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Review

Adaptation of the communicative brain to post-lingual deafness. Evidence from functional imaging

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ABSTRACT

Not having access to one sense profoundly modifies our interactions with the environment, in turn producing changes in brain organization. Deafness and its rehabilitation by cochlear implantation offer a unique model of brain adaptation during sensory deprivation and recovery. Functional imaging allows the study of brain plasticity as a function of the times of deafness and implantation. Even long after the end of the sensitive period for auditory brain physiological maturation, some plasticity may be observed. In this way the mature brain that becomes deaf after language acquisition can adapt to its modified sensory inputs. Oral communication difficulties induced by post-lingual deafness shape cortical reorganization of brain networks already specialized for processing oral language. Left hemisphere language specialization tends to be more preserved than functions of the right hemisphere. We hypothesize that the right hemisphere offers cognitive resources re-purposed to palliate difficulties in left hemisphere speech processing due to sensory and auditory memory degradation. If cochlear implantation is considered, this reorganization during deafness may influence speech understanding outcomes positively or negatively. Understanding brain plasticity during post-lingual deafness should thus inform the development of cognitive rehabilitation, which promotes positive reorganization of the brain networks that process oral language before surgery.

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1. Introduction

Not having access to one sense profoundly modifies interactions with the environment (Merabet and Pascual-Leone, 2010; Strelnikov et al., 2010). Advances in functional imaging (Friston, 2009) and animal models (see Kral et al., 2013 for a review) have contributed to the exploration and better understanding of sensory deprivation, especially illuminating the effect of deafness on brain adaptation. Sensory deprivation leads to modifications in relative connectivity between cortical areas, and particularly in interactions across sensory areas, depending on the age at which the deprivation occurs (for a review, see Merabet and Pascual-Leone, 2010). In both humans and animals, the loss of one sensory modality induces compensatory mechanisms leading to increases in performance of the spared modalities (for reviews, see Bavelier et al., 2006; Rauschecker, 1995; Röder and Rosler, 2004). Among the sensory losses, deafness causes significant handicap as it prevents social interactions through oral communication. Helen Keller who was deaf–blind used to say that "Blindness separates people from things, deafness separates people from people".

Thanks to sign language (visual-based communication) and cochlear implantation (which provides the brain with auditory inputs through electric stimulation), models of sensory deprivation, adaptation and re-afferentation have allowed great steps in the understanding of brain plasticity in pre- and post-lingually deaf subjects. The distinction between pre-lingual and post-lingual deafness is important because learning a language is a long

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process that starts peri-natally in people with normal hearing (Dehaene-Lambertz et al., 2002). Hearing experience during the first year of life (phonemic contrasts in particular) drives brain maturation and central physiological organization related to speech perception and production (see Kral, 2007 for a review). Using a variety of brain imaging methods, it has been shown that the congenitally-deafened brain does not show the same developmental organization as a brain that is exposed to normal auditory inputs from birth to the age of approximately 5 years, when the basics of language are considered acquired and language learning tends to stabilize (Bavelier et al., 2001; Fine et al., 2005; Finney et al., 2001).

The effect of non-rehabilitated pre-lingual deafness on the remaining visual and somatosensory senses (Bavelier et al., 2006; Dye and Bavelier, 2010), as well as auditory development after cochlear implantation in childhood (Kral and Sharma, 2012; Sharma et al., 2009, 2007) has been previously reviewed. The effects are complex and vary depending on the compensatory modality, state of development, and individual factors (Kral and O'Donoghue, 2010). We provide here a brief overview of the findings concerning central modifications related to congenital deafness, but will subsequently focus on reorganization related to oral communication in post-lingually deaf adults. Developmental studies show that a high potential for plasticity exists within the first 3 years after birth and that the brain takes advantage of the senses available by potentiating them (Bavelier et al., 2006). During this developing period, competition between the dominant senses determines final differentiation within multi-sensory areas (Levanen et al., 1998). If one sense is missing, such as hearing, the spared modalities are boosted, leading to supra-normal compensation (Bavelier and Neville, 2002; Bavelier et al., 2006). Thus, in congenitally-deaf subjects, enhanced spatial attention and reactivity to visual events presented mainly in the peripheral visual field have been observed (Bavelier et al., 2006; Dye and Bavelier, 2010; Neville and Lawson, 1987). The beneficial changes in visual skills are however selective to traits that normally interact with available auditory input during audio–visual convergence (see Bavelier et al., 2006 for a review). So deaf individuals generally do not exhibit better performance in simple visual discrimination tasks. Once the sensitive period of plasticity is over, after the age of 7 years, specific organizations/specializations may not be reversible. This phenomenon has been related primarily to extensive synaptogenesis between 2 and 4 years of age, followed by synaptic elimination (central pruning) from 4 to 16 years (Huttenlocher and Dabholkar, 1997). Consequently, brains deafened for too long may not allow satisfactory auditory rehabilitation by a cochlear implant (CI) if surgery occurs after the end of the sensitive period (Giraud and Lee, 2007; Lee et al., 2005, 2007b; Sharma et al., 2009; Sharma et al., 2007).

After the sensitive period is over, primary and secondary auditory areas are no longer able to develop new functional interactions, even though the CI provides auditory inputs. Non-auditory functions, such as sign language processing (Lambertz et al., 2005; Nishimura et al., 1999), may be observed in the secondary auditory areas, and in the case of late implantation, auditory activations have been observed in visual and parieto-temporal areas without any benefit to speech comprehension (Sharma et al., 2007, 2009). Further, early deafness likely affects top–down influence (from high-order areas), leading to the functional decoupling of primary auditory cortex (Kral and Eggermont, 2007). The decrease of top–down modulation in deafness seems to negatively impact on related high-level abilities, such as auditory object categorization, or attentional processes (Kral and Eggermont, 2007).

The same principle applies to non-deprived brains: functional organization tends to be permanent, even though some plasticity and reorganization are possible in adulthood due to lesions (e.g. Cramer et al., 2011; Kell et al., 2009; van Oers et al., 2010) or post-lingual deafness (Lazard et al., 2013; Rouger et al., 2012). Because most cognitive functions are asymmetrically implemented in the brain (Formisano et al., 2008; Hickok and Poeppel, 2007; Hugdahl, 2000), engaging the contralateral cortex to palliate deficits or injury in language processing may be less efficient than the primary functional organization, and hence maladaptive (Kell et al., 2009; Marsh and Hillis, 2006; Naeser et al., 2005; Preibisch et al., 2003; van Oers et al., 2010).

Based on the idea that deafness impoverishes social interactions, principally when it occurs in subjects who were used to hearing (post-lingually deafened), this review will focus on functional imaging findings concerning central adaptation to oral communication loss induced by post-lingual deafness (for animal models, refer to Kral et al., 2013). We hypothesize that central repurposing is driven by communication needs. To understand the observed reorganizations, the physiology of speech perception and reading will be examined. Evidence of adaptation to acquired deafness and its consequences on the observed variability in speech understanding once post-lingual subjects have received a CI will be reviewed.

2. Prerequisites

To understand plasticity, a few terms need to be defined. *Multi-modal* brain areas receive and process inputs from different modalities. *Intra-modal* reorganization/plasticity refers to the potentiation of dedicated areas (uni-modal areas) in their usual modality or function (e.g. increased activity within the visual cortex during lip-reading, a communication relying on visual inputs (Doucet et al., 2006)). *Cross-modal* reorganization/plasticity refers to cortical areas that become under-stimulated by their usual sensory inputs and are taken over by other modalities (e.g. activation of auditory areas by sign language (Finney et al., 2001)). *Meta-modal* reorganization/plasticity applies to originally multi-modal sensory areas that come to favor one modality (or several modalities) over another modality, when sensory input in this latter modality is reduced.

Except for very limited specific etiologies for which subjects become abruptly profoundly deaf (meningitis, bilateral temporal bone fracture, bilateral sudden idiopathic hearing loss), post-lingually deaf people usually face a period of progressive hearing deterioration from moderate to profound deafness (from a pure tone average loss of 40 decibels (dB HL) to 90 dB HL). The duration of moderate hearing loss is defined as the time from which the pure tone average hearing loss is more than 40 dB HL, and/or the time of the first use of hearing aids, until the time of severe to profound deafness. When people become severely or profoundly deaf, they may become a candidate for a CI (UKCISG, 2004). This period of progressively worsening hearing has been minimally investigated in functional imaging studies, which generally focus on the period of total auditory deprivation. However, in a large sample of post-lingual CI recipients, we have shown that the duration of moderate hearing loss impacts CI outcome negatively (Fig. 1) (Lazard et al., 2012b). This study also showed that hearing aids may improve post-implantation speech understanding if worn during the period of severe to profound hearing loss. Wearing two hearing aids pre-implant was related to better post-implant speech outcomes than not having any hearing aid, suggesting that even minimal stimulation tends to preserve auditory functions and areal specificity (Lazard et al., 2012b). The hypothesis is that hearing aids have a protective effect against deleterious plasticity such as visual take-over of auditory areas (Doucet et al., 2006). These factors may

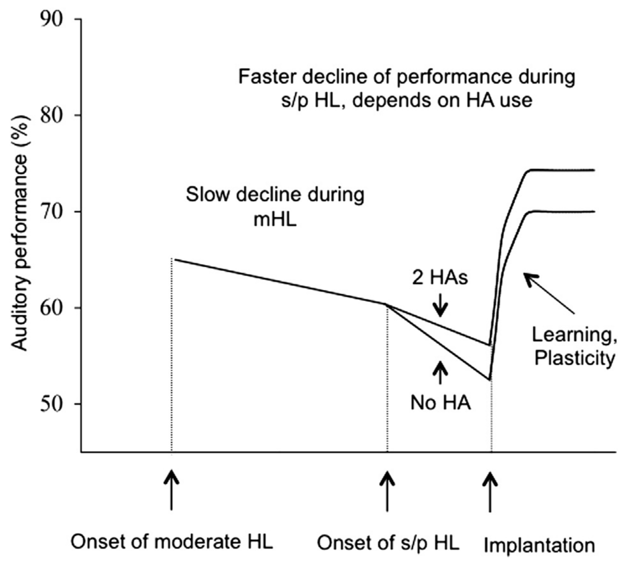

Fig. 1. Theoretical model of mean expected speech performance over time for a hypothetical "average cochlear implant recipient". From Lazard et al. (2012b). Pre-, Per- and Postoperative Factors Affecting Performance of Postlinguistically Deaf Adults Using Cochlear Implants: A New Conceptual Model over Time. PLoS One 7, e48739. This model was developed using data from 2251 post-lingually deafened adult CI recipients (retrospective multi-centric study). Auditory performance on the vertical axis refers to the expected speech performance with a CI if the hypothetical patient were to receive a CI. It was assumed about 20 years of moderate hearing loss for this hypothetical patient, so auditory performance decreases down to 60%, where the patient presents with a severe to profound hearing loss. It was then assumed about 10 years of severe to profound hearing loss. During this period, the decrease in mean expected performance depends on HA use, at about 0.45% per year if 2 HAs are worn, and 0.89% if no HAs are worn. It is to note that HA use during the period of moderate hearing loss was not known in this study. The final stage represents the post-operative learning curve related to CI experience. mHL: moderate hearing loss; s/p HL: severe to profound hearing loss, HA: hearing aid.

open a wide investigation area as, to the knowledge of the authors, just one functional imaging study has investigated the effects of moderate hearing loss on central auditory processing (Lazard et al., 2013).

The last prerequisite is that although the CI allows speech understanding, the sensation it provides is an ersatz of acoustic hearing. In brief, CI speech coding strategies filter the incoming auditory signal into a defined number of band-pass channels, and secondarily extract the envelopes of the band-passed waveforms, i.e., the slowly varying amplitude modulations of the speech waveform. Envelope extraction can be achieved either by full or half-wave rectification followed by low pass filtering or by Hilbert transform (see Loizou, 2006). The envelope amplitude in each filter channel is then transformed into pulse amplitude (electric current level) applied to independent electrodes. Envelope modulations provide temporal cues and tonotopic electrode placements provide spectral cues. Coding strategies do not convey the full information content of speech signals, especially in terms of fine temporal structure (Lorenzi et al., 2006). Spectral coding is also sparse with 12–22 electrodes depending on the manufacturer (Friesen et al., 2001). We can add to these limitations possible tonotopic shifts in the frequency-to-place mapping of spectral information due to electrode-array placement (Friesen et al., 2001), and overlapping excitation patterns of adjacent channels due to the large spread of electric stimulation (Shannon, 1983). The limitations in speech understanding with a CI, even in quiet, are evidenced by the need to maintain high audio–visual cooperation, even after 5 years of CI use (Rouger et al., 2007).

3. Language processing in normally-hearing adults

To understand the reorganization induced by the degradation of oral interactions in post-lingually deaf adults, we first review language processing in non-deprived, normal-hearing listeners. In the normally-hearing population, communication is mainly based on speech through verbal exchange and its written transcription. Verbal exchange becomes very difficult when hearing is lost, and writing may become a major means of communication.

3.1. Oral speech processing through the auditory modality in normally-hearing adults

The first step of oral speech processing is speech *sound* processing: the capacity to process phonemes and their acoustical features (i.e. basic features and symbolic units of speech) (Chomsky and Halle, 1968). This takes place within bilateral primary auditory areas and early auditory associative areas (Fig. 2). The second step is speech processing in itself. This is a higher-level task which generates access to understanding through semantic/linguistic memory-based comparisons and motor reproduction/planning (Hickok and Poeppel, 2007). Speech processing involves asymmetrical bi-hemispheric participation (Hickok et al., 2008), with the left hemisphere demonstrating specialization in fine rapid temporal processing (speech syllables perception), and the right hemisphere being more specialized in slower spectral processing (Abrams et al., 2008; Formisano et al., 2008; Poeppel et al., 2008; Zatorre and Belin, 2001; Zatorre and Gandour, 2008; for a review see Lazard et al., 2012a). In the model developed by Hickok and Poeppel (2007), speech processing follows a dorso-ventral dissociation with a dorsal sensori-motor analysis and a ventral lexico-semantic analysis (Fig. 2). The dorsal sensori-motor stream is

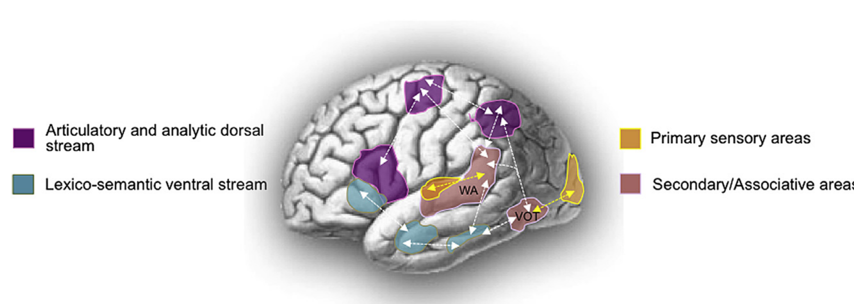

Fig. 2. Schematic representation of oral and written language processing (left hemisphere). Primary sensory areas (auditory A1 and visual V1) are represented in orange. Information is then processed in specialized higher-order areas, in Wernicke's area (WA) and planum temporale on one hand and ventral occipito-temporal area (VOT or visual word form area) on the other hand (pink blobs). The two following streams, the dorsal (purple blobs) and ventral (blue blobs) routes, are common to both specialized sensory entries. Arrows show extensive bottom up and top down interactions.

strongly left-lateralized and maps acoustic speech signals to the parieto-frontal lobes through articulatory and analysis networks. The ventral stream is bilateral, and processes speech signals through lexico-semantic analysis (occipito-temporal and inferior frontal lobes), giving fast access to comprehension.

3.2. Written speech processing through the visual modality in normally-hearing adults

Apart from the sensory entry point, reading involves very similar networks to those of oral language. After passing through primary visual cortex, written material is processed beginning with letter string deciphering within the ventral occipito-temporal cortex, also called the visual word form area (Cohen et al., 2000; Price and Devlin, 2011). A dorso-ventral dissociation exists, similarly to speech processing (Fig. 2). Two reading strategies depending on the frequency of the words encountered are described. The dorsal phonological route involves the left superior temporal cortex, the left inferior parietal cortex and the inferior frontal gyrus in its posterior part (opercular part). This route allows for conversion from graphemes to phonemes and post-assembly phonetic segmentation associated with articulatory planning (Fiebach et al., 2002; Jobard et al., 2003). The dorsal phonological route is also called the indirect route because semantic meaning is accessed secondarily. This strategy is used for new words that need an inner representation of their pronunciation because of their unfamiliarity and for phonologic comparison (for a review see Price, 2012). It overlaps with the dorsal stream described in speech processing. For frequent irregularly spelled words, the ventral stream, or direct lexico-semantic strategy, retrieves phonology directly from global orthography analysis of the whole word (their correct pronunciation has been integrated during reading learning) (Fiebach et al., 2002; Jobard et al., 2003). It involves the middle temporal gyrus and the inferior frontal gyrus in its anterior (triangular) part (Price, 2012), overlapping the ventral stream described in speech processing. As with speech processing, reading strategies are strongly left-lateralized (Price, 2012).

4. Language processing in congenital deaf signers and in post-lingually deafened subjects

When hearing is absent, new modes of communication may develop: sign language is one of them. Interestingly, in the congenitally deaf, brain structure and function related to communication are very similar to that in hearing brains, even though the main sense used is visual. In contrast, people who become deaf after oral language acquisition have to adapt to their sensory loss with a central nervous system that has matured with harmonious multi-sensory inputs.

4.1. Congenital deaf signers

Sign language processing and production uses the visual modality only without any sound-based phonological correspondence. Similarly to spoken language, processing of sign language involves left hemisphere speech dedicated areas: Broca's and Wernicke's areas, left perisylvian areas, and the parieto-temporal junction (for a review see Campbell et al., 2008). However, sign language processing also recruits the right hemisphere in a more extensive way than speech. This right hemisphere involvement is related to its higher functions in processing spatial syntactic properties such as facial recognition, emotional expression, body movements and position – all intrinsic features of sign language (Campbell et al., 2008; MacSweeney et al., 2002). Independently of input modality (auditory or visuo-spatial), the human brain shows highly preserved organization for language processing, especially on the left side.

4.2. Post-lingually deafened subjects

When deafness appears after language acquisition and stabilization, the sensitive period of maximal plasticity has elapsed and major brain specializations are fixed. This was confirmed in the left auditory cortex of post-lingually deafened adults by the study of late cortical auditory evoked potentials (AEP) in response to CI stimulation. The morphology of long-latency AEPs was similar to that of normal-hearing controls (Eggermont, 2008), contrarily to developing brains that display evolution of AEP morphology according to age and duration of auditory deprivation (Eggermont, 2008; Eggermont et al., 1997). Late AEPs are generated in the left planum temporale that is an associative auditory area within Wernicke's area. It is an important region where speech sensory-motor transformation is carried out (Hickok et al., 2009). Unlike in congenital deafness, high-order left auditory areas of the post-lingually deafened brain maintain their specialization in language processing through auditory input or their viseme correspondence after total sensory loss. This specialization may be maintained by fast disinhibition of latent visual circuits mapping visual cues from lip-reading onto former phonetic representations (visemes) (Lee et al., 2007a; Suh et al., 2009). As described later, post-lingual deafness induces reorganization, but we may hypothesize that the left hemisphere is more resilient than the right hemisphere, because communication disabilities may require potentiation of left hemispheric capacities in language processing (Lazard et al., 2012a). Another hypothesis would simply be that the right hemisphere is more prone to plasticity by essence, and especially to visual plasticity in case of deafness (Sandmann et al., 2012). This is in agreement with findings showing that cortical plasticity differentially affects the right and left hemispheres after unilateral deafness (Hanss et al., 2009).

Post-lingually deafened people adapt to their handicap with anatomical and functional constraints that are in part fixed. However, some reorganization is possible, allowing continuation of their social habits (i.e., not switching to a signed mode of communication). As indicated in the prerequisite section, the reorganization of sensory areas can be either meta-modal (non-impaired senses are favored in originally multi-modal sensory areas when input from one sense is reduced) and/or cross-modal (take over by other modalities of normally uni-modal areas under-stimulated by their usual sensory inputs). Both these aspects of plasticity are present in post-lingually deaf subjects and are described below.

5. Meta-modal reorganization as an adaptation to post-lingual deafness

To understand neurofunctional changes that may occur during post-lingual deafness, brain networks for language and environmental sound processing were compared between normal-hearing controls and post-lingually deaf subjects. Fig. 3 shows areas of activation found in functional magnetic resonance imaging (fMRI) or positron emission tomography (PET) experiments during three different tasks: phonological tasks (written rhyming tasks), lip-reading tasks, and environmental sound imagery tasks (mental imagery of sounds produced by animals or noisy objects; for methods and details, see Lazard et al., 2010, 2011, 2013; Lee et al., 2007a; Rouger et al., 2012). Written and imagery tasks were used to recruit auditory areas and related networks in post-lingual profoundly deaf subjects, as their hearing loss precluded the use of real auditory stimuli. Brain activation when auditory imagery tasks are used has been shown to be very similar to when real auditory stimuli are used – the only difference being a lack of primary

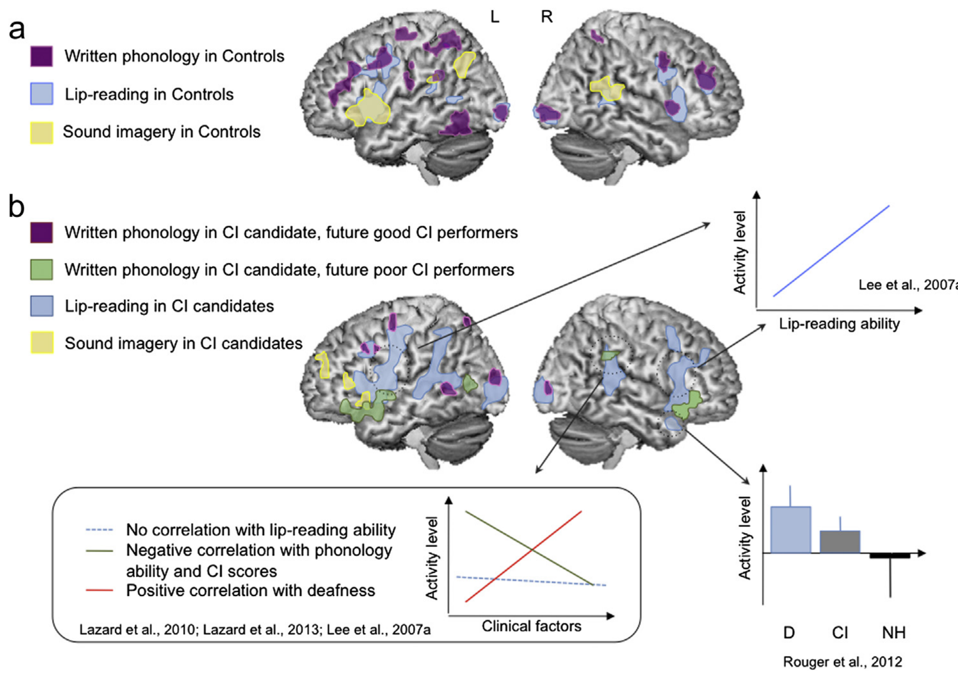

Fig. 3. Comparative neural involvement in normal-hearing subjects (a) and post-lingual deaf subjects (b) during phonological tasks, lip-reading, and environmental sound imagery. Phonological processing involved rhyming tasks in written material (pairs of words). Lip-reading was studied by showing recorded silent lip movements. Sound imagery was tested using black and white images of noisy objects or animals. To better evidence deafness-induced plasticity during phonological processing, whole brain correlation with cochlear implant (CI) speech scores (assessed 6 months post-surgery by monosyllabic words) was performed in deaf subjects (3b, purple and green blobs). The additional graphs represent the regression lines of individual neural activations (*y* axes) plotted according to behavioral performance (*x* axes) during lip-reading and rhyming tasks just before implantation, and speech understanding with a CI 6 months after implantation. The additional histogram represents the means (+standard deviation) of individual neural activations of three groups: deaf subjects before CI activation (D), the same subjects tested with their CI after speech intelligibility recovery (CI), and normal-hearing controls (NH). Adapted from (Lazard et al., 2011; Lazard et al., 2013; Lazard et al., 2010; Lee et al., 2007a; Rouger et al., 2012). L: left, R: right.

auditory activation in the imagery tasks (Bunzeck et al., 2005). Therefore we will talk about environmental sound *processing*, even though real sounds were not used in the study described. In normal-hearing controls, areas activated by lip-reading (Fig. 3a, blue blobs) bilaterally overlap with the dorsal articulatory and analytic indirect route (purple blobs, Fig. 2). In post-lingual deaf subjects, a much larger network is involved (Fig. 3b, blue blobs). However it encompasses the same areas as those activated by controls during phonological tasks when mapping graphemes to phonemes and making internal auditory conversion (Burton et al., 2005), i.e. bilateral pre-central cortices and prefrontal lobes (purple blobs in Fig. 3a). Moreover, neural activation of bilateral prefrontal gyri is positively correlated with lip-reading ability in post-lingual deaf subjects (top graph in Fig. 3b). This effect takes advantage of the multi-modal nature (audio–visual in particular) of inferior frontal areas that are involved in hierarchical language processing (Sahin et al., 2009) and in language production planning (Hickok and Poeppel, 2007; Turkeltaub and Coslett, 2010). Similarly, an expanse of recruitment of the left posterior temporal cortex is observed in post-lingual deaf subjects, corresponding to meta-modal potentiation following predominantly uni-modal visual access to language in an audio-visual area *per se* (Burton et al., 2005).

In the case of post-lingual deafness, meta-modal reorganization potentiates the visual modality to process language information accessible from lip-reading.

6. Right cross-modal take-over to adapt to difficult phonological processing

With increasing periods of auditory deprivation, auditory memory and phonological correspondences with visemes tend to fade out in post-lingual deaf subjects (Andersson et al., 2001; Lazard et al., 2010, 2011), especially if lip-reading has not been used before profound deafness when auditory inputs were still usable (Suh et al., 2009; Lazard et al., unpublished data). To palliate these difficulties, the brains of some post-lingual deaf subjects develop new strategies or recruit areas that were not formerly specialized in phoneme analysis. Fig. 3b shows that some post-lingual deaf subjects have adopted a direct access to semantic areas (bilateral anterior part of inferior frontal lobes, green blobs), even though processing phonology.

It can also be seen that bilateral posterior temporal cortices are more involved during lip-reading by post-lingual deaf subjects than controls during either lip-reading or phonology processing (stronger activation within overlapping areas between deaf subjects and controls, but also expansion of the activation, blue blobs, Fig. 3b). In the normally-hearing brain, the left posterior temporal cortex is more specialized in phonology (Hickok et al., 2009), and is a major area in language processing as it performs speech sensory-motor transformation from multi-modal inputs (Hickok et al., 2009), and orthography-to-phonology mapping (Graves et al., 2010) (left purple and blue blobs, Fig. 3a). By contrast, the right posterior temporal cortex is largely involved in environmental sound processing (Beauchamp et al., 2004; Binder et al., 1996; Bunzeck et al., 2005; Lewis et al., 2004) (right yellow blob, Fig. 3a). In the case of increasing duration of post-lingual deafness, the right posterior temporal area tends to be progressively reorganized (red line, bottom graph, Fig. 3b) to perform lip-reading and phonology (blue and green blobs, Fig. 3b). However, these neural activations do not correlate or negatively correlate with behavioral performance recorded during lip-reading tasks (blue dotted line, bottom graph, Fig. 3b), and phonological tasks (written phonology during the period of profound hearing loss and speech understanding with a CI [green line, bottom graph, Fig. 3b]), respectively.

It means that this reorganization is not relevant to understanding visual speech, and may even be deleterious when processing oral speech. This effect that may seem paradoxical is related to the re-purposing of areas already highly specialized in performing different tasks.

Another example of right hemisphere recruitment following post-lingual deafness is the visual take-over of the area which normally processes the human voice (right anterior superior temporal cortex) (Rouger et al., 2012) (blue bob, Fig. 3b). This area is usually uni-modal (auditory modality), dedicated to human voice processing and speaker identification (Belin et al., 2000; Kriegstein and Giraud, 2004; von Kriegstein and Giraud, 2006). The bar graphs in the bottom right of Fig. 3b show that this area does not normally respond to visual inputs (black bar: no activity in normal-hearing controls during lip-reading). By contrast, in post-lingual deaf subjects this cortical region is involved in processing lip-reading (blue bar) but this visual cross-modal reorganization is reversible with time after auditory rehabilitation (Rouger et al., 2012) (gray bar, same subjects after few months of CI use).

These examples of right hemisphere involvement in processing language represent evidence of cortical reorganization tending to adapt to sensory loss. Unfortunately, using cognitive resources that were not initially highly specialized in processing the function required may result in a more pejorative than beneficial effect, resulting in maladaptive plasticity (Merabet and Pascual-Leone, 2010) with regards to future auditory restoration by a CI. As previously outlined, examples of deafness-related plastic effects in the right hemisphere are more numerous than in the left (Finney et al., 2001; Sandmann et al., 2012). Our hypothesis is that some cognitive functions that are not highly relevant to inter-individual communication (e.g. environmental sound processing) tend to be used less as hearing worsens. The cortical areas associated with these functions are then available to be re-purposed in order to compensate for language processing difficulties induced by sensory loss and the progressive degradation of auditory memory. Because of the asymmetric hemispheric functioning in speech processing, the resources to be re-purposed may be more available on the right side. From the intrinsic properties of the right hemisphere (lower rate of myelination and lower cell density), it is more suited to processing of slow temporal events such as spectral content (Zatorre and Belin, 2001), and may consequently be less efficient in processing rapid events such as speech. In the case of post-lingual deafness, involvement of the right hemisphere aims at processing phonology when hearing worsens from moderate hearing loss (Lazard et al., 2013) and at processing visual speech accessible from lip-reading when deafness becomes profound (Lee et al., 2007a).

Once plasticity has occurred during deafness, knowing how the brain recovers auditory function with a CI is an important issue. Do all the modifications reverse? How is the crude CI sound quality processed? Some answers have emerged and may explain part of the variability observed in speech understanding outcomes of post-lingually deaf CI recipients.

7. Consequences of auditory rewiring

As the brain adapts to the new sensory input provided by a CI, speech understanding scores gradually improve over time (Fig. 1). PET studies have shown a progressive reactivation of the auditory system that includes the neuronal network involved in language processing (Green et al., 2005; Naito et al., 1995; Wong et al., 1999). Activation of the auditory areas increases progressively with respect to CI experience and is also related to the level of speech comprehension with the implant (Giraud et al., 2001; Mortensen et al., 2006; Nishimura et al., 2000). Auditory information provided by the CI is sometimes insufficient to be understood on its own and needs reinforced audio–visual cooperation (Rouger et al., 2007). Up to 3 years post-implantation, CI recipients learn to differentiate speech from noise within secondary auditory areas (intra-modal plasticity) and visual cortex (cross-modal plasticity) (Giraud et al., 2001). Extracting meaningful information is not straightforward with a CI and brain reorganization is required (Pantev et al., 2006). Speech understanding with a CI varies from 100% to 0% for CI recipients tested in the same conditions (Blamey et al., 2013). Only 22% of this variability can be related to the clinical factors such as duration of deafness, age at implantation, residual hearing, and hearing aid use that are routinely available from clinical assessments (Lazard et al., 2012b). Understanding those neurofunctional changes influenced by other factors that remain to be elucidated may explain part of the remaining variance: poorer outcomes would reflect either reduced capacity in central adaptation or maladaptive plasticity (Lazard et al., 2010; Merabet and Pascual-Leone, 2010). Recent findings support this idea: in the case of phonological reuse of right posterior temporal cortex, it was shown that those subjects who disengaged the most from environmental sound processing would become the least-proficient CI users (Lazard et al., 2013). Visual reorganization of the voice area was reversible with time post-implantation in proficient CI users (Fig. 3b) (Rouger et al., 2012), but not in poor CI performers who did not present any activation of this area to voice stimuli even two years after cochlear implantation (Coez et al., 2008). The amount of some of these modifications implying poor outcome was related to longer durations of auditory deprivation (Lazard et al., 2010, 2013; Sandmann et al., 2012). Further, during lip-reading and audio-visual tasks (word recognition) in CI recipients shortly after cochlear implantation, it was consistently found that activation within the early visual cortex was positively correlated with successful CI outcome, while activation within the right anterior temporal area was negatively correlated with CI outcome. It was hypothesized that marked intra-modal compensation in the visual cortex and slight visual cross-modal reorganization of the right auditory areas (including the voice area) were associated with better CI outcome (Strelnikov et al., 2013). The positive influence of the visual cortex in the efficiency of auditory speech perception suggests the existence of neural mechanisms that build up synergy between the two modalities (Strelnikov et al., 2009).

Whether cross-modal visual processing of speech is deleterious (Doucet et al., 2006; Sandmann et al., 2012) or beneficial (Barone and Deguine, 2011) is still controversial, and presumably depends on the areas involved and the amount of reorganization. It suggests that the success of CI rehabilitation relies, at least partly, on the functional plasticity of the brain and involves a subtle balance between intra- and cross-modal reorganization during deafness and the period of adaptation to the implant.

In some CI candidates, strategies adopted during deafness may not reverse despite auditory rehabilitation. This failure to correctly re-organize brain function based on new inaccurate auditory sensory input may be one of the causes of poor post-implant speech understanding performance. Understanding these reorganizations is consequently our next challenge. One study has shown that learning lip-reading at the beginning of deafness, even though more cognitively demanding than using written communication, maintains normal auditory-viseme matching and auditory processes: only severely deaf proficient lip-readers showed brain activation in the audio–visual left posterior temporal cortex during a rhyming task on written material. The same subjects became proficient CI users. This suggests that left phonological memory maintains auditory representations that will later be critical to map the crude sounds of CI speech processors onto phonological representations. Conversely, switching to a strategy based on visual written communication was a predictor of poorer outcome: those deaf subjects incapable of learning lip-reading and communicating instead by writing developed a reorganization of the secondary visual area and right posterior temporal cortex toward meaningful written material, giving faster access to Broca's area, but compromising future auditory processing (Lazard et al., unpublished data). Detecting those patients who have specialized in written communication by a simple behavioral test in the clinic seems within easy reach (Lazard et al., unpublished data).

8. Conclusion and perspectives

Altogether, beyond the theoretical insights about the intra- and cross-modal adaptive mechanisms provided by the analysis of functional reorganization in deafness, the studies reviewed are of high clinical significance as they suggest that brain imaging or dedicated behavioral tests performed before cochlear implantation could inform CI prognosis. Based on that prediction, a specific cognitive rehabilitation program can be adapted for each patient in order to speed up or optimize speech comprehension recovery. The guidance of central modifications may be one therapy in a close future. Awaiting this step, we may encourage hearing-impaired patients to wear hearing aids as soon as possible, before they start to profoundly adapt to their handicap (Fig. 1). Developing lip-reading should also start earlier than practiced nowadays (in profound hearing loss) to avoid skipping progressively to a reading-based strategy. Once severe hearing loss has been reached, dedicated training should be proposed promoting auditory memory and phonological processing, preserving hemispheric specialization.

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References

Abrams, D.A., Nicol, T., Zecker, S., Kraus, N., 2008. Right-hemisphere auditory cortex is dominant for coding syllable patterns in speech. J. Neurosci. 28, 3958–3965.
Andersson, U., Lyxell, B., Ronnberg, J., Spens, K.E., 2001. Cognitive correlates of visual speech understanding in hearing-impaired individuals. J. Deaf Stud. Deaf Educ. 6, 103–116.
Barone, P., Deguine, O., 2011. Multisensory processing in cochlear implant listeners. In: Zeng, F.G., Popper, A.N., Fay, R. (Eds.), Auditory Prostheses: Cochlear Implants and Beyond, Springer Handbook of Auditory Research, vol. 39, pp. 365–382. New-York.
Bavelier, D., Neville, H.J., 2002. Cross-modal plasticity: where and how? Nat. Rev. Neurosci. 3, 443–452.
Bavelier, D., Dye, M.W., Hauser, P.C., 2006. Do deaf individuals see better? Trends Cogn. Sci. 10, 512–518.
Bavelier, D., Brozinsky, C., Tomann, A., Mitchell, T., Neville, H., Liu, G., 2001. Impact of early deafness and early exposure to sign language on the cerebral organization for motion processing. J. Neurosci. 21, 8931–8942.
Beauchamp, M.S., Lee, K.E., Argall, B.D., Martin, A., 2004. Integration of auditory and visual information about objects in superior temporal sulcus. Neuron 41, 809–823.
Belin, P., Zatorre, R.J., Lafaille, P., Ahad, P., Pike, B., 2000. Voice-selective areas in human auditory cortex. Nature 403, 309–312.
Binder, J.R., Frost, J.A., Hammeke, T.A., Rao, S.M., Cox, R.W., 1996. Function of the left planum temporale in auditory and linguistic processing. Brain 119 (Pt 4), 1239–1247.
Blamey, P., Artieres, F., Baskent, D., Bergeron, F., Beynon, A., Burke, E., Dillier, N., Dowell, R., Fraysse, B., Gallego, S., Govaerts, P.J., Green, K., Huber, A.M., Kleine-Punte, A., Maat, B., Marx, M., Mawman, D., Mosnier, I., O'Connor, A.F., O'Leary, S., Rousset, A., Schauwers, K., Skarzynski, H., Skarzynski, P.H., Sterkers, O., Terranti, A., Truy, E., Van de Heyning, P., Venail, F., Vincent, C., Lazard, D.S., 2013. Factors affecting auditory performance of postlinguistically deaf adults using cochlear implants: an update with 2251 patients. Audiol. Neurootol. 18, 36–47.
Bunzeck, N., Wuestenberg, T., Lutz, K., Heinze, H.J., Jancke, L., 2005. Scanning silence: mental imagery of complex sounds. Neuroimage 26, 1119–1127.
Burton, M.W., Locasto, P.C., Krebs-Noble, D., Gullapalli, R.P., 2005. A systematic investigation of the functional neuroanatomy of auditory and visual phonological processing. Neuroimage 26, 647–661.
Campbell, R., MacSweeney, M., Waters, D., 2008. Sign language and the brain: a review. J. Deaf Stud. Deaf Educ. 13, 3–20.
Chomsky, N., Halle, M., 1968. The Sound Pattern of English. MIT Press, Cambridge.
Coez, A., Zilbovicius, M., Ferrary, E., Bouccara, D., Mosnier, I., Ambert-Dahan, E., Bizaguet, E., Syrota, A., Samson, Y., Sterkers, O., 2008. Cochlear implant benefits in deafness rehabilitation: PET study of temporal voice activations. J. Nucl. Med. 49, 60–67.
Cohen, L., Dehaene, S., Naccache, L., Lehericy, S., Dehaene-Lambertz, G., Henaff, M.A., Michel, F., 2000. The visual word form area: spatial and temporal characterization of an initial stage of reading in normal subjects and posterior split-brain patients. Brain 123 (Pt 2), 291–307.
Cramer, S.C., Sur, M., Dobkin, B.H., O'Brien, C., Sanger, T.D., Trojanowski, J.Q., Rumsey, J.M., Hicks, R., Cameron, J., Chen, D., Chen, W.G., Cohen, L.G., deCharms, C., Duffy, C.J., Eden, G.F., Fetz, E.E., Filart, R., Freund, M., Grant, S.J., Haber, S., Kalivas, P.W., Kolb, B., Kramer, A.F., Lynch, M., Mayberg, H.S., McQuillen, P.S., Nitkin, R., Pascual-Leone, A., Reuter-Lorenz, P., Schiff, N., Sharma, A., Shekim, L., Stryker, M., Sullivan, E.V., Vinogradov, S., 2011. Harnessing neuroplasticity for clinical applications. Brain 134, 1591–1609.
Dehaene-Lambertz, G., Dehaene, S., Hertz-Pannier, L., 2002. Functional neuroimaging of speech perception in infants. Science 298, 2013–2015.
Doucet, M.E., Bergeron, F., Lassonde, M., Ferron, P., Lepore, F., 2006. Cross-modal reorganization and speech perception in cochlear implant users. Brain 129, 3376–3383.
Dye, M.W., Bavelier, D., 2010. Attentional enhancements and deficits in deaf populations: an integrative review. Restor. Neurol. Neurosci. 28, 181–192.
Eggermont, J.J., 2008. The role of sound in adult and developmental auditory cortical plasticity. Ear Hear. 29, 819–829.
Eggermont, J.J., Ponton, C.W., Don, M., Waring, M.D., Kwong, B., 1997. Maturational delays in cortical evoked potentials in cochlear implant users. Acta Otolaryngol. 117, 161–163.
Fiebach, C.J., Friederici, A.D., Muller, K., von Cramon, D.Y., 2002. fMRI evidence for dual routes to the mental lexicon in visual word recognition. J. Cogn. Neurosci. 14, 11–23.
Fine, I., Finney, E.M., Boynton, G.M., Dobkins, K.R., 2005. Comparing the effects of auditory deprivation and sign language within the auditory and visual cortex. J. Cogn. Neurosci. 17, 1621–1637.
Finney, E.M., Fine, I., Dobkins, K.R., 2001. Visual stimuli activate auditory cortex in the deaf. Nat. Neurosci. 4, 1171–1173.
Formisano, E., De Martino, F., Bonte, M., Goebel, R., 2008. "Who" is saying "what"? Brain-based decoding of human voice and speech. Science 322, 970–973.
Friesen, L.M., Shannon, R.V., Baskent, D., Wang, X., 2001. Speech recognition in noise as a function of the number of spectral channels: comparison of acoustic hearing and cochlear implants. J. Acoust. Soc. Am. 110, 1150–1163.
Friston, K.J., 2009. Modalities, modes, and models in functional neuroimaging. Science 326, 399–403.
Giraud, A.L., Lee, H.J., 2007. Predicting cochlear implant outcome from brain organisation in the deaf. Restor. Neurol. Neurosci. 25, 381–390.
Giraud, A.L., Price, C.J., Graham, J.M., Truy, E., Frackowiak, R.S., 2001. Cross-modal plasticity underpins language recovery after cochlear implantation. Neuron 30, 657–663.
Graves, W.W., Desai, R., Humphries, C., Seidenberg, M.S., Binder, J.R., 2010. Neural systems for reading aloud: a multiparametric approach. Cereb. Cortex 20, 1799–1815.
Green, K.M., Julyan, P.J., Hastings, D.L., Ramsden, R.T., 2005. Auditory cortical activation and speech perception in cochlear implant users: effects of implant experience and duration of deafness. Hear Res. 205, 184–192.
Hanss, J., Veuillet, E., Adjout, K., Besle, J., Collet, L., Thai-Van, H., 2009. The effect of long-term unilateral deafness on the activation pattern in the auditory cortices of French-native speakers: influence of deafness side. BMC Neurosci. 10, 23.
Hickok, G., Poeppel, D., 2007. The cortical organization of speech processing. Nat. Rev. Neurosci. 8, 393–402.
Hickok, G., Okada, K., Serences, J.T., 2009. Area Spt in the human planum temporale supports sensory-motor integration for speech processing. J. Neurophysiol. 101, 2725–2732.
Hickok, G., Okada, K., Barr, W., Pa, J., Rogalsky, C., Donnelly, K., Barde, L., Grant, A., 2008. Bilateral capacity for speech sound processing in auditory comprehension: evidence from Wada procedures. Brain Lang. 107, 179–184.
Hugdahl, K., 2000. Lateralization of cognitive processes in the brain. Acta Psychol. (Amst) 105, 211–235.
Huttenlocher, P.R., Dabholkar, A.S., 1997. Regional differences in synaptogenesis in human cerebral cortex. J. Comp. Neurol. 387, 167–178.
Jobard, G., Crivello, F., Tzourio-Mazoyer, N., 2003. Evaluation of the dual route theory of reading: a metanalysis of 35 neuroimaging studies. Neuroimage 20, 693–712.
Kell, C.A., Neumann, K., von Kriegstein, K., Posenenske, C., von Gudenberg, A.W., Euler, H., Giraud, A.L., 2009. How the brain repairs stuttering. Brain 132, 2747–2760.

Kral, A., 2007. Unimodal and cross-modal plasticity in the 'deaf' auditory cortex. Int. J. Audiol. 46, 479–493.
Kral, A., Eggermont, J.J., 2007. What's to lose and what's to learn: development under auditory deprivation, cochlear implants and limits of cortical plasticity. Brain Res. Rev. 56, 259–269.
Kral, A., O'Donoghue, G.M., 2010. Profound deafness in childhood. N. Engl. J. Med. 363, 1438–1450.
Kral, A., Sharma, A., 2012. Developmental neuroplasticity after cochlear implantation. Trends Neurosci. 35, 111–122.
Kral, A., Popper, A.N., Fay, R.R., 2013. Deafness. Springer Science + Business Media LLC, New York.
Kriegstein, K.V., Giraud, A.L., 2004. Distinct functional substrates along the right superior temporal sulcus for the processing of voices. Neuroimage 22, 948–955.
Lambertz, N., Gizewski, E.R., de Greiff, A., Forsting, M., 2005. Cross-modal plasticity in deaf subjects dependent on the extent of hearing loss. Brain Res. Cogn. Brain Res. 25, 884–890.
Lazard, D.S., Collette, J.L., Perrot, X., 2012a. Speech processing: from peripheral to hemispheric asymmetry of the auditory system. Laryngoscope 122, 167–173.
Lazard, D.S., Giraud, A.L., Truy, E., Lee, H.J., 2011. Evolution of non-speech sound memory in postlingual deafness: implications for cochlear implant rehabilitation. Neuropsychologia 49, 2475–2482.
Lazard, D.S., Lee, H.J., Truy, E., Giraud, A.L., 2013. Bilateral reorganization of posterior temporal cortices in post-lingual deafness and its relation to cochlear implant outcome. Hum. Brain Mapp. 34, 1208–1219.
Lazard, D.S., Lee, H.J., Gaebler, M., Kell, C.A., Truy, E., Giraud, A.L., 2010. Phonological processing in post-lingual deafness and cochlear implant outcome. Neuroimage 49, 3443–3451.
Lazard, D.S., Vincent, C., Venail, F., Van de Heyning, P., Truy, E., Sterkers, O., Skarzynski, P.H., Skarzynski, H., Schauwers, K., O'Leary, S., Mawman, D., Maat, B., Kleine-Punte, A., Huber, A.M., Green, K., Govaerts, P.J., Fraysse, B., Dowell, R., Dillier, N., Burke, E., Beynon, A., Bergeron, F., Baskent, D., Artieres, F., Blamey, P.J., 2012b. Pre-, per- and postoperative factors affecting performance of post-linguistically deaf adults using cochlear implants: a new conceptual model over time. PLoS One 7, e48739.
Lee, H.J., Truy, E., Mamou, G., Sappey-Marinier, D., Giraud, A.L., 2007a. Visual speech circuits in profound acquired deafness: a possible role for latent multimodal connectivity. Brain 130, 2929–2941.
Lee, H.J., Kang, E., Oh, S.H., Kang, H., Lee, D.S., Lee, M.C., Kim, C.S., 2005. Preoperative differences of cerebral metabolism relate to the outcome of cochlear implants in congenitally deaf children. Hear Res. 203, 2–9.
Lee, H.J., Giraud, A.L., Kang, E., Oh, S.H., Kang, H., Kim, C.S., Lee, D.S., 2007b. Cortical activity at rest predicts cochlear implantation outcome. Cereb. Cortex 17, 909–917.
Levanen, S., Jousmaki, V., Hari, R., 1998. Vibration-induced auditory-cortex activation in a congenitally deaf adult. Curr. Biol. 8, 869–872.
Lewis, J.W., Wightman, F.L., Brefczynski, J.A., Phinney, R.E., Binder, J.R., DeYoe, E.A., 2004. Human brain regions involved in recognizing environmental sounds. Cereb. Cortex 14, 1008–1021.
Loizou, P.C., 2006. Speech processing in vocoder-centric cochlear implants. Adv. Otorhinolaryngol. 64, 109–143.
Lorenzi, C., Gilbert, G., Carn, H., Garnier, S., Moore, B.C., 2006. Speech perception problems of the hearing impaired reflect inability to use temporal fine structure. Proc. Natl. Acad. Sci. U. S. A. 103, 18866–18869.
MacSweeney, M., Woll, B., Campbell, R., Calvert, G.A., McGuire, P.K., David, A.S., Simmons, A., Brammer, M.J., 2002. Neural correlates of British sign language comprehension: spatial processing demands of topographic language. J. Cogn. Neurosci. 14, 1064–1075.
Marsh, E.B., Hillis, A.E., 2006. Recovery from aphasia following brain injury: the role of reorganization. Prog. Brain Res. 157, 143–156.
Merabet, L.B., Pascual-Leone, A., 2010. Neural reorganization following sensory loss: the opportunity of change. Nat. Rev. Neurosci. 11, 44–52.
Mortensen, M.V., Mirz, F., Gjedde, A., 2006. Restored speech comprehension linked to activity in left inferior prefrontal and right temporal cortices in postlingual deafness. Neuroimage 31, 842–852.
Naeser, M.A., Martin, P.I., Nicholas, M., Baker, E.H., Seekins, H., Kobayashi, M., Theoret, H., Fregni, F., Maria-Tormos, J., Kurland, J., Doron, K.W., Pascual-Leone, A., 2005. Improved picture naming in chronic aphasia after TMS to part of right Broca's area: an open-protocol study. Brain Lang. 93, 95–105.
Naito, Y., Okazawa, H., Honjo, I., Hirano, S., Takahashi, H., Shiomi, Y., Hoji, W., Kawano, M., Ishizu, K., Yonekura, Y., 1995. Cortical activation with sound stimulation in cochlear implant users demonstrated by positron emission tomography. Brain Res. Cogn. Brain Res. 2, 207–214.
Neville, H.J., 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.
Nishimura, H., Doi, K., Iwaki, T., Hashikawa, K., Oku, N., Teratani, T., Hasegawa, T., Watanabe, A., Nishimura, T., Kubo, T., 2000. Neural plasticity detected in short- and long-term cochlear implant users using PET. Neuroreport 11, 811–815.
Nishimura, H., Hashikawa, K., Doi, K., Iwaki, T., Watanabe, Y., Kusuoka, H., Nishimura, T., Kubo, T., 1999. Sign language 'heard' in the auditory cortex. Nature 397, 116.
Pantev, C., Dinnesen, A., Ross, B., Wollbrink, A., Knief, A., 2006. Dynamics of auditory plasticity after cochlear implantation: a longitudinal study. Cereb. Cortex 16, 31–36.
Poeppel, D., Idsardi, W.J., van Wassenhove, V., 2008. Speech perception at the interface of neurobiology and linguistics. Philos. Trans. R Soc. Lond B Biol. Sci. 363, 1071–1086.
Preibisch, C., Neumann, K., Raab, P., Euler, H.A., von Gudenberg, A.W., Lanfermann, H., Giraud, A.L., 2003. Evidence for compensation for stuttering by the right frontal operculum. Neuroimage 20, 1356–1364.
Price, C.J., 2012. A review and synthesis of the first 20 years of PET and fMRI studies of heard speech, spoken language and reading. Neuroimage 62, 816–847.
Price, C.J., Devlin, J.T., 2011. The interactive account of ventral occipitotemporal contributions to reading. Trends Cogn. Sci. 15, 246–253.
Rauschecker, J.P., 1995. Compensatory plasticity and sensory substitution in the cerebral cortex. Trends Neurosci. 18, 36–43.
Röder, B., Rosler, F., 2004. Compensatory plasticity as a consequence of sensory loss. In: Calvert, G., Spence, C., Stein, B.E. (Eds.), The Handbook of Multisensory Processes. MIT Press, Cambridge, Mass, pp. 719–747.
Rouger, J., Lagleyre, S., Fraysse, B., Deneve, S., Deguine, O., Barone, P., 2007. Evidence that cochlear-implanted deaf patients are better multisensory integrators. Proc. Natl. Acad. Sci. U. S. A. 104, 7295–7300.
Rouger, J., Lagleyre, S., Demonet, J.F., Fraysse, B., Deguine, O., Barone, P., 2012. Evolution of crossmodal reorganization of the voice area in cochlear-implanted deaf patients. Hum. Brain Mapp. 33, 1929–1940.
Sahin, N.T., Pinker, S., Cash, S.S., Schomer, D., Halgren, E., 2009. Sequential processing of lexical, grammatical, and phonological information within Broca's area. Science 326, 445–449.
Sandmann, P., Dillier, N., Eichele, T., Meyer, M., Kegel, A., Pascual-Marqui, R.D., Marcar, V.L., Jancke, L., Debener, S., 2012. Visual activation of auditory cortex reflects maladaptive plasticity in cochlear implant users. Brain 135, 555–568.
Shannon, R.V., 1983. Multichannel electrical stimulation of the auditory nerve in man. II. Channel interaction. Hear Res. 12, 1–16.
Sharma, A., Nash, A.A., Dorman, M., 2009. Cortical development, plasticity and re-organization in children with cochlear implants. J. Commun. Dis. 42, 272–279.
Sharma, A., Gilley, P.M., Dorman, M.F., Baldwin, R., 2007. Deprivation-induced cortical reorganization in children with cochlear implants. Int. J. Audiol. 46, 494–499.
Strelnikov, K., Rouger, J., Barone, P., Deguine, O., 2009. Role of speechreading in audiovisual interactions during the recovery of speech comprehension in deaf adults with cochlear implants. Scand. J. Psychol. 50, 437–444.
Strelnikov, K., Rouger, J., Demonet, J.F., Lagleyre, S., Fraysse, B., Deguine, O., Barone, P., 2010. Does brain activity at rest reflect adaptive strategies? Evidence from speech processing after cochlear implantation. Cereb. Cortex 20, 1217–1222.
Strelnikov, K., Rouger, J., Demonet, J.-F., Lagleyre, S., Fraysse, B., Deguine, O., Barone, P., 2013. Visual activity predicts auditory recovery from deafness after cochlear implantation in adult. Brain in press.
Suh, M.W., Lee, H.J., Kim, J.S., Chung, C.K., Oh, S.H., 2009. Speech experience shapes the speechreading network and subsequent deafness facilitates it. Brain 132, 2761–2771.
Turkeltaub, P.E., Coslett, H.B., 2010. Localization of sublexical speech perception components. Brain Lang. 114, 1–15.
UKCISG, 2004. Criteria of candidacy for unilateral cochlear implantation in post-lingually deafened adults I: theory and measures of effectiveness. Ear Hear. 25, 310–335.
van Oers, C.A., Vink, M., van Zandvoort, M.J., van der Worp, H.B., de Haan, E.H., Kappelle, L.J., Ramsey, N.F., Dijkhuizen, R.M., 2010. Contribution of the left and right inferior frontal gyrus in recovery from aphasia. A functional MRI study in stroke patients with preserved hemodynamic responsiveness. Neuroimage 49, 885–893.
von Kriegstein, K., Giraud, A.L., 2006. Implicit multisensory associations influence voice recognition. PLoS Biol. 4, e326.
Wong, D., Miyamoto, R.T., Pisoni, D.B., Sehgal, M., Hutchins, G.D., 1999. PET imaging of cochlear-implant and normal-hearing subjects listening to speech and nonspeech. Hear Res. 132, 34–42.
Zatorre, R.J., Belin, P., 2001. Spectral and temporal processing in human auditory cortex. Cereb. Cortex 11, 946–953.
Zatorre, R.J., Gandour, J.T., 2008. Neural specializations for speech and pitch: moving beyond the dichotomies. Philos. Trans. R Soc. Lond B Biol. Sci. 363, 1087–1104.