Crossmodal reorganisation in deafness: mechanisms for functional preservation and functional change

Velia Cardin[1], Konstantin Grin[1], Valeria Vinogradova[2] and Barbara Manini[1]

1. Deafness, Cognition and Language Research Centre, UCL, London, UK.
2. School of Psychology, University of East Anglia, Norwich, UK.

Abstract

The study of deafness and blindness has contributed unique knowledge to our understanding of the brain, showing that environmental experience critically shapes neural structure and function. Nevertheless, the most prevalent theories of crossmodal plasticity propose opposed views about the function of reorganised cortical regions. Some theories agree on functional preservation, where in the absence of early sensory stimulation, cortical regions respond to a different sensory modality, but perform the same function. Others propose that the absence of sensory stimulation from birth results in cortical regions changing their "typical" sensory processing function to higher-order cognition. Both deafness and blindness have provided vast evidence in support of each of these theories. Here we use examples from the study of deafness to explore organisational mechanisms that would allow functional preservation and functional change to co-exist either in the same or adjacent regions. We provide a set of predictions and testable hypotheses that support each of these accounts, and lay out some steps that will move us towards more specific theories of cortical reorganisation.

Introduction

The study of deafness and blindness allows us to understand how the brain develops under different environmental conditions. In these cases, the variation is not in the environment *per se*, but in the types of sensory inputs that provide information about the environment. Understanding reorganisation in congenital deafness and blindness provides fundamental insights into brain function and its potential for change and enhancement, with important implications for the development of sensorimotor substitution devices and neural prostheses, for the planning of inclusive policies and for the design of better educational practices.

One of the most prominent questions on neural reorganisation concerns the function of sensory cortices when the preferred sensory input is missing. Studies in deaf and blind individuals have revealed significant reorganisation in sensory cortices as a consequence of sensory loss (Rauschecker et al., 1995; Bavelier and Neville, 2002; Merabet and Pascual-Leone, 2010; Ricciardi and Pietrini., 2011). In deaf individuals, the superior temporal cortex (STC), a region typically considered auditory, responds to other sensory inputs, such as vision and touch (Finney et al., 2001, 2003; MacSweeney et al., 2002; Fine et al., 2005; Auer et al., 2007; Emmorey et al., 2011; Leonard et al., 2012, Bottari et al., 2014; Karns et al., 2012; Cardin et al., 2013). In blind individuals, occipital regions usually involved in visual processing are activated by sound and touch (Arno et al., 2001; Amedi et al., 2002, 2007; Gougoux et al, 2005; Poirier et al, 2006; Collignon et al., 2007; Voss et al., 2008; Merabet et al., 2008). This type of reorganisation is known as crossmodal plasticity, where brain regions that usually process sensory information from a given modality adapt to process sensory information from a different modality (e.g. Rauschecker, 1995, 2002; Merabet and Pascual-Leone, 2010).

Several studies of deafness and blindness in animals and humans propose that one of the mechanisms of crossmodal plasticity is preservation of function, where cortical regions keep their original function but adapt to respond to a different sensory input (Pascual-Leone et al., 2005; Ricciardi et al., 2009; Lomber et al., 2010; Renier et al., 2013; Heimler et al., 2015). However, research in humans has also shown that sensory deprived regions take on higher-order cognitive functions such as working memory and language (Buchsbaum et al., 2005; Cardin et al., 2013; Ding et al., 2015; Röder et al., 2000, 2002; Watkins et al., 2012; Bedny et al., 2011, 2012, 2015; Bedny, 2017). Executive functions such as working memory are usually associated with activity in frontoparietal brain regions involved in cognitive control (D'Esposito and Postle, 2015), whereas the auditory and visual cortices are typically considered sensory regions. Thus, these findings raise the possibility of a change of function from sensory processing to executive functions, suggesting great malleability in the functional future of cortical areas. Researchers have referred to these theories in different ways, but here we summarise them into two main theoretical accounts, using a nomenclature that highlights function, the topic at the core of our discussion:

1. **Functional Preservation:** This theory proposes that after cross-modal reorganisation, cortical regions preserve the function they previously had, but adapt to process a sensory input in a different modality (Pascual-Leone et al., 2005; Ricciardi et al., 2009; Lomber et al., 2010; Renier et al., 2013; Heimler et al., 2015). For example, regions of the brain that in hearing cats are involved in sensory processing of auditory motion are involved in sensory processing of visual motion in deaf cats (Lomber et al., 2010). In both cases the function is the same -- motion -- but the modality of the input is different. This preservation is also observed for higher cognitive functions such as language, where superior temporal regions involved in speech processing in hearing individuals are recruited for sign language processing in deaf individuals, but not in hearing native signers (MacSweeney et al., 2002; Cardin et al., 2013, 2016a; Twomey et al., 2017).
2. **Functional Change:** This theory proposes a change in both the function of the cortex and the sensory modality to which it responds (see Bedny 2017 for a review). For example, auditory sensory areas in hearing individuals respond to visual working memory in deaf individuals (Buchsbaum et al., 2005; Cardin et al., 2013; Ding et al., 2015), and visual occipital regions are involved in language processing in blindness (Röder et al., 2000, 2002; Watkins et al., 2012; Bedny et al., 2011, 2012, 2015; Bedny, 2017).

It has been challenging to converge these findings on a single theory because there is extensive experimental evidence supporting both functional preservation and functional change. In fact, in some cases, there is evidence supporting preservation and change in the same cortical region. In this review, we use examples from the study of deafness to discuss mechanisms that could explain evidence supporting both accounts in the same or adjacent cortical regions. We will start with a summary of the evidence from deafness and blindness supporting each theory, and then describe two specific examples from the study of deafness that provide evidence in support of preservation and change of function in the same portion of the posterior Superior Temporal Cortex (STC). We first concentrate on the left pSTC, exploring the physiological and anatomical changes that could explain both language and working memory effects. We then move onto considering whether a single functional reorganisation theory could explain both effects. In the last section, we use the right pSTC as an example to discuss whether effects are arising from independent but adjacent cortical regions. Our aim is to reconcile findings that may initially seem contradictory, and provide a theoretical framework with testable hypotheses for future research.

Evidence for functional preservation

Theories of functional preservation propose that crossmodal reorganisation results from cortical regions preserving the function they would usually have, but adapting to processing a different sensory modality (Amedi et al., 2002; Pascual-Leone et al., 2005; Ricciardi et al., 2009; Lomber et al., 2010; Renier et al., 2013; Heimler et al., 2015). In some accounts of this theory, researchers propose that crossmodal plasticity is a product of the brain being organised into processing modules that perform a specific computation, regardless of the modality of the sensory input. They propose that regional preferences for a certain sensory modality in sighted and hearing individuals are due to better suitability of such modality for the computation the region performs (Pascual-Leone et al., 2005; Reich et al., 2011; Renier et al., 2013), and not necessarily due to pre-determined wiring to sensory organs.

Both deafness and blindness have provided compelling evidence supporting functional preservation (MacSweeney et al., 2002; Poirier et al., 2006; Capek et al., 2010; Lomber et al., 2010; Cardin et al., 2013; Striem-Amit et al., 2015; Bola et al., 2017; Benetti et al., 2017, 2018). One of the clearest examples of functional preservation comes from the study of deafness in cats. Lomber et al. (2010) causally demonstrated that cortical auditory regions that had a role in sound localisation in hearing cats were involved in the localisation of visual stimuli in deaf cats. Furthermore, these additional cortical resources conferred deaf cats with behavioural visual advantages over hearing animals. Studies in humans have also suggest a functional preservation in the deaf auditory cortex – regions processing voice identity and auditory rhythm in hearing individuals are involved respectively in face (Benetti et al., 2017; 2018) and visual rhythm processing in deaf individuals (Bola et al., 2018). For higher-order functions, regions involved in spoken language processing in hearing speakers are recruited for audiovisual language processing in deaf individuals (Neville et al., 1998; Emmorey et al., 2003, 2007; Horwitz et al., 2003; MacSweeney et al., 2002, 2008; Capek et al., 2010; Cardin et al., 2013; Twomey et al., 2017). Indeed, regions processing spoken language in hearing individuals maintain their specific role in phonological, semantic and syntactic processing in deaf individuals, either for speechreading (lipreading) or sign language (see Corina and Knapp, 2006; MacSweeney et al., 2008; Campbell and MacSweeney, 2012). In some cases, these are language regions that respond to sign and spoken language also in hearing individuals, suggesting a supramodal language network. Nevertheless, for more anterior auditory regions in the superior temporal cortex, the evidence shows activation in these areas for sign language processing in deaf signers, but not in hearing native signers (Söderfeldt et al., 1994; MacSweeney et al., 2002; Cardin et al., 2013; Emmorey et al, 2014; Twomey et al., 2017).

The study of the visual cortex of congenitally blind individuals has also provided evidence in support of functional preservation. A region in the left ventral occipito-temporal cortex of blind individuals, which in sighted individuals is more responsive to visually-presented letters than to other visual object categories (Cohen and Dehaene, 2004), responds more strongly to letters presented either in Braille (Sadato et al., 1996; Burton et al., 2002) or in the auditory modality by means of a sensory substitution algorithm (Striem-Amit et al., 2012). Functional preservation for spatial processing has also been shown in the visual cortex of the congenitally blind, where occipital regions were activated during an auditory- or tactile- spatial processing tasks in a congenitally blind group (Reiner et al., 2010; Collignon et al., 2011). These regions are typically involved in visuospatial- and motion-processing in sighted individuals. Functional preservation has also been demonstrated for category selectivity in the ventral-temporal cortex in early blind adults (Pietrini et al., 2004; Van den Hurk et al., 2017). In blind individuals, the patterns of neural activity for tactile or auditory face-, body-, scene-, and object-related stimuli is similar and could predict the response patterns for the same categories in the visual modality in sighted individuals.

Evidence for functional change

Functional change theories propose not only a change in the sensory modality recruiting a sensory deprived cortex, but fundamentally a change in the underlying function of this region (Uhl et al., 1991; Sadato et al., 1996, Cohen et al., 1997; Röder et al., 2002; Bedny et al., 2011; Burton et al, 2012; Lane et al., 2015; Bedny, 2017). In the case of deafness, evidence supporting this theory comes from the study of working memory in humans, where typically auditory regions are recruited for visual working memory tasks (Buchsbaum et al., 2005; Ding et al., 2015; Cardin et al., 2018). Sensory regions, such as the auditory cortex of hearing individuals, usually store information in working memory and are fundamental components in sensorimotor theories of working memory (D'Esposito and Postle, 2015). However, the effects found in deaf individuals seem to reflect a role beyond sensory storage, which had led to the proposal that this region is involved in higher-order cognitive control. Studies have shown enhanced functional connectivity in deaf individuals between STC regions recruited for working memory and frontoparietal regions (Ding et al., 2016; Cardin et al., 2018). There is also a correlation between behavioural performance and STC recruitment during a working memory task (Ding et al., 2015). Performance on working memory tasks also correlates with the strength of resting-state functional connectivity between STC and frontoparietal regions (Ding et al., 2016). In addition, hearing and deaf individuals have different profiles of activity in frontoparietal areas during working memory tasks, pointing to a network-wide reorganisation of working memory functions in deaf individuals (Cardin et al., 2018). Working memory is usually associated with activity in frontoparietal brain regions involved in cognitive control, whereas the auditory cortex is typically considered a sensory region. In other words, findings from the study of working memory suggest the possibility of a significant change of function, from sensory processing to executive functions in the auditory cortices of deaf individuals.

Human congenital deafness provides a unique approach to the study of plasticity effects, given that several factors contribute to brain reorganisation in deaf individuals. These include lack of sensory inputs, but also the acquisition of language in the visual domain, and in many cases a delay in language acquisition (Lyness et al., 2013). As such, when studying deafness, it is essential to ensure that the observed effects are not due to language delay or language processing, in particular when looking at superior temporal regions involved in auditory and speech processing in hearing individuals. The study by Cardin et al. (2018) controlled those variables by comparing deaf and hearing native signers, and by using linguistic and non-linguistic stimuli that did not differ in their component visual features. They observed recruitment of pSTC for working memory only in deaf individuals (and not in the control group of hearing native signers), independently of the linguistic content of the stimuli and the sign language knowledge of the participants. These findings excluded the possibility of language effects confounding the working memory results and provided support for a functional change towards higher-order cognitive processing in a region typically linked to sensory processing.

Evidence from the study of blindness also support a functional change. The occipital cortex, which is usually involved in visual processing, is selectively recruited for functions such as working memory in blind individuals (Amedi et al., 2003; Bonino et al., 2008; Park et al., 2011; Rimmele et al., 2019), maths (Kanjlia et al., 2016) and language (Röder et al., 2002; Amedi et al., 2004; Bedny et al., 2011; Watkins et al., 2012). These effects are not found in sighted individuals. These findings are not related to low-level sensory processing, given that: a) responses to spoken language in the blind occipital cortices are modulated by the grammatical and semantic properties of linguistic stimuli (Röder et al., 2002; Bedny et al., 2011); b) repetitive TMS applied to the occipital lobe in blind individuals interferes with semantic processing (Amedi et al., 2004); c) working memory effects cannot be attributed to sensory imagery (Watkins et al., 2012). Furthermore, the functional profile of visual areas of blind individuals mirrors the responses of classical language regions, suggesting again a functional change in the crossmodally reorganised cortex (Bedny et al., 2011, 2012)

Functional preservation and functional change in the same cortical region: the case of the deaf posterior Superior Temporal Cortex

The evidence summarised above suggests that crossmodal plasticity does not follow a single rule. It is likely that different brain regions undergo functional change or functional preservation depending on the weight and utility of outputs and inputs they receive, and the computations that are possible in such regions. Nonetheless, there are situations in which evidence for both these phenomena have been found in the same cortical area (Reich et al., 2011; Striem-Amit et al., 2012; Cardin et al., 2013, 2018; Kim et al., 2017). Here we will discuss one such example from the study of deafness: the posterior Superior Temporal Cortex (pSTC). This region has been shown to have a role in language processing, which at least in the left hemisphere supports preservation of function, but has also been shown to have a role in working memory, which suggests functional change.

Language processing has been functionally assigned to the STC of deaf individuals in several studies of sign language and lipreading (Emmorey and Corina, 1993; Bavelier et al., 1998; MacSweeney et al., 2002, 2004; Emmorey et al, 2003; Capek et al., 2008, 2010; Emmorey et al., 2013; Pénicaud et al., 2013; Cardin et al., 2013; Campbell et al., 2014; Twomey et al., 2017). Here we will use the study by Cardin et al. (2013) as a working example. In this study, the authors dissociated plasticity effects due to language processing from more general visuo-spatial processing effects. To achieve this, Cardin et al. (2013) conducted an fMRI experiment in which sign language stimuli were shown to three different groups: 1) deaf native signers; 2) deaf non-signers (English speakers) and 3) hearing non-signers. Participants' task was to press a button when they saw a sign that was produced in a cued location or when the sign contained a cued handshape. This task could be performed by both signers and nonsigners, but for signers it was the equivalent of a phoneme-monitoring task, and it tapped into processes underlying sign language comprehension. The rationale of this study was that any plasticity effect that reflected general visuo-spatial processing will be a consequence of deafness *per se* (lack of auditory inputs) and will be present in both groups of deaf participants, but not in the group of hearing non-signers. On the other hand, a plasticity effect that reflected language processing will be found only in deaf signers. Plasticity effects associated with sign language processing were found in deaf signers both in the left and right STC (Fig. 1), and only when stimuli had linguistic content. Specifically, in the left STC, a region that is involved in auditory speech and language processing in hearing individuals, plasticity effects were mainly associated with sign language processing. This finding suggested that after plastic reorganisation cortical regions develop their typical function, in this case language, but adapt to a different type of sensory input, not only to aid perception (Lomber et al., 2010), but also for higher-order cognitive functions (Cardin et al., 2018).

In contrast, a different study also in deaf individuals provides support for functional change in the left pSTC. Cardin et al. (2018) showed that pSTC is recruited for visual working memory in deaf individuals. In this study, the authors were interested in understanding the neural networks involved in linguistic and non-linguistic working memory in deaf individuals. Previously, when studies addressed this question, stimuli in the linguistic and non-linguistic conditions differed considerably in their component sensory features (see Rudner et al., (2009) for a review). To avoid this issue and results driven by low-level sensory properties, Cardin et al. (2018) used point-light displays of British Sign Language signs (linguistic) or of moving non-sense objects (non-linguistic). Results showed recruitment of bilateral pSTC for working memory, but only in deaf participants. Because of the previous findings allocating language processing to pSTC, this effect was expected for the condition with linguistic content, but a working memory effect was observed with both types of stimuli, linguistic and non-linguistic. Thus, the effect seemed to be related to working memory *per se*, and not to the linguistic processing of the stimuli.

Both these studies, one of language and one of working memory, showed recruitment of pSTC in deaf individuals. As can be seen in Fig. 1, there is considerable overlap in the location of such effects in pSTC, with the language effect extending more anteriorly in the STC. Nonetheless, both studies demonstrated the specificity of the observed effects - the effect of language in Cardin et al. (2013) was only present in deaf signers, the only group that had access to the linguistic content of the stimuli; in Cardin et al. (2018) the effect of working memory was only found in the group of deaf individuals and only during the working memory task, not during the control condition, which excludes an effect of deafness on general visuospatial processing. Furthermore, the tasks that participants performed in each study were very different. The task used for the working memory effect is a demanding 2-back task on videos of point light displays. In the experiment showing a language effect, participants performed a monitoring task, that did not have a strong working memory component. In both cases, effects of task demands were eliminated by comparing activations across groups. Properties of the stimuli were also very different between both studies, as one used point-light displays and the other used videos of a person signing. In summary, activation in left pSTC in these studies cannot be explained by similarities in the composition and demands of the tasks between both studies.

What is compelling about these findings is that the language effect supports preservation of function, whereas the working memory effect suggests the possibility of a functional change. In the following section, we discuss neurophysiological processes that could explain both effects, including mechanisms by which both effects could co-exist, or by which a single process or theory can explain both effects.

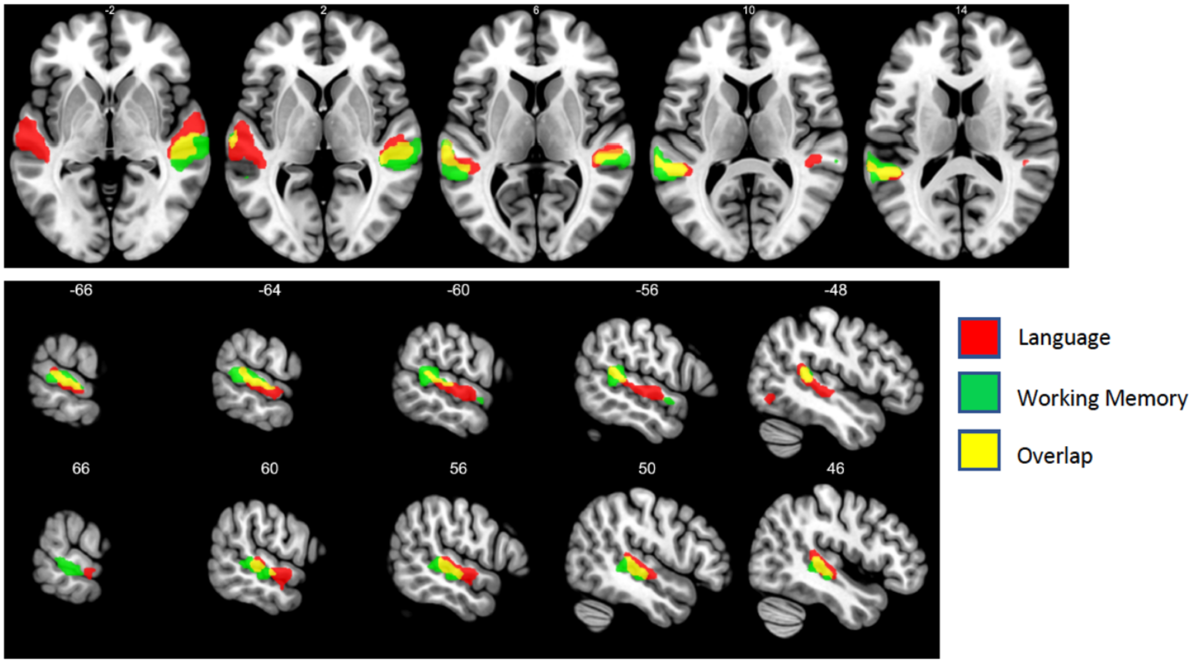

Fig. 1. Language and working memory effects in the Superior Temporal Cortex of deaf individuals. Language effect: regions that were more active during a phoneme monitoring task only in deaf native signers, but not in deaf non-signers or in hearing controls (results from Cardin et al., 2013). Working memory effect: regions that were more active for working memory only in deaf individuals (results from Cardin et al., 2018). Both effects displayed at $p < .001$ (language) and $p < .005$ (working memory) for visualisation purposes, but all peaks or clusters significant at $p < .05$, FWE.

Anatomical and physiological substrates for functional preservation and functional change

When discussing the anatomical and physiological mechanisms that could support functional preservation and functional change, it is important to consider certain anatomical and technical constraints. It is known that only a few new neuronal projections are found in crossmodally reorganised areas (Barone et al., 2013; Meredith et al., 2016; Meredith and Lomber, 2017). As such, plasticity likely arises from local and opportunistic changes such as unmasking of silent inputs, lack of pruning during development, and sprouting or extension of connections from neighbouring regions (see for a review Rauschecker, 1995). This is a constraint for both theories, functional change and functional preservation.

In addition, there are differences in the neuronal composition and physiology of primary and higher-order deaf auditory cortices. Even though plasticity has been shown in primary auditory cortex (e.g. Karns et al., 2012), crossmodal plasticity has been more consistently observed in higher-order areas (see for a review Kral 2007; Butler and Lomber 2013), in particular for visual cross-modal plasticity (Steward and Starr, 1970; Kral et al., 2003; Yusuf et al., 2017; Cardin et al., 2013, 2016b). Therefore, we will concentrate on evidence from animal and human studies in higher-order auditory areas, so that we can better understand the mechanisms of reorganisation in human pSTC.

Lastly, the working examples discussed, and much of the evidence supporting different theories of plasticity in humans, have come from fMRI studies. BOLD fMRI measures haemodynamic changes reflected in the blood-oxygen-level-dependent (BOLD) signal, which can be used as an index of neural activity. The neural composition of the BOLD signal is complex, reflecting the firing of cortical neurons (Mukamel et al., 2005; Lee et al., 2010), but also local processing which may not produce changes in spiking, such as presynaptic activity, neuromodulation and changes in the excitation-inhibition balance of a cortical region (Logothetis, 2008). As such, two fMRI found in the same cortical region will not necessarily reflect the same physiological events.

Keeping this in mind, what sort of physiological and anatomical mechanisms could give rise to preservation and change in the same cortical region? One way in which both effects could be located in the same area is through reflecting activity in different populations of neurons. For example, the dorsal zone (DZ) of the cat's auditory cortex, which has a role in visual motion detection in deaf cats (Lomber et al., 2010), contains cells that respond to auditory inputs (when these inputs are restored), as well as an increased number of cells responding to visual stimulation (Land et al., 2016). Whereas the number of auditory-responsive neurons is the same in deaf and hearing animals, a significant amount of visually-responsive neurons is only found in deaf cats. Visually- and auditory- responsive neurons were part of two different populations with different latencies and electrophysiological profiles (Land et al., 2016). The deaf human pSTC does not necessarily have the same populations of neurons that are found in the cat's DZ, but these results clearly demonstrate different populations of neurons in the deaf secondary auditory cortex, which could give rise to different functional effects.

Different effects could also reflect presynaptic inputs from different cortical areas. These presynaptic inputs will elicit local processing and will be reflected in the BOLD signal, but will not necessarily result in spiking. Inputs to neurons showing crossmodal responses are likely to originate from ectopic projections from visual, somatosensory and multimodal brain regions (Barone et al., 2013; Butler et al., 2017). A small number of such projections from the same non-auditory regions are also found in the same areas in hearing individuals (Meredith and Lomber, 2011), in agreement with crossmodal plasticity being a consequence of unmasked connections or extension of pre-existing or neighboring projections. We could only assume that a similar increase in ectopic connections will be found in humans, arising from cortico-cortical connections that are already present in the same or neighboring regions. In support of this, MEG/EEG studies show that visual responses only arise in the human STC in a late time window, suggesting that inputs to this region also originate from other cortical areas (Neville and Lawson, 1987; Finney et al., 2003; Bottari et al., 2014), and not from subcortical sensory processing (Leonard et al., 2012). A variety of cortico-cortical projections connect the human pSTC to visual and frontoparietal areas, and could differentially mediate functional preservation and a functional change towards higher-order cognitive functions. For example, the Middle Longitudinal Lateral Fasciculus connects pSTC with higher-order visual and multisensory areas (Makris et al., 2017). On the other hand, portions of this tract, together with the Arcuate Fasciculus, connect superior temporal regions to parietal and frontal areas involved in motor and higher-order cognitive functions such as language and working memory (Catani et al., 2005; Rilling et al., 2008; Makris et al., 2017).

There are also differences in the cytoarchitecture of the deafened auditory cortex that could explain different effects in the same region. The mammalian cerebral cortex has a structured composition of six well-defined cytoarchitectonic layers (Rockland and Pandya, 1979, 1981). This anatomical organisation gives rise to top-down, bottom-up and local processing, with distinct computations being performed in each layer (Rockland and Pandya, 1979, 1981; Sallin and Bullier, 1995). In a study in which the laminar organisation of the auditory cortex was compared between deaf and hearing cats, Berger et al. (2017) found that layer 4 and infragranular layers are thinner in deaf cats, both in area DZ (secondary auditory) and A1 (primary auditory), with no difference in thickness in supragranular layers. This is not surprising, as layer 4 and infragranular layers are the ones receiving stronger auditory inputs from the thalamus and earlier auditory regions (Sakata and Harris, 2009), and in cases of deafness these inputs are not present or very significantly reduced. Infragranular layers send feedback projections to earlier cortical and subcortical regions, which suggest that feedback loops might also be compromised (Butler and Lomber, 2013). Berger et al. (2017) suggest that "*to allow the differential dystrophic effects between these layers, the coupling of supragranular to infragranular layers must be abnormal in congenital deafness*". This is interesting, because perhaps this "abnormal" coupling is what allows for a functional change in the auditory cortex, or for different functions in supragranular and infragranular layers. In support of the latter, it is known that cortical layers can perform different computations, and that neuronal networks simulations have shown supragranular and infragranular layers can have different functions (Rolls and Mills, 2017). This could be achieved by superficial layers operating as a discrete attractor network useful for categorisation and feeding information forward up the cortical hierarchy, whereas the deep layers could operate as a continuous attractor network useful for providing a spatially and temporally smooth output to output systems in the brain (Rolls and Mills, 2017). Specifically, Rolls and Mills (2017) suggest that the more continuous representations in deep cortical layers could be useful in functions such as language production, facilitating a smooth transition between different motor outputs. This is a compelling possibility, where perhaps supragranular layers of pSTC contribute information to working memory storage and infragranular layers to outputs such as language production. This is a testable hypothesis with current advances in high spatial resolution laminar fMRI (Lawrence et al., 2017).

A compelling observation from the studies described so far is that, in deafness, a preserved cortical physiology and architecture in auditory areas is not needed to effectively influence behaviour in other sensory modalities. We conclude this from the fact that area DZ contributes to visual perception, providing deaf cats with behavioral advantages in visual motion detection (Lomber et al., 2010), even though: a) its cortical composition and columnar dynamics are altered, and 2) the number of cells with visual crossmodal responses is small, with most neurons in DZ responding to restored visual stimulation. The fact that most neurons preserve their capability to respond to auditory stimuli after a life of deafness is striking - what is the function of these neurons when auditory inputs are not restored? It is possible that they respond to somatosensory stimulation, but somatosensory projections to DZ are scarce (Kok and Lomber, 2017) and the neuronal response to somatosensory stimulation is significantly smaller than the visual response (Meredith and Lomber, 2017). Another possibility is that if regions were to change function, these auditory-responsive neurons could be the candidates to support higher-order functions. It is possible to speculate that in the absence of the strong auditory input that usually drives this region, projections from frontal and parietal areas might drive activity in secondary auditory areas, and dramatically alter the columnar physiology. This is more likely to be the case in humans, where in comparison to other primate species white-matter volume in the frontal and temporal lobes, as well as white matter projections between frontal and temporal areas, are significantly increased (Schoenemann, 2006; Rilling et al., 2011).

Assuming similar physiological and anatomical changes in the auditory cortex of deaf humans and animals, it seems that secondary auditory cortices contribute to functions such as working memory and language even though the columnar physiology and auditory cortico-cortical interactions are altered. Understanding laminar computations during working memory and language in hearing individuals can aid us in explaining patterns of reorganisation in deaf individuals. A few studies using high-resolution fMRI in humans have started to investigate laminar physiology in humans (Lawrence et al., 2017), but most of the evidence comes from animal models. We cannot address questions about language with invasive techniques in animal models, but we do have knowledge of the cortical laminar dynamics that support working memory (Bastos et al., 2018; Markowitz et al., 2015). In frontal regions, gamma power (50–250 Hz) activity, which is strongest in superficial layers, has been associated with sensory information held in working memory (Howard et al., 2003; Roux et al., 2012; Markowitz et al., 2015; Bastos et al., 2018), correlating with the number of objects stored in working memory (Howard et al., 2003; Roux et al., 2012). The alpha/beta band (4–22 Hz), which is strongest in deep layers (Bastos et al., 2018), has been associated with top-down information (e.g., task rules) and with inhibitory functions. Authors found that local field potentials (LFPs) from superficial and deep layers were synchronized in the alpha/beta band, with deep layers regulating activity in the superficial layers and hence the maintenance of the contents of WM.

In early sensory areas such as the primary visual cortex, item-specific working memory traces are reflected in activity in supragranular layers and infragranular layer 5, but not in layer 4 (Lawrence et al., 2017). This item-specific activity disappears when there is other incoming sensory information such as a visual mask, but is reinstated when the mask is gone, consistent with top-down inputs sustaining this pattern of activity (Lawrence et al., 2017; Van Kerkoerle et al., 2017). Beyond V1, working-memory-related activity is present at all depths in V2 and V3 (Lawrence et al., 2017).

It is not clear what the contribution to working memory is of regions such as pSTC, both in hearing and deaf individuals. If the profile of activity during working memory in pSTC is similar to that observed in sensory areas such as V2/V3, then pSTC is likely to have preserved its function and its recruitment during working memory is likely to reflect the storage of sensory information. Alternatively, the composition and dynamics of pSTC could change to emulate frontal cortices involved in working memory control, which will support functional change and the idea that sensory regions take on higher-order functions as a consequence of sensory absence. The first step in order to answer this question is to understand further the role of pSTC in auditory working memory in hearing individuals, characterising the dynamics and representation of information in this region, to then compare this to the representations observed in the crossmodally reorganised pSTC of deaf individuals.

Different effects may reflect the same underlying function

Working memory and language findings in the deaf pSTC could be easily explained if both effects were a manifestation of the same underlying function. The most parsimonious interpretation for our present examples is that they both reflect either language or working memory activity.

We start by considering whether the working memory effects observed by Cardin et al. (2018) could be explained by labeling or phonological coding of the stimuli, which is a common strategy in working memory tasks (Hicks, 1980; Palmer, 2000). In Cardin et al. (2018), the effect of working memory was observed both in the linguistic and the non-linguistic conditions. The non-linguistic stimuli did not have pre-existing labels, but participants could have created labels on the go, with activations in pSTC reflecting language processing or rehearsal in both conditions. If this was the case, it will be expected that all participants, deaf and hearing, would use this strategy to perform the task. Either hearing native signers could have used sign language to label the stimuli, or any of the hearing groups could have used spoken language to label the stimuli. In any such cases, activation of pSTC should have been found if this was linked to labeling or vocalisation; neither of these effects was found. Furthermore, recruitment of pSTC for working memory in deaf individuals has also been observed in other studies of working memory that use pure visuospatial displays (Ding et al., 2015, Manini et al., 2019), for which labeling is not a useful strategy, supporting the argument that this effect is independent of language processing.

The evidence summarised above suggests it unlikely that working memory effects could be explained as language processing. But what about the reverse situation, could the language effects be explained as working memory? The task used in Cardin et al. (2013) did not have a strong working memory component, deeming this explanation unlikely.

Finally, the observed effects in pSTC could be a common function that subserves both WM and language. This notion is supported by studies of auditory working memory and speech processing in hearing individuals and stroke patients. Previous studies in hearing individuals have shown the involvement of pSTC in language and auditory working memory (Hickok et al., 2003; Leff et al., 2009; Koenigs et al., 2011; Kumar et al., 2016). Hickok et al. (2003) conducted a study in which participants had to listen and covertly rehearse non-sense speech sentences or melodic tonal sequences. Their results showed recruitment of posterior temporal regions during perception and rehearsal of both types of stimuli, speech and music. Because of the recruitment during the music condition, the authors excluded an explanation related only to phonological storage. Leff et al. (2009) used voxel-based morphometry in 210 structural scans from stroke patients and identified that the structural integrity of the left pSTC is necessary for spoken sentence comprehension and auditory short-term memory. Damage to this region did not affect auditory word and non-word repetition, highlighting that the effect was specific to working memory and language, and not a general auditory processing deficit. These findings suggested a shared substrate for auditory short-memory and speech comprehension, or for a common function that supports both. Findings from Koenigs et al. (2011) also supported this account, showing that patients with damage to the inferior frontal and posterior temporal areas were impaired on digit span, as well as on tests requiring the production and comprehension of language.

It is possible that the role of pSTC in hearing individuals could be a domain-general cognitive control mechanism used for language and working memory. Supporting this account, tasks with increased difficulty tend to elicit higher activations in left pSTC (e.g. Twomey et al., 2017; Cardin et al., 2018). As such, it is expected that areas involved in control will be recruited to a greater extent with increased difficulty. Furthermore, the involvement of this region in cognitive control in the visual domain in deaf individuals could be a remnant of the connections that are pruned during development -- a study comparing brain activations during cognitive control tasks in children and adults showed that children, but no adults, activate a region in the left pSTC when they successfully inhibit a response or when they suppress interference (Bunge et al., 2002). Children also recruited frontal regions to a lesser extent or not at all, showing a developmental shift from posterior to anterior brain regions involved in cognitive control, and towards more successful control. Thus, it is possible that in the absence of auditory inputs reaching the STC during development, the role of that region in cognitive control persists through adulthood or that it is enhanced.

Whether a common function reflects preservation or change depends on the role of pSTC in hearing individuals. If pSTC is involved in cognitive control in deaf individuals, it seems to be at least a change from the function it has in hearing adults, but it could be a preservation of the role it had during development. This poses the question of whether functional change effects observed in blind individuals also reflect the preservation of roles visual cortices have during development, before full maturation of the adult brain.

Functional preservation and functional change may co-exist in adjacent, but distinct anatomical locations

Most of the evidence from humans discussed so far, and our two working examples, are fMRI results from group averages. However, it could be the case that an effect which seems to originate from the same cortical region, arises indeed from adjacent regions and merges into a single activation when smoothing and averaging is performed across participants. Plasticity effects in the right pSTC of deaf individuals can clearly exemplify why this is a potential issue in the study of deafness. Many fMRI studies in humans use univariate analyses to study crossmodal plasticity. In such studies, functional plasticity is often inferred from an increase in the amplitude of brain activity to visual or somatosensory stimulation in deaf individuals, compared to hearing individuals ([Deaf > Hearing]). Using univariate analyses and fMRI, the right pSTC has been consistently shown to undergo functional plasticity in deaf individuals across a variety of tasks, stimuli, and sensory modalities (Fig. 2). This evidence includes studies using visual stimulation as well as somatosensory stimulation, studies using simple stimuli such as moving dots or complex stimuli such as sign language, and studies with low-level perceptual tasks as well as more difficult working memory tasks (Fine et al., 2005; Emmorey et al., 2011; Karns et al., 2012; Cardin et al., 2013; Twomey et al., 2017; Bola et al., 2017; Benetti et al., 2018; Cardin et al., 2018). This broad plasticity effect is located in the right pSTC, but it is not found in other typically auditory regions. (As discussed above, crossmodal plasticity effects in the left pSTC are specific for working memory and language, but not for lower-level visuospatial tasks; Emmorey et al., 2011; Cardin et al., 2013, 2018; Twomey et al., 2017).

What do this task flexibility and overlap of visual and somatosensory responses in right pSTC mean for the mechanisms of plasticity? They suggest a role either in multisensory processing or in a higher cognitive function across sensory modalities, such as reorientation of attention. These proposed roles have been associated with adjoining temporo-parietal junction (TPJ) and posterior temporal multisensory regions (Geng et al., 2011; Beauchamp et al., 2008; Corbetta et al., 2008) (Fig. 2), providing a possible mechanism for plasticity based on anatomical vicinity. Furthermore, activity in right pSTC correlates with performance in a visual attention task in deaf and hearing individuals (Seymour et al., 2017), suggesting that this region may indeed have a role in attention in both populations. Despite the likelihood of a higher-order function for the reorganised right pSTC, plasticity in this region has often been associated with crossmodal responses and functional preservation (Benetti et al., 2017; Bola et al., 2017). For example, it has been suggested that the same region that is involved in processing voice identity and auditory rhythm in hearing individuals is involved in face processing (Benetti et al., 2017) and visual rhythm perception in deaf individuals (Bola et al., 2017). Thus, research so far suggests several possibilities for the mechanism of plasticity in right pSTC:

- pSTC changes its function from auditory processing to higher-order attentional processing, supporting a functional change
- pSTC preserves its function but responds to other modalities, which supports functional preservation

- The region usually identified as pSTC is part of multisensory temporal regions or TPJ, but with stronger responses to vision and touch due to the loss of auditory inputs. This also indicates a functional preservation, but in a region that is also strongly multisensory in hearing individuals.

Because of the close vicinity between TPJ, posterior multisensory regions and other temporal areas typically considered auditory, it is possible that different plasticity mechanisms are mixed and averaged across adjacent anatomical regions in whole-brain group studies (Fig. 2). Future studies contrasting these different tasks and hypotheses, but also looking at the distribution of effects in a subject by subject basis, should provide answers to this.

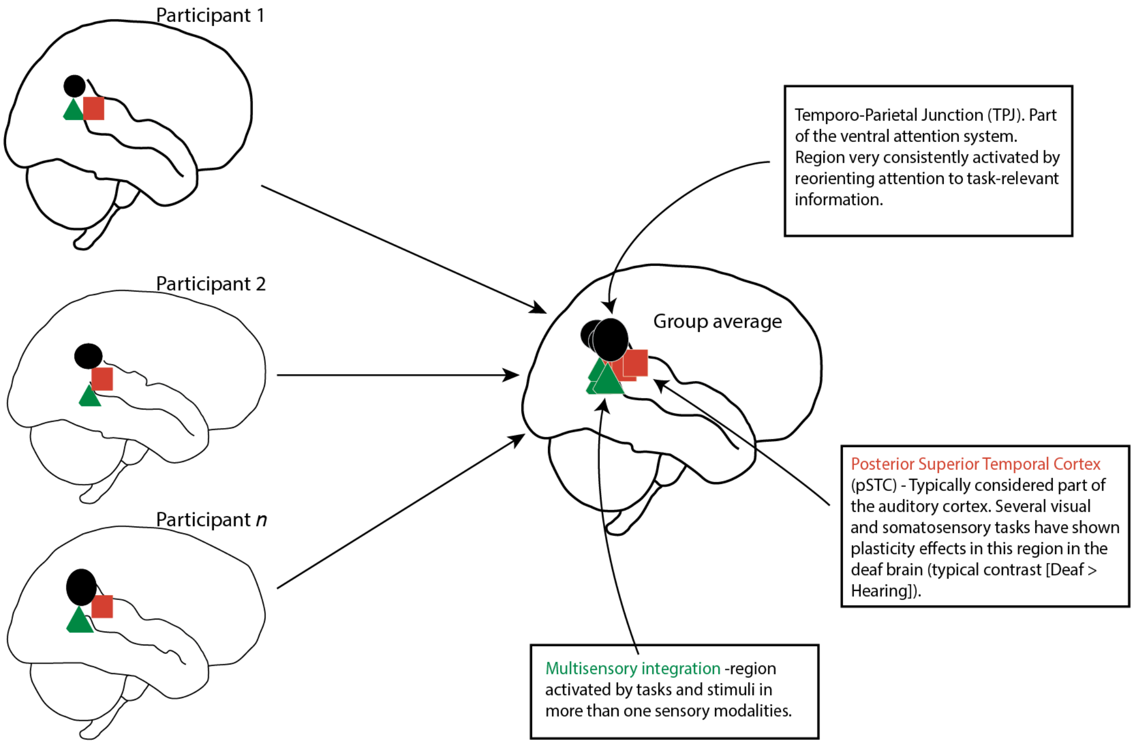

Fig. 2. Schematic representation of right pSTC and neighbouring regions. The extent, location and shape of each of these regions is different from participant to participant. Group averages are then likely to result in overlapped activations from adjacent regions.

Can the same principles be applied to the study of blindness?

A detailed review of the literature on blindness is beyond the scope of this review, but it is important to consider whether the accounts discussed above can also explain potentially contradicting results in the literature on crossmodal plasticity in the blind brain. Evidence for functional change and functional preservation in the same region in blind individuals has been reported in the Visual Word Form Area (VWFA). This is a portion of the left ventral occipitotemporal cortex (VOTC), which is suggested to have a specific role in reading (McCandliss et al., 2003; Shaywitz et al., 2008; Dehaene et al., 2010; but see also Price and Devlin, 2003;

2011). Typically, it is found to be more active when individuals look at words than when they look at scrambled letters or objects.

Evidence in support of functional preservation in the blind brain shows that this region also responds preferentially to letters presented in the somatosensory (Braille; Sadato et al., 1996; Burton et al., 2002; Reich et al., 2011) or in the auditory modality (using sensory substitution; Striem-Amit et al., 2012). The general consensus from these studies is that the "reading" specialization of the VWFA develops independently of visual experience, and that the function of the cortex is preserved.

On the other hand, Bedny and collaborators proposed a functional change in the VWFA of blind individuals, where this region shifts its function from processing written words to a more general language function (Bedny et al., 2011; Bedny, 2017; Kim et al., 2017). Their research in blind individuals shows that the VWFA not only responds preferentially to letters and words, but also to language stimuli in general (e.g. auditory sentences), with activity in this region being modulated by syntactic complexity. In their view, a common function can indeed explain both sets of results, where the VWFA's stronger response to letters in the somatosensory and auditory modality in blind individuals is due to its shift towards a more general role in language processing, and not because of preserved specialisation for reading, indicating that specialisation for reading does indeed require visual experience.

Interestingly, the specificity of the VWFA is not present at birth and instead develops with literacy. VWFA specificity for words increases as children learn to read, with word selectivity only observed in fully literate children, and with selectivity for words correlating with reading skills in 7-12 years old children (Dehane-Lambertz et al., 2018; Kubota et al., 2019). Increased selectivity to tactile words can also arise in VWFA in sighted individuals as they learn to read Braille (Siuda-Krzywicka et al., 2016). Given this change in specificity as a function of literacy, it is possible that this region of the VOTC has a general language function early in infancy and before reading develops, and that this function could persist in blind adults. It will be interesting to investigate changes in selectivity in the VWFA in blind individuals as they learn to read Braille, and see whether this shift towards letter selectivity is also observed. If this is the case, the increase in letter selectivity may be accompanied by a reduction in sensitivity to syntactic complexity, indicating an increased specialisation for reading and reduced general linguistic processing.

Another possibility is that both these effects do indicate a role of this region in language processing, but they do not necessarily represent a functional change. Price and Devlin (2003; 2011) propose that the ventral occipito temporal cortex, including the region called VWFA, has a role in integrating incoming bottom-up visual information with top-down conceptual and phonological knowledge, such as speech sounds, actions and meanings (Price and Devlin, 2011). They have argued against the existence of a brain specialisation for reading in VOTC, suggesting that the name WVFA is misleading (Price and Devlin, 2003). The authors have based their argument on evidence showing that the ventral occipital cortex is activated not only by reading but also by tasks not involving any visual word component, such as observing and naming pictures, manipulating unfamiliar objects, naming colours, and processing of auditory and tactile stimuli. In their view, neurons in the VOTC are not selectively tuned to orthographic inputs, and the observed specialization from orthography is part of an ongoing interaction between bottom-up visual features and top-down modulations (Price and Devlin, 2011). If this account holds, and the role of this region is indeed language processing also in sighted individuals, the findings in blind individuals will be reflecting the same common function, but supporting functional preservation for language processing, and not a functional change.

Further research in sighted and blind individuals is needed to disambiguate between these possibilities. Specifically, MEG research could demonstrate whether these effects coincide in time, and developmental and learning studies could clarify whether word selectivity is a function of literacy also in the blind population. Moreover, these are excellent examples of how the study of deafness and blindness provides insights on crossmodal plasticity, but more generally on the principles of brain organisation.

Conclusion and future directions

The study of plasticity in deaf and blind individuals has revealed a striking capacity of the brain for adaptation and change. Theories of crossmodal plasticity propose either a functional preservation or a functional change. Evidence from both sets of theories have made important contributions to our understanding of crossmodal reorganisation, but more generally to knowledge of the brain, challenging traditional models of neural function. These include theories such as the pluripotentiality of the cortex (Bedny, 2017) or experience-based modality-independent organisation of processing structures (Pascual-Leone and Hamilton, 2001; Lomber et al., 2010; Reich et al., 2011; Heimler et al., 2015).

It is clear that there is substantial evidence supporting functional preservation and functional change, in some cases from the same model and the same research group. Instead of contrasting both theories, here we tried to identify neural mechanisms that could support both accounts in the same or adjacent regions. We suggest that these two mechanisms could co-exist across the cortex, reflecting either different processes in distinct groups of neurons or cytoarchitectonic layers within the same cortical region. Evidence from the study of deaf cats has shown the existence of populations of neurons with distinct functional profiles in the secondary auditory cortex (Land et al., 2016). Some neurons show crossmodal responses, probably due to unmasking or sprouting of pre-existing connections, but a large proportion of neurons can respond to restored inputs and seem to preserve their wiring, with very few neurons showing bimodal responses. It is unlikely these auditory-responsive neurons are dormant in deaf cats, and they could potentially be more susceptible to top-down modulations from higher areas and have a role in cognition. Future studies aimed at identifying neurons involved in cognitive processes in crossmodally reorganised areas would shed light onto the principles of reorganisation and its substrate.

Moreover, as a research field, we need more characterisation of plasticity effects in a layer-specific fashion, especially in human experimental research. The existence of separate functions in different layers has been proposed in models of sensory-typical individuals (Rolls and Mills, 2017), showing that this could be a general principle of neural organisation and function, and not only a consequence of early sensory absence. In the light of this, a future challenge for our scientific field will be to incorporate evidence and predictions about which cortical layers are the substrate of crossmodal changes, so that more precise theories of reorganisation could be developed. The technology now exists for high-resolution layer fMRI (Lawrence et al., 2017). This is not without challenges, as 7T scanners are less user-friendly than more common 3T or 1.5T, which is particularly problematic within populations with sensory loss, but it is an exciting possibility.

Another possibility for seemingly distinct effects in the same cortical regions is that they both underlie the same function. Here we discussed this possibility with examples of working memory and language in deaf individuals. Indeed, the effects observed in the left pSTC could underlie a common function, but we do not know what that function is. To answer this question, we need to know more about the role of pSTC in auditory working memory and cognitive control in hearing individuals, and more studies of executive functions with auditory paradigms. With this information, we will be then well equipped to confirm whether pSTC undergoes a functional change or a preservation. For example, working memory effects in pSTC could reflect functional preservation in the same way that sensorimotor cortices maintain sensory information during working memory. On the other hand, support for functional change will come if pSTC has a role in working memory control that is not observed in auditory working memory tasks in hearing individuals.

Finally, a likely explanation for functional preservation and functional change effects is that different cortical regions undergo different reorganisation, and that the opposing effects observed in the same cortical area are a consequence of smoothing and averaging across groups of participants. Here we discussed how this is an issue in the study of crossmodal reorganisation in the right pSTC of deaf individuals, but this is also a problem in many fMRI studies. A more meticulous mapping of several sensory and cognitive paradigms at subject-level would provide clues onto what regions undergo what type of crossmodal changes. If segregated organisation is the rule, it is likely that a fine balance between environmental influences and innate wiring will shift regions in different ways. Following the developmental trajectory of these changes is an exciting opportunity to reveal such organisational principles.

All these open questions will only be answered by continuing the joint effort to understand crossmodal reorganisation in animal and human models. Studies in animals provide invaluable information from invasive techniques that are not feasible in human populations. It will be intriguing to find out whether higher-order functions such as working memory are also reorganised to sensory-deprived regions in animal models and what are the cellular substrates of such reorganisation. On the other hand, only research in humans can address the effect of language in cortical development and crossmodal reorganisation. This is particularly important in models of deafness, where language deprivation is unfortunately a very common reality (see for a review Lyness et al., 2013). In the past few years, multivariate neuroimaging techniques have provided more detailed information about reorganisation (Peelen et al., 2014; Almeida et al., 2015; Handjaras et al., 2017; Mattioni et al., 2017), and the future challenge for our field is to expand this while also employing high-resolution imaging techniques. Deafness and blindness research in humans is challenging because the populations of interest are small and difficult to recruit, which calls for our field to embark in cross-laboratory projects such as those used in other research with similar obstacles (Frank et al., 2018).

Figure Legends

Fig. 1. Language and working memory effects in the Superior Temporal Cortex of deaf individuals. Language effect: regions that were more active during a phoneme monitoring task only in deaf native signers, but not in deaf non-signers or in hearing controls (results from Cardin et al., 2013). Working memory effect: regions that were more active for working memory only in deaf individuals (results from Cardin et al., 2018). Both effects displayed at $p < .001$ (language) and $p < .005$ (working memory) for visualisation purposes, but all peaks or clusters significant at $p < .05$, FWE.

Fig. 2. Schematic representation of right pSTC and neighbouring regions. The extent, location and shape of each of these regions is different from participant to participant. Group averages are then likely to result in overlapped activations from adjacent regions.

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References

Almeida, J., He, D., Chen, Q., Mahon, B.Z., Zhang, F., Gonçalves, Ó.F., Fang, F., Bi, Y. Decoding visual location from neural patterns in the auditory cortex of the congenitally deaf. Psychol. Sci. 26, 1771-1782 (2015).

Amedi, A., Jacobson, G., Hendler, T., Malach, R., Zohary, E. Convergence of visual and tactile shape processing in the human lateral occipital complex. Cereb. Cortex. 12, 1202–1212 (2002).

Amedi, A., Raz, N., Pianka, P., Malach, R., Zohary, E. Early ‘visual’ cortex activation correlates with superior verbal memory performance in the blind. Nat. Neurosci. 6(7), 758-766 (2003).

Amedi, A., Floel, A., Knecht, S., Zohary, E., Cohen, L.G. Transcranial magnetic stimulation of the occipital pole interferes with verbal processing in blind subjects. Nat. Neurosci. 7(11), 1266-1270 (2004).

Amedi, A., Stern, W.M., Camprodon, J.A., Bermpohl, F., Merabet, L., Rotman, S., Hemond, C., Meijer, P., Pascual-Leone, A. Shape conveyed by visual-to-auditory sensory substitution activates the lateral occipital complex. Nat. Neurosci. 10(6), 687-689 (2007).

Arno, P., De Volder, A.G., Valierde, A., Wanet-Defalque, M.C., Streel, E., Robert, A., Sanabria-Bohórquez, S., Veraart, C. Occipital activation by pattern recognition in the early blind using auditory substitution for vision. Neuroimage. 13(4), 632-645 (2001).

Auer, E., Bernstein, L., Sungkarat, W., Signh, M. Vibrotactile activation of the auditory cortices in deaf versus hearing adults. Neuroreport. 18, 645-648 (2007).

Barone, P., Lacassagne, L., Kral, A. Reorganization of the connectivity of cortical field DZ in congenitally deaf cat. PloS One 8(4), e60093 (2013).

Bastos, A.M., Loonis, R., Kornblith, S., Lundqvist, M., Miller, E.K. Laminar mechanisms for working memory. Proc. Natl. Acad. Sci. 115(15), 1117-1122 (2018).

Bavelier, D., Corina, D., Jezzard, P., Clark, V., Karni, A., Lalwani, A., Rauschecker, J.P., Braun, A., Turner, R., Neville, H.J. Hemispheric specialization for English and ASL: left invariance-right variability. Neuroreport. 9(7), 1537-1542 (1998).

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

Beauchamp, M.S., Yasar, N. E., Frye, R.E., Ro, T. Touch, sound and vision in human superior temporal sulcus. Neuroimage. 41(3), 1011–20 (2008).

Bedny, M., Pascual-Leone, A., Dodell-Feder, D., Fedorenko, E., Saxe, R. Language processing in the occipital cortex of congenitally blind adults. Proc. Natl. Acad. Sci. 108(11), 4429-4434 (2011).

Bedny, M., Pascual-Leone, A., Dravida, S., Saxe, R. A sensitive period for language in the visual cortex: Distinct patterns of plasticity in congenitally versus late blind adults. Brain Lang. 122(3), 162-170 (2012).

Bedny, M., Richardson, H., Saxe, R. “Visual” Cortex Responds to Spoken Language in Blind Children. J. Neurosci. 35(33), 11674–11681 (2015).

Bedny, M. Evidence from Blindness for a Cognitively Pluripotent Cortex. Trends Cogn. Sci. 21(9), 637-648 (2017).

Benetti, S., Van Ackeren M.J., Rabini, G., Zonca, J., Foa, V., Baruffaldi, F., Rezk, M., Pavani, F., Rossion, B., Collignon, O. Functional selectivity for face processing in the temporal voice area of early deaf individuals. Proc. Natl. Acad. Sci. 114(31), 6437–6446 (2017).

Benetti, S., Novello, L., Maffei, C., Rabini, G., Jovicich, J., Collignon, O. White matter connectivity between occipital and temporal regions involved in face and voice processing in hearing and early deaf individuals. Neuroimage. 179, 263–274 (2018).

Berger, C., Kühne, D., Scheper, V., Kral, A. Congenital deafness affects deep layers in primary and secondary auditory cortex. J. Comp. Neurol. 525(14), 3110-3125 (2017).

Bola, Ł., Zimmermann, M., Mostowski, P., Jednoróg, K., Marchewka, A., Rutkowski, P., Szwed, M. Task-specific reorganization of the auditory cortex in deaf humans. Proc. Natl. Acad. Sci. 114(4), 600-609 (2017).

Bonino, D., Ricciardi, E., Sani, L., Gentili, C., Vanello, N., Guazzelli, M., Vecchi, T., Pietrini, P. Tactile spatial working memory activates the dorsal extrastriate cortical pathway in congenitally blind individuals. Arch Ital Biol. 146(3-4), 133–146 (2008).

Bottari, D., Heimler, B., Caclin, A., Dalmolin, A., Giard, M.H., Pavani, F. Visual change detection recruits auditory cortices in early deafness. Neuroimage. 94, 172-184 (2014).

Buchsbaum, B., Pickell, B., Love, T., Hatrak, M., Bellugi, U., Hickok, G. Neural substrates for verbal working memory in deaf signers: fMRI study and lesion case report. Brain Lang. 95(2), 265-72 (2015).

Bunge, S.A., Dudukovic, N.M., Thomason, M.E., Vaidya, C.J., Gabrieli, J.D.E. Immature Frontal Lobe Contributions to Cognitive Control in Children: Evidence from fMRI. Neuron. 33(2), 301-311 (2002).

Burton, H., Snyder, A.Z., Conturo, T.E., Akbudak, E., Ollinger, J.M., Raichle, M.E. Adaptive Changes in Early and Late Blind: A fMRI Study of Braille Reading. J Neurophysiol. 87(1), 589-607 (2002).

Burton, H., Sinclair, R.J., Agato, A. Recognition memory for Braille or spoken words: An fMRI study in early blind. Brain Res. 1438, 22-34 (2012).

Butler, B. E., Lomber, S. G. Functional and structural changes throughout the auditory system following congenital and early-onset deafness: Implications for hearing restoration. Front Syst Neurosci. 7, 92 (2013).

Butler, B.E., Chabot, N., Kral, A., Lomber, S.G. Origins of thalamic and cortical projections to the posterior auditory field in congenitally-deaf cats. Hear Res. 343, 118–127 (2017).

Campbell, R., MacSweeney, M. Brain bases for seeing speech: FMRI studies of speechreading, in: Bailly, G., Perrier, P., Vatikiotis-Bateson, E. (Eds.), Audiovisual Speech Processing. Cambridge University Press, Cambridge. 76-103 (2012).

Campbell, R., MacSweeney, M., Woll, B. Cochlear implantation (CI) for prelingual deafness: the relevance of studies of brain organization and the role of first language acquisition in considering outcome success. Front. Hum. Neurosci. 8, 834 (2014).

Capek, C.M., Waters, D., Woll, B., MacSweeney, M. Brammer, M.J., McGuire, P.K., David, A.S., Campbell, R. Hand and mouth: cortical correlates of lexical processing in British Sign Language and speechreading English. J. Cog. Neurosci. 20(7), 1220-34 (2008).

Capek, C.M., Woll, B., MacSweeney, M., Waters, D., McGuire, P.K., David, A.S., Brammer, M.J., Campbell, R. Superior temporal activation as a function of linguistic knowledge: Insights from deaf native signers who speechread. Brain Lang. 112(2), 129-134 (2010).

Cardin, V., Orfanidou, E., Rönnberg, J., Capek, C.M. Rudner, M., Woll, B. Dissociating cognitive and sensory neural plasticity in human superior temporal cortex. Nat. Commun. 4, 1473 (2013).

Cardin, V., Orfanidou, E., Kästner, L., Rönnberg, J., Woll, B., Capek, C.M., Rudner, M. Monitoring Different Phonological Parameters of Sign Language Engages the Same Cortical Language Network but Distinctive Perceptual Ones. J. Cog. Neurosci. 28(1), 20-40 (2016a).

Cardin, V., Smittenaar, R.C., Orfanidou, E., Rönnberg, J., Capek, C.M., Rudner, M., Woll, B. Differential activity in Heschl's gyrus between deaf and hearing individuals is due to auditory deprivation rather than language modality. Neuroimage. 124, 96-106 (2016b).

Cardin, V., Rudner, M., De Oliveira, R.F, Andin, J., Su, M.T., Beese, L., Woll, B., Rönnberg, J. The Organization of Working Memory Networks is Shaped by Early Sensory Experience. Cereb. Cortex. 28(10), 3540–3355 (2018).

Catani, M., Jones, D.K., Ffytche, D.H. Perisylvian language networks of the human brain. Ann. Neurol. 57, 8-16 (2005).

Cohen, L.G., Celnik, P., Pascual-Leone, A., Corwell, B., Falz, L., Dambrosia, J., Honda, M., Sadato, N., Gerloff, C., Catalá, M.D., Hallett, M. Functional relevance of cross-modal plasticity in blind humans. Nature. 389(6647), 180-183 (1997).

Cohen, L., Dehaene, S. Specialization within the ventral stream: the case for the visual word form area. Neuroimage. 22(1), 466-476 (2004).

Collignon, O., Lassonde, M., Lepore, F., Bastien, D., Veraart, C. Functional cerebral reorganization for auditory spatial processing and auditory substitution of vision in early blind subjects. Cereb. Cortex. 17(2), 457-465 (2007).

Collignon, O., Vandewalle, G., Voss, P., Albouy, G., Charbonneau, G., Lassonde, M., Lepore, F. Functional specialization for auditory-spatial processing in the occipital cortex of congenitally blind humans. Proc. Natl. Acad. Sci. 108(11), 4435-4440 (2011).

Corbetta, M., Patel, G., Shulman, G.L. The reorienting system of the human brain: from environment to theory of mind. Neuron. 58(3), 306–24 (2008).

Corina, D.P., Knapp, H. Sign Language Processing and the Mirror Neuron System. Cortex. 42(4), 529-39 (2006).

Dehaene-Lambertz, G., Monzalvo, K., Dehaene, S. The emergence of the visual word form: Longitudinal evolution of category-specific ventral visual areas during reading acquisition. PLoS Biol. 16(3), e2004103 (2018).

D'Esposito, M., Postle B.R. The cognitive neuroscience of working memory. Annu. Rev. Psychol. 66, 115-42 (2015).

Ding, H., Qin, W., Liang, M., Ming, D., Wan, B., Li, Q., Yu, C. Cross-modal activation of auditory regions during visuo-spatial working memory in early deafness. Brain. 138(9), 2750–2765 (2015).

Ding, H., Ming, D., Wan, B., Li, Q., Qin, W., Yu, Ch. Enhanced spontaneous functional connectivity of the superior temporal gyrus in early deafness. Sci. Rep. 6, 23239 (2016).

Emmorey, K., Corina, D. Hemispheric specialization for ASL signs and English words: Differences between imageable and abstract forms. Neuropsychologia. 31(7), 645-653 (1993).

Emmorey, K., Grabowski, T., McCullough, S., Damasio, H., Ponto, L.L.B., Hichwa, R.D., Bellugi, U. Neural systems underlying lexical retrieval for sign language. Neuropsychologia. 41, 85–95 (2003).

Emmorey, K., Mehta, S., Grabowski, T.J. The neural correlates of sign versus word production. NeuroImage, 36, 202–208 (2007).

Emmorey, K., Xu, J., Braun, A. Neural responses to meaningless pseudosigns: evidence for sign-based phonetic processing in superior temporal cortex. Brain Lang. 117, 34–38 (2011).

Emmorey, K., McCullough, S., Mehta, S., Ponto, L.L., Grabowski, T.J. The biology of linguistic expression impacts neural correlates for spatial language. J. Cogn. Neurosci. 25(4), 517-533 (2013).

Emmorey, K., McCullough, S., Mehta, S., Grabowski, T.J. How sensory-motor systems impact the neural organization for language: Direct contrasts between spoken and signed language. Front Psych. 5, 484 (2014).

Fine, I., Finney, E.M., Boynton, G.M., Dobkins, K.R. Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. J. Cogn. Neurosci. 17, 1621–1637 (2005).

Finney, E.M., Fine, I., Dobkins, K.R. Visual stimuli activate auditory cortex in the deaf. Nat. Neurosci. 4, 1171–1173 (2001).

Finney, E.M., Clementz, B.A., Hickok, G., Dobkins, K.R. Visual stimuli activate auditory cortex in deaf subjects: evidence from MEG. Neuroreport. 14, 1425-1427 (2003).

Frank, M.C., Bergelson, E., Bergmann, C., Cristia, A., Floccia, C., Gervain, J., Hamlin, J.K., Hannon, E.E., Kline, M., Levelt, C., Lew-Williams, C., Nazzi, T., Panneton, R., Rabagliati, H., Soderstrom, M., Sullivan, J., Waxman, S.R., Yurovsky, D. A Collaborative Approach to Infant Research: Promoting Reproducibility, Best Practices, and Theory-Building. Infancy. 22(4), 421-435 (2017).

Geng, J.J., Mangun, G.R. Right temporoparietal junction activation by a salient contextual cue facilitates target discrimination. Neuroimage. 54(1), 594–601 (2011).

Gougoux, F.,Zatorre, R.J., Lassonde, M., Voss, P., Lepore, F. A Functional Neuroimaging Study of Sound Localization: Visual Cortex Activity Predicts Performance in Early-Blind Individuals. PloS Biol. 3(2),e27 (2005).

Handjaras, G., Leo, A., Cecchetti, L., Papale, P., Lenci, A., Marotta, G., Pietrini, P., Ricciardi, E. Modality-independent encoding of individual concepts in the left parietal cortex. Neuropsychologia. 105, 39-49 (2017).

Heimler, B., Striem-Amit, E., Amedi, A. Origins of task-specific sensory-independent organization in the visual and auditory brain: Neuroscience evidence, open questions and clinical implications. Curr Opin Neurobiol. 35, 169–177 (2015).

Hickok, G., Buchsbaum, B., Humphries, C., Muftuler, T. Auditory–motor interaction revealed by fMRI: speech, music, and working memory in area Spt. J. Cogn. Neurosci. 15(5), 673-682 (2003).

Hicks, C. The ITPA visual sequential memory task: An alternative interpretation and the implications for good and poor readers. Br. J. Educ. Psychol. 50(1), 16-25 (1980).

Horwitz, B., Amunts, K., Bhattacharyya, R., Patkin, D., Jeffries, K., Zilles, K., Braun, A.R. Activation of Broca’s area during the production of spoken and signed language: A combined cytoarchitectonic mapping and PET analysis. Neuropsychol. 41(14), 1868-1876 (2003).

Howard, M.W., Rizzuto, D.S., Caplan, J.B., Madsen, J.R., Lisman, J., Aschenbrenner-Scheibe, R., Schulze-Bonhage, A., Kahana, M.J. Gamma oscillations correlate with working memory load in humans. Cereb Cortex. 13(12), 1369-1374 (2003).

Hribar, M., Suput, D., Carvalho, A.A., Battelino, S., Vovk., A. Structural alterations of brain grey and white matter in early deaf adults. Hear. Res. 318, 1-10 (2014).

Kanjlia, S., Lane, C., Feigenson, L., Bedny, M. Absence of visual experience modifies the neural basis of numerical thinking. Proc. Natl. Acad. Sci. 113(40), 11172-11177 (2016).

Karns, C.M., Dow, M.W., Neville, H.J. 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 (2012).

Karns, C.M., Stevens, C., Dow, M.W., Schorr, E.M., Neville, H.J. Atypical white-matter microstructure in congenitally deaf adults: A region of interest and tractography study using diffusion-tensor imaging. Hear. Res. 343, 72-82 (2017).

Kim, D.J., Park, S.Y., Kim, J., Lee, D.H., Park, H.J. Alterations of white matter diffusion anisotropy in early deafness. Neuroreport. 20, 1031-1036 (2009).

Kim, J.S., Kanjlia, S., Merabet, L.B., Bedny, M. Development of the visual word form area requires visual experience: Evidence from blind Braille readers. J. Neurosci. 37, 11495-11504 (2017).

Koenigs, M., Acheson, D.J., Barbey, A.K., Solomon, J., Postle, B.R., Grafman, J. Areas of left perisylvian cortex mediate auditory–verbal short-term memory. Neuropsychologia. 49(13), 3612-361 (2011).

Kok, M., Lomber., S. Origin of the thalamic projection to dorsal auditory cortex in hearing and deafness. Hear. Res. 343, 108-117 (2017).

Kral, A., Schröder, J.H., Klinke, R., Engel, A.K. Absence of cross-modal reorganization in the primary auditory cortex of congenitally deaf cats. Exp. Brain. Res. 153, 605–613 (2003).

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

Kubota, E.C., Joo, S.J., Huber, E., Yeatman, J.D. Word selectivity in high-level visual cortex and reading skill. Dev Cogn Neurosci. 36, 100593. (2019).

Kumar, S., Joseph, S., Gander, P.E., Barascud, N., Halpern, A.R., Griffiths, T.D. A brain system for auditory working memory. J. Neurosci. 36, 4492-4505 (2016).

Land, R., Baumhoff, P., Tillein, J., Lomber, S.G., Hubka, P., Kral, A. Cross-Modal Plasticity in Higher-Order Auditory Cortex of Congenitally Deaf Cats Does Not Limit Auditory Responsiveness to Cochlear Implants. J. Neurosci. 36(23), 6175-6185 (2016).

Lane, C., Kanjlia, S., Omaki, A., Bedny, M. “Visual” Cortex of Congenitally Blind Adults Responds to Syntactic Movement. J. Neurosci. 35(37), 12859-12868 (2015).

Lawrence, S.J., Formisano, E., Muckli, L., de Lange, F.P. Laminar fMRI: Applications for cognitive neuroscience. Neuroimage. (2017).

Lee, J.H., Durand, R., Gradinaru, V., Zhang, F., Goshen, I., Kim, D.S., Fenno, L.E., Ramakrishnan, C., Deisseroth, K. Global and local fMRI signals driven by neurons defined optogenetically by type and wiring. Nature. 465(7299), 788-792 (2010).

Leff, A.P., Schofield, T.M., Crinion, J.T., Seghier, M.L., Grogan, A., Green, D.W., Price, C.J. The left superior temporal gyrus is a shared substrate for auditory short-term memory and speech comprehension: evidence from 210 patients with stroke. Brain. 132(12), 3401-3410 (2009).

Leonard, M.K., Ferjan Ramirez, N., Torres, C., Travis, K.E., Hatrak, M., Mayberry, R.I., Halgren, E. Signed words in the congenitally deaf evoke typical late lexicosemantic responses with no early visual responses in left superior temporal cortex. J. Neurosci. 32, 9700-9705 (2012).

Logothetis, N.K. What we can do and what we cannot do with fMRI. Nature. 453(7197), 869-878 (2008).

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

Lyness, R., Woll, B., Campbell, R., Cardin, V. How does visual language affect crossmodal plasticity and cochlear implant success? Neurosci Biobehav Rev. 37(10), 2621-2630 (2013).

Lyness, R.C., Alvarez, I., Sereno, M.I., MacSweeney, M. Microstructural differences in the thalamus and thalamic radiations in the congenitally deaf. Neuroimage. 100(100), 347-357 (2014).

MacSweeney, M., Woll, B., Campbell, R., McGuire, P.K., David, A.S., Williams, S.C.R., Suckling, J., Calvert, G.A., Brammer, M.J. Neural systems underlying British Sign Language and audio-visual English processing in native users. Brain. 125(7), 1583-1593 (2002).

MacSweeney, M., Campbell, R., Woll, B., Giampietro, V., David, A.S., McGuire, P.K., Calvert G.A., Brammer, M.J. Dissociating linguistic and nonlinguistic gestural communication in the brain. Neuroimage. 22(4), 1605-1618 (2004).

MacSweeney, M., Capek, C.M., Campbell, R., Woll, B. The signing brain: The neurobiology of sign language. Trends. Cogn. Sci. 12(11), 432-440 (2008).

Makris, N., Zhu, A., Papadimitriou, G.M., Mouradian, P., Ng, I., Scaccianoce, E., Baselli, G., Baglio, F., Shenton, M.E., Rathi, Y., Dickerson, B., Yeterian, E., Kubicki, M. Mapping temporo-parietal and temporo-occipital cortico-cortical connections of the human middle longitudinal fascicle in subject-specific, probabilistic, and stereotaxic Talairach spaces. Brain Imaging Behav. 11.5, 1258-1277 (2017).

Manini, B., Vinogradova, V., Woll, B., Eimer, M., Cameron, D., Saada, J., Cardin, V. Functional reorganization for visuo-spatial working memory in the STC of deaf individuals. Organization for Human Brain Mapping Conference (2019).

Markowitz, D. A., Curtis, C. E., & Pesaran, B. Multiple component networks support working memory in prefrontal cortex. Proc. Natl. Acad. Sci. 112, 11084-11089 (2015).

Mattioni, S., Rezk, M., Cuculiza, K., Battal, C., Bottini, R., Van Ackeren, M., Oosterhof, N., Collignon, O. A-modal versus Cross-modal: How input modality and visual experience affect categorical representation in the "visual" cortex. J. Vis. 17, 281 (2017).

Merabet, L.B., Hamilton, R., Schlaug, G., Swisher, J.D., Kiriakopoulos, E.T., Pitskel, N.B., Kauffman T., Alvaro Pascual-Leone A. Rapid and reversible recruitment of early visual cortex for touch. PLoS One. 3(8), e3046 (2008).

Merabet, L. B., Pascual-Leone, A. Neural reorganization following sensory loss: the opportunity of change. Nat. Rev. Neurosci. 11, 44–52 (2010).

Meredith, M.A., Lomber, S.G. Somatosensory and Visual Crossmodal Plasticity in the Anterior Auditory Field of Early-Deaf Cats. Hear. Res. 280(1-2), 38–47 (2011).

Meredith, M.A., Clemo, H.R., Corley, S.B., Chabot, N., Lomber, S.G. Cortical and thalamic connectivity of the auditory ectosylvian cortex of early deaf cats: Implications for neural mechanisms of crossmodal plasticity. Hear. Res. 333, 25-36 (2016).

Meredith, M.A. and Lomber, S.G. Species-dependent role of crossmodal connectivity among the primary sensory cortices. Hear. Res. 343, 83–91 (2017).

Mukamel, R., Gelbard, H., Arieli, A., Hasson, U., Fried, I., Malach, R. Coupling between neuronal firing, field potentials, and FMRI in human auditory cortex. Science. 309(5736), 951-954 (2005).

Neville, H.J., Lawson, D. 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(2), 268-283 (1987).

Neville, H.J., Bavelier, D., Corina, D., Rauschecker, J., Karni, A., Lalwani, A., Braun, A., Clark, V., Jezzard, P., Turner, R. Cerebral organization for language in deaf and hearing subjects: biological constraints and effects of experience. Proc. Natl. Acad. Sci. 95(3), 922-929 (1998).

Palmer, S. Working memory: A developmental study of phonological recoding. Memory. 8(3), 179-193 (2000).

Park, H.J., Chun, J.W., Park, B., Park, H., Kim, J.I., Lee, J.D., Kim, J.J. Activation of the occipital cortex and deactivation of the default mode network during working memory in the early blind. J. Int. Neuropsychol. Soc. 17(3), 407-422 (2011).

Pascual-Leone, A., Amedi, A., Fregni, F., Merabet, L.B. The Plastic Human Brain Cortex. Annu. Rev. Neurosci. 28, 377-401 (2005).

Pascual-Leone, A., Hamilton, R. The metamodal organization of the brain. Prog. Brain. Res. 134, 427-45 (2001).

Peelen, M. V., He, C., Han, Z., Caramazza, A., Bi, Y. Nonvisual and visual object shape representations in occipitotemporal cortex: evidence from congenitally blind and sighted adults. J. Neurosci, 34, 163-170 (2014).

Pénicaud, S., Klein, D., Zatorre, R.J., Chen, J.K., Witcher, P., Hyde, K., Mayberry, R.I. Structural brain changes linked to delayed first language acquisition in congenitally deaf individuals. Neuroimage. 66, 42-49, (2013).

Pietrini, P., Furey, M.L., Ricciardi, E., Gobbini, M.I., Wu, W.H.C., Cohen, L., Guazzelli, M., Haxby, J.V. Beyond sensory images: Object-based representation in the human ventral pathway. Proc. Natl. Acad. Sci. 101(15), 5658-5663 (2004).

Poirier, C., Collignon, O., Scheiber, C., Renier, L., Vanlierde, A., Tranduy, D., Veraart, C., De Volder, A.G. Auditory motion perception activates visual motion areas in early blind subjects. Neuroimage. 31(1), 279-285 (2006).

Rauschecker, J.P. Compensatory plasticity and sensory substitution in the cerebral cortex. Trends Neurosci. 18, 36–43 (1995).

Rauschecker, J.P. Cortical map plasticity in animals and humans. Prog Brain Res. 138, 73-88 (2002).

Reich, L., Szwed, M., Cohen, L., Amedi, A. A ventral visual stream reading center independent of visual experience. Curr. Biol. 21(5), 363-368 (2011).

Renier, L.A., Anurova, I., De Volder, A.G., Carlson, S., VanMeter, J., Rauschecker, J.P. Preserved functional specialization for spatial processing in the middle occipital gyrus of the early blind. Neuron. 68(1), 138-148 (2010).

Renier, L., Cuevas, I., Grandin, C.B., Dricot, L., Plaza, P., Lerens, E., Rombaux, P., De Volder, A.G. Right occipital cortex activation correlates with superior odor processing performance in the early blind. PLoS One. 8:e71907 (2013).

Ricciardi, E., Bonino, D., Sani, L., Vecchi, T., Guazzelli, M., Haxby, J.V., Fadiga, L., Pietrini, P. Do We Really Need Vision? How Blind People “See” the Actions of Others. J. Neurosci. 29, 9719-9724 (2009).

Ricciardi, E., Pietrini, P. New light from the dark: what blindness can teach us about brain function. Curr Op Neurol. 24(4), 357–363 (2011).

Rilling, J.K., Glasser, M.F., Preuss, T.M., Ma, X., Zhao, T., Hu, X., Behrens, T.E. The evolution of the arcuate fasciculus revealed with comparative DTI. Nat. Neurosci. 11(4), 426-428 (2008).

Rimmele, J.M., Gudi-Mindermann, H., Nolte, G., Röder, B., Engel, A.K. Working memory training integrates visual cortex into beta-band networks in congenitally blind individuals. Neuroimage. 194, 259-271 (2019).

Rockland, K.S., Pandya, D.N. Laminar origins and terminations of cortical connections of the occipital lobe in the rhesus monkey. Brain Res. 179(1), 3-20 (1979).

Rockland, K.S., Pandya, D.N. Cortical connections of the occipital lobe in the rhesus monkey: interconnections between areas 17, 18, 19 and the superior temporal sulcus. Brain Res. 212(2), 249-270 (1981).

Röder, B., Rösler, F., Neville, H.J. Event-related potentials during auditory language processing in congenitally blind and sighted people. Neuropsychol. 38(11), 1482-1502 (2000).

Röder, B., Stock, O., Bien, S., Neville, H., Rösler, F. Speech processing activates visual cortex in congenitally blind humans. Eur. J. Neurosci. 16(5), 930-936 (2002).

Rolls, E.T., Mills, W.P.C. Computations in the deep vs superficial layers of the cerebral cortex. Neurobiol Learn Mem. 145, 205-221 (2017).

Roux, F., Wibral, M., Mohr, H.M., Singer, W., Uhlhaas, P.J. Gamma-band activity in human prefrontal cortex codes for the number of relevant items maintained in working memory. J. Neurosci. 32(36), 12411-12420 (2012).

Rudner, M., Andin, J., Rönnberg, J. Working memory, deafness and sign language. Scand. J. Psychol. 50(5), 495-505. (2009).

Sadato, N., Pascual-Leone, A., Grafman, J., Ibañez, V., Deiber, M.P, Dold, G., Hallett, M. Activation of the primary visual cortex by Braille reading in blind subjects. Nature. 380(6574), 526-28 (1996).

Sakata, S., Harris, K.D. Laminar structure of spontaneous and sensory-evoked population activity in auditory cortex. Neuron. 64(3), 404-418 (2009).

Salin, P.A., Bullier, J. Corticocortical connections in the visual system: structure and function. Physiol. Rev. 75(1), 107-154 (1995).

Seymour, J. L., Low, K.A., Maclin, E.L., Chiarelli, A.M., Mathewson, K.E., Fabiani, M., Gratton, G., Dye, M.W. Reorganization of neural systems mediating peripheral visual selective attention in the deaf: An optical imaging study. Hear. Res. 343, 162–175 (2017).

Schoenemann, P.T. Evolution of the Size and Functional Areas of the Human Brain. Annu. Rev. Anthropol. 35, 379-406 (2006).

Shore, S.E., Koehler, S., Oldakowski, M., Hughes, L.F., Syed, S. Dorsal cochlear nucleus responses to somatosensory stimulation are enhanced after noise-induced hearing loss. Eur. J. Neurosci. 27(1), 155-168 (2008).

Siuda-Krzywicka, K., Bola, Ł., Paplińska, M., Sumera, E., Jednorog, K., Marchewka, A., Śliwińska, M.W., Amedi, A., Szwed, M. Massive cortical reorganization in sighted Braille readers. Elife, 5, e10762 (2016).

Söderfeldt, B., Rönnberg, J., Risberg, J. Regional cerebral blood flow in sign language users. Brain Lang., 46, 59–68 (1994).

Stewart, D.L., Starr, A. Absence of visually influenced cells in auditory cortex of normal and congenitally deaf cats. Exp Neurol. 28(3): 525–528 (1970).

Striem-Amit, E., Cohen, L., Dehaene, S., Amedi, S. Reading with sounds: sensory substitution selectively actives the visual word form area in the blind. Neuron. 75(3), 640-652 (2012).

Striem-Amit, E., Ovadia-Caro, S., Caramazza, A., Margulies, D. S., Villringer, A., Amedi, A. Functional connectivity of visual cortex in the blind follows retinotopic organization principles. Brain. 138(6), 1679-1695 (2015).

Twomey, T., Waters, D., Price, C.J., Evans, S., MacSweeney, M. How Auditory Experience Differentially Influences the Function of Left and Right Superior Temporal Cortices. J. Neurosci. 37(39), 9564–9573 (2017).

Uhl, F., Franzen, P., Lindinger, G., Lang, W., Deecke, L. On the functionality of the visually deprived occipital cortex in early blind persons. Neurosci. Lett. 124(2), 256-259 (1991).

Van den Hurk, J., Van Baelen, M., de Beeck, H.P.O. Development of visual category selectivity in ventral visual cortex does not require visual experience. Proc. Natl. Acad. Sci. 114(22), 4501-4510 (2017).

Van Kerkoerle, T., Self, M.W., Roelfsema, P.R. Layer-specificity in the effects of attention and working memory on activity in primary visual cortex. Nat Comm. 8, 13804 (2017).

Voss, P., Gougoux , F., Zatorre, R.J., Lassonde, M., Lepore, F. Differential occipital responses in early- and late-blind individuals during a sound-source discrimination task. Neuroimage. 40, 736-758 (2008).

Watkins, K.E., Cowey, A., Alexander, I., Filippini, N., Kennedy, J.M., Smith, S.M., Ragge, N., Bridge, H. Language networks in anophthalmia: maintained hierarchy of processing in 'visual' cortex. Brain. 135(5), 1566-1577 (2012).

Yusuf, P.A., Hubka, P., Tillein, J., Kral, A. Induced cortical responses require developmental sensory experience. Brain. 140(12), 3153-3165 (2017).

Zeng, C., Yang, Z., Shreve, L., Bledsoe, S., Shore, S. Somatosensory projections to cochlear nucleus are upregulated after unilateral deafness. J. Neurosci. 32(45), 15791-15801 (2012).