Human Language

From Genes and Brains to Behavior

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Insights into the Neurobiology of Language from Individuals Born Blind or Deaf

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In this chapter we discuss insights into theories of the neurobiology of language from work with individuals who are born blind or deaf. Why should language acquired under atypical circumstances be of interest to those striving toward a general theory of language? An answer to this question was articulated by Lila Gleitman and her colleagues twenty years ago in the context of behavioral research on language acquisition (e.g., Landau & Gleitman, 1985; Gleitman & Newport, 1995). Children acquiring language with different access to the environment offer unique insights into the contribution of nature and nurture to the language faculty. Landau and Gleitman (1985) showed that children born blind acquire the meanings of words such as *red* and *look* at around the same time as sighted children do. Deaf children growing up without access to either a signed or spoken language develop language-like communication systems called homesign (Goldin-Meadow, chapter 16 of this volume). Language acquisition turns out to be surprisingly robust to dramatic changes in the environment.

An analogous argument applies to the neurobiology of language. The anatomical substrates of language are remarkably consistent across languages and cultures. Left-lateralized perisylvian cortices are a core neurobiological mechanism across users of English, German, Russian, and Mandarin Chinese (Chee et al., 1999; Rüschemeyer, Fiebach, Kempe, & Friederici, 2005). What predisposes language toward these cortical systems? Has evolution uniquely programmed the left perisylvian cortices for language processing? Are there any circumstances under which regions outside the classic network take on language functions? Alternatively, since many aspects of the acquisition experience are shared across cultures, do these commonalities give rise to a similar neural phenotype? For example, most people learn language through audition. We might therefore suppose that lateral temporal areas become involved in language because of their proximity to auditory cortices. Research with those born deaf allows us to test this hypothesis. Conversely, studies with individuals who are born blind have the potential to uncover how and whether absence of vision changes the neurobiological instantiation of concrete concepts. As it turns out, studies of blindness also reveal a surprising capacity of language to colonize unused cortical territory in the visual cortex. Research with individuals who grow up with distinctive experiences thus provides unique insights into the contributions of nature and nurture to the neurobiology of language.

1. The Cognitive and Neural Basis of Language in Blind Individuals

1.1. Representation of Word Meanings in Blindness: Insights into the Relationship of Meaning and Sensory Experience

When philosophers and psychologists consider the effects of blindness on language, they often focused on the meanings of concrete words, supposing such meanings to be very different in people who are blind from birth (Berkeley, 1709; Hume, 1748; Locke, 1690). Vision is a key source of information about objects, actions, events, properties, and agents. Sighted people use information from the eyes to distinguish lions from hippos and rolling from spinning. Prominent philosophical, cognitive, and neural theories of concepts posit that understanding concrete words involves reactivating recollections of modality-specific experiences with referents. For example, the meaning of the word *run* includes visual memories of seeing others run, motor memories of running, and the sound of running footsteps. At the neurobiological level, these different modality-specific aspects of meaning are said to be stored in distinct neural systems (e.g., visual image of running stored in visual motion areas, e.g., middle temporal complex (MT+), and the motor program for running in motor cortex) (Barsalou, Simmons, Barbey, & Wilson, 2003; Kable, Kan, Wilson, Thompson-Schill, & Chatterjee, 2005; Martin, 2007; Martin, Haxby, Lalonde, Wiggs, & Ungerleider, 1995; Patterson, Nestor, & Rogers, 2007; Pulvermüller, 2001; Warrington & Shallice, 1984). Different versions of such embodied theories have been proposed (see Meteyard, Cuadrado, Bahrami, & Vigliocco, 2012, for a review). Many current versions of such theories posit additional binding mechanisms or domain-general convergence zones that retrieve and weigh the modality-specific representations (Patterson, Nestor, & Rogers, 2007; Damasio, 1989). Some further claim that words and concepts depend not on primary sensory cortices but rather on secondary sensory areas or even sensory-derived representations in regions that are immediately adjacent to sensory cortices. Nevertheless, what makes all such theories "embodied" is the shared claim that modality-specific aspects of experience are causally relevant to the cognitive and neural instantiation of the meanings of words.

Such theories predict that changes in sensory experience should translate to changes in language comprehension. Some evidence consistent with this idea comes from studies of expertise. For example, hockey players activate different neural systems when listening to descriptions of hockey actions than nonhockey players do (Beilock, Lyons, Mattarella-Micke, Nusbaum, & Small, 2008), as do left- as opposed to right-handed individuals (Willems, Hagoort, & Casasanto, 2010). One interpretation of these results is that action experiences change the representation of action-verb meanings. Theories that predict changes to hockey players' concept of actions due to sensory-motor experience also predict that in blindness representations of concrete language should be substantially different. We would expect changes to the meanings for visual words such as *blue* and *sparkle*, as well as names of concrete objects (e.g., *lion*) and concrete events (e.g., *rolling*).

Contrary to this straightforward prediction, studies of linguistic behavior in blind children and adults reveal that blind individuals have rich "visual" concepts. As noted, Landau and Gleitman (1985) showed that the acquisition of color adjectives and verbs of perception (look and see) is preserved in blind children. For example, a blind five-year-old understood that a car could be yellow but an idea could not. Blind adults also know something about which colors are more similar to each other (e.g., orange to red more than to blue) (Connolly, Gleitman, & Thompson-Schill, 2007; Marmor, 1978; Shepard & Cooper, 1992). We recently found that blind adults' knowledge of visual perception and light emission verbs is indistinguishable from that of the sighted. Like the sighted, blind individuals distinguish between prolonged and brief acts of looking (e.g., *stare* vs. *glance*) and represent light emission verbs along dimensions of intensity (*blaze* vs. *shimmer*) and temporal stability (*blaze* vs. *flash*). Together these studies demonstrate that direct first-person sensory access is not necessary for the acquisition of concrete word meanings. Either first-person sensory experience is not relevant or at the very least equivalent information is redundantly present in nonsensory sources (e.g., language).

These behavioral data nevertheless leave open the possibility that representations of concrete meanings are qualitatively different in format across blind and sighted individuals, albeit behaviorally equivalent. For example, the meaning of *red* might be modality-specific and visual in the sighted, while abstract, linguistic, or represented in some other modality for people who are blind. Studies of the neural basis of word meanings can provide insight into this problem.

A key signature of semantic retrieval is that different categories of concepts depend on partially nonoverlapping neural mechanisms (Hart, Berndt, & Caramazza, 1985; Warrington & Shallice, 1984). The cognitive and neural interpretation of these category-specific differences have long been debated. According to the embodied theories outlined above, such neural differences reflect the degree to which different types of sensory experiences (e.g., visual, auditory, or motor) contribute to different categories of words. For example, retrieving the meanings of motion verbs depends disproportionately on regions within the left posterior temporal lobe that are partially overlapping with or near visual motion perception areas (MT+ and RSTS, right superior temporal sulucus). Such activation is said to reflect retrieval of visual motion features associated with verbs such as *roll* (Kable et al., 2005; Kemmerer, Castillo, Talavage, Patterson, & Wiley, 2008; Martin et al., 1995). Contrary to this interpretation, congenitally blind individuals activate the same posterior temporal regions when making semantic judgments about motion verbs (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012; Noppeney, 2003). Crucially, it is not merely that blind individuals activate the same cortical area, rather the response profile of this region is identical across blind and sighted speakers across multiple different categories of words (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012). As it turns out both in the sighted and blind participants, this region responds more to all verbs than to all nouns, including verbs like *believe* that have no apparent motion associations (Bedny, Caramazza, Grossman, Pascual-Leone, & Saxe, 2008).

Analogous evidence comes from studies of object nouns. Different categories of objects activate distinct parts of the ventral temporal cortices, and it has been suggested that these neural differences reflect the retrieval of modality-specific visual representations of object color and shape (Martin, 2007; Martin et al., 1995). Yet ventral temporal category-specific responses to objects names are also preserved in blindness. Large objects (e.g., *castle*) activate a region of medial ventral temporal cortex that overlaps with the parahippocampal place area (Bi, Wang, & Caramazza, 2016; He et al., 2013). Names of tools activate a medial region in the ventral stream and a region of inferior parietal cortex (Mahon, Anzellotti, Schwarzbach, Zampini, & Caramazza, 2009; Mahon, Schwarzbach, & Caramazza, 2010) and spatial propositions activate the supramarginal gyrus (Struiksma, Noordzij, Neggers, Bosker, & Postma, 2011). Further studies are needed to characterize the details of the information represented within these brain regions in blind individuals. Nevertheless, the few studies that have attempted to do so find similar content across blind and sighted speakers. Peelen, He, Han, Caramazza, and Bi (2014) used multivoxel pattern analysis with concrete object nouns to show similar spatial patterns of activation among blind and sighted individuals.

In sum, all of the behavioral and neural evidence from blindness suggests that dramatic changes to sensory experience leave word meanings unaltered. This does not imply the phenomenological experiences, memories, and knowledge of sighted and blind people do not differ. On the contrary, there is ample evidence that cortical systems that typically store and process sensory visual representations do change quite dramatically in blindness. What is remarkable is that these changes do not carry forward into conceptual systems. Evidence from blindness thus challenges the idea that sensory motor representations play a major role in semantics. Word meaning representations appear to develop independent of modality-specific experiences.

It remains possible that future studies will reveal some differences not only in blind individual's sensory perception but also in semantic knowledge. Indeed such differences seem quite possible when it comes to knowledge of appearance information (e.g., the color differences between *deer* and *kangaroo*). Such differences are of interest and could reveal the unique contribution of vision to information gathering. The available evidence suggests, however, that such differences, if they do exist, are a small change to the overall semantic knowledge about concrete categories. They do not lead to any fundamental change in the neural or cognitive architecture of word meanings or concepts. As such, they are no different from the typical variation in expertise across domains in the population. We therefore make two claims about semantics. First, sensory experience per se plays a rather peripheral role. Abstract aspects of experience are more likely to yield semantic differences, that is, the hockey-related concepts of a hockey player are different not merely because the player has different muscular and sensory motor memory, but because they have much richer knowledge about hockey. Second, the meanings of words are not faithful reflections of our own first-person histories but rather shared cultural constructs. It is this property of words that enables us to communicate with each other, whether we are sighted, blind, musicians, or athletes. This property of words also makes their gross neural signatures robust to idiosyncratic variation in individual experience.

1.2. Frontotemporal Language System in Blindness During language acquisition, blind children have reduced access to extralinguistic information such as object referents and visual social cues (e.g., eyegaze). There is some evidence that this causes subtle and temporary delays in the earliest milestones of language acquisition: blind children are slightly late to produce first words and first multiword utterances (Bigelow, 1987; Landau & Gleitman, 1985; Urwin, 1987). There is also some recent evidence of transient delays in the functional maturation of cortical systems that support language processing. We found that in blind children, the degree of inferior frontal selectivity for language is reduced relative to that for sighted children. Interestingly, no such delay is observed in lateral temporal cortices (Bedny, Richardson, & Saxe, 2015). This finding is consistent with reports that development of prefrontal language regions is sensitive to early deafness (MacSweeney, Waters, Brammer, Woll, & Goswami, 2008) and variability in socioeconomic status (Raizada, Richards, Meltzoff, & Kuhl, 2008).

Importantly, both the neural and behavioral delays described resolve. Older blind children and adults have similar linguistic competence as sighted individuals do (Lane, Kanjlia, Omaki, & Bedny, 2015). We recently found that blind adults actually perform better on comprehension of grammatically complex sentences (Loiotile, Omaki, & Bedny 2019) and multiple studies show superior verbal working memory performance in blindness (Amedi, Raz, Pianka, Malach, & Zohary, 2003; Raz, Striem, Pundak, Orlov, & Zohary, 2007). Paralleling preserved linguistic competence, the functional signatures of the frontotemporal language system are similar in blind and sighted adults. Prefrontal language selectivity increases in blind children between ages 4 and 17, and frontotemporal neural specialization for language is similar in blind and sighted adults (Bedny et al., 2015). In blind individuals, regions of the inferior frontal and lateral temporal cortices are active during sentence processing, word comprehension, reading, and production (Bedny, Pascual-Leone, Dodell-Feder, Fedorenko, & Saxe, 2011; Burton, 2002; Röder, Stock, Bien, Neville, & Rösler, 2002; Watkins et al., 2012). Activity in these frontotemporal areas is sensitive to phonological, lexical, and syntactic information, in the same way as that of sighted adults (e.g., sensitive to the grammatical complexity of sentences) (Bedny et al., 2011; Lane, et al., 2015; Röder et al., 2002). Specialization within the perisylvian language network is also preserved. Like sighted individuals, blind individuals show larger responses to verbs than nouns in the posterior lateral temporal and inferior frontal cortices (Bedny, Caramazza, Pascual-Leone, & Saxe, 2012).

One exception to this general pattern of preservation within the frontotemporal language network is lateralization. During auditory sentence processing, congenitally blind individuals are more likely to have right-lateralized or bilateral frontotemporal responses (Lane et al., 2015, Röder et al., 2002; Röder, Rösler, & Neville, 2000). Importantly, reduced left-lateralization in blindness does not appear to be associated with reduced language performance. An intriguing possibility is that reduced laterality is a neural vestige of early delays in language acquisition (see Bishop, 2013). It has been suggested that the maturational phase of cortex at the time of language acquisition affects lateralization (Bates et al., 1997; Bishop, 2013; Corballis & Morgan, 2010; Locke, 1997). If so, then delayed acquisition early in life could reduce the likelihood of left-lateralization in adulthood.

1.3. Visual Cortex Recruited for Language Processing in Blindness: Insights into Function Structure Mapping The biggest change to the neurobiology of language in blindness is not within the perisylvian language network but outside it. In blindness, parts of the so-called visual cortices appear to be incorporated into the language network. Visual cortices are active when blind individuals listen to spoken sentences, generate verbs from heard nouns, retrieve lists of words from long-term memory, and read Braille (Amedi et al., 2003; Bedny et al., 2011; Burton, 2002; Burton et al., 2002; Röder et al., 2002; Watkins et al., 2012). Language responses are observed in lateral and ventral occipital cortices, as well as V1 (Bedny et al., 2011). Visual cortex responses to spoken language and Braille are part of a broader phenomenon known as cross-modal plasticity, where regions of the brain that normally respond primarily to visual input come to respond to auditory and tactile stimuli (Pascual-Leone, Amedi, Fregni, & Merabet, 2005). However, visual cortex responses to language go beyond sensory responses to sound or touch. Visual cortices respond more to auditory and tactile language tasks than to nonlinguistic auditory and tactile control tasks that are matched on low-level sensory and working memory demands. Responses to language are anatomically separable from responses to nonlinguistic auditory tasks within visual cortices (Kanjlia, Lane, Feigenson, & Bedny, 2016). Most importantly, visual cortices are sensitive to the grammatical and lexical properties of linguistic stimuli. Visual cortex activity scales with amount of sentence-level structure and lexical information. As in frontotemporal language areas, highest responses are observed for sentence stimuli, followed by Jabberwocky and lists of words, and lowest to lists of nonwords (Bedny et al., 2011). Among sentences, larger responses are observed for those that are grammatically complex (Lane et al., 2015; Röder et al., 2002). Visual cortices are also sensitive to subtle semantic manipulations. For example, the N400 component has a more posterior distribution in blind as compared to sighted individuals (Röder et al., 2000). The functional profile of language-responsive visual areas is thus similar in several important respects to that of frontotemporal language regions (see figure 37.1).

There is also some evidence that in blindness visual cortex activity is functionally relevant to some linguistic tasks. Transiently disrupting visual cortex activity with transcranial magnetic stimulation causes semantic verb generation errors in blind but not sighted participants (Amedi, Floel, Knecht, Zohary, & Cohen, 2004). Transcranial magnetic stimulation to the occipital pole impairs reading Braille words and letters and abolishes repetition priming (Cohen et al., 1997; Kupers et al., 2007). Across blind individuals, a greater amount of visual cortex activity correlates with superior linguistic performance (Amedi et al., 2003; Lane et al., 2015).

In blindness, language-responsive visual cortices also become functionally connected with frontotemporal language networks. In resting state data, correlations between frontoparietal networks are higher in blind than in sighted individuals (Bedny et al., 2011; Deen, Saxe, & Bedny, 2015; Watkins et al., 2012). Those areas of visual cortex that are active during language tasks are also more correlated with prefrontal language areas. By contrast, areas of visual cortex that are involved in nonlinguistic processing correlate with different regions of prefrontal and parietal cortices (Kanjlia et al., 2016). Finally, in blind individuals, the laterality of occipital language responses follows the laterality of frontotemporal cortices. Blind individuals that have right-lateralized responses to spoken language in frontotemporal cortices also show larger responses on the

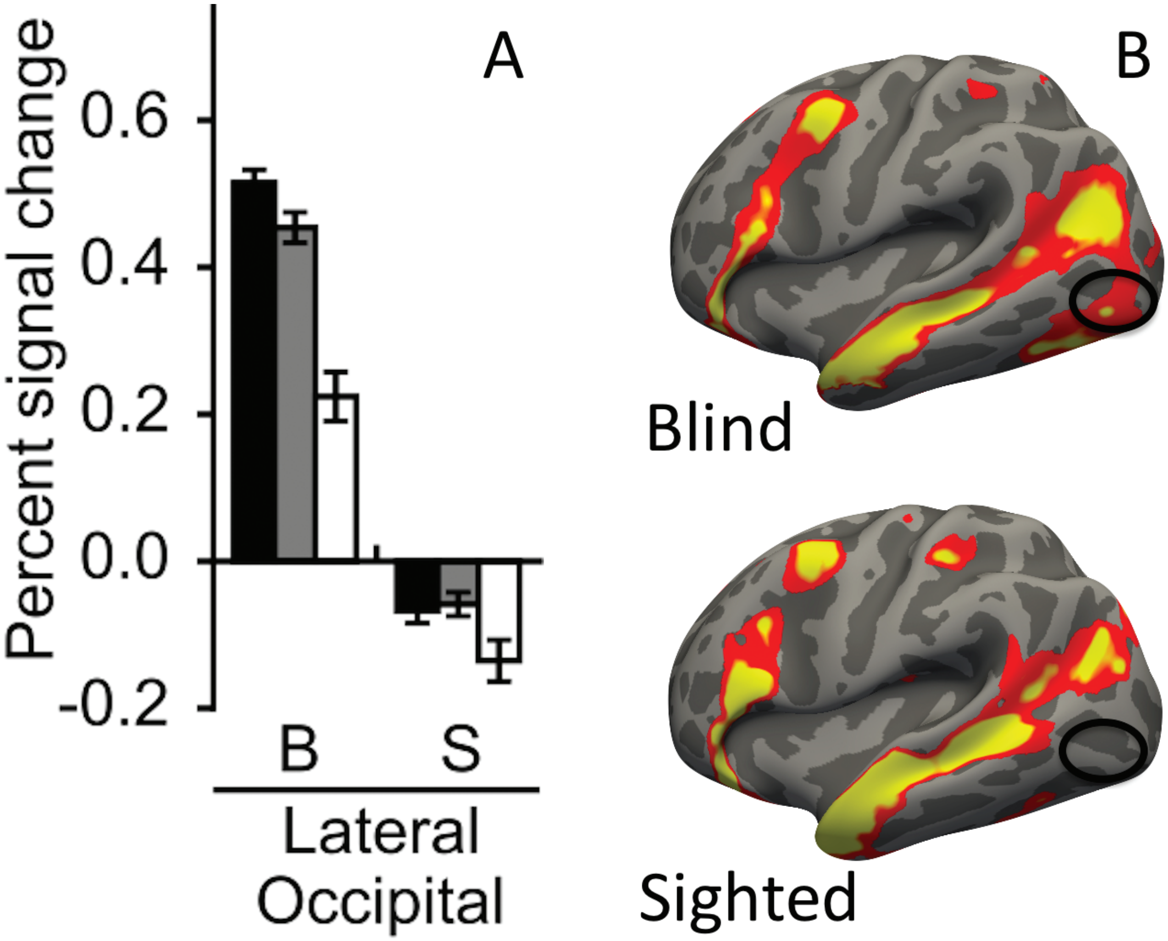

Figure 37.1 (A) Visual cortex responses to spoken sentences with syntactic movement (black) and without syntactic movement (light gray) as well as matched lists of nonwords (white) in sighted (S) and blind (B) groups. (B) Whole-brain responses to sentences (average of +Move and −Move) greater than nonword lists in blind and sighted.

right in occipital cortices (Lane et al., 2015). Together, the available evidence suggests that parts of visual cortices become functionally incorporated into the language network in blindness.

How and when does language colonize the visual cortices of blind individuals? We hypothesize that in the absence of bottom-up visual input, signals from higher cognitive networks in frontoparietal and temporal cortices dominate activity in the visual system during development (Bedny et al., 2011; Deen et al., 2015; Watkins et al., 2012). In sighted individuals, these systems typically modulate activity in the visual cortices based on goals, attention, and conceptual content. In blindness, they incorporate the visual system into higher cognitive networks. There is evidence that language-related plasticity in the occipital cortex occurs early in life and follows a sensitive period. In blind children, occipital responses to spoken language are observed by four years of age and do not require Braille literacy (Bedny et al., 2015). Selective responses to language in the visual system do not appear to be present in adult-onset blind individuals, even after many years of blindness (Bedny, Pascual-Leone, Dravida, & Saxe, 2012; Burton, 2002).

The striking neural reorganization of the language system in blindness has implications for theories of language neurobiology. Frontotemporal networks are involved in language processing across variation in experience, including blindness and deafness, and therefore may well be predisposed for language processing. However, evidence from blindness also suggests that development of the language system is not well described as the gradual maturation of a preordained set of frontotemporal areas. Despite its usual consistency, the neural phenotype of language emerges as a result of a dynamic process. When other brain regions are available at the right time (i.e., not already doing something else), they can be incorporated into the language system. Studies of blindness further suggest that regions that did not evolve for language can nevertheless participate in language processing. The neural phenotype of language is influenced by the state of other neurocognitive systems during development (e.g. the visual system).

1.4. NEURAL BASIS OF BRAILLE-READING IN BLINDNESS: INSIGHTS INTO THE NEUROBIOLOGY OF READING

The blind community uses a tactile reading system called Braille. Like visual reading systems, Braille translates spoken language into permanent written record. As such it enables blind readers to do all of the things that print makes possible for the sighted: to take notes, to scan text and reread important passages, to label and organize, to write down and pore over mathematical equations. Yet Braille is also different from visual print in interesting respects. Most obviously Braille is tactile, while print is visual. Each Braille cell is composed of a two-row-by-three-column grid of raised dots that are perceived by passing the palm of the finger over the dots. Each English Braille letter corresponds to a letter of the print English alphabet. For example, the Braille character for the letter K is <⠅> and for the letter T is <⠞>. Proficient Braille readers of English use a contracted form of Braille in which single characters and character combinations stand for larger units, such as frequent letter combinations and words. For example, the single character K <⠅> also stands for the whole word "knowledge." There are also single character Braille contractions for commonly used bound morphemes such as "ing" and "ed." The most commonly used form of English Braille text is a combination of contractions and letter-by-letter spelling.

There are some differences in the way Braille and print are recognized. A key challenge in the recognition of visual letters and words is the invariance problem. Sighted readers must recognize different instances of A a *a* as the same, while remaining sensitive to the subtle shape difference that distinguishes *e* from *c*. By contrast, Braille has no font variation. Braille dots are of a standardized size and spacing and even capital letters are indicated by a preceding dot and not by changing the character itself. Proficient Braille readers are believed to recognize letters through shear patterns on the finger (Millar, 2008). Like print readers, proficient readers of Braille represent orthographic sublexical structure beyond single letters (Fischer-Baum & Englebretson, 2016). However, while expert sighted print readers read words in parallel and do not show word-length effects on reading speed (Adelman, Marquis, & Sabatos-DeVito, 2010), even for highly skilled Braille readers, reading speed per word scales with letter length because the finger must pass in sequence over each character (Bertelson, Mousty, & Radeau, 1992; Daneman, 1988; Legge, Madison, & Mansfield, 1999). Thus, reading by touch has some consequences for the cognitive properties of orthography. Does it also influence the neurobiology of reading?

Sighted print readers recruit a consistent network of areas during reading. A key node this network is the so-called *visual word form area* (VWFA), located in the ventral occipitotemporal cortex. The VWFA is situated among object-selective regions such as the fusiform face area and the parahippocampal place area (Epstein & Kanwisher, 1998; Kanwisher, McDermott, & Chun, 1997). According to one prominent hypothesis, the VWFA supports the recognition of letter and word forms (Dehaene & Cohen, 2007, 2011; Tsapkini & Rapp, 2010; Vinckier et al., 2007; see Price & Devlin, 2011, for an alternative account). The VWFA is of particular theoretical importance within cognitive neuroscience because it is the only category-specific brain region that is known to acquire its function as a result of learning (Dehaene et al., 2010).

Different nonmutually exclusive hypotheses have been proposed regarding the causal mechanisms that lead this particular part of the ventral occipital temporal cortex to specialize for reading (Dehaene & Cohen, 2007, 2011; Price & Devlin, 2011). One possibility is that the VWFA develops at the nexus of visual and linguistic inputs, because reading involves extracting linguistic content from visual symbols (Dehaene & Dehaene-Lambertz, 2016; Saygin et al., 2016; Kravitz, Saleem, Baker, Ungerleider, & Mishkin, 2013). Alternatively, it has been suggested that the VWFA has an intrinsic preference for representing the types of forms found in written alphabets (e.g., line junctions) (Szwed, Cohen, Qiao, & Dehaene, 2009). At face value, all of these hypotheses predict that the VWFA should not become reading-selective in blindness. Braille has no line junction and does not require connecting vision and language.

Surprisingly, there is evidence that congenitally blind readers of Braille activate the VWFA during reading (Burton et al., 2002; Reich, Szwed, Cohen, & Amedi, 2011; Sadato et al., 1996). The occipitotemporal cortex responds more when blind individuals read Braille words than when they pass their fingers over strings of raised dots without linguistic content and the response to Braille words is larger than to spoken words (Reich et al., 2011). A VWFA-like response is also observed when blind subjects listen to letters through a sensory substitution device (Striem-Amit, Cohen, Dehaene, & Amedi, 2012). Remarkably, the peak response to Braille words within the occipitotemporal cortex is located in the same location as the peak response to printed words in sighted readers (Reich et al., 2011). Based on this finding, it has been suggested that like sighted print readers, blind Braille readers develop a VWFA reading-selective region in the ventral stream. In an effort to account for the

Braille findings, it was recently suggested that the VWFA is suited for processing shape, independent of modality (Hannagan, Amedi, Cohen, Dehaene-Lambertz, & Dehaene, 2015). This, along with connectivity to language networks, is said to account for both print and Braille reading-specialization in this part of the brain (Hannagan et al., 2015). It remains unclear, however, how well such an account squares with either the nature of Braille reading, which may depend on shear patterns more so than shape recognition, or the function of the occipitotemporal cortex, which is involved in view-invariant object recognition, rather than shape extraction per se (DiCarlo, Zoccolan, & Rust, 2012).

We recently tested an alternative prediction: Since the VWFA has strong anatomical connectivity to the frontotemporal language network prior to literacy, we predicted that in the absence of visual input, this region would become incorporated into the frontotemporal language network. Consistent with this possibility, we found that in individual blind Braille readers, the same occipitotemporal area that responds to Braille also responds to the grammatical complexity of spoken sentences (Kim, Kanjlia, Merabet, Bedny, 2017). By contrast, in sighted print readers, reading-responsive VWFA was insensitive to grammatical complexity. This observation is consistent with evidence that large parts of the visual system become incorporated into language networks in blindness. Indeed, the VWFA may serve as a gateway region for the language to enter the visual system. These data suggest that in the sighted, the VWFA develops where it does, in part because print is read through the visual modality. Thus, the neurobiology of tactile reading is at least in part different from that of reading visual print. Whether Braille depends on other, reading-specific neural mechanisms, or whether VWFA-like category specificity is unique to the visual system, remains to be determined.

The case of the VWFA in blindness is a powerful illustration that activating the same region during language tasks in two different populations does not necessary imply that the region is performing the same computations. Determining whether a region is functionally similar requires measuring its response across a range of cognitive manipulations. At the end of the chapter, we return to this issue and the flexibility of the mind to brain mapping more generally.

2. The Cognitive and Neural Basis of Language in Individuals Who Are Deaf

Children born severely or profoundly deaf offer unique insights into the neurobiology of language that cannot be gained from working with hearing people alone. First, we can ask whether the neurobiology of language changes when language is not auditory. Only 5% to 10% of deaf children are born to deaf parents and are therefore likely to be exposed to a fully accessible native language—a sign language. Sign languages are natural human languages that are perceived in the visual modality alone. Examining the neural systems that support sign language processing is interesting in its own right. However, sign languages are also a powerful tool with which to test constraints and plasticity of the language system. Determining commonalities between how signed and spoken languages are processed allows identification of language processes and language networks that are recruited *independent of modality*. First, in section 2.1, we will therefore review the current knowledge about the neural systems supporting language in deaf native signers and the insights that have been gained about plasticity of the language system from this group. Second, in section 2.2, we consider the impact of absence of auditory input on plasticity of sensory cortices and specifically whether auditory regions play a role in linguistic or nonlinguistic processing in those born deaf.

Finally, in section 2.3, we discuss the impact of impoverished early access to language. As many as 90% to 95% of deaf children are born to hearing parents. These children do not have early access to sign language. Furthermore, as is the case for all deaf children, they have impoverished access to the auditory component of *spoken language*. Unlike the subtle consequences of impoverished access to visual aspects of speech for blind children, the impact of deafness on spoken language processing can be severe. There have been tremendous improvements in recent years in digital hearing aids and in cochlear implants. However, there are large individual differences in the extent to which deaf children's spoken language benefits from these forms of amplification. There is a broad continuum from those who learn the spoken language around them well to those who do not. Hearing parents may or may not decide to learn a sign language. Furthermore, the age at which a deaf child of hearing parents encounters a signed language in an educational or social environment can vary greatly. Thus deaf children of hearing parents have extremely heterogeneous early language experiences. Here, we consider sign language processing in these individuals who have learned a sign language late, building on impoverished early access to a spoken language. These studies provide insights into the consequences of delayed access to language for the development of the language system in the brain. Research with deaf individuals with different language histories provides unique insights into the environmental constraints that influence the development of the language system.

2.1. USING SIGN LANGUAGES AS A TOOL TO IDENTIFY MODALITY-INDEPENDENT LANGUAGE NETWORKS: STUDIES WITH NATIVE SIGNERS

One of the goals within the field of the neurobiology of language is to identify the neural systems supporting higher order language processing *regardless of modality*. Studies with deaf signers provide a unique opportunity to answer this question because it is only in this population that we can rule out activation of auditorily derived representations (see MacSweeney, Capek, Campbell, & Woll, 2008, for review). Sign languages arise wherever Deaf[1] communities come together, and they differ across countries (e.g., American Sign Language [ASL], British Sign Language [BSL]). Children born to signing parents grow up to be native signers. Studies have clearly shown that deaf children learning a sign language from deaf parents show the same developmental milestones in their language acquisition as hearing children learning a spoken language do (Morgan & Woll, 2002). By identifying regions of overlapping activation during tasks performed in signed and spoken languages, we can then propose the testable hypothesis that the linguistic computations and processes being carried out in these regions are truly modality-independent.

As in spoken language users, lesion studies in signers overwhelmingly indicate that left hemisphere damage leads to severely impaired language processing (aphasia) while right hemisphere damage does not (e.g., Klima & Bellugi, 1979; Marshall, Atkinson, Woll, & Thacker, 2005). Neuroimaging studies also indicate a critical role for the left hemisphere in sign language processing. Despite differences in the articulators used, both covert and overt sign production rely predominantly on the left hemisphere (Gutierrez-Sigut et al., 2015; Gutierrez-Sigut, Payne, & MacSweeney, 2016) and specifically on the left inferior frontal gyrus, as does speech production. Critically, whether the right or left hand is used to produce signs has little impact on the recruitment of this left-lateralized network (Corina, San Jose-Robertson, Guillemin, High, & Braun, 2003). Furthermore, although sign languages are well suited to represent the visual features of referents (i.e., to be iconic) this appears to have little direct impact on the neural systems supporting sign language production (Emmorey et al., 2004). Finally, hearing people who have grown up as bilinguals, having learned a signed language from their deaf parents and a spoken language from the broader hearing community, engage the same left frontoparietal network during both sign and speech production (Emmorey, McCullough, Mehta, & Grabowski, 2014).

With regard to language perception, we used conjunction analysis across different groups, to identify the regions involved in processing audiovisual speech in hearing people and BSL in deaf native signers (MacSweeney, Woll, Campbell, McGuire et al., 2002). We identified a primarily left frontotemporal network involving the superior temporal gyrus and sulcus as well as the left inferior frontal gyrus, extending into the prefrontal gyrus, that was involved in processing both sign and speech (see also Sakai, Tatsuno, Suzuki, Kimura, & Ichida, 2005). Numerous studies of sign language perception alone have also identified a primarily left-lateralized frontotemporal network involved in sign language perception when contrasted with non-sense movement (MacSweeney et al., 2004), gesture (Newman, Supalla, Fernandez, Newport, & Bavelier, 2015), or transitive actions (Corina et al., 2007). Together these studies suggest that the classic left-lateralized perisylvian network is resilient to change in the sensory modality of language.

In summary, in native users, signed and spoken languages engage very similar left-perisylvian networks for perception and production of sign and speech. This similarity appears to extend to metalinguistic judgments regarding the phonological structure of sign and speech, which have been shown to engage a left frontoparietal network (MacSweeney, Waters, et al., 2008).

The fact that signed languages, like spoken languages, are predominantly processed in the left hemisphere is an important finding that should be taken into account in theories of hemispheric lateralization of language processing. It has been argued by some that the left hemisphere shows a predisposition to process certain temporal aspects of auditory information that are critical to speech processing (see McGettigan & Scott, 2012; Scott & McGettigan, 2013, for reviews and comment). The inference is then made, explicitly or implicitly, that this is the cause of left hemisphere lateralization for language processing. That sign languages are also predominantly processed in the left hemisphere poses a problem for any purely auditory-based account. Although the finding with sign languages does not answer *why* language is predominantly left-lateralized in most people, it should prompt the field to generate hypotheses that are modality-independent and can account for left hemisphere lateralization of both sign and speech.

2.2. BEYOND COMMONALITIES: MODALITY-/LANGUAGE-DEPENDENT DIFFERENCES BETWEEN SIGNED AND SPOKEN LANGUAGE PROCESSING NETWORKS

Although the overlap between the networks supporting sign and speech processing is extensive, there are some differences. Not surprisingly, direct contrasts have highlighted differences reflecting early sensory processing. Audiovisual speech elicits greater activation than sign language in auditory processing regions in superior temporal cortices. In contrast, sign languages elicit greater activation than audiovisual speech does, in biological motion processing regions of the posterior middle temporal gyri, bilaterally (Emmorey, McCullough, & Weisberg, 2014; MacSweeney, Woll, Campbell, McGuire, et al., 2002; Söderfeldt et al., 1997). Above and beyond sensory demands of visual motion processing, the posterior middle temporal gyri also appear to be recruited when visual movement is specifically linguistic, such as in the perception of classifiers representing movement of a referent (MacSweeney, Woll, Campbell, Calvert, et al., 2002; McCullough, Saygin, Korpics, & Emmorey, 2012). This finding is in line with the proposal from the blindness literature that regions primarily involved in visual processing can also be engaged in linguistic processing.

There is also growing evidence suggesting that the left inferior and superior parietal lobules appear to play a greater role in sign language processing than spoken language processing (see MacSweeney, Capek, et al., 2008, for review). Greater activation has been reported in the inferior and superior parietal lobules during sign language compared to spoken language production (Emmorey, Mehta, & Grabowski, 2007) and during short-term memory tasks for sign compared to speech (e.g., Bavelier, 2008). It has been suggested that the left superior parietal lobule may be involved in motor rehearsal during memory tasks (Buchsbaum et al., 2005) and/or in proprioceptive monitoring during sign production (Emmorey, McCullough, & Weisberg, 2016). Online monitoring of language production is, by necessity, different for sign and speech. The feedback received by a hearing person during their own speech production is almost equivalent to that heard by their interlocutor. In contrast, a signer's perception of their own hands while signing is very different to that perceived by their communication partner. There are likely to be important implications of this difference between languages in the online feedback loop for the neural systems supporting language production. The current state of knowledge suggests that the superior parietal lobe plays an important role in this monitoring for sign production (see Emmorey et al., 2016).

In contrast to the superior parietal lobule, the left supramarginal gyrus in the inferior parietal lobule appears to play a particularly important role in phonological processing of sign language. Corina et al. (1999) found that direct stimulation to the left supramarginal gyrus elicited errors in selecting appropriate handshapes and movements during sign production. Furthermore, phonological similarity judgments for signs elicit greater activation in the superior portion of the left supramarginal gyrus, extending into the superior parietal lobule, than phonological similarity judgments for speech (MacSweeney, Waters, et al., 2008). The inferior parietal lobule is reliably recruited during the imitation and production of hand configurations or movements and also when such stimuli are passively viewed or imagined (Rizzolatti & Craighero, 2004). The need to attend to the location and configuration of the hands in space in any task involving sign language processing could explain the enhanced involvement of this region. The focus on these features during a sign language phonological task is likely to increase these processing demands further.

A critical question regarding the influence of sensory experience on language processing in deafness that relates to the blindness literature is whether deaf individuals additionally recruit auditory cortices during sign language processing, as blind individuals recruit visual cortices for spoken and written language. Unlike in the case of blindness, the evidence is mixed regarding whether sign language, or any other visual stimuli, activates the primary auditory cortices (see Cardin et al., 2016; Scott, Karns, Dow, Stevens, & Neville, 2014). However, there are now numerous reports of increased activation in secondary auditory and auditory association cortices in the superior temporal cortex (STC) in deaf individuals that is greater than that in hearing individuals during sign language perception, even when sign language experience is matched across deaf and hearing groups (Capek et al., 2010; MacSweeney et al., 2004). In addition to the influence of deafness, however, there is a further influence of sign language experience. For example, the left STC has been shown to be more active in deaf signers than in *deaf nonsigners* during sign language perception (Cardin et al., 2013). It has also been shown that responses in left STC in deaf signers are larger for sign language stimuli than for other nonlinguistic visual stimuli (e.g., MacSweeney et al., 2004).

Unlike in the case of blindness, it is not clear whether responses to sign language in auditory cortices of deaf signers are language-specific. Studies in deaf cats suggest that portions of the STC, that are typically auditory cortex in hearing cats, are recruited for visuospatial tasks. For example, Lomber, Meredith, & Kral (2010) demonstrated that regions involved in auditory localization in hearing cats are recruited during visual localization in deaf cats. It is therefore possible that larger auditory responses to sign than nonsign stimuli in signers are partially due to the visual complexity of the signed input and subsequent increased visual processing demands. There is also evidence that portions of the posterior STC, that typically participate in higher order auditory processing, are recruited by deaf individuals in visual tasks that do not involve language, such as a visual rhythm discrimination task (Bola et al., 2017) and a visuospatial working memory (Ding et al., 2015). Ding et al. (2015) found that auditory cortex activity is active not only when complex visual stimuli are displayed, but also during the maintenance phase of a visual working memory task, during which only a static crosshair was visible on the screen. Furthermore, the effects were load-dependent, with larger responses when more information was maintained in working memory during the delay. Ding et al. (2015) also reported correlations between amplitude of response in STG and task performance in deaf but not hearing participants. They argue therefore that auditory association cortices play an important role in visuospatial working memory in those born deaf (see MacSweeney & Cardin, 2015, for commentary). Furthermore, in a recent study, we find that these STC regions are particularly involved in sign language tasks in which the visual working memory and visual imagery demands are high—a picture-based BSL phonological judgment task (Twomey, Waters, Price, Evans, & MacSweeney, 2017). We hypothesize that plasticity within the left STC is most likely an interaction between deafness and sign language knowledge. As discussed in section 2.3, this interaction is likely to be further influenced by age of sign language acquisition and sign language proficiency (MacSweeney, Waters, et al., 2008; Mayberry, Chen, Witcher, & Klein, 2011).

Future studies are needed to determine whether the linguistic and nonlinguistic cognitive processes recruit distinct portions of auditory association cortices in deaf individuals, as they appear to do in the visual cortices of blind adults. Or instead whether activity during sign language tasks is related to nonlinguistic cognitive functions. We would expect that some general principles of plasticity in sensory loss apply across deafness and blindness. For example, as reviewed, in both deaf and blind humans, there is evidence that sensory cortices are recruited for higher cognitive functions (e.g., language and working memory in deafness). However, the specific patterns of functional reorganization in deafness and blindness will depend in part on the connectivity patterns of auditory and visual cortices, respectively. Furthermore, other aspects of experience that differ among deaf as opposed to blind individuals may lead to differences in cortical repurposing. Language-related plasticity in sensory cortices could be less likely in cases of reduced language experience early in life (e.g., deaf individuals who lack access to spoken and signed language). Uncovering the similarities and differences between patterns of functional reorganization in deafness and blindness is an important future avenue for understanding plasticity mechanisms.

2.3. CONSEQUENCES OF IMPOVERISHED ACCESS TO EARLY LANGUAGE: EVIDENCE FROM DEAF LATE LEARNERS OF A SIGN LANGUAGE

The vast majority of deaf children are not exposed to a sign language from birth. They are born to hearing parents, who may or may not decide to learn a sign language. Often these children are exposed to a sign language at school or on leaving school, at an age past the point that would normally be considered the critical period for language development (see Mayberry & Lock, 2003; Mayberry, Lock, & Kazmi, 2002). These children have extremely heterogeneous language experiences and can provide unique insights into the influence of timing on the language system.

The impact of late sign language acquisition on sign language processing has been investigated extensively at the behavioral level. Studies have reported poorer syntactic (Morford, 2003; Johnson & Newport, 1989) and phonological (Mayberry & Fischer, 1989) performance by this group (see Mayberry, 2007, for review). The impact of late sign language acquisition on the neural systems supporting language has yet to be fully explored. Newman, Bavelier, Corina, Jezzard, and Neville (2002) reported greater right angular gyrus activation in hearing native than hearing non-native signers while watching ASL. Newman et al. (2002) argued that this reflected the spatial-linguistic processing requirements of a sign language. However, hearing late learners of sign have already successfully acquired a first (spoken) language; deaf late learners of a sign language have not. When a deaf person learns a sign language later in life, it is typically built on impoverished early access to a spoken language. That is, it cannot always be considered a second language, as is clearly the case for hearing late learners of a signed language. As a consequence, it is unclear to what extent findings from hearing late learners of sign can be extrapolated to late sign language learners who are deaf.

To date only a handful of studies have examined the impact of late sign language acquisition on the neural systems supporting sign language processing in those born deaf. MacSweeney, Waters, et al. (2008) tested deaf native and non-native signers. The non-native signers had learned BSL between the ages of 4 and 21 years and importantly the deaf native and non-native signers did not differ significantly on measures of English proficiency (reading, speech reading [lipreading], and English vocabulary). Participants were asked to make phonological judgments about signs (same location?) and speech (rhyme?) in response to picture pairs. We found increased activation in the left inferior frontal gyrus in the non-native compared to in the native signers (MacSweeney, Waters, et al., 2008). Critically, this was the case not only for BSL, which was learned late, but also for English, of which both groups had similar experience and had also shown equal levels of performance on English online (rhyme task) and offline tasks. The deaf late learners of sign language, needed to call on left frontal cortices to a greater extent for both sign and speech tasks, even when their performance on the tasks was equivalent to that of the native signers. Such recruitment might reflect more effortful processing. One interpretation of these data, therefore, is that having a robust first language (here a signed language) provides a solid basis on which to learn a second language (here English). These data support behavioral data underlining the critical importance of early language experience, in any modality, for later language development (see Mayberry, 2007, for review).

Mayberry et al. (2011) also investigated the influence of age of sign language acquisition by testing participants whose age of onset of ASL acquisition ranged from birth to 14 years old. Participants were tested on phonemic and grammatical judgments in response to ASL sentences. In contrast to the findings of MacSweeney, Waters, et al. (2008), Mayberry et al. (2011) found *decreased* recruitment of left frontal regions in late compared to early signers. Late signers, in contrast, showed enhanced recruitment of occipital cortices. There were a number of stimulus (ASL video/static pictures) and task differences between the MacSweeney, Waters, et al. (2008) and Mayberry et al. (2011) studies that may have contributed to the different pattern of results. One key difference appears to be language skills of those tested. In the MacSweeney, Waters, et al. (2008) study, the deaf late signers had a relatively high level of English, as measured by reading and speech reading tests. In contrast, the deaf late learners of ASL tested by Mayberry et al. (2011, p. 18) rated their spoken language communication skills as not able to "understand spoken language sufficiently for functional communication." The discrepancy in language skills of the participants tested could explain the different patterns observed across studies. Future studies should examine how proficiency and task demands interact with age-of-language acquisition in predicting inferior frontal recruitment during sign language processing.

Whatever the cause for the difference in results between these two studies, it is clear that the left inferior frontal cortices are sensitive (in one direction or another) to the age of sign language acquisition and/or to the consequences of impoverished first language input. These findings align well with data from blind children reviewed in section 1, suggesting that the left frontal cortices are sensitive to early language experience (Bedny et al., 2011). Future studies are needed to dissociate those effects that are related to age of sign language exposure and those related to sign language proficiency.

Mayberry and colleagues (Ramirez et al., 2014; Ferjan Ramirez et al., 2016) have also had the opportunity to examine ASL processing in two deaf adolescents who moved to the United States from Central America and who are described as having no first language (spoken language) before encountering ASL at the age of 14 years (Ramirez et al., 2014). Critically, only in cases of extreme deprivation could such cases be argued to be found in the hearing population. These case studies therefore offer unique insights into the consequences of severe early language deprivation.

Using magnetoencephalography, Ferjan Ramirez et al. (2016) showed that even after three years of exposure to ASL, the teenager's responses to single signs were highly atypical, engaging right dorsal frontoparietal regions, rather than the typical left-lateralized frontotemporal network. When followed up just over a year later, these cases still showed atypical neural processing for less familiar signs. However, interestingly, for more familiar signs, they started to show activation in the typical left perisylvian network. Ferjan Ramirez et al. (2016) argued that even though timing of language experience inevitably affects the organization of neural language processing, language representation in the human brain can continue to evolve with experience, even into adolescence. Continuing to study the language development of these individuals and testing them on more complex language input will provide unique insights into the consequences of extremely impoverished early language experience on the neural bases of language processing.

3. Conclusion

Studies of blindness and deafness highlight that language is an abstract system of phonological, semantic, and syntactic representations that can be realized as speech sounds, combinations of hand shapes and movements, printed words or tactile Braille. Even in the absence of optimal sensory access, children acquire language by hook or by crook, as long as linguistic information is available to them in some format. Blind children acquire language without seeing colors, without pointing, eye-gaze, or the sight of moving lips. Children who are born deaf can acquire a visuospatial signed language, provided they have access to the language early in life. Like the behavioral phenotype of language, the neuroanatomical layout and functional profile of the perisylvian language system is robust to dramatic changes in sensory experience. This suggests that whatever predisposes perisylvian systems to take on language processing, these predispositions are related to the computational demands of language as a system of thought and communication and not to a particular sensory instantiation.

By contrast to sensory change per se, reduced or delayed access to language in childhood impacts language competence and changes language neurobiology. In blindness, delays to language acquisition are subtle and do not affect ultimate language competence, but nevertheless, may modify the time course of functional maturation in prefrontal language areas during childhood and reduce the left-lateralization of frontotemporal language systems. In deaf children of hearing parents, language access can be severely reduced. Impoverished exposure to signed and spoken language early in life can have significant consequences for later language proficiency and affects the neural systems supporting language. Reports of extreme case studies with deaf individuals who had no access to sign language, and limited spoken language exposure, during childhood suggest that severe delays in first language acquisition can lead to large-scale and long-term functional changes in frontotemporal language networks (e.g., Ferjan Ramirez et al., 2016). By contrast, early access to a sign language leads to a preserved frontotemporal system and provides robust foundations for later spoken language processing. An interesting question is whether, in the absence of access to language early in life, frontotemporal systems merely diminish in their language capabilities or whether in the absence of language experience the perisylvian cortices are colonized by nonlinguistic functions, akin to the colonization of sensory systems of deaf and blind individuals by nonsensory functions. Such colonization, if it occurs, could affect the capacity of perisylvian cortices to support language.

Conversely, an important insight from studies of blindness is that there is more than one neural solution to the computational problem of language. Blind adults perform the same or better on language tasks as compared to matched groups of sighted individuals. Nevertheless, blind individuals show reduced left-lateralization of frontotemporal language areas and recruit "visual cortices" during language processing. It is therefore an oversimplification to consider the infant brain as a miniature version of the adult language system (Bates et al., 1997; Karmiloff & Karmiloff-Smith, 2009). Rather the language-ready brain contains predispositions, which are then amplified and transformed during acquisition. As a result there is potential for nonverbal experience and the maturation of other brain systems to influence the neural basis of language.

Studies of blindness and deafness furthermore demonstrate that cortical location and cognitive computation are not inextricably linked at birth. When experience is dramatically changed, brain regions can assume drastically different functional profiles (e.g., visual cortex in blindness). This could also be true on a smaller scale across speakers of different languages. For example, computing sentence structure depends to different degrees on word order as opposed to morphology depending on the language. Perisylvian cortices participate in sentence processing across speakers of different languages but the precise information they represent is different. What are the limits on such cortical flexibility? Studies with adult-onset blind individuals suggest that once the cognitive role of a cortical area is established during development, there are limits on how much it can change. For example, even after years of blindness, the visual cortices are limited in their ability to take on linguistic functions in those who become blind later in life (e.g., Bedny, Pascual-Leone, Dravida, et al., 2012). On the other hand, smaller scale cognitive reorganization is possible in adult learning (e.g., Merzenich et al., 1984). Such flexibility may also exist within an individual across contexts. For example, it has been suggested that the same cortical region could contribute to syntactic or semantic processing depending on the other areas and networks engaged during a given language task (Hagoort, 2014). We might say then that a cortical region has a cognitive range that depends on its connectivity and microcircuitry. At birth this range is wide and discontinuous, encompassing cognitively unrelated functions. With experience and age the range narrows and becomes more cognitively homogenous, but nevertheless it does not boil down to a single cognitive operation.

Many further opportunities remain open for insights into the neurobiology of language from blindness and deafness and recent methodological advances continue to open new avenues of inquiry. When individuals with different developmental histories activate the same brain regions (e.g., the VWFA or perisylvian cortices) during similar tasks, are the same representations being processed in the same way for both groups (Amedi, Hofstetter, Maidenbaum, & Heimler, 2017)? If not, what are the differences? Conversely, when different cortical areas are activated by groups with different developmental histories, do different cortical areas nevertheless perform the same computations across groups? An important goal for future research is to use multivariate approaches to examine in greater detail the linguistic representations and computations of cortical systems involved in language processing across populations. This would provide insight into the degree to which the information represented and processed within language-responsive cortical systems is similar across blind, sighted, hearing, and deaf individuals.

There is also a need for research into the neurobiology of language in blind and deaf *children*. Only a single imaging study has looked at the neurobiology of language development in blind children, and there are no published studies with deaf children using techniques with high spatial resolution such as functional MRI. Examining the developing neural system supporting language, rather than only the end state, will provide unique insights into how language and sensory experience influences development of language networks in the human brain. These, and many other open questions, remain to be answered. Studying language in individuals with diverse developmental experiences continues to be an important source of insight into human language.

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NOTE

1. In line with convention, “Deaf” is used when referring to those who use a signed language as their primary language.

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