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Sensitive periods in cortical specialization for language: insights from studies with Deaf and blind individuals

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Studies with Deaf and blind individuals demonstrate that linguistic and sensory experiences during sensitive periods have potent effects on neurocognitive basis of language. Native users of sign and spoken languages recruit similar fronto-temporal systems during language processing. By contrast, delays in sign language access impact proficiency and the neural basis of language. Analogously, early but not late-onset blindness modifies the neural basis of language. People born blind recruit 'visual' areas during language processing, show reduced left-lateralization of language and enhanced performance on some language tasks. Sensitive period plasticity in and outside fronto-temporal language systems shapes the neural basis of language.

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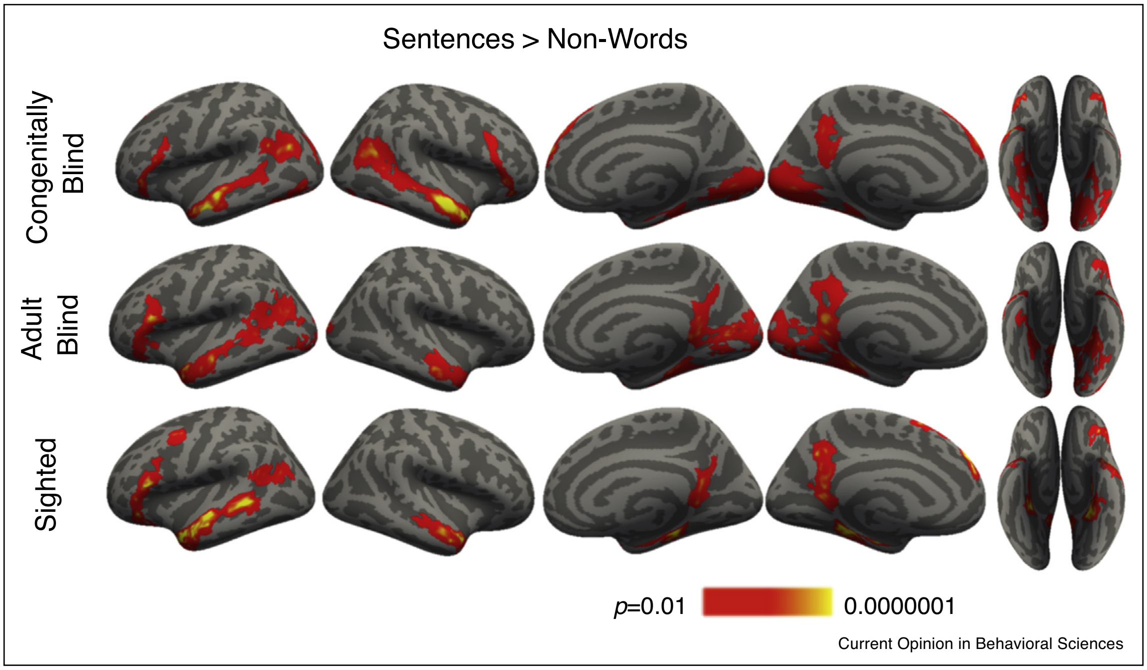
Introduction

Unlike learning calculus, political science or learning to cook, language acquisition proceeds more quickly and effectively in childhood. Lenneberg was one of the first proponents of the idea that language acquisition follows a critical period, akin to those found in sensory systems [1]. Critical or sensitive periods are windows during the lifespan where neural systems exhibit enhanced plasticity, resulting in enhanced learning capacities as well as enhanced vulnerability to negative environmental influence. Perhaps the best studied sensitive period is that of visual cortex in amblyopia. Monocular deprivation during, but not before or after, the sensitive period causes the 'good eye' to take over cells that would normally respond to input from the deprived eye [2,3]. In recent decades, there has been tremendous progress in uncovering the neurochemical mechanisms that mediate the opening and closing of sensitive periods in sensory systems. For example, maturation of inhibitory gamma-aminobutyric acid (GABA) circuits, itself partially experience-dependent, is a key step in sensitive period opening and molecular breaks, such as perineuronal nets mediate sensitive period closure [4].

At present it is not possible to measure cellular properties of language related cortical circuits in humans. Whether putative sensitive periods for language acquisition are mediated by similar neural mechanisms to those found in sensory systems is not known. Nevertheless, studies of behavior and cortical function in humans strongly suggest that the juvenile brain is optimally suited to language acquisition. Evidence for the sensitive period hypothesis in language comes from a variety of sources, including second language acquisition, language training with children and adults and acquisition of language by children with early brain damage [5–7]. The current review centers on recent evidence from studies with individuals who are born either deaf or blind, focusing specifically on higher-order aspects of language, including grammar and semantics [see Refs. 8,9 for reviews of sensitive periods in speech perception]. Studies of sensory loss provide unique insights into how experience shapes the neurocognitive development of a first language. Comparing the effects of early life experience to those of experience in adulthood (early versus late access to a sign language and early versus late blindness) reveals the unique malleability of the neural basis of language early in life.

Language acquisition is resilient to sensory loss *per se*. Children born blind acquire language effectively despite reduced access to the referents of sentences such as 'Look at the red cup' [10]. Children born deaf acquire language in similar ways to hearing children, provided they have access to a manual sign language early in life [11]. In hearing speakers and deaf native signers, language likewise depends on a left-lateralized fronto-temporal network. (For an example of fronto-temporal response during spoken sentence comprehension see Figure 1). However, delays in exposure to sign language among people born deaf affect ultimate language proficiency, modify cortical responses to language and affect cortical anatomy. Consistent with the idea that the neural basis of language is more malleable during sensitive periods, early but not late blindness incorporates parts of occipital 'visual' cortices into language networks and

Figure 1



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Language processing networks of congenitally blind (n = 22), adult-onset blind (n = 15) and sighted adults (n = 18). Activation for sentences as compared to lists of non-words, cluster corrected, $p < 0.05$. Adapted from Ref. [56••].

reduces left-lateralization of language. Evidence from blindness and deafness converges on the idea that the neural basis of language is maximally flexible and maximally vulnerable during sensitive periods of development. At the same time, the different patterns of plasticity observed in these populations raise new questions. In Deaf individuals, delayed language access is associated with a modified neural basis of language and lower linguistic proficiency. By contrast, blindness-related changes to the neural basis of language have either no behavioral consequences (reduced left-lateralization) or are associated with performance enhancements (addition of occipital areas to fronto-temporal networks). This evidence highlights the complexity of brain-behavior relationships.

Language-related plasticity in Deafness as a result of delayed sign language access

Spoken language is the most prevalent form of human communication and being born deaf affects access to speech. Even with the aid of hearing devices and speech training, deaf children have variable and often limited access to spoken language. About 5–10% of Deaf individuals are born into households with fluent users of a sign language and exposed to a fully accessible, visual-manual, language from birth [12]. Deaf native learners acquire sign language in the same way as hearing children acquire a spoken language and become proficient users of phonology, morphology, grammar and semantics in the particular sign language they are exposed to [see Ref. 11 for review]. In Deaf native signers, sign languages depend on similar fronto-temporal neural mechanisms as spoken languages [13,14]. Evidence from native signers illustrates the modality-independent nature of fronto-temporal systems. Just as the intrinsic developmental plasticity of fronto-temporal systems accommodates English, Hindi and Urdu acquisition, it also enables the acquisition of Brazilian, American or Chinese sign languages.

In contrast to native learners, the majority of Deaf individuals are born to hearing non-signing parents. For these children, access to a fully accessible language, sign language, is often limited and variable early in life. The current review focuses on the consequences of these delays for linguistic behavior and the neural basis of language. Studies of delayed language access among people born deaf are a strong test of the sensitive period hypothesis, since Deaf individuals experience delayed access to a first language (L1), despite typical social and physical experience.

Most Deaf individuals will eventually acquire sign language when entering a sign language education program, or when encountering the Deaf community. A large body of work shows that delaying access to sign language limits ultimate language proficiency [16–18 see Ref. 19•for a review]. Recent behavioral case studies with Deaf individuals who have no hearing compensation and severely delayed access to L1 highlight the importance of language exposure during early development. When individuals with severely delayed access finally get exposed to a sign language community, in adolescence or adulthood, early vocabulary and basic word order is acquired [20,21]. However, later emerging aspects of grammar, such as topicalization and grammatical markers, plateau before reaching full native proficiency [20, Mayberry *et al*., unpublished]. Even when presented with simple transitive sentences, severely delayed language learners privilege real world knowledge over syntactically relevant word order, interpreting sentences such as 'the egg bites a boy' as the boy biting an egg [Cheng and Mayberry, unpublished]. In one case report, an individual who acquired British Sign Language (BSL) in his late 20 s and was tested 25 years after exposure, attained grammatical skills comparable to a 5-year-old Deaf native signer, and showed inconsistent phonological and grammatical use in spontaneous production [22].

Severe delays in language access are also associated with changes to the neural basis of language. As noted above, Deaf native signers recruit left fronto-temporal language network during comprehension and production [15]. A series of studies recently examined the neural basis of language processing in three individuals with severely delayed access to sign language, no hearing compensation and no formal schooling. Two of these individuals were first exposed to a signing community in late adolescence and one at 20 years of age. The adolescent learners were first scanned 2–3 years after initial exposure to a signing community, while the adult learner had been signing for 20 years at the time of the study. Relative to native signers, all three individuals show reduced activation in typical fronto-temporal language networks during word comprehension [23,24,25••]. By contrast, increased activity is observed in occipital regions, possibly reflecting increased reliance on visuo-spatial processing, and in right frontal and parietal regions [23,25••], possibly reflecting increased reliance on domain general working memory systems. After an additional year of ASL exposure, the two adolescent learners showed some shift from right fronto-parietal and occipital to left fronto-temporal regions, especially when processing familiar words [24]. All three severely delayed learners show reduced connectivity in the left arcuate fasciculus, a white matter pathway that connects temporal and frontal language regions [26].

Since severe language delays are fortunately rare, the sample sizes of the studies reviewed above are necessarily small. Convergent evidence comes from studies with larger samples of Deaf individuals with late sign language onset but shorter delays or somewhat less impoverished early language experience (e.g. used hearing technology such as hearing aids or cochlear implants). These studies find similar behavioral and neural changes to cases of severe delay, but the effects are more moderate and more variable, possibly reflecting variable access to spoken language before sign language acquisition. Delaying sign language access reduces ultimate proficiency in grammar [27,28], phonology [29–31] and vocabulary for the sign language being acquired [32,33]. Moreover, earlier sign language access facilitates spoken and written language attainment [34,35], again showing the crucial role of a fully accessible language during the sensitive periods. Late access to sign language also reduces activation in left fronto-temporal language regions during phonological and sentence processing tasks and increases occipito-parietal involvement [36,37••,38 for evidence of anatomical occipital changes see Ref. 39]. In summary, studies of sign language acquisition in Deaf individuals provide clear evidence that delayed exposure to a first language impacts phonological and grammatical proficiency and changes the neural networks that support language processing.

Language-related plasticity in blindness

Unlike deafness, vision loss does not substantially alter access to speech. Blindness changes access to the referents of linguistic expression, that is to the objects, events and qualities to which languages refer. This observation led to the hypothesis that blindness would significantly delay or fundamentally changes the acquisition of meanings of linguistic expressions. Empirical evidence shows, on the contrary, that blind children acquire language in largely the same way as sighted children and converge on similar meanings [10,40]. This is true even for seemingly 'visual' words, such *sparkle*, *peek* and *blue* [41–43]. Rather than being hindered, linguistic communication enables people born blind to construct mental models of visual phenomena and appearance that are similar to those of sighted people living in the same culture [44•]. As reviewed below, aspects of language processing are in fact enhanced in blindness, either because of increased reliance on language as a source of information, because of availability of extra cortical resources or both [45•].

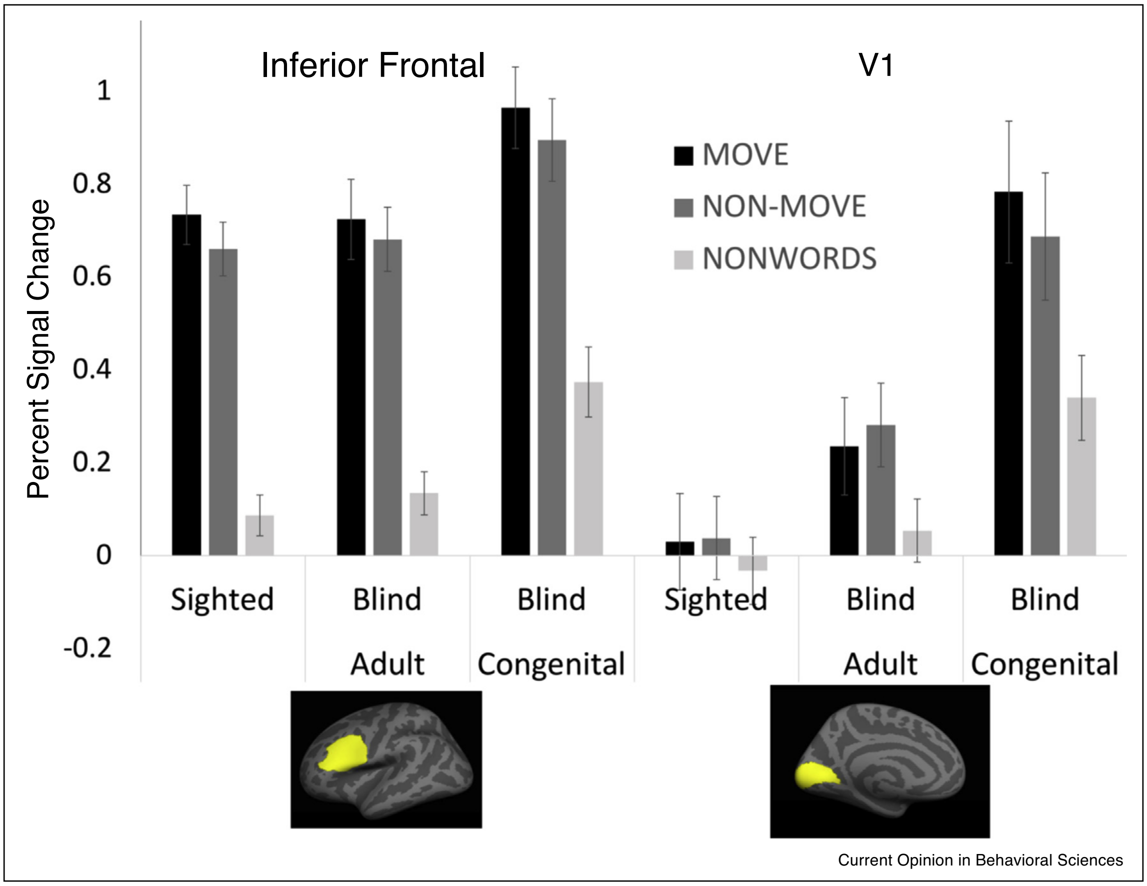
Blindness from birth also modifies the neural basis of language by changing neural dynamics during cortical development. In addition to classic fronto-temporal language networks, people who are born blind recruit 'visual' cortices during language tasks [46, see Ref. 47 for recent review]. This functional reorganization is part of a broader phenomenon known as 'cross-modal' plasticity, whereby deafferented visual cortices upregulate their responses to other modalities and cognitive domains [48]. In blind adults, but not blindfolded sighted controls, 'visual' cortices are active when listening to sentences and words, when generating verbs to heard nouns and when reading

Braille via touch (Figure 1) [49–52]. Apart from language, 'visual' cortices of blind individuals are active during tasks such as sound localization, mathematical calculation and auditory motion perception [48]. Language recruits a distinctive subset of 'visual' cortices, relative to these non-linguistic tasks [52]. Responses to spoken language are observed in secondary visual regions of lateral and ventral occipito-temporal cortex, including the so called 'visual word form area,' as well as in primary visual cortex (V1) (Figure 1, top row) [53]. A recent study reported that different parts of 'visual' cortex respond to sentence comprehension, verb generation, long term memory and executive demands [54]. Occipital regions that are active during language tasks also change in their functional connectivity, becoming coupled with fronto-temporal language networks at rest [51,55].

Crucially, in blindness, language-responsive 'visual' areas are sensitive to high-level linguistic information that is, semantics and grammar. For example, 'visual' regions respond more to sentences than lists of words and more to Jabberwocky than lists of non-words [57]. In blindness, 'visual' cortices are also sensitive to grammatical complexity of spoken sentences, responding more to sentences with syntactic movement (Figure 2) [46,58].

There is some evidence that occipital responses to language are behaviorally relevant. Transcranial Magnetic Stimulation (TMS) applied to 'visual' cortices of blind individuals impairs verb generation and Braille reading [59–61]. In one study, blind individuals with larger responses to grammatical complexity in 'visual' cortex were more accurate when answering comprehension questions about grammatically complex sentences [58]. One recent study found that, people born blind are on average better at comprehending complex grammatical constructions, particularly garden path sentences than sighted controls [45•]. There is also evidence for faster

Figure 2



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Responses to sentences with syntactic movement (MOVE), sentences without syntactic movement (NONMOVE) and lists of nonwords (NONWORDS) in congenitally blind (CB), adult-onset blind (AB) and sighted (S) participants in V1 and left inferior frontal regions of interest. Analysis was done in individual functional ROIs defined within the anatomical search spaces using data from a separate experiment (sentences > equations contrast). Error bars represent standard errors of the mean. Adapted from Ref. [56••].

lexical access and superior verbal memory in blindness [62,63]. Whether these cognitive enhancements are related to occipital recruitment, habitual processing of spoken language in the absence of visual cues, increased reliance on language or all of the above remains to be determined.

Apart from occipital plasticity, the lateralization of fronto-temporal language networks is more variable across congenitally blind than sighted people. In one study just under half of the blind participants sampled showed bilateral or right-lateralized fronto-temporal responses during spoken language comprehension [64•]. Interestingly, across blind individuals, fronto-temporal and occipital responses to language are co-lateralized: blind individuals who show right-lateralized responses to language in inferior frontal cortex, also show right-lateralized responses to language in occipital cortex. However, there is no relationship between the degree of occipital recruitment and language lateralization across individuals, suggesting that changes in laterality and occipital plasticity are driven by different mechanisms. The mechanisms of blindness-related laterality changes are not known. One possibility is that blindness alters competitive processes between language and other cognitive domains (e.g. visuo-spatial processes) that typically ‘push’ language to the left hemisphere during cortical development.

Both reduced lateralization of fronto-temporal networks and addition of ‘visual’ cortex regions to the language system follow sensitive periods. People who become blind as adults show responses to language that are as left-lateralized as those of sighted people, even after many years of blindness (Figure 1) [58]. Occipital responses to language are less pronounced in people who become blind as adults and upregulation of resting state correlation between occipital and fronto-temporal language regions is present but reduced [56••,57,65,66, see Ref. 67 for review of sensitive period effects in cross-modal plasticity]. Occipital sensitivity to grammatical structure appears to be absent in people who become blind in adulthood [56••,67]. There is also evidence that behavioral relevance of occipital responses is unique to people born blind [68]. Together, these studies suggest that blindness early in life is uniquely capable of modifying the neural basis of language.

Conclusions

Evidence from studies with Deaf and blind individuals provides complementary support for the sensitive period hypothesis of language acquisition and gives insight into human cortical specialization. Delays in access to sign language among people born deaf reduce ultimate language proficiency and modify the neural basis of language [13,15]. In cases of severe delay in language access, fronto-temporal involvement during language tasks appears to be reduced. Attainment of native proficiency may, therefore, depend on the enhanced plasticity of fronto-temporal networks during sensitive periods. The evidence also raises a potential link between the recruitment of left fronto-temporal networks for language and proficiency in some language domains, such as grammar.

On the other hand, studies with people born blind show that fronto-temporal regions are not the only ones that can participate in language processing and that not all changes to the neural bases of language have negative behavioral consequences. Adults born blind perform the same or better than sighted people on language tasks but show reduced left-lateralization of language and recruit occipital, in addition to fronto-temporal areas, during language processing. Moreover, even in ‘visual’ occipital cortices, specialization for language occurs only during sensitive periods. Cortical specialization for language may, therefore, depend on sensitive period plasticity in and outside fronto-temporal systems.

Evidence from blindness also suggests that competitive interactions between cognitive domains play an important role in human cortical specialization [69,70]. As noted in the introduction, in primary visual cortex the two eyes compete for cortical neurons during sensitive periods [2]. Analogous competition appears to occur at the network scale, with language encroaching into occipital cortices in the absence of competing visual inputs during development. An open question is whether non-linguistic cognitive domains analogously colonize fronto-temporal networks in the absence of timely language access. By contrast, exposure to any language, whether spoken or signed, may establish language specialization in fronto-temporal systems and prevent colonization by other cognitive functions. According to this hypothesis, human cortex does not wait around for a specific type of information to arrive but rather becomes specialized, as best it can, for whatever information is available during sensitive periods. Future work could test this hypothesis by studying whether fronto-temporal language regions acquire responses to non-linguistic domains in Deaf individuals with delayed language access.

Conflict of interest statement

Nothing declared.

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