Title: Neurobiological insights from the study of deafness and sign language

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ABSTRACT

The study of deafness and sign language has provided a means of dissociating modality specificity from higher level abstract processes in the brain. Differentiating these is fundamental for establishing the relationship between sensorimotor representations and functional specialisation in the brain. Early deafness in humans provides a unique insight into this problem, because the reorganisation observed in the adult deaf brain is not only due to neural development in the absence of auditory inputs, but also due to the acquisition of visual communication strategies such as sign language and speechreading. Here we report research by scholars who have collaborated with Prof. Bencie Woll in understanding the neural reorganisation that occurs as a consequence of early deafness, and its relation to the use of different visual strategies for language. We concentrate on three main topics: functional specialisation of sensory cortices, language and working memory.

INTRODUCTION

For many people, the word language automatically means speech. It is perhaps not surprising that most of our knowledge of the neurobiology of language comes from the study of speech in hearing individuals. Similarly, our knowledge about perception derives mainly from studying the auditory cortex of hearing people or the visual cortex of sighted individuals. However, evidence obtained from exceptions to these rules has provided equally compelling yet unique insights into the capacities and limitations of the human brain.

Here, we discuss work that the authors have conducted together with Prof. Bencie Woll in the fields of sign language, speechreading and deafness, which we believe has contributed to our knowledge of language and cognition in the brain. Congenital deafness is an excellent model for the study of brain function and reorganisation, as adaptive changes develop not only in response to the lack of auditory stimulation, but also in response to visual mechanisms for language acquisition. This is because deaf individuals acquire language through the visual modality, and because language acquisition in deaf children is often delayed. Furthermore, because signed and spoken languages differ regards to their underlying sensory and motor processes (sign languages are visual/manual languages, spoken languages are auditory/oral languages), they are excellent tools for investigating to what degree mental representations and processes are based on, or are independent of, underlying sensory and motor mechanisms. Focusing on neural plasticity, language and working memory, we discuss how neuroscience research on deafness has allowed us to better understand the effect of different developmental sensory and communication experiences on the structure and function of the adult brain.

NEURAL PLASTICITY

Critical periods for the development of specific cognitive skills such as language have been proposed since the work of Lenneberg (1967; and see chapter 6, Lillo-Martin et al., this volume). They indicate time-limited periods in development when the acquisition of a cognitive skill may be achieved readily (or at all). This concept maps onto that of neural plasticity, which refers to the functional and structural capacity of the brain to reorganise in response to physiological or pathological environmental events (Merabet and Pascual-Leone, 2010). Neural events occurring at specific time points during development underlie such critical periods, and are mediated in the developing brain by enhanced cortical plasticity which allows the neural system to reorganise in response to environmental information (Hensch, 2004). In deaf individuals, one of the main causes of reorganisation is the absence of auditory inputs during a proposed critical period for development of the auditory system in the brain (Kral, 2013). However, there are other factors that drive plastic changes in the deaf brain, the most

important ones being those related to the acquisition of language in the visual modality (Lyness et al., 2013). Because cortical plasticity varies as a function of sensory stimulation (and other environmental factors) during early sensitive periods (Lyness et al., 2013), we will only discuss studies of plasticity as consequence of congenital or very early deafness. Individuals with late-acquired deafness or with cochlear implants may have access to auditory information during these critical periods, which will result in different developmental pathways for cortical regions involved in auditory and language processing (see section "*What are the consequences of impoverished access to early language?*").

The role of the "auditory" cortex in Deaf individuals.

Cortical auditory processing in hearing individuals is located largely in the Superior Temporal Cortex (STC). In some of the first neuroimaging studies in deaf individuals, it was shown that the STC of congenitally deaf humans responded to basic visual stimulation (moving dots; Finney et al. 2001), and to sign language (Nishimura et al., 1999). This "crossmodal plasticity", reflects the fact that regions typically involved in auditory processing can become responsive to other sensory inputs (Merabet and Pascual-Leone, 2010; Glick and Sharma, 2017). However, studying the effects of deafness on neural reorganisations is challenging because of deafness has consequences beyond sensory processing, affecting may cognitive skills, including but not limited to language (see Dye & Thompson, Chapter 8 this volume). Given such heterogeneity, it is not surprising that in many studies of neural plasticity as a consequence of deafness, it is difficult to categorically establish if differences between hearing and deaf groups are due to differences in auditory experience, or due to delayed or poor language acquisition and skills.

In an effort to dissociate the effects of absence of auditory inputs during the critical periods from those of acquiring and using a signed or a spoken language, Cardin et al. (2013) conducted an fMRI experiment in which sign language stimuli were shown to three different groups of participants: 1) deaf native signers; 2) deaf non-signers – a group of individuals who were congenitally or early deaf, grew up using a spoken language, and did not know any sign language; and 3) hearing non-signers. The rationale of this study was that any plasticity effect that was due to a lack of auditory inputs during development will be present in both groups of deaf participants, but not in the group of hearing non-signers. On the other hand, given the linguistic content of the sign language stimuli, a plasticity effect as a consequence of early sign language acquisition will be found only in the group of deaf signers. The results showed that the absence of auditory inputs during infancy caused plasticity in the right posterior superior temporal cortex (STC – see figure 1). Plasticity effects as a consequence of sign language use were found in both the left and right STC, and were evident only when stimuli had linguistic content. These regions recruited for sign language processing in deaf individuals

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corresponded to those supporting speech in hearing individuals. This suggests that in the absence of early sensory experience cortical regions develop their typical function, but adapt to a different type of sensory input, not only in terms of perception (Bennetti et al. 2017; Lomber et al. 2010), but also higher-order cognitive function. As we discuss in the section below, it is indeed the case that regions involved in spoken language processing in hearing individuals maintain their specific role, at least to some extent, in phonological, semantic and syntactic processing in deaf individuals, either for speechreading (lipreading) or sign language (Corina and Knapp, 2006; MacSweeney et al., 2008a; Campbell and Macsweeney, 2012; Twomey et al., 2017).

The types of stimuli and tasks that reveal plasticity effects in STC suggest an involvement of this region in higher order sensory processing. This is supported by studies that used other brain imaging techiques such as EEG and MEG to investigate the timing of this response. In an MEG study, Leonard et al. (2012) showed that responses to sign language (and static pictures) arose from the STC of deaf individuals during a late time window (~300 ms) associated to lexicosemantic processing. Early sensory processing responses (~ 100 ms) were constrained to visual cortices in both hearing and deaf adults. (For a further example see Bottari et al., 2014).

The next step for understanding the role of the superior temporal regions in deaf individuals is to go beyond language and low-level vision, and investigate other cognitive functions. In the past few years, studies have shown that the STC is involved in visual working memory (Buchsbaum et al., 2005; Ding et al., 2015; Cardin et al., 2018) . This effect is independent both of the linguistic content of the stimuli, and of the language knowledge of the deaf participants, which indicates is not directly related to language processing in STC (Cardin et al., 2018). Instead, it suggests a different role for some regions of the deaf STC; a role which is distinct from the one this cortical region has in hearing individuals. Analogous functional changes have been reported in the visual cortex of blind individuals (Röder et al., 2002; Amedi et al., 2004; Bedny et al., 2015). These functional changes suggest considerable malleability in the function of brain region that are usually considered unisensory, and the function of such regions in the adult brain will strongly depend on the type and quality of early environmental experience. Together, these findings point to two co-existing plasticity mechanisms: functional preservation and functional change, and future efforts should be directed towards delineating the physiological and anatomical principles behind each of them.

MODALITY DEPENDENT AND INDEPENDENT LANGUAGE NETWORKS

Visual speech in deaf and hearing individuals.

The movement of the speech articulators can be felt by the speaker, and is seen as well as heard. Sensitivity to seen speech can be demonstrated from the first months of life in hearing infants (e.g.

Dodd, 1980; Mercure et al., 2018) and, while audition dominates, speech processing continues to be essentially multimodal throughout life (Campbell, 2008). Behavioral studies show that seeing the speaker enhances the perception of heard speech – especially, but not exclusively, when speech is noisy (Dodd and Campbell, 1988).

It might be assumed that deaf children, denied access to heard language, must become efficient speechreaders. However, younger deaf children can be worse speechreaders than hearing children (Kyle et al., 2013), although deaf adults often outperform hearing people on tests of speechreading (Mohammed et al., 2006). It is likely that skilled speechreading in deaf adults makes use of multiple strategies to infer the meaning of the speechread message (Feld and Sommers, 2009), and see section on working memory, below). Skilled speechreading is effortful, and it can make greater demands on general cognitive processes than hearing speech (e.g. Hornsby, 2013). The hearing speechreader has less need to develop these skills, which could explain the difference in performance in the adult populations.

Figure 1. *Schematic of left hemisphere lateral surface showing perisylvian regions centred on 'A', (secondary) auditory cortex in the superior temporal lobe (STC – see text). The dark arrow indicates the dorsal projection stream and the stippled arrow the approximate route of the ventral projection – both to inferior frontal regions.*

Many speech actions are hidden within the mouth, leading to suboptimal identification of phonemes by sight alone. That does not necessarily mean that speechreading is ineffective as a route into language for someone who cannot hear, but its utility varies not just with the content of speech and its general visibility, but also with the language experience of the speechreader. For instance, knowledge of the statistical structure of words in the language can often make good the lack of phonological detail (Auer and Bernstein, 1997). There can be a good deal of variability in speechreading skill in deaf people, reflecting, amongst other factors, their varied exposure to and affiliation with spoken language. A partial analogue, for hearing people, would be the ability to interpret noisy or degraded speech: that too shows marked individual variation (Rönnberg et al., 2013; Tamati et al., 2013).

Neural bases of audiovisual speech processing in hearing individuals

Neural models of speech processing in hearing adults can provide a template against which to explore speechreading in hearing and deaf populations. These models differ in several regards, but they propose that in order to extract a linguistic message, speech processing is supported by a network of left-lateralised perisylvian regions (Fig. 1). Sounds reaching the primary auditory cortex in Heschl's gyrus within the superior temporal plane (hidden from view in the surface representation of Figure 1) are then processed in STC. Activation in STC maps, via connection tracts, onto regions in the inferior frontal gyrus (IFG) which are specialised for articulatory processing (a 'dorsal route'). This route is thought to effect the processing of speech structure, including phonology. A complementary route for the processing of semantic speech-based entities maps from anterior STC to inferior frontal regions (Hickok and Poeppel, 2007; Rauschecker and Scott, 2009 - a 'ventral route' and see previous section). The left-lateralization of all these processes is age-dependent, and evidence of left-lateralization for speech processing is less secure in children than adults (Neville and Bavelier, 1998; Holland et al., 2007).

Neuroscientific studies of audiovisual speech processing have shown that perisylvian auditory speech regions are also activated by seen speech (Calvert et al., 1997). These activations in STC seem to follow a modality gradient: auditory speech preferentially activates more anterior regions, visual speech (speechreading) more posterior regions, while mid-regions of the sulcus preferentially specialize for audiovisual speech processing (Bernstein and Liebenthal, 2014; Venezia et al., 2017). In accordance to this gradient, more anterior regions of the STS show greater activation for speech and language processing (Beauchamp, 2015; Deen et al., 2015), whereas more posterior parts of STS show greater activation for bodily and facial gestures (non-verbal signals; see Figure 2). In addition, visual perception of nonverbal biological signals, such as those seen when someone speaks, also engages regions

specialized for the perception of face actions and biological movement in the parieto-temporo-occipital junction region (Calvert and Campbell, 2003).
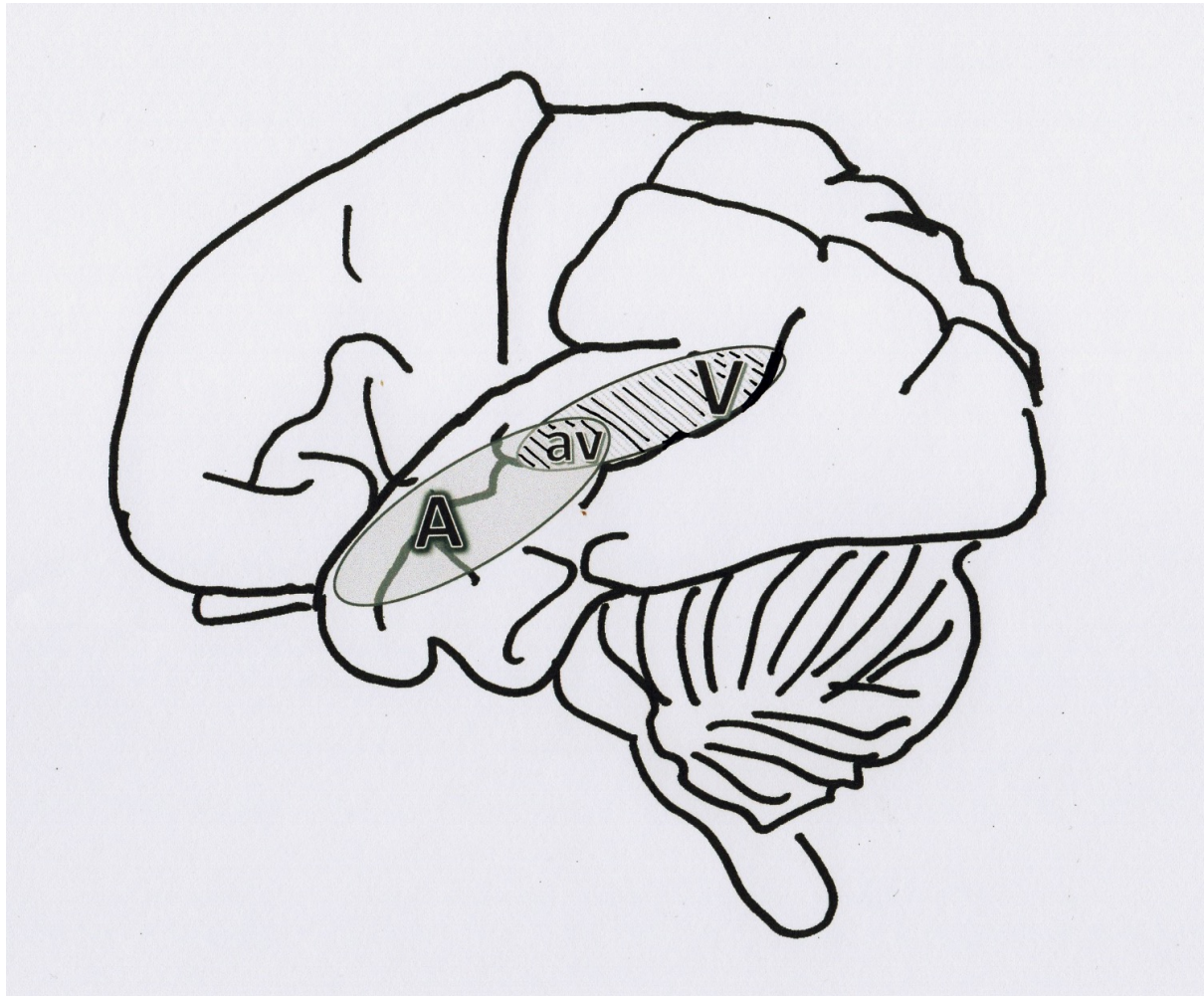

Figure 2. Schematic of left hemisphere lateral surface indicating approximate regions within superior temporal cortex specialized for auditory processing of speech (A: open region) and visual gesture processing (V: stippled region). Regions specialized for auditory-visual processing of speech are in the mid regions of these superior temporal structures, with projections from both auditory and visual processing.

Neural bases for speechreading in deaf people

Given these findings in hearing people, how might seen speech localise in deaf brains? Would we expect to find evidence of more extensive - or different - patterns of activation? Might deaf brains show greater activation in 'purely' visual regions than hearing brains, since deaf people rely more on speechreading?

One study (Capek et al., 2008a), compared deaf and hearing adults on a simple speechreading task (identifying a videoclip of a spoken word 'yes' by sight among other silently spoken unconnected words). The deaf participants showed more extensive activation than the hearing group in left STC, specifically. Ludman et al. (2000) previously showed that speechreading skill in hearing people correlated specifically with activation in STC, so this difference between groups could reflect

differences in speechreading skill, which was better for the deaf participants. Activations in anterior STC did correlate with speechreading skill in both deaf and hearing people (Capek et al, 2008a). However, the differences between groups persisted when speechreading skill was controlled. This finding, then, suggests that when hearing is absent, anterior parts of the left STC that process heard speech in hearing people can 'take over' speechreading.

Speech actions in sign language and in seen speech: neural correlates

The deaf participants in the Capek et al (2008 a,b) study were all bimodal bilingual – that is they were similarly proficient in both BSL and speechreading. Could the more extensive left STC activation observed for speechreading in these deaf people simply reflect their bimodal language skills? This particular study formed part of a set of explorations of perception of mouth actions in both sign language and speech. Sign languages incorporate mouth actions alongside manual ones, and their role has been explored by sign linguists (Baker and Padden, 1978; Sutton-Spence and Woll, 1999). The comparison of activation patterns for seen speech compared with mouth actions in BSL that were not speechlike re-iterated and extended the previous finding: speechreading activated more anterior parts of STC, while BSL non-speechlike mouth actions activated more posterior parts (Capek et al., 2008a, 2010). When these bimodal bilingual deaf adults were compared to hearing adults born into signing families (hearing bimodal bilinguals), deafness itself was found to have an influence on the pattern: once again, deaf speechreaders showed greater activation in anterior parts of STC than did bilingual hearing people (Capek et al., 2008b).

Taken together, these findings suggest that early developmental experience modulates functional specialization in STC. These regions appear to show plasticity reflecting both early auditory experiences AND language processing. In this respect the findings for speechreading recapitulate those described previously, in the section on sign language processing. However, the cortical regions that show plasticity may differ depending on the nature of the visual language signal. Plasticity for speechreading in deaf brains is seen in anterior STC (Capek et al., 2008a); those regions that are regularly activated by heard speech in hearing people. By contrast, sign language plasticity is seen in more posterior regions, specialized for visual processing, where deaf people show greater activation than hearing people (Cardin et al., 2013; 2016).

Sign languages as a window into modality-independent language processing.

Studies with native users of a signed language provide a unique opportunity to identify the neural systems supporting higher order language acquisition and processing *regardless of modality.*

Identification of regions of overlapping activation during tasks performed in signed and spoken languages allows us to directly test the hypothesis that these regions are involved in language development and processing independently of modality.

Here we review neural systems which are recruited by native adult users of sign language (studies with children are lacking at present).

In accordance with lesion studies of hearing patients, studies of native signers with lesions overwhelmingly indicate that left hemisphere damage leads to severely impaired language processing (aphasia) while right hemisphere damage does not (e.g. Hickok et al., 1996; Marshall et al., 2005). Neuroimaging studies also indicate a critical role for the left hemisphere in sign language processing. Despite differences in the articulators used to produce sign and speech, both modalities of language production predominantly engage left hemisphere regions (Emmorey et al., 2014; Gutierrez-Sigut et al., 2015, 2016). With regard to language *perception*, a left fronto-temporal network involving the superior temporal gyrus and sulcus (STC) as well as the left inferior frontal gyrus, extending into the prefrontal gyrus, was shown to be involved in processing both sign and speech (see also Sakai et al., 2005). Numerous studies have also identified a primarily left lateralized fronto-temporal network involved in sign language perception when contrasted with gesture (Newman et al., 2015), transitive actions (Corina et al., 2007) or non-sense movement (MacSweeney et al., 2004). These studies suggest that the core left-lateralized language network is resilient to change in language modality. In summary, even though language development in native users of signed and spoken languages involves different sensorimotor mechanisms, very similar left-perisylvian networks are engaged for the perception and production of sign and speech. This similarity appears to extend to metalinguistic judgments regarding the sublexical, phonological, structure of sign and speech, which have been shown to engage a left fronto-parietal network (MacSweeney et al., 2008b).

Although the overlap between the networks supporting sign and speech processing is extensive, there are some differences. As indicated in previous parts of this chapter, direct contrasts have highlighted differences reflecting early sensory processing. Audio-visual speech elicits greater activation than sign language in auditory processing regions in STC. In contrast, signed languages elicit greater activation than audio-visual speech in biological motion processing regions of the posterior middle temporal gyri, bilaterally (Söderfeldt et al., 1997; MacSweeney et al., 2002b; Emmorey et al., 2014). 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 et al., 2002a; McCullough et al., 2012).

There is also growing evidence suggesting that the left inferior and superior parietal lobules play a greater role in sign language processing than spoken language processing (see MacSweeney et al.,

2008 for review). 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 et al., 2016). Within the inferior parietal lobule (IPL), the left supramarginal gyrus appears to play a particularly important role in phonological processing of signed language (Corina et al., 1999; MacSweeney et al., 2008b; Cardin et al., 2016).

The summary of the literature regarding signed and spoken language processing presented above, refers to both deaf and hearing signers. It is worth noting that in addition to the networks described above deaf signers appear to recruit parts of STC that are not activated in hearing sign users (MacSweeney et al., 2002b; Cardin et al., 2016; Twomey et al., 2017). As described in the section on plasticity, the STCs are involved in auditory processing in the hearing. In congenitally deaf participants, these regions are available to process input from other modalities. Of particular relevance to this section, posterior parts of the left STC in deaf signers appear to be particularly sensitive to the demands of sign language processing and not to general low-level visuo-spatial processing demands (Cardin et al., 2013; Twomey et al., 2017). It is unlikely that this effect is language specific, but rather due to the complexity the visual components of the language and the potential increased processing demands. However, further studies are necessary to explore this hypothesis directly.

What are the neural consequences of impoverished access to early language?

All of the studies reviewed above have focused on studies of deaf native signers. However, the vast majority of deaf children are not exposed to a signed language from birth. They are born to hearing parents, who may or may not decide to learn a signed language. Often these children are exposed to a signed language at school or upon 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 development of the language system.

Although the impact of late sign language acquisition on sign language processing has been investigated extensively at the behavioral level (see Lillo-Martien et al., this volume), the impact of late sign language acquisition on the neural systems supporting language has yet to be fully explored. Hearing late learners of sign have already successfully acquired a first (spoken) language; deaf late learners of a signed 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.

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 et al., (2008b)

tested deaf native and non-native signers. Participants were asked to make phonological judgements about signs (same location?) and speech (rhyme?) in response to picture pairs. Increased activations were found in the left inferior frontal gyrus in the non-native compared to the native signers (MacSweeney et al., 2008). Critically, this was the case not only for the task in BSL, which was learnt late, but also for the task in English, of which both groups had similar experience and had also shown equal levels of performance on English online (rhyme task) and offline tasks. One interpretation of these data is that having a robust first language, here a signed language, provides a solid basis upon 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 (Mayberry et al., 2002).

Mayberry et al. (2011) also investigated the influence of age of sign language acquisition by testing participants whose age of onset of American Sign Language (ASL) acquisition ranged from birth to 14 years old. Participants were tested on phonemic and grammatical judgements in response to ASL sentences. In contrast to the findings of MacSweeney et al. (2008b), Mayberry et al. (2011) found *decreased* recruitment of left frontal regions in late compared to early signers. Late signers showed enhanced recruitment of occipital cortices. There were a number of stimulus (ASL video/ static pictures) and task differences between the MacSweeney et al. (2008b) and Mayberry et al. (2011) studies that may have contributed to the different pattern of results. One key difference is that the participants in the MacSweeney et al. (2008b) are likely to have had better spoken language skills than those in the Mayberry et al. (2011) study. 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. Future studies are needed to dissociate effects that are related to age of sign language exposure and those related to sign language proficiency.

Mayberry and colleagues have also had the opportunity to examine ASL processing in two deaf adolescents who moved to the US from Central America and who are described as having no first language (spoken language) before encountering ASL at the age of 14 years (Ferjan 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 MEG the authors showed that even after three years of exposure to ASL, the teenager's responses to single signs were highly atypical, engaging right dorsal fronto-parietal regions, rather than the typical left-lateralized fronto-temporal network (Ferjan Ramirez et al., 2016). 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. The authors argue 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 (Ferjan Ramirez et al., 2016). 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.

WORKING MEMORY FOR LANGUAGE IN DEAF AND HEARING INDIVIDUALS

The general notion of a working memory is that of a limited-capacity mental work-bench that allows for storage and manipulation of information (Baddeley and Hitch, 1974; Daneman and Merikle, 1996). Although working memory is in place already in infancy (Zosh and Feigenson, 2015), it develops steadily during childhood (Cowan, 2016), and it represents one of the most central cognitive functions in the adult brain. Furthermore, there is a well-supported proposal that the development of working memory and the acquisition of native phonology and first words are closely and reciprocally linked (Gathercole and Baddeley, 1993). How this plays out in relation to language processing in deaf children and adults is the topic of this section which reviews studies of working memory for sign and spoken language.

Linguistic representations and working memory development. Due to its relevance for cognitive models of working memory (Baddeley and Hitch, 1974; Rönnberg et al., 2013; Ronnberg et al., 2018), many efforts have concentrated in understanding the role of phonological representations during WM for sign language. According to the Ease of Language Understanding model (ELU, Rönnberg et al., 2013), lexical access (irrespective of language modality) is mediated by phonological representations that "unlock" the lexical/semantic meaning. Whether there is an actual match in the number of phonological and semantic attributes is assumed to be set by a threshold. Below threshold, lexical access is denied. In this case, a mismatch is said to have occurred (Rudner et al., 2009; Rönnberg et al., 2013). Considering the importance of phonological matching during speech processing, a role for phonology during sign language processing may be expected. While speech phonology is based on sound patterns generated through the vocal tract, sign phonology is mainly based on the articulatory patterns of the moving hands in terms of shape, position, movement and orientation. Work by Wilson and Emmorey (1997) using ASL provided evidence for a sign version of the phonological loop (Baddeley, 2012). We have reported evidence of a phonological similarity effect for Swedish Sign Language (SSL, Rudner and Rönnberg, 2008; Andin et al., 2013) although we did not find such an effect in BSL (Andin et al., 2013), possibly due to methodological differences. Subsequent work shows that phonological representations play less prominent role in working memory for sign language than in

suggested by generic models of working memory (Rudner et al., 2016; Rudner, 2018; Rudner and Ronnberg, 2019). Rather, it is the nature of the underlying motor representations that is important for explicit processing of signs (Rudner, 2015; Cardin et al., 2016; Rudner et al., 2016), in line with the notion of embodied cognition (Wilson, 2001; Rönnberg et al., 2004)

Holmer et al. (2016) investigated the role of sign-phonology representations for sign language WM in the developing cognitive system. In their study, Holmer et al. (2016) found that requiring children to imitate (lists of) manual gestures improved performance more for deaf and hard-of-hearing signing children than for hearing non-signing children. For successful imitation to occur representations are needed to be kept in mind before a judgement can be passed, which means that the ability to imitate is dependent on WM. Thus, the steeper development in the hard-of-hearing signing children than the hearing non-signing children reported by Holmer et al. (2016) is likely to reflect a supportive role of existing phonological representations of signs in developing WM for signs. On a similar note, Pierce et al. (2017) argued that the role of early language experience in establishing linguistic representations is crucial for the development of phonological WM. In addition, they proposed that the state of phonological WM at any given time will constrain further learning.

However, linguistic representations seem not only to influence the development of WM for linguistic material but also non-linguistic WM. In a study by Marshall et al. (2015), individual differences in non-linguistic WM was in part explained by level of vocabulary in a group of deaf signing children. In a later study, Botting et al. (2017) reported that language skills mediated executive functioning skill, including working memory. Experiences that prepare the brain for language processing, by establishment of linguistic representations, are also important for the emerging WM system in the brain.

Modality-specific and modality-independent working memory mechanisms. Working memory seen from a communicative perspective is assumed to serve both predictive and postdictive linguistic functions (Rönnberg, et al., submitted), the predictive function is related to the ability to maintain focus while e.g. inhibiting distracting information (Sörqvist and Rönnberg, 2012) or improving recognition by means of phonological or semantic priming (Signoret et al., 2018). The postdictive aspect is about reconstructing and repairing what has been missed or misperceived in a more elaborative way than for prediction. Here, rehearsal of elements of the dialogue, combined with retrieval from semantic long-term memory may be used to infer the missing information (Rönnberg et al., 2013).

Within this framework, the study of working memory for sign language and speech allow us to understand what aspects of working memory in a communication setting are due to the specific sensorimotor mechanisms used for perception and production of the language (modality specific), and

what aspects are shared across language modalities, potentially based on higher level linguistic representations (modality-independent).

In a study of WM for sign and speech in bimodal bilingual hearing individuals, Rönnberg et al. (2004) demonstrated that working memory for signs and speech obey similar laws of memory. In terms of an analysis of serial position effects, typical bow-shaped curves were obtained, demonstrating both recency and pre-recency effects, with an overall superiority for spoken tokens. A subset of *early*, hearing native bilinguals even showed that the effect of language modality was non-significant. Thus, this result means that there are modality-independent commonalities across linguistic modalities.

Nevertheless, imaging data from studies of WM for sign language, both in deaf and hearing individuals, showed language modality-specific bilateral parietal and occipital activations for the contrast of signs over speech (Rönnberg et al., 2004; Rudner et al., 2007; Pa et al., 2009). These differences could be explained by activation differences in sensorimotor cortex elicited by the two different types of stimuli – signs will result in activations in parieto-occipital regions, whereas speech will result in activations in temporal areas. To test whether parieto-occipital activations during working memory for sign language were due to modality-specific linguistic processing or sensorimotor processing, we conducted an experiment in which we compared working memory for lexical signs and working memory for nonsense moving objects in groups of deaf and hearing participants with and without knowledge of sign language (Cardin et al., 2018). Crucially, we used point-light stimuli, significantly reducing the differences in low-level features between the stimuli. Our results showed no specific activation for working memory for signs compared with nonsense objects, suggesting that differences in working memory for linguistic and non-linguistic visual stimuli identified in previous less well-controlled studies were driven by activations in areas involved in sensorimotor processing of the stimuli, which could also be involved in storing information during working memory tasks.

In spite of this, there is a possibility that it is the type of processing (or mechanism involved in the particular processing invoked) that is crucial for language modality specific effects to occur, and not necessarily the types of stimuli used. For example, Rudner et al. (2007) investigated the episodic buffer of WM in bimodal bilinguals using n-back lists. The task requires that subjects keep track of the sequence of events (signs/words) in order to retrieve one that may match one presented earlier – just how many steps back varied from trial to trial (hence 'n-back'). The critical (mixed) list contained both lexical signs and spoken words to be compared across modality/language. These mixed lists demanded deep semantic analysis, a kind of binding process in the episodic buffer of WM between the lexical meaning of signs and words. Compared to unimodal lists, the mixed list data produced activity in right middle temporal brain areas. This may indicate that there is a neural correlate of the episodic buffer that actually connects signs with speech by binding phonological representations in the speech and

sign loops of working memory to semantic memory representations in long-term memory (Rudner et al., 2007). Furthermore, using an n-back task, Rudner et al. (2013) also showed language-modality specific effects at different levels of processing stimuli (semantic, phonological and orthographic).

The overall picture that arises from these WM studies is that language modality specificity seems to lie in the type of mental operations induced rather in the sensory input as such (Wilson and Emmorey, 1997). What type of operation within working memory is actually asked for: semantic judgements, serial recall, phonological comparisons, same/different judgments) appears to be the main determinant of brain signatures.

CONCLUSION

Bencie Woll's pioneering and ongoing studies into sign language processes have allowed us, as her colleagues and collaborators, to develop a variety of insights into the impact of deafness and sign language exposure on the development of functional specialisations in the adult brain. Sign language studies of language and working memory processing have shown largely modality-independent mechanisms. These are used for general-purpose processing, independently of the sensorimotor properties of the stimuli, and ultimately challenge theories based on sensorimotor properties of specific signals. Furthermore, neuroscience research on deafness and sign language has provided unique information about the potential of the brain for change throughout development, including infancy (when the roots of language are laid down). It is clear that neural plasticity effects can be observed as a consequence of deafness, both in auditory and non-auditory cortices, and that deafness as a model allows a much fuller interpretation of the plastic possibilities of the adult brain. Evidence from the study of deafness shows that regions considered to be dedicated to specific sensory and articulatory processes are also activated by inputs and outputs from another modality. In addition, the study of the deaf brain has clarified the function(s) of those modality-independent networks which support language processing, whether signed or spoken. However, a bigger issue is still pending – what is the functional and behavioural relevance of the reorganisation observed in the brain of deaf individuals? In animal models, a causal relationship has been established between enhanced performance in specific visual tasks and crossmodal plasticity in the auditory cortex. In humans, plastic reorganisation as a consequence of deafness also seems to impact behaviour (Bottari et al., 2011; Karns et al., 2012; Ding et al., 2015), but we are far from understanding the all-encompassing implications of these effects and the principles governing them.

Altogether, the study of deafness and sign language have allowed us to gain a better understanding of the developmental adaptability of the neural system and its largely modality-independent processes.

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