Crossmodal Plasticity, Sensory Experience, and Cognition

Valeria Vinogradova[1,2]

Velia Cardin[1]

1. Deafness, Cognition and Language Research Centre, UCL, London UK.
2. Center for Language and Brain, HSE University, Moscow Russia.

Summary

Crossmodal plasticity occurs when sensory regions of the brain adapt to process sensory inputs from different modalities. This is seen in cases of congenital and early deafness and blindness, where, in the absence of their typical inputs, auditory and visual cortices respond to other sensory information. Crossmodal plasticity in deaf and blind individuals impacts several cognitive processes, including working memory, attention, switching, numerical cognition, and language. Crossmodal plasticity in cognitive domains demonstrates that brain function and cognition are shaped by the interplay between structural connectivity, computational capacities, and early sensory experience.

Keywords: crossmodal plasticity, sensory experience, cognition, deafness, blindness, language, attention, executive functions, numerical cognition

Introduction

Crossmodal plasticity refers to the phenomenon where brain regions that usually process sensory information from one modality adapt to processing sensory information from a different modality (Bavelier & Neville, 2002; Merabet & Pascual-Leone, 2010; Rauschecker, 1995). Some of the most striking cases of crossmodal plasticity arise in congenital and early deafness and blindness, where in the absence of the typical input, auditory and visual cortices, respectively, reorganise to process other available sensory inputs (Burton et al., 2004; Finney et al., 2001, 2003; Kral, 2007; Levänen et al., 1998; Lomber et al., 2010; Nishimura et al., 1999; Reich et al., 2011; Röder et al., 2002; Striem-Amit et al., 2012).

Critically, this neural reorganisation in sensory areas also affects cognitive processing. Studies in deaf and blind humans have shown that, following early sensory deprivation, auditory and visual cortices can also acquire prominent roles in cognition (Bedny, 2017; Bedny et al., 2011, 2015; Cardin et al., 2018; Ding et al., 2015; Kanjlia et al., 2016; Manini et al., 2022). Evidence from these studies provides unique insights into the nature of crossmodal plasticity and our understanding of cognition and functional specialisation in the brain.

This article will review the evidence of crossmodal changes that impact, in humans, different cognitive domains, including language, executive function, and social cognition. It will present evidence showing that the functional properties of brain areas, including those involved in cognitive processing, are the result of the interaction between computational capacities, connectivity, plasticity, and environmental experience.

Theories of Crossmodal Plasticity

The study of crossmodal plasticity is grounded in the pioneering work on sensory deprivation conducted by Hubel and Wiesel in the late 1950s and early 1960s. They studied the ocular selectivity of cortical cells in kittens who had unilateral visual deprivation (by having one eyelid sutured early in life) (Wiesel & Hubel, 1963; Wiesel & Hubel, 1965). In fully sighted cats, most cells in the primary visual cortex (V1) respond to some degree to stimulation to both eyes. In addition, a smaller proportion of cells show ocular dominance, responding preferentially to input from either the contralateral or ipsilateral eye (Hubel and Wiesel, 1962). In kittens who had several months of unilateral monocular visual deprivation, the majority of the cells responded only to the non-deprived eye, even after eyesight was restored (Wiesel & Hubel, 1963). This experience-dependent plasticity was limited to a brief developmental time-window, suggesting that early in life there are critical periods of enhanced plasticity during which the organisation of cortical systems is strongly influenced by environmental experience (Hubel & Wiesel, 1970). This work paved the way for decades of research showing changes in the structural and functional organisation of sensory cortices in animals and humans with altered sensory experience (Fine et al., 2005; Finney et al., 2001, 2003; Kujala et al., 1997; Lomber et al., 2010; Sadato et al., 1996). These studies found crossmodal plasticity effects in visual (Kujala et al., 1997; Sadato et al., 1996) and auditory (Fine et al., 2005; Finney et al., 2001, 2003) cortices, showing that after sensory deprivation, if the main sensory input is not restored, sensory cortices will respond to other sensory information (Fine et al., 2005; Finney et al., 2001, 2003; Kujala et al., 1997; Lomber et al., 2010; Sadato et al., 1996). Further research showed a degree of flexibility in the early periods of enhanced plasticity, suggesting sensitive periods of enhanced plasticity, rather than strict critical periods (Kujala et al., 1997; Sadato et al., 2004).

The development of non-invasive neuroimaging techniques in the late 20th century allowed this research to accelerate in humans, further showing that plasticity effects not only affect sensory processing, but also higher-order cognitive functions. In congenitally and early blind humans, visual areas process inputs from other modalities (Collignon et al., 2009; Poirier et al., 2006). For example, tactile discrimination recruits primary and secondary visual cortices in blind individuals, while in sighted controls, these regions are deactivated during these tasks (Sadato et al., 1996). However, visual cortices in blind individuals also have a role in higher-order cognitive processing, such as verbal memory, verb generation (Amedi et al., 2003), language comprehension (Bedny et al., 2011; Röder et al., 2002), and response inhibition (Kanjlia et al., 2021). Similar effects are found in the auditory cortex of deaf individuals, where there is increased activity in response to visual and tactile inputs (Bavelier et al., 2001; Benetti et al., 2021; Finney et al., 2001; Karns et al., 2012). In addition, auditory areas in deaf individuals are also recruited for higher-order cognitive functions including language processing, working memory, and task switching (Buchsbaum et al., 2005; Capek et al., 2008; Cardin et al., 2013; Ding et al., 2015; MacSweeney et al., 2004; Manini et al., 2022; Neville et al., 1998).

These findings have led to two main theories of crossmodal plasticity in deafness and blindness. Several studies propose a preservation of function in sensory areas, where regions maintain their original computation but adapt to respond to a different sensory modality (Benetti et al., 2017, 2021; Bola et al., 2017; Cardin et al., 2013; Heimler et al., 2015; Lomber et al., 2010; Ricciardi et al., 2009). For example, the visual motion area hMT+/V5 of blind individuals is recruited during auditory and tactile motion processing (Collignon et al., 2011; Matteau et al., 2010; Poirier et al., 2006). In deaf individuals, temporal brain areas usually involved in voice processing in hearing individuals are activated by visual faces (Benetti et al., 2017). Other studies have shown responses to higher-order cognitive tasks in sensory-deprived areas, suggesting a functional change, where cortices change their computations and contribute to higher-order cognitive processes (Cardin et al., 2013; Ding et al., 2015; Manini et al., 2022). Evidence such as language responses in visual areas in blind individuals (Amedi et al., 2004; Bedny et al., 2011; Burton, Snyder, Conturo, et al., 2002), or working memory responses in auditory areas of deaf individuals, support this view (Cardin et al., 2013; Ding et al., 2015).

The following sections of this article will provide a discussion on how changes in the processing of cognitive functions occur under both instances of functional preservation and change, showing that sensory experience is fundamental for establishing cognitive processing networks. The focus will be on evidence from congenital or early sensory deprivation, as studies of plasticity effects on cognition have been undertaken among such cohorts. However, it should be kept in mind that the existing studies of cognition and plasticity in late-onset deafness and blindness also suggest a degree of reorganisation for these functions (Bedny et al., 2012; Campbell & Sharma, 2014).

Language

Language has been widely studied in the context of crossmodal plasticity. In natural communication, human languages use multi modal sensory streams to convey meaning and aid human communication (Holler & Levinson, 2019). Spoken languages are produced by the movement of orofacial articulators and accompanying body gestures, and they are perceived auditorily and visually (Gullberg, 2022; Holler & Levinson, 2019). The importance of visual signals for spoken languages was especially evident during the COVID-19 pandemic, where face masks significantly hindered face-to-face spoken communication (Saunders et al., 2021). In addition, the existence of phenomena such as the McGurk effect, where altered visual lip patterns make a person perceive a sound differently from what was actually said (McGurk & MacDonald, 1976), emphasise the relevance of visual information in decoding speech. Sign languages, on the other hand, rely on articulations of the hands, arms, and face (Sutton-Spence & Woll, 1999; Valli & Lucas, 2000). While most sign languages are perceived visually, there are also tactile varieties that are used by deaf-blind individuals (Mesch, 2001).

Individuals who are born deaf, or become deaf very early in life, acquire and process language relying more on visual information. Similarly, early blind individuals rely more strongly on auditory language information than their hearing peers. Consequently, language comprehension through these accessible modalities can be developed to a higher level in deaf and blind individuals. For instance, superior speechreading (lipreading) has been described in deaf individuals (Bernstein et al., 2001; Elphick, 1996; Mohammed et al., 2006), and blind individuals show better auditory speech perception (measured as resilience to noise; Rokem & Ahissar, 2009). These effects indicate behavioural compensation that could be related to crossmodal changes in the neural processing of language. Results from neuroscience studies addressing this topic show that specialisation for language within the classical perisylvian network is reliably found in blind (Dietrich et al., 2013; Röder et al., 2002) and deaf adults (Corina, 1998; Hickok et al., 1998, 2002; MacSweeney et al., 2004; MacSweeney, Woll, Campbell, McGuire, et al., 2002; Nishimura et al., 1999; Poizner et al., 1990). Nevertheless, there are also differences that suggest an impact of sensory experience on language processing.

Different responses to language stimuli between deaf and hearing individuals have been found in the left temporal areas, such as the superior temporal cortex (STC) (MacSweeney, Woll, Campbell, McGuire, et al., 2002; Twomey et al., 2017, 2020) and the posterior parietal cortex (Bavelier et al., 2001). However, because several studies of language in deaf individuals study sign languages, differences between deaf and hearing individuals can be due to modality effects (sign language vs spoken language), or plasticity induced by reduced auditory inputs. Dissociating between these factors is important to successfully isolate the effects of sensory experience. For example, it has been shown that the left superior parietal lobule and the left supramarginal gyrus are activated more for sign production in deaf signers than for speech production in hearing speakers (Emmorey et al., 2007). However, this effect is also found in hearing signers (Braun et al., 2001; Emmorey et al., 2014), indicating that these increased activations are specific to sign language knowledge, rather than sensory experience.

One reliable effect associated with the different sensory experience of deaf individuals is the recruitment of middle and anterior portions of the left STC for sign language processing. In hearing individuals, these regions are involved in auditory and speech processing, including speechreading, but they are not recruited for sign language processing (MacSweeney, Woll, Campbell, Calvert, et al., 2002; Söderfeldt et al., 1997). MacSweeney et al. (2002) showed activations along the left STC in deaf signers during a sentence acceptability task. This was not found in hearing native signers, where activations were constrained to more posterior parts of the STC. Similar results were found when comparing activations in deaf and hearing signers during a sign comprehension task (Sadato et al., 2004), working memory task (Rönnberg et al., 2004), sign phonological processing task (Twomey et al., 2017), when comparing sign processing vs gestural processing (MacSweeney et al., 2004), during a semantic judgement task (Twomey et al., 2020), or when comparing point-light signs to point-light nonsense objects (Cardin et al., 2018). In all these cases, activations for the sign language condition were found in deaf signers, but not in the control group of hearing signers.

Further work confirmed that the left STC had a role in linguistic processing of sign languages, and not general visuo-spatial processing crossmodal plasticity effects. Cardin et al. (2013) showed that fMRI activations in anterior portions of the left STC were only present in deaf signers, and not in deaf non-signers, highlighting that this is a language- specific effect. Furthermore, in a MEG study of sign language processing, Leonard et al. (2012) showed that lexicosemantic processing in deaf signers activates the left frontotemporal language network, including left STC, only during a late time window associated with lexicosemantic integration, but not during an earlier time window associated with sensory processing (Leonard et al., 2012).

Differences are also found between deaf and hearing individuals when studying speechreading. While both these groups recruit superior temporal cortices during speechreading, these activations are stronger in deaf signers (Capek et al., 2010), suggesting a plasticity effect. Moreover, activations in the posterior portion of the superior temporal gyrus were positively associated with speechreading scores in deaf, but not in hearing, participants. These findings suggest that, in deaf individuals, the STC could develop to respond to visual language, while in hearing individuals it could be more strongly tuned to auditory speech (Capek et al., 2008).

Together, these studies show that language processing in the left STC can be modulated by sensory experience: regions that typically engage in auditory and speech processing in hearing individuals start responding more strongly to visual language information – either sign language or speechreading – when auditory inputs are significantly reduced from early development. These findings establish that language processing in the brain is not determined by a specific modality of sensory input, and that traditional spoken language processing areas, such as anterior portions of the left STC, can process language in different modalities.

In blind individuals, reorganisation for language processing has been observed in the extrastriate and striate visual cortices. This includes neural responses to speech comprehension (Bedny et al., 2011; Röder et al., 2002), verb generation (Amedi et al., 2003; Burton, Snyder, Diamond, et al., 2002), and Braille reading (Burton, Snyder, Conturo, et al., 2002). These responses to spoken language processing in the visual cortex are modulated by grammatical properties of the stimuli, such as syntactic complexity (Bedny et al., 2011; Kanjlia et al., 2016; Lane et al., 2015; Röder et al., 2002), phonological, and lexical information (Bedny et al., 2011). These modulations suggest that such responses are not related to sound processing, but rather, to the linguistic complexity of the signal. Moreover, in blind adults, transcranial magnetic stimulation (TMS) applied to the occipital lobe interferes with semantic verb generation (Amedi et al., 2004) and Braille reading (Cohen et al., 1997), suggesting that language processing in visual areas impacts behavioural outcomes.

One of the regions where language has been studied in more detail in blind individuals is the left ventral occipito-temporal cortex (VOTC), or the visual word form area (VWFA). This region is associated with reading skills in sighted individuals (Brem et al., 2020; Dehaene et al., 2010), but it has also been shown to be active during several visual language tasks (Price & Devlin, 2003; Waters et al., 2007). In blind adults, this region is recruited during Braille reading (Kim et al., 2017; Reich et al., 2011) and when listening to sound-coded visual letters (Striem-Amit et al., 2012). Critically, this area is sensitive to the grammatical complexity of spoken sentences only in blind adults, suggesting that it is less selective for reading and that it takes on a higher-order language processing function in blind individuals (Kim et al., 2017), potentially serving as “a gateway region for the language to enter the visual system” (Bedny and MasSweeney, 2019).

Overall, there is considerable evidence of a specialisation for language processing in blind individuals in cortical areas that are typically considered “visual”. Some of these effects could be linked to linguistic processing that is already localised to such regions, such as is the case of the VWFA. However, the recruitment of the primary visual cortex for language processing in blind individuals suggests a functional change. This has significant implications for our understanding of the neural specialisation for natural language in the human brain. Bedny and MacSweeney (2019) suggest that occipital areas that show crossmodal plasticity in blind individuals in language processing are incorporated into the frontotemporal language network. Evidence showing functional connectivity between the left occipital areas reorganised for language and the left prefrontal language regions and thalamus is higher in blind individuals than in sighted controls further supports this view (Bedny et al., 2011).

In summary, patterns of crossmodal plasticity from language studies support accounts of both, functional preservation and functional change. Activations in the left superior temporal cortices during sign language processing and speechreading in deaf individuals suggest preservation of function, but with responses to a different sensory modality. Instead, language responses in early visual cortices of blind individuals suggest a functional change. More importantly, these results indicate that while there is a core network of areas involved in language processing, additional regions can be integrated into this network depending on sensory input and language modality.

Executive Functions

Executive functions comprise cognitive domains that support goal-directed behaviours, including sustained attention, working memory (WM), inhibition, planning, and flexibility (Niendam et al., 2012). In deaf and blind adults, compensatory changes have been suggested in key domains of executive processing (Arcos et al., 2022; Ding et al., 2015). One domain that has been studied extensively in blind and deaf individuals is working memory. Blind children (Withagen et al., 2013) and adults (Dormal et al., 2016) show enhanced auditory WM abilities compared to sighted controls. Enhanced visual WM abilities have also been reported in deaf individuals (Cardin et al., 2018; Ding et al., 2015), although this evidence is not consistent (Andin et al., 2021; Manini et al., 2022) and may be heavily dependent on language experience (as in studies of deaf children; Botting et al., 2017; Marshall et al., 2015). While it is still unclear whether all these behavioural differences are linked to crossmodal plasticity effects, there is substantive evidence showing that sensory experience modulates WM processing in the brain. In blind individuals, tactile spatial WM (Bonino et al., 2008), and auditory identity, pitch, and location WM tasks (Park et al., 2011) activate visual occipital areas. In deaf individuals, but not in hearing controls, the STC is recruited during visual and somatosensory WM tasks (Andin et al., 2021; Bonna et al., 2021; Buchsbaum et al., 2005; Cardin et al., 2013; Ding et al., 2015). This is accompanied by an increase in connectivity between STC and frontal regions involved in cognitive control, attention, and salience/alerting (Andin et al., 2021; Cardin et al., 2018; Ding et al., 2016). Furthermore, in deaf individuals, the amplitude of the crossmodal activation during the maintenance period of a visuo-spatial WM task is associated with faster reaction times (Ding et al., 2015).

One possibility is that these effects are not specific to WM, but that they reflect a more general involvement of reorganised auditory and visual cortices in cognitive control, mimicking the role of frontoparietal brain regions involved in WM and other executive function tasks. Manini, Vinogradova, et al. (2022) addressed this question in deaf individuals using four visuospatial executive tasks: WM, inhibition, planning, and switching. Only task switching induced significant responses across auditory regions, including the bilateral planum temporale and posterior STC, and left primary auditory cortex (Heschl's gyrus) (Manini et al., 2022). Furthermore, activity in these areas predicted behavioural performance in the switching task in the group of deaf individuals, indicating a behavioural relevance for this functional reorganisation. This finding suggests a change in function in superior temporal areas of deaf individuals, from auditory to cognitive processing. However, it is unlikely that the function of reorganised auditory regions is cognitive control or a subprocess of WM such as storage or updating, given that, of the four executive function tasks, only switching resulted in significant recruitment of superior temporal areas. These findings suggest that the role of reorganised auditory regions might be linked to shifting between tasks or mental states. This is supported by evidence from resting state connectivity studies showing increased connectivity in deaf individuals between auditory areas and regions of the salience/ventral attention network (Cardin et al., 2023).

In understanding the origins of these functional changes, it is important to consider the developmental trajectory of executive processing in the brain. Evidence from developmental studies shows that temporal cortices are recruited during visual switching tasks in typically hearing children (Engelhardt et al., 2019). Thus, it is possible that early during development this cortex has a role in switching in deaf and hearing individuals. Later in life, given the increased computational needs for auditory processing in hearing individuals, the function of these regions follows different developmental pathways in deaf and hearing individuals. Another possibility is that the recruitment of the temporal cortex for task switching is guided by top-down projections from adjacent temporal and parietal regions, such as the temporoparietal junction (TPJ). TPJ is involved in reorientation of attention (Corbetta & Shulman, 2002; Dugué et al., 2018) and changing tasks sets (Geng & Mangun, 2011). Its vicinity to the auditory cortex could influence its functional role in deaf individuals.

Indeed, it has been suggested that specific aspects of visual attention are modified by early sensory experience, including enhanced peripheral attention in deaf individuals (Bavelier et al., 2000; Dye et al., 2007; Neville & Lawson, 1987; Parasnis & Samar, 1985; Proksch & Bavelier, 2002; C. Stevens & Neville, 2006). Evidence suggests that at least some of these effects can be supported by crossmodal plasticity changes. Using optical imaging, Seymour et al. (2017) found increased activations in deaf individuals in the right posterior STC during a peripheral selective attention task (Seymour et al., 2017). Activations in the superior temporal cortex (Bavelier et al., 2001; Benetti et al., 2021; Fine et al., 2005) have also been described during visual motion processing in deaf individuals, and one interpretation is that these activations could also be related to allocation of attention to relevant items and locations.

Blind individuals also show enhanced attention abilities in the periphery in an auditory localisation experiment (Fieger et al., 2006; Röder et al., 1999). Blind individuals respond faster in spatial attention detection/localisation tasks but are slower in nonspatial frequency discrimination tasks, which could indicate the enhancement of the posterior-dorsal "where" pathway but not the anterior-ventral "what" pathway (Chen et al., 2006). Evidence also suggests that, in blind individuals, crossmodal reorganisation of visual cortices support some of these auditory attention effects (Garg et al., 2007; Stevens et al., 2007). In blind individuals, but not in sighted controls, the medial occipital cortex is activated with the presentation of a cue signalling a discrimination trial, but not with cues that signal a no-trial (Stevens et al., 2007). Furthermore, the pattern of activation resembles the preparatory effects observed in visual selective attention paradigms in sighted individuals (Stevens et al., 2007). The medial occipital cortex is also recruited during a covert auditory attention switching task in blind individuals, with the peak of the response coinciding with the appearance of the target stimuli, suggesting a bottom-up reallocation of attention effect or increased processing of targets, rather than a top-down orientation of attention role (Garg et al., 2007). Tasks of numerical cognition (Kanjlia et al., 2016) or inhibition (Kanjlia et al., 2021) also activate overlapping regions of the visual cortex, and one suggestion is that attention may be a common underlying process for these effects (Röder et al., 1997; Sadato et al., 1996; Weaver & Stevens, 2007)

In summary, the evidence presented in this section shows that several executive function tasks activate visual and auditory areas in blind and deaf individuals, independently of the sensory composition of the stimuli. One possibility is that a shared process, such as reorienting of attention, is the common underlying process for these effects. In any event, crossmodal plasticity findings suggest that the scope of function for “sensory” regions transcends processing sensory features, and that under circumstances such as reduced sensory inputs during the sensitive periods, these regions can develop to implement components of complex cognition.

Numerical Cognition

Numerical cognition encompasses abilities related to understanding and manipulating numerical information and is involved in many aspects of life in modern society (Bull, 2008). One of the prevailing theoretical accounts of numerical processing is the triple code model (Dahaene, 1992) that suggests a dissociation between different arithmetic operations in the brain (Dehaene & Cohen, 1997; Dehaene et al., 2005). The model identifies a visual code that is used for processing digits visually, a verbal code that relies on accessing verbal memory and linguistic functions, and a magnitude code, which requires representing numbers on a mental number line.

Studies of numerical processing in deaf and blind individuals show experience-driven changes in neural correlates of different aspects of numerical processing, and in distinct types of brain areas. The right inferior parietal sulcus is an area typically involved in magnitude manipulation (Dehaene et al., 2005). It has been shown that, during simple multiplication, deaf adults activate this region more strongly than hearing controls (Andin et al., 2019). Further studies did not find any other significant differences between deaf and hearing participants in numerical processing, other than a stronger involvement of the left inferior frontal gyrus in the hearing group (Andin et al., 2023). Overall, these findings suggest enhanced involvement of the magnitude system in deaf adults, and a lack of cross-modal plasticity effects in sensory areas, as the whole-brain analysis does not identify differences between groups in arithmetic processing (Andin et al., 2019). In blind individuals, on the other hand, numeric processing recruits the visual cortex (Kanjlia et al., 2016; Crollen et al., 2019). One of the proposed explanations for these effects is the early developmental changes allowing high functional flexibility and the incorporation of the visual areas into the frontoparietal number network, as shown by the increased connectivity between the maths-responsive cortices in blind individuals (Kanjlia et al., 2016). An alternative account suggests that when cross-modal plasticity occurs in visual areas in blind individuals during numeric processing, visual cortices preserve their computational properties, namely in the spatial processing domain (Crollen et al., 2019). Visual cortices in blind participants are activated during subtraction, but not during multiplication (Crollen et al., 2019). Subtraction has been associated with representations along the “mental number line” and may be decoded within the same region that is responsible for eye movements along the left-right continuum (Knops et al., 2009). The selective response for subtraction in the visual cortex of blind individuals can be explained through the preservation of the spatial processing function of the visual dorsal stream (Milner & Goodale, 1995; Mishkin et al., 1983), suggesting that cross-modal plasticity results from common computational properties of the regions (Crollen et al., 2019).

The distinct phenomena observed in studies of numerical processing in deaf and blind individuals may point to the role of the computational properties of the sensory regions in shaping cross-modal plasticity for cognition (if spatial representations in the visual cortex allow their recruitment for subtraction in blind participants), but also to the role of experience in other cognitive domains, such as language. Multiplication is processed differently in the brain of deaf individuals (Andin et al., 2019), but this has not been found in blind individuals (Crollen et al., 2019). Deaf participants seem to rely more on the non-verbal, magnitude system of numerical processing for multiplication than hearing controls (Andin et al., 2019), while typically multiplication involves verbal processing (Dehaene et al., 1997, 2005). Behaviourally, deaf adults have been found to be less accurate or slower in tasks involving the verbal code, such as multiplication (Nunes et al., 2009; Andin et al., 2014, 2023). In a group of deaf signing adults, but not in hearing non-signers, multiplication skills were linked to alphabetical and phonological processing skills (Andin et al., 2014), suggesting that successful acquisition of sign language phonology can aid multiplicative reasoning.

Social Perception and Cognition

Social cognition refers to the psychological processes that allow individuals to interact (Frith & Frith, 2007). Face and voice perception and recognition are of paramount importance for social cognition (Streri et al., 2013), providing valuable cues that facilitate communication and interaction. In sign languages, facial expressions can take on linguistic meaning (Liddell, 1980; Wilbur, 2000), and speechreading is an important source of access to spoken language in deaf and hearing individuals (R. Campbell, 2011; Worster et al., 2018). Voice perception is also critical for human social communication, as it not only allows us to extract meaning from speech, but it also provides important affective and identity information (Belin et al., 2004), both in sighted and blind individuals (Hölig et al., 2014a).

Studies of face identity suggest that crossmodal reorganisation in deaf individuals supports this process. Face selectivity has been shown in deaf individuals in the right mid-STC (Benetti et al., 2017; McCullough et al., 2005; Weisberg et al., 2012), an area that overlaps with a region involved in voice processing in hearing individuals (Belin et al., 2000; Latinus et al., 2011). This activation is accompanied by a face-selective evoked component peaking at ~192ms (Benetti et al., 2017).

Face selectivity in mid-STC was not found in hearing signers, suggesting that this is an effect of sensory experience, and not of sign language use (Benetti et al., 2017). This enhancement for face selectivity in the mid-STC in deaf individuals may be supported by reorganisation of long-range functional connectivity between early visual and reorganised STC areas (Benetti et al., 2017). Alternatively, it could be triggered by the anatomical proximity to the posterior superior temporal sulcus (STS) that is suggested to be a “people-selective, heteromodal” region supporting social-information processing (Watson et al., 2014). Cross modal plasticity changes in face processing have also been found using EEG source reconstruction, where significant activations were localised to the auditory cortices of deaf native signers during an individual face discrimination task, but not during face-object categorisation task (Bottari et al., 2020).

In blind individuals, there are categorical responses to sounds (including voices) in visual cortical areas, but there is no consistent evidence showing specific voice processing and recognition effects. Categorical membership of sounds is reliably encoded in the ventral occipito-temporal cortex of blind individuals (Mattioni et al., 2022). In this study, Mattioni et al. (2022) demonstrated differences in categorical representation between blind and sighted groups in temporal and occipital regions, with enhanced decoding accuracies for sound categories in the occipital regions of the blind participants and decreased decoding accuracy in their temporal cortex. While these differences were observed across several categories, suggesting that the effect is not specific to voices, the representation of the voice category was one of the most significantly altered in blind groups compared to sighted individuals.

Stronger activations are found in the left STS in blind individuals during voice processing (Gougoux et al., 2009), suggesting an intra-modal effect as a consequence of sensory experience. Gougoux et al. (2009) also found crossmodal activations in the occipital cortex of blind individuals, but these were present when comparing sounds to silence, and were also not specific to voices. Hölig and colleagues (2014b) used an fMRI priming paradigm and showed increased activation during voice processing in the right anterior fusiform gyrus in blind individuals and in the right posterior STS in the sighted group. The increased activations in the right fusiform gyrus suggest crossmodal plasticity effects during voice recognition, but it is unclear whether this effect is specific to voices. In a study addressing this question, (Dormal et al., 2018) found that, when contrasted to scrambled voices, vocal sounds only elicited preferential responses in blind individuals in a small area of the bilateral fusiform gyrus, but this area also showed larger responses for object sounds compared to voices. They also found that the functional connectivity between the left temporal voice area and the right fusiform gyrus was enhanced in blind individuals in comparison to sighted controls. This increased connectivity, according to the authors, may support general crossmodal plasticity for processing vocal and non-vocal auditory objects in the visual cortex of early blind individuals (Dormal et al., 2018).

The development of aspects of social cognition such as face and voice processing coincides, to a certain extent, with the periods during early infancy of maximum plasticity in sensory cortices (Hensch, 2005; Spolidoro et al., 2009). However, other aspects of social cognition, such as Theory of Mind (ToM), take longer to develop, spanning through adolescence and early adulthood (Valle et al., 2015). ToM is the ability to attribute mental states of others and to predict behaviour based on these states (Premack & Woodruff, 1978). While some components of ToM develop in childhood, other aspects continue developing into adolescence (Valle et al., 2015), with the behavioural maturation of ToM being associated with age-related changes in white matter in temporoparietal regions, the precuneus, and medial prefrontal cortex (Grosse Wiesmann et al., 2017).

Neuroscience studies of social cognition studies suggest that the functional profile for ToM is similar in blind and sighted individuals (Arioli et al., 2021; Bedny et al., 2009; Ricciardi et al., 2009). For example, representations of the sensory modality of mental states of others (whether a person has seen or heard something) are successfully decoded in the same cortical regions (specifically, the TPJ) in blind and sighted adults (Koster-Hale et al., 2014). In a meta-analysis, Arioli et al. (2021) did not find evidence for consistent crossmodal recruitment of the visual cortex in social functions in blind individuals. The authors suggest that the lack of consistent crossmodal recruitment in the visual cortex of blind individuals is due to the ability of the higher-level regions to mediate social tasks without recruiting additional resources in blind individuals. Behaviourally, blind children have been suggested to experience delays in ToM development (Brown et al., 1997; Peterson et al., 2000) including auditory versions of the false-belief task (McAlpine & Moore, 1995; Minter et al., 1998; Peterson et al., 2000). However, blind adolescents have been shown to catch up with their peers (Brambring & Asbrock, 2010), and blind adults develop effective ToM (Bedny et al., 2009), suggesting that, at most, early visual experiences may affect the trajectory of development of ToM, but not its final outcome.

Differences in performance in ToM tasks have not been found when comparing deaf native signers and hearing non-signers (Meristo et al., 2007; Peterson & Siegal, 1999; Woolfe et al., 2002). Both these groups of individuals typically have early and fully accessible language development (e.g. deaf native signers; Meristo et al., 2007; Peterson & Siegal, 1999; Woolfe et al., 2002). However, differences are found between such groups and deaf children with other language experiences, such as those who were raised in a spoken language environment (Meristo et al., 2007; Peterson et al., 2000; Peterson & Siegal, 1999; Russell et al., 1998; Schick et al., 2007; Woolfe et al., 2002). These differences in ToM tasks cannot be due to a different sensory experience, since they are not found in deaf native signers, and have been attributed to a lack of early access to language (Schick et al., 2007), early conversational experiences (Woolfe et al., 2002), and sharing language about mental states (Meristo et al., 2012). This is also supported by neuroimaging evidence showing that deaf children who experienced delayed access to language not only show deficits in ToM tasks, but also have a different neural response profile in the right TPJ, a critical region for ToM (Richardson & Saxe, 2020).

The conversational account of differences in ToM development can be extended to blind children, potentially explaining the differences in the development of ToM in this population. Blindness affects the nature and extent of parent-child communication in blind infants and preschoolers, with blind infants having difficulties in sharing opinions about objects with their mothers in infancy (Preisler, 1991). Social restrictions in discourse and exchange of information about mental state that arise in the context of blindness and deafness in sighted and hearing families, respectively, may explain the differences in both populations, if indeed ToM arises from experience with discussing mental states, beliefs, and intentions (Dunn, 1994; Peterson et al., 2000).

In summary, while there are crossmodal modulations in face and voice processing due to deafness and blindness, such effects have not been found in more complex social cognition tasks. This could be because social cognition has a longer period of development, spanning through adolescence and early adulthood, while the periods of maximum plasticity in sensory cortices are during early infancy (Hensch, 2005; Spolidoro et al., 2009). It is also likely that typically sensory regions lack the computational capacity and connectivity required for advanced social cognition, unlike the brain's "higher-order, evolutionarily newer" (Sydnor et al., 2021) association cortices which have evolved to implement these.

Conclusion

Studies of crossmodal plasticity in deafness and blindness have provided unique insights into our understanding of human cognition. They have shown that sensory experience significantly shapes cognitive processing in the brain. In blind individuals, there is recruitment of early visual cortices for language, numerical, and working memory processing, functions that are not typically associated with these cortical regions. Likewise, evidence of recruitment of auditory areas for working memory and cognitive switching in deaf individuals also suggest a functional change, where these areas can be incorporated into cognitive functional networks. In addition, evidence from studies of deaf individuals showing modulation of face processing responses in areas typically involved in voice identity, or accounts of sign language processing in regions associated with speech processing, suggest a functional preservation but a change in the input modality. Thus, it is clear that in both cases of functional preservation and functional change, sensory experience and crossmodal plasticity influence cognitive processing. The term "crossmodal plasticity" may be at times confusing when describing cases of cognitive processing in sensory cortices of deaf and blind individuals. “Cross-functional” plasticity may be a more fitting term for such cases where cognitive functions recruit sensory areas. However, it is not yet clear whether these plasticity effects reflect drastic changes of function, and indeed need a different terminology.

Understanding plasticity effects can provide crucial insights into the neural constraints and requirements of different cognitive processes, and enable us to harness them for developing effective treatments and interventions. For instance, the development of sensory restoration and sensory substitution devices is reliant on our understanding of neural plasticity mechanisms (Bubic et al., 2010). Sensory substitution – a technique based on conveying information from one modality into another – may have a capacity to support cognitive skills through facilitating the processing of input from other modalities in the brain areas of deaf and blind individuals. The role of crossmodal plasticity in sensory restoration procedures has been controversial in relation to both audition and vision (Heimler et al., 2014), but especially with regard to hearing restoration and visual language. While factors such as the duration of deafness have been linked to cochlear implant outcomes and cortical activity in the temporal regions (Green et al., 2005; Lazard et al., 2013), the variance in the performance outcomes can remain largely unexplained by predictors based on durations of deafness or cochlear implant use, etiology, and age of onset (Lazard et al., 2012). Crossmodal reorganisation takes place even in cases of adult-onset hearing loss (Campbell & Sharma, 2014), and there is evidence of cortical reorganisation not only in temporal but also in frontal areas in early-stage adult-onset hearing loss (Campbell & Sharma, 2013), demonstrating a potential relevance of interactions with cognition. Recently, a study showed that the recruitment of auditory cortices for visual language after hearing restoration with a cochlear implant is linked to better speech understanding (Anderson et al., 2017). Experienced cochlear implant users show greater activity in the left middle temporal cortex, an area of multisensory integration, suggesting development of cooperation between auditory and visual language strategies after cochlear implantation, and emphasising the role of audio-visual plasticity in speech recovery (Barone et al., 2013; Strelnikov et al., 2015). Research that takes into account different aspects of cognitive functioning, such as the role of sensitive periods for language acquisition and experience with visual language, has been lacking in the field of sensory restoration, and language and cognitive development should be taken into account when developing rehabilitation tools (Lyness et al., 2013).

Regardless of whether crossmodal plasticity manifests as sensory processing of inputs from other modalities, or during the execution of cognitive tasks, there might be shared underlying mechanisms and anatomical constraints. Specifically, crossmodal plasticity depends strongly on the connectivity and computational capacities of sensory regions. Evidence suggests that crossmodal plasticity builds on pre-existing functional connectivity biases (Collignon et al., 2009, 2013; Kanjlia et al., 2016) and innate structural connectivity (Benetti et al., 2018). This reliance on pre-existing connections will apply for cases of both, functional preservation and functional change. For instance, it has been proposed that direct structural connections between the fusiform face area and the temporal voice area (Blank et al., 2011) can facilitate the functional reorganisation found in the temporal voice area of deaf individuals during face processing (Benetti et al., 2017) and crossmodal plasticity during voice recognition in blind individuals in the fusiform gyrus (Hölig et al., 2014b). Bonna et al. (2021) also propose that altered connectivity between the salience, frontoparietal and default mode networks in deaf individuals may support enhanced performance in attentional and working memory tasks (Bonna et al., 2021).

The computational capacities of reorganised areas will also constrain the nature and extent of plastic changes. For theories of functional preservation, the assumption is that the computations are the same (Crollen et al., 2019; Lingnau et al., 2014; Pascual-Leone & Hamilton, 2001; Renier et al., 2014), so no additional computations would have to be implemented. This could also be the case for reorganisation that suggests a functional change. It has been proposed that higher-order cognitive functions that activate sensory cortices in blind individuals might have common computational properties to the functions typically performed by the visual cortices, even in numerical cognition (Crollen et al., 2019). For example, one of the proposed explanations for the involvement of the visual cortex in subtraction in blind individuals is that because subtraction engages “spatial” processing, which has common computational properties to the right dorsal occipital cortex region that is selectively activated for subtraction but not multiplication (Crollen et al., 2019).

Alternatively, some of the computational changes proposed in cases such as language processing in the visual cortex of blind individuals or switching in the auditory cortices of deaf individuals could be facilitated by pre-existing connections. Functional and structural neuroimaging studies propose the existence of broad sensory-biassed networks within the human frontal cortex (Braga et al., 2017; Michalka et al., 2015; Tobyne et al., 2017). These structural and functional connections between frontoparietal and sensory areas may selectively guide crossmodal reorganisation for higher-order cognitive functions in deaf and blind individuals. Similarly, vicinity of auditory temporal areas to the TPJ might influence some of the crossmodal effects observed in deaf individuals. The TPJ-pSTS has been proposed as a hub that coordinates different brain networks and underlies social abilities in humans (Patel et al., 2019). It integrates inputs from the thalamus, the limbic system, as well as sensory areas (Decety & Grèzes, 2006). Its heteromodality may aid the crossmodal plasticity observed in the adjacent temporal cortices during face processing (Benetti et al., 2017) and cognitive switching (Manini et al., 2022) in deaf individuals.

Neural processing of higher-order cognitive functions in sensory areas of deaf and blind individuals could also be explained through quantitative changes in the balance between sensory and cognitive processing occurring during development in these areas. Switching and inhibition result in activations in the temporal and occipital cortices in hearing and sighted children with a mean age of 10 (Engelhardt et al., 2019), and have been shown to engage sensory-deprived temporal and occipital cortices in deaf and blind adults (switching, deaf: Manini et al., 2022; inhibition, blind: Kanjlia et al., 2021).

So far, crossmodal plasticity effects related to cognition are found in domains such as language, attention, working memory, and face/voice processing, but there is no evidence of an effect on complex social cognition, such as Theory of Mind. Potentially, the connectivity and computational capacities of “sensory” areas can be adequate for facilitating processes such as attention and working memory, but they are unlikely to sustain complex social cognition. Notwithstanding, research in this area is limited, and further evidence might reveal unknown effects on complex social cognition.

In conclusion, crossmodal plasticity in sensory areas of deaf and blind individuals suggests that reorganisation is not restricted to sensory processing in other modalities. Sensory areas can also be involved in cognitive processes such as working memory, attention, switching, and language processing. The implications of these plasticity effects are multifaceted. It shows that the interplay between connectivity, computational capacities and experience fundamentally shapes the functionality of a given region within the brain. It also suggests that cognitive processes can be influenced by sensory experiences through either mechanisms of functional preservation or functional change. Moreover, changes are not symmetrical across sensory cortices and cognitive functions, if we consider evidence from studies on deafness and blindness together. Differences can arise from the environmental experiences of the populations, as in the case of deaf individuals, for whom reduced access to language can have long-standing effects on cognition and brain function, or functional capacities of the sensory regions. Critically, a comprehensive understanding of the physiological and behavioural mechanisms accompanying these crossmodal changes could allow us to harness this computational power for cognition.

Further Reading

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