behavioral and Brain Sciences*, 33(2–3), 61–83.
<https://doi.org/10.1017/S0140525X0999152X>

Hickok, G., Bellugi, U., & Klima, E. S. (1996). The neurobiology of sign language and its implications for the neural basis of language. *Nature*, 381(6584), 699–702.
<https://doi.org/10.1038/381699a0>

Hickok, G., Bellugi, U., & Klima, E. S. (1998). The neural organization of language: Evidence from sign language aphasia. *Trends in Cognitive Sciences*, 2(4), 129–136.
[https://doi.org/10.1016/S1364-6613\(98\)01154-1](https://doi.org/10.1016/S1364-6613(98)01154-1)

Hickok, G., Klima, E., Kritchevsky, M., & Bellugi, U. (1995). A case of ‘sign blindness’ following left occipital damage in a deaf signer. *Neuropsychologia*, 33(12), 1597–1606. [https://doi.org/10.1016/0028-3932\(95\)00111-5](https://doi.org/10.1016/0028-3932(95)00111-5)

Hickok, G., Kritchevsky, M., Bellugi, U., & Klima, E. S. (1996). The role of the left frontal operculum in sign language aphasia. *Neurocase*, 2(5), 373–380.
<https://doi.org/10.1080/13554799608402412>

Hickok, G., Say, K., Bellugi, U., & Klima, E. S. (1996). The basis of hemispheric asymmetries for language and spatial cognition: Clues from focal brain damage in two deaf native signers. *Aphasiology*, 10(6), 577–591.
<https://doi.org/10.1080/02687039608248438>

Hosemann, J., Herrmann, A., Sennhenn-Reulen, H., Schlesewsky, M., & Steinbach, M. (2018). Agreement or no agreement. ERP correlates of verb agreement violation in German Sign Language. *Language, Cognition and Neuroscience*, 1–21.

<https://doi.org/10.1080/23273798.2018.1465986>

Hosemann, J., Herrmann, A., Steinbach, M., Bornkessel-Schlesewsky, I., & Schlesewsky, M. (2013). Lexical prediction via forward models: N400 evidence from German Sign Language. *Neuropsychologia*, 51(11), 2224–2237.

<https://doi.org/10.1016/j.neuropsychologia.2013.07.013>

Inubushi, T., & Sakai, K. L. (2013). Functional and anatomical correlates of word-, sentence-, and discourse-level integration in sign language. *Frontiers in Human Neuroscience*, 7.

<https://doi.org/10.3389/fnhum.2013.00681>

Jednoróg, K., Bola, Ł., Mostowski, P., Szwed, M., Boguszewski, P. M., Marchewka, A., & Rutkowski, P. (2015). Three-dimensional grammar in the brain: Dissociating the neural correlates of natural sign language and manually coded spoken language. *Neuropsychologia*, 71, 191–200.

<https://doi.org/10.1016/j.neuropsychologia.2015.03.031>

Klann, J., Kastrau, F., & Huber, W. (2005). Lexical decision with no iconicity effect in German Sign Language: An fMRI-study. *Brain and Language*, 95(1), 167–169.

<https://doi.org/10.1016/j.bandl.2005.07.091>

Klima, E. S., Bellugi, U., Battison, R., Boyes-Braem, P., Fischer, S., Frishberg, N., Lane, H., Lentz, E. M., Newkirk, D., Newport, E. L., Pedersen, C. C., & Siple, P. (1979). *The signs of language*. Harvard UP.

- Krauska, A., & Lau, E. (2023). Moving away from lexicalism in psycho- and neuro-linguistics. *Frontiers in Language Sciences*, 2, 1125127.
<https://doi.org/10.3389/flang.2023.1125127>
- Labache, L., Mazoyer, B., Joliot, M., Crivello, F., Hesling, I., & Tzourio-Mazoyer, N. (2020). Typical and atypical language brain organization based on intrinsic connectivity and multitask functional asymmetries. *eLife*, 9, e58722.
<https://doi.org/10.7554/eLife.58722>
- Lenneberg, E. H. (1964). The capacity for language acquisition. In J. A. Fodor & J. J. Katz (Eds.), *The structure of language: Readings in the philosophy of language* (pp. 579–603). Prentice-Hall.
- Lenneberg, E. H. (1967). *Biological foundations of language*. Wiley.
- Lenneberg, E. H. (1969). On explaining language. *Science*, 164(3880), 635–643.
<https://doi.org/10.1126/science.164.3880.635>
- Lenneberg, E. H. (1970). What is meant by a biological approach to language? *American Annals of the Deaf*, 115(2), 67–72.
- Levanen, S. (2001). Cortical Representation of Sign Language: Comparison of Deaf Signers and Hearing Non-signers. *Cerebral Cortex*, 11(6), 506–512.
<https://doi.org/10.1093/cercor/11.6.506>
- Luck, S. J., & Gaspelin, N. (2017). How to get statistically significant effects in any ERP experiment (and why you shouldn't): How to get significant effects. *Psychophysiology*, 54(1), 146–157. <https://doi.org/10.1111/psyp.12639>

MacSweeney, M., Campbell, R., Woll, B., Brammer, M. J., Giampietro, V., David, A. S., Calvert, G. A., & McGuire, P. K. (2006). Lexical and sentential processing in British Sign Language. *Human Brain Mapping*, 27(1), 63–76.
<https://doi.org/10.1002/hbm.20167>

MacSweeney, M., & Cardin, V. (2015). What is the function of auditory cortex without auditory input? *Brain*, 138(9), 2468–2470. <https://doi.org/10.1093/brain/awv197>

MacSweeney, M., Woll, B., Campbell, R., Calvert, G. A., McGuire, P. K., David, A. S., Simmons, A., & Brammer, M. J. (2002). Neural correlates of British Sign Language comprehension: Spatial processing demands of topographic language. *Journal of Cognitive Neuroscience*, 14(7), 1064–1075.
<https://doi.org/10.1162/089892902320474517>

MacSweeney, M., Woll, B., Campbell, R., McGuire, P. K., David, S. A., Williams, S. C. R., Suckling, J., Calvert, G. A., & Brammer, M. J. (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. *Brain*, 125(7), 1583–1593. <https://doi.org/10.1093/brain/awf153>

Maran, M., Friederici, A. D., & Zaccarella, E. (2022). Syntax through the looking glass: A review on two-word linguistic processing across behavioral, neuroimaging and neurostimulation studies. *Neuroscience & Biobehavioral Reviews*, 142, 104881.
<https://doi.org/10.1016/j.neubiorev.2022.104881>

Maran, M., Numssen, O., Hartwigsen, G., & Zaccarella, E. (2022). Online neurostimulation of Broca's area does not interfere with syntactic predictions: A combined TMS-EEG approach to basic linguistic combination. *Frontiers in Psychology*, 13, 968836.
<https://doi.org/10.3389/fpsyg.2022.968836>

- Marshall, J., Atkinson, J. R., Smulovitch, E., Thacker, A., & Woll, B. (2004). Aphasia in a user of British Sign Language: Dissociation between sign and gesture. *Cognitive Neuropsychology*, 21(5), 537–554. <https://doi.org/10.1080/02643290342000249>
- Matchin, W., İlkbaşaran, D., Hatrak, M., Roth, A., Villwock, A., Halgren, E., & Mayberry, R. I. (2021). The cortical organization of syntactic processing is supramodal: Evidence from American Sign Language. *Journal of Cognitive Neuroscience*, 1–12. https://doi.org/10.1162/jocn_a_01790
- Mathur, G., & Rathmann, C. (2012). Verb agreement. In R. Pfau, M. Steinbach, & B. Woll (Eds.), *Sign language: An international handbook* (pp. 136–157). de Gruyter.
- Mathur, G., & Rathmann, C. (2014). The structure of sign languages. In M. A. Goldrick, V. S. Ferreira, & M. Miozzo (Eds.), *The Oxford handbook of language production* (pp. 379–392). Oxford UP.
- Mayberry, R. I. (2002). Cognitive development in deaf children: The interface of language and perception in neuropsychology. In S. J. Segalowitz & I. Rapin (Eds.), *Handbook of Neuropsychology* (2nd ed., Vol. 8, pp. 71–107). Elsevier.
- Mayberry, R. I., Chen, J.-K., Witcher, P., & Klein, D. (2011). Age of acquisition effects on the functional organization of language in the adult brain. *Brain and Language*, 119(1), 16–29. <https://doi.org/10.1016/j.bandl.2011.05.007>
- Mayberry, R. I., Davenport, T., Roth, A., & Halgren, E. (2018). Neurolinguistic processing when the brain matures without language. *Cortex*, 99, 390–403. <https://doi.org/10.1016/j.cortex.2017.12.011>

Mayberry, R. I., & Squires, B. (2006). Sign Language: Acquisition. In *Encyclopedia of Language & Linguistics* (pp. 291–296). Elsevier. <https://doi.org/10.1016/B0-08-044854-2/00854-3>

McCullough, S., & Emmorey, K. (2021). Effects of deafness and sign language experience on the human brain: Voxel-based and surface-based morphometry. *Language, Cognition and Neuroscience*, 36(4), 422–439.
<https://doi.org/10.1080/23273798.2020.1854793>

McCullough, S., Saygin, A. P., Korpics, F., & Emmorey, K. (2012). Motion-sensitive cortex and motion semantics in American Sign Language. *NeuroImage*, 63(1), 111–118.
<https://doi.org/10.1016/j.neuroimage.2012.06.029>

McGarry, M. E., Midgley, K. J., Holcomb, P. J., & Emmorey, K. (2023). How (and why) does iconicity effect lexical access: An electrophysiological study of American sign language. *Neuropsychologia*, 183, 108516.
<https://doi.org/10.1016/j.neuropsychologia.2023.108516>

McGuire, P. K., Robertson, D., Thacker, A., David, A. S., Kitson, N., Frackowiak, R. S. J., & Frith, C. D. (1997). Neural correlates of thinking in sign language. *NeuroReport*, 8, 695–698.

Meier, R. P. (2016). *Sign language acquisition*. Oxford University Press.
<https://doi.org/10.1093/oxfordhb/9780199935345.013.19>

Mesch. (2010). *Perspectives on the Concept and Definition of International Sign*. World Federation of the Deaf. http://wfdeaf.org/wp-content/uploads/2016/11/Perspectives-on-the-Concept-and-Definition-of-IS_Mesch-FINAL.pdf

Miranda, M., Arias, F., Arain, A., Newman, B., Rolston, J., Richards, S., Peters, A., & Pick, L. H. (2022). Neuropsychological evaluation in American Sign Language: A case study of a deaf patient with epilepsy. *Epilepsy & Behavior Reports*, 19, 100558. <https://doi.org/10.1016/j.ebr.2022.100558>

Mitchell, R. E., & Karchmer, M. A. (2004). Chasing the Mythical Ten Percent: Parental Hearing Status of Deaf and Hard of Hearing Students in the United States. *Sign Language Studies*, 4(2), 138–163. <https://doi.org/10.1353/sls.2004.0005>

Moreno, A., Limousin, F., Dehaene, S., & Pallier, C. (2018). Brain correlates of constituent structure in sign language comprehension. *NeuroImage*, 167, 151–161. <https://doi.org/10.1016/j.neuroimage.2017.11.040>

Neville, H. J., Bavelier, D., Corina, D., Rauschecker, J., Karni, A., Lalwani, A., Braun, A., Clark, V., Jezzard, P., & Turner, R. (1998). Cerebral organization for language in deaf and hearing subjects: Biological constraints and effects of experience. *Proceedings of the National Academy of Sciences*, 95(3), 922–929. <https://doi.org/10.1073/pnas.95.3.922>

Neville, H. J., Coffey, S. A., Lawson, D. S., Fischer, A., Emmorey, K., & Bellugi, U. (1997). Neural systems mediating American Sign Language: Effects of sensory experience and age of acquisition. *Brain and Language*, 57(3), 285–308. <https://doi.org/10.1006/brln.1997.1739>

Newman, A. J., Supalla, T., Fernandez, N., Newport, E. L., & Bavelier, D. (2015). Neural systems supporting linguistic structure, linguistic experience, and symbolic communication in sign language and gesture. *Proceedings of the National Academy of Sciences*, 112(37), 11684–11689. <https://doi.org/10.1073/pnas.1510527112>

Newman, A. J., Supalla, T., Hauser, P., Newport, E. L., & Bavelier, D. (2010). Dissociating neural subsystems for grammar by contrasting word order and inflection. *Proceedings of the National Academy of Sciences*, 107(16), 7539–7544.

<https://doi.org/10.1073/pnas.1003174107>

Newport, E. L., & Meier, R. P. (1985). The acquisition of American Sign Language. In D. I. Slobin (Ed.), *The crosslinguistic study of language acquisition* (pp. 881–938). Psychology Press.

Obretenova, S. (2010). Neuroplasticity associated with tactile language communication in a deaf-blind subject. *Frontiers in Human Neuroscience*, 3.

<https://doi.org/10.3389/neuro.09.060.2009>

Olulade, O. A., Koo, D. S., LaSasso, C. J., & Eden, G. F. (2014). Neuroanatomical Profiles of Deafness in the Context of Native Language Experience. *The Journal of Neuroscience*, 34(16), 5613–5620. <https://doi.org/10.1523/JNEUROSCI.3700-13.2014>

Pallier, C., Devauchelle, A.-D., & Dehaene, S. (2011). Cortical representation of the constituent structure of sentences. *Proceedings of the National Academy of Sciences of the United States of America*, 108(6), 2522–2527.

<https://doi.org/10.1073/pnas.1018711108>

Payne, H., Gutierrez-Sigut, E., Woll, B., & MacSweeney, M. (2019). Cerebral lateralisation during signed and spoken language production in children born deaf. *Developmental Cognitive Neuroscience*, 36, 100619. <https://doi.org/10.1016/j.dcn.2019.100619>

Peperkamp, S., & Mehler, J. (1999). Signed and spoken language: A unique underlying system? *Language and Speech*, 42(2–3), 333–346.

<https://doi.org/10.1177/00238309990420020901>

Petitto, L. A. (1987). On the autonomy of language and gesture: Evidence from the acquisition of personal pronouns in American sign language. *Cognition*, 27(1), 1–52.
[https://doi.org/10.1016/0010-0277\(87\)90034-5](https://doi.org/10.1016/0010-0277(87)90034-5)

Petitto, L. A., Zatorre, R. J., Gauna, K., Nikelski, E. J., Dostie, D., & Evans, A. C. (2000). Speech-like cerebral activity in profoundly deaf people processing signed languages: Implications for the neural basis of human language. *Proceedings of the National Academy of Sciences*, 97(25), 13961–13966. <https://doi.org/10.1073/pnas.97.25.13961>

Pfau, R., Salzmann, M., & Steinbach, M. (2018). The syntax of sign language agreement: Common ingredients, but unusual recipe. *Glossa: A Journal of General Linguistics*, 3(1). <https://doi.org/10.5334/gjgl.511>

Pfau, R., Steinbach, M., & Woll, B. (Eds.). (2012). *Sign language: An international handbook*. de Gruyter.

Pickell, H., Klima, E., Love, T., Kritchevsky, M., Bellugi, U., & Hickok, G. (2005). Sign language aphasia following right hemisphere damage in a left-hander: A case of reversed cerebral dominance in a deaf signer? *Neurocase*, 11(3), 194–203.
<https://doi.org/10.1080/13554790590944717>

Poeppel, D., & Embick, D. (2013). Defining the relation between linguistics and neuroscience. In A. Cutler (Ed.), *Twenty-first century psycholinguistics: Four cornerstones* (pp. 103–118). Psychology Press.

Poeppl, D., Emmorey, K., Hickok, G., & Pylkkänen, L. (2012). Towards a New Neurobiology of Language. *The Journal of Neuroscience*, 32(41), 14125–14131.
<https://doi.org/10.1523/JNEUROSCI.3244-12.2012>

Poizner, H., Klima, E. S., & Bellugi, U. (1987). *What the hands reveal about the brain*. MIT Press.

Quer, J., & Steinbach, M. (2019). Handling Sign Language Data: The Impact of Modality. *Frontiers in Psychology*, 10, 483. <https://doi.org/10.3389/fpsyg.2019.00483>

Ramírez, N. F., Lieberman, A. M., & Mayberry, R. I. (2013). The initial stages of first-language acquisition begun in adolescence: When late looks early. *Journal of Child Language*, 40(2), 391–414. <https://doi.org/10.1017/S0305000911000535>

Sadato, N., Yamada, H., Okada, T., Yoshida, M., Hasegawa, T., Matsuki, K.-I., Yonekura, Y., & Itoh, H. (2004). Age-dependent plasticity in the superior temporal sulcus in deaf humans: A functional MRI study. *BMC Neuroscience*, 5(1), 56.
<https://doi.org/10.1186/1471-2202-5-56>

Saito, K., Otsuki, M., & Ueno, S. (2007). Sign language aphasia due to left occipital lesion in a deaf signer. *Neurology*, 69(14), 1466–1468.
<https://doi.org/10.1212/01.wnl.0000277455.08067.9c>

Sakai, K. L., Tatsuno, Y., Suzuki, K., Kimura, H., & Ichida, Y. (2005). Sign and speech: Amodal commonality in left hemisphere dominance for comprehension of sentences. *Brain*, 128(6), 1407–1417. <https://doi.org/10.1093/brain/awh465>

San José-Robertson, L., Corina, D. P., Ackerman, D., Guillemin, A., & Braun, A. R. (2004). Neural systems for sign language production: Mechanisms supporting lexical

selection, phonological encoding, and articulation: Neural Systems for Sign Language Production. *Human Brain Mapping*, 23(3), 156–167.
<https://doi.org/10.1002/hbm.20054>

Sandler, W., & Lillo-Martin, D. C. (2001). Natural sign languages. In M. Aronoff & J. Rees-Miller (Eds.), *The handbook of linguistics* (pp. 533–562). Blackwell.

Sandler, W., & Lillo-Martin, D. C. (2008). *Sign language and linguistic universals*. Cambridge UP.

Schönwiesner, M., Rübsamen, R., & Von Cramon, D. Y. (2005). Hemispheric asymmetry for spectral and temporal processing in the human antero-lateral auditory belt cortex: Spectro-temporal processing in human auditory cortex. *European Journal of Neuroscience*, 22(6), 1521–1528. <https://doi.org/10.1111/j.1460-9568.2005.04315.x>

Sehyr, Z. S., Caselli, N., Cohen-Goldberg, A. M., & Emmorey, K. (2021). The ASL-LEX 2.0 Project: A Database of Lexical and Phonological Properties for 2,723 Signs in American Sign Language. *The Journal of Deaf Studies and Deaf Education*, 26(2), 263–277. <https://doi.org/10.1093/deafed/enaa038>

Skeide, M. A., & Friederici, A. D. (2016). The ontogeny of the cortical language network. *Nature Reviews Neuroscience*, 17(5), 323–332. <https://doi.org/10.1038/nrn.2016.23>

Söderfeldt, B., Ingvar, M., Rönnberg, J., Eriksson, L., Serrander, M., & Stone-Elander, S. (1997). Signed and spoken language perception studied by positron emission tomography. *Neurology*, 49(1), 82–87. <https://doi.org/10.1212/WNL.49.1.82>

Stokoe, W. C. (1960). Sign language structure: An outline of the visual communication systems of the American deaf. *Studies in Linguistics*, 8.

- Stroh, A., Grin, K., Rösler, F., Bottari, D., Ossandón, J., Rossion, B., & Röder, B. (2022). Developmental experiences alter the temporal processing characteristics of the visual cortex: Evidence from deaf and hearing native signers. *European Journal of Neuroscience*, ejn.15629. <https://doi.org/10.1111/ejn.15629>
- Stroh, A.-L., Rösler, F., Dormal, G., Salden, U., Skotara, N., Hänel-Faulhaber, B., & Röder, B. (2019). Neural correlates of semantic and syntactic processing in German Sign Language. *NeuroImage*, 200, 231–241.
<https://doi.org/10.1016/j.neuroimage.2019.06.025>
- Tang, G., & Lau, P. (2012). Coordination and subordination. In R. Pfau, M. Steinbach, & B. Woll (Eds.), *Sign language: An international handbook* (pp. 340–365). de Gruyter.
- Terrace, H., Petitto, L., Sanders, R., & Bever, T. (1979). Can an ape create a sentence? *Science*, 206(4421), 891–902. <https://doi.org/10.1126/science.504995>
- Trettenbrein, P. C., & Friederici, A. D. (2023). Functional and structural brain asymmetries in language processing. In P. Corballis & C. Papagno (Eds.), *Handbook of Clinical Neurology*.
- Trettenbrein, P. C., Papitto, G., Friederici, A. D., & Zaccarella, E. (2021). Functional neuroanatomy of language without speech: An ALE meta-analysis of sign language. *Human Brain Mapping*, 42(3), 699–712. <https://doi.org/10.1002/hbm.25254>
- Trettenbrein, P. C., Pendzich, N.-K., Cramer, J.-M., Steinbach, M., & Zaccarella, E. (2021). Psycholinguistic norms for more than 300 lexical signs in German Sign Language (DGS). *Behavior Research Methods*, 53, 1817–1832. <https://doi.org/10.3758/s13428-020-01524-y>

Turkeltaub, P. E., Eickhoff, S. B., Laird, A. R., Fox, M., Wiener, M., & Fox, P. (2012).

Minimizing within-experiment and within-group effects in activation likelihood estimation meta-analyses. *Human Brain Mapping*, 33(1), 1–13.

<https://doi.org/10.1002/hbm.21186>

Uddén, J., Hultén, A., Schoffelen, J.-M., Lam, N., Harbusch, K., van den Bosch, A., Kempen, G., Petersson, K. M., & Hagoort, P. (2022). Supramodal Sentence Processing in the Human Brain: fMRI Evidence for the Influence of Syntactic Complexity in More Than 200 Participants. *Neurobiology of Language*, 3(4), 575–598.

https://doi.org/10.1162/nol_a_00076

van der Burght, C. L., Friederici, A. D., Maran, M., Papitto, G., Pyatigorskaya, E., Schroen, J., Trettenbrein, P. C., & Zaccarella, E. (2023). *Cleaning up the Brickyard: How Theory and Methodology Shape Experiments in Cognitive Neuroscience of Language* [Preprint]. PsyArXiv. <https://doi.org/10.31234/osf.io/6zpjq>

Vigneau, M., Beaucousin, V., Hervé, P.-Y., Jobard, G., Petit, L., Crivello, F., Mellet, E., Zago, L., Mazoyer, B., & Tzourio-Mazoyer, N. (2011). What is right-hemisphere contribution to phonological, lexico-semantic, and sentence processing? *NeuroImage*, 54(1), 577–593. <https://doi.org/10.1016/j.neuroimage.2010.07.036>

Warrington, S., Bryant, K. L., Khrapitchev, A. A., Sallet, J., Charquero-Ballester, M., Douaud, G., Jbabdi, S., Mars, R. B., & Sotiroopoulos, S. N. (2020). XTRACT - Standardised protocols for automated tractography in the human and macaque brain. *NeuroImage*, 217, 116923. <https://doi.org/10.1016/j.neuroimage.2020.116923>

Wilson, S. M., Entrup, J. L., Schneck, S. M., Onuscheck, C. F., Levy, D. F., Rahman, M., Willey, E., Casilio, M., Yen, M., Brito, A. C., Kam, W., Davis, L. T., de Riesthal, M.,

& Kirshner, H. S. (2023). Recovery from aphasia in the first year after stroke. *Brain*, 146(3), 1021–1039. <https://doi.org/10.1093/brain/awac129>

Woolfe, T., Herman, R., Roy, P., & Woll, B. (2010). Early vocabulary development in deaf native signers: A British Sign Language adaptation of the communicative development inventories. *Journal of Child Psychology and Psychiatry*, 51(3), 322–331. <https://doi.org/10.1111/j.1469-7610.2009.02151.x>

Yang, C., Crain, S., Berwick, R. C., Chomsky, N., & Bolhuis, J. J. (2017). The growth of language: Universal Grammar, experience, and principles of computation. *Neuroscience & Biobehavioral Reviews*.

<https://doi.org/10.1016/j.neubiorev.2016.12.023>

Zaccarella, E., & Trettenbrein, P. C. (2021). Neuroscience and syntax. In N. Allott, T. Lohndal, & G. Rey (Eds.), *A Companion to Chomsky* (pp. 325–347). Wiley-Blackwell. <https://doi.org/10.1002/9781119598732.ch20>

Zaidel, E. (1978). The Elusive Right Hemisphere of the Brain. *Engineering and Science*, 42, 10–32.

Zatorre, R. J., Belin, P., & Penhune, V. B. (2002). Structure and function of auditory cortex: Music and speech. *Trends in Cognitive Sciences*, 6(1), 37–46. [https://doi.org/10.1016/S1364-6613\(00\)01816-7](https://doi.org/10.1016/S1364-6613(00)01816-7)

Zwitserlood, I. (2012). Classifiers. In R. Pfau, M. Steinbach, & B. Woll (Eds.), *Sign language: An international handbook* (pp. 158–185). de Gruyter.