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Chapter 7

Cross-modal integration and plasticity in the superior temporal cortex

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Abstract

In congenitally deaf people, temporal regions typically believed to be primarily auditory enhance their response to nonauditory information. The neural mechanisms and functional principles underlying this phenomenon, as well as its impact on auditory recovery after sensory restoration, yet remain debated. In this chapter, we demonstrate that the cross-modal recruitment of temporal regions by visual inputs in congenitally deaf people follows organizational principles known to be present in the hearing brain. We propose that the functional and structural mechanisms allowing optimal convergence of multisensory information in the temporal cortex of hearing people also provide the neural scaffolding for feeding visual or tactile information into the deafened temporal areas. Innate in their nature, such anatomo-functional links between the auditory and other sensory systems would represent the common substrate of both early multisensory integration and expression of selective cross-modal plasticity in the superior temporal cortex.

INTRODUCTION[1]

Decades of research into cognitive neuroscience have evidenced the extraordinary ability of the human brain to adapt its anatomo-functional components in response to experience, typically referred to as brain neuroplasticity. Most humans can interact appropriately with the surrounding environment thanks to multiple senses and specialized sensory organs that capture and integrate multisensory signals. It is now widely accepted that both experiential exposure and endogenous constraints influence the development of the dynamic neural connections and functional units that subtend unified and coherent sensory experiences (Knudsen, 2004; Hensch, 2005; Takesian and Hensch, 2013). There is also consistent evidence that multisensory convergence and integration increase perceptual accuracy by allowing access to redundant sensory cues that are necessary for full object characterization (Calvert and Thesen, 2004; Stein and Stanford, 2008).

Some individuals, however, cannot rely on all their sensory systems since they were born without, or have lost early or late in life, one or more senses. This is, for example, the case of blind and deaf individuals. Early views, mostly based on “deficiency” theories of sensory deprivation (Myklebust and Brutten, 1953; Axelrod, 1959) predicted that sensory deprivation would substantially impair the remaining sensory and high-level cognitive systems. In contrast to such views, it has become clear that sensory-deprived individuals can impressively compensate for their sensory loss thanks to enhanced abilities in the remaining senses and that such

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[1] Abbreviations used in the chapter are listed at the end of the chapter before References section.

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*Correspondence to: Olivier Collignon Sr. Phd, 10, Place du Cardinal Mercier, Louvain-La-Neuve, 1348, Belgium. Tel: +32-10-47-44-75, E-mail: olivier.collignon@uclouvain.be adaptation is paralleled by concurrent brain changes (Rauschecker, 1995; Merabet and Pascual-Leone, 2010; Voss et al., 2010; Frasnelli et al., 2011). Sensory deprivation can induce changes at different brain levels: changes involving brain regions dedicated to the processing of the remaining senses are referred to as *intramodal plasticity*, whereas changes occurring in regions that normally would process the lost sensory modality are referred to as *cross-modal plasticity*. Since intra- and cross-modal plasticity plausibly reflect different neural mechanisms of adaptation, the study of individuals with sensory deprivation is a unique model to test how sensory experience and intrinsic genetic constraints interact to shape the development of functional brain specialization.

The purpose of this chapter is to provide an overview of the impact that early auditory deprivation exerts on the functional specialization of the superior temporal cortex (STC), and the extent and properties of cross-modal plasticity in this region and its relationship with early multisensory processing in the brain. Severe hearing loss (congenital or early/late acquired) is the most frequent sensory deficit in the human population with a world prevalence estimated 6.1% (466 millions) among adults and 1.7% (34 millions) among children (WHO report on hearing, 2021). Despite the remarkable degree of adaptation and compensation that deaf children and adults show as they interact with the surrounding environment, a significant portion of them require substantial rehabilitative and educational support. Cochlear implants (CIs) are modern devices that allow hearing to be partially restored by electrical stimulation of the human cochlea, provided that the auditory nerve is intact. Despite the fast development of CI technology, the degree of auditory recovery after cochlear implantation yet remains variable, particularly as age and duration of hearing loss at implantation increases (Sharma et al., 2005) and concurrent cross-modal reorganization of auditory regions takes place (Kral and Sharma, 2012; Sharma et al., 2015). It follows that an additional, translational aim of neurocognitive research focusing on cross-modal plasticity and auditory deprivation is to evaluate whether and to what extent cortical reorganization interferes with auditory restoration interventions. Further, the study of cross-modal plasticity can contribute in characterizing the potential resources that this neural mechanism might provide and inform the adaptation of rehabilitative and educational interventions.

The chapter starts out by reviewing the existing knowledge on behavioral compensation in deafness and its relationship with cross-modal plasticity (Section "Adaptation and Cross-Modal Plasticity in the STC"). Then, it presents the most recent investigations that documented functional selectivity of cross-modal plasticity (Section "Cross-Modal Functional Selectivity in the STC") and that explored the neural mechanisms subtending cross-modal reorganization in the STC (Section "Neural Mechanisms Mediating Selective Cross-Modal Plasticity in the STC"), before discussing innate anatomical and functional constraints on the expression of cross-modal plasticity in this brain region (Section "Cortical Multisensory Convergence and Intrinsic Constraints of Cross-Modal Plasticity"). In the last section, outstanding questions and future challenges for research in the field of sensory deprivation and restoration will be introduced (Section "Outstanding Questions and Concluding Remarks").

ADAPTATION AND CROSS-MODAL PLASTICITY IN THE STC

The notion of brain plasticity has been particularly adduced when discussing the compensatory mechanisms that might emerge in some cases of early sensory deprivation (Bavelier and Neville, 2002; Pascual-Leone et al., 2005). For deaf individuals, environmental and interpersonal information critically relies on the binocular visual field, whereas in hearing individuals additional information can be attained from the auditory system covering all directions in space. Importantly, they can access language mostly through the visual modality by reading lip movements of a talking person or by relying on sign language. However, despite living in a world without sounds, deaf individuals can adapt themselves by interacting with the surrounding environment, communicate with others, and achieve impressive accomplishments in their lives. There are anecdotal reports of deaf persons demonstrating enhanced abilities with their remaining senses, the most prominent example being the last masterpieces composed by Ludwig van Beethoven. Turned profoundly deaf by his forties, Beethoven continued composing piano sonatas and symphonies by using a wooden stick between his teeth to touch the piano soundboard and feel the vibrations produced while playing the instrument (Stevens and Hemenway, 1970).

Behavioral research has shown that enhanced visual abilities in congenitally deaf individuals are not pervasive, but rather appear bounded by specific areas of visual and somatosensory perception (Bavelier et al., 2006a; Pavani and Bottari, 2012). Pioneering research reported that low-level perceptual thresholds, such as contrast sensitivity (Finney et al., 2001), motion sensitivity (Bosworth and Dobkins, 1999, 2002), motion velocity (Brozinsky and Bavelier, 2004), and brightness discrimination (Bross, 1979) do not appear to be enhanced in deaf individuals. Instead, heightened visual skills had been primarily reported for visual perceptual processing of the peripheral visual field (Neville and Lawson, 1987; Hong Loke and Song, 1991; Bavelier et al., 2000; Proksch and Bavelier, 2002; Sladen et al., 2006). More recent investigations, however, have reported advantages in early deaf adults also for visual stimuli presented at both fixation and perifoveal locations (Bottari et al., 2010; Heimler and Pavani, 2014). In addition, enhanced performances have been observed also for tactile/vibratory temporal order processing (Levänen et al., 1998; Levänen and Hamdorf, 2001; Heming and Brown, 2005; Moallem et al., 2010; Van Dijk et al., 2013) in deaf compared to hearing individuals.

It has been proposed that cross-modal plasticity might be an adaptive mechanism responsible, at least in part, for the compensatory enhancement described in individuals with sensory deprivation or loss (Bavelier and Neville, 2002). More specifically, following the loss of a sensory modality, behavioral compensation might be causally related to the capability of the sensory-deprived cortex to adapt itself and process inputs coming from a spared sensory modality (Rauschecker, 1995; Röder et al., 1999; for reviews, see Frasnelli et al., 2011; Merabet and Pascual-Leone, 2010; Voss et al., 2010). Therefore, in the case of deafness, the auditory regions in the STC, divested of their preferred sensory input, would become favorable candidates for nesting cross-modal plasticity and support behavioral compensation.

Animal models provided initial evidence that the primary auditory cortex (A1) could be recruited by visual information in the absence of auditory inputs: surgical rewiring of visual inputs from the thalamus to A1 induced responses to visual information in A1 (Pallas et al., 1990) that were strikingly similar to those observed in the primary visual cortex (Roe et al., 1992) of ferrets. In humans, early neuroimaging studies have shown cross-modal recruitment of auditory regions of the STC in response to visual motion in deaf compared to hearing individuals. For example, in deaf individuals, visual recruitment of the right auditory cortex was observed during attended visual motion (Finney et al., 2001, 2003; Shibata et al., 2001; Fine et al., 2005) and vision of lip movements and hand gestures/signs (Sadato et al., 2005), with or without a language component, using fMRI. Notably, such cross-modal motion sensitivity is not driven by the use of visual sign language in deaf participants since a similar effect was not observed in hearing individuals who were also native sign language users (Fine et al., 2005). More recently, imaging studies in humans have also provided evidence in favor of cross-modal responses to visual change detection (Bottari et al., 2014) and peripheral visual stimulation (Scott et al., 2014) in primary and associative auditory regions of profoundly deaf individuals.

Several neuroimaging studies also focused on cross-modal reorganization of superior temporal regions that typically respond to spoken/heard language in hearing individuals. Most of these earlier studies compared visual sign language stimuli with still images of the signers and did not match sign language stimuli with nonlinguistic motion conditions, thus not directly addressing cross-modal reorganization of temporal regions that typically process spoken/heard language. Nevertheless, they provided initial evidence that cross-modal plasticity, in deaf individuals, might follow organizational principles known to be present in the "hearing" brain. Two pioneering studies used positron emission tomography (PET) in congenitally deaf individuals, who were also native sign language users, and showed increased cerebral blood flow activity in response to viewing signs in the STC bilaterally (Nishimura et al., 1999; Petitto et al., 2000). More specifically, the cross-modal response was mostly overlapping with the *planum temporale*, a region implicated in auditory speech processing (Scott and Johnsrude, 2003; for a review see Price, 2012). In the following years, additional observations were collected that consistently reported cross-modal activations for sign language processing in bilateral secondary auditory cortices of the mid-posterior STC (MacSweeney, 2002; Campbell et al., 2011), more prominently in the left hemisphere (Neville et al., 1998; Emmorey et al., 2007; Mayberry et al., 2011). Importantly, visual recruitment of the superior temporal regions by sign language processing was greater in deaf native signers compared to hearing native signers (MacSweeney, 2002), suggesting that cross-modal recruitment of these regions is not an exclusive by-product of sign language acquisition and exposure. This observation was recently corroborated by a series of studies comparing deaf native users of British Sign Language with deaf and hearing speakers of English while they responded to sign-based material that could convey or not language content (Cardin et al., 2013, 2016). In deaf individuals, sensory deprivation and sign language exposure induced plastic changes in distinct anatomical and functional areas: sign-language stimulation was associated with cross-modal activity in the left STC and anterior-medial part of the right STC, while cross-modal activity in the right mid-posterior STC and the primary auditory regions was associated, to a greater extent, with visual nonlinguistic stimulation.

Only a few studies have investigated whether cross-modal reorganization occurs with the somatosensory modality, possibly due to the primary focus that neurocognitive research focusing on cross-modal plasticity has allocated to the visual modality (Bavelier et al., 2006a; Heimler et al., 2014). An earlier single-case study (Levänen et al., 1998) recorded MEG signals in a congenitally deaf adult while a vibro-tactile stimulation was applied on his palm and fingers and showed, not only cross-modal recruitment of the bilateral primary and secondary auditory cortices, but also that these regions were able to discriminate across different vibration frequencies. This initial evidence was subsequently supported by two fMRI investigations that reported both widespread somatosensory responses in the "deaf" auditory cortical regions, partly modulated by the life-long experience with hearing aids (Auer et al., 2007), and visual-haptic responses in Heschl's gyrus mostly overlapping with the primary auditory cortex (Karns et al., 2012). Interestingly, Karns et al. (2012) also reported that somatosensory cross-modal responses in the primary auditory regions were larger than those elicited by visual stimulation, while the opposite was observed for visual cross-modal responses in secondary and high-order auditory regions of the STC.

Overall, the neurocognitive research presented so far confirms the emergence of functional reorganization of the "deaf" auditory regions in the STC following early auditory deprivation. However, despite the growing body of work on this topic, only few studies showed a significant correlation between cross-modal activations and behavioral outcomes (Bolognini et al., 2012; Karns et al., 2012). In an elegant study involving transcranial magnetic stimulation (TMS), Bolognini et al. (2012) reported cross-modal functional responses to temporal and spatial tactile stimulation within an early time window (<120 ms) in the STC of deaf individuals and that their behavioral performance on temporal and spatial processing was disrupted by applying TMS over the same STC regions, similar to what was observed in the primary somatosensory areas of hearing individuals (Bolognini et al., 2012). Karns et al. (2012) exploited a double-flashed somatosensory illusion in which a single flash of light paired with two (or more) somatosensory stimuli is wrongly perceived as two flashes (Artem et al., 2005) and showed that the strength of somatosensory cross-modal responses in the auditory cortices were positively correlated with the strength of the touch-induced visual illusion in deaf individuals. A more recent series of studies reported only indirect evidence of causality between neural reorganization and behavioral adaptation by showing that both cortical thickness (Shiell et al., 2016) and white matter connectivity indices (Shiell and Zatorre, 2017) in a portion of the human right *planum temporale* (hPT), typically involved in auditory motion processing (Baumgart et al., 1999; Battal et al., 2019), were correlated with motion-detection thresholds in deaf individuals.

Altogether, the studies presented in this section provided initial evidence that cross-modal recruitment does not occur uniformly across the auditory regions deprived of their preferred input; rather, it appears to emerge in discrete subregions of the auditory cortex and to involve specific visual or somatosensory functions. It naturally follows, therefore, to ask what functional principles drive and constrain the selective cross-modal plasticity reported in the STC and how this relates to the functional organization and specialization of the "hearing" STC.

CROSS-MODAL FUNCTIONAL SELECTIVITY IN THE STC

An influential study investigating cross-modal plasticity and its functional relevance in congenitally deaf cats (Lomber et al., 2010) proposed that selective cross-modal plasticity is more likely to occur in cortical modules that rely on functional attributes commonly shared between sensory modalities. Moreover, the output function of the reorganized cortical modules would be preserved after cross-modal reorganization since it would be dependent on the domain specialization of the deprived sensory cortex. According to this proposition, visual localization or visual motion could anchor into regions typically supporting auditory spatial localization and auditory motion perception, for instance, because they share a common computational goal. In contrast, visual acuity or color perception, which are prominently modality-specific functions, might not find a computational niche sufficiently close in function to remap into the temporal cortex of the "deaf" brain (Lomber et al., 2010; Dormal and Collignon, 2011).

In order to address the existence of a causal link between "supranormal" visual abilities and cross-modal visual recruitment of the auditory cortex following auditory deprivation, Lomber et al. (2010) surgically implanted deaf cats with cortical *cryoloops* (Lomber et al., 1999) that permitted selective and reversible deactivation of auditory regions through cortical cooling. They demonstrated that the heightened performances in visual spatial localization and motion detection observed in congenitally deaf cats were selectively and separately impaired by a transient deactivation of discrete portions of the dorsal auditory cortex. These regions, the posterior auditory field and the dorsal zone, are known to typically process auditory spatial and motion information, respectively, in hearing cats (Malhotra and Lomber, 2007; Malhotra et al., 2008). Critically, none of the cortical manipulations implemented in the study altered either the performance of the hearing cats in the same visual functions or the performance of the deaf cats in other visual functions such as visual acuity or velocity discrimination. A second study by the same group (Meredith et al., 2011b) further showed that the auditory field of the anterior ectosylvian sulcus, typically implicated in auditory spatial localization in hearing cats, was causally related to visual spatial orienting behaviors in early-deafened cats.

One of the first studies that tested functionally specific cross-modal plasticity in deaf humans failed to observe significant selective cross-modal responses to visual motion detection in motion-sensitive auditory regions (Shiell et al., 2015). However, the group of deaf individuals participating in the study was heterogeneous as to both the onset of hearing loss (congenital vs acquired during infancy) and the extent of hearing aid use (spanning from 21% to 92% of a lifetime). Therefore, given that studies of sensory-deprived individuals rarely imply large sample sizes, interindividual variability might have impacted the discovery power of the study. Indeed, cross-modal activity in the posterior STC was observed at a subthreshold statistical significance and the extent of hearing use was found to negatively correlate with the strength of such cross-modal recruitment, i.e., deaf individuals that used hearing aids longer were also those showing the weaker cross-modal recruitment of auditory motion-sensitive regions in the STC.

More recently, it was tested whether cross-modal responses to visual rhythm could be detected in specific portions of the "deaf" auditory STC (Bola et al., 2017). In this study, deaf and hearing individuals were compared while they discriminated between visual sequences of flashes that were temporally complex. Cross-modal visual responses were observed, for deaf individuals, in portions of the STC and the superior temporal sulcus (STS) that responded to matched temporally complex auditory sequences of beeps in hearing individuals. The cortical portion responding to both auditory and visual temporal sequences encompassed auditory regions along the STC/STS that are also known to subtend different auditory functions such as motion (Baumgart et al., 1999; Battal et al., 2019), voice (Belin et al., 2000), and speech (Scott and Johnsrude, 2003; for a review, see Price, 2012) processing. Accordingly, these STC/STS subregions might altogether, each with their specific functional specialization, contribute to higher-level functions that involve processing temporal sequences, such as audio-visual speech and language processing (Bernstein and Liebenthal, 2014).

Benetti and colleagues aimed at specifically assessing the functional selectivity of cross-modal responses in the temporal cortex of deaf humans by investigating two distinct brain functions that maximally benefit from multisensory convergence: person identity recognition and coherent motion processing (Benetti et al., 2017, 2021). The functional selectivity of cross-modal plasticity was ascertained by including, in each study, a specific fMRI localizer for the localization of voice or auditory motion-sensitive auditory regions in hearing individuals. Additionally, in order to control for potential confounding effects of language experience (i.e., oral/spoken language vs visual sign language, native vs late sign-language acquisition) in these studies, a group of hearing individuals who were native sign-language users (born to deaf parents) or had acquired the Italian sign language (LIS) in school (LIS interpreters) were also included. In the first study (Benetti et al., 2017), deaf and hearing individuals were compared while they processed visual information depicting human faces or houses during both fMRI and MEG experiments. This contrast was chosen since these visual stimuli are known to engage distinct cortical circuits in the human brain (Haxby et al., 2001). In addition, a second sophisticated adaptation-suppression fMRI experiment (Grill-Spector and Malach, 2001; Gentile and Rossion, 2014) was employed to elucidate further the computational attributes of potential cross-modal reorganization. In deaf individuals, selective cross-modal responses to faces were detected in a small portion of the mid-STC/STS, which mostly overlapped with the region selectively responding to human voice information in hearing individuals; also known as the temporal voice-sensitive area (TVA; Belin et al., 2000); while no selective responses were elicited by the perception of houses (Fig. 7.1A). In this region of the "deaf" temporal cortex, face-selective responses emerged very fast, 192 ms following stimulus onset, which was only milliseconds later than the activation observed at 176 ms in the main face recognition area, the fusiform face area (FFA; Kanwisher et al., 1997). In addition, the reorganized "deaf" TVA showed functional adaptation (i.e., decreased activity) in response to same face identity when compared to different face identities, demonstrating that this region can discriminate across face identities similar to what it is observed in the visual FFA (Gentile and Rossion, 2014) and in the "hearing" TVA for voices (Belin and Zatorre, 2003). Notably, when the relationship between face-selective recruitment of STC/STS in deaf individuals and their ability to recognize and recollect previously seen faces was assessed, deaf individuals outperformed hearing individuals and the strength of face-selective responses in the "deaf" TVA was positively correlated with the ability to recognize and recollect face identity. Overall, these findings suggest that the reorganized "voice" region participates in face identity processing and responds selectively to faces early in time, putatively maintaining a relation to the computational structure of the problems it solves in hearing individuals: discriminating between people identities.

In a second investigation (Benetti et al., 2021), functional selective cross-modal responses for visual coherent motion processing were examined. In this study, two visual motion trajectories were specifically contrasted, lateral-horizontal and approaching-radial motion, based on the assumption that both benefit from audio-visual convergence, but that audition might

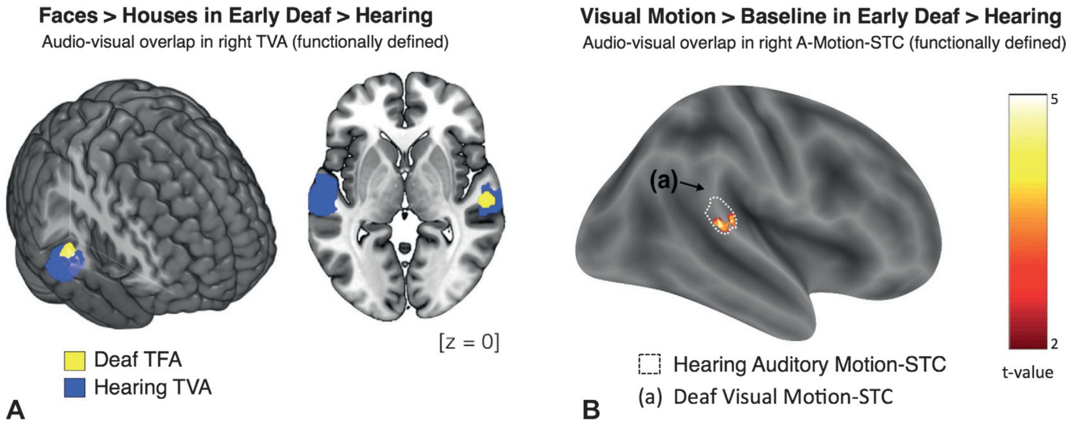

Fig. 7.1. Selective cross-modal recruitment of the "deaf" superior temporal cortex. (A) Depiction of the spatial overlap between the face-selective response in deaf subjects (*yellow*) and the voice-selective response in hearing subjects (*blue*) in the right hemisphere. (B) Visual motion sensitivity within the right deaf auditory motion-STC, outlined in the *black dotted line* is the auditory motion-STC as functionally defined in hearing controls for [auditory motion > static]. *TVA*, temporal voice-sensitive area; *TFA*, temporal face-sensitive area; *A-Motion-STC*, auditory motion-sensitive area in STC. Modified with permission from Benetti S, van Ackeren MJ, Rabini G, Zonca J, Foa V, Baruffaldi F, Rezk M, Pavani F, Rossion B, Collignon O (2017). Functional selectivity for face processing in the temporal voice area of early deaf individuals. Proc Natl Acad Sci U S A 114: E6437–E6446. doi:10.1073/pnas.1618287114; Benetti S, Zonca J, Ferrari A, Rezk M, Rabini G, Collignon O (2021). Visual motion processing recruits regions selective for auditory motion in early deaf individuals. Neuroimage 230. doi:10.1016/j.neuroimage.2021.117816.

convey more relevant sensory information for the latter. In fact, a perceptual priority for approaching/receding compared to static or horizontal moving sounds is observed for the auditory modality in hearing humans (Neuhoff, 1998; Moore and King, 1999), suggesting that adaptive and selective cross-modal recruitment might be more likely to occur in the circuits subtending the perception of approaching/receding audio-visual objects. Accordingly, at the behavioral level, deaf individuals were previously found to be faster and more accurate when detecting subtle changes from horizontal to diagonal motion (Hauthal et al., 2013). Adding on to previous findings (Finney et al., 2001, 2003; Fine et al., 2005), cross-modal responses to both horizontal and radial visual motion were reported in a portion of the right hPT that selectively processed both these motion trajectories in hearing individuals (Fig. 7.1B). In addition, selective visual responses to approaching-radial motion were also observed in a more anterior subregion of the hPT that preferentially responds to this motion trajectory compared to lateral-horizontal motion in the "hearing" brain. This suggests that ecological biases for approaching/receding audio-visual objects (Soto-Faraco et al., 2004; Cappe et al., 2009) might provide a preferential ground for adaptive cross-modal plasticity in the STC. Further, a multivoxel pattern analysis was implemented to assess motion-decoding capabilities in the reorganized portion of the "deaf" hPT and reported increased discrimination accuracies among motion trajectories in this region similar to what was observed in the visual hMT+/V5 complex, a region in the occipito-temporal cortex sensitive to coherent motion perception (Zeki et al., 1991; Watson et al., 1993; Braddick et al., 2001) and known to implement multivariate responses to distinct motion trajectories (Kamitani and Tong, 2010; Rezk et al., 2020) in hearing individuals. Interestingly, it was also observed that the decoding accuracies of different motion trajectories decreased in the hMT+/V5 in deaf individuals, suggesting a reallocation of computational load between auditory and visual brain regions that typically support the multisensory processing of motion information (see Dormal et al., 2016, for similar conclusions in the "blind" brain).

In summary, the study of animal models of congenital deafness together with the recent imaging studies conducted in early-deaf humans provide convincing evidence that the lack of auditory experience early in life induces functionally specific cross-modal plasticity. More specifically, these selective cross-modal changes follow organizational principles that maintain the functional specialization of the colonized "deaf" brain regions. Furthermore, selective cross-modal reorganization appears to emerge preferentially in conditions where the spared sensory modality, such as vision, alone is not sufficiently informative and where cross-modal convergence is typically most beneficial in hearing and sighted individuals (Dormal and Collignon, 2011). In the next sections, we will discuss the neural mechanisms that might mediate such selective cross-modal plasticity with a specific focus on the interaction between sensory experience, intrinsic constraints, and multisensory convergence in the STC.

NEURAL MECHANISMS MEDIATING SELECTIVE CROSS-MODAL PLASTICITY IN THE STC

The research presented in the previous sections compellingly illustrates how nature and nurture might interact in brain development by suggesting that specific brain areas have evolved to anticipate particular computations while remaining flexible relative to the sensory input they receive (see also Amedi et al., 2017; Heimler and Amedi, 2020, for recent theoretical proposals on task-selective functional specialization of the human brain). As a consequence, selective cross-modal recruitment of a sensory-deprived region would "*find 'neuronal niches' in a set of circuits that perform functions sufficiently close to the ones required by the remaining senses"* (Collignon et al., 2011). Yet, beyond the functional principles that appear to drive the emergence of selective cross-modal plasticity, an important question remains unanswered that concerns the neural mechanisms mediating such reorganization.

Initial suggestions come from the available animal literature and indicate that, compared to changes in subcortical connectivity, long-range cortico-cortical connections with preserved sensory cortices might play a crucial role in the expression of cross-modal plasticity (for a review, see Bavelier and Neville, 2002). More specifically, visual information might access the auditory-deprived temporal cortex through either unmasking or ingrowth of existing heteromodal synapses, as well as via rewiring of new cortico-cortical connections. In deaf animals, tracing studies have so far suggested that a combination of both preserved heteromodal (e.g., audiovisual) structural connections and minor functional reorganization of cortico-cortical connectivity, prevalently at the synaptic level, might support cross-modal reorganization in early deafness (Barone et al., 2013; Butler et al., 2017).

Only a few studies have addressed the role of long-range cortico-cortical connections between auditory and nonauditory regions, either at the structural or at the functional level (as well as their relationship), in deaf humans. Of the research groups specifically investigating selective cross-modal plasticity, Shiell et al. (2014) and Bola et al. (2017) have both reported increased functional connectivity between the reorganized auditory regions in the STC and visual regions in the calcarine (Shiell et al., 2014) and the dorsal occipito-temporal (Bola et al., 2017) cortices that are typically engaged by visual motion processing and perception of dynamic visual stimuli in hearing individuals. In addition, we reported that increased functional coupling between early visual regions (V2/V3) and the reorganized "deaf" TVA was specifically associated with face processing in deaf compared to hearing individuals (Benetti et al., 2017). Functional connectivity, however, mostly describes patterns of temporal statistical dependence between neural events (Friston, 2011), such as the cross-modal activation in the STC and the visual responses in the occipital regions, but it does not allow inferring any causal relationship between them.

Benetti and colleagues contributed to elucidating this open question by characterizing the directional flow of information between visual regions responding to faces and motion and the reorganized regions of the STC that responded to the same visual stimulations in deaf individuals (Benetti et al., 2017, 2021). To this purpose, dynamic causal modeling and the analysis of effective connectivity—which refers explicitly to the influence that a dynamic neural system exerts over another, either at a synaptic or a population level (Friston, 2011)—were applied to the face- and motion-selective cross-modal responses previously detected in deaf individuals (Benetti et al., 2017, 2021). It was found that face-selective activity in the right "deaf" TVA was primarily sustained by increased feed-forward effective connectivity from early extra-striate visual regions (Benetti et al., 2017; Fig. 7.2A). Similarly, cross-modal recruitment of the "deaf" right hPT in response to visual motion was best explained by direct feed-forward visual inputs from earlier visual regions and visual-motion selective regions in the occipito-temporal cortex (Benetti et al., 2021; Fig. 7.2B). Moreover, in both studies Benetti and colleagues demonstrated that the reorganized auditory regions in STC/STS become part of the visual brain networks dedicated to face identity and visual motion perception, respectively, and that their contributions remarkably resemble those of the specialized visual regions (i.e., FFA and hMT+/V5, respectively) in terms of interregional dynamics within each respective system (Fig. 7.2A, B). In a third study (Benetti et al., 2018), the relationship between face-selective cross-modal recruitment of the "deaf" TVA and potential reorganization of underlying anatomical connections was also addressed, given the evidence of direct white matter connections between the TVA and FFA (Blank et al., 2011) and between extra-striate visual and temporal auditory regions (Beer et al., 2011) in humans. In this study, preserved macrostructural features of the anatomical connections between auditory and visual regions were found to be associated with face-selective cross-modal plasticity, while microstructural indices of white matter integrity—such as fractional anisotropy and radial diffusivity—were marginally altered and might reflect subtle axonal atrophy due to the lack of auditory stimulation (but see Benetti et al., 2018, for a full interpretation).

The evidence reviewed above suggests that functional reorganization of temporal regions, following early auditory deprivation, builds on anatomical links with

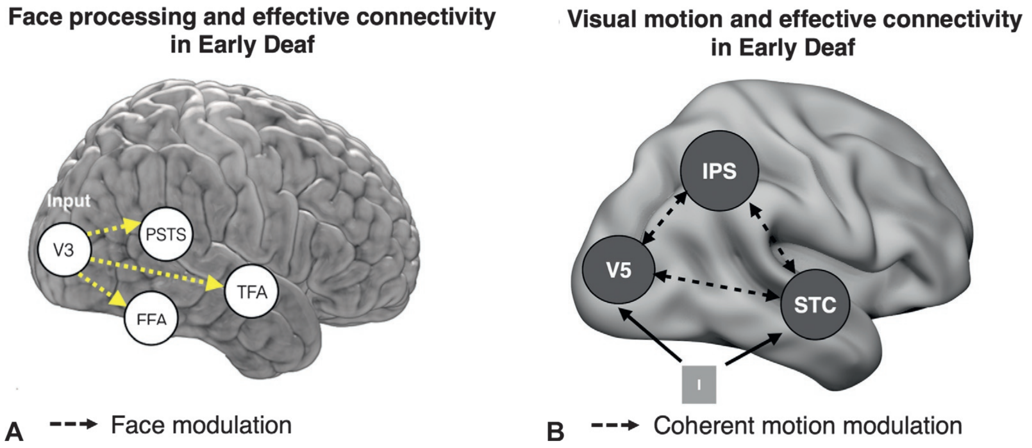

Fig. 7.2. Selective cross-modal reorganization of the "deaf" superior temporal cortex is best predicted by direct feed-forward effective connectivity with early visual regions for both face (A) and visual motion (B) processing. *I*, input; V3 and V5 are subregions of the occipito-temporal visual cortex; *FFA*, face fusiform area; *PSTS*, posterior superior temporal sulcus; *TFA*, temporal face area; *STC*, superior temporal cortex; *IPS*, inferior parietal sulcus. Modified with permission from Benetti S, van Ackeren MJ, Rabini G, Zonca J, Foa V, Baruffaldi F, Rezk M, Pavani F, Rossion B, Collignon O (2017). Functional selectivity for face processing in the temporal voice area of early deaf individuals. Proc Natl Acad Sci U S A 114: E6437–E6446. doi:10.1073/pnas.1618287114; Benetti S, Zonca J, Ferrari A, Rezk M, Rabini G, Collignon O (2021). Visual motion processing recruits regions selective for auditory motion in early deaf individuals. Neuroimage 230. doi:10.1016/j.neuroimage.2021.117816.

nonauditory regions that are mostly genetically predetermined (Innocenti et al., 1988; Innocenti and Price, 2005) and that might provide the neural substrate for feeding of early visual information into the deafened temporal areas (Benetti et al., 2018). This proposition is in line with the observation, consistently reported by previous investigations of cortico-cortical connectivity in congenitally or early deaf (ototoxically deafened < 50 days of life) cats, that newly formed projections from nonauditory regions represent only a small portion of the cross-modal inputs to the deprived auditory regions (Barone et al., 2013; Chabot et al., 2015; Meredith et al., 2016; Butler et al., 2017). Therefore, the emergence of functional cross-modal plasticity might be mostly supported by preserved heteromodal connections and only minor reorganization of cortico-cortical connectivity in early deafness (Barone et al., 2013; Butler et al., 2017; Benetti et al., 2018).

CORTICAL MULTISENSORY CONVERGENCE AND INTRINSIC CONSTRAINTS OF CROSS-MODAL PLASTICITY

Environmental events are usually detected by different sensory systems almost simultaneously. However, in order for multisensory integration to happen and yield coherent percepts and behavioral responses, salient multisensory information must converge onto shared neural populations for information from the different sensory systems to influence one another (Stein and Meredith, 1993; Meredith, 2002). The initial dominant paradigm assumed that unisensory information would be completely processed within specific sensory regions and cortical pathways before the processed signals would converge in polysensory cortical areas (Ungerleider and Mishkin, 1982; Rauschecker and Tian, 2000). Accordingly, it was suggested that the presence of audio-visual signals in occipital or temporal regions would mostly rely on feedback projections from higher-level multimodal areas (Driver and Spence, 2000; Soto-Faraco and Kingstone, 2004). However, over the past two decades, this view has been challenged by substantial evidence in favor of early auditory-visual interactions, occurring as early as 50 ms after stimulus presentation, which cannot not be explained exclusively by feedback from the polysensory cortical areas (Foxe and Schroeder, 2005; Murray et al., 2005; Shams et al., 2005; see also Ferraro et al., 2020, for a recent stereotactic electroenchelography study). These observations led to the appreciation that early multisensory interactions are much more pervasive than previously assumed and may affect brain regions traditionally considered modality-specific (Ghazanfar and Schroeder, 2006).

In the STC, in particular, invasive recordings in animals have reported multisensory responses in brain regions classically considered modality-specific (Schroeder and Foxe, 2002; Brosch et al., 2005; Ghazanfar et al., 2005;Kayser et al., 2005 ; Lakatos et al., 2007). For example, visual influences on the secondary and even primary auditory cortex were documented in nonhuman primates during voice processing (Ghazanfar et al., 2005; Perrodin et al., 2014), auditory categorization (Brosch et al., 2005), and passive listening (Schroeder and Foxe, 2002). Similarly, it has also been observed that tactile stimuli can modulate the response to auditory stimuli (Kayser et al., 2005; Lakatos et al., 2007). In humans, the upper bank of the STS and the posterior portion of the superior temporal gyrus are known to respond to a range of multisensory costimulations such as: low-level audio-visual stimulation (Martuzzi et al., 2007; Ferraro et al., 2020), audio-visual presentation of human-made tools (Beauchamp et al., 2004), audio-visual speech processing (Calvert et al., 1999, 2001; Miller and D'Esposito, 2005), and face-voice processing during a speaker's recognition (von Kriegstein et al., 2005).

Assuming that early cross-modal interactions are the rule and not the exception, it naturally follows to ask what neural pathways could underlie their unfolding in the human brain. Over the past two decades, insight into early cross-modal interactions has been paralleled by the overturning of another classical assumption: connectivity of early sensory areas would be restricted to areas of the same sensory modality and, therefore, no direct long-range connectivity would exist between sensory regions (Jones and Powell, 1970). Indeed, mounting evidence for cortico-cortical anatomical connectivity among sensory cortical areas has been documented in both animal and human connectivity studies, challenging such earlier assumption. In nonhuman primates, monosynaptic connections from the primary auditory into the primary visual cortex (Falchier et al., 2002; Clavagnier et al., 2004), bidirectional fibers between the auditory belt and primary visual areas (Rockland and Ojima, 2003) as well as between the auditory belt and somatosensory subregions (Hackett et al., 2007) have been found. Consistently, tract-tracing studies in mammals have revealed anatomical connections between both early auditory and visual regions (Bizley et al., 2007) and between auditory subregions and somatosensory/olfactory regions. Further, anatomical connections were also reported between the motion-sensitive visual complex (i.e., *MT+/V5)* and secondary auditory subregions in the caudal parabelt (Palmer and Rosa, 2006) and middle lateral belt (Majka et al., 2019), known to be sensitive to auditory motion in nonhuman primates.

Initial and growing evidence of long-range anatomical connectivity between early sensory regions in humans has also become available thanks to modern neuroimaging techniques, such as in vivo white matter fiber-tracing based on diffusion-tensor imaging data (Catani et al., 2002; Mori and van Zijl, 2002; Jones, 2008). Beer et al. (2011) investigated the existence of white matter connections from Heschl's gyrus and the hPT to occipital and parietal regions and reported direct long-range connections between the primary auditory and visual cortex. The same year (Blank et al., 2011), white matter connections were also characterized between the face-selective area in the fusiform gyrus and the TVA, which are both implicated in early audio-visual interactions during the speaker's recognition (von Kriegstein et al., 2005). Both these observations were subsequently replicated in both hearing and early deaf individuals (Benetti et al., 2018). Recently, Gurtubay-Antolin et al. (2021) further described, for the first time, direct anatomical connections between motion-selective regions in the human hMT+/V5 complex and the hPT. Intriguingly, these findings naturally follow and fit with the observation that the hMT+/V5 complex, a region classically considered as being uniquely visual, also contains information about auditory motion (Rezk et al., 2020). It is noteworthy that no connection could be reconstructed between the hPT and the FFA (Gurtubay-Antolin et al., 2021), supporting the notion that the hMT+/V5-hPT connection might play a key role in the emergence of functional selectivity for visual motion in the "deaf" hPT. Importantly, the anatomical plausibility of the connections virtually characterized in these studies is supported by postmortem dissection studies and tractography-based atlases that have described the main anatomical pathways potentially nesting such specific connections (Catani and Thiebaut de Schotten, 2008).

Overall, the observations reported at the macrostructural level suggest that direct anatomical links between sensory regions might provide the neural substrate not only for feeding of nonauditory information in the "deaf" temporal regions (Benetti et al., 2017, 2021), but also for early multisensory interactions. The functional specificity that is observed in the reconstruction of white matter tracts connecting TVA-FFA and hMT+/V5-hPT, based on functional responses for faces/voices and auditory/visual motion, respectively, additionally reinforces this hypothesis. We further propose that it is precisely the existence of such innate anatomical substrate that constrains the expression of selective cross-modal plasticity in the STC of deaf individuals by providing structural scaffolding for the expression of functional reorganization according to organizational principles, which might also have determined the development of such intrinsic connections in the human brain. For example, the existence of anatomical pathways linking visual and auditory regions implicated in face and voice processing would constrain the functional remapping of faces in the deprived temporal voice area in contrast to other visual stimuli (e.g., houses; see Benetti et al., 2017). We speculate that through evolutionary pressure for optimal convergence and integration of salient multisensory information (e.g., for face-voice, see Sheehan and Nachman, 2014), phylogenetic and ontogenetic experiences might have favored the development of anatomo-functional links between regions in the auditory and other sensory systems that are involved in the same computational function. For instance, regions selective to faces, in the fusiform cortex, and to voices, in the temporal cortex, would be linked since those regions constantly exchange information in order to integrate audio-visual information (e.g., on speech, identity, sex, and age) during social interaction. Similarly, visual (hMT+/V5) and auditory (hPT) motion-selective regions might link to each other to exchange audio-visual information about the presence, direction, and speed of moving objects. Such genetically privileged functional connections might represent the common substrate of both early multisensory integration and expression of selective cross-modal plasticity in the STC. Normally, these connections might facilitate the modulation of sensory-specific processing for the main sensory modality in each of the connected areas (e.g., boosting processing of visual motion in extrastriate and occipito-temporal cortex, when the visual event coincides with sudden approaching sounds). However, if one sensory area becomes deprived of the typical sensory input, as is the case in profound deafness, influences from the remaining sense might then become selectively potentiated.

OUTSTANDING ISSUES AND CONCLUDING REMARKS

An important challenge for the future is to further elucidate the cellular mechanisms underlying and constraining cross-modal selectivity in the reorganized temporal auditory cortex, and more generally in sensory-deprived brain regions. Recent findings in animal studies appear to converge on the notion that synaptic reorganization affects existing projections that typically provide subthreshold cross-modal inputs to the auditory regions (Butler et al., 2017; Kral et al., 2017). However, whether such heteromodal connections are strengthened as a result of local synaptic sprouting, ingrowth of existing or unmasking of silent synapses, or alterations in developmental synaptic pruning remains mostly unanswered. Animal studies are, at present, the more likely to provide initial insight into this issue. For instance, Clemo et al. (2016, 2017) have documented increases in the spine density of neurons in early and high-order auditory regions in deaf cats. Nevertheless, laminar high-resolution imaging in humans (Lawrence et al., 2019) also offers a promising and exciting possibility to investigate the synaptic contributions to cross-modal plasticity and reorganization of cortico-cortical connectivity in deafness, and more widely in sensory deprivation.

A further intriguing issue for future research is the characterization of the computational contributions implemented in the reorganized temporal auditory cortex: would reorganized auditory regions act as duplicates of the nonauditory areas typically dedicated to specific nonauditory functions? Further, how would the strengthened computational role of reorganized auditory regions impact on nonauditory regions subtending the same nonauditory functions? Research from our group (Benetti et al., 2017, 2021) suggests that the reorganized auditory regions might implement computations on faces and visual motion that are temporally and qualitatively similar to those implemented in the nonauditory regions typically subtending these visual functions. This observation is in line with an earlier EEG study (Bottari et al., 2014) that revealed, in early deaf individuals, the recruitment of auditory cortices for visual change detection within the typical time window reported for visual cortices. The same study also showed a reduction of response within the visual cortex that was paralleled by our finding (Benetti et al., 2021) of enhanced visual motion decoding in the motion-selective hPT of the deaf and concomitant reduction of decoding accuracy in hMT+/V5 compared to hearing individuals. This initial evidence suggests that cross-modal reorganization, within brain systems typically dedicated to multisensory functions, might support a large-scale reallocation of computational resources from spared nonauditory to reorganized auditory regions.

Moreover, to what extent the age of onset of deafness impacts on the expression of cross-modal plasticity, as suggested by research on blindness, remains an open question since, to the best of our knowledge, only one study has specifically compared early and late-onset deafness (Sadato et al., 2004). In the previous section, we suggested that privileged links between auditory and nonauditory regions may be nested in the temporal cortex early during human brain development and might remain particularly susceptible to functional reorganization after auditory deprivation. In the absence of acoustic information, it is plausible that the brain remains able to reorganize itself, throughout developmental maturation, by building on existing cross-modal inputs in the right temporal regions. In support of our proposition, Sadato et al. (2004) found cross-modal responses in the middle STC of both early and late-onset deaf individuals compared to hearing individuals. However, cross-modal recruitment was modulated by deafness onset and early deaf individuals showed the strongest reorganization in this auditory area. Indeed, there are also a number of studies showing cross-modal recruitment of temporal regions by vision in postlingually (age onset > age 6 and after full acquisition of speech and language) deaf people, who are also CI users (Rouger et al., 2012; Strelnikov et al., 2013; Stropahl et al., 2015; Chen et al., 2016). However, no decisive conclusion can be drawn based on the existing cross-sectional studies investigating early and late deaf individuals separately and we advocate for the need for further research specifically investigating the role of deafness onset.

Finally, a compelling translational issue that remains highly debated concerns the relationship between cross-modal recruitment of the temporal auditory cortex and the outcome of auditory restoration with CIs. Early investigations on this topic suggested that cross-modal visual recruitment of the auditory cortex has a maladaptive effect on the ability to recovery auditory functions, typically quantified as verbal language recovery/development, after CI (Nishimura et al., 1999; Lee et al., 2001, 2007; Giraud and Lee, 2007; Strelnikov et al., 2013). Animal models of auditory restoration have in part confirmed this hypothesis by suggesting that cross-modal reorganization triggers a functional decoupling of bottom-up and top-down connections in the auditory cortex, preventing subsequent full development of the auditory system (Sharma et al., 2005; Kral, 2007, 2013). Accordingly, exposure to a sign language prior to cochlear implantation has long been discouraged by clinicians, as visual linguistic inputs are thought to facilitate the takeover of the auditory cortex and prevent the proper recovery of audition. However, most of early human studies (Lee et al., 2001, 2005, 2007; Giraud and Lee, 2007) supporting the notion of maladaptive cross-modal plasticity presented some methodological issues. For instance, visual recruitment was mostly inferred from resting-state activity and based on reported sign-language use rather than on actual imaging of visual processing. In addition, more recent studies have focused only on late-onset deaf individuals (Doucet et al., 2006; Rouger et al., 2012; Sandmann et al., 2012). Critically, animal studies did not take into account that every specific function, or "functional unit" (e.g., speech, object/voice recognition, spatial or motion perception), within a cortical region has specific critical and sensitive periods of development (Knudsen, 2004; Lewis and Maurer, 2005) that might be independent of critical periods for the physiological development of the auditory system. It might, therefore, be possible that a different sensory modality than audition might trigger proper development of such specific units and, in turn, pave the way for successful recovery of these functions in the auditory domain after CI (Hassanzadeh, 2012; for critical reviews, see Heimler et al., 2014 and Lyness et al., 2013). This suggestion opens an exciting prospect in which functional selective cross-modal plasticity might be exploited in integrated multisensory approaches to habilitation/rehabilitation following CI intervention. Promising observations appear to support this proposition by showing that early exposure to multisensory training (e.g., sign- and spoken-language pairing, speech-reading, and audio-visual speech training) substantially improved the language CI outcome (Bergeson et al., 2005; Strelnikov et al., 2011, 2015).

In conclusion, the main aim of this chapter was to attempt a characterization of the impact of early sensory deprivation on the STC, the extent and properties of cross-modal plasticity and its relationship with early multisensory processing in the brain, and to introduce further research questions that also bear translational relevance. The fields of cross-modal perception and plasticity research have rapidly broadened since the first attempt was made to answer the question of where and how cross-modal plasticity occurs in the human brain following early sensory deprivation (Bavelier and Neville, 2002). First, it is now well established and widely accepted that cross-modal reorganization does not occur uniformly across the auditory regions deprived of their preferred input, rather it appears to emerge in discrete subregions of the auditory cortex and to involve specific visual or somatosensory functions, as observed for behavioral compensation or enhancement. Second, selective cross-modal plasticity appears to follow organizational principles that maintain the functional specialization of the colonized "deaf" temporal regions and appears to emerge preferentially in conditions where cross-modal convergence is typically most beneficial in hearing individuals (Lomber et al., 2010; Collignon et al., 2011; Dormal and Collignon, 2011). Third, functional reorganization of temporal regions might build on innate anatomical connections with nonauditory regions that might provide the structural substrate for feeding nonauditory information into the deafened temporal areas (Benetti et al., 2018). Finally, we speculated that such privileged connections might represent the common substrate of both early multisensory integration and expression of selective cross-modal plasticity in the STC. These observations and our proposal provide an enthralling illustration of how the brain handles cross-modal perception and plasticity in the STC, with several new principles emerging in addition to many new opportunities for future research.

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ABBREVIATIONS

A1, primary auditory cortex; CI, cochlear implants; FFA, fusiform face area; fMRI, functional magnetic resonance imaging; *h*MT+/V5, human extrastriate visual areas sensitive to motion; hPT, human *Planum Temporale*; LIS, Italian sign language; MEG, magnetoencephalography; PET, positron emission tomography; STC, superior temporal cortex; STS, superior temporal sulcus; TMS, transcranial magnetic stimulation; TVA, temporal voice area; V2/V3, areas of extrastriate visual cortex.

REFERENCES

Amedi A, Hofstetter S, Maidenbaum S et al. (2017). Task selectivity as a comprehensive principle for brain organization. Trends Cogn Sci 21: 307–310. https://doi.org/10.1016/j.tics.2017.03.007.

Artem V, Shinsuke S, Ladan S (2005). Touch-induced visual illusion. Neuroreport 16: 1107–1110.

Auer ET, Bernstein LE, Sungkarat W et al. (2007). Vibrotactile activation of the auditory cortices in deaf versus hearing adults. Neuroreport 18: 645–648.

Axelrod S (1959). Effects of early blindness: Performance of blind and sighted children on tactile and auditory tasks. No. 7. American Foundation for the Blind.

Barone P, Lacassagne L, Kral A (2013). Reorganization of the connectivity of cortical field DZ in congenitally deaf cat. PLoS One 8: e60093. https://doi.org/10.1371/journal.pone.0060093.

Battal C, Rezk M, Mattioni S et al. (2019). Representation of auditory motion directions and sound source locations in the human planum temporale. J Neurosci 39: 2208–2220. https://doi.org/10.1523/JNEUROSCI.2289-18.2018.

Baumgart F, Gaschler-Markefski B, Woldorff MG et al. (1999). A movement-sensitive area in auditory cortex [9]. Nature 400: 724–726. https://doi.org/10.1038/23390.

Bavelier D, Neville HJ (2002). Cross-modal plasticity: where and how? Nat Rev Neurosci 3: 443–452.

Bavelier D, Tomann A, Hutton C et al. (2000). Visual attention to the periphery is enhanced in congenitally deaf individuals. J Neurosci 20: RC93.

Bavelier D, Dye MWG, Hauser PC (2006a). Do deaf individuals see better? Trends Cogn Sci 10: 512–518.

Beauchamp MS, Lee KE, Argall BD et al. (2004). Integration of auditory and visual information about objects in superior temporal sulcus. Neuron 41: 809–823. https://doi.org/10.1016/S0896-6273(04)00070-4.

Beer AL, Plank T, Greenlee MW (2011). Diffusion tensor imaging shows white matter tracts between human auditory and visual cortex. Exp Brain Res 213: 299–308.

Belin P, Zatorre RJ (2003). Adaptation to speaker's voice in right anterior temporal lobe. Neuroreport 14: 2105–2109. https://doi.org/10.1097/01.wnr.0000091689.94870.85.

Belin P, Zatorre RJ, Lafaille P et al. (2000). Voice-selective areas in human auditory cortex. Nature 403: 309–312.

Benetti S, van Ackeren MJ, Rabini G et al. (2017). Functional selectivity for face processing in the temporal voice area of early deaf individuals. Proc Natl Acad Sci U S A 114: E6437–E6446. https://doi.org/10.1073/pnas.1618287114.

Benetti S, Novello L, Maffei C et al. (2018). White matter connectivity between occipital and temporal regions involved in face and voice processing in hearing and early deaf individuals. Neuroimage 179: 263–274. https://doi.org/10.1016/j.neuroimage.2018.06.044.

Benetti S, Zonca J, Ferrari A et al. (2021). Visual motion processing recruits regions selective for auditory motion in early deaf individuals. Neuroimage 230: 117816. https://doi.org/10.1016/j.neuroimage.2021.117816.

Bergeson TR, Pisoni DB, Davis RAO (2005). Development of audiovisual comprehension skills in prelingually deaf children with cochlear implants. Ear Hear 26: 149–164. https://doi.org/10.1097/00003446-200504000-00004.

Bernstein LE, Liebenthal E (2014). Neural pathways for visual speech perception. Front Neurosci 8: 386. https://doi.org/10.3389/fnins.2014.00386.

Bizley JK, Nodal FR, Bajo VM et al. (2007). Physiological and anatomical evidence for multisensory interactions in auditory cortex. Cereb Cortex 17: 2172–2189. https://doi.org/10.1093/cercor/bhl128.

Blank H, Anwander A, von Kriegstein K (2011). Direct structural connections between voice- and face-recognition areas. J Neurosci 31: 12906–12915.

Bola Ł, Zimmermann M, Mostowski P et al. (2017). Task-specific reorganization of the auditory cortex in deaf humans. Proc Natl Acad Sci U S A 114: E600–E609. https://doi.org/10.1073/pnas.1609000114. Early Edit.

Bolognini N, Cecchetto C, Geraci C et al. (2012). Hearing shapes our perception of time: temporal discrimination of tactile stimuli in deaf people. J Cogn Neurosci 24: 276–286.

Bosworth R, Dobkins K (1999). Left-hemisphere dominance for motion processing in deaf signers. Psychol Sci 10: 256–262.

Bosworth R, Dobkins K (2002). Visual field asymmetries for motion processing in deaf and hearing signers. Brain Cogn 49: 170–181.

Bottari D, Nava E, Ley P et al. (2010). Enhanced reactivity to visual stimuli in deaf individuals. Restor Neurol Neurosci 28: 167–179. https://doi.org/10.3233/RNN-2010-0502.

Bottari D, Heimler B, Caclin A et al. (2014). Visual change detection recruits auditory cortices in early deafness. Neuroimage 94: 172–184.

Braddick OJ, O'Brien JMD, Wattam-Bell J et al. (2001). Brain areas sensitive to coherent visual motion. Perception 30: 61–72. https://doi.org/10.1068/p3048.

Brosch M, Selezneva E, Scheich H (2005). Nonauditory events of a behavioral procedure activate auditory cortex of highly trained monkeys. J Neurosci 25: 6797–6806. https://doi.org/10.1523/JNEUROSCI.1571-05.2005.

Bross M (1979). Residual sensory capacities of the deaf: a signal detection analysis of a visual discrimination task. Percept Mot Skills 48: 187–194. https://doi.org/10.2466/pms.1979.48.1.187.

Brozinsky CJ, Bavelier D (2004). Motion velocity thresholds in deaf signers: changes in lateralization but not in overall sensitivity. Cogn Brain Res 21: 1–10. https://doi.org/10.1016/j.cogbrainres.2004.05.002.

Butler BE, de la Rua A, Ward-Able T et al. (2017). Cortical and thalamic connectivity to the second auditory cortex of the cat is resilient to the onset of deafness. Brain Struct Funct 223: 819–835. https://doi.org/10.1007/s00429-017-1523-y.

Calvert GA, Thesen T (2004). Multisensory integration: methodological approaches and emerging principles in the human brain. J Physiol Paris 98: 191–205. https://doi.org/10.1016/j.jphysparis.2004.03.018.

Calvert GA, Brammer MJ, Bullmore ET et al. (1999). Response amplification in sensory-specific cortices during crossmodal binding. Neuroreport 10: 2619–2623. https://doi.org/10.1097/00001756-199908200-00033.

Calvert GA, Hansen PC, Iversen SD et al. (2001). Detection of audio-visual integration sites in humans by application of electrophysiological criteria to the BOLD effect. Neuroimage 14: 427–438. https://doi.org/10.1006/nimg.2001.0812.

Campbell R, Capek CM, Gazarian K et al. (2011). The signer and the sign: cortical correlates of person identity and language processing from point-light displays. Neuropsychologia 49: 3018–3026.

Cappe C, Thut G, Romei V et al. (2009). Selective integration of auditory-visual looming cues by humans. Neuropsychologia 47: 1045–1052.

Cardin V, Orfanidou E, Rönnberg J et al. (2013). Dissociating cognitive and sensory neural plasticity in human superior temporal cortex. Nat Commun 4: 1473.

Cardin V, Smittenaar RC, Orfanidou E et al. (2016). Differential activity in Heschl's gyrus between deaf and hearing individuals is due to auditory deprivation rather than language modality. Neuroimage 124: 96–106. https://doi.org/10.1016/j.neuroimage.2015.08.073.

Catani M, Thiebaut de Schotten M (2008). A diffusion tensor imaging tractography atlas for virtual in vivo dissections. Cortex 44: 1105–1132.

Catani M, Howard RJ, Pajevic S et al. (2002). Virtual in vivo interactive dissection of white matter fasciculi in the human brain. Neuroimage 17: 77–94. Elsevier B.V., Section of Old Age Psychiatry, Institute of Psychiatry, London, United Kingdom.

Chabot N, Butler BE, Lomber SG (2015). Differential modification of cortical and thalamic projections to cat primary auditory cortex following early- and late-onset deafness. J Comp Neurol 523: 2297–2320. https://doi.org/10.1002/cne.23790.

Chen LC, Sandmann P, Thorne JD et al. (2016). Crossmodal functional reorganization of visual and auditory cortex in adult cochlear implant users identified with fNIRS. Neural Plast 2016, 1–13. https://doi.org/10.1155/2016/4382656.

Clavagnier S, Falchier A, Kennedy H (2004). Long-distance feedback projections to area V1: Implications for multisensory integration, spatial awareness, and visual consciousness. In: Cognitive, affective and behavioral neuroscience, Psychonomic Society Inc. pp. 117–126. https://doi.org/10.3758/CABN.4.2.117.

Clemo HR, Lomber SG, Meredith MA (2016). Synaptic basis for cross-modal plasticity: enhanced supragranular dendritic spine density in anterior ectosylvian auditory cortex of the early deaf cat. Cereb Cortex 26: 1365–1376. https://doi.org/10.1093/cercor/bhu225.

Clemo HR, Lomber SG, Meredith MA (2017). Synaptic distribution and plasticity in primary auditory cortex (A1) exhibits laminar and cell-specific changes in the deaf. Hear Res 353: 122–134. https://doi.org/10.1016/j.heares.2017.06.009.

Collignon O, Vandewalle G, Voss P et al. (2011). Functional specialization for auditory-spatial processing in the occipital cortex of congenitally blind humans. Proc Natl Acad Sci U S A 108: 4435–4440.

Dormal G, Collignon O (2011). Functional selectivity in sensory-deprived cortices. J Neurophysiol 105: 2627–2630.

Dormal G, Rezk M, Yakobov E et al. (2016). Auditory motion in the sighted and blind: early visual deprivation triggers a large-scale imbalance between auditory and "visual" brain regions. Neuroimage 134: 630–644. https://doi.org/10.1016/j.neuroimage.2016.04.027.

Doucet ME, Bergeron F, Lassonde M et al. (2006). Crossmodal reorganization and speech perception in cochlear implant users. Brain 129: 3376–3383.

Driver J, Spence C (2000). Multisensory perception: beyond modularity and convergence. Curr Biol 10: R731–R735. https://doi.org/10.1016/S0960-9822(00)00740-5.

Emmorey K, Mehta S, Grabowski TJ (2007). The neural correlates of sign versus word production. Neuroimage 36: 202–208. https://doi.org/10.1016/j.neuroimage.2007.02.040.

Falchier A, Clavagnier S, Barone P et al. (2002). Anatomical evidence of multimodal integration in primate striate cortex. J Neurosci 22: 5749–5759.

Ferraro S, Van Ackeren MJ, Mai R et al. (2020). Stereotactic electroencephalography in humans reveals multisensory signal in early visual and auditory cortices. Cortex126: 253–264. https://doi.org/10.1016/j.cortex.2019.12.032.

Fine I, Finney EM, Boynton GM et al. (2005). Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. J Cogn Neurosci 17: 1621–1637. https://doi.org/10.1162/089892905774597173.

Finney EM, Fine I, Dobkins KR (2001). Visual stimuli activate auditory cortex in the deaf. Nat Neurosci 4: 1171–1173.

Finney EM, Clementz BA, Hickok G et al. (2003). Visual stimuli activate auditory cortex in deaf subjects: evidence from MEG. Neuroreport 14: 1425–1427. Department of psychology, University of California-San Diego, La Jolla, CA, USA.

Foxe JJ, Schroeder CE (2005). The case for feedforward multisensory convergence during early cortical processing.

Neuroreport 16: 419–423. https://doi.org/10.1097/00001756-200504040-00001.

Frasnelli J, Collignon O, Voss P et al. (2011). Crossmodal plasticity in sensory loss. In: Progress in brain research, Elsevier B.V. 233–249. https://doi.org/10.1016/B978-0-444-53752-2.00002-3.

Friston KJ (2011). Functional and effective connectivity: a review. Brain Connect 1: 13–36. https://doi.org/10.1089/brain.2011.0008.

Gentile F, Rossion B (2014). Temporal frequency tuning of cortical face-sensitive areas for individual face perception. Neuroimage 90: 256–265.

Ghazanfar AA, Schroeder CE (2006). Is neocortex essentially multisensory? Trends Cogn Sci 16: 278–285. https://doi.org/10.1016/j.tics.2006.04.008.

Ghazanfar AA, Maier JX, Hoffman KL et al. (2005). Multisensory integration of dynamic faces and voices in rhesus monkey auditory cortex. J Neurosci 25: 5004–5012. https://doi.org/10.1523/JNEUROSCI.0799-05.2005.

Giraud A-L, Lee H-J (2007). Predicting cochlear implant outcome from brain organisation in the deaf. Restor Neurol Neurosci 25: 381–390.

Grill-Spector K, Malach R (2001). fMR-adaptation: a tool for studying the functional properties of human cortical neurons. Acta Psychol (Amst) 107: 293–321. https://doi.org/10.1016/S0001-6918(01)00019-1.

Gurtubay-Antolin A, Battal C, Maffei C et al. (2021). Direct structural connections between auditory and visual motion-selective regions in humans. J Neurosci 41: 2393–2405. https://doi.org/10.1523/jneurosci.1552-20.2021.

Hackett TA, Smiley JF, Ulbert I et al. (2007). Sources of somatosensory input to the caudal belt areas of auditory cortex. Perception 36: 1419–1430. https://doi.org/10.1068/p5841.

Hassanzadeh S (2012). Outcomes of cochlear implantation in deaf children of deaf parents: comparative study. J Laryngol Otol 126: 989–994.

Hauthal N, Sandmann P, Debener S et al. (2013). Visual movement perception in deaf and hearing individuals. Adv Cogn Psychol 9: 53–61.

Haxby JV, Gobbini MI, Furey ML et al. (2001). Distributed and overlapping representations of faces and objects in ventral temporal cortex. Sci (New York, NY) 293: 2425–2430.

Heimler B, Amedi A (2020). Are critical periods reversible in the adult brain? Insights on cortical specializations based on sensory deprivation studies. Neurosci Biobehav Rev 116: 494–507. https://doi.org/10.1016/j.neubiorev.2020.06.034.

Heimler B, Pavani F (2014). Response speed advantage for vision does not extend to touch in early deaf adults. Exp Brain Res 232: 1335–1341. https://doi.org/10.1007/s00221-014-3852-x.

Heimler B, Weisz N, Collignon O (2014). Revisiting the adaptive and maladaptive effects of crossmodal plasticity. Neuroscience 283: 44–63.

Heming JE, Brown LN (2005). Sensory temporal processing in adults with early hearing loss. Brain Cogn 59: 173–182. https://doi.org/10.1016/j.bandc.2005.05.012.

Hensch TK (2005). Critical period plasticity in local cortical circuits. Nat Rev Neurosci 6: 877–888. https://doi.org/10.1038/nrn1787.

Hong Loke W, Song S (1991). Central and peripheral visual processing in hearing and nonhearing individuals. Bull Psychon Soc 29: 437–440. https://doi.org/10.3758/BF03333964.

Innocenti GM, Price DJ (2005). Exuberance in the development of cortical networks. Nat Rev Neurosci 6: 955–965. https://doi.org/10.1038/nrn1790.

Innocenti GM, Berbel P, Clarke S (1988). Development of projections from auditory to visual areas in the cat. J Comp Neurol 272: 242–259. https://doi.org/10.1002/cne.902720207.

Jones DK (2008). Studying connections in the living human brain with diffusion MRI. Cortex 44: 936–952.

Jones EG, Powell TPS (1970). An anatomical study of converging sensory pathways within the cerebral cortex of the monkey. Brain 93: 793–820. https://doi.org/10.1093/brain/93.4.793.

Kamitani Y, Tong F (2010). Decoding motion direction from activity in human visual cortex. J Vis 5: 152. https://doi.org/10.1167/5.8.152.

Kanwisher N, McDermott J, Chun MM (1997). The fusiform face area: a module in human extrastriate cortex specialized for face perception. J Neurosci 17: 4302–4311. https://doi.org/10.1098/Rstb.2006.1934.

Karns CM, Dow MW, Neville HJ (2012). Altered cross-modal processing in the primary auditory cortex of congenitally deaf adults: a visual-somatosensory fMRI study with a double-flash illusion. J Neurosci 32: 9626–9638.

Kayser C, Petkov CI, Augath M et al. (2005). Integration of touch and sound in auditory cortex. Neuron 48: 373–384. https://doi.org/10.1016/j.neuron.2005.09.018.

Knudsen EI (2004). Sensitive periods in the development of the brain and behavior. J Cogn Neurosci 16: 1412–1425. https://doi.org/10.1162/0898929042304796.

Kral A (2007). Unimodal and cross-modal plasticity in the 'deaf' auditory cortex. Int J Audiol 46: 479–493.

Kral A (2013). Auditory critical periods: a review from systematic's perspective. Neuroscience 247: 117–133.

Kral A, Sharma A (2012). Developmental neuroplasticity after cochlear implantation. Trends Neurosci 35: 111–122.

Kral A, Yusuf PA, Land R (2017). Higher-order auditory areas in congenital deafness: top-down interactions and cortico-cortical decoupling. Hear Res 343: 50–63. https://doi.org/10.1016/j.heares.2016.08.017.

Lakatos P, Chen C, Connell MNO et al. (2007). Neuronal oscillations and multisensory interaction in primary auditory cortex. Neuron 53: 279–292. https://doi.org/10.1016/j.neuron.2006.12.011.

Lawrence SJD, Formisano E, Muckli L et al. (2019). Laminar fMRI: applications for cognitive neuroscience. Neuroimage 197: 785–791. https://doi.org/10.1016/j.neuroimage.2017.07.004.

Lee DS, Lee JS, Oh SH et al. (2001). Cross-modal plasticity and cochlear implants. Nature 409: 149–150.

Lee H-J, Kang E, Oh SH et al. (2005). Preoperative differences of cerebral metabolism relate to the outcome of cochlear implants in congenitally deaf children. Hear Res 203: 2–9. https://doi.org/10.1016/j.heares.2004.11.005.

Lee H-J, Giraud A-L, Kang E et al. (2007). Cortical activity at rest predicts cochlear implantation outcome. Cereb Cortex (New York, NY 1991) 17: 909–917.

Levänen S, Hamdorf D (2001). Feeling vibrations: enhanced tactile sensitivity in congenitally deaf humans. Neurosci Lett 301: 75–77. https://doi.org/10.1016/S0304-3940(01)01597-X.

Levänen S, Jousmäki V, Hari R (1998). Vibration-induced auditory-cortex activation in a congenitally deaf adult. Curr Biol 8: 869–872.

Lewis TL, Maurer D (2005). Multiple sensitive periods in human visual development: evidence from visually deprived children. Dev Psychobiol 46: 163–183. https://doi.org/10.1002/dev.20055.

Lomber SG, Payne BR, Horel JA (1999). The cryoloop: an adaptable reversible cooling deactivation method for behavioral or electrophysiological assessment of neural function. J Neurosci Methods 86: 179–194.

Lomber SG, Meredith MA, Kral A (2010). Cross-modal plasticity in specific auditory cortices underlies visual compensations in the deaf. Nat Neurosci 13: 1421–1427.

Lyness CR, Woll B, Campbell R et al. (2013). How does visual language affect crossmodal plasticity and cochlear implant success? Neurosci Biobehav Rev 37: 2621–2630.

MacSweeney M (2002). Neural systems underlying British Sign Language and audio-visual English processing in native users. Brain 125: 1583–1593. https://doi.org/10.1093/brain/awf153.

Majka P, Rosa MGP, Bai S et al. (2019). Unidirectional monosynaptic connections from auditory areas to the primary visual cortex in the marmoset monkey. Brain Struct Funct 224: 111–131. https://doi.org/10.1007/s00429-018-1764-4.

Malhotra S, Lomber SG (2007). Sound localization during homotopic and heterotopic bilateral cooling deactivation of primary and nonprimary auditory cortical areas in the cat. J Neurophysiol 97: 26–43. https://doi.org/10.1152/jn.00720.2006.

Malhotra S, Stecker GC, Middlebrooks JC et al. (2008). Sound localization deficits during reversible deactivation of primary auditory cortex and/or the dorsal zone. J Neurophysiol 99: 1628–1642. https://doi.org/10.1152/jn.01228.2007.

Martuzzi R, Murray MM, Michel CM et al. (2007). Multisensory interactions within human primary cortices revealed by BOLD dynamics. Cereb Cortex 17: 1672–1679. https://doi.org/10.1093/cercor/bhl077.

Myklebust HR, Brutten M (1953). A study of the visual perception of deaf children. Acta Otolaryngol 105: 1–126.

Mayberry RI, Chen JK, Witcher P et al. (2011). Age of acquisition effects on the functional organization of language in the adult brain. Brain Lang 119: 16–29.

Merabet LB, Pascual-Leone A (2010). Neural reorganization following sensory loss: the opportunity of change. Nat Rev Neurosci 11: 44–52. https://doi.org/10.1038/nrn2758.

Meredith MA (2002). On the neuronal basis for multisensory convergence: a brief overview. Cogn Brain Res 14: 31–40. https://doi.org/10.1016/S0926-6410(02)00059-9.

Meredith MA, Kryklywy J, McMillan AJ et al. (2011b). Crossmodal reorganization in the early deaf switches sensory, but not behavioral roles of auditory cortex. Proc Natl Acad Sci U S A 108: 8856–8861. https://doi.org/10.1073/pnas.1018519108.

Meredith MA, Clemo HR, Corley SB et al. (2016). Cortical and thalamic connectivity of the auditory anterior ectosylvian cortex of early-deaf cats: implications for neural mechanisms of crossmodal plasticity. Hear Res 333: 25–36. https://doi.org/10.1016/j.heares.2015.12.007.

Miller LM, D'Esposito M (2005). Perceptual fusion and stimulus coincidence in the cross-modal integration of speech. J Neurosci 25: 5884–5893. https://doi.org/10.1523/JNEUROSCI.0896-05.2005.

Moallem TM, Reed CM, Braida LD (2010). Measures of tactual detection and temporal order resolution in congenitally deaf and normal-hearing adults. J Acoust Soc Am127: 3696–3709. https://doi.org/10.1121/1.3397432.

Moore DR, King AJ (1999). Auditory perception: the near and far of sound localization. Curr Biol 9: R361–R363.

Mori S, van Zijl PCM (2002). Fiber tracking: principles and strategies—a technical review. NMR Biomed 15: 468–480.

Murray MM, Molholm S, Michel CM et al. (2005). Grabbing your ear: rapid auditory-somatosensory multisensory interactions in low-level sensory cortices are not constrained by stimulus alignment. Cereb Cortex 15: 963–974. https://doi.org/10.1093/cercor/bhh197.

Neuhoff JG (1998). Perceptual bias for rising tones [4]. Nature 95: 123–124. https://doi.org/10.1038/25862.

Neville HJ, Lawson D (1987). Attention to central and peripheral visual space in a movement detection task: an event-related potential and behavioral study. II. Congenitally deaf adults. Brain Res 405: 268–283. https://doi.org/10.1016/0006-8993(87)90296-4.

Neville HJ, Bavelier D, Corina D et al. (1998). Cerebral organization for language in deaf and hearing subjects: biological constraints and effects of experience. Proc Natl Acad Sci U S A 95: 922–929. https://doi.org/10.1073/pnas.95.3.922.

Nishimura H, Hashikawa K, Doi K et al. (1999). Sign language 'heard' in the auditory cortex. Nature 397: 116.

Pallas SL, Roe AW, Sur M (1990). Visual projections induced into the auditory pathway of ferrets. I. Novel inputs to primary auditory cortex (AI) from the LP/pulvinar complex and the topography of the MGN-AI projection. J Comp Neurol 298: 50–68. https://doi.org/10.1002/cne.902980105.

Palmer SM, Rosa MGP (2006). Quantitative analysis of the corticocortical projections to the middle temporal area in the marmoset monkey: evolutionary and functional implications. Cereb Cortex 16: 1361–1375. https://doi.org/10.1093/cercor/bhj078.

Pascual-Leone A, Amedi A, Fregni F et al. (2005). The plastic human brain cortex. Annu Rev Neurosci 28: 377–401.

Pavani F, Bottari D (2012). Visual abilities in individuals with profound deafness a critical review. In: MM Murray, MT Wallace (Eds.), The neural bases of multisensory processes. CRC Press, Boca Raton (FL).

Perrodin C, Kayser C, Logothetis NK et al. (2014). Auditory and visual modulation of temporal lobe neurons in voice-sensitive and association cortices. J Neurosci 34: 2524–2537.

Petitto LA, Zatorre RJ, Gauna K et al. (2000). Speech-like cerebral activity in profoundly deaf people processing signed languages: implications for the neural basis of human language. Proc Natl Acad Sci U S A 97: 13961–13966. https://doi.org/10.1073/pnas.97.25.13961.

Price CJ (2012). A review and synthesis of the first 20years of PET and fMRI studies of heard speech, spoken language and reading. Neuroimage 62: 816–847. https://doi.org/10.1016/j.neuroimage.2012.04.062.

Proksch J, Bavelier D (2002). Changes in the spatial distribution of visual attention after early deafness. J Cogn Neurosci 14: 687–701. MIT PressOne Rogers Street, Cambridge, MA 02142-1209USAjournals-info@mit.edu, Department of Brain and Cognitive Sciences, University of Rochester, Rochester, NY 14627-0268, USA.

Rauschecker JP (1995). Compensatory plasticity and sensory substitution in the cerebral cortex. Trends Neurosci18: 36–43. https://doi.org/10.1016/0166-2236(95)93948-W.

Rauschecker JP, Tian B (2000). Mechanisms and streams for processing of “what” and “where” in auditory cortex. Proc Natl Acad Sci U S A 97: 11800–11806. https://doi.org/10.1073/pnas.97.22.11800.

Rezk M, Cattoir S, Battal C et al. (2020). Shared representation of visual and auditory motion directions in the human middle-temporal cortex. Curr Biol 30: 2289–2299. https://doi.org/10.1016/j.cub.2020.04.039.

Rockland KS, Ojima H (2003). Multisensory convergence in calcarine visual areas in macaque monkey. Int J Psychophysiol 50: 19–26. https://doi.org/10.1016/S0167-8760(03)00121-1.

Röder B, Teder-Sälejärvi W, Sterr A et al. (1999). Improved auditory spatial tuning in blind humans. Nature 400: 162–166. https://doi.org/10.1038/22106.

Roe AW, Pallas SL, Kwon YH et al. (1992). Visual projections routed to the auditory pathway in ferrets: receptive fields of visual neurons in primary auditory cortex. J Neurosci 12: 3651–3664. https://doi.org/10.1523/jneurosci.12-09-03651.1992.

Rouger J, Lagleyre S, Démonet J-F et al. (2012). Evolution of crossmodal reorganization of the voice area in cochlear-implanted deaf patients. Hum Brain Mapp 33: 1929–1940.

Sadato N, Yamada H, Okada T et al. (2004). Age-dependent plasticity in the superior temporal sulcus in deaf humans: a functional MRI study. BMC Neurosci 5: 1–6. https://doi.org/10.1186/1471-2202-5-56.

Sadato N, Okada T, Honda M et al. (2005). Cross-modal integration and plastic changes revealed by lip movement, random-dot motion and sign languages in the hearing and deaf. Cereb Cortex 15: 1113–1122. https://doi.org/10.1093/cercor/bhh210.

Sandmann P, Dillier N, Eichele T et al. (2012). Visual activation of auditory cortex reflects maladaptive plasticity in cochlear implant users. Brain 135: 555–568.

Schroeder CE, Foxe JJ (2002). The timing and laminar profile of converging inputs to multisensory areas of the macaque neocortex. Cogn Brain Res 14: 187–198. https://doi.org/10.1016/S0926-6410(02)00073-3. Elsevier.

Scott SK, Johnsrude IS (2003). The neuroanatomical and functional organization of speech perception. Trends Neurosci 26: 100–107. https://doi.org/10.1016/S0166-2236(02)00037-1.

Scott GD, Scott G, Karns CM et al. (2014). Enhanced peripheral visual processing in congenitally deaf humans is supported by multiple brain regions, including primary auditory cortex. Front Hum 8: 1–9.

Shams L, Iwaki S, Chawla A et al. (2005). Early modulation of visual cortex by sound: an MEG study. Neurosci Lett 378: 76–81. https://doi.org/10.1016/j.neulet.2004.12.035.

Sharma A, Dorman MF, Kral A (2005). The influence of a sensitive period on central auditory development in children with unilateral and bilateral cochlear implants. Hear Res 203: 134–143.

Sharma A, Campbell J, Cardon G (2015). Developmental and cross-modal plasticity in deafness: evidence from the P1 and N1 event related potentials in cochlear implanted children. Int J Psychophysiol 95: 135–144.

Sheehan MJ, Nachman MW (2014). Morphological and population genomic evidence that human faces have evolved to signal individual identity. Nat Commun 5: 4800. https://doi.org/10.1038/ncomms5800.

Shibata DK, Kwok E, Zhong J et al. (2001). Functional MR imaging of vision in the deaf. Acad Radiol 8: 598–604. https://doi.org/10.1016/S1076-6332(03)80684-0.

Shiell MM, Zatorre RJ (2017). White matter structure in the right planum temporale region correlates with visual motion detection thresholds in deaf people. Hear Res 343: 64–71. https://doi.org/10.1016/j.heares.2016.06.011.

Shiell MM, Champoux F, Zatorre RJ (2014). Reorganization of auditory cortex in early-deaf people: functional connectivity and relationship to hearing aid use. J Cogn Neurosci 21: 1–14.

Shiell MM, Champoux F, Zatorre RJ (2015). Reorganization of auditory cortex in early-deaf people: functional connectivity and relationship to hearing aid use. J Cogn Neurosci 27: 150–163. https://doi.org/10.1162/jocn_a_00683.

Shiell MM, Champoux F, Zatorre RJ (2016). The right hemisphere planum temporale supports enhanced visual motion detection ability in deaf people: evidence from cortical thickness. Neural Plast. https://doi.org/10.1155/2016/7217630.

Sladen DP, Tharpe AM, Ashmead D et al. (2006). Visual attention in deaf and normal hearing adults residual auditory processing deficits in adolescents and young adults view project using immersive virtual reality to evaluate pedestrian street crossing decisions at a roundabout View project. Artic J Speech Lang Hear Res 48: 1529–1537. https://doi.org/10.1044/1092-4388(2005/106).

Soto-Faraco S, Kingstone A (2004). Multisensory integration of dynamic information. In: GA Calvert, BE Spence (Eds.), The handbook of multisensory processes. MIT Press. pp. 49–67.

Soto-Faraco S, Spence C, Lloyd D et al. (2004). Moving multisensory research along. Curr Dir Psychol Sci13: 29–32. https://doi.org/10.1111/j.0963-7214.2004.01301008.x.

Stein BE, Meredith MA (1993). The merging of the senses, MIT Press, Cambridge, MA.

Stein BE, Stanford TR (2008). Multisensory integration: current issues from the perspective of the single neuron. Nat Rev Neurosci 9. https://doi.org/10.1038/nrn2331255–226.

Stevens KM, Hemenway WG (1970). Beethoven's deafness. JAMA J Am Med Assoc 213: 434–437. https://doi.org/10.1001/jama.1970.03170290030006.

Strelnikov K, Rosito M, Barone P (2011). Effect of audiovisual training on monaural spatial hearing in horizontal plane. PLoS One 6: 18344. https://doi.org/10.1371/journal.pone.0018344.

Strelnikov K, Rouger J, Demonet J-F et al. (2013). Visual activity predicts auditory recovery from deafness after adult cochlear implantation. Brain 136: 3682–3695.

Strelnikov K, Rouger J, Lagleyre S et al. (2015). Increased audiovisual integration in cochlear-implanted deaf patients: independent components analysis of longitudinal positron emission tomography data. Eur J Neurosci 41: 677–685.

Stropahl M, Plotz K, Schönfeld R et al. (2015). Cross-modal reorganization in cochlear implant users: auditory cortex contributes to visual face processing. Neuroimage 121: 159–170. https://doi.org/10.1016/j.neuroimage.2015.07.062.

Takesian AE, Hensch TK (2013). Balancing plasticity/stability across brain development. Prog Brain Res 3–34. https://doi.org/10.1016/B978-0-444-63327-9.00001-1. Elsevier B.V.

Ungerleider LG, Mishkin M (1982). Two cortical visual systems. In: D Ingle, M Goodale, R Mansfield (Eds.), Analysis of visual behavior. MIT Press, pp. 549–586.

Van Dijk R, Kappers AML, Postma A (2013). Superior spatial touch: improved haptic orientation processing in deaf individuals. Exp Brain Res 230: 283–289. https://doi.org/10.1007/s00221-013-3653-7.

von Kriegstein K, Kleinschmidt A, Sterzer P et al. (2005). Interaction of face and voice areas during speaker recognition. J Cogn Neurosci 17: 367–376. https://doi.org/10.1162/0898929053279577.

Voss P, Collignon O, Lassonde M et al. (2010). Adaptation to sensory loss. Wiley Interdiscip Rev Cogn Sci 1: 308–328. https://doi.org/10.1002/wcs.13.

Watson JD, Myers R, Frackowiak RS et al. (1993). Area V5 of the human brain: evidence from a combined study using positron emission tomography and magnetic resonance imaging. Cereb Cortex 3: 79–94. https://doi.org/10.1093/cercor/3.2.79.

Zeki S, Watson JD, Lueck CJ et al. (1991). A direct demonstration of functional specialization in human visual cortex. J Neurosci 11: 641–649. https://doi.org/10.1523/JNEUROSCI.11-03-00641.1991.