



Centre for Mind/Brain Sciences

PhD Thesis

# Plasticity following auditory deafferentation and reafferentation

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“Plasticity, then, in the wide sense of the word, means the possession of a structure weak enough to yield to an influence, but strong enough not to yield all at once. Each relatively stable phase of equilibrium in such a structure is marked by what we may call a new set of habits. Organic matter, especially nervous tissue, seems endowed with a very extraordinary degree of plasticity of this sort; so that we may without hesitation lay down as our first proposition the following, that *the phenomena of habit in living beings are due to plasticity of the organic materials of which their bodies are composed.*”

William James

*The laws of habit*, 1887

“Of course I myself see *all* my stuff – I mean see it in each case – as an action; but there are degrees and proportions and *kinds* of plasticity – and everything isn’t theatrically [...] workable to what I call the peculiar and special and ideal tune”.

Henry James

*Notes*, 1909

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## General abstract

The present thesis investigates the effects of auditory deafferentation and reafferentation with a unimodal and multisensory perspective. Aim of the thesis is the understanding of issues concerning functional plasticity resulting from long-term auditory deprivation, and the effects of reafferentation through a cochlear implant (CI) on audition, vision, and their interaction. The thesis is divided into three parts: Part I explores the effects of auditory deafferentation on the visual modality to understand whether a long-term sensory deprivation leads one of the remaining senses to reorganise in a cross-modal fashion. In particular, Chapter 1 reviews animal and human findings on cross-modal plasticity after sensory deafferentation and introduces the particular case of deafness, focusing on the sensory modality that seems to reorganise the most after profound deafness: vision. In Chapter 2 I present the study we conducted to explore an underinvestigated issue of cross-modal reorganisation after long-term auditory deprivation. We investigated visual temporal processing in a group of profoundly deaf individuals by testing their ability to make temporal order judgments. Our results show comparable accuracy in processing visual temporal sequences in deaf individuals and hearing controls, but an enhanced reactivity in the deaf population particularly when responding to stimuli appearing towards the periphery of the visual field. Our findings suggest that long-term auditory deprivation does not alter temporal processing abilities, and that the reactivity observed in the deaf group may instead constitute a central aspect of the functional changes occurring after auditory deafferentation.

Part II of the thesis addresses the effects of auditory reafferentation through a cochlear implant on the adult auditory system. Chapter 3 reviews findings that

document plasticity in the adult brain and the role of experience in determining the extent for plasticity to occur. In addition, a review on auditory spatial hearing introduces the two studies we conducted to investigate the recovery of sound localisation abilities after bilateral and unilateral cochlear implantation (chapter 4 and 5, respectively). Results from the first study show that partial recovery of spatial hearing after bilateral implantation occur with different time course as a function of the recipient's experience with auditory cues. Results from the second study show that some sound localisation abilities can emerge even in prelingually deafened adults fitted with a single implant, at least in a laboratory setting. Importantly, this ability appears to be constraint by the years of experience with the CI, and again as a function of previous auditory experience of the CI recipient.

Part III addresses the question of the effects of auditory reafferentation on the visual system and its interaction with audition. Chapter 6 reviews the issue of cross-modal plasticity after auditory reafferentation. In particular, we investigated whether visual abilities are modified after cochlear implantation in a group of prelingual and postlingual deaf recipients (Chapter 7). In this study we found that prelingual deaf recipients, compared to postlingual deaf, had an advantage in detecting the onset of rapidly presented visual stimuli in the periphery of the visual field. In a further experiment (Chapter 8) we investigated whether auditory and visual information are integrated after cochlear implantation in prelingual and postlingual deaf recipients and found that their abilities are comparable to hearing controls.

Finally, Chapter 9 summarises all the presented results and draws the major conclusions.



# **PART I**

The effects of auditory  
deafferentation on vision

# **CHAPTER 1**

## Introduction

## 1.1 Plastic changes after sensory deafferentation

The term 'plasticity' broadly refers to the ability of the nervous system to change as a function of experience. During development, three forms of plasticity can be observed that allow the brain to functionally organise, and to process and transform the sensory input in a behavioural output. The first of these can be termed "experience-independent plasticity", and it is a condition in which connections are set regardless of any influence of experience (Gottlieb, 1976). In the second condition called "experience-expectant plasticity" (Greenough & Alcantara, 1976), the effects of experience manifest as initial overproduction of connections and subsequent pruning of exceeding synapses. The third form of plasticity has been termed "experience-dependent" (Knudsen, 1999; King et al., 2000) and is the result of experience on the brain to reinforce existing connections or to form new synapses, or to produce changes at the behavioural level ("adaptive plasticity").

In the context of such extensive brain plasticity, particularly during early development and during sensitive periods of the maturational process (e.g., Berardi et al., 2000; Stiles, 2000; Hensch, 2005), a still ongoing and debated issue of cognitive neuroscience is the understanding of how, and to what extent the brain plastically reorganises in case of altered sensory experience (e.g., blindness, deafness). In particular, a key issue remains the understanding of the mechanisms underpinning plasticity from both an anatomical and behavioural point of view. There are different types of changes that can occur whenever plasticity is observed, and definitions about these types of changes are sometimes ambiguous and seem to overlap with each other. Here we will start with an initial distinction between *intramodal* and *intermodal* changes. The first one speaks for changes that occur within a sensory modality, the second one for changes that occur across modalities.

We will then move to examine some of the behavioural consequences of these types of changes. Finally, we will discuss how these changes can also occur, to some extent, with short-term deprivation.

### *1.1.1 Intramodal plasticity*

This first type of plasticity occurs within a sensory modality as a consequence of an altered use of that sensory modality, be it increased or decreased. This type of plasticity appears mediated by local changes within a limited set of cortical areas, and it can appear during normal development and maturation, as a consequence of extended training in that particular modality. This latter case speaks for an *increased* use of that sensory modality, as it happens, for example, in experienced musicians (for a review, see Münte et al., 2002), who were found to have a cortical enlargement of some brain areas, including the planum temporale. The primary somatosensory cortex has proven to be particularly plastic even in the shortest period. An example for this comes from Schaefer et al. (2004), who found an enlarged cortical representation for the first and fifth digit during tool use in which these particular digits were stimulated. Similar findings were found in anatomical studies on sensory deprived animals: in case of peripheral lesion in a region of the skin, the adjacent sensory areas have documented to extend into the deafferented area, with a consequent enlargement of the neighbouring representations (Buonomano & Merzenich, 1984; Kaas, 2000). These studies suggest that sensory maps in the cortex are adaptively altered to reflect recent experience and learning, and the cortex seems to be able to re-allocate representations of the particular peripheral input that is mostly used. Similarly, in animals that are surgically deprived of the visual

modality, neurons that originally had receptive fields in a particular retinal location develop new receptive fields at the border of the retinal lesion (Kaas, 1990).

In the context of intramodal plasticity elicited by sensory deprivation, as it is the case of blindness or deafness, for example, the changes are seen in the remaining associated sensory modalities as a result of the greater reliance of an individual on that particular sensory system, and are a direct consequence of a *decrease* in use of the deprived sensory modality. This type of change does not imply re-allocation of sensory functions originally belonging to the deafferented sense to the other sensory systems, but only speaks for neural changes within a functional system that is linked to a specific brain region. In this view, compensatory changes that have been documented for both blind and deaf individuals in terms of an increase in processing efficiency could be ascribed into intramodal changes.

Also, when referring to any type of change that may occur after sensory deprivation, a neuroanatomical perspective has to be taken. In other words, plastic changes documented in behavioural studies that do not include neuroimaging techniques can only speculate on the type of plasticity observed. In addition, while there are several animal studies that have documented intramodal changes in terms of increased or decreased arbour growth after sensory deafferentation in the remaining senses (Antonini et al., 1999), advances in the neuroimaging techniques have allowed observing these types of changes in the human brain as well. The following examples coming from the blind and the deaf could account for intramodal changes, though future studies are expected to investigate reorganisation in the primary and secondary cortices of the remaining sensory modalities in the blind and in the deaf.

### Intramodal plasticity in the blind

Pascual-Leone and Torres (1993) recorded somatosensory evoked potentials from proficient Braille readers and demonstrated that the cortical representation of the index finger was larger than that of sighted controls and blind non-Braille readers (similar to findings in animal studies, for example Buonomano & Merzenich, 1998). In addition, suppression of tactile stimulation through TMS appeared to occur after larger number of sites over the somatosensory cortex were disrupted compared to sighted controls and non-Braille readers, suggesting that blind individuals demonstrate remarkable neuroplastic changes in response to sensory deprivation and the acquisition of Braille-reading skills. Interestingly, these neuroanatomical changes did not correspond to functional changes. Blind individuals were found to have comparable sensitivity thresholds and tactile discrimination abilities compared to sighted controls, suggesting that intramodal changes may sometime have neuroanatomical correlates only. Similar findings were also found when considering the auditory cortex after blindness. Elbert et al. (2002) explored the changes in the auditory cortex of blind individuals as a consequence of enhanced auditory processing. An expansion of regions within the auditory areas was found as measured with MEG, indicating a use-dependent cortical reorganisation.

Intramodal changes that also include a functional change in behaviour have been documented by a series of studies by Röder et al. (1996; 1999). One of these studies (Röder et al., 1996), found shorter latencies for auditory and somatosensory brain ERPs in blind individuals compared to sighted controls that additionally corresponded to shorter reaction times in a discrimination task that compared blind and sighted controls. These results suggest that blind individuals may have increased their processing efficiency in the auditory and somatosensory domain. To

further investigate compensatory changes in the auditory modality as a consequence of blindness, Röder et al. (1999) compared behavioural and electrophysiological indices of spatial tuning within central and peripheral auditory space in congenitally blind and sighted controls. Individuals were asked to detect the 'deviant' sound among standard auditory stimuli that could be presented from central or peripheral spatial locations. Behavioural and electrophysiological measures were found to correlate, in that blind were found to have better localisation abilities compared to hearing controls, particularly for stimuli presented in the periphery of the auditory space. In addition, electrophysiological recording revealed sharper tuning of early spatial attention mechanisms in the blind. Difference in the scalp distribution of the brain electrical activity suggests a compensatory reorganisation of brain areas in the blind that may improve spatial resolution. Although this latter change could speak for supra-modal changes (i.e., reorganisation of high-level cognitive functions), it should be noted that attention in this case appears only as an aspect of auditory reorganisation due to blindness, in other words, sensory-dependent.

#### Intramodal plasticity in the deaf

Similar intramodal changes as a consequence of sensory loss have been found in the deaf population as well, as revealed by a series of ERPs and fMRI studies. In an early study by Neville et al. (1983), visual-evoked potentials were recorded from occipital, parietal and temporal areas while participants fixated a white dot presented in the centre of a screen. A white rectangle appeared randomly either at centre or to the left or right of fixation. Visual-evoked potentials in the deaf were found to be enhanced for a component (N150) particularly for stimuli appearing in the periphery of the visual field, suggesting compensatory changes selectively for

peripheral sensory reception due to greater reliance on vision for the detection of events in the periphery. In addition, the increased amplitude in response of components in the occipital areas speaks for structural changes that occur within the visual system (intramodally).

More recently, Bavelier et al. (2000) measured brain activity using functional magnetic resonance (fMRI) in congenitally deaf individuals and hearing controls while monitoring visual moving stimuli that could either be presented in the periphery or in the centre of the visual field. Results showed that deaf had increased activation of the motion-selective complex MT/MST compared to hearing controls when monitoring the periphery of the visual field, indicating enhanced activity of visual motion areas for the deaf. It is worth noting though that the enhancement found for the visual motion areas was modulated by attentional demands towards the periphery. Deaf individuals in fact had comparable activation to hearing controls when they viewed dots randomly distributed over the whole visual field. Overall results suggested specific changes in the organisation of the visual motion areas in deaf individuals, and, similarly to the previous study, it suggested that an increased activation of this complex depends upon a different representation of the peripheral space that arises as a consequence of early auditory deprivation.

It should be mentioned that some early-deafened individuals are trained to sign language, which is a visuospatial language. It could be argued that sign language then, similarly to Braille-reading, induces plasticity as a consequence of extended use of that particular sensory modality, and thus any observed change may not depend upon deafness *per se*. Although this would not argue against the type of change, which is use-dependent, it remains to be ascertained whether early sensory loss triggers plasticity phenomena that are selective for that particular case.



Bavelier et al. (2001) addressed this question by measuring brain activity with fMRI in a group of deaf signers, hearing controls, and native hearing signers. All participants were scanned during presentation of static dots and moving flowfields under different conditions of spatial (fullfield, centre, periphery) and featural (luminance, velocity) attention. The task consisted in reporting the number of blocks containing three or more changes. From a behavioural point of view, deaf signers tended to perform better than hearing controls and hearing signers in the peripheral location of attention conditions, but hearing controls were found to perform better for central location of attention conditions. fMRI data confirmed this pattern of behavioural results, documenting higher activation of area MT/MST in hearing controls and hearing signers when attention was directed towards the centre of the visual field and higher activation of this area in deaf signers when attention was directed towards the periphery of the visual field. In particular, a shift towards the left hemisphere in MT/MST greater activity in deaf signers and hearing signers documented that use-dependent plasticity changes may be found in terms of lateralisation. A greater activation of MT/MST in deaf signers only for peripheral conditions compared to the two hearing controls suggested that this change occurs as a consequence of deafness per se. In addition, during the visual motion task, the posterior superior temporal sulcus was activated in the deaf signers only, establishing that even polymodal areas may undergo reorganisation that specifically occurs as a consequence of auditory deafferentation. Modifications in these areas should be considered intramodal.

### Polymodal plasticity

Polymodal association areas in the cortex receive and integrate inputs from multiple sensory modalities. Although it may sound counterintuitive to consider changes in these areas as intramodal, as they are thought to be multisensory by nature, these areas should somehow be considered as a unique area, comparable to unisensory areas that, instead of processing a single sensory function, respond to more than one sensory input. The development of polymodal areas is shaped by the incoming signals from unimodal systems, which means that the absence of signal from one sensory system causes polymodal areas to reorganise *within*, in that the remaining sensory systems compete for higher representation in these areas in a compensatory fashion. In other words, the activity level of the remaining sensory modalities expands into the neural representation of the deprived sensory modality. Examples of polymodal changes have been documented in several animal studies. After visual deprivation in juvenile rats (Vidyasagar, 1978), cats (Rauschecker, 1996) and monkeys (Hyvärinen et al., 1981), there is an increase in the number of neurons that respond to somatosensory and auditory information in multimodal areas, including the superior colliculus (SC), the anterior ectosylvian cortex (AEC) in cats and the parietal cortex in monkeys. Rauschecker and Korte (1993) deprived cats of vision from birth, and found that neurons of the visual area in AES had become mostly responsive to auditory stimulation but also to tactile stimulation, meaning that the remaining sensory modalities had expanded into the formerly visual area. In addition, Rauschecker and Kniepert (1994) also found a corresponding behavioural compensatory effect, in that visually deprived cats showed improved auditory localisation abilities and greater auditory spatial tuning of cells in the AEC. In addition, the part of the region that typically responds to visual stimulation in sighted

animals becomes predominantly auditory and somatosensory, as to document an increased representation of the latter sensory maps in a field of the region not originally devoted to process those sensory inputs.

Similar findings were also found in blind and deaf humans (Alho et al., 1993; De Volder et al., 1997; Röder et al., 1996), whose compensatory abilities in the remaining sensory modalities could be due to reorganisation of polymodal areas. For example, Röder et al. (1996) reported an enhancement and a posterior shift of the N2 potential as measured with ERPs in the blind. The N2 component is believed to be generated in polymodal areas, thus leading to hypothesise that reorganisation of these areas may contribute to compensatory changes in the blind. Furthermore, Röder and Neville (2003) proposed that reorganisation in these areas are constrained by age, in particular to critical periods for typical development of these polymodal areas. The authors found that in early blind individuals, whose cataracts were removed in adulthood, impairment in higher visual functions was observed. These functions included depth perception, spatial attention and face recognition, all visual features that highly rely on polymodal areas. Interestingly, reorganisation in these areas seem to occur only during early childhood, and seem to be constraint by experience in sensory deprivation (as previously seen in Bavelier et al., 2001), namely they remain unchanged after extensive training of a single sensory modality.

Finally, it should be noted that intramodal changes that occur in unisensory and polymodal areas may somehow overlap, and establishing a clear border to keep these changes separated would not capture the complexity underlying plasticity phenomena. A step towards further understanding of anatomical and functional plastic changes after deafferentation is represented by *intermodal* changes.

### *1.1.2 Intermodal plasticity*

This type of change refers to the engagement of an intact sensory modality in processing the information of a deprived sensory modality. More precisely, the absence of the stream of information coming from one sensory modality causes the brain to reorganise in a cross-modal fashion, in that the intact senses respond to cortical functions originally belonging to the deafferented sensory modality. Intermodal changes somehow derive from the one previously described, and cannot really exist unless intramodal changes have not taken place before. One may rethink of intermodal changes as a “saturation” of cortical areas that are reorganised after sensory deprivation and have to re-balance their functions by recruiting neurons in other cortical areas. Moreover, neurons that are usually responsive to a particular stimulation in a region of the brain will respond to stimulation that was originally specific for the processing of other sensory functions.

Several animal models have addressed the question of cross-modal plasticity by re-routing the input of one sensory modality to the primary cortex of another modality (Sur et al., 1990; Sharma et al., 2000; von Melchner et al., 2000). For instance, Sur et al. (1988; 1990) conducted a series of experiments by re-routing retinal axons of newborn ferrets into the auditory thalamus, thereby providing a pathway for visual inputs to drive the auditory thalamus first, and the auditory cortex then. The rationale beyond these experiments was to change the input activity projected to the auditory cortex without altering the anatomical structure. For this reason, newborns were tested, whose anatomical structure is still highly immature. These experiments addressed the question of whether and how input activity influences initial formation of intracortical connections. In other words, if the rewired auditory cortex develops networks that are similar to those in the visual cortex, it

could suggest that the formation of visual processing networks in the cortex are shaped by instructions given by vision itself, despite any intrinsic developmental programme. In addition, these anatomical changes present behavioural consequences as well, in that one may question on whether visual activation of the rewired projections are interpreted by the animal as a visual input or an auditory one. If the behavioural role of a cortical area is independent of its input, then activation of the auditory cortex by any stimulus would be interpreted as auditory. Per contra, if the nature of the input has a role in determining the function of a cortical area, then rewired animals should interpret visual activation in the auditory cortex as a visual stimulus. Von Melchner et al. (2000) addressed this question by training ferrets rewired in the left hemisphere to discriminate between a visual and an auditory stimulus. Visual stimuli were presented in the left monocular field, while auditory stimuli were presented at different locations. Through a reward procedure, animals learned to associate one location with visual stimuli, another location with auditory stimuli. After this first training, visual stimuli were presented in the right monocular field, and animals obviously responded to the visual stimulus, since the rewired left hemisphere now contained two parallel pathways coming from the eye. In the second part of the testing, the lateral geniculate nucleus in the rewired hemisphere was ablated, and animals were still able to recognise visual stimuli. However, when the auditory cortex was lesioned, animals responded at chance level, indicating that the animals were blind in the right visual field because the auditory cortex became in the meanwhile functionally responsive to visual stimulation.

Most importantly, some form of rewiring seems to emerge even without forcing the deprived sensory channel towards another modality. Studies conducted on adult cats have shown that early sensory deprivation of either the auditory

(Rebillard et al., 1977) or the visual system (Rauschecker, 1993) elicits for the first case neural activation in the primary auditory cortex when a visual stimulation is presented, and elicits for the second case neural activation in the visual areas when an auditory stimulation is presented. The conclusion that cortical areas derive function from their inputs is consistent with studies conducted on early blind and deaf humans, who show recruitment of visual and auditory cortices, respectively, when performing a task that is not specific for the modality tested.

#### Intermodal plasticity in the blind

In early blind individuals, this type of change has been massively documented for the tactile modality, in that the occipital cortex is activated in association with the performance of tactile tasks (Sadato et al., 1996; Cohen et al., 1997). Sadato et al. (1996) used PET to measure activation during Braille reading and during the performance of a tactile discrimination task. Blind individuals showed activation of primary and secondary visual cortices particularly during Braille reading, and lesser activation of these cortices during performance of different tactile tasks. On the contrary, sighted controls showed no visual activation during any of the tactile tasks. Interestingly, no visual activation was found when blind individuals were asked to perform a tactile task not involving spatial discrimination. Cohen et al. (1997) further investigated this issue by addressing the question of the functional role of this occipital activation, namely whether these areas contributed to performance of the tactile task or were incidentally activated. Using TMS they studied the effects of disrupting the activity of different cortical visual regions during Braille reading. Individuals were asked to identify letters and read them aloud as accurately and quickly as possible. Results showed that application on occipital areas disrupted

somatosensory perceptions in the blind but not in the controls. These results indicate functional recruitment of the occipital areas for tactile discrimination. A striking additional example comes from a single case: Hamilton et al. (2000) reported of a blind woman who, after bilateral ischemic stroke involving the occipital cortex, lost her Braille reading skills, suggesting that regions of the visual cortex are essential in functionally compensating the sensory loss.

Similar findings were found for auditory sound localisation as well. For example, Weeks et al. (2000) measured brain activity in a group of congenitally blind individuals and sighted controls using PET scanning. Participants were asked to localise sounds coming from seven different spatial locations (sounds were synthesised and presented through headphones) by moving a joystick towards the perceived location. Behavioural results showed no difference in localisation abilities between blind and sighted controls. However, neuroimaging results demonstrated that there was recruitment of the occipital cortex during auditory localisation in the blind, which was absent in the sighted controls. These findings suggest that particularly the right occipital cortex in the blind has become part of the functional network for auditory localisation.

#### Intermodal plasticity in the deaf

Evidence of intermodal changes in the deaf are comparably less than in blind individuals, possibly because the interest in the deaf has a more recent history. However, fMRI and MEG studies have consistently provided evidence for intermodal plasticity in deaf individuals with early sensory loss.

Levänen et al. (1998) recorded magnetic signals using MEG from a single congenitally deaf individual during vibrotactile stimulation applied on the palm and

fingers of his left hand. To test the reactivity of the brain to sudden changes in tactile stimulation, the sequence of stimuli consisted in 'standard' frequent vibrations and 'deviant' infrequent vibrations differing in frequency. The vibration-induced activation in the primary somatosensory cortex were comparable between the deaf participants and the hearing controls, but only in the deaf individual there was a strong bilateral activation of the supratemporal (ST) auditory cortices. In addition, the 'deviant' stimulus produced two to three times stronger signals in the ST compared to 'standard' stimuli, suggesting that the auditory cortex contributes to the discrimination of tactile frequency.

A unique finding comes from Finney et al. (2001), who measured visually evoked activity in auditory areas of deaf individuals hearing controls using fMRI and found activation of the primary auditory cortex.

In a first study, participants were asked to simply view a moving dot pattern that was presented in either the right or left visual field. In a second study, participants were asked to perform a dimming task on the fixation spot while the motion visual stimulus was presented. In both studies, deaf participants demonstrated recruitment of the primary auditory cortex when processing visual stimuli. The effect was smaller in the second study because individuals were not attending the visual stimulus. Nonetheless, the fact that auditory activation was found even under non-attentional demands speaks for robust effect of intermodal changes due to sensory loss. In a further study, Fine et al. (2005) investigated neural plasticity resulting from early auditory deprivation and the use of sign language, to disambiguate the role of these two factors in triggering plastic changes. To this aim, a group of deaf signers, hearing signers and hearing controls were recruited to take part in the fMRI study. Similar to the previous study, participants had to either attend



a visual moving stimulus or ignore it. The results showed recruitment of the auditory cortex under visual stimulation, which was absent in both hearing signers and hearing controls, suggesting that such intermodal changes may be due to deafness per se. In addition, larger recruitment of the auditory cortex was found under attentional demands, suggesting that attention may play a crucial role in modulating and enhancing intermodal changes.

### *1.1.3 Behavioural and functional plasticity*

The general assumption is that if the properties of the neural circuitry change throughout life, a change in behaviour will probably be seen as well, and vice versa. This change in behaviour is often referred to as *compensatory* to underlie the improved functionality of the intact senses after the loss of one sensory modality in order to reduce the cost of the loss. Studies on the blind population have documented behavioural changes (i.e., enhanced performance) in several different tasks (for a review see Röder & Rösler, 2004), reporting better discrimination abilities in the tactile domain (Van Boven et al., 2000), better auditory localisation abilities (for a review see Collignon et al., 2009), and several better abilities for the discrimination of features in the auditory and tactile domain, such as spectrum (Doucet et al., 2004) pitch (Gougoux et al., 2004), and processing of fine spatial cues (Lessard et al., 1998; Voss et al., 2004). An interesting example comes from studies that focused on compensatory behaviours for the spatial processing of sounds in the blind (Lessard et al., 1998; Lewald, 2002; Fieger et al., 2006). In the study by Lessard et al. (1998), a group of blind individuals were tested in an auditory spatial localisation task, for signals presented in the frontal hemifield, under binaural and monaural listening conditions (the latter was obtained by obstructing one ear). In the binaural listening

condition, blind individuals were found to perform comparably to sighted controls, indicating that vision is not strictly necessary for sound localisation. In addition, under monaural listening condition, blind individuals outperformed sighted controls. In the sighted group, obstruction of one ear produced a localisation bias towards the non-obstructed ear in all participants. By contrast, only half of the blind participants showed a similar localisation error. Half of the blind were able to localise sounds correctly with a single ear in almost 100% of the trials, suggesting that blind individuals can use monaural spatial cues more efficiently than sighted controls. In another experiment (Voss et al., 2004), blind individuals were tested in a localisation task where stimuli were presented in far space, to see whether their compensatory abilities could be observed in a condition in which they cannot make use of sensory-motor feedback (such as using touch to calibrate the sound source or using a cane). Even under this condition blind individuals were found to be better than sighted controls in mapping the auditory space beyond their reaching space. In addition, even late-onset blind individuals were found to develop compensatory changes, in that they were found to have better spatial abilities compared to sighted controls. It is worth noting though that the latter result was found only for sounds presented at peripheral locations. As we shall see, this finding is in line with the main compensatory change that was found for the deaf as well, namely a higher performance for visual stimuli presented in the periphery of the visual field (Neville & Lawson, 1987; Loke & Song, 1991; Bavelier et al., 2000). The following paragraph will explore sensory compensation in the deaf in more detail. Here, it is worth mentioning that despite a higher reorganisation found in the deaf for the visual modality, this population was also found to have enhanced tactile sensitivity. In a study by Levänen and Hamdorf (2001), a group of congenitally deaf individuals were

tested for their tactile accuracy in a frequency discrimination and detection for suprathreshold frequency changes in a sequence of vibratory stimuli. The latter task showed a better performance for deaf individuals compared to hearing controls, suggesting higher tactile sensitivity as a consequence of auditory deprivation. Interestingly, no difference between the two groups was found in the discrimination task, suggesting that compensation mechanisms in the deaf for the tactile domain are selective for some aspects (detection of changes, as seen in the tactile detection task).

Overall results for blind and deaf individuals suggest that enhancement in the remaining sensory modalities are highly selective for the given task. Also, when comparing blind and deaf performances, it should be noted that the attentional component seem to be stronger in deaf than in blind, in that it is mainly under attentional conditions that deaf individuals show enhanced performances compared to hearing controls, suggesting a different role of attention that is sensory specific.

#### *1.1.4 Rapid plastic changes in the human brain*

Finally, it should be mentioned that behavioural plastic changes have been observed even in the shortest period after deprivation in sighted individuals, blindfolded for several days (Kauffman et al., 2000; Pascual-Leone & Hamilton, 2001). Pascual-Leone and Hamilton (2001) asked a group of sighted individuals to remain visually deprived for 5 days, during which they underwent training for tactile and auditory spatial discrimination tasks. In addition to behavioural testing, participants also underwent two fMRI tasks to record any cortical plastic change that could appear after deprivation. In the auditory fMRI task, participants had to compare a novel tone with a previous one, and decide whether the two tones were same or

different. Similarly, in the tactile fMRI task, participants were presented with pairs of Braille symbols and had to decide whether they were same or different. Result from both tasks showed activation of the visual cortex during auditory and tactile stimulation. Remarkably, activation of contralateral somatosensory cortex was present even on the first day of blindfolding, while activation in occipital areas started emerging by the second day of visual deprivation. In particular, an occipital activation was seen during tactile or auditory stimulation, documenting fast cross-modal changes occurring after short-term visual deprivation. Another striking change was observed when blindfolding was removed: after less than 24 hours, activation in the occipital areas for tactile and auditory stimuli disappeared, suggesting that recruitment of the deprived sensory modality for processing information in the remaining sensory modalities was only transient and reversed as soon as the normal function was made available again. Overall, these results have led the authors to suggest that the visual cortex has a *metamodal* structure that receives visual as well as auditory and tactile stimuli. These inputs can be unmasked whenever a visual deprivation is applied, and the visual cortex seems to subserve spatial discrimination tasks, regardless of the sensory input processed. The hypothesis beyond this is that the brain shapes sensory input and cortical modules for the demands of the sensory modalities (as seen whenever sensory deprivation is observed) that perform particular operations without specific reference to type of sensory input. The direct consequence to this is that tactile and auditory input into visual areas (as in this case) are present in any human being, and can be unmasked if behaviourally desirable in the shortest period as a consequence of adaptation. Although the speed of the changes does not allow establishing of new connections, these behavioural changes parallel the findings on animal studies after sensory rewiring.

## **1.2 Visual abilities in early deafness: what's enhanced, what's not**

The previous paragraph has shown the great interest that has particularly been devoted to phenomena of plasticity in the blind. However, an increasing number of studies have recently focused on the consequences of profound hearing loss on perception and cognition (for reviews, see Bavelier et al., 2006; Marschark & Hauser, 2008). Data available thus far suggest that enhancements for this population as a consequence of compensation are predominantly evident for specific aspects of visual cognition. Although some studies have argued for difficulties in deaf children and adults in sustaining attention leading to increased distractibility (Quittner et al., 1994; Parasnis et al., 2003), deaf individuals have generally proven to have comparable performances to hearing controls in most visual tasks involving accuracy and sensitivity thresholds. These include brightness discrimination (Bross, 1979), contrast sensitivity (Finney & Dobkins, 2001; Stevens & Neville, 2006), motion direction (Bosworth & Dobkins, 2002a, 2002b), and motion velocity (Brozinsky & Bavelier, 2004). Recent studies have suggested that there are three main conditions under which visual performance of the deaf is enhanced:

1. whenever central and peripheral visual targets are compared;
2. whenever the task involves attention;
3. whenever reactivity above accuracy is considered.

In a classic study by Loke and Song (1991) a group of deaf individuals and a group of hearing controls were asked to detect the onset of a visual target presented at central or peripheral locations, at 0.5 and 25 degrees of visual angle, respectively. Results showed a difference in speed of response: deaf individuals were found to be

faster in detecting the onset of peripheral targets, while they had comparable performance to hearing controls for stimuli presented in the centre of the visual field. In a similar experiment that documented selective effects of deafness on visual cognition, Neville and Lawson (1984) compared performance of a group of deaf individuals with hearing controls in a motion task, in which participants were asked to detect the visual motion. Deaf individuals were found to perform faster when asked to detect the direction of motion of peripheral targets at an attended location. Instead, the two groups had comparable performance for stimuli presented in the centre of the visual field.

To examine whether such effect may result from enhanced peripheral attention in the deaf, Proksch and Bavelier (2002) studied the effect of flanker distractors on a target identification task, in which participants were asked to identify a target shape presented in one of six circular frames arranged in a ring around fixation. A distracting shape (either a potential target shape or a neutral one) was presented either in the centre of the ring (i.e., perifoveal) or outside the ring (i.e., peripheral). Results showed that spatial distribution of visual attention differed between deaf and hearing controls, with deaf individuals being more distracted by flankers presented in the periphery, unlike hearing controls, who were more distracted by flankers presented at perifoveal locations. Additionally, to disentangle whether the observed reorganisation of the allocation of attention over the visual field is a consequence of auditory deprivation per se or a consequence of experience with sign language, the experiment was repeated on hearing signers born to deaf parents and exposed to sign language from birth. Interestingly, the latter group showed a similar pattern of results compared to hearing controls, with less attentional resources over the periphery than deaf signers. Therefore, these results show that

the plastic compensatory changes observed in the deaf are given by early auditory deprivation itself, not by practice in sign language, which requires a higher monitoring of the peripheral visual field.

Enhanced performance in the periphery of the visual field may be compatible with the notion that under normal hearing conditions, the auditory system provides information about the environment that is outside the field of view. As a consequence of auditory deprivation, compensatory changes may occur in enhancing visual processing directed towards the periphery of the visual field. Other evidence in support to this account comes from a recent study by Dye et al. (2009), who showed that in a complex attentional task deaf individuals outperformed hearing controls. An adaptation of the Useful Field of View task (UFOV) was used, in which participants had to identify a central target and localise a peripheral target in the presence of distractors. This type of task is supposed to measure how visual attention is distributed across central and peripheral targets, and examine whether deaf individuals have enhanced visual attention towards the periphery. Deaf individuals were proved faster at performing the task compared to hearing controls, suggesting enhanced visual selective attention particularly for stimuli presented in the periphery.

As attention seems to play a key role in enhanced visual abilities of the deaf, one main question is which aspect of attention is modified after profound deafness. In particular, do deaf individuals endogenously direct their attention towards visual targets, or is their attention exogenously captured? Bosworth and Dobkins (2002) investigated three aspects of spatial attention (orienting of attention, divided attention and selective attention) adopting a motion discrimination task on three groups: deaf signers, hearing signers and hearing controls (to keep the effects of auditory deprivation and experience with sign language as separate variables). In order to

investigate the ability to orient attention, similar to a previous study (Parasnis & Samar, 1985), participants' motion discrimination thresholds and reaction times to a cued and uncued target were compared. In the first condition, attention orienting towards the target occurs prior to its appearance, while in the second condition, orienting occurs when target appears, which presumably also occurs at the expenses of reaction times. Thus, if deaf signers are faster than controls in orienting attention endogenously towards a stimulus, then their performance would be better regardless of condition. In order to investigate the ability to divide attention across multiple visual stimuli, participants were asked to detect a single motion target presented either alone or among distractors. If deaf individuals are faster than hearing controls at detecting the target presented among distractors that would document greater attentional resources for the deaf group, as already suggested by Stivalet et al. (1998) and Rettenbach et al. (1999), who previously adopted a visual search task and found that deaf individuals were less influenced by the increasing number of distractors compared to hearing controls. At last, selective spatial attention was investigated by comparing thresholds for a single cued motion target with a motion target presented among distractors. As seen in previous studies, this ability has found to be enhanced in the deaf population for stimuli presented in the periphery of the visual field while ignoring centrally presented distractors (Parasnis & Samar, 1985; Reynolds, 1993).

Results showed that deaf individuals did not benefit of the cue in the orientation task, particularly for stimuli presented in the periphery, confirming the enhanced performance of deaf individuals as a function of eccentricity of the stimulus. Since this effect was not found in the other two groups, it appears that it is not due to experience with sign language but a consequence of auditory deprivation



per se. In the divided attention paradigm, participants did not show any difference, suggesting (contrarily to previous studies) comparable discrimination of motion direction for deaf and hearing controls. In the last experiment investigating selective attention, deaf individuals were found to perform better in the multiple condition (cued target presented among distractors). Overall, the three experiments showed that two aspects of attention, namely orienting and selective attention are altered as a consequence of early auditory deprivation.

Other aspects of visual attention that may change after deafness were investigated by Dye et al. (2007), who conducted two experiments adopting the Attentional Network Test (ANT) to investigate which aspects of visual attention are changed by deafness. More precisely, the ANT measures three aspects of visual attention: alerting, orienting and executive control. In the first experiment, all participants were presented with flankers represented by two horizontal arrows aligned on either side of the central target arrow. Flankers could either point in the same direction than the target arrow (congruent condition) or point in the opposite direction of the target arrow (incongruent condition). In addition, a single or double asterisk representing the cue and presented in different spatial locations appeared before target onset, and was used precisely with the aim to investigate alerting and orienting effects. Results showed no difference in performance between deaf individuals and hearing controls, suggesting comparable alerting and orienting processing in both groups. Also, no flanker interference effect difference was reported between groups, suggesting comparable executive control. Experiment 2 addressed the question whether deaf and hearing controls may differ in the latter aspect by manipulating the spatial locations of the flankers (i.e., spacing the distance between target and flanker arrows). Despite still comparable alerting and orienting

effects between groups, a flanker interference effect was found this time in the deaf population, presumably reflecting the more peripheral location now adopted for the flanker.

Overall the results I have reviewed from these previous studies point to the saliency of enhancement in the deaf population selectively for stimuli presented in the periphery of the visual field, and also suggest that this occurs under attentional demands, particularly under endogenous directing of attention.

A recent series of studies conducted by Bottari and co-workers (2008; 2009a; 2009b) have challenged the notion that endogenous attention shift is sufficient for enhanced performance to emerge. In a first study, Bottari et al. (2008) evaluated the endogenous component of attention by testing a group of deaf individuals on a change blindness task. Participants were presented with two visual scenes comprising 4 or 8 images, appearing half in central locations, the other half in peripheral locations. The two scenes were separated by a single blank and participants had to report whether the two scenes were same or different. Crucially, participants were asked to either attend to the centre or the periphery of the visual field or distribute attention across the whole visual scene. Results of this first study showed comparable performance among groups, regardless of the attention conditions. Furthermore, no benefit for processing peripheral changes was observed. Contrarily to previous findings, this study showed that deaf individuals do not have enhanced endogenous attention directed by default to the periphery of the visual field. To further investigate the role of endogenous and exogenous attention in the deaf population, Bottari et al. (2009a) conducted a second study and adopted the change blindness paradigm previously described with the exception that this time a valid or invalid cue was introduced in half of the trials (superimposed on the blank

screen), in order to explore the effects of an exogenous capture of attention. In addition, a simple detection task was introduced as well, in which participants only had to detect as quickly as possible the onset of the target stimulus that could appear either in the centre or the periphery of the visual field. Again, no between group difference emerged. Remarkably however, a substantial speed of response advantage emerged in deaf than hearing controls, regardless of stimulus spatial position.

In a third study, Bottari et al. (2009b) compared performance of deaf and hearing controls in a simple detection task and in a discrimination task, with the aim to evaluate reactivity in a distributed attention context (simple detection task) as well as in a selective spatial attention context (discrimination task). Results of this third study confirmed that deaf individuals are faster than hearing controls at detecting visual targets. However, no benefit in the discrimination task emerged.

The studies discussed so far have evidenced that compensatory visual changes in the deaf are highly selective, and only occur under specific conditions. However, an important aspect that has lacked substantial investigation concerns the temporal perception in this population.

### **1.3 Temporal abilities in the deaf population**

As discussed in the previous paragraph, many studies have investigated perceptual and attentive abilities in the deaf population, suggesting enhanced visual abilities that are strictly selective for the task demands and involve only some aspects of vision. A central and underinvestigated issue concerns how temporal

information is processed after auditory loss. The lack of interest for this issue is quite surprising if one thinks that the auditory system serves temporal components of perception, and that, more in general, temporal processing is essential to the functioning of the organisms in everyday life. For example, perception of simultaneity, the judgment of an event as preceding or following another, or the estimation of time duration are essential to have a temporal representation of the environment surrounding us. One could therefore assume that the lack of the auditory input could impact on at least some aspects of temporal processing. However, in the general view that a sensory deprivation leads to compensatory effects in the remaining sensory modalities, one may predict that, as in the case of deafness, the visual system may take over temporal abilities typically pertaining to the auditory system in a cross-modal fashion. A study by Bross et al. (1980) documented that hearing individuals auditory deprived for 24 hours showed enhanced visual temporal resolution in a flicker frequency threshold task, suggesting rapid compensatory changes in the functioning sensory systems.

So far, temporal processing in the deaf population has received little attention, and the different tasks used to investigate this aspect have led to contrasting results. For example, Kowalska and Szelag (2006) tested congenitally deaf adolescents with the aim to investigate their temporal accuracy in a reproduction task in the range of seconds. They chose this range purposely because it corresponds to the length of words and phrases. Since deaf individuals who were born deaf show disturbed language articulation, the question of whether they may also have difficulties in processing temporal duration has a second fall on the relationship between time and language. Participants performed two experiments: in the first one, they were asked to reproduce intervals of several durations of visually

presented stimuli, by pressing a button when they perceived that the duration of the second stimulus was as long as the first presented stimulus. In the second experiment, participants were required to produce different durations up to 6 seconds, by pressing on the button the requested duration presented on the monitor. Results showed that deaf individuals were overall worse than hearing controls in both experiments. In particular, deaf individuals overestimated intervals when shorter than 3 seconds, and underestimated intervals longer than 3 seconds in both reproduction and production tasks. Various factors may be responsible for the differences between deaf and hearing controls, including different attentional resources and working memory differences. An important factor that should be considered whenever the time interval spans over several seconds is the possibility that participants may adopt counting strategies. Therefore, instead of a difference in time perception, deaf individuals may be impaired in their counting abilities. However, some studies (Zarfaty et al., 2004) have demonstrated that deaf individuals are not impaired in their counting abilities, therefore any difference that could be found in their temporal processing compared to hearing controls should be explained as a consequence of auditory deprivation per se.

A crucial point that has arisen from this study is the close relationship between temporal perception and the acquisition of language. Children who were born deaf or acquired deafness before the age of 3 not surprisingly perform worse in most of the language domains compared to their hearing peers (Svirsky et al., 2000). However, language is a complex function that is made up of more low levels of cognition that constitute language in its different components. One of these components is the ability to correctly process the temporal information. Evidence of a relationship between language and temporal processing comes from studies with

language-impaired children (Farmer & Klein, 1995; Wright et al., 1997; Tallal et al., 1998). Wright et al. (1997) measured the detection thresholds for a brief tone presented before, during or after different masking noises in language-impaired children and controls. Children with language impairment showed to be significantly worse than controls in separating a brief sound from a rapidly following sound of similar frequency, and in detecting a brief tone by exploiting a frequency difference between the target tone and the co-occurring or masking sound. These results suggest that auditory deficits can impair perception of briefly acoustic elements of speech. Similarly, Farmer and Klein (1995) reviewed several studies suggesting a relationship between temporal processing impairment and dyslexia. In particular, dyslexic individuals were found to have a deficit in temporal order judgments in both the auditory and visual modality, and in the discrimination of stimulus sequences composed of more than two elements. Interestingly, since the stimuli used for the temporal tasks involved both linguistic and non-linguistic stimuli (i.e., tones, syllables, words, flashes), the hypothesis that dyslexia is only caused by language impairment per se does not hold, suggesting that more low-level cognitive aspects are linked to the deficit, particularly the impairment in temporal processing. Similarly, Tallal et al. (1998) tested language-impaired children and controls who were presented with two rapid tones (75 ms) differing in frequency and separated by different ISI, and who were asked to discriminate or reproduce their perceived order. Results showed that controls were able to respond accurately even when stimuli were spaced 10 ms apart. On the contrary, the language-impaired children took 150 ms to reach the same level of accuracy, leading the authors to conclude that this population is impaired when processing temporal events that are presented in rapid succession.

Conclusions of these studies suggest that language impairments can be somehow predicted by deficits shown in auditory perception, particularly for brief tones presented in rapid succession. It could be speculated that there may be a relationship between language and temporal perception, in that not only the latter determines language impairment, but also viceversa, with language deficits leading to temporal processing impairment. In this view, deaf individuals who are impaired on most of the linguistic skills may also show impairment in the temporal dimension.

From the previously studies discussed, two main hypothesis emerge for temporal processing abilities that may have profoundly deaf individuals: on the one side, deaf individuals could have enhanced or comparable temporal processing abilities than hearing controls because of compensatory abilities shown in the remaining sensory modalities; on the other side, deaf individuals may have impaired temporal processing abilities as a consequence of language impairment that involves temporal aspects of speech.

#### **1.4 Aim of Part I of the thesis**

In the following chapter we will examine how visual temporal information is processed after long-term auditory deprivation. While we have seen that some initial work on the deaf population has been done in the range of seconds, leaving the possibility that other factors might have played a role in determining a difference in performance between deaf and hearing controls, here we adopted a task in which stimuli were in the range of milliseconds. Specifically, we adopted a temporal order judgment task (TOJ) and asked participants to determine the order of two visual

stimuli presented in rapid succession. In addition, since enhanced performance in the deaf for the visual modality has been found particularly for stimuli presented in the periphery of the visual field, we positioned stimuli at two different eccentricities in each hemifield (at perifoveal and peripheral locations).



## CHAPTER 2

# Visual temporal order judgment in profoundly deaf individuals

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## **2.1 Abstract**

We investigated temporal processing in profoundly deaf individuals by testing their ability to make temporal order judgments (TOJs) for pairs of visual stimuli presented at central or peripheral visual eccentricities. Ten profoundly deaf participants judged which of the two visual stimuli appearing on opposite sides of central fixation was delivered first. Stimuli were presented symmetrically, at central or peripheral locations, or asymmetrically (i.e. one central and the other peripheral) at varying stimulus onset asynchronies (SOAs) using the method of constant stimuli. Two groups of hearing controls were also tested in this task: 10 hearing controls auditory-deprived during testing and 12 hearing controls who were not subjected to any deprivation procedure. Temporal order thresholds (i.e. just noticeable differences) and points of subjective simultaneity for the two visual stimuli did not differ between groups. However, faster discrimination responses were systematically observed in the deaf than in either group of hearing controls, especially when the first of the two stimuli appeared at peripheral locations. Contrary to some previous findings, our results show that a life-long auditory deprivation does not alter temporal processing abilities in the millisecond range. In fact, we show that deaf participants obtain similar temporal thresholds to hearing controls, while also responding much faster. This enhanced reactivity is documented here for the first time in the context of a temporal processing task, and we suggest it may constitute a critical aspect of the functional changes occurring as a consequence of profound deafness.

## 2.2 Introduction

In the last decade, an increasing number of studies have investigated perceptual and attentional abilities in the profoundly deaf with the aim of understanding the functional and neural mechanisms of multisensory plasticity following long-term auditory deprivation (e.g., see Bavelier et al., 2006; Bavelier and Neville, 2002 for reviews). Since the early observations of Neville and colleagues suggesting behavioural as well as electrophysiological enhancements of visual processing in the profoundly deaf (Neville, 1995; Neville and Lawson, 1987; Neville et al., 1983), many contributions have clarified under which circumstances these compensatory effects can emerge (e.g. Armstrong et al., 2002; Bottari et al., 2008a, b; Bavelier et al., 2001; Bavelier et al., 2000; Finney and Dobkins, 2001). However, one aspect that remains to be ascertained is whether such compensatory effects extend to temporal processing abilities. In the present work, we examine temporal processing abilities in the profoundly deaf by using a temporal order judgment (TOJ) task.

Enhanced visual abilities in the profoundly deaf have been consistently reported in behavioural, event-related potentials (ERPs), and functional neuroimaging (fMRI) studies involving processing of visual motion stimuli (e.g., Armstrong et al., 2002; Bavelier et al., 2000, 2001; Neville and Lawson, 1987; Stevens and Neville, 2006). In addition, faster detection has been documented in response to simple visual target onsets (e.g., Bottari et al. 2008b; Loke and Song, 1991; Reynolds, 1993), or during re-orienting of attentional resources towards invalidly cued regions of the visual field (e.g., Colmenero et al., 2004; Parasnis and Samar, 1985). Importantly, visual enhancement seems to be particularly prevalent for stimuli appearing towards the periphery of the visual field (e.g., Bavelier et al.,

2000, 2001; Loke and Song, 1991; Parasnis and Samar, 1985; Reynolds, 1993), in agreement with the interpretation that compensatory abilities in the visual modality reflect higher reliance on peripheral vision for monitoring the surrounding environment in the deaf population (e.g., Colmenero et al., 2004; Loke and Song, 1991).

Despite the increasing interest for visual and attentional mechanisms in the deaf, much less work has been devoted to temporal processing abilities in this population. This is rather surprising when considering that the auditory system finely processes temporal events, and it is still debated whether temporal processing abilities in the profoundly deaf are impaired, intact or even enhanced with respect to hearing individuals. On the one hand, it could be hypothesized that whenever the auditory system has been deprived from birth, decreased temporal processing should emerge. Audition is the typical dominant sensory modality for time processing (e.g., Morein-Zamir et al., 2003; Shams et al., 2000), and its absence could undermine normal development of temporal perception. On the other hand, there is evidence in the literature that enhanced temporal resolution in the visual modality, as measured by lowering of flicker frequency thresholds (Bross et al., 1980), can emerge in hearing individuals deprived of auditory stimulation for 24 consecutive hours. This finding would predict that a lifelong auditory deprivation in the deaf could determine enhanced temporal processing instead of a decreased ability.

Initial work on time perception in the profoundly deaf focused on temporal abilities of this population in the range of seconds. Worse performance in the deaf than hearing controls was documented using tasks in which participants were asked to produce or reproduce the duration of visually presented stimuli (Kowalska and Szelag, 2006; Rileigh and Odom, 1972; Sterritt et al., 1966). In a typical production

task, participants receive a semantic instruction on screen (e.g., 'How long is 3 seconds') and are subsequently asked to interrupt the presentation of a visual stimulus when they judge that the requested duration has been achieved (e.g., Kowalska and Szelag, 2006, Exp.2). In a typical reproduction task, participants are exposed to a visual stimulus of defined duration (e.g., 3 seconds) and are subsequently asked to reproduce the perceived sample duration by interrupting the presentation of a stimulus delivered on screen (e.g., Kowalska and Szelag, 2006, Exp.1). As pointed out by Mills (1985, p. 483), it is not clear whether poor performance with production and reproduction tasks is due to a deficiency in encoding/remembering the exact temporal duration requested by the experimenter, or a deficiency in reproducing that duration. In addition, whenever the time interval spans over several seconds, it is always possible that participants adopt counting strategies, and therefore it cannot be excluded that any worse performance partially reflects counting rather than time processing difficulties (particularly for the profoundly deaf individuals; e.g. see Wood et al., 1984). Interestingly, no difference between deaf and hearing controls emerged using measures of temporal perception that did not involve duration reproduction, such as judging whether pairs of tactile stimuli presented in sequence (Kracke, 1975) or pairs of rhythmic patterns presented through vision (Mills, 1985) are same or different.

Other studies have examined temporal processing in the profoundly deaf in the range of milliseconds, rather than seconds (Bross and Sauerwein, 1980; Heming and Brown, 2005; Poizner and Tallal, 1987). Poizner and Tallal (1987) conducted four experiments to test temporal processing abilities in congenitally deaf individuals, but found no difference between this population and a group of hearing controls. Two experiments examined flicker fusion thresholds for a single circle flickering on and off

at different frequencies, or for two circles presented in sequence with variable inter-stimulus interval (Poizner and Tallal, 1987, Exp. 1 and 2, respectively). Although this paradigm was in many aspects similar to that adopted by Bross et al. (1980) with hearing participants auditory-deprived for 24 hours, no significant difference between deaf and hearing individuals was found (see also Bross and Sauerwein, 1980 for similar results). A comparable performance for deaf and hearing controls also emerged in one additional experiment that tested temporal order judgment abilities for pairs or triplets of visual targets presented in sequence (Poizner and Tallal, 1987, Exp. 3). All visual targets appeared from the same central spatial location on the computer screen, at either fixed (500 ms) or variable inter-stimulus intervals (0–400 ms), and participants were asked to tap the correct order of target appearance. Finally, the deaf and hearing participants also performed similarly in a serial memory task, in which sequences of three to seven items were presented at 2-Hz rate (i.e., one every 500 ms) and participants were asked to tap out the order of the presented stimuli on the computer keyboard (Poizner and Tallal, 1987, Exp. 4). Based on this series of results, Poizner and Tallal (1987) concluded that deaf individuals do not show deficits of temporal processing, at least when considering time intervals in the millisecond range.

This conclusion has recently been challenged by a study in which temporal processing in deaf and hearing individuals was examined using tactile and visual simultaneity judgment tasks (Heming and Brown, 2005). Tactile or visual stimuli were delivered in pairs, and the interval between the stimuli was adjusted using ascending or descending staircases until the participant was no longer able to determine whether the two stimuli were simultaneous or not. In the tactile task, vibrotactile stimuli were delivered to the index and middle fingers of one of the two hands

(unimanual condition) or to the index fingers of both hands (bimanual condition). In the visual task, light flashes were delivered from two out of six possible light emitting diodes (LEDs), horizontally arranged and regularly spaced with respect to central fixation (three LEDs on each side of fixation, with 3.3° of separation from one another). All pairs of flashes were delivered from adjacent LEDs, either on the same side or on opposite sides with respect to fixation. Regardless of target modality, results showed significantly higher temporal thresholds for congenitally deaf participants than hearing controls, leading Heming and Brown (2005) to suggest that different reorganisation of neural pathways subtending temporal processing can emerge after long-term auditory deprivation.

When comparing the results of these two studies that examined visual temporal processing in the deaf within the millisecond range (i.e., Heming and Brown, 2005; Poizner and Tallal, 1987) one methodological difference is evident. While Poizner and Tallal (1987) presented all visual stimuli from the same location in space (at central fixation), Heming and Brown (2005) presented all stimuli from different eccentricities with respect to central fixation, including locations in the periphery of the visual field. As anticipated earlier, performance differences between deaf and hearing participants emerged particularly for visual targets appearing towards the periphery of the visual field (e.g., Bavelier et al. 2000, 2001; Loke and Song, 1991; Parasnis and Samar, 1985; Proksch and Bavelier, 2002; Reynolds, 1993). This suggests that differences in temporal perception between deaf and hearing participants could also be particularly pronounced when stimuli occur at peripheral (as in Heming and Brown, 2005) than central locations (as in Poizner and Tallal, 1987).

In the present study, we used a TOJ task to examine whether the location of targets in the visual field can modulate temporal processing in the millisecond range for deaf and hearing participants. To make sure that any difference between deaf and hearing controls could not be merely explained in terms of task-irrelevant auditory experience affecting the performance of the hearing participants during testing (e.g., uncontrolled noise occasionally distracting the hearing participants from their main visual task), ten of the hearing controls performed the visual task with substantial auditory deprivation (see later for details on this procedure). Note that such a control group was not included in most previous studies on visual abilities in the deaf. However, it actually provides an important control for concluding that any differential ability in the profoundly deaf is linked to long-term auditory deprivation. Several reports have suggested that task-irrelevant noise can be detrimental for the performance of hearing participants (see Smith, 1989 for a review). For instance, task-irrelevant background noise can result in prolonged reaction times during visuo-spatial attention tasks (Trimmel and Poelzl, 2006).

In the current work, the three groups of participants (deaf, non-deprived hearing controls, and auditory-deprived hearing controls) were asked to determine the temporal order of two visual stimuli, presented in brief succession at different eccentricities on the computer screen. The two stimuli always appeared on opposite sides with respect to central fixation, and were either symmetrical (i.e., both central or both peripheral) or asymmetrical with respect to fixation (i.e., one central and the other peripheral). We hypothesised that a difference between deaf and hearing participants could be mostly pronounced when visual stimuli appear at peripheral locations.



## 2.3 Methods

### *Participants*

Twelve profoundly deaf participants (three females and nine men; mean age = 32 years, range from 18 to 40 years; all right-handed) were recruited to take part in the study through the National Association for the Deaf (Ente Nazionale Sordi, Trento, Italy). All deaf participants had bilateral profound hearing loss (>85 dB). Two deaf participants were subsequently excluded from data analysis: one was unable to understand the task; the other was unable to focus on the task. Among the remaining ten deaf participants, two had congenital deafness, three acquired deafness before the age of two (i.e. pre-verbal onset), and the remaining five acquired deafness between 2 and 4 years of age (i.e., post-verbal onset). All were proficient users of sign language, but were also capable of using oral communication.

Twenty-two hearing controls also took part in the study. Twelve of the hearing controls (eight females and four men, mean age = 21 years, range from 19 to 32 years; all right-handed) were tested in a quiet room, not specifically shielded for noise (non-deprived hearing controls). The remaining ten hearing controls (six females and four men, mean age = 30 years, range from 27 to 34 years; two were left-handed) were tested in an auditory-deprived condition (see procedure for details), inside a sound-attenuated booth (auditory-deprived hearing controls).

Both deaf and hearing controls gave their informed consent before taking part to the study that was conducted according to the principles of the Helsinki declaration. All were naive as to the purpose of the experiment, and varied in their previous experience with psychophysical testing procedures. All participants had

normal or corrected-to-normal vision. The experiment took approximately 30 minutes to complete.

### *Apparatus and stimuli*

Visual stimuli were generated and presented using a Latitude Dell 820 laptop, connected to a Dell E773C-CRT video monitor with a 17-inch display (screen resolution 1023 x 768 pixel, refresh rate 75 Hz). Stimulus programming, presentation and response collection was done using E-Prime (<http://www.pstnet.com>). Visual targets were blue circles (diameter =  $0.5^\circ$  of visual angle) presented for 15 ms. Fixation was a white cross presented at the centre of the screen. All stimuli were presented on a uniform light-grey background.

In one subgroup of hearing controls, a combination of sound-attenuation methods (earplugs plus closed headphones reducing auditory input up to 50 dB) was used to obtain substantial auditory deprivation during visual testing. In addition, these participants were tested inside a sound-attenuated anechoic booth (Amplifon G2 x 2.25; floor area = 200 x 250 cm, height = 220 cm).

### *Procedure and design*

The experiment was conducted in a dimly lit room. Participants sat at table, approximately 60 cm from the computer monitor. In each trial, central fixation appeared for 500 ms, and after a random interval ranging between 500 and 1,000 ms the two visual targets appeared in rapid succession using the method of constant stimuli. Stimulus onset asynchrony (SOA) between the visual targets was either -110, -90, -55, -30, -20, +20, +30, +55, +90 or +110 ms. Negative SOAs indicate that the right visual target was presented first, whereas positive SOAs indicate that the

left visual target was presented first. The two visual targets were always presented on opposite sides with respect to central fixation, at 3° or 8° of eccentricities with respect to fixation. Visual targets were presented according to four possible spatial arrangements: (1) both targets at 3° from fixation ('both central' condition); (2) both targets at 8° from fixation ('both peripheral' condition); (3) the first target at 3° and the second target at 8° ('central first' condition); (4) the first target at 8° and the second target at 3° ('peripheral first' condition). Note that the term 'central' is adopted here by analogy with other studies on the deaf population (e.g. Bottari et al., 2008a, b; Bavelier et al., 2000; Neville and Lawson, 1987; Proksch and Bavelier, 2002), but actually denotes locations that were peri-foveal. From now on we will refer to the first presented stimulus as 'S1' and the second presented stimulus as 'S2'.

Participants were informed that the two visual targets could appear on either side of fixation and that their task was to determine which visual target had been presented first. Participants were also informed that they should use the two mouse buttons for their response (left button to indicate 'left stimulus first', right button to indicate 'right stimulus first'). All participants, including the left-handed, used two fingers of the right hand to give their responses, namely, index finger to press on the left button, and middle finger to press on the right button. They were also told that accuracy was more important than response speed. Finally, participants were required to keep their head still and gaze at central fixation throughout each block of trials (no chinrest was used). For each of the ten possible SOAs, the experiment comprised eight trials for each of the symmetrical stimulus arrangements (i.e. 'both central' and 'both peripheral' conditions) and eight trials for the asymmetrical stimulus arrangements (i.e. 'central first' and 'peripheral first' conditions). This resulted in 480 trials overall, divided in three experimental blocks. All experimental

conditions were fully randomised within each block. A short practice of ten trials preceded the experimental blocks that were separated by short resting breaks.

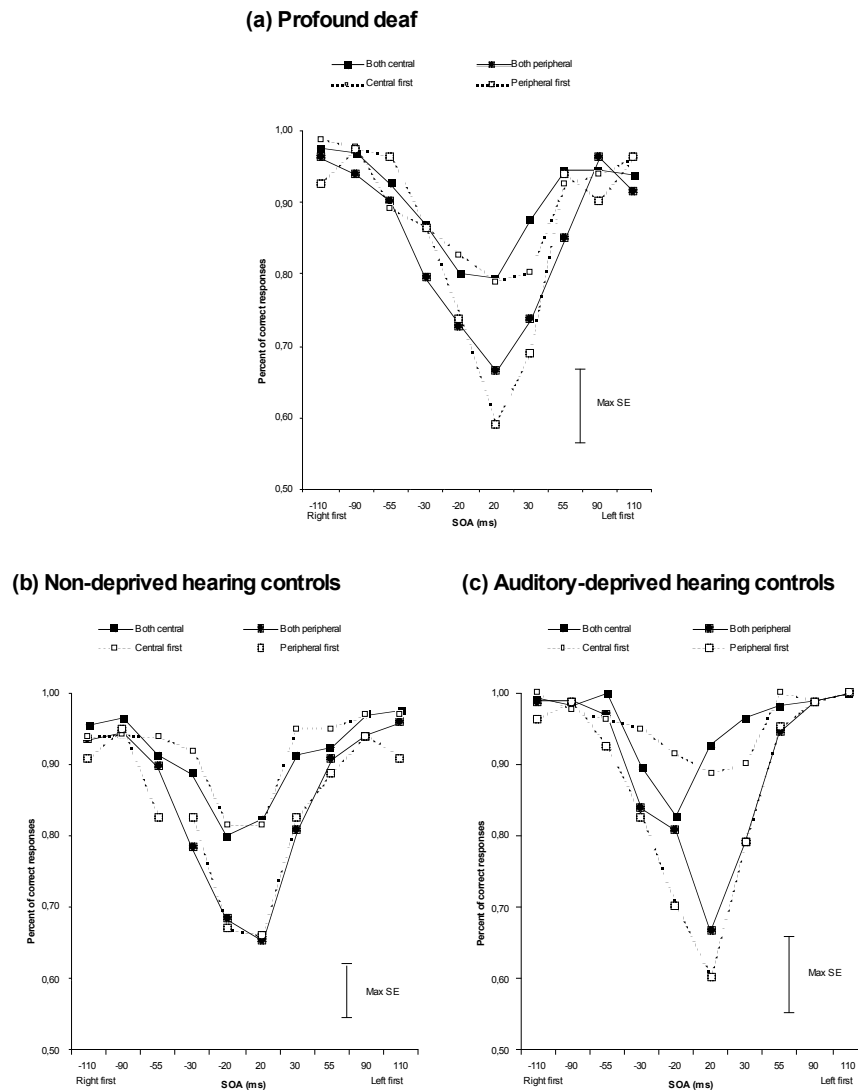
## **2.4 Results**

### *Proportion of correct responses*

Proportions of correct responses as a function of SOA and spatial arrangement of the visual target are shown in Fig. 1, separately for profoundly deaf individuals (Fig. 1a), non-deprived hearing controls (Fig. 1b) and auditory-deprived hearing controls (Fig. 1c). As can be seen from this figure, all groups showed higher accuracy for the spatial arrangements in which the first of the two visual targets appeared from central locations (i.e. 'both central' and 'central-first' conditions) than spatial arrangements in which the first of the two visual targets appeared from peripheral locations (i.e. 'both peripheral' and 'peripheral-first' conditions). This was particularly evident at the shortest SOAs.

To confirm this pattern of results statistically, proportions of correct responses for each participant were entered into a mixed analysis of variance (ANOVA) with S1 eccentricity (central or peripheral), S1 side (left or right), S1-S2 relative position (symmetrical or asymmetrical) and SOA (20, 30, 55, 90 or 110 ms) as within-participants factors. Group (deaf, non-deprived hearing controls and auditory-deprived hearing controls) was entered into the analysis as between-participants factor. Post hoc tests were corrected for multiple comparisons using the Bonferroni procedure.

Figure 1



**Fig. 1** Proportion of correct responses as a function of SOA and spatial arrangement of the visual targets, separately for (a) deaf, (b) non-deprived hearing controls, and (c) auditory-deprived hearing controls. *Bold squares* indicate performance when both S1 and S2 appeared at central locations, *bold circles* indicate performance when both S1 and S2 appeared at peripheral locations. *Empty squares* indicate performance when S1 appeared centrally (and S2 peripheral), *empty circles* indicate performance when S1 appeared peripherally (and S2 central).

This analysis revealed a main effect of S1 eccentricity,  $F(1,29) = 51.2$ ,  $P < 0.0001$ , caused by participants responding more correctly on trials in which S1 appeared at central (mean = 0.92, SE = 0.01) than peripheral locations (mean = 0.86, SE = 0.02). The main effect of SOA was also significant,  $F(4,116) = 97.3$ ,  $P < 0.0001$ , reflecting higher accuracy for longer than shorter SOAs. Finally, there was a significant interaction between S1 eccentricity and SOA,  $F(4,116) = 19.2$ ,  $P < 0.0001$ , caused by worse performance at the shortest SOAs (i.e.  $\pm 20$  and  $\pm 30$  ms) for peripheral than central S1 eccentricities (all  $P$ s  $< 0.01$ , on paired  $t$  tests). This interaction was more pronounced when S1 appeared on the left than right side, resulting also in a significant three-way interaction between S1 eccentricity, S1 side and SOA,  $F(4,116) = 2.9$ ,  $P < 0.02$ . The interaction between S1 eccentricity and side was also significant,  $F(1,29) = 4.2$ ,  $P < 0.05$ , but subsidiary to the three-way interaction described above. Importantly, however, neither the main effect of group, nor any of the interactions involving the group factor reached significance (all  $F$ s  $< 2.4$ ).

#### *Just noticeable differences and points of subjective simultaneity*

As a standard approach to the analysis of psychophysics functions (including those resulting from TOJ studies, as here) we computed for each participant the just noticeable difference (JND) and the point of subjective simultaneity (PSS). The JND represents the temporal interval between two stimuli needed for participants to be able to judge reliably which stimulus came first. The PSS indicates the amount of time by which one stimulus had to lead the other in order for synchrony to be perceived (i.e., for participants to make the 'left first' and 'right first' responses equally often).

We started by calculating these functions with respect to the side (i.e. which side was presented first) of the stimulus. The proportion of 'left-first' responses was fitted with a cumulative Gaussian function and we calculated JND and PSS as the standard deviation and mean of the fitting distribution, respectively. All analyses on JND and PSS values were done using GnuPlot software for Linux platforms. JND and PSS values for each experimental group, computed with respect to side are reported in the upper part of Table 1. The two measures were entered separately into a mixed ANOVA with S1 eccentricity (central or peripheral) as within-participants factors, and group (deaf, hearing controls and auditory-deprived hearing controls) as between-participants factor.

The analysis of JND revealed a main effect of S1 Eccentricity,  $F(1,29) = 14.4$ ,  $P < 0.001$ , caused by larger JNDs for S1 appearing at peripheral (mean = 45.5, SE = 9.7) than central locations (mean = 26.8, SE = 5.3). This finding is shown in Fig. 2. Notably there was no main effect of group,  $F(1,29) = 0.8$ , n.s., and no interaction between S1 eccentricity and group,  $F(2,29) = 1.4$ , n.s. A similar analysis conducted on PSS showed no significant main effect of group,  $F(1,29) = 0.9$ , n.s., or S1 eccentricity,  $F(1,29) = 0.1$ , n.s. Only the interaction between group and S1 eccentricity approached significance,  $F(2,29) = 2.7$ ,  $P = 0.08$ . However, note that for all of the groups PSS was not significantly different from zero (see upper part of Table 1, all  $P$ s  $> 0.05$  on  $t$  test against zero). This indicates that no groups showed a significant temporal bias for stimuli appearing on the left versus the right side of fixation.

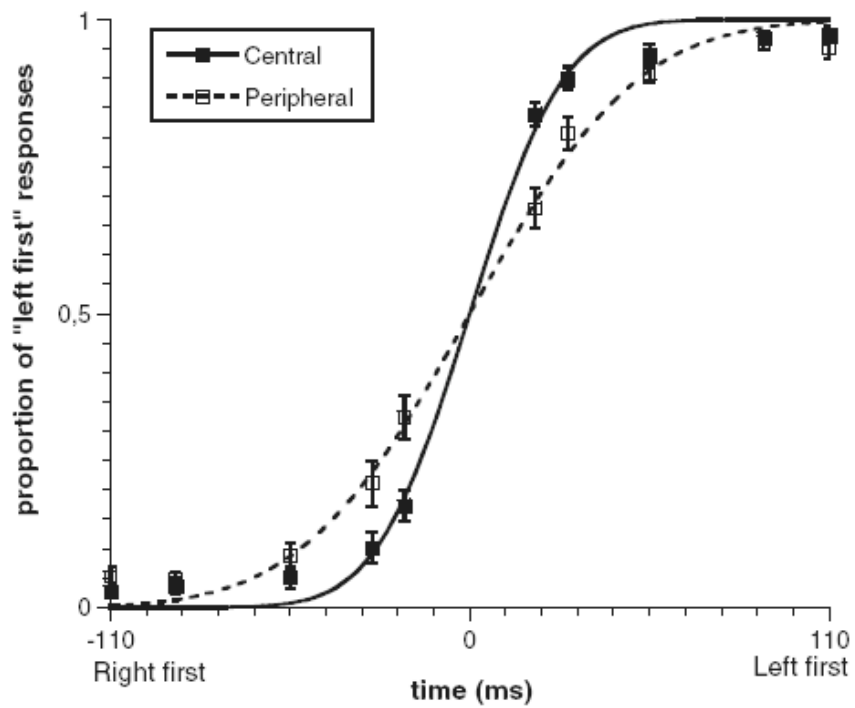
Table 1

	JND (ms)	PSS (ms)
Computed with respect to side		
Profound deaf	36 (13)	-5 (4)
Non-deprived hearing controls	47 (12)	2 (4)
Auditory-deprived hearing controls	25 (13)	1 (4)
Computed with respect to eccentricity		
Profound deaf	36 (12)	6 (2)
Non-deprived hearing controls	43 (11)	9 (2)
Auditory-deprived hearing controls	22 (12)	10 (2)

**Table 1** Mean JND and PSS (in ms) as a function of group, computed with respect to side (i.e., which side lead; see upper part of the table) or with respect to eccentricity (i.e. which eccentricity lead; see lower part of the table).



Figure 2



**Fig. 2** Proportion of left-first responses (i.e. psychophysical function computed with respect to side), as a function of S1 position (central or peripheral). Note that this plot describes performance collapsed across groups, as no significant group difference emerged from the analysis (see text). *Error bars* indicate the standard error of the mean.

We then computed JND and PSS with respect to the eccentricity of the stimuli (i.e. which eccentricity was presented first). To this aim, we re-coded our data so that negative SOAs now indicate that the central stimulus was presented first, and positive SOAs indicate that the peripheral stimulus was presented first. As before, we fitted the proportion of 'peripheral-first' responses with a cumulative Gaussian function and calculated JND and PSS as the standard deviation and mean of the fitting distribution, respectively. JND and PSS values for each experimental group, computed with respect to eccentricity are reported in the bottom part of Table 1. The two measures were entered separately into a mixed ANOVA with S1-S2 relative position (symmetrical or asymmetrical) as within-participant factors and group (deaf, non-deprived hearing controls and auditory-deprived hearing controls) as between-participant factor.

The analysis of JND showed no main effect of S1-S2 relative position or group, nor any interaction between these two factors (all  $F_s < 1.6$ ). This confirmed that temporal sensitivity was comparable across groups and was unaffected by whether the two stimuli appeared at symmetrical or asymmetrical locations. The analysis on PSS also revealed no significant main effect or interaction (all  $F_s < 1.0$ ). Importantly, however, mean PSS was now significantly larger than zero (overall, mean = 8.2 ms, SE = 1.3,  $t(31) = 6.3$ ,  $P < 0.0001$ ), indicating that the peripheral stimulus had to lead on average by 8 ms to be perceived simultaneous with the central one (see Fig. 3).

### *Response time*

Having established that the three groups did not differ in their temporal sensitivity (as measured by accuracy and JND) and in their PSS, we turned to

examine whether readiness of response was also comparable between the groups. Although our instructions to participants favoured accuracy over speed of response (as mostly requested in TOJ paradigms), we also considered reaction times (RTs) as dependent measure because a large part of the literature on visual abilities in the deaf found differences between this population and hearing participants, specifically when readiness of response was considered (e.g., Bavelier et al., 2000; Bottari et al., 2008b; Colmenero et al., 2004; Loke and Song, 1991; Neville and Lawson, 1987; Parasnis and Samar, 1985; Proksch and Bavelier, 2002; Sladen et al., 2005).

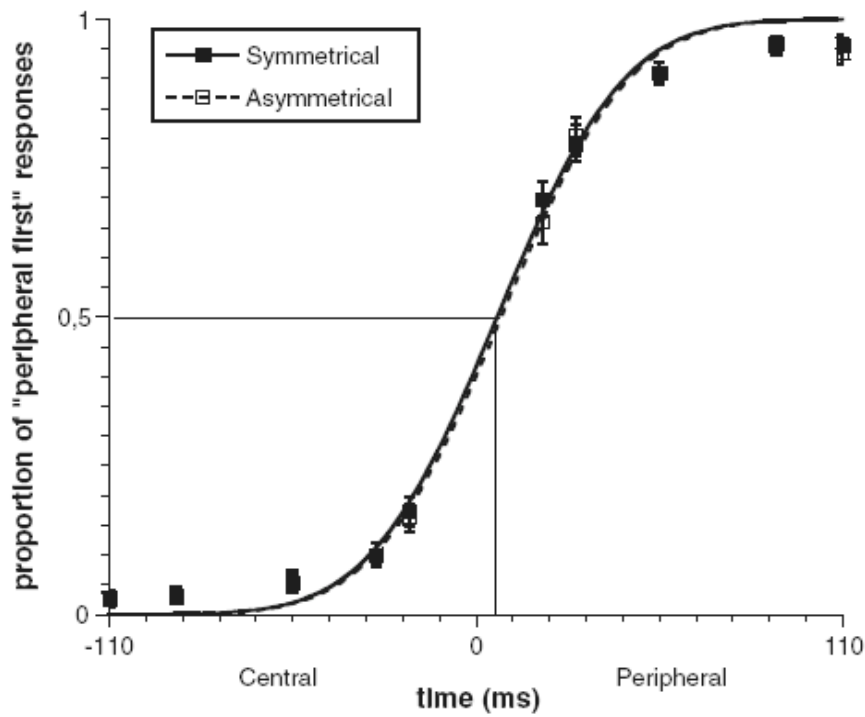
Mean reaction times for correct trials are shown in Table 2 as a function of S1 eccentricity and group.

Table 2

	S1 eccentricity		
	Central	Peripheral	Difference
Profound deaf	508 (30)	550 (46)	42
Non-deprived hearing controls	516 (28)	638 (42)	122
Auditory-deprived hearing controls	487 (30)	600 (45)	113

**Table 2** Mean reaction time (with standard error in parenthesis) for correct responses as a function of S1 position and group.

Figure 3

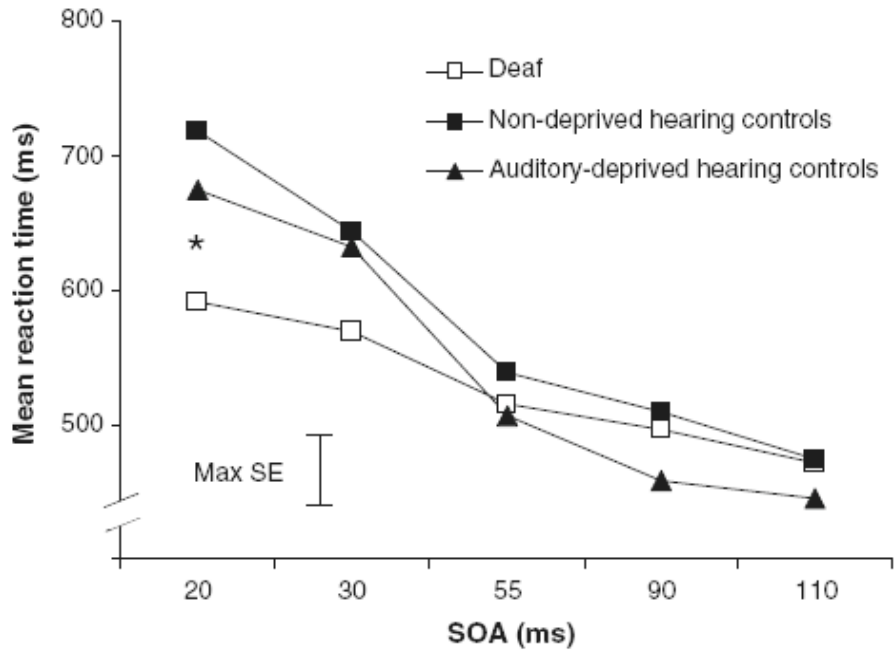


**Fig. 3** Proportion of centre-first responses (i.e. psychophysical function computed with respect to eccentricity), as a function of S1-S2 relative position (symmetrical or asymmetrical). Note that this plot describes performance collapsed across groups, as no significant group difference emerged from the analysis (see text). *Error bars* indicate the standard error of the mean.

Median RTs for each participant were entered into an ANOVA similar to the one used above for accuracy data. This analysis revealed a main effect of SOA,  $F(4,116) = 48.1$ ,  $P < 0.0001$ , reflecting longer RTs for the shortest SOAs (i.e. 30 and 20 ms), in accord with the increased complexity of the task at short intervals. There was also a main effect of S1 eccentricity,  $F(1,29) = 34.2$ ,  $P < 0.0001$ , caused by faster RTs when S1 appeared at central (mean = 503 ms, SE = 17) than peripheral locations (mean = 596 ms, SE = 25). Such a difference was most pronounced at the shortest SOAs (i.e. 30 and 20 ms), resulting in a significant interaction between S1 eccentricity and SOA,  $F(4,116) = 10.5$ ,  $P < 0.0001$ . In addition, slower responses to peripheral than central stimuli were specific to S1 appearing on the left than on the right, as indicated by a significant interaction between S1 eccentricity and S1 side,  $F(1,29) = 8.5$ ,  $P = 0.007$ .

Most importantly, the interaction between SOA and group was also significant,  $F(8,116) = 2.1$ ,  $P = 0.04$  ( $P = 0.1$  with Huynh–Feldt sphericity correction,  $\epsilon = 0.43$ ). This was caused by profoundly deaf participants responding faster than either group of hearing controls at the shortest SOA. As can be seen from Fig. 4, when the two visual stimuli were separated by 20 ms, deaf participants were on average 126 ms faster than the non-deprived hearing controls ( $P < 0.0006$  on Newman–Keuls post hoc test) and 83 ms faster than auditory-deprived hearing controls ( $P < 0.03$  on Newman–Keuls post hoc test). By contrast, no significant response speed advantage emerged at the other SOAs. In addition, no significant difference emerged between the two groups of hearing controls.

Figure 4



**Fig. 4** Mean reaction times as a function of SOA in the deaf and in the two groups of hearing controls. *Asterisk* indicates a significant difference between the deaf and either group of hearing controls (see text for details).

Visual inspection of Table 2 suggests that this lower response speed in the deaf may depend upon the smaller cost paid by deaf participants when S1 appeared at peripheral than central locations (note that the RT difference between central and peripheral locations is 42 ms for the profoundly deaf, 122 ms for the auditory-deprived hearing controls, and 113 ms for the auditory-deprived hearing controls; see Table 2). To confirm this pattern of results statistically, we calculated the difference between RTs at central and peripheral locations for each participant, and ran planned comparisons (two-tailed independent-samples  $t$  test, with equal variance not assumed) to compare the performance of the deaf group with the performance of each of the hearing control groups. These planned comparisons confirmed a reduced RT cost for deaf participants when responding to peripheral than central targets, both with respect to non-deprived hearing controls,  $t(17.9) = 2.1$ ,  $P = 0.05$ , and with respect to auditory-deprived hearing controls,  $t(17.7) = 2.3$ ,  $P = 0.03$ .

## **2.5 Discussion**

The present study examined whether long-term auditory deprivation can modify temporal abilities in the millisecond range, and whether the eccentricity of visual targets play a role in modulating temporal processing. To this aim, we compared the performance of one group of profoundly deaf individuals and two groups of hearing controls in a TOJ task for visual stimuli appearing at central versus peripheral eccentricities in opposite visual fields. Our findings reveal that temporal sensitivity (as measured by accuracy, JND and PSS) did not differ between groups,

regardless of stimulus eccentricity. However, deaf participants were systematically faster than either group of hearing controls at the SOA corresponding to the most difficult temporal order judgments, especially when the first of the two stimuli appeared at peripheral locations.

### *Deaf are not impaired in TOJs*

The results of the present study show that basic temporal abilities in the millisecond range are not altered in the profoundly deaf population. This finding expands the earlier report of Poizner and Tallal (1987, Exp.3), by showing that comparable accuracy in temporal order judgment emerges also when visual stimuli are presented towards the periphery of the visual field (as here) instead of directly at fixation (as in Poizner and Tallal, 1987). In addition, it is in agreement with the literature showing that temporal abilities in the range of seconds are comparable in the deaf and in hearing controls (Kracke, 1975; Mills, 1985). Instead, our findings are in contrast with a recent result showing that simultaneity thresholds are higher for deaf than hearing participants (Heming and Brown, 2005). One obvious reason for such a discrepancy may relate to the different adopted task. While Heming and Brown (2005) asked participants to perform a simultaneity judgment (SJ) task, we instructed participants to judge which stimulus came first ('left' or 'right', TOJ task). Recent evidence suggests that SJ and TOJ tasks may involve somewhat different aspect of temporal perception (e.g. Schneider and Bavelier, 2003; Vatakis et al., 2007). Thus, it is possible that the poorer performance of deaf participants documented by Heming and Brown (2005) reflects a selective difficulty of this population when judging the simultaneity of visual events, rather than an overall deficit of temporal processing.



### *Readiness of response differs between deaf and hearing individuals*

The novel finding of the present study is the observation that a difference between profoundly deaf and hearing participants in the TOJ task can emerge in terms of readiness of response, rather than accuracy. In spite of comparable temporal sensitivity, deaf participants were on average 100 ms faster than hearing controls when judging the temporal order of the visual stimuli under the most demanding SOA (i.e.  $\pm 20$  ms). Importantly, this advantage in response speed cannot be merely explained in terms of task-irrelevant auditory noise distracting the hearing participants from their visual task. Previous evidence in the literature suggests that task-irrelevant background noise can indeed result in prolonged reaction times in visual tasks (e.g. Trimmel and Poelzl, 2006). However, as clearly illustrated in Fig. 4, deaf participants in our study were faster (at the 20 ms SOA) also with respect to auditory-deprived hearing controls. Thus, the mere absence of background noise was not sufficient to make hearing controls responding as fast as the profoundly deaf. It also interesting to note that the RT advantage we have documented in the deaf is specific for the shortest SOA (i.e.  $\pm 20$  ms) and particularly pronounced when S1 appears at peripheral locations. These specificities of the effect argue against an overall response-speed enhancement due to higher motivation or increased alertness in the deaf. Instead, our findings suggest that the differential performance of the profoundly deaf may reflect some temporally and spatially selective modulations of reactivity in this sensory-deprived population.

Reaction time enhancements in the deaf have previously been reported in tasks requiring discrimination of visual motion (Neville and Lawson, 1987) or visual detection (Colmenero et al., 2004; Parasnis and Samar, 1985). Recently, we also

reported that deaf participants respond on average 50 ms faster in a simple detection task, for simple visual targets appearing at 3° or 8° from central fixation (Bottari et al., 2008b; see also Loke and Song, 1991, for related findings). To our knowledge, however, RT advantages for deaf than hearing participants during a temporal processing task have not been previously described in the literature. The fact that enhanced readiness of response characterises the performance of profoundly deaf individuals in such a variety of behavioural tasks (from simple detection to temporal order judgment) suggests that speeding of response may constitute a critical aspect of functional reorganisation following long-term auditory deprivation. In this respect, it is interesting to note that several authors have linked the visual compensatory mechanisms occurring in profound deafness to modification occurring in the dorsal visual pathway (e.g. Stevens and Neville, 2006). The dorsal visual pathway is known for fast and parallel processing of visual stimuli (e.g. Paradiso, 2002). Areas reaching from V1 to MST and the frontal eye field (FEF) are almost simultaneously activated within the first 50 ms from stimulus presentation (Lamme and Roelfsema, 2000).

Finally, as anticipated above, reaction times differences between deaf and hearing individuals were more pronounced when S1 appeared at peripheral locations. Both groups of hearing participants paid a substantial reaction time cost when S1 appeared at peripheral than central locations. By contrast, the difference between peripheral and central S1 locations was much reduced in deaf participants (see Table 2). This pattern of results has been previously observed for detection or discrimination tasks (e.g. Loke and Song, 1991; Neville and Lawson, 1987). It has been interpreted as the consequence of a greater need of this population to use peripheral vision for monitoring the environment, and it has been linked with

modifications occurring in the dorsal visual stream (e.g. Stevens and Neville, 2006). Interestingly, a somewhat similar pattern of results was also documented by Heming and Brown (2005), albeit for simultaneity thresholds rather than reaction times. In their study, hearing participants showed significantly higher thresholds for the outer (i.e. more peripheral) than inner (i.e. more central) locations of the stimuli. By contrast, deaf showed comparable temporal thresholds regardless of whether the stimuli appeared at inner or outer locations (Heming and Brown, 2005, pp. 179).

*Better performance for central than peripheral visual targets*

A final point worth discussing concerns the modulations of PSS and JND as a function of eccentricity of the first stimulus. PSS differed as a function of the eccentricity of the first stimulus. When data were recoded with respect to stimulus eccentricity (i.e. which eccentricity came first), it became evident that the peripheral stimulus had to lead on average by 8 ms to be simultaneously perceived with the central one (see Fig. 3). One possible explanation for the PSS finding relates to the different saliency of central stimuli with respect to the peripheral ones. Because visual stimuli in our paradigm were not corrected for cortical magnification, central stimuli were inevitably more salient than peripheral ones. Several evidence suggests that the perceived temporal order of visual stimuli is modulated by their relative luminance (e.g. Allik and Kreegipuu, 1998; Arden and Weale, 1954), with the brighter stimulus that needs to be presented later in time in order to be perceived simultaneous with the less bright one. Extrapolating here to visual saliency, one could argue that the central (more salient) stimuli were detected earlier than peripheral ones in our paradigm, thus leading to the observed modulation of PSS.

JND was better in both groups when the first of the two visual targets originated from central than peripheral locations in the visual field. Specifically, participants showed smaller temporal thresholds (JNDs) and faster RTs when S1 appeared at central locations (i.e. 'both central' or 'central-first' conditions) than when S1 appeared at peripheral locations (i.e. 'both peripheral' or 'peripheral-first' conditions). Note that this result is evident even for the two asymmetric conditions, for which distance in external space between S1 and S2 was held constant (11°). Namely, temporal order judgments were easier in the central-first condition (mean JND = 30 ms) than in the peripheral-first condition (mean JND = 47 ms), suggesting that this pattern of results does not reflect the changing distance in external space between S1 and S2 across conditions (see Allik and Kreegipuu, 1998; Westheimer and McKee, 1977, for an example of TOJ modulation as a function of distance in the visual domain; see Shore et al., 2005 for an example in the tactile domain). We can also exclude that the modulation of TOJ as a function of S1 eccentricity reflects some sort of response bias, because participants were always instructed to report the side of the first stimulus and not its eccentricity. One possible explanation for this unpredicted JND modulation relates to the combination of two factors: on the one hand the specific instructions we gave to participants (i.e. 'which stimulus came first'), on the other hand the salience difference between central and peripheral stimuli. Specifically, the judgment as to which stimulus came first, could have been easier (i.e. lower JNDs) for the more salient stimuli presented at central locations. Importantly, this unpredicted effect on JND did not interact with the group factor, indicating that our main finding concerning the absence of a performance difference between deaf and hearing controls cannot be interpreted on the basis of this additional phenomenon.

## **2.6 Conclusions**

Taken together our findings challenge the idea that deaf participants show poorer temporal processing abilities than hearing controls, and suggest instead that their temporal thresholds in the millisecond range can be entirely comparable to that of hearing controls. In fact, our findings reveal that deaf participants reach a comparable level of accuracy with respect to hearing controls, while also responding considerably faster. This was particularly evident when the first visual target appeared at the periphery of the visual field. This novel finding indicates that readiness of response rather than accuracy could differentiate between profoundly deaf and hearing individuals, leading to the suggestion that reactivity could be a critical aspect of the functional changes following long-term auditory deprivation.

## **Acknowledgments**

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## **2.7 Interim conclusions**

The present study investigated temporal processing of rapid visual events in a group of deaf adults. The main finding consists in having established, contrarily to previous literature, that deaf individuals are not impaired in temporally processing stimuli in the millisecond range. This may suggest that, in their language acquisition impairment, the temporal component does not play a critical role, unlike the case of language learning impaired children. The second finding, which is in line with previous research on the deaf population, concerns the enhanced reactivity found particularly for stimuli presented in the periphery of the visual field. This result speaks out for the role played by readiness of response, which could be one of the most salient aspects that change as a consequence of auditory deprivation.

Overall, the first part of the thesis has added support to the notion that some compensatory plastic changes can be observed at a behavioural level, and that long-term auditory deprivation leads to changes that are highly selective for the visual modality.

## **PART II**

The effects of auditory  
reafferentation on the adult brain



# **CHAPTER 3**

## Introduction

### **3.1 Functional plasticity in the adult brain and the role of experience**

Until quite recently, the common thought was that no new connection could be formed in the adult brain, suggesting that once the nervous system had achieved complete maturation, no other change would be possible. Pioneering studies on adult neurogenesis (Gould et al., 1999; Kornack & Rakic, 1999; Kempermann et al., 2004; Leedo et al., 2006) were the first to document the production of new neurons in the adult brain (though constraint to few regions and yet not clear about their functional benefit). These studies share the common idea that neurogenesis occurs in restricted areas in the adult mammalian brain (hippocampus and olfactory system), and that the main challenge remains the understanding of the functions that these newborn neurons may have. For instance, Kempermann (2002) speculated that the possible function of adult neurogenesis in the hippocampus could be to sustain the ability of this structure to accommodate continuous modulations given by cortical inputs.

Further evidence that some degree of plasticity is observable even in the adult brain comes from neurophysiological and neuroanatomical studies in animals and non-invasive methods used in human beings (for a review, see Ramachandran, 1993). For example, early animal studies showed that the adult brain can undergo cortical remapping following surgical changes of peripheral sensory input. Merzenich and colleagues (1983, 1984) conducted several studies on adult monkeys to assess the spatial representations of sensory input in primary sensory areas and documented dramatic and rapid reorganisation as a result of modified sensory input. In one of their studies, for example, Merzenich and colleagues (1984) surgically amputated one finger of adult monkey hands and found a change of the somatosensory map following the digit amputation. The representation of the

remaining digits increased and expanded to locations within the former cortical territories of the amputated digit. The results suggested that cortical representations of the skin surface are alterable by new sensory input given in adulthood. In addition, these experience-dependent changes of sensory maps account for the concomitant changes in tactual abilities observed at a behavioural level (for an extended review on the topic, see Kaas, 1991). Similar conclusions were also reached for the visual system (Kaas et al., 1990; Chino, 1995) by removing part of the retina in adult mammals. Kaas et al. (1990) showed that cortical neurons that normally have receptive fields corresponding to the lesioned region of the retina of the adult monkey acquired new receptive fields in the portions of the retina surrounding the lesion. This corresponded to a systematic altering of the representation of the retina in the primary and secondary visual cortex. Remarkably, Chino (1995) found that all regions in the lesioned zone of cortex acquired new receptive fields within hours of deafferentation.

### *3.1.1 Plasticity in the adult human brain*

Neuroimaging techniques have allowed investigating cortical plasticity in the adult human brain as well. As for animal studies, plasticity has been documented in different sensory systems. A first evidence came from the somatosensory system, in which Mogilner et al. (1993) conducted a MEG study on two adults with syndactyly (a condition where two or more fingers are fused together) before and after surgical correction of this dismorphism. Before surgery, the hand representation in cortical maps had shrunken; after surgery, the somatosensory map was reorganised and correlated with the new functional status of the separated fingers, suggesting that reorganisation of the cortical maps can be observed even in the human adult brain.

Plasticity in the auditory system has been investigated by several researchers (Scheffler et al., 1998; Ponton et al., 2001). For example, Scheffler et al. (2001) conducted an fMRI study to compare patterns of cortical activation produced by monaural stimulation in normal-hearing individuals and unilaterally deaf adults. Normal-hearing individuals showed strong lateralisation of cortical contralateral response when stimulated monaurally. On the contrary, deaf subjects did not show such lateralisation of the functional response, maintaining instead a response comparable to the one observed in normal hearing during binaural stimulation. This result suggested the presence of plasticity in the auditory system of adult deaf individuals or some kind of reorganisation of the auditory pathways following sensory deprivation. It should be emphasised that in this study both individuals with early and late deafness onset were included, failing to disambiguate whether the observed plasticity was due to long-term deprivation and/or deprivation acquired in childhood. In another study, Ponton et al. (2001) precisely examined whether plasticity can be observed in the adult brain by measuring auditory evoked potentials in late deafened individuals with profound deafness in one ear only, by studying the time course of the cortical activation changes. Ponton et al. (2001) found enhanced activation in the hemisphere ipsilateral to the stimulated ear, indicating significant changes in the central nervous system following adult deafness. Since auditory evoked potentials were not recorded immediately after deafness onset, it cannot be excluded that some changes in the auditory system may have occurred right after deafness onset. However, significant changes between unilateral deaf and hearing controls appeared more robust for those who had been deaf for more than 2 years (than less than 2 years), suggesting that the more the experience with auditory deprivation increases, the more the changes in cortical activation increase as well.

The latter studies, as well as the other discussed in the first part of the thesis and concerning sensory deprivation, lead to the question of whether there exists a difference between plasticity in early life and plasticity observed in adulthood, if there are different mechanisms underpinning them, and how these two may even interact.

### *3.1.2 Plasticity during sensitive periods*

There are some fundamental aspects that differentiate plasticity in early life and in adulthood. Studies in animals have shown that during limited time windows in early life, the effects of experience are unusually strong in shaping the brain and behaviour (Knudsen, 2004). These periods occur early in life and have been commonly named 'sensitive periods'. A particular class of sensitive periods is represented by the so-called 'critical periods', which represent the strict time window during which experience provides information that is essential for normal development and during which each sensory input can permanently alter behaviour (Knudsen, 2004; Hensch, 2005). By contrast, in mature circuits plastic changes are somehow impeded by the stability achieved by the brain during development. In support to this view, early studies by Knudsen et al. (1984; 1986) on young barn owls examined the effects of plugging one ear at different times in life to study to what extent re-calibration of the sound localisation circuitry is based upon early sensory experience. To this aim, a group of young barn owls were chronically occluded in one ear at different ages (from a few weeks after birth to adulthood) and performed a localisation task consisting in orienting the head towards either a sound or a light stimulus. Results showed that barn owls monaurally occluded before 6 weeks of age adjusted their sound localisation abilities relatively quickly, and those occluded between 6 and 8 weeks also readjusted but taking longer. On the contrary,

barn owls occluded after 8 weeks of age did not recover sound localisation abilities, suggesting that there is a relatively short critical period for experience to shape behaviour (in the case of auditory localisation, it seems to be constrained to head and ears reaching adult size). Beyond that, no new experience can be achieved. This somehow 'strict' view raises the question of whether adult plasticity, that has proven to occur at an anatomical and cortical level, can be somehow manifested by behavioural changes. To understand the functional plastic mechanisms that can be observed in adulthood, a concept should be put forward first, namely the crucial role of experience in promoting and shaping adult plasticity.

### *3.1.3 Different types of experience shape plasticity in the adult brain*

Whenever we refer to the term 'experience', two closely linked aspects need to be considered. On the one side, experience is the familiarity and knowledge we have acquired of a particular skill, event, or object in a specific phase of life (i.e., *when* experience takes place). On the other side, experience can be seen as the duration of training we do with that skill (i.e., *how long* the experience occurred for). As for the first idea of experience, the role of sensitive periods is representative of this view: if an experience occurs within the closure of critical periods, it will determine and favour enhanced plasticity in adulthood. In other words, a particular ability acquired during sensitive periods will enable the brain to re-establish that experience later in life, even if there was no use of it in the meanwhile. An example for this concept comes from a study by Knudsen et al. (1998), who compared capacity for audio-visual localisation adjustments in two groups of adult barn owls. One group experienced normal audio-visual correspondences throughout the sensitive period; the second group had an altered audio-visual experience caused by

wearing of prisms in juvenile age that shifted the normal audio-visual tuning. Both groups were tested after the second group had regained normal audio-visual tuning. The experiment consisted in exposing both groups to chronic displacement of the visual field through prisms. The group who had normal experience during the sensitive period had to wear the prisms for 6 months before readjusting audio-visual correspondence. On the contrary, the group that had experienced prisms adaptation during the sensitive period took only 17 days to calibrate adaptive audio-visual correspondence. Results from this study show that experience during a sensitive period leaves traces in the adult brain, in that experience in adulthood can re-establish functional connections that were grown during the sensitive period, regardless of the disuse of these connections even for a long time.

Similar results have also been obtained from studies on ocular dominance shift after monocular deprivation (Pizzorusso et al., 2002; Hofer et al., 2006). Hofer et al. (2006) showed that monocular deprivation in mice during the sensitive period, and subsequent deprivation in adulthood caused the visual cortex to shift more rapidly ocular dominance towards the non-deprived eye. This suggests that an early-altered experience can enhance effectiveness of a second altered experience in adulthood, even if the cortex has completely recovered during the first and second period of induced deprivation. In addition, Hofer et al. (2006) have expanded the idea of experience, in that the authors found that even by depriving monocularly the first and second time during adulthood, mice showed high degrees of plasticity, suggesting that any experience achieved in the past (not only during development) facilitates reproducing the same experience a second time. Overall, these results suggest that plasticity can be observed regardless of whether the first experience occurred during sensitive or were both experienced in adulthood. It should be noted

though that different plasticity mechanisms underlie juvenile and adult plasticity, in that adult ocular dominance shifts were mediated mainly by an increase in the response strength of the non-deprived ipsilateral eye, while in juvenile mice the dominance shift corresponded to a weakening of the deprived inputs. Nonetheless, this study is of particular interest because it suggests that despite different plasticity mechanisms, the strength and rapidity with which experience-induced plasticity is observed is similar in the juvenile and adult brain.

The second idea of experience addresses the question of *how long* an experience should last to induce plastic changes in adulthood. Clearly, this aspect is closely linked with the concept of learning, i.e., the process by which individuals' behaviour is changed through interaction with the environment. A study by King et al. (2000) showed that by plugging one ear of adult ferrets, their performance in sound localisation reached almost normal levels after several months of occlusion (6 months), indicating that experience with a new sensory input (without specific training) enables even the adult brain to reshape, given enough time. In addition, King et al. (2000) specifically trained another group of adult-plugged ferrets on the same task and found that their performance improved over the first few weeks, documenting the role of training in determining how fast a new experience can be achieved. These two experiments point to a causal relationship between adult plasticity and experience. In fact, as suggested by King et al. (2001), it is unlikely that, particularly for sound localisation, an anatomical remodelling may take place after altered experience in adulthood (contrarily to what happens during early childhood, in which experience strengthens both neural connections and behaviour). Instead, it may be possible that re-weighting of acoustic cues take place as a consequence of adaptation (i.e., in this case, monaural pinna cues can become



more reliable than in normal binaural conditions). Similarly, Linkenhoker and Knudsen (2002) exposed a group of adult owls to prismatic spectacles that caused a large horizontal shift of the visual field. Since in the optic tectum of the barn owl auditory and visual maps of space are aligned, the tectal neurons are tuned to the values of auditory localisation cues, such as interval time difference (ITD), that corresponds to the visual location of the sound source. The capacity of the optic tectum to acquire new representations of auditory cues is usually considered to be restricted in the adult animal (King, 1993), while young owls reared with prisms can readjust within few months to the new input. In this study, the authors verified the effects of training on adult plasticity by exposing two groups of adult owls to prismatic shift differing in prism strength (in terms of degrees) delivered in a single large step (i.e., in a unique session) or incrementally (i.e., in different sessions with increasing prism strength). The group that had a single large step in prism strength was found to have no difference in ITD tuning after the long experience. On the contrary, the second group, which underwent small incremental training, was found to have shifted ITD tuning after only 21 days. This study demonstrated that by constantly and slowly increasing the prism strength, the final and largest shift in ITD tuning corresponded to the one observed in juvenile owls. The difference between juvenile and adult owls consisted in time of exposure to the experience before reaching adjustment, and in the gradual exposure to the shift. Overall results suggest that the adult brain is capable of great plasticity, and that, in order to observe this capacity, the training increments for adults have to be smaller compared to the ones given to juvenile animals. The difference found between adult and developmental plasticity taps again into the different mechanisms characterising early and adult plasticity. As suggested by the authors, the need for adults to learn gradually indicates that adult

plasticity is less effective in producing changes in patterns of connectivity compared to early developmental plasticity. This also leads to the suggestion that while in young animals adaptability might be the priority to develop properties of the individual, adult animals may rely more on already established and functional networks.

### *3.1.4 The effects of learning: the special case of musicians*

While all the mentioned studies have investigated the effects of learning after exposing the animal to atypical experiences or even by sensory depriving them, intriguing evidence of plastic changes after extensive training comes from studies conducted on musicians. Musicians represent a useful group for documenting adult plasticity after long experience of a sensory modality, in that it shows that plastic changes may occur in the typically developed brain due to increased use of a particular sensory modality, as it is the case of audition (Pantev et al., 1998; 2003) and tactile performance (Ragert et al., 2004) for this population. Pantev et al. (2003) conducted a series of MEG studies to investigate the changes that occur in the human auditory system when learning to play a musical instrument. Results showed an enlarged cortical representation of tones of the musical scale compared to control pure tones in trained musicians. Interestingly, this pattern of result was correlated with the age at which musicians began to play the instrument. Further investigations also showed enhanced cortical representations for notes produced by different instruments that were actually enhanced in those musicians trained on that particular instrument. Finally, even cross-modal plasticity was proven to occur in musicians, in that when the lips of trumpet players are stimulated at the same time as a trumpet tone, activation in the somatosensory cortex is increased more than it is during the

sum of the separate lip and trumpet tone stimulation. Similarly, Ragert et al. (2004) found enhanced tactile performance in expert pianists by investigating their tactile spatial acuity in a two-point discrimination task. This psychophysical measure was considered to be an indirect marker of plastic changes in the pianists. Musicians were found to have lower spatial discrimination thresholds compared to non-musicians, and, more interestingly, the single performance had a linear correlation with the extent of training, indicating a link between functional plastic changes and the amount of practicing. Since musicians were also found to present different anatomical structures compared to non-musicians, it would be interesting to understand if, though speculative, these anatomical differences exist prior to any learning and may somehow induce an inclination to music.

### *3.1.5 Top-down influences facilitate plasticity*

A final aspect underlying the relationship between adult plasticity and experience is the role that higher cognitive functions have in facilitating plasticity. Evidence from this comes from a series of studies on animals documenting top-down influences in favouring plasticity in the adult brain (for a review, see Keuroghlian & Knudsen, 2007). Keuroghlian and Knudsen (2007) suggested that in order to induce adaptive plasticity in the adult central auditory system, acoustic stimuli have to be behaviourally relevant, which means that they have to attract attention. In addressing the question using animals, it appears evident that attention has to be triggered under reward contingencies. In a study by Polley et al. (2006), adult rats were exposed either passively to a sound or trained to detect particular features of the stimulus. In animals that learned to respond to a particular frequency, the representation of the target frequency largely extended in the auditory cortex

compared to controls, suggesting that adult plasticity can be induced by stimuli that are important to the animal, and that simple exposure to the stimulus does not drive plasticity (this latter point being in line with previous results by Linkenhoker and Knudsen, 2007). Since these studies were conducted on animals and constraints by several factors (such as conditioning and rewarding), any hypothesis on whether top-down influences may promote plasticity in the adult human brain should be considered speculative. However, this factor, as well as the role of learning in promoting plasticity particularly in the adult, allows understanding to what extent the brain maintains optimal functional properties through a lifespan. From a clinical perspective, investigation of the possibilities and limits of the adult brain may allow understanding how to ameliorate or reverse disease, damage or dysfunction, as it is the case, for example, of auditory loss and the possibility to restore hearing through a device called cochlear implant.

### **3.2 Cochlear implants: what plasticity can tell**

A cochlear implant (see Figure 1) is a neuroprosthetic device that allows reafferenting the auditory pathway by electrically stimulating the nerve, and therefore allows observing how the brain functionally adapts to the new auditory input. In case of profound hearing loss, the cause is usually the loss or damage of hair cells that allow transduction of the auditory input.

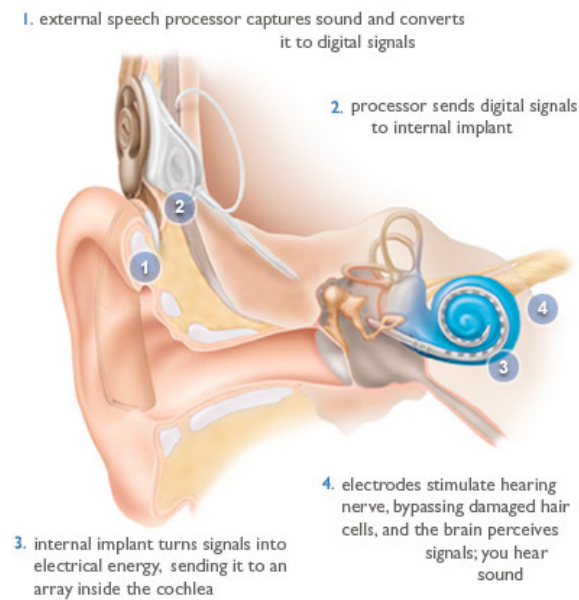


Figure 1

The cochlear implant bypasses the hair cells through a system comprising an external sound processor (microphone), a headpiece (radio frequency transmitter), an implanted cochlear stimulator underneath the skin (radio frequency receiver), and an array of microelectrodes implanted into the cochlea. This system replaces the auditory system that, under normal conditions, interprets the complex spectral and temporal aspects of sounds by mapping them onto the cochlea. Although the device provides the brain with peripheral input that is unnatural and impoverished compared

to the normal-functioning cochlea, a large number of adults and children have so far largely benefited of the implant. According to the Food and Drug Administration's 2005 data, nearly 100,000 people worldwide have received cochlear implants. In the United States, roughly 22,000 adults and nearly 15,000 children have received them, which means that mainly adults benefit of the device. This statistics underlies the social relevance in addressing issues such as plasticity in the adult brain, to understand to what extent adult cochlear implant recipients can benefit from the fitting. Since the first single-electrode implant was approved in 1984 in the U.S. (Zeng, 2004), several technical advances have been made, and nowadays the mostly adopted multielectrode device allows some recipients even to talk on the telephone. The possibility to observe the effects of auditory reafferentation from a psychophysical, speech rehabilitation and cognitive perspective has made the implant literature grow fast since the early 1990s.

Most of the studies conducted so far have focused on the recovery of language perception in quiet and noise (Schleich et al., 2004; Van Hoesel & Tyler, 2002; Van Hoesel et al., 2002; Long et al., 2006), as the cochlear implant is firstly meant to allow recipients to enhance communicative skills. Most of the recipients still receive a unilateral cochlear implant, but the practice of implanting two devices (i.e., bilateral cochlear implant) has rapidly increased, allowing to address the question of whether cochlear implants can improve sound localisation (Nopp et al., 2004; Verschuur et al., 2005; Grantham et al., 2007). Since bilateral cochlear implants can be implanted either sequentially or simultaneously, (i.e., one device implanted months or years before the second, or implanted together, respectively), recent studies have focused on the comparison between unilateral and bilateral cochlear implants, reaching the shared idea that "two is better than one", both in sequential

implant condition (Tyler et al., 2002; Nopp et al., 2004; Schleich et al., 2004; Laszig et al., 2004; Grantham et al., 2007) and simultaneous implantation (Laszig et al., 2004; Litovsky et al., 2006).

Despite a general benefit encountered by most of the recipients, the extent of the improvements on several auditory tasks (i.e., speech perception and discrimination, sound localisation, perception of music) and for different age groups over different time courses are still very variable. Intriguingly, these variables are precisely what make the study of cochlear implants a neuroscientific topic, not only a technological one. The outcome of cochlear implantation depends on several factors, such as cochlear implant processor, position of electrodes on the cochlea, but also status of the central auditory system, and its capability to adapt to the new auditory input. In this view, it is not only cochlear implants that may provide evidence of plasticity in the human brain and behaviour, but it is the understanding of plasticity mechanisms that can tell about the ability of the brain to interpret the signal given by the implant, and somehow predict cochlear implantation outcome.

### *3.2.1 The role of sensitive periods in determining cochlear implant outcome*

In rethinking the role of sensitive periods, as well as the role of experience in favouring plasticity in different periods in life as discussed in the previous section, some literature has provided evidence that these characteristics apply to cochlear implants too. For example, electrophysiological techniques have shown that sensitive periods in the development of the central auditory system can impact on auditory recovery following cochlear implantation (Ponton et al., 1996; Sharma et al., 2002; Sharma et al., 2005). Ponton et al. (1996) was the first to demonstrate differential cortical auditory evoked potential (CAEP morphologies) in children and

adults fitted with a cochlear implant compared to hearing controls matched for age. Results showed that the P1 latency (which is considered an index of the auditory pathway maturation) is delayed in the implanted than hearing individuals. Similarly, Sharma et al. (2002) examined P1 latencies in congenitally deaf children who received a cochlear implant and found that those implanted before 3.5 years of age had normal P1 latencies, while children who received their implant after 7 years of age had abnormal latencies. This suggests the existence of a sensitive period for central auditory development that persists up to 3.5 years of age, but no longer. In a further study, Sharma et al. (2005) assessed the time course of central auditory development in early and late congenitally deaf children implanted unilaterally either before 3.5 years of age or after 7 years of age. In addition, two bilaterally implanted children were also tested: one child was fitted with both implants within the sensitive period; the other received the second implant beyond the sensitive period. Overall results showed a different pattern of P1 development for early and late implanted children. While early implanted children reached almost normal P1 latencies within a week of implant use, late implanted children showed atypical response that remains atypical until the 18<sup>th</sup> month follow-up. Interestingly, results from the two bilaterally implanted children speak for different pattern of development for the two ears if sequentially implanted at different ages. The one who received both devices by the end of the sensitive period showed similar CAEP morphology and P1 latency compared to early-implanted children (ipsilateral to the second implanted device), while the one who received the second implant after the end of the sensitive period had a pattern similar to the late-implanted children. This suggests that stimulation of the auditory pathway contralateral to an implant does not preserve the ipsilateral auditory pathway. If this is the case, stimulation from a second implant will reach a



cortex that does not have normal connections within cortical layers, suggesting limited benefits of a second implant if fitted after a sensitive period. While the latter study suggests that sensitive periods constrain the rapidity with which any recovery in central auditory development can be observed, a more definite conclusion about sensitive periods was drawn by Lee et al. (2001), who investigated the role of cross-modal plasticity in determining the possibility to restore hearing through a cochlear implant. In this study, glucose metabolism was adopted as an index of brain activity as measured with PET. A group of prelingually deaf individuals with different ages was tested before implantation to compare their glucose metabolism in the auditory and related cortices with that of hearing controls. Results showed that the degree of hypometabolism before implantation correlated with the hearing abilities achieved after implantation. Interestingly, the extent of the metabolic area was reduced as a function of duration of deafness. In addition, this result was put in relation with the possibility of visual or somatosensory afferents that may have increased as a cause of auditory deafferentation. Therefore, if cross-modal plasticity takes place in the auditory cortex before implantation, no improvement in hearing function will be seen after implantation. In this view, the onset of cross-modal reorganisation signals the end of the sensitive period (around 7 years of age).

These results overall extend on humans the role of sensitive periods in shaping the brain and behaviour, as seen in the previous paragraph where animal studies were described. However, also the notion of experience (in its two forms) can be applied in the case of cochlear implantation, and this is well represented by the studies conducted on the performance of postlingually deafened adults implanted late in life.

### *3.2.2 The role of experience in prelingual and postlingual cochlear implant recipients*

In case of deafness acquired after normal development of the main sensory functions (as well as more complex ones, like language; i.e., typical development during sensitive periods) adult recipients have proven to recover more accurately and rapidly on both speech perception skills (Hinderink et al., 1995) and sound localisation abilities (Nopp et al., 2004) compared to prelingually deaf peers. While we will explore behavioural outcomes for both postlingual and prelingual deaf adult recipients in the following paragraph, here we will point to some neuroimaging studies that have explained the role of experience 'from the inside'. For example, Okazawa et al. (1996) tested the efficacy of cochlear implants in transmitting auditory information to the brain in 5 postlingually and 5 prelingually deafened adults as measured with PET. They delivered both white noise and verbal stimuli through the electrodes of the cochlear implant, and examined the activation of primary auditory and language cortices to observe whether previously different experience with sounds and particularly language could determine a different response in auditory and language areas of prelingual and postlingual deaf recipients. Verbal stimuli caused greater activation of the primary auditory cortex than noise signals in both postlingually deafened individuals and hearing controls. On the contrary, the prelingual group did not show significant activation of the auditory cortex in both stimulation conditions. However, for all groups the language areas (Wernicke's and Broca's areas) were activated during verbal stimulation, but not during noise stimulation. Overall results showed almost normal functions in the primary auditory cortex for the postlingual group, suggesting that while cortical representation of language does not depend upon previous auditory experience, processing in the primary auditory cortex is experience dependent. In addition, postlingually deafened

adults had greater activation of the language areas and a better speech comprehension, which further demonstrates the relationship with auditory experience acquired before deafness and the possibility to restore those abilities after reafferentation of the auditory pathways. In support to these results, similar findings were achieved by Giraud et al. (2001), who studied the functional neuro-anatomy of the auditory system in a small group of postlingually deafened adults. Responses to sounds were obtained even after the first week post-activation in both primary auditory and non-primary auditory cortices, suggesting that postlingually deafened recipients' auditory pathways respond rapidly after implantation. However, it is worth noting that the extent to which the auditory cortex recovers in postlingually deafened adults is correlated to the duration of deafness, as shown by Lee et al. (2003): the more the auditory system remains deprived, the more it will undergo cross-modal reorganisation and therefore be not able to benefit from an implant (as previously seen for prelingually deaf children, Lee et al., 2001).

Finally, in highlighting the effects of training and learning on adult implant recipients, it may be hypothesised that the simple exposure to a new auditory input over time may constitute an implicit form of training (i.e., the environment itself provides sufficient stimuli for the brain to learn how to interpret them). This is partially true and documented by behavioural studies that have investigated the time-course of cochlear implant outcome (Laszig et al., 2004; Grantham et al., 2007). Nonetheless, other studies have shown the benefits of an active training particularly in recovering speech perception skills in the short period (Fu et al., 2005; Fu & Galvin, 2007), but also in sound localisation (Luntz et al., 2004). Fu and Galvin (2005), for example, developed a computer-assisted speech-training programme to provide auditory rehabilitation at home (including vowel and consonant recognition,

word and sentence recognition). Subjects were required to train each day for at least one hour, 5 days a week, and underwent retesting in the labs every two weeks. Overall results showed an improvement for all individuals following 4 weeks of moderate auditory training. As predictable, subjects showed a great variability both in rate and time course of improvement. Note however that in this study both prelingual and postlingual individuals were included, and no correlation between deafness onset and duration of deafness were made, suggesting that such variability could have been caused by these factors. Nonetheless, none of the participants to the training had the same speech scores after 4 weeks as those measured on initial testing (baseline), suggesting that training helps improving speech perception despite individual characteristics.

Despite contrasting results on rate and time course of auditory recovery after implantation, overall results seem to suggest that some speech perception skills are recovered or learned even in the case of implantation in adulthood, adding evidence to the notion that some degree of plasticity can be observed even in the adult brain and behaviour. A still underinvestigated issue remains the recovery of spatial auditory abilities after cochlear implantation, which involves the understanding of whether and how unilaterally and bilaterally implanted recipients can localise sounds surrounding them.

### **3.3 Auditory spatial hearing**

#### *3.3.1 Human sound localisation*

The human auditory system allows us to identify with substantial accuracy where a sound is coming from in space. Unlike the visual system, which is topographically organised (so that any point in the outside world corresponds on a specific point on the retina), the auditory space is tonotopically organised. The basilar membrane responds to specific frequencies and amplitude, but does not directly inform our cognitive system about the position of the sound in space. Therefore, localisation of sounds in space implies the use of cues. The primary auditory cues that normal-hearing listeners experience with two ears are the spectral content, interaural time difference (ITD), and interaural level difference (ILD) of the sound. They are determined by the frequency content of the sound and by the location of the external sound source relative to the listener's head. Spectral information is mainly used for identifying source elevation (Middlebrooks & Green, 1991), while ITD and ILD are used for sound localisation on the horizontal plane (azimuth). The ITD is the difference in arrival time of a sound reaching the two ears, so a sound coming from one side will reach the nearest ear 0.6 ms before reaching the other one. Although it is not a consciously perceivable difference, the auditory system can take advantage of this difference. The ILD is the difference in intensity (sound pressure level) of the sound between ears, so that when the sound reaches the two ears it will be more intense on one side with respect to the other side. Related to this latter cue is the role of the head. The head produces a sound shadow, a barrier that reduces the intensity of the sound. This head shadow effect is particularly strong for high-frequency sound waves, and is proportional to the size of the head (i.e., the head is "large" relative to high-frequency sounds and "small"

relative to low-frequency sounds). More generally, while ILD is a particularly useful cue for high-frequency sounds, ITD is more useful for low-frequency sounds. ITD and ILD are useful cues for the left-right angle of the sounds presented on the azimuthal plane, but cannot help when trying to determine the elevation of the sound-source (i.e, the vertical direction, as ears are placed symmetrically on both sides of the head) and the front-back direction. To determine the direction of these sound-sources, the pinna comes as a useful tool, as its particular shape reflects and diffracts sounds coming from different directions. Spectral cues enable listeners to determine elevation and front-back direction and are available monaurally (i.e., to one ear).

A classical way that has been adopted to investigate monaural hearing has been to plug one ear in animal models (King et al., 2000) or humans (Oldfield & Parker, 1986; Butler, 1986). However, it has been claimed that this method has some limits (Wightman & Kistler, 1997): first, complete deprivation of one ear is difficult to achieve, leaving the question open of which residual frequencies were available to the ear; second, plugging one ear does not completely suppress ITD and ILD cues; it only enlarges ILD while shrinking ITD. Van Wanrooij & Van Opstal (2004) examined the role of head shadow and pinna shape in monaurally deafened adults to see to what extent they may rely on intensity and spectral cues when localising sounds. Participants were asked to perform three different paradigms to test for different auditory and non-auditory cues in monaural sound localisation. In the “intensity paradigm”, participants were presented with auditory stimuli at different intensities and in different spatial locations in the frontal hemifield. In the “spectral paradigm” participants had to localise sounds presented in different spatial positions and at varying intensities under perturbed spectral cues (i.e., by putting wax molds in

the pinna of their intact ear). In the third paradigm, participants were trained to localise a single auditory stimulus with fixed intensity, and they had to localise it with or without visual feedback. Results showed that all monaural listeners relied on both head shadow effect and spectral cues to localise sounds on the azimuth and for elevation localisation. This result contrasts with the one obtained by Wightman and Kistler (1997), who found no monaural localisation ability for their participants. This difference in results may be attributed to the long experience with monaural hearing achieved by the unilaterally deaf participants compared to the short-term monaurally deprived controls in the other study. In accord with the notion that experience may have played a significant role, when unilaterally deafened participants were asked to localise with wax molds in the pinna of their intact ear, they were no longer able to localise, also suggesting that complex spectral cues need time to be learned. On the contrary, intensity cues can be easily learned for a variety of sounds, thus allowing unilaterally deaf individuals to adopt this strategy to localise sounds.

### *3.3.2 Sound localisation after cochlear implantation*

Bilateral implantation is somehow a new clinical procedure that has attracted attention for not more than ten years, despite the clear benefit that may derive from binaural hearing, particularly for allowing the localisation of sounds in the environment and – as a result - in discriminating speech in noisy contexts. When considering several of the studies conducted to investigate sound localisation in bilateral cochlear recipients, two commonly reported results seem to emerge:

1. bilateral implantation allows great recovery in spatial hearing (Tyler et al., 2002; Van Hoesel & Tyler, 2003; Nopp et al., 2004; Schleich et al., 2004; Schoen et al., 2005);

2. the use of two devices compared to one is significantly better for localisation performance (Van Hoesel et al., 2002; Laszig et al., 2004; Grantham et al., 2007).

However, several important issues remain underinvestigated or present contrasting results. One of these concerns the time course of spatial recovery after implantation.

#### The time course of spatial hearing recovery after cochlear implantation

On the one side, most studies have adopted a transversal approach, by testing different recipients at different intervals from activation (Nopp et al., 2004; Litovsky et al., 2004; Schleich et al., 2004), lacking to investigate the exact time course of spatial recovery within each single recipient, which would be possible by adopting a longitudinal approach. Since a commonly met problem in testing groups of recipients is the great variability determined by clinical factors (e.g., deafness onset, years of auditory deprivation, etiology of deafness, etc.), any result that does not take in consideration these factors may be taken with caution. By testing the same individuals at different follow-up intervals, on the contrary, the time course of recovery can be observed at net of their individual differences. On the other side, recipients have commonly been tested after at least 3 months from activation (Nopp et al., 2004; Verschuur et al., 2005; Grantham et al., 2007), leaving unanswered the question of when the recipients start recovering sound localisation abilities. To our knowledge, only a few studies have made follow-up investigations (Grantham et al., 2007), and no study has tested recipients before 1 month from activation. Grantham et al. (2007) tested 22 postlingually deafened adults at 5 months after activation and 12 individuals at 15-month follow-up. Recipients were tested on a localisation task



comprising 43 loudspeakers spanning an arc from  $-90^{\circ}$  to  $90^{\circ}$ . Out of 43 loudspeakers, only 17 were actually active for sound presentation of the two stimuli used (a noise burst and a speech stimulus). Participants had to call out the number of the loudspeaker from where they considered the sound to have originated, not being aware that only some of the loudspeakers were active. Overall results showed that CI recipients could localise well above chance with their two implants active. Interestingly, there was no longitudinal effect, namely participants did not show any improvement between performance measured at 5 months post-implant activation and 15-month follow-up. This result suggests that asymptote performance may be reached around the fifth month after activation. However, as previously pointed out when discussing individual variability, it is worth noting that in Grantham's et al. (2007) study, two out of 12 recipients were found to dramatically improve over 10 months, suggesting that some individuals may develop binaural listening more slowly than other recipients. Also, since recipients were tested after 5-month experience with their implants, it remains to be ascertained whether their localisation abilities might have reached asymptote performance before then. In support to the view that asymptote performance in localisation abilities may occur around 5 months after activation, a study by Litovsky et al. (2006) measured sound localisation abilities in 17 adults, and found that their performance after 3 months with bilateral CIs was only slightly above chance, suggesting that more time is needed for the brain to adapt to a new auditory input and particularly to be able to re-weight binaural cues.

Nopp et al. (2004), on the contrary, tested 19 postlingually deafened adults and one prelingual deaf with at least 1-month experience with their second implant, but did not re-test them at different follow-up intervals. In addition, recipients with 1-month experience were averaged together with other recipients with different

experience with their implant at testing (range between 1 month and 6 years), leaving the question open of whether any benefit observed in the ability to localise sounds is due to the implant itself or to the different experience in implant use. Nonetheless, this study is of particular interest because it raises an issue of concern: performance of prelingual deaf individuals. In their study, Nopp et al. (2004) recruited a 17 years old congenital deaf who was sequentially implanted late in life (at 11 years in his first implanted ear). While all postlingually deaf participants were found to perform above chance when using two devices, he was the only one who performed at chance, leading authors to conclude that early-deafened individuals who receive an implant in adulthood may not benefit of bilateral implantation. Although this issue raises intriguing questions about the role of previously acquired auditory experience in determining the outcome of cochlear implantation, studies that included prelingually deafened adults in sound localisation tasks (for example, Litovsky et al., 2004) did not consider separately the performance of these recipients, averaging results across all participants, regardless of deafness onset. Also, since the common thought is that prelingually deafened adults may not benefit from cochlear implantation (be it unilateral or bilateral), some studies have purposely selected postlingually deafened adults to test their sound localisation abilities (Verschuur et al., 2005; Grantham et al., 2007). However, while this applies to sound localisation tasks, some evaluation of cochlear implant benefits for prelingually deafened recipients, particularly for speech, have been undertaken. In addition, it should be noted that investigations on children implanted at different ages (Manrique et al., 2004; Harrison et al., 2005; Sharma et al., 2005) have suggested that children implanted early in life may develop typical behaviour for both speech perception and production. On the contrary, congenital deaf children or with early deafness onset

who do not receive an implant within a critical period (3 years) may not be able to develop typical behaviours (as seen in previous paragraphs). These results may partially explain the lack of interest in late-implanted adults with early deafness onset. Nonetheless, a few studies conducted between the 1980s and 1990s have precisely investigated this aspect selectively for language outcome (Clark et al., 1987; Skinner et al., 1992; Waltzman et al., 1992). Overall studies suggest poor performance in speech perception skills, but these early studies used processing strategies that have now improved, suggesting that new generations of cochlear implants may aid more auditory recovery in this population. For example, Hinderink et al. (1995) evaluated speech discrimination performance in a group of postlingually deafened adults and in a group of prelingually deafened adults using the same type of implant (either single-channel or multichannel) at various intervals during a 2-year follow-up. Results showed that the average performance improved significantly for all four groups of recipients, particularly between 3 and 6 months, but not after the 6-month follow-up. However, postlingually deafened recipients performed better than prelingually deafened recipients particularly in achieving greater and prolonged improvement over time (but note that the performance of the prelingually deafened group was on average above chance). In addition, postlingually deafened recipients were found to have better performance than prelingually deaf on an audio-visual test where lipreading skills are evaluated (using the Continuous Discourse Tracking) than visual only performance. In a more recent study, Teoh et al. (2004) examined speech understanding in late-implanted, prelingually deaf adult recipients over 12-month follow-up. Overall results demonstrated that after 3 months, significant improvement was observed in all participants, although their scores were below those of postlingually deafened adults.

### Sound localisation abilities with one and two ears

Another question of concern when considering bilateral implantation is the interplay between monaural and binaural sound localisation abilities during binaural spatial recovery. In order to investigate the benefits of bilateral implantation, most studies have tested recipients on the same task in two listening conditions: monaural and binaural (Van Hoesel & Tyler, 2003; Nopp et al., 2004; Schleich et al., 2004; Verschuur, 2005; Schoen et al., 2005), and compared the two performances. However, particularly when the two implants are implanted sequentially, it remains unclear to what extent any previously developed plasticity to monaural hearing might interact with the new inputs arising from binaural implantation. For instance, the experience a recipient might have had with a single implant before bilateral implantation may influence results on both unilateral and bilateral performance (particularly in the short period), in that the latter may be worse than unilateral performance because previously acquired monaural cues need to reweight the binaural input.

A way to investigate this issue without the confound of sequential implantation is to look at simultaneous implantation. Although it is still a rare clinical practice, some studies have investigated bilateral sound localisation in this small population, giving the opportunity to observe the ability of the two ears to adjust simultaneously to the new auditory input over the same time period. In addition, this condition allows observing monaural hearing abilities as arising from same bilateral experience, and any result from this is comparable to those studies that plugged one ear to observe monaural listening in hearing individuals (Wightman & Kistler, 1997).

In an initial study by Van Hoesel et al. (2002) 5 postlingually deafened adults fitted simultaneously with their implants were tested on a sound localisation task in

which 8 loudspeakers spanning the frontal horizontal arc were present. Stimuli consisted of a sequence of four pink-noise bursts, and participants were asked to indicate which loudspeaker had sounded. Note that, although participants were asked to keep their head in a straightforward position, loudspeakers were not prevented from being seen, suggesting that results from this type of set-up have to include the possibility that subjects were partially relying on their visual abilities as well. Results showed that all subjects had clear benefit when performing with two ears rather than with a single ear. Nonetheless, when visually exploring monaural performance for each recipient, it seems that for two participants, monaural listening - at least with one of the two ears - was similar to bilateral hearing, suggesting that some monaural listening abilities are present after bilateral implantation. This variability in monaural performance may have depended upon a factor: although all participants were tested after 12 months experience with the two implants, deafness onset for 3 participants out of 5 was asymmetrical (hearing loss in one ear preceded of some time the other ear), suggesting that in considering monaural abilities after simultaneous bilateral implantation, also previous extent of auditory deprivation should be included. This result also applies to Litovsky et al. (2004), who tested 17 adults, 3 of which had prelingual deafness onset. The participants not only had variable deafness onset, but also had asymmetrical auditory deprivation experience per ear.

Grantham et al. (2007) tested 22 postlingually deafened adults on a localisation task, 20 of which were simultaneously implanted. Deafness onset for these recipients was variable (ranging between 1 and 16 years), but all had symmetrical deafness onset for both ears, and all were tested around 5 months after activation. Of the 18 subjects tested with their single implants, 10 had a better

performance with their right ear in both speech and noise stimuli conditions, 6 had a better performance with their left ear in both conditions, and 2 had asymmetrical ear performance depending on stimuli condition. In addition, in addressing monaural hearing, also the two subjects who were sequentially implanted were included. Overall, performance with either left or right ear was not significantly different from chance. However, when considering only performance with the single ear with higher score (computed as the difference between actual sound source and reported sound position), group performance was found to be on average significantly better than chance, suggesting that some individuals with bilateral implant can localise with their better single ear. Interestingly, the two best unilateral performers were the ones who received their implants sequentially, and their better ear performance corresponded to the first implanted ear, suggesting that their ability to use monaural cues may have depended upon previously more extended experience with the single ear. Consequently, this also suggests that simultaneously implanted recipients adjust to binaural cues in a symmetrical way. This is further evidenced by the strong bias showed by the simultaneously implanted recipients when listening monaurally, namely by reporting the sounds as all coming from the side of the active device. As suggested by Grantham et al. (2007), this pattern of results may document that under temporal monaural hearing (after binaural hearing is experienced) the tendency is to hear sounds as originating from the side of the stimulated auditory nerve.

Results of the previous studies show that considering monaural hearing abilities after simultaneous bilateral implantation may be a good way to test performance with a single ear. However, several individual factors should be

controlled before this type of testing, such as deafness onset of each ear and experience with bilateral hearing.

To gather more information about monaural hearing and the possible cues achieved with that particular hearing condition, the most efficient way could be to consider sound localisation abilities in single CI recipients. As to our knowledge, only a few studies have investigated sound localisation abilities in this population. A first evaluation comes from a study by Luntz et al. (2002), who tested 3 adults and a child on a localisation task with 5 loudspeakers positioned on the horizontal plane in front of them. Aim of this study was to investigate the effects of training on sound localisation performance, by re-testing periodically each subject on the same task. Results from this study and also from a second one by Luntz et al. (2005) showed that after initial poor performance, an improvement in sound localisation abilities was found for all participants (on average after 6 weeks of training).

Buhagiar et al. (2004) tested 18 postlingually deafened adults on a localisation task with different stimuli. All participants had at least one-year experience with their implant and had not more than 10 years auditory deprivation prior to implantation. All participants performed at chance level, leading the authors to conclude that monaural CI recipients do not benefit of their single implant for localising sounds in space. A similar conclusion was also reached by Tyler et al. (2006), who found that unilateral CI recipients generally perform worse than bilateral CI recipients.

Mixed results come from a study by Grantham et al. (2007), who tested 6 postlingually deafened adults implanted monaurally, with a one-year experience with their implant. Authors found that 3 out of 6 recipients could perform at a better than chance level. Nonetheless, overall results from these studies suggest that monaural

implantation does not offer great sound localisation improvement, and the few data of better than chance performance seem to be constraint to controlled situations, be it preservation of frequency cues (Grantham et al., 2007) or training on pure tones of fixed intensity (Luntz et al., 2002; 2005).

#### Auditory cues in cochlear implant recipients

Finally, a last issue that needs to be discussed is how bilateral and unilateral CI recipients localise sounds, namely, what type of cues they use. In addressing the question of which auditory cues are used after bilateral implantation, several authors have investigated the role of ILD and ITD underlying sound localisation abilities (Van Hoesel et al., 2002; Schoen et al., 2005; Grantham et al., 2007; Grantham et al., 2008). Although ILD is commonly acknowledged to be the primary auditory cue underlying horizontal plane localisation for most bilateral cochlear implant recipients (Van Hoesel et al., 2003; Van Hoesel, 2004; Verschuur et al., 2005; Grantham et al., 2007), some studies have indicated that subjects can sometimes make use of the ITD cue (Van Hoesel, 2004; Schoen et al., 2005). However, note that most of the studies that have investigated these cues have used different stimulus delivery, which are far from reproducing natural settings. The first type delivers electrical pulse trains directly to the electrodes of the implant, therefore assessing both ITD and ILD thresholds (see Van Hoesel & Tyler, 2003). The second method delivers electrical signals to the speech processor of the implant, which means that the signal bypasses the processor microphone and the compression circuits (AGC), resulting in a higher ILD threshold (Laback et al., 2004; Senn et al., 2005). The third method consists in delivering acoustic signals over headphones, which is the most 'everyday life condition' compared to the other two methods, because the signal has to go



through initial compression and speech transduction before reaching the electrodes. Grantham et al. (2008), for example, assessed ITD and ILD sensitivity with white noise presented over the headphones to reproduce the most everyday-life hearing situation. In addition, since Grantham et al. (2008) tested the same recipients who performed the sound localisation task (2007) previously presented, results were put in relationship to the latter performance. Results for ITD and ILD sensitivity confirmed previous studies, in that subjects were found to have poor ITD thresholds. In seeking for correlations with the sensitivity task and the localisation task, results showed no correlation between ITD thresholds and localisation error scores, suggesting that ITD cues cannot contribute to the ability of localising sounds. Nonetheless, since ITD cues may contribute to localising sounds in peripheral azimuthal regions (as suggested by Van Hoesel (2004), ILD cues become more ambiguous in the periphery), Grantham et al. (2008) correlated ITD thresholds with the most peripheral stimuli. However, even in this case, no significant correlation was found. On the contrary, ILD cues were found to significantly correlate particularly with the positions closer to midline (i.e., the positions mostly in front of the participant). Overall results suggest that ILD cues entirely dominate sound localisation performance in bilaterally implanted recipients. An interesting finding comes from Schoen et al. (2005), who investigated sound localisation in 12 postlingual deaf recipients. Participants were seated in the centre of a semicircle with 7 loudspeakers positioned between  $-90^\circ$  and  $90^\circ$ , and were asked to indicate the loudspeaker of the perceived direction of stimulus presentation. In a first experiment, the general abilities to localise sound sources were investigated by presenting noise bursts at different sound levels and with two signals of different spectral shape. To assess sensitivity to binaural cues (ILD and ITD), two other experiments were conducted:

ILD was investigated by performing the localisation test with the two speech processors unbalanced while signal level was fixed; ITD was investigated by measuring lateralisation as a function of the time difference between two signals, each directed to one of the subject's speech processor microphones by way of headphones. Although overall results showed that bilateral cochlear implant recipients mainly adopt interaural level differences to localise sounds, a correlation between lateralization and localisation test was found, suggesting that the more a subject can lateralise sounds on the basis of ITD, the more he/she can localise sounds.

### **3.4 Aim of Part II of the thesis**

The second part of the thesis addresses the role of experience in determining plasticity in the adult. To this aim, we conducted two sound localisation experiments on both bilateral and unilateral implanted recipients who differed in deafness onset and experience with auditory cues. In the first experiment, we compared the performance of two bilaterally implanted recipients on a sound localisation task. The two participants were comparable for age and experience with both implants, but had achieved different experience with auditory cues, in that one became deaf early in life, the other in adulthood. In this experiment we assessed the role of auditory cues achieved before deafness onset in determining the time course of recovery after bilateral implantation.

The second experiment investigated sound localisation abilities in two groups of unilaterally implanted adults who were both implanted in adulthood but differed in

deafness onset (prelingual vs. postlingual deafness onset). Here we investigated both the role of experience with auditory cues prior to deafness onset, and the effects of training with the new auditory input in determining some localisation improvement.

## CHAPTER 4

### Hearing again with two ears: recovery of spatial hearing after bilateral cochlear implantation

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#### **4.1 Abstract**

Bilateral cochlear implants (CI) offer a unique opportunity for the study of spatial hearing plasticity in humans. Here we studied the recovery of spatial hearing in two sequential bilateral CI recipients, adopting a longitudinal approach. Each recipient was tested in a sound-source identification task shortly after bilateral activation and at 1, 6, and 12 months follow-up. The results show fast recovery (1 month from CI activation) in the recipient who had substantial experience with auditory cues in adulthood. By contrast, the bilateral CI recipient who developed profound deafness in childhood, regained spatial hearing abilities only 12 months after CI activation. These findings provide the first direct evidence that recovery of auditory spatial abilities in bilateral CI recipients can occur shortly after activation of the two devices. In addition, they suggest that previous auditory experience can constrain the time course of this recovery.

## 4.2 Introduction

Functional and neural reorganization after sensory deafferentation is a widely documented phenomenon (for recent reviews see Bavelier & Neville, 2002; Pascual-Leone, Amedi, Fregni, & Merabet, 2005). By contrast, much less is known about plasticity following sensory reafferentation (e.g., Giraud, Truy, & Frackowiak, 2001). A unique opportunity for the study of sensory reafferentation is offered by cochlear implants (CI). CIs are neuroprosthetic devices routinely adopted in the clinical practice that restore functional hearing through direct electrical stimulation of the auditory nerve. Although the vast majority of CIs are implanted monaurally, an increasing number of recipients now receive bilateral CIs, thus giving the opportunity to examine the recovery of binaural spatial hearing in humans.

Several studies have documented a substantial recovery of spatial hearing in bilateral CI users (e.g., Neuman, Haravon, Sislian, & Waltzman, 2007; Schoen, Mueller, Helms, & Nopp, 2005; Van Hoesel & Tyler, 2003). However, a number of important issues remain to be addressed. First, the earliest recovery of spatial hearing in bilateral CI recipients has been documented to appear 3 months after implant activation (Nopp, Schleich, & O’Hease, 2004; Verschuur, Lutman, Ramsden, Greenham, & O’Driscoll, 2005), suggesting that a relatively long period of adaptation to binaural hearing is necessary before spatial hearing abilities can be restored. These previous studies, however, adopted a transversal approach (i.e., different recipients tested at different intervals from activation), lacking to investigate the exact time course of binaural hearing recovery within each single recipient. Second, the role of previous auditory experience in modulating recovery of spatial hearing is still an open issue. Although some investigators have proposed that the rapidity and efficacy of recovery may be closely linked to the amount of auditory experience

acquired by the recipient before deafness-onset (Grantham, Ashmead, Ricketts, Labadie, & Haynes, 2007; Litovsky et al., 2004), to date there has been no systematic study addressing the role of previous auditory experience on spatial hearing recovery. Finally, a third unexplored issue concerns the interplay between monaural and binaural sound localisation abilities during binaural recovery. Particularly when the two CIs are implanted sequentially (i.e., the second CI is implanted after several months or years of experience with the first monaural implant; e.g., Nopp et al., 2004; Verschuur et al., 2005), it remains unclear to what extent any previously developed plasticity to monaural hearing might interact with the new inputs arising from binaural implantation.

In the current study, we had the opportunity to test two sequential bilateral CI recipients (S.P. and P.A.), with comparable characteristics with respect to CI surgery (age at first and second implant and years of experience using the first monaural implant), but substantially different clinical histories with respect to their exposure to auditory cues. S.P. became deaf late in life when aged 39, whereas P.A. became deaf during childhood when aged 4. Both recipients were tested in a sound-source identification task, with their first CI active (monaural testing condition) or with both CIs active (binaural testing condition). S.P. and P.A. were tested on the very first day of the second CI activation, and in several follow-up sessions within the first 12 months from activation. The longitudinal approach adopted here for the first time allowed the assessment of both the exact time course of binaural recovery after bilateral CI and the potential interplay between monaural and binaural hearing strategies.

### 4.3 Methods

#### *Participants*

S.P. is a 46-year-old man, who became progressively deaf at around 30 years of age due to otosclerosis. He wore acoustic external prosthesis until he became profoundly deaf (>90 dB) when aged 39. He received his first implant in the right ear when aged 40, and the second implant in the left ear when aged 46 (MED-EL Pulsar with FSP strategy in both ears).

P.A. became progressively deaf at around 4 years of age for unknown causes. He used acoustic prosthesis from the age of 6. However, when tested with the prosthesis before the first CI surgery, his auditory abilities for verbal materials were rather poor even at maximal stimulation intensities. He received his first implant in the left ear when aged 36, and the second implant in the right ear when aged 40 (Cochlear Freedom Contour Advance with ACE strategy in the left ear, Cochlear Nucleus 24 Contour with ACE strategy in the right ear).

The bilateral audiogram threshold for case P.A. was 25 dB HL for all frequencies between 250 Hz and 4 kHz, when measured 1 month after bilateral activation and 30 dB HL when measured 12 months from activation. The bilateral audiogram threshold for case S.P. for the same frequency range was 35 dB HL when measured 1 month after bilateral activation.

#### *Apparatus, stimuli and procedure*

The two recipients performed the sound-source identification test in a silent room. The set-up consisted of eight loudspeakers, positioned in a circle (radius 60 cm) around the participant who sat in the centre. With respect to the straight-ahead



position ( $0^\circ$ ), loudspeakers were positioned at  $+30^\circ$ ,  $+60^\circ$ ,  $+120^\circ$  and  $+150^\circ$  on the right side of the participant, and at  $-30^\circ$ ,  $-60^\circ$ ,  $-120^\circ$  and  $-150^\circ$  on the left side of the participant. Stimuli were generated using Matlab and consisted of a sequence of four 20ms noise bursts, separated by 80ms intervals (overall stimulus duration was 400ms). Each stimulus was randomly delivered six times from each loudspeaker, in three separated blocks (48 trials per block; 144 fully randomised presentations in total). We also randomly varied the intensity level of each speaker ( $\pm 4$  dB) so that minimal intensity differences between speakers could not aid source identification. In addition, an acoustically transparent close weave cloth, specifically designed for mounting on loudspeaker grilles when cut smaller than the complete sheet used here (Model: KS50E, Maplin, UK), covered all frontal loudspeakers to avoid visual cues to localisation.

Participants were asked to verbally identify the loudspeaker from which they considered the sound to have originated. To provide their answer, participants were given a diagram with the representation of all possible loudspeakers' spatial positions. The experimenter arbitrarily timed stimulus presentation by pressing a button on the computer keyboard (approximately 1 stimulus every 3 s). The two recipients performed the sound-source identification test, both monaurally and binaurally, in 4 separate experimental sessions: immediately after bilateral activation, and at 1, 6 and 12 months follow-up. Note that monaural testing was always performed with the first implanted device for each recipient (i.e., right CI for S.P. and left CI for P.A.). Within each session the order of monaural and binaural blocks was counterbalanced and the participant rested between blocks. No repeats were allowed and no feedback was given. Each session took approximately 45 min to complete.

#### 4.4 Results

##### *Recipient S.P.*

The performance of S.P. (late deafness-onset) is illustrated in Fig. 1. When S.P. was tested shortly after activation of the second implant, he performed worse with binaural than monaural hearing. Mean absolute error in this first session was  $57^\circ$  (S.E. = 7) with monaural hearing, and  $90^\circ$  (S.E. = 7) with binaural hearing ( $t(116) = 3.3$ ,  $p < 0.001$ ; chance performance with this set-up was  $90^\circ$  error). On most monaural trials, S.P. was able to discriminate the location of stimuli in azimuth (net azimuth error computed by collapsing front and back locations was  $24^\circ$ , S.E. = 4). This value is lower than the minimal spatial separation between speakers (i.e.,  $30^\circ$ ).

Strikingly, S.P.'s performance with binaural hearing improved substantially already in the first follow-up session, 1 month after activation of the second implant (see Fig. 2a). Mean absolute error in the binaural testing condition was reduced to  $27^\circ$  (S.E. = 3;  $t(124) = 8.9$ ,  $p < 0.0001$ , with respect to binaural performance in the activation session). By contrast, his monaural localisation ability dropped to  $78^\circ$  overall (S.E. = 5) with respect to the activation session ( $t(94) = 2.3$ ,  $p = 0.02$ ). S.P. localised almost all sounds to the right hemispace (i.e., the side of the first monaural implant; net azimuth error was  $51^\circ$ , S.E. = 4; see monaural hearing bubble plot at 1month in Fig. 1).

This improved performance with binaural over monaural hearing was confirmed also at the 6 and 12 months follow-up sessions. In fact, S.P.'s binaural localisation improved even further in the 6 months follow-up (mean absolute error =  $20^\circ$ , S.E. = 3;  $t(286) = 2.0$ ,  $p = 0.05$ ; net azimuth error was  $8^\circ$ , S.E. = 1), and in the 12 months follow-up (mean absolute error =  $14^\circ$ , S.E. = 2;  $t(277) = 1.9$ ,  $p = 0.03$ ,

one-tail; net azimuth error was 7°, S.E. = 1). By contrast, monaural performance remained stable in both sessions (6 months: mean absolute error = 79°, S.E. = 4; 12 months: mean absolute error = 79°, S.E. = 4).

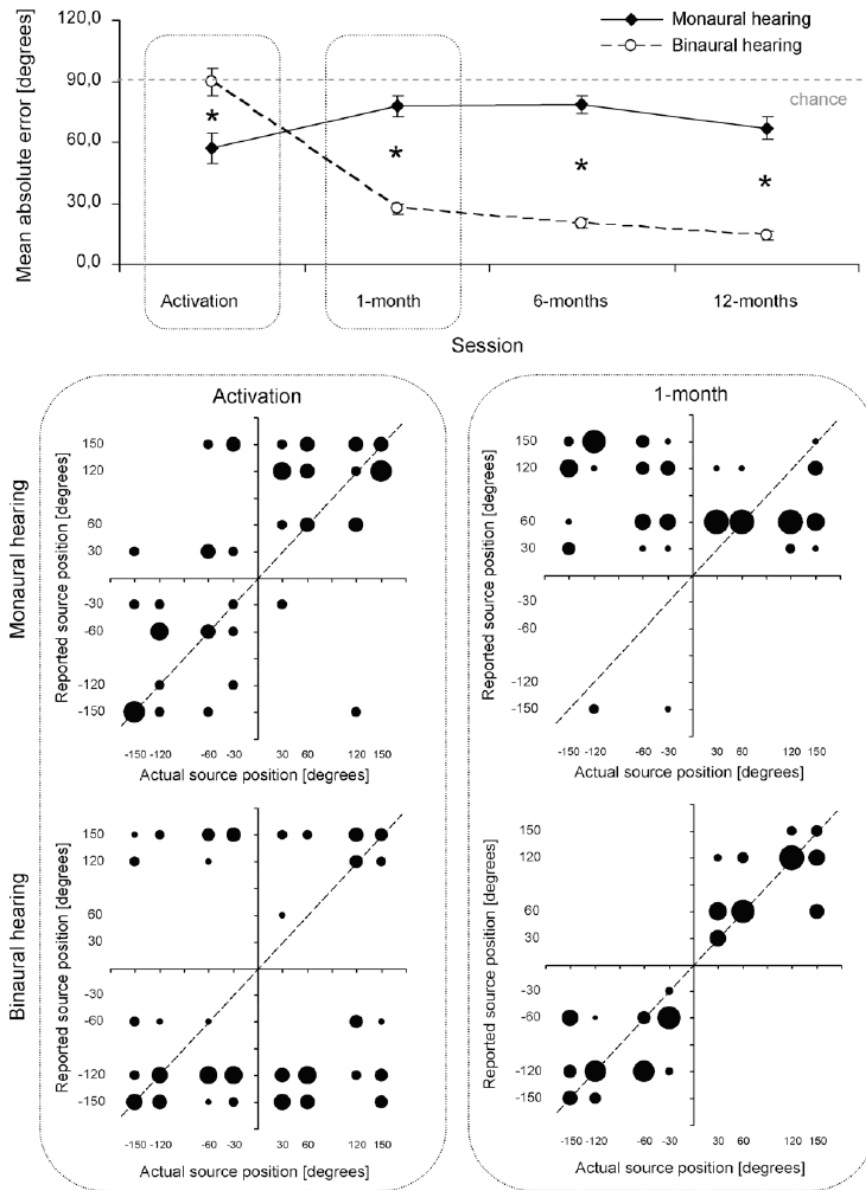
*Recipient P.A.*

The performance of P.A. (early deafness-onset) is illustrated in Fig. 2. When P.A. was tested shortly after activation of the second implant, he showed comparable performance with both binaural and monaural hearing. Mean absolute error in the first session was 58° (S.E. = 4) for the monaural testing condition, and 65° (S.E. = 4) for the binaural testing condition ( $t(283) = 1.2, p = 0.2$ ); significantly below chance for both monaural ( $t(143) = 8.1, p < 0.0001$ ) and binaural hearing ( $t(143) = 5.7, p < 0.0001$ ). His error in azimuth was 32° (S.E. = 3) with both hearing conditions.

Critically, however, no modulation of performance emerged for P.A. in the 1 and 6 months follow-up sessions. Binaural hearing abilities remained stable in these two follow-up sessions (1 month: mean absolute error = 56°, S.E. = 5; 6 months: mean absolute error = 58°, S.E. = 4). Similarly, monaural hearing abilities were approximately identical across sessions (1 month: mean absolute error=59°, S.E. = 5; 6 months: mean absolute error = 60°, S.E. = 5).

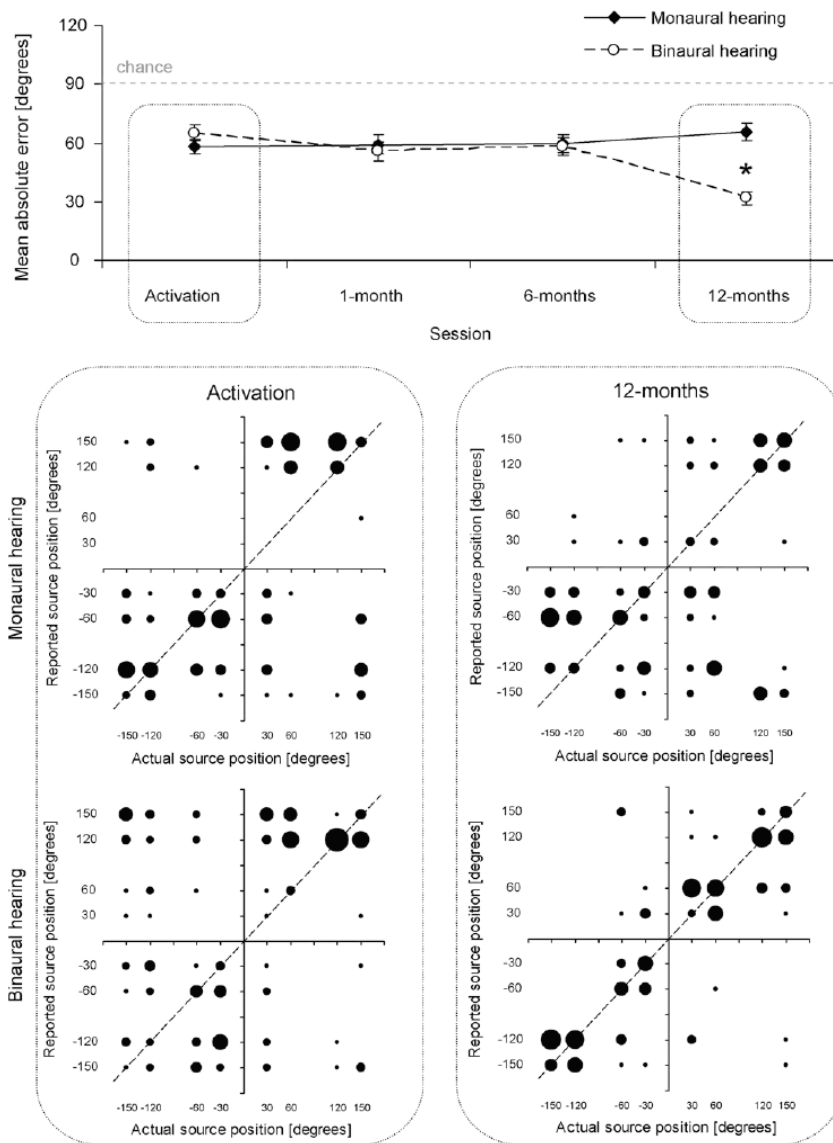
A significant change in binaural abilities emerged instead 12 months after activation. Mean absolute error in the binaural condition improved to 32° (S.E. = 3;  $t(143) = 5.01, p < 0.0001$ ). Note that this is comparable to the absolute mean error showed by recipient S.P. in the 1 month follow-up session.

Figure 1



**Fig. 1** Mean absolute error in the four testing sessions for recipient S.P. Error bars indicate the standard error of the mean; asterisks indicate significant differences between monaural and binaural performance. Bubble plots illustrate distribution of responses during monaural and binaural testing, in the day of bilateral activation and in the 1-month follow-up (i.e., the session in which the first improvement of binaural spatial hearing emerged for this recipient).

Figure 2



**Fig. 2** Mean absolute error in the four testing sessions for recipient P.A. Error bars indicate the standard error of the mean; asterisks indicate significant differences between monaural and binaural performance. Bubble plots illustrate distribution of responses during monaural and binaural testing, in the day of bilateral activation and in the 12-month follow-up (i.e., the session in which the first improvement of binaural spatial hearing emerged for this recipient).

## 4.5 Discussion

The current study provides the first longitudinal investigation of spatial hearing recovery in bilateral CI recipients, examined here from the moment of bilateral implant activation and in several follow-up sessions within the first 12 months of regained binaural hearing. Our findings demonstrate that recovery of spatial hearing can emerge already 1 month from bilateral CI activation, suggesting the possibility of fast plastic changes in spatial hearing after bilateral reafferentation of the auditory pathways. This is clearly illustrated by the performance of recipient S.P., who acquired profound deafness in adulthood. Despite a poor bilateral performance immediately after activation, S.P. shows substantial recovery of spatial hearing abilities with two active implants already in the first follow-up session (1 month), and improved even further at the 6 and 12 months follow-up. Intriguingly, this fast recovery of binaural spatial hearing appears to have occurred at the expenses of the preexisting monaural abilities, suggesting a possible interplay between monaural and binaural sound localisation strategies in sequential CIs.

Fast plastic changes of spatial hearing have been previously documented in individuals with normal hearing abilities whose spectral-shape cues were perturbed using binaural (Hofman, Van Riswick, & Van Opstal, 1998) or monaural molds on the participant's pinnae (Van Wanrooij & Van Opstal, 2005). Listeners tested with these paradigms relearned sound localisation within a few weeks from ear molding. In addition, immediately after removal of the molds, all participants regained a level of sound localisation accuracy comparable to that recorded at the beginning of the experiment several weeks earlier (Hofman et al., 1998). Similarly, in the classic studies by Knudsen and colleagues (1984), young barn owls that were monaurally occluded after having developed adult binaural cues, relearned to localize normally

with the two ears after the monaural earplug removal. This suggests that recovery of well-acquired mappings between auditory cues and space can occur very fast even after substantial intervening changes affecting auditory perception, such as ear molding (Van Wanrooij & Van Opstal, 2005), monaural ear occlusion (Knudsen, Knudsen, & Esterly, 1984) or a period of profound deafness as reported here.

In agreement with this notion that fast recovery of spatial hearing may be closely dependent upon well-acquired experience with auditory cues, the current study reveals that recovery of auditory spatial abilities is substantially slower when previous experience with auditory cues has been limited. This is clearly illustrated by the performance of recipient P.A., who acquired profound deafness in childhood. Unlike recipient S.P., recipient P.A. did not show an improvement of binaural abilities until 12 months from bilateral CI activation. The striking difference between time of recovery of our two bilateral CI recipients clearly suggests that fast recovery may be constrained by the recipient's previous experience with auditory localisation cues. Intriguingly, the current findings indicate that despite sound localisation maturity was likely impaired (if not entirely compromised) in P.A., it did not prevent progressive relearning of systematic mappings between auditory cues and space. Thus, despite complex aspects of hearing, such as sound localisation, achieve maturity during the years of adolescence (Moore, 2002), the brain appears nonetheless capable of learning how to interpret auditory cues in adulthood as well (see also Hofman et al., 1998; King et al., 2000, 2001).

Which auditory cues could have supported the recovery of spatial hearing abilities of our two recipients in the binaural hearing condition? Monaural spectral cues from each of the two ears unlikely account for the improved localisation performance, because these cues minimally contribute to localisation in azimuth in

normal hearing individuals (e.g., Van Wanrooij & Van Opstal, 2004, 2005) and are substantially limited with multi-electrode implants. Instead, we cannot exclude that monaural cues related to the head-shadow effect (HSE; systematic changes in the proximal stimulus intensity at each ear as a function of the azimuthal location of the sound-source; Van Wanrooij & Van Opstal, 2004) could have played some role, due to the limited range of sound intensity variations in our study ( $\pm 4$  dB, while HSE variations are in the range of  $\pm 10$  dB). However, a number of systematic studies addressing specifically the contribution of different auditory cues in bilateral recipients suggest that binaural cues may indeed return available when two devices are active. In particular, several recent studies point to a key role of interaural level differences (instead of interaural time differences) in regained localisation abilities of bilateral CI recipients (Grantham, Ashmead, Ricketts, Haynes, & Labadie, 2008; Seeber & Fastl, 2007).

In conclusion, the results of the present study demonstrate that recovery of spatial hearing with bilateral CI can emerge in the shortest period after reafferentation, at least for the recipient who had the most extensive experience with auditory cues. Intriguingly, this binaural recovery in S.P. appears to have occurred at the expenses of his monaural abilities, as if 1 month of binaural hearing overcame the experience acquired in 5 years of monaural hearing. This fast recovery is compatible with reprogramming of the auditory spatial mappings that S.P. acquired before deafness-onset. By contrast, the longer time-course of recovery of case P.A. could reflect the gradual process of learning auditory spatial mappings which were not fully acquired before deafness onset.



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## CHAPTER 5

# Spatial hearing with a single cochlear implant in late-implanted adults

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## **5.1 Abstract**

We assessed sound localisation abilities of late-implanted adults fitted with a single cochlear implant (CI) and examined whether these abilities are affected by the duration of implant use. Ten prelingually and four postlingually deafened adults who received a unilateral CI were tested in a sound-source identification task. Above chance performance was observed in those prelingual CI recipients who had worn their implant for longer time (9 years on average), revealing some monaural sound localisation abilities in this population but only after extensive CI use. On the contrary, the four postlingual recipients performed equal or better with respect to the best prelingual participants despite shorter experience with the monaural implant (11 months on average). Our findings reveal that some sound localisation ability can emerge in prelingually deafened adults fitted with a single implant, at least in a controlled laboratory setting. This ability, however, appears to emerge only after several years of CI use. Furthermore, the results of four postlingually deafened adults suggest that early experience with auditory cues may result in more rapid acquisition of spatial hearing with a single CI.

## 5.2 Introduction

The ability to localise sounds in space is crucial for many aspects of cognition and behaviour. The process through which the brain constructs auditory space by taking advantage of the localisation cues at the two ears (inter-aural intensity and timing differences), as well as the localisation cues available at the single ear (monaural spectral and intensity changes) has been widely studied and it is relatively well understood (e.g., Blauert, 1997; Moore, 1997). However, recent technical advances in hearing science pose new clinical and theoretical issues for spatial hearing. In particular, there is growing interest in the auditory spatial abilities of individuals fitted with one or two cochlear implants (CIs). The CI is a neuroprosthetic device that can partially restore functional hearing through direct electrical stimulation of the auditory nerve. Although CIs are routinely adopted in the clinical practice for the great benefit they provide in terms of recovery of communication skills, it remains to be clearly assessed to what extent they can restore spatial hearing.

Several studies have documented that bilateral CIs can partially restore sound localisation abilities in deafened adults to a greater extent than monaural CI (e.g., Van Hoesel and Tyler, 2003; Laszig et al., 2004; Verschuur et al., 2005; Neuman et al., 2007; Grantham et al., 2007). For example, Grantham et al. (2007) examined 22 postlingually deafened adults fitted with bilateral CIs in a localisation task in which participants were asked to call out the loudspeaker number they believed produced the sound. Localisation measurements were conducted with either CI alone and with both devices activated together. Results showed that all recipients could localise at a better than chance level when both devices were active (adjusted constant error for noise signals =  $24^\circ$ ), but performed at chance level on

average when one of the two implants was switched off (adjusted constant error for noise signals = 51°; chance level with this set-up was 50°). The procedure adopted in the study by Grantham and colleagues (2007) to test monaural localisation abilities (i.e., deactivation of one of the two implants) is representative of the approach used by most investigators when addressing the issue of monaural abilities in CI recipients (e.g., Laszig et al., 2004; Verschuur et al., 2005; Nopp et al., 2007; Neuman et al., 2007). However, this procedure does not entirely capture the sound localisation abilities that can be achieved with a single implant, because these recipients have in the meanwhile experienced hearing with two ears (see Grantham et al., 2008 for a similar argument). In the case of sequential bilateral CI recipients, any acquired monaural skill could somehow decrease due to the presence of the more used and potent binaural cue. For instance, we documented exactly this pattern of results in one bilateral CI recipient, tested longitudinally in a sound-source identification task (Nava et al., 2009). That recipient showed recovery of binaural spatial hearing, but at the same time lost the monaural abilities he had acquired in the previous 5 years of monaural experience. One month after implantation of the second device, his binaural localisation abilities improved while his monaural localisation skills decayed. Given these considerations, the most informative context for assessing sound localisation abilities with a single CI are the recipients who are only implanted unilaterally, or the sequentially implanted recipients tested before activation of the second implant. Remarkably, only a minority of studies has conducted such investigations in CI recipients fitted with a single device (Luntz et al., 2002, 2005; Buhagiar et al., 2004; Tyler et al., 2006, 2007; Dunn et al., 2008; Grantham et al., 2008; Noble et al., 2008). Furthermore, the majority of these investigation focused primarily on postlingually deaf CI recipients.

Luntz and colleagues (2002) were the first to evaluate sound localisation abilities in recipients fitted with a single CI. They asked three postlingually deafened adults and one prelingual deaf child (7 years old) to localise a random series of ten stimuli (1000 Hz tones, delivered for 3 s at 95 dB nHL) produced by five loudspeakers positioned on the horizontal plane in front of the participant. After the first testing session, each participant underwent several weeks of training (6.5 on average) in which they repeated the same task with feedback. Participants were not allowed to move their head when performing the localisation test. Despite poor performance in the very first testing session (mean score = 43), repeated training increased performance consistently for all participants (mean score = 74; note that each response was scored on a 0–2 scale, with 0 indicating a mistake by two or more loudspeakers, 1 a mistake by one loudspeaker and 2 correct speaker identification; the maximum score possible for an entire series of 50 stimuli was 100). These results suggested that initially poor sound localisation abilities in monaural CI recipients can be improved by training. In a subsequent study, Luntz and colleagues (2005) used the same paradigm to evaluate sound localisation abilities in 5 postlingual CI adults (aged 16–75 years old) and 4 prelingual deaf children (aged 8–14 years old). This second study examined monaural localisation performance as a function of duration of deafness and duration of CI use. Results showed a comparably poor performance for both prelingual and postlingual participants at the initial testing session (median score = 41 for the postlingual deaf; median score = 45 for the prelingual deaf). In addition, there was a significant positive correlation between duration of CI use and performance. After the training sessions, however, sound localisation abilities improved reliably only for postlingually deafened adults (median score = 85), but not for the prelingual ones (median score = 50). The

substantial age difference between the prelingual and the postlingual participants, however, limit considerably any generalisation of these results.

In a study by Buhagiar and colleagues (2004), 18 postlingual monaural recipients were tested in a localisation task with different stimuli (pink noise, white noise, or speech samples), presented in separate blocks. All stimuli in the study were changed every trial both in intensity ( $\pm 5$  dBs) and frequency content, to prevent use of absolute intensity cues and frequency content cues while performing the task. Participants reached overall a close to chance performance (ranging from  $57^\circ$  to  $61^\circ$  of mean absolute error; chance level was  $65^\circ$  with this set-up), leading the authors to conclude that monaural CI recipients have poor localisation abilities. Performance remained at chance level also when the same participants repeated the test with head movements allowed (mean absolute error:  $49^\circ$ ).

A similar conclusion was also reached by a series of studies that tested bilateral and unilateral CI recipients in a source identification task using everyday sounds (e.g., dog barking, buzzer, telephone ring). Sounds were presented at 70 dB from each of 8 loudspeakers spaced  $15.5^\circ$  from one another and forming an arc in the frontal horizontal plane. Tyler and colleagues (2006) found that unilateral CI recipients were generally poor localisers with respect to the bilateral CI users. However, one 'exceptional' monaural CI recipient who performed comparably to the bilateral CI users was also reported. The authors suggested that monaural localisation ability for this participant could reflect "spectral changes resulting from head movements, knowledge that louder sounds are more likely from the implanted side, [and/or] knowledge that sounds with less high-frequency energy are likely from the non-implanted side" (Tyler et al., 2006, p. S114). In one further study, using the same sound identification paradigm, Tyler et al. (2007) tested 6 postlingually

deafened adults and 1 prelingual deafened adult who received two CIs sequentially (with a range between the first and second implant from 6.8 years to 17 years). Although the main aim of that study was to document binaural abilities in sequentially implanted patients, 2 participants out of 7 were also tested for their monaural localisation abilities prior to their second implantation. Both of these patients performed near chance with a single implant, but improved shortly after receiving the second CI (see also Nava et al., 2009 for similar evidence of fast acquisition of binaural spatial abilities after implantation of the second device). Dunn et al. (2008) compared 12 bilateral CI users with 12 unilateral CI users (all postlingually deaf) and confirmed the better performance of the bilateral CIs group, whereas the single CI group performed near chance. Finally, Noble et al. (2008) studied 10 monaural CI recipients and 12 sequential CI recipients (tested prior to the implantation of the second device) and found better than chance performance ( $46^\circ$ ) for both CI groups.

In addition, 6 postlingually deafened adults implanted unilaterally were recently tested by Grantham and co-workers (2008). All participants had worn their CI for at least one year. The adopted sound localisation paradigm was similar to that described above for the study on bilateral CI recipients (Grantham et al., 2007). In separate runs, participants were asked to verbally localise which source produced either a noise-burst or a speech sample. Frequency content of the stimuli was kept constant, whereas intensity was changed in each trial ( $\pm 5$  dB). This design allowed monaural spectral information to be available, similar to real-life situations. Results showed that three monaural CI recipients could perform better than chance (performance ranged between  $35^\circ$  and  $44^\circ$ ), while the other three performed at chance level ( $51^\circ$ ; chance level for this experiment was  $51^\circ$ ).



Taken together, the studies discussed above suggest that sound localisation abilities in monaural CI recipients are either at chance level or very limited (both with respect to hearing controls and with respect to bilateral CI recipients). Nonetheless, some localisation abilities have been documented when frequency cues were preserved (Grantham et al., 2008; see also Noble et al., 2008) or when monaural CI recipients were trained using pure tones of fixed intensity (Luntz et al., 2002, 2005). In addition, the study by Luntz et al. (2005) suggests that the longer the experience with the CI, the better the monaural localisation abilities, regardless of deafness onset. Remarkably, all of the previous studies on monaural localisation abilities with a single CI have been conducted on recipients who acquired deafness postlingually. The only exceptions to this are the 5 cases reported by Luntz and colleagues (2002, 2005), which however were children of considerably different ages (from 8 to 14 years old), and the single prelingual adult reported by Tyler et al. (2007).

In the present study, we conducted a cross-sectional investigation on sound localisation abilities of 10 prelingual monaural recipients with different years of CI experience (range from 2 to 12 years). In addition to the clinical relevance of providing for the first time systematic evidence on the localisation ability of this subgroup of monaural CI users, the investigation of monaural localisation ability in prelingual CI recipients has also the theoretical interest of showing to what extent individuals who had minimal or no auditory experience can learn to localise sounds in space. Four postlingually deafened adults implanted monaurally were also tested in the study for preliminary comparisons with the prelingual group.

### 5.3 Methods

#### *Participants*

Fourteen unilateral CI recipients were recruited at the “Santa Maria del Carmine” hospital in Rovereto (Italy) to take part in the study. All recipients were assessed to be profoundly deaf in both ears prior to implantation (>90 dB). Ten recipients became deaf before 1 year of age (i.e., prelingual onset; 4 females and 6 males, mean age = 26 years, range 23–53) and four became deaf postlingually (3 male, 1 female, mean age = 40 years, range 31–53). Deafness aetiology was unknown for most recipients, except for recipient S5 who became deaf due to a cytomegalovirus infection, S6 who was deaf for genetic causes (connexin 26), and S13 who had a car accident when aged 29. All participants were implanted in adulthood with a single cochlear device (either MED-EL, Nucleus or Clarion). The device was worn in the standard over-the-ear position, with the microphone located over the top front of the pinna. Details on the adopted CI for each participant are reported in Table 1, together with time from CI surgery and other demographic information. None of the participants made use of hearing aids on the non-implanted ear after the CI surgery, but all had experience using bilateral hearing aids prior to cochlear implantation.

Before starting the experimental session, participants were mapped to optimally adjust the threshold (T) and maximum comfort (MC) levels (i.e., the standard clinical mapping in which T and MC levels are measured for each electrode). Furthermore, all had implant thresholds of 35–45 dB HL for warble tones presented in sound field condition. Prior to the testing session, participants were instructed to select the program and volume settings they were more accustomed to

using. No further change to the CI sensitivity was allowed during testing. The study has been approved by the Institutional Review Board where the study was performed.

Table 1

Participants	Sex [degrees]	Age [years]	Ear implanted [degrees]	Time form CI activation	CI type
<i>Prelingual</i>					
S1	F	23	Right	6 yrs	Med EI
S2	F	18	Left	10 yrs	Nucleus
S3	F	23	Right	4 yrs	Med EI
S4	M	19	Right	12 yrs	Med EI
S5	M	19	Right	6 yrs	Nucleus
S6	M	32	Right	2 yrs	Nucleus
S7	M	20	Right	6 yrs	Clarion
S8	M	30	Right	7 yrs	Nucleus
S9	M	24	Right	11 yrs	Med EI
S10	M	24	Right	4 yrs	Nucleus
<i>Postlingual</i>					
S11	M	53	Right	2 months	Med EI
S12	F	31	Left	11 months	Med EI
S13	M	36	Left	2 yrs	Med EI
S14	M	38	Left	6 months	Med EI

**Table 1** Demographic information

*Apparatus, stimuli and procedure*

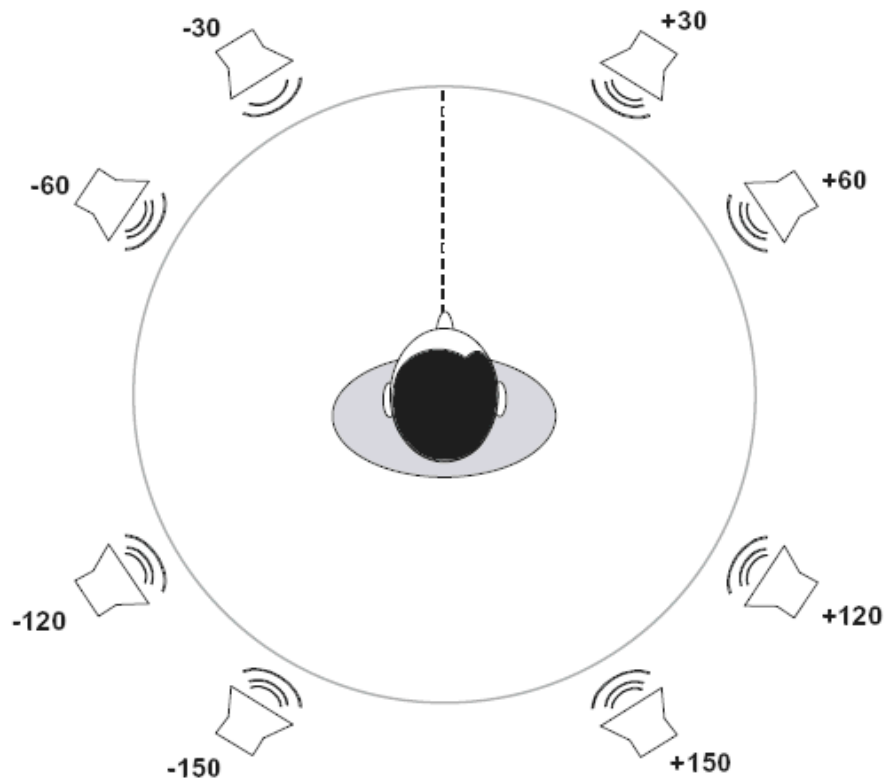
All recipients performed the localisation test in a silent, but not anechoic, room. The room measured 610 cm × 270 cm, with 310 cm height, and was fully furnished. The set-up consisted of 8 loudspeakers, positioned in a circle (radius 60 cm) around the participant who sat in the centre (see Fig. 1). With respect to the straight-ahead position (0°), loudspeakers were positioned at +30°, +60°, +120° and

+150° on the right side of the participant, and at -30°, -60°, -120° and -150° on the left side of the participant. Stimuli were generated using Matlab and consisted of a sequence of four 20 ms noise-bursts, separated by 80 ms intervals (overall stimulus duration was 320 ms). Noise-bursts consisted of unfiltered Gaussian noise (sample frequency 44,100), including 0.2 ms linear ramps, delivered at 70 dB. Each stimulus was randomly delivered six times from each loudspeaker, in three separated blocks (48 trials per block; 144 fully randomised presentations in total). We also randomly varied the intensity level of each speaker ( $\pm 3$ –4 dB) between trials. Note that such a small decibel variation had only the purpose to mask minimal loudness differences between loudspeakers, but likely did not overwhelm monaural localisation cues based on the head-shadow effect (which are in the range of  $\pm 10$  dB; Van Wanrooij and Van Opstal, 2004). Finally, an acoustically transparent close weave cloth, specifically designed for mounting on loudspeaker grilles when cut smaller than the complete sheet used here (Model: KS50E, Maplin, UK), covered all frontal loudspeakers to avoid visual cues to localisation.

Participants were asked to verbally identify the loudspeaker from which they considered the sound to have originated. To provide their answer, participants were given a diagram with the representation of all possible loudspeakers' spatial positions. The experimenter arbitrarily timed stimulus presentation by pressing a button on the computer keyboard (approximately 1 stimulus every 3 s). All patients performed the sound localisation test in a single experimental session. The localisation procedure was immediately obvious to all participants and no practice or training was needed prior to the testing session. No head movements were allowed during stimulus presentation, and the experimenter started each trial only when the participant complied with the instruction to face straight ahead. No repeats were

allowed and no feedback was given. Each session took approximately 45 min to complete.

Figure 1



**Fig. 1** Set-up. Overhead schematic view of the experimental set-up.

## 5.4 Results

### *Prelingual CI recipients*

The mean absolute error for each prelingual participant (with error bars indicating the standard error of the mean computed over the three sessions) is shown in Fig. 2, as a function of years from CI activation. White circles indicate better than chance localisation performance (chance-level 90° with our experimental set-up), black circles indicate performance that was not statistically different from chance. Mean absolute error for each stimulus location was computed as the difference between the actual sound-source location and the response given by the participant. Mean absolute error across the prelingual participants ranged from 68° to 97° (see Table 2 for details and Fig. 3 for percentage of occurrence of absolute error values for each of the participants).

Un-paired t-tests (with unequal variance assumed) were carried out to investigate whether the performance of each recipient was statistically different from chance. These tests revealed that 5 recipients out of 10 performed statistically better than chance (all  $p < 0.03$ ; white circles in Fig. 2, and bold figures in Table 2). These 5 prelingual deaf recipients had worn their implant longer (mean = 9 years, SE = 5) than those who performed at chance level (mean = 5 years, SE = 5;  $t(4) = 3.69$ ,  $p = 0.02$ ). However, a one-tailed correlation analysis between time from CI activation and mean absolute error did not reach significance (Pearson correlation = - 0.50,  $p = 0.07$ ). In addition, inspection of Fig. 2 shows that some cases (i.e. S1 and S8) performed at chance level despite comparable time from CI activation to others (i.e. S5 and S7), thus acknowledging the existing variability among participants.

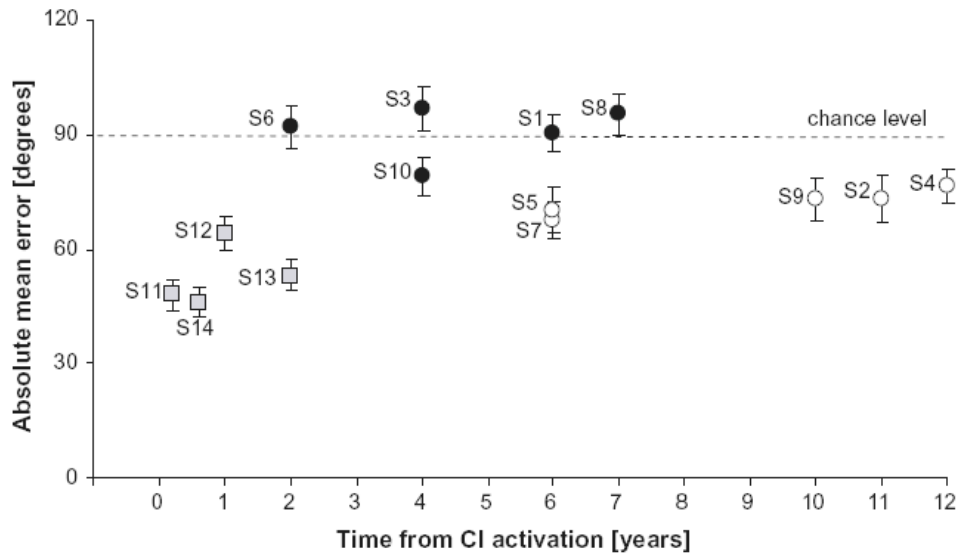
The mean absolute error reported above includes both errors in azimuth and errors in the front/back dimension. In the following two analyses we examined the azimuth error after front–back response resolution (resolved azimuth error) and the errors in the front–back dimension separately. To disentangle accuracy of the response in azimuth from that in the front–back discrimination we collapsed stimulus and response azimuths across front and back locations (i.e., we considered a response as correct whenever the azimuthal component was accurately recognised, regardless of whether it was localised in front or back space).

Table 2

Participants	Overall mean error [degrees]	Resolved azimuth error [degrees] Chance = 52°	Directional bias [degrees] No bias = 0°	Front hemifield	Front-back [% errors] Back hemifield	Overall
<i>Prelingual</i>						
S1	90	65	37	18%	58%	<b>38%</b>
S2	<b>73</b>	<b>44</b>	43	69%	10%	<b>40%</b>
S3	97	60	18	44%	63%	53%
S4	<b>76</b>	<b>34</b>	–21	51%	60%	56%
S5	<b>68</b>	39	16	18%	61%	<b>40%</b>
S6	92	57	–20	56%	48%	52%
S7	<b>70</b>	47	5	30%	38%	<b>34%</b>
S8	95	61	<b>55</b>	23%	73%	48%
S9	<b>73</b>	45	8	33%	42%	<b>38%</b>
S10	79	51	<b>85</b>	40%	39%	<b>40%</b>
<i>Postlingual</i>						
S11	<b>48</b>	22	–21	40%	32%	<b>36%</b>
S12	<b>64</b>	<b>28</b>	1	67%	26%	47%
S13	<b>54</b>	<b>24</b>	–28	29%	4%	<b>17%</b>
S14	<b>45</b>	23	–6	29%	6%	<b>17%</b>

**Table 2** Individual performance of each CI recipients in the study. Bold figures indicate performance significantly above chance. Direction biases towards the right are indicated by positive numbers.

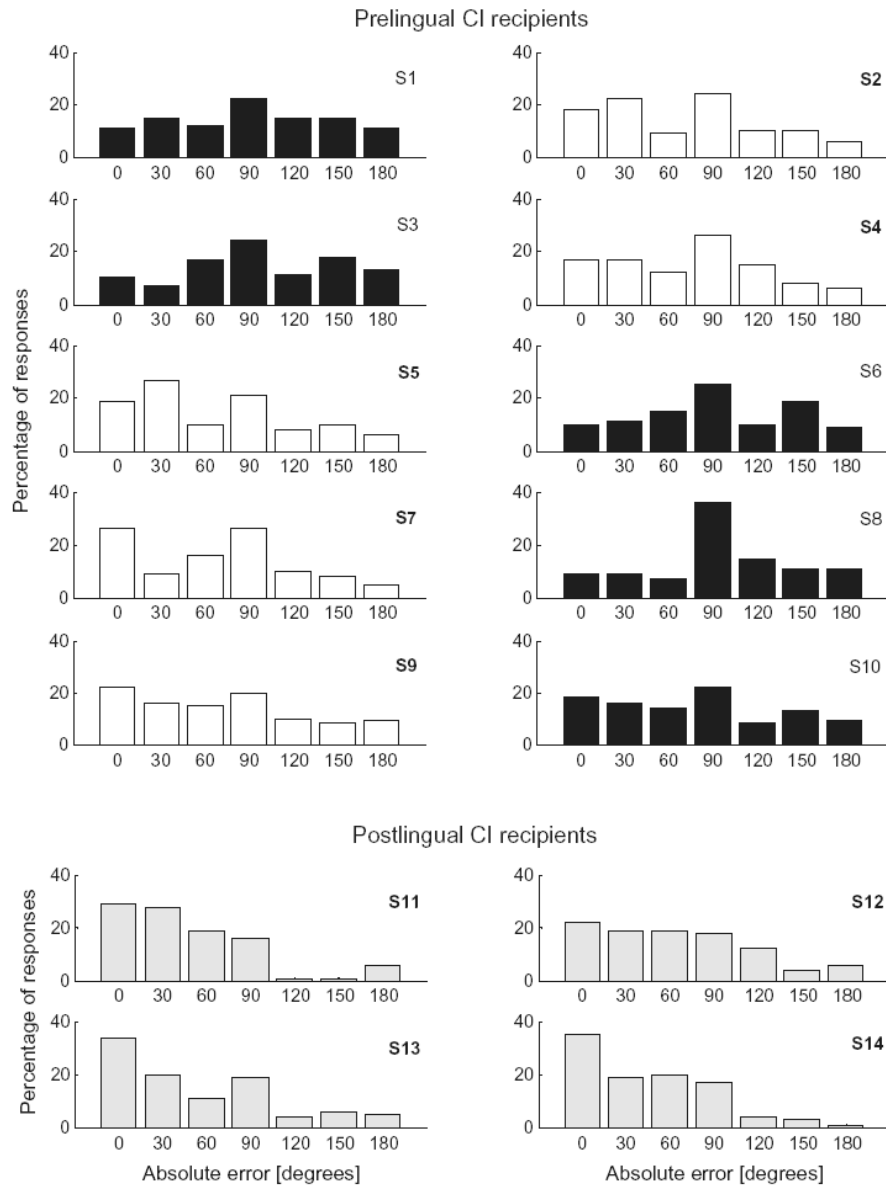
Figure 2



**Fig. 2** Mean absolute error. Mean absolute error (in degrees) for each participant as a function of time from CI activation (in years). Prelingual recipients are indicated with circles, postlingual recipients are indicated with squares. Open circles and open squares indicate better than chance localisation performance (chance-level 90° with our experimental settings). Filled circles indicate performance not statistically different from chance. Error bars indicate the standard error of the mean.



**Figure 3**



**Fig. 3** Interparticipant absolute error distribution percentage of occurrence of absolute error values for each of the participants. Bars are colour-coded to correspond to Fig. 2: prelingual recipients who perform better than chance (white), prelingual recipients who perform at chance (black), postlingual recipients (gray).

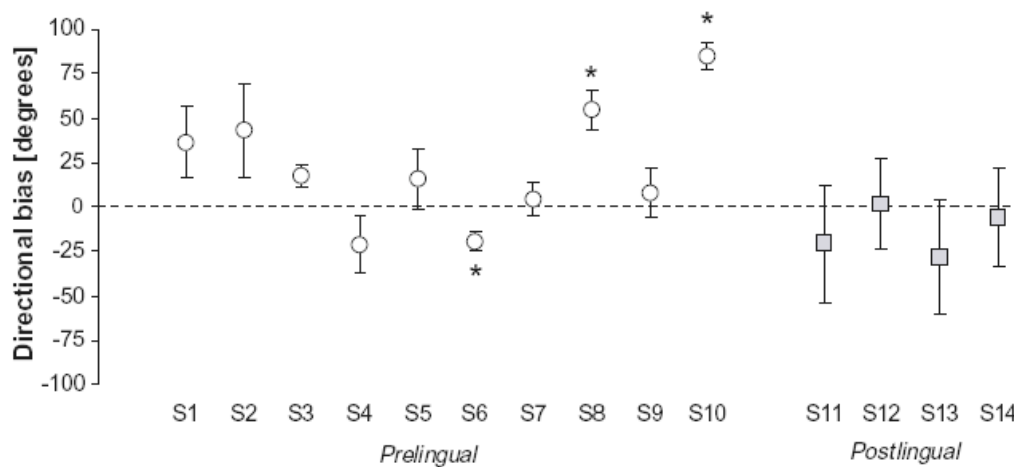
Resolved azimuth errors across participants ranged from 34° to 65°, and unpaired t-tests revealed again that 5 recipients performed better than chance (see bold figures in Table 2; note that these are the same 5 recipients who performed above chance in the mean absolute error analysis). Notably, the correlation between time from CI activation and resolved azimuth error reached significance when considered one-tail (Pearson correlation = - 0.62,  $p = 0.03$ ).

Percent errors in the front–back dimension across participants ranged from 34% to 56% (44% mean error overall). We considered a response to be correct whenever the participant responded correctly to a stimulus being presented in the front or the back, regardless of its side. Individual  $\chi^2$  tests revealed that 6 recipients performed better than chance in the front–back dimension (see bold figures in the column reporting the overall front–back discrimination errors in Table 2). Although this finding may suggest some front–back discrimination ability in the prelingual participants, this result should be taken with great caution. Inspection of percent errors separately for front and back hemifields in Table 2 suggests that part of the observed accuracy could mainly be driven by the performance in the front hemifield. This leaves open the possibility that the apparent ability in front–back discrimination could reflect a response bias (perhaps due to a preference to locate the stimuli in the portion of space towards which the CI microphone is directed), rather than true discrimination sensitivity.

Finally, we computed the directional bias of each participant as the arithmetic average of the signed responses (negative and positive values indicate an overall bias towards the left and right side, respectively; e.g., see Grantham et al., 2007). This allowed us to examine to what extent localisation responses were biased towards the side of the monaural CI. As illustrated in Fig. 4, all prelingual recipients

except one (S6) showed a numerical directional bias towards the side of their active implant (i.e., a rightward bias when wearing a right CI, and a leftward bias when wearing a left CI). The sole exception was case S6, who showed a leftward bias despite having a CI on the right ear. Statistically significant differences (as revealed by un-paired t-test against 0) are indicated by asterisks in Fig. 4 and bold numbers in Table 2.

**Figure 4**



**Fig. 4** Localisation bias. Directional bias for each participant, computed as the arithmetic average of the signed responses. Negative and positive values indicate a bias towards the left or right side, respectively. All participants were fitted with a CI on the right ear, except participants S4 and S12 who had their CI on the left ear.

### *Postlingual CI recipients*

The mean absolute error for the four postlingual participants (with error bars indicating the standard error of the mean) is also shown in Fig. 2 using gray squares. The overall mean error of the 4 postlingual participants was 53°. Due to the limited number of cases, instead of performing a between group analysis (i.e., prelingual group vs. postlingual group comparisons), we opted for treating each postlingual participant as a single case. Accordingly, we compared each postlingual case performance to the distribution of the prelingual CI recipients using the procedure developed by Crawford and Garthwaite (2002) for the investigation of single case studies in neuropsychology. This procedure tests whether an individual's score is significantly different from a control or normative sample.

The mean absolute error for case S11, case S13 and case S14 were significantly smaller with respect to the prelingual group (in all cases  $p < 0.03$ ; see means in Table 2). For case S12, the mean absolute error (64°, SE = 4) was instead comparable to that of the prelingual group ( $p = 0.2$ ). Performance of case S12 was significantly different with respect to both S11 and S14 ( $p < 0.01$ ) and marginally different with respect to S13 ( $p = 0.09$ ), whereas cases S11, S13 and S14 were all statistically comparable. Importantly, all cases had a significantly better than chance performance ( $p < 0.001$ ), despite having been tested after much shorter time from CI activation than the prelingual group. S11 was tested 2 months from activation, S12 was tested 11 months from activation, S13 was tested 2 years after activation and S14 after 6 months from activation (recall that minimum time from activation in the prelingual group was 2 years).

The analysis on resolved azimuth error for the 4 postlingual cases confirmed entirely the pattern described above. For all cases the resolved azimuth error (see

Table 2) was better than chance ( $p < 0.0001$ ), and was significantly smaller with respect to the prelingual group for cases S11, S13 and S14 ( $p < 0.03$ ), but only marginally significantly smaller for case S12 ( $p < 0.06$ ). Front–back discrimination also overall better in the postlingual cases. With the sole exception of case S12 (who showed a systematic bias for locating sounds in back space), all cases performed significantly better than chance (as assessed by  $\chi^2$  tests). Furthermore, unlike the performance of prelingual recipients which we suggest could be primarily driven by a response bias, cases S11, S13 and S14 were accurate both when the stimulus originated from front space and when it originated from back space (see Table 2). No significant bias emerged for the postlingual recipients (as assessed by unpaired t-test against zero).

## **5.5 Discussion**

The present study investigated sound localisation abilities in a group of adults fitted with a single CI. Contrarily to previous works (Buhagiar et al., 2004; Dunn et al., 2008; Grantham et al., 2008; Luntz et al., 2002; Noble et al., 2008; Tyler et al., 2006, 2007), which tested such abilities in adult recipients who became deaf late in life, the present investigation focused primarily on a group of CI recipients with early deafness (i.e., prelingual recipients). In addition, we report the performance of 4 postlingual CI recipients.

### *Monaural spatial abilities can emerge with time in prelingual CI recipients*

Overall, monaural localisation performance of prelingual CI recipients was rather poor. However, some prelingual recipients fitted with a single CI in adulthood did achieve better than chance localisation performance. Interestingly, we found that the prelingual recipients who performed better than chance were the ones who had worn their implant for longer time (mean = 9 years). This suggests that there may be a close relationship between years of implant use and the development of monaural localisation abilities in CI recipients. The only previous report of monaural localisation abilities in a group of 4 prelingual CI users was conducted by Luntz et al. (2005) and documented chance performance in this population. However, it should be emphasised that the duration of implant use in their study was relatively short (range 1 and 7 months), whereas our prelingual recipients had an experience with their monaural implant that ranged between 2 and 12 years. Furthermore, the study by Luntz et al. (2005) tested children of considerably different age (8, 10, 12 and 14 years old). Our findings expand the current knowledge on monaural spatial abilities of prelingual CI recipients, by testing for the first time a sample of adult prelingual CI users and by showing a relationship between years of implant use and acquired monaural abilities.

The profile of our data suggests that monaural localisation abilities in prelingual recipients start emerging at least after 6 years of CI use. However, closer inspection of Fig. 2 also shows a clear interparticipant variability. For example, case S8 performed below chance level despite she was tested 7 years from CI activation. In-depth understanding of the impact of variability across recipients was beyond our aims, as it would require a larger group of cases than the one reported here. At present we can only suggest as potential sources of performance variability the

amount of perceptual experience that the recipients had with the localisation cues, as well as the cognitive skills they developed (e.g., as a consequence of scholar experience, the amount of speech therapy before and after CI, or their socio-cultural background). From a theoretical perspective, our study may also prove informative for the general issue of auditory spatial plasticity in adulthood (e.g., Hofman et al., 1998; Van Wanrooij and Van Opstal, 2004). We show that even CI recipients who were minimally exposed to auditory cues can develop some sound localisation abilities with a single ear, given enough time. This finding is in agreement with the results from animal studies that suggest that neural circuits responsible for sound localisation can be recalibrated throughout life (King et al., 2000). Whether our findings of acquired monaural abilities in prelingual CI recipients reflect learning of novel associations between auditory cues and spatial locations in adulthood, or instead reflect re-weighting of the different auditory cues, remains an open issue. Although the early onset of deafness in our CI recipients could point to the first interpretation, the re-weighting account is still the most parsimonious explanation that can be offered. The unknown aetiology of most of the recipients we tested, as well as the absence of systematic audiometric data from their period of deafness, leaves open the possibility that our CI recipients had occasions of learning some auditory cues after their deafness onset, which could then be recalibrated after implant activation.

#### *Comparison between postlingual cases and the prelingual group*

A second finding of the present study emerged when comparing the performance of the prelingual group with the performance of the 4 postlingually deafened adults who underwent the same sound-source identification test. Although

this finding should be considered preliminary, given the limited sample of postlingually deaf adults recruited in the present study, it should be noted that prelingual and postlingual CI recipients of comparable age have not been previously tested on the same sound localisation task.

The most striking aspect, which is apparent from Fig. 2, is that the four postlingual cases reached a comparable (or even better) performance to the best prelingual recipients despite a much shorter experience with the CI (see gray squares in Fig. 2). Recipients S11, S13 and S14 outperformed all prelingual CI recipients despite being tested 2 months, 2 years and 6 months after implant activation, respectively. Recipient S12 achieved comparable performance to the best prelingual participants (e.g., S5 and S7) despite being tested 11 months from implant activation<sup>1</sup>. If confirmed on a larger sample of cases this finding would suggest that the time-course for the acquisition of monaural hearing may be different as a function of whether the recipient had prelingual or postlingual deafness onset. Such a difference could reflect the differential exposure to auditory cues to sound localisation in the two populations. Further evidence in support of the notion that the amount of exposure to auditory cues can constrain the time-course of acquisition of spatial abilities comes from a recent observation on two postlingual bilateral CI recipients, who had substantially different deafness onset (Nava et al., 2009). We found that the recipient with longer auditory experience (deafness onset when aged 39 years) recovered binaural sound localisation abilities shortly after implant activation (1 month), whereas the recipient with less auditory experience (deafness onset when aged 4 years) recovered binaural localisation abilities after 12 months from activation. Taken together, the results of the present work and the results of the previous study we conducted on bilateral CI recipients (Nava et al., 2009) lead to the



prediction that whenever auditory cues are made available through the CI, postlingual recipients can rapidly re-weight previously learned auditory spatial mappings even after several years of sensory deprivation.

*What type of auditory cues can serve localisation in monaural implant recipients?*

The existence of above chance localisation abilities in monaural CI recipient raises the issue of which auditory cues may serve this partially recovered auditory spatial ability. Two types of monaural auditory cues could in principle have played a role. First, monaural spectral cues, which depend on how the sounds coming from different directions in space are spectrally shaped as a function of the shape of the head and pinnae (e.g., Hofman et al., 1998). These cues typically allow discrimination of sound location in the near–far, front–back and elevation dimensions, but can also contribute, to some extent, to localisation in azimuth (Butler, 1987). Second, monaural intensity cues, which depend on how sounds coming from different locations in azimuth are attenuated as a function of the shadow cast by the head on the receiving ear (the so-called head-shadow effect (HSE); Van Wanrooij and Van Opstal, 2004). Because HSE can attenuate sounds up to 25 dB (depending on frequency), it can be used as monaural intensity cue to determine positions in azimuth even when some intensity jitter is applied to the stimuli (see also Buhagiar et al., 2004; Grantham et al., 2008).

It is very likely that part of the monaural abilities of our participants depended upon the use of the HSE monaural cue. As clearly documented by van Wanrooij and Van Opstal (2004), the monaural intensity cues related to HSE can be easily learned and applied to a variety of sounds. However, whether monaural spectral cues played a role in the monaural abilities of our CI recipients remains an open question. On the

one hand, evidence in support of a role of monaural spectral cues comes from the observation that randomly changing the spectral characteristics of the sound (as in the study by Buhagiar et al., 2004) results in chance localisation performance in monaural CI recipients (Grantham et al., 2008). Furthermore, the discrimination ability documented in monaural CI recipients in far–near localisation (Grantham et al., 2008, p.150) and in front–back discrimination (the postlingual recipients of the present study) points to a role of monaural spectral cues even for localisation in azimuth. Finally, Grantham et al. (2008) found better localisation performance in monaural CI recipients with speech stimuli rather than noise; this is in agreement with the notion that monaural spectral cues can be learned more easily for familiar than unfamiliar stimuli (Van Wanrooij and Van Opstal, 2004). On the other hand, it is noteworthy to point that CI speech processor might not capture spectral cues provided by the external ear filtering due to the placement of the microphone.

One final aspect worth discussing concerns the discrepancy between the good performance of the four postlingual participants in the present study and the postlingual participants tested in the study by Grantham et al. (2008). In that work, monaural abilities in the postlingual recipients were rather poor and emerged only for some of the participants (despite several years of experience with the CI). By contrast, our four postlingual participants achieved better than chance performance already within a short time from activation. Several different aspects could have contributed to this discrepancy. First, unlike the study by Grantham et al. (2008) we tested all our participants in a silent room which was not anechoic. In such an environment, reverberation cues may contribute to localisation of the sound sources (but see Buhagiar et al., 2004). Second, Grantham et al. presented the sounds from one of 9 locations embedded among 43 visible dummy loudspeakers. On the

contrary, our set-up consisted of 8 loudspeakers that, although not visible to the participant, were not embedded among others, though giving to the participants only 8 choices for a decision to be made. Therefore, the set-up by Grantham et al. (2008) could have resulted in a much more difficult task than the setup used in the present study. Third, stimulus presentation level was varied over a range of 10 dB in the study by Grantham et al. (2008), whereas in the present study it varied over a 6 dB range. Hence, the extent to which recipients could have access to level cues could have been different in the two studies.

### *Conclusions*

We have shown that some prelingually deafened adults implanted with a single CI can learn to localise sounds at a better than chance level, provided that they had substantial experience with their device (at least over 6 years). This ability is likely to reflect monaural intensity cues (HSE), although a role of monaural spectral cues cannot be excluded, and in this respect it may have been particularly favoured by the controlled laboratory setting we have adopted. Finally, we observed that postlingually deafened adults who have experienced auditory cues earlier in life can reach a more accurate performance than prelingual CI recipients and in the shortest period after activation. If confirmed on a larger sample of cases this finding would suggest a different time-course for the acquisition of monaural hearing in prelingual and postlingual recipients.

### *Footnotes*

1. It should be remarked that among the four postlingual cases, S12 is the only one that had an extensive period of auditory deprivation. Her deafness started when she was 4 years old and, although it emerged progressively and was corrected through hearing aids, it severely limited her auditory spatial experience until she was implanted at the age of 30 years. This anecdotal observation could lead to the prediction that among the postlingual CI recipients those who remained deaf for longer time will need more time to learn how to re-weight auditory cues after implantation.

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## **5.6 Interim conclusions**

Results from the two experiments have shown that even the adult brain maintains some degree of plasticity. Particularly the first experiment has shown that the rapidity of the recovery in auditory sound localisation is constraint to the experience achieved with auditory cues: the recipient who became deaf in adulthood recovered in the shortest period, while the recipient who did not experience normal hearing for years took longer to achieve a comparable performance. Given that both recipients acquired deafness postlingually (excluding the role of a sensitive period in shaping auditory cues), their different time course in spatial recovery could possibly be attributed to the different duration of deafness experienced before implantation.

The second experiment has shown that some sound localisation abilities can be achieved even with a single cochlear implant, and even in some cases of prelingual deafness onset. However, results from prelingually deafened adults suggest that their localisation performance may improve only after several years of implant use, if improved at all. Results from the postlingually deafened adults confirmed the role of experience in allowing a more rapid recovery compared to prelingual deaf recipients, possibly due to their previous hearing experience and to the duration of deafness that seemed to modulate the time course of their recovery.

## **PART III**

The effects of auditory  
reafferentation on visual abilities  
and audio-visual interactions

# **CHAPTER 6**

## Introduction

## **6.1 Visual abilities after auditory reafferentation**

This final part of the thesis will investigate a further issue concerning the interplay between adult plasticity, cochlear implantation, and experience. In particular, we will explore what happens to visual abilities after implantation and the nature of the interactions between vision and the reafferented auditory input. In addressing this issue, it is crucial to take into consideration the occurrence of plastic changes prior to cochlear implantation.

In the previous sections of the thesis we have shown that both neural and compensatory changes may occur as a consequence of early sensory loss (Neville et al., 1983; Röder et al., 1996; Bavelier et al., 2000). In case of profound deafness, compensatory changes have proved to occur particularly for some aspects of the visual modality (Neville & Lawson, 1987; Loke & Song, 1991). In addition, plastic changes have been documented to be particularly strong and rapid during sensitive periods in early life (Knudsen, 2004). These salient aspects characterising plasticity following early auditory deprivation lead to hypothesise that if auditory input is restored through a cochlear implant in adulthood, it may likely leave unchanged the plastic changes that occurred early in life. In addition, given the strength of these changes, they may likely persist even after extensive use of the cochlear device.

Plastic changes in case of postlingual deafness onset have been documented as a consequence of duration of deafness. For instance, Lee et al. (2003) measured metabolic activity in the auditory cortex of postlingually deafened adults before implantation with the assumption that glucose levels in this deafferented area should increase if cross-modal reorganisation has taken place. This indeed was the case in postlingually deafened adults compared to hearing controls in auditory cortex. However, metabolic activity increased as a function of



duration of deafness, suggesting that a prolonged auditory deprivation leads to cross-modal changes (i.e., recruitment of the auditory cortex by other sensory modalities). Overall, these results showed that plastic changes can occur in the adult brain depending on the duration of the atypical experience. Similar results were also found by Lee et al. (2001) in a previous study, where the same measures were used to investigate cross-modal plasticity in a group of prelingually deafened children before implantation. A comparison between the two studies suggests that similar pattern of cross-modal reorganisation can emerge as a consequence of early sensory loss (Lee et al., 2001), or duration of deafness in adulthood (Lee et al., 2003). Since these metabolic changes were not correlated to functional compensatory changes in the other sensory modalities, a direct comparison between neuronal and functional changes is not possible.

However, given our results for postlingually deafened adults in Part II of the thesis, and the notion that plasticity exhibited after sensitive periods is restricted (King et al., 1993; Knudsen, 1990), a hypothesis on how visual abilities will be processed after cochlear implantation may be formulated: postlingually deafened adults may not exhibit compensatory changes by the time they receive a cochlear implant.

Nonetheless, postlingually deafened adults may develop compensatory changes after cochlear implantation as a consequence of an incomplete auditory reafferentation. Evidence of this comes from a study by Giraud et al. (2001), who investigated the recruitment of visual cortex in CI recipients during auditory language tasks in a series of PET experiments. Postlingually deafened adults had 2 years auditory deprivation before to implantation and 1 year cochlear implant experience when tested. In the first two experiments, greater activation of the visual cortex was

found for both presentations of meaningful and meaningless words compared to hearing controls. To disambiguate whether visual activation reflected a process that emerged after cochlear implantation or as an effect of cross-modal plasticity established during the period of deafness, Giraud et al. (2001) performed another experiment in which a group of postlingually deafened adults was tested in the first week following implant activation (i.e., prior to any experience with the cochlear implant). Interestingly, these CI recipients had less visual activation compared to the other two groups tested in the other experiments, suggesting that, in contrast to Lee's study (2003), responses in the visual cortex may not be due to cross-modal changes that occur during deafness but appear as a consequence of cochlear implantation. Overall results show that CI recipients recruit the visual cortex when listening to speech-sounds, and this activation increases with implant use, suggesting that restoration of hearing is followed by a mutual reinforcement of vision. This latter study leads to another issue of concern, namely how visual and auditory stimuli interact after auditory reafferentation.

## **6.2 Multisensory interactions**

The way we perceive objects and events in the environment is made possible by the brain being able to encode, decode and interpret information through each sensory modality. Although every single sensory modality provides its unique qualitative perception, we constantly combine two or more senses to have a more unitary and coherent representation of the environment, and to increase our ability to identify objects or events of interest. However, a question of concern is how and to

what extent these multisensory perceptions are actually combined in the brain, namely, whether they really fuse to produce a unique percept or whether they simply lead to a behavioural enhancement. A second question is whether typical or atypical experiences during developmental stages constrain the ability to integrate in a multisensory fashion.

### *6.2.1 The view from the single neuron*

The classical animal studies by Meredith & Stein (for reviews, see Meredith & Stein, 1993; Stein & Stanford, 2008) have largely contributed to the understanding of the neural correlates of multisensory integration, documenting that sensory inputs need to have access to the same neurons for the brain to be able to integrate them. In particular, their studies have mainly focused on a subcortical structure in the cat – the superior colliculus – that was proved to be rich of multisensory neurons, in that it responded to stimuli from more than a single sense. However, some multisensory neurons not only respond to different sensory inputs, but their activity is suppressed if they do not receive multisensory stimulation. Meredith and Stein (1993) reported of single neurons that responded to very low-level-intensity auditory stimulus, and were completely suppressed when the visual stimulus was made unavailable to the animal (i.e., by either covering the animal's eyes or by turning the lights off). In order to weight the magnitude of multisensory integration, three types of computations were suggested: 1) additivity, in which the multisensory response equals the arithmetic sum of the responses to the component stimuli; 2) subadditivity, in which the multisensory response is smaller than the arithmetic sum of the responses to the component stimuli; 3) superadditivity, in which the multisensory response is larger than the arithmetic sum of the responses to the component stimuli. On the

behavioural side, these types of multisensory integration computations lead to enhanced or decreased responses to cross-modal stimuli, for example in case of speed of response (Colonius & Diederich, 2004; Rowland et al., 2007).

Multisensory neurons seem sensitive to two main principles, namely the role of space and time: the more the stimuli coincide spatially and temporally, the more they will be able to elicit a multisensory response. Evidence for these two principles comes from investigations of the spatial distribution of sensory receptive fields in multisensory neurons. Each neuron has different receptive fields (i.e., area of sensory space in which presentation of a particular sensory stimulus elicitates a response) on which the single sensory modality is represented. Since some of these receptive fields spatially overlap, it is not only the stimulation of the single sensory modality itself to trigger activity in multisensory neurons, but the location of the event to determine activation of that neuron. For example, the two receptive fields of audio-visual neurons overlap in space, which means that if one of the two sensory modalities activates that neuron, it will activate the other sensory modality as well, regardless (in theory) of their incoming spatial congruency or incongruency (Kadunce et al., 2001).

A similar logic applies to time as well: stimuli that reach the nervous system within a comparably long time window will enable integration to take place. In this view, the magnitude of the integrated response will be proportional to the temporal overlap of each sensory input. In sum, when sensory stimuli appear in close spatial and temporal proximity, their firing rate can increase dramatically, and this facilitation occurs particularly when responses to the individual inputs are weak. In other words, the more the combined stimuli are weak, the more they will produce enhancement in multisensory neurons (inverse effectiveness).

These features of multisensory integration seem to apply particularly for the superior colliculus, since it was found to contain 80% of multisensory neurons (Wallace & Stein, 1997). However, polysensory areas were found to have multisensory neurons as well, including the anterior ectosylvian fissure and lateral sulcus of the cat, parietal cortex and anterior superior temporal sulcus in the monkey.

Several neuroimaging techniques (fMRI, MEG, PET) have been used to identify the neural correlates of multisensory interactions in the human brain, documenting the existence of multisensory areas. In particular, activity to trisensory stimulation (audio-visual-tactile) was found in the premotor cortex and posterior parietal cortex, while audio-visual activity occurs particularly in the posterior superior temporal sulcus, a region in the auditory cortex.

Some initial studies (Calvert et al., 1999; 2000) investigated the neural bases of cross-modal gains for linguistic interactions, having the notion that a superadditive improvement is achieved in audio-visual speech comprehension when both auditory and visual stimuli are made available to the subject. In one of their studies, Calvert et al. (2000) scanned individuals while listening to excerpts of a book in the presence of matched or mismatched lip and mouth movements. In addition, individuals also listened to the words without visual cue and viewed lip and mouth movements without auditory cue (unimodal conditions). This design allowed identification of brain areas that are in line with previous findings on animals that are sensitive to the principle of spatial congruency. In particular, the left superior temporal sulcus was identified as putatively involved in audiovisual speech when the two stimuli are spatially coincident.

Similar gains for audio-visual integration occur for non-linguistic stimuli as well, and appeal to the temporal role. For example, Bushara et al. (2001) conducted a PET scan on a group of subjects required to detect whether an auditory tone and a visual stimulus (a colored circle) were presented synchronously or not. Onset asynchrony could vary in order to have three difficulty levels. The authors found a network of polymodal brain areas that are involved in audio-visual temporal synchrony detection, including the right insular, posterior parietal and prefrontal regions. Further and more detailed analyses documented that the right insula participated more when the task became more difficult (i.e., at decreasing asynchronies). Only a functional interaction between insula and superior colliculus was found, leading the authors to conclude that these two regions are mostly involved in synthesising cross-modal interactions on the basis of their temporal congruency. However, conclusions about the involvement of specific regions of the brain in processing the temporal aspect underpinning multisensory integration should be taken with caution, as it is possible that spatial and temporal factors somehow influence each other. For example, the classical ventriloquist effect (which is a spatial illusion) occurs as a consequence of synchronous stimuli onset, and asynchronous presentation of the audio-visual components does not lead to the perceptual illusion.

#### *6.2.2 Disruption of multisensory integration after sensory deprivation*

The capacity to combine information across different sensory channels to form a coherent and unified percept of the environment derives from the way these senses interact during development. The developmental approach is of particular importance when addressing early sensory loss, in that it could determine to what

extent some multisensory interactions are innate or learned through experience. In other words, it would speak for abilities that early sensory-deprived individuals may or may not achieve through experience.

Animal studies conducted on both cats (Wallace & Stein, 1997) and monkeys (Wallace & Stein, 2001) have shown different patterns of multisensory development from a neural point of view. Electrophysiological recordings obtained in the cat in the very first postnatal days have revealed little sensory activity in the layers of the superior colliculus. The only sensory response in these layers is given by somatosensory cues. The second sensory response to appear is that driven by auditory input, and this coincides with the appearance of the first multisensory neurons in the superior colliculus responsive to audio-tactile cues. On the contrary, monkeys show somatosensory, auditory and visual responses in the superior colliculus immediately after birth. The most evident developmental change that occurs in both species in the neuron of the superior colliculus is the shrinkage of the receptive fields, with sensory representation taking an increasingly fine-grained resolution. Furthermore, the growth of multisensory neurons is paralleled by the growth of the different sensory-responsive cell types, so that the growth, for example, in visual responses, will coincide with visually responsive multisensory neurons. Another difference between developing and mature multisensory neurons features is the magnitude in response. While combination of stimuli from multiple modalities results in enhancement in the adult (Meredith & Stein, 1986; 1993), early multisensory neurons respond with the same intensity compared to individual stimuli or their combination, and are not sensitive to the spatial and temporal rule. Multisensory integration, in an adult-like fashion (i.e., providing superadditive

effects), occurs several weeks after appearance of the first neurons, suggesting that multisensory development may be a gradual process.

Multisensory neurons receive most of the inputs from polysensory areas, namely the anterior ectosylvian sulcus and the lateral suprasylvian cortex. This means that the development of multisensory integration in the superior colliculus will also depend on the development of these polysensory areas (i.e., cortical development).

Despite the early existence of multisensory neurons, their ability to integrate in a multisensory fashion is not an innate capability. This ability is driven by experience, and upon the correct development of sensory experience depends the maturation of multisensory integration as well (Wallace & Stein, 1997; 2000; Wallace et al., 2004). Wallace et al. (2004) documented this issue by rearing cats without any visual experience, and by observing whether the absence of early sensory experience could affect the development of multisensory neurons in the superior colliculus and their ability to integrate multisensory information. Recording of single neurons was performed when cats had achieved maturation. Results showed that visual deprivation did not prevent animals from developing multisensory neurons. However, sensory deprivation led to an altered distribution of sensory-responsive neurons in the superior colliculus, with an expansion of auditory and somatosensory responses, but did not completely suppress visually responsive neurons. In addition, these neurons had larger receptive fields (as in neonatal animals), which degrades the spatial register of the single neuron's receptive fields, leading to the inability to integrate multiple sensory cues. The parallel between adult-deprived multisensory neurons and neonatal neurons suggests that sensory deprivation could result in immature shaping of these neurons in adulthood. Most importantly, the main



difference of multisensory neurons in deprived animals and controls was observed in their response to multisensory stimuli. Neurons in deprived animals did not respond with substantial enhancement of activity when presented with spatially and temporally coincident multisensory stimuli. Rather, their responses were comparable to those given to one modality-specific stimuli component, reflecting a lack in multisensory integration. In addition, a general decline in non-visually responsive neurons was seen as well, further documenting that impairment in one modality influences general development of the other sensory component. The latter aspect leads to question of whether the visual modality represents a particular case of sensory modality. This issue was addressed by some studies (King et al., 1988; Knudsen & Brainard, 1991), who found in both avian and mammalian species that displacement of the visual field during development leads to a gradual shift of the auditory space map. In other words, the altered visual experience given by placing prisms in the animals' eyes (Knudsen & Brainard, 1991) caused an immediate misalignment between locations of the auditory and visual receptive fields. However, prolonged exposure to prisms caused the auditory receptive fields to realign with the visual ones, suggesting the crucial role played by vision in calibrating auditory cues in order to benefit of bimodal stimulation.

The previous studies speak for multisensory integration particularly as a consequence of visual experience in shaping its normal development. However, whether the loss of auditory or somatosensory input leads to lack of development of multisensory processes, still remains to be investigated. A way to document whether the development of multisensory processes is also driven by other sensory modalities different from vision is represented by the case of cochlear implant recipients. In particular, prelingually deafened adults, implanted late in life, represent

a challenging population to address the question of whether multisensory abilities are strongly shaped during early childhood.

### **6.3 Audio-visual interplay after cochlear implantation**

The previous paragraph has shown that the ability to integrate multisensory information results in enhanced responses, both from a physiological and behavioural point of view. In addition, multisensory integration largely contributes to speech recognition, which is based on the simultaneous integration of visual information coming from lip movements and the auditory information produced by the talker. Most of the studies that have investigated how vision and hearing interact after cochlear implantation have focused on audio-visual speech interaction. Audio-visual speech integration in cochlear implants has commonly been investigated by either presenting the auditory component alone or with lipreading (visual component), with the aim to investigate the outcome of speech comprehension after cochlear implantation, particularly in children (Tyler et al., 1997; Lachs et al., 2001; Geers et al., 2003). For example, Bergeson et al. (2005) conducted a longitudinal study on a group of prelingually deafened children to observe their development in audio-visual speech comprehension over a period of 5 years after cochlear implantation. Bergeson et al. (2005) measured comprehension of sentences presented in the auditory or visual modality alone or in a combined audio-visual fashion. In addition, they investigated the role of communication mode experienced before implantation (oral vs. total communication, i.e., oral and sign language) and the age at implantation. All children acquired deafness before the age of 3 years and

received their CI before 9 years of age. The results showed that children performed better during audio-visual sentence comprehension compared to auditory or visual comprehension alone. This ability improved over 5 years after cochlear implantation. Interestingly, auditory and audio-visual conditions improved at a greater rate compared to visual alone condition, suggesting the auditory benefit that CIs can give for speech comprehension skills. Similar results were documented by Kaiser et al. (2003) for the adult population. They examined how postlingually deafened adults with cochlear implant combine visual information from lipreading with auditory cues in an open-set word recognition task, with presentation of words under auditory-only, visual-only or audio-visual condition. Results showed that word recognition was highest for audiovisual presentation, followed by auditory-only and visual-only conditions. CI users made better use of visual cues compared to the hearing controls, relying more on the visual component in ambiguous situations, but were overall better in auditory-alone conditions than visual-only conditions. The finding that postlingually deafened adults fitted with a cochlear implant performed comparably to hearing controls in audio-visual speech comprehension tasks is interesting because it suggests that even an altered sound perception given by the device does not impair the previously acquired multisensory linguistic experience. Interestingly, even prelingually deafened adults seem to have a pattern of results similar to postlingually deafened individuals. Moody-Antonio et al. (2005) determined whether congenitally deafened adults implanted in adulthood achieved improved speech perception with auditory and visual speech information simultaneously available. Subjects were aged between 18 and 55, had profound congenital bilateral hearing loss and had at least 1-year experience with their implant. The results showed that subjects were on average better in the audiovisual condition compared

to the auditory and visual alone condition, suggesting that even congenitally deaf individuals, who receive a cochlear implant in adulthood, can integrate auditory information with visual speech information despite the lack of auditory experience before implantation.

Results so far speak for good audio-visual speech abilities in cochlear implant recipients, who seem to gain in integrating the two sensory information to better discriminate speech perception. However, these studies seem to point out to a benefit derived from summation of the two sensory information, and it remains unclear whether cochlear implant recipients can really *integrate* the visual and auditory information. A study by Rouger et al. (2007) has precisely addressed the question of whether cochlear implant recipients can fuse visual speech information with auditory information in a similar fashion to hearing controls. To this aim, 97 postlingually deafened adults were tested on unimodal (auditory or visual only) and bimodal (audio-visual) conditions over a period of 8 years (stimuli were disyllabic words). At the time of activation, speechreading performance for cochlear implant users was found to be much higher compared to hearing controls, and, interestingly, it did not decrease as a function of implant use. In audio-visual conditions, cochlear implant recipients reached a near-perfect performance level after only two months from implantation, compared to the unisensory conditions. This result suggests that cochlear implant recipients develop greater ability in speechreading during the period of deafness, which induces this population to improve multisensory integration skills after implantation. To further investigate whether this ability occurs as a consequence of enhanced visual abilities acquired during deafness prior to implantation, or as enhanced audio-visual integration abilities per se, the visuo-auditory gain in cochlear implant recipients tested at activation was compared with

that of a group of hearing controls exposed to a degraded auditory signal. In addition, to further test the hypothesis that the difference between cochlear implant recipients and hearing controls for multisensory integration do not mainly derive from a different visual performance, a subgroup of cochlear implant recipients with low visual performance was selected. Results showed a difference in favour of cochlear implant users, leading to the conclusion that cochlear implant recipients are better multisensory integrators compared to hearing controls.

Although the latter study provides evidence of multisensory abilities that are even enhanced in cochlear implant recipients, it is worth noting that the audio-visual stimulus was always congruently paired, leaving the question open of whether cochlear implant recipients can also segregate incongruent audio-visual information. A recent study by Champoux et al. (2009) tested a group of prelingual and postlingual deaf recipients on an auditory speech recognition task in the presence of 3 incongruent visual stimuli that could be either a color-shift, a dot-motion or a lip motion. The recipients were divided in two groups ('proficient users' vs. 'non-proficient users') according to their performance on the auditory-alone condition. All recipients were matched with hearing controls who were exposed to a degraded auditory signal. Results showed that presentation of visual stimuli impaired concurrent auditory stimuli in non-proficient cochlear implant users but not in proficient cochlear implant users. In addition, this pattern of results was present either with linguistic and non-linguistic stimuli. Overall results suggest that in non-proficient CI users (i.e., with low speech perception scores) vision, if not congruently matched, may interfere with the auditory signal provided by the implant.

Finally, it is worth pointing out that audio-visual speech perception may constitute a special case of multisensory integration, and the issue is still debated.

On the one side, some studies (Massaro, 2004) suggest that audio-visual speech perception is fundamentally a prototypical situation of audio-visual integration, in which information conveyed through face and voice are tightly processed to impose a face-to-face communication. On the other side, other studies suggest (Meltzoff & Moore, 1997) that speech perception may be supramodal, in that it is the representation of bodily gestures that go far beyond the single sensory modalities.

### **6.3 Aim of part III of the thesis**

The last part of the thesis investigates the effects of auditory reafferentation through a cochlear implant on visual and audio-visual abilities in both prelingually and postlingually deafened adults who received their CI in adulthood. In addressing these issues, we tested two different groups of prelingual and postlingual deaf who received their implant in adulthood on two tasks. In a first study, we investigated the consequences of auditory reafferentation on the visual modality, and prelingual and postlingual recipients' performance was measured on a detection task, in which speed of response was measured. In a second study, we tested other two groups of prelingual and postlingual deaf adult recipients on an audio-visual task, consisting in the presentation of rapid, non-linguistic, visual and auditory stimuli that could be either congruently or incongruently paired. Aim of both studies was to compare performance between the two groups, with the hypothesis that both compensatory visual reorganisation prior and after implantation could lead to different processing of the visual input as well as its integration with the reafferented sensory system.

# **CHAPTER 7**

Enhanced visual abilities in  
prelingual but not postlingual CI  
recipients

## **7.1 Abstract**

Studies on profoundly deaf individuals suggest that this population undergoes compensatory plastic changes that appear for some aspects of the visual modality, particularly for stimuli presented in the periphery of the visual field. However, no study to date has addressed the question of whether visual compensatory changes may be reversed after reafferentation of the auditory system after cochlear implantation. Here we measured reaction times to visually presented stimuli appearing in central and peripheral locations on a computer monitor in two groups of adult cochlear implant recipients, who experienced auditory loss either early or late in life (prelingual vs. postlingual deafness onset), and received their implant in adulthood. Results showed that prelingually deafened recipients were faster than postlingually deafened recipients for stimuli appearing in the periphery of the visual field. While prelingual deaf had comparable speed of response for stimuli presented in central and peripheral locations, postlingually deafened individuals paid a cost for stimuli presented in the periphery of the visual field, as typically found in hearing controls adopting identical task and stimuli. These findings lead to suggestion that compensatory changes that occur early in life cannot be reversed in adulthood in case of sensory reafferentation.



## 7.2 Introduction

The present study investigated the effects of auditory reafferentation on visual abilities in a group of prelingual and postlingual recipients, implanted late in life, adopting a visual detection task. The novelty of this study consists in having addressed the question of what happens to the remaining sensory modalities once auditory abilities are partially restored. In addition, this is also the first study that adopted non-linguistic stimuli with the aim to observe reactivity to rapid visual stimuli appearing in 8 different spatial locations on the computer monitor.

The visual detection task was adapted from a study by Bottari et al. (2009, in press), which compared reaction times for a group of deaf individuals and a group of hearing controls for visual targets appearing at 3 or 8 degrees from central fixation, and at two different time intervals after warning at fixation (short interval: 400-800 ms; long interval: 1800 ms). The reason why we adopted this task is that, as seen in Part I of the work, not all aspects of vision are enhanced as a consequence of auditory deafferentation. However, a general observation concerning visual processing in the deaf is that enhanced abilities at the behavioural level mainly emerge in tasks measuring speed of response rather than accuracy (Loke & Song, 1991; Colmenero et al., 2004). In addition, this enhanced visual reactivity seems to be spatially selective, as it occurs particularly for stimuli presented in the periphery of the visual field (Loke & Song, 1991; Parasnis & Samar, 1985). Bottari et al. (2009, in press) found overall faster reaction times in deaf individuals than hearing controls. In addition, they documented that deaf individuals responded equally fast to central and peripheral visual targets compared to controls, who instead paid an RT cost when stimuli occurred at the visual periphery, confirming an advantage for peripheral target locations in the deaf. This difference in performance between group as a function of

eccentricity approached significance when the time interval between the warning and the target was long (i.e., 1800 ms), whereas was clearly evident for target appearing after shorter time intervals (i.e., 400 to 800 ms). This modulation of enhanced visual abilities as a function of the ISI between warning and target has also been recently replicated in a ERP study conducted by Bottari and colleagues (Bottari, Giard, Caclin & Pavani, in preparation). In this view, the rationale beyond our study was to observe the effects of auditory reafferentation through a cochlear implant on this particular visual aspect that seems to characterise in a compensatory fashion the visual system in the deaf.

For the present study we recruited both prelingual and postlingual deaf individuals. For the prelingual deaf, our working hypothesis was that any visual ability that developed in this population as a consequence of compensatory changes would not be reversed by auditory reafferentation. For the postlingual deaf, our hypothesis was that the late auditory deprivation would determine smaller or negligible reorganisation of the visual system. As suggested by King (2001), adult plasticity is more the consequence of adaptation, and does not involve anatomical remodelling. Our previous studies (Nava et al., 2009a; Nava et al., 2009b) have indeed shown that whenever auditory cues are restored in postlingually deafened adults, their recovery occurs in the shortest period. Therefore, it could be hypothesised that postlingually deafened adults, implanted late in life, may not show any enhanced visual ability for the periphery of the visual field.

### 7.3 Methods

#### *Participants*

15 prelingual and 10 postlingual deaf recipients were recruited to take part in the study. Among these, 21 (all prelingual and 6 postlingual) were recruited through collaboration with the hospital “Santa Maria del Carmine” (Rovereto, Italy), 3 postlingual were recruited through collaboration with the hospital of Vicenza (Italy) and 1 postlingual deaf was recruited through collaboration with the hospital of Reggio Emilia. The prelingual deaf group was on average 25 years old (SE = 6, range between 16 and 40 years) when tested, and 4 among them were congenitally deaf. The postlingual deaf group was on average 45 years old (SE = 11, range between 35 and 68 years) when tested. Participants’ experience with their implant ranged between 0 (time of activation of the implant) and 9 years, with an average of 4 years for the prelingual and 3 years for the postlingual recipients (see Table 1 for further details on participants). All participants had normal or corrected-to-normal vision and were right-handed by self-report. Before testing, all participants signed an informed consent. The study was approved by the Ethical Committee of the University of Trento.

<i>ID</i>	<i>age</i>	<i>deafness onset</i>	<i>type of deafness</i>	<i>etiology</i>	<i>implanted ear</i>	<i>years from activation</i>	<i>type of implant</i>
1	22	1	prelingual	unknown	left	1	MED-EL
2	40	2	prelingual	unknown	right	7	MED-EL
3	16	0	prelingual	connexin	right	6	Clarion
4	27	0	prelingual	connexin	right	7	MED-EL
5	24	2	prelingual	unknown	right	7	Clarion
6	24	2	prelingual	unknown	right	0,1	MED-EL
7	20	2	prelingual	unknown	right	0	MED-EL
8	26	1	prelingual	unknown	left	7	MED-EL
9	26	2	prelingual	unknown	left	4	Clarion
10	19	1	prelingual	unknown	right	0,3	Clarion
11	29	0	prelingual	unknown	right	5	Cochlear
12	31	0	prelingual	unknown	right	9	MED-EL
13	31	3	prelingual	unknown	left	0,1	MED-EL
14	23	2	prelingual	unknown	right	7	Clarion
15	22	2	prelingual	ototoxic drugs	left	6	MED-EL
16	47	5	postlingual	unknown	left	0	MED-EL
17	56	25	postlingual	otosclerosis	bilateral	1	MED-EL
18	38	4	postlingual	virus	bilateral	0,6	MXM
19	38	38	postlingual	virus	left	0,1	MED-EL
20	68	66	postlingual	trauma	bilateral	2	MXM
21	36	27	postlingual	unknown	right	0,1	MED-EL
22	43	12	postlingual	virus	left	7	Cochlear
23	35	29	postlingual	trauma	right	7	Cochlear
24	55	20	postlingual	Turner syndrome	right	5	MXM
25	37	5	postlingual	unknown	left	9	Cochlear

Table 1

*Apparatus and stimuli*

All stimuli were presented on a 17 inches monitor (1024 × 768 pixel resolution), and the experiment was programmed with E-Studio 1.1.4.1 and controlled with E-Prime 1.1.4.1 (<http://www.pstnet.com/products/e-prime>). Visual fixation was a small white cross (approximately 1 degree of visual angle) presented at the centre of the screen throughout the trial. A flickering red square was presented around the white cross for 500 ms at the beginning of each trial to warn the

participant of the upcoming target and to attract fixation to the centre. After the red square disappeared, fixation could remain still for either 500 ms or 1800 ms before target onset. Stimuli consisted of letters “C” either oriented rightwards or leftwards, which could appear in 8 possible spatial locations: 4 locations at 3 degrees of visual angle from central fixation (central locations), 4 locations at 8 degrees of visual angle from central fixation (peripheral locations, see Figure 1). Peripheral stimuli were corrected for the cortical magnification factor, so that central stimuli had 1.5 degrees of visual angle and peripheral stimuli had 2.6 degrees of visual angle. All stimuli had duration of 50 ms.

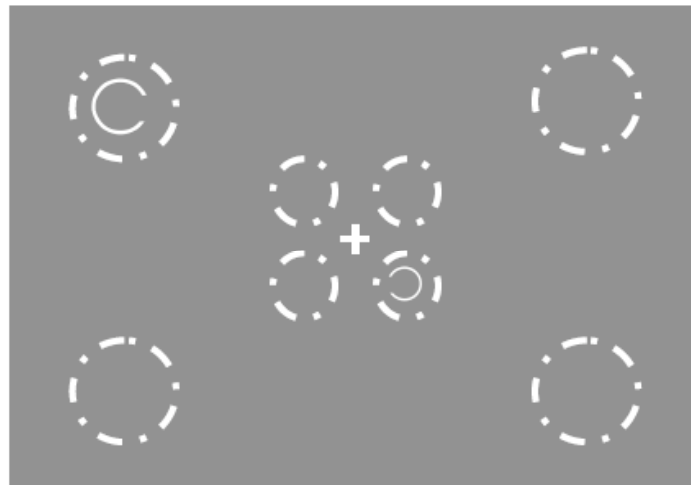


Figure 1

### *Procedure and design*

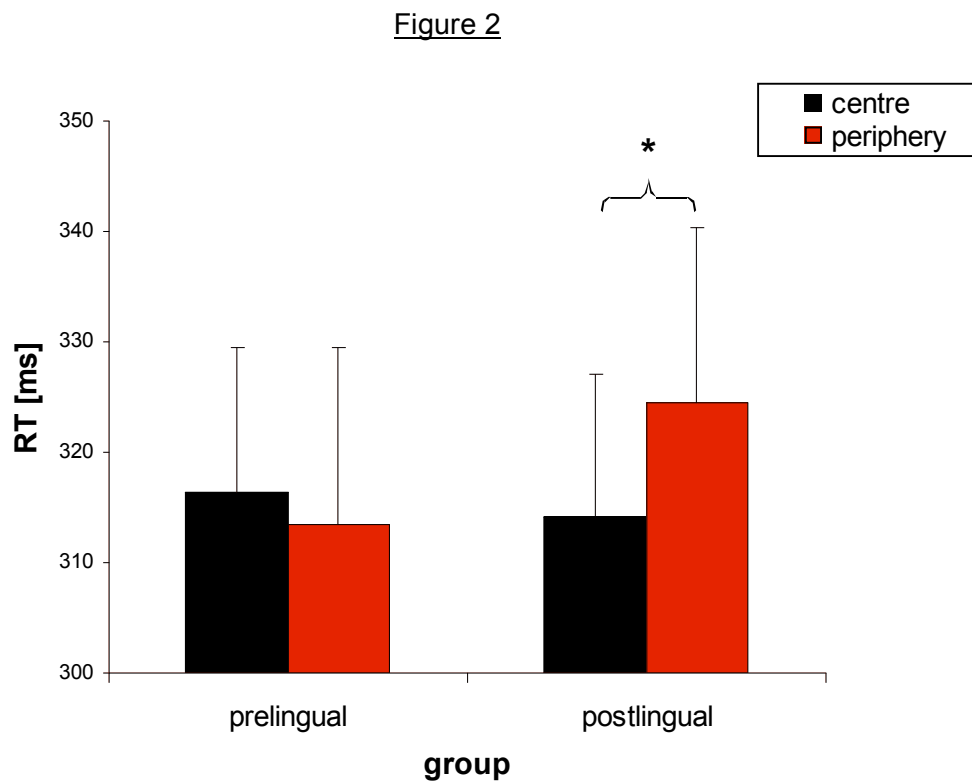
All participants were tested in silent rooms provided by the hospitals. Participants sat at approximately 60 cm from the computer monitor and were instructed to keep fixation on the white cross throughout the experimental session. The detection task comprised 4 blocks of 96 trials each (with equal distribution of all stimuli in the 8 different spatial positions), separated by pauses that participants could freely decide to take or skip. The experiment took approximately 30 minutes to complete. Participants were asked to simply press on the space bar as soon as they detected the stimulus, irrespective of stimulus location.

### **7.4 Results**

Median reaction times were computed for each participant and entered into a mixed Analysis of Variance (ANOVA) with target location (central or peripheral) and ISI (long or short) as within-participants factor, as well as group (prelingual, postlingual) as between-participants factor. This first analysis revealed a main effect for ISI ( $F(1, 23) = 48, p < 0.0001$ ), given by all participants being more rapid for stimuli presented at longer (mean = 297 ms, SE = 12) than shorter intervals (mean = 301 ms, SE = 12). In addition, there was a nearly significant interaction between target location and group ( $F(1, 23) = 4.3, p = 0.051$ ), caused by postlingual individuals tending to respond faster to central than peripheral targets (296 ms vs. 303 ms, respectively), unlike prelingual individuals who showed no difference in response time as a function of target eccentricity (299 ms vs. 299 ms, respectively). No other main effect or interaction reached significance.

As anticipated in the Introduction, previous evidence has revealed that differences between deaf and hearing individuals in reacting to visual events is more pronounced at short than long ISIs between warning and target (Bottari et al., in press; Bottari, Giard, Caclin & Pavani, in preparation). For this reason, we further explored the difference between groups as a function of eccentricity specifically for the shortest ISI. This follow-up analysis revealed a significant interaction between eccentricity and group ( $F(1, 23) = 4.4, p = 0.046$ ).

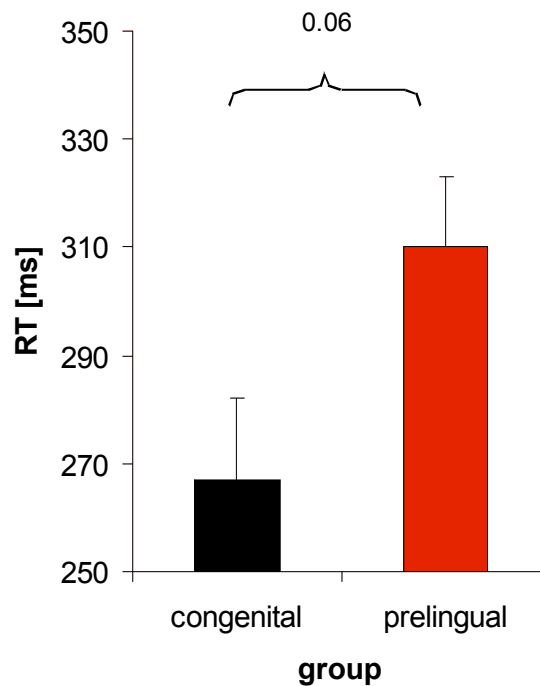
Figure 2 illustrates this interaction. In order to see whether there was a difference between responses given to central and peripheral targets, we performed paired samples t-test for the two groups separately. While there was no difference in response for prelingual deaf recipients ( $p = 0.5$ ), a significant difference emerged for postlingual deaf ( $t(9) = 2.6, p = 0.03$ ).



To examine the role of deafness onset for the prelingual deaf and duration of deafness for the postlingual deaf, we considered groups separately, and created subgroups among prelingual and postlingual deaf, namely: for prelingual deaf, congenital deaf were kept separated by the other participants with deafness onset after 1 year of age. For postlingual deaf, we separated those who had deafness duration of less than 10 years from those who had more than 10 years auditory deprivation prior to implantation.

When considering reaction times (shorter ISI only) for prelingual deaf (congenital vs. prelingual deafness onset), regardless of eccentricity, we found a trend towards significance ( $p = 0.06$ , see Figure 3), but note that we only had 4 congenital deaf out of 15.

Figure 4





In considering postlingually deafened adults, we divided this group into < 10 years of deafness duration vs. > 10 years of deafness duration, and calculated their reaction times at the shortest ISI but separately for eccentricity, as they were found to perform differently per target location. We found no difference between these two groups, but note that we only had 10 postlingually deafened adults (4 individuals < 10 years deafness duration; 6 individuals > 10 years deafness duration).

Finally, to confirm that the previous patterns of results derive from changes that occur before implantation, and that they are not reversed through extensive use of cochlear implant use, we correlated the differences in reaction times between peripheral and central locations with the years of the single individual in implant use. Figure 4 shows the trend as a function of implant use separately for prelingual and postlingual deaf. Note that no significant correlation was found.

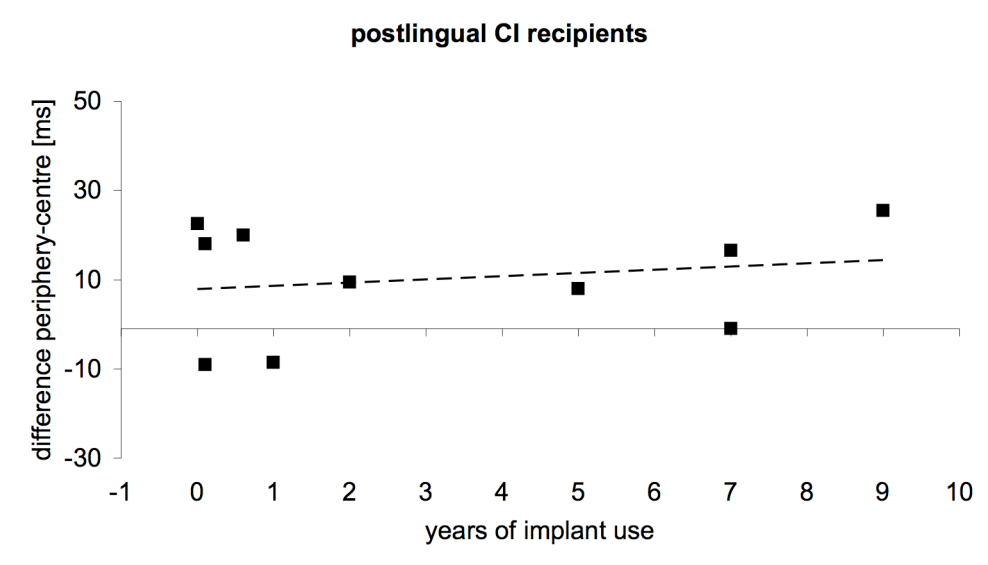
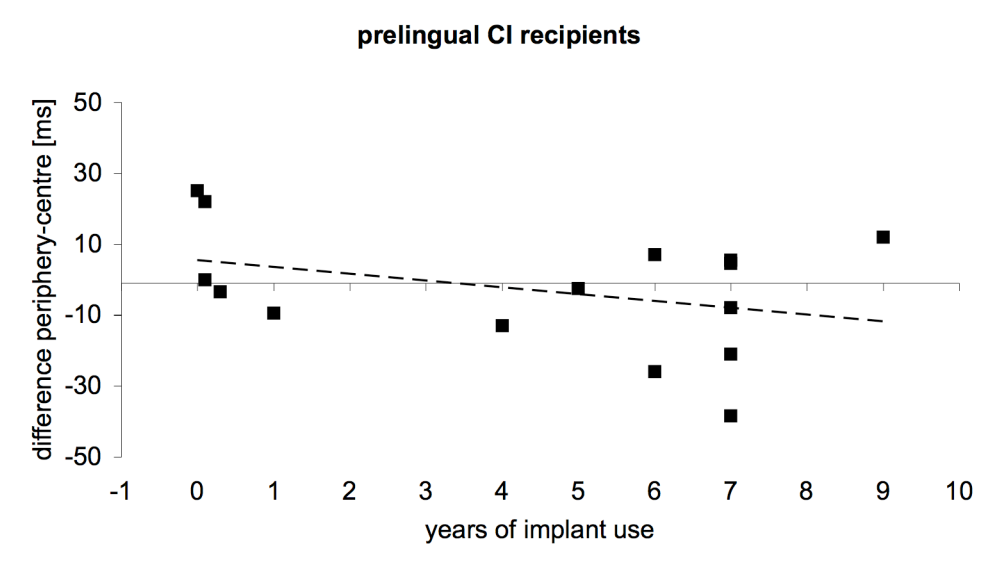


Figure 4

## 7.5 Discussion

Recent findings on profoundly deaf individuals (Bottari et al., in press; Bottari, Giard, Caclin & Pavani, in preparation) show that when presented with visual stimuli, deaf individuals are more rapid than hearing controls in detecting the onset of rapid visual stimuli. In addition, when comparing performance of deaf and hearing controls for central and peripheral spatial locations, deaf individuals show no RT cost when processing peripheral targets unlike hearing controls, who show a difference in speed of response between central and peripheral target locations. As suggested by Bottari et al. (in press), this advantage for peripheral targets in deaf individuals may be caused by a reorganisation in the representation of the periphery of the visual field from an anatomical point of view. In other words, the consequences of an early auditory loss may result in an expansion of visual neurons devoted to the processing of peripheral events. Because this hypothesis speaks for neural changes that likely occur early in life, it leads to the strong prediction that these structural changes cannot be reversed in adulthood through reafferentation of the deprived sensory modality.

To address these questions, the present study tested the effects of auditory reafferentation through a cochlear implant on visual abilities in prelingually and postlingually deafened adults implanted late in life. The task adopted allowed observing an aspect which has proven to be central as a consequence of compensatory changes for the visual modality in profoundly deaf individuals: speed of response, particularly for stimuli presented in the periphery of the visual field. Here we investigated whether speed of response changes after auditory reafferentation, and whether it changes selectively for spatial location. We found that prelingual deaf recipients showed faster reaction times compared to postlingually deafened

individuals for stimuli presented in the periphery of the visual field. In particular, when considering speed of response within the group, we found that prelingual deaf recipients did not have, contrarily to postlingually deafened adults, a significant difference between central and peripheral targets. This result is particularly interesting because it matches the one found by Bottari et al. (2009, in press), who documented an overall advantage in terms of speed of response for deaf individuals compared to hearing controls. However, while the latter group paid a cost in reaction times for stimuli presented in the periphery of the visual field, deaf individuals had no difference in response between the two spatial locations.

In a further analysis prelingual deaf recipients were divided into congenital and early-deafened adults to test for additional differences within the same group, and to underline the role of age at deafness onset in case of prelingual deafness. Interestingly, we found a nearly significant difference between congenital and early deafened adults. This latter result suggests that there may be great difference between those who were never exposed to any auditory experience (congenital deafness) and those who have experienced even a very short period of hearing. Finally, our results showed that enhanced abilities in the prelingual deaf do not decrease as a function of implant use, as even after years of device experience the pattern of results remains unchanged. In addition, this latter result speaks for plastic changes that have occurred before implantation, not as a consequence of auditory reafferentation.

The fact that prelingual and postlingual deaf adults showed a pattern previously documented in deaf and hearing controls respectively, adds evidence to the notion that whenever an experience (be it typical or atypical) is achieved early in development, it will have particular strength in shaping the brain and behaviour

(Knudsen, 2004). In this view, it could be hypothesised that the development of neural representations of the central and peripheral visual fields are not altered by adult experience. To the best of our knowledge, the only evidence that documented that visual abilities can remain unchanged after cochlear implantation comes from Doucet et al. (2006), who measured evoked potentials involved in the processing of visual stimuli in prelingual and postlingual deaf. However, their results showed that all participants had greater activation of the visual cortex compared to hearing controls, suggesting greater reliance on visual cues after auditory reafferentation. However, in this study participants were asked to passively view a high contrast sinusoidal concentric grating followed by a star-shaped grating (overall stimulus duration = 1 sec). By contrast, in our study participants had to actively respond to a visual stimulus, suggesting that our data speak for functional changes that become evident under attentional demands.

In conclusion, this is the first study to document that functional compensatory changes occurring as a consequence of early hearing loss do not reverse after auditory reafferentation through a cochlear implant. Future research may shed light on the neural correlates of the present findings, achieving evidence of structural changes that underpin these very stable compensatory changes.

## **CHAPTER 8**

Visual illusions induced by  
sounds in prelingual and  
postlingual CI recipients

## **8.1 Abstract**

Most of the studies that have investigated multisensory interactions in cochlear implant recipients have so far focused on audio-visual speech perception, leaving open the possibility that any observed interaction could derive from linguistic rather than perceptual abilities. The present study investigated, for the first time, audio-visual interactions for non-linguistic stimuli in prelingual and postlingual deaf adults who received a cochlear implant late in life. We adopted a task in which 1, 2 or 3 visual flashes could be presented either alone or combined with congruent or incongruent number of auditory beeps. We hypothesised that particularly prelingually deafened individuals would rely more on the visual component than postlingually deafened adults and hearing controls. Notably, our results showed that prelingual deaf CI recipients performed comparably to postlingual deaf CI recipients and hearing controls, suggesting comparable audio-visual interactions on this type of conflict paradigm. However, our findings speak more about the nature of this multisensory illusion, and any conclusion about multisensory abilities in cochlear implant recipients cannot be drawn from this particular task.

## 8.2 Introduction

In the past years, several studies (Schleich et al., 2004; Van Hoesel & Tyler, 2002; Verschuur et al., 2005) have examined the effects of auditory reafferentation through a cochlear implant on perceptual functions, particularly focusing on the reafferented modality (i.e., audition). The study we reported in Chapter 7 has documented, for the first time, the effects of auditory reafferentation on the visual modality. However, a further issue that has to date received little attention concerns the interaction between the reafferented modality (hearing) and the remaining sensory modality. In fact, the study of multisensory integration in cochlear implant recipients has so far been investigated only for audio-visual interactions involved in seen and heard speech. For example, Bergeson et al. (2005) measured comprehension of sentences presented in the auditory or visual modality alone or in a combined audio-visual fashion in prelingually deafened children. This study showed a benefit in audio-visual sentence comprehension compared to auditory or visual comprehension alone. Similar results were documented by Kaiser et al. (2003) for the adult population, in which perception of words presented unimodally (i.e., lipreading or hearing alone) or bimodally (i.e., audio-visual) were compared. Word recognition was higher for audiovisual presentation, although cochlear implant users made better use of visual cues compared to the hearing controls, relying more on the visual component in ambiguous situations. Finally, Moody-Antonio et al. (2005) determined whether congenitally deafened adults implanted in adulthood could achieve improved speech perception with auditory and visual speech information simultaneously available. Even for these individuals, who were never exposed to sounds, audiovisual speech comprehension was higher compared to unimodally presented information.



A particularly relevant study in this domain has been conducted by Schorr et al. (2005). They examined whether a critical period exists in the development of the ability to fuse the auditory and visual information to achieve a unified percept. To this aim, Schorr et al. (2005) studied the so-called McGurk effect, in which a listener presented with a spoken syllable (e.g., /pa/) while watching a video-recorded mouth articulating another syllable (e.g., /ka/), usually perceives a third syllable (e.g., /ta/) emerging from the fusion of the other two. In that study, 36 children (age-range between 5 and 14 years), profoundly deaf from birth, and implanted at least 1 year before testing, were presented with unimodal (auditory and visual alone syllables) and bimodal congruent or incongruent syllables pairs. All children were able to discriminate the unimodally presented visual and auditory stimuli, as well as the bimodal congruent syllables. However, on incongruent trials (McGurk effect), 70% of the children had very few fusion effects. Interestingly, when comparing type of answer in the poor fusion trials (whether a visual or auditory answer was given) between CI recipients and hearing controls, the latter group tended to respond to the auditory component, while CI children reported the visual component of the stimulus, suggesting a higher dependence on lip-reading than auditory information. Interestingly, A further finding of this study was that the likelihood of consistent fusion depended on the age of the child at implantation: children who received their implant before 2.5 years of age exhibited more bimodal fusion compared to children who received their implant after this age, suggesting that there may be a critical period for developing typical and strong bimodal fusion.

In the present study, we investigated how multisensory information is processed in prelingual and postlingual CI adult recipients who received their implant late in life, adopting for the first time a non-linguistic task. The task we used was

adapted for these participants from a well-known audio-visual illusion: the sound-induced illusory effect (Shams et al., 2002), in which adults, when presented with a single flash accompanied with multiple auditory beeps, usually report more flashes than actually presented. This paradigm presents some advantages in that, besides making use of non-linguistic auditory and visual stimuli, it presents them from the same spatial location, avoiding any problem with localisation abilities. As seen in Nava et al. (2009), spatial localisation abilities particularly for prelingually deafened adults implanted monaurally are poor, and in administering audio-visual tasks, the spatial component should be taken in consideration.

Here we tested recipients with the hypothesis that audio-visual performance would differ between prelingual and postlingual deaf. In particular, given our previous results on enhanced visual abilities in prelingual deaf recipients even after several years of implant use, and given that this task does not make use of linguistic stimuli (i.e., that can somehow help in building a sense out of audio-visual information), we hypothesised that prelingual recipients would rely more on vision and not be able to integrate the audio-visual compound. Based on similar reasons, we hypothesised that postlingually deafened adults would equally rely on auditory and visual information, and perceive more illusion compared to the prelingual group.

### 8.3 Methods

#### *Participants*

20 naïve volunteers participated in the study after informed consent was given. All participants were recruited through collaboration with the hospital “Santa Maria del Carmine” (Rovereto, Italy). Among these participants, 9 were postlingually deaf (mean age = 43, SE = 4, range between 31 and 60 years), and 11 were prelingually deaf recipients (mean age = 22, SE = 2, range between 18 and 41) when tested. Participants’ experience with their implant ranged between 0 (implant activation) and 11 years. Participants signed and informed consent before testing. The study was approved by the Ethical Committee of the University of Trento. Further details are shown in Table 1.

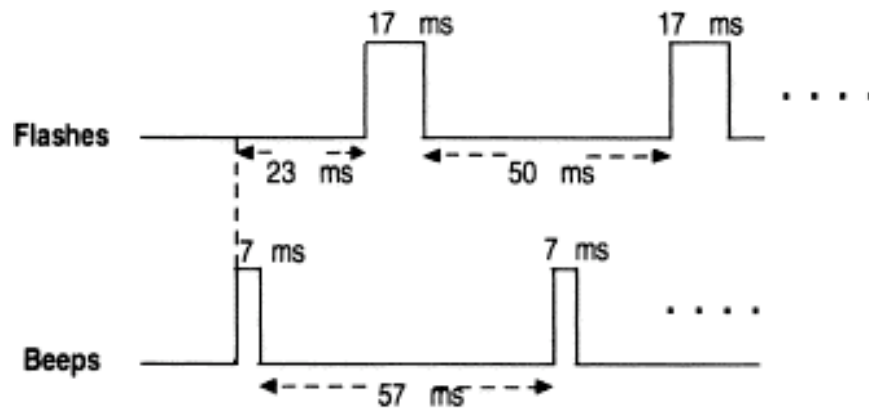
<b>ID</b>	<b>age</b>	<b>deafness onset</b>	<b>type of deafness</b>	<b>etiology</b>	<b>implanted ear</b>	<b>years from activation</b>	<b>type of implant</b>
1	18	1	prelingual	unknown	right	10	Cochlear
2	23	0	prelingual	unknown	right	4	Cochlear
3	20	2	prelingual	unknown	right	1	MED-EL
4	19	1	prelingual	cytomegalovirus	left	6	Cochlear
5	32	0	prelingual	connexin	left	2	Cochlear
6	40	0	prelingual	connexin	left	0	Clarion
7	18	1	prelingual	unknown	right	0	MED-EL
8	24	1	prelingual	unknown	right	11	MED-EL
9	18	0	prelingual	connexin	right	5	Cochlear
10	16	0	prelingual	connexin	right	5	MED-EL
11	53	52	postlingual	unknown	right	0,1	MXM
12	38	38	postlingual	virus	left	0	MED-EL
13	31	5	postlingual	unknown	left	1	MED-EL
14	56	25	postlingual	otosclerosis	bilateral	1	MED-EL
15	32	18	postlingual	otosclerosis	left	1	MED-EL
16	38	4	postlingual	virus	bilateral	0,3	MXM
17	36	27	postlingual	unknown	right	0	MED-EL

Table 1

### *Apparatus and stimuli*

Visual stimuli (flash) consisted of a uniform yellow disk subtending 2° of visual angle presented at 5° eccentricity below fixation point positioned at the centre of a black-background computer monitor. Auditory stimuli (beep) consisted of a 65 dB beep at 3.5 kHz frequency presented from two loudspeakers positioned on the two sides of the monitor. The pitch was chosen arbitrarily, according to Shams et al. (2002), who found no difference in results for varying frequencies. Visual stimuli could be presented either alone (unimodal condition: 1, 2 or 3 flashes) or combined with 1, 2 or 3 auditory beeps (bimodal condition, either congruent or incongruent). Each beep had duration of 7 ms, and in bimodal conditions beeps preceded the flashes by 23 ms and were spaced 57 ms from each other. Flashes had duration of 17 ms and were spaced 50 ms from each other (see Figure 1).

Figure 1



(Shams et al., 2002)

### *Procedure*

Participants sat at approximately 60 cm from the monitor and were asked to judge the number of sequentially presented flashes, while ignoring the concurrent beeps. Responses were given by pressing the corresponding number on a computer keyboard. The experiment consisted of a short practice session and two blocks of 120 trials each (20 trials per condition), randomly presented. In addition, a block of 30 randomised auditory stimuli alone (1, 2 or 3 beeps) was presented in order to test participants' sensitivity to the single beeps. Participants were asked to keep their fixation towards a small white cross, presented at the centre of the monitor throughout the experiment.

The bimodal conditions could lead to congruent conditions (i.e., 2 beeps together with 2 flashes) or illusory trials (incongruent presentation of flashes and beeps). When the number of beeps exceeds the number of flashes, a so-called 'fission' is experienced, given by participants usually reporting more flashes than actually presented. By contrast, when the number of beeps is less than the number of flashes, a so-called 'fusion' is experienced, with participants usually reporting fewer flashes than actually presented.

## 8.4 Results

### *Auditory baseline*

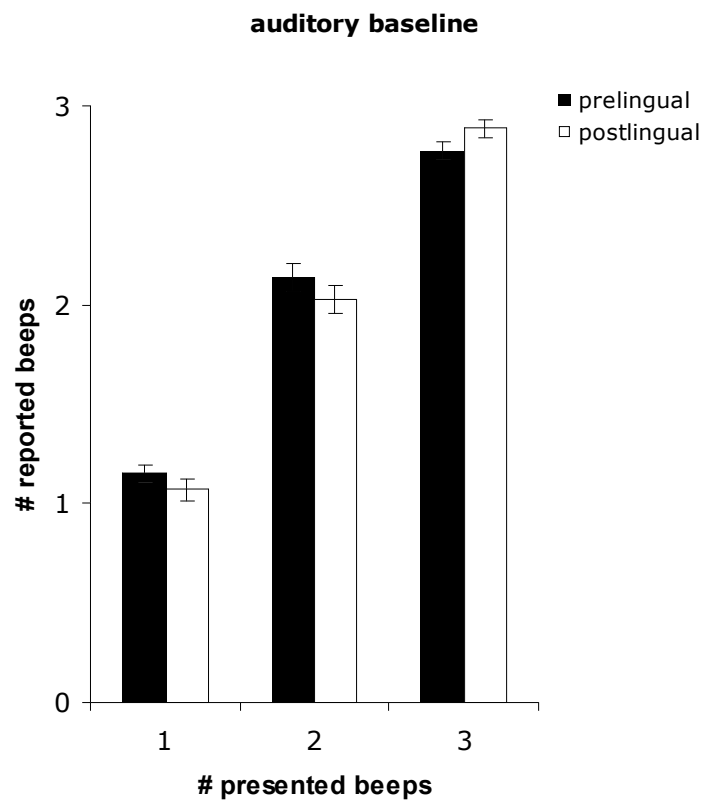
We started by analysing the auditory baseline for each participant, i.e., the accuracy in discriminating between 1, 2 or 3 beeps when presented unimodally. Auditory baselines were extracted from a single block of auditory stimuli that participants performed prior to the multisensory task. Three participants (one prelingual and two postlingual deaf) were excluded from further analyses. One prelingual and one postlingual participant were excluded because their auditory discrimination performance was on average lower than 60%. The remaining postlingual participant was excluded because of insufficient data collection.

Average response for each stimulation was entered into an ANOVA with number of beeps (1, 2, and 3) as within-subjects factor and group (prelingual and postlingual) as between-participants factor. Note that this auditory baseline was collected on cochlear implant recipients only because pilot observations on hearing controls showed ceiling or near-ceiling performance in this unisensory task. Results showed no difference in response between groups, documenting no difference in auditory sensitivity to multiple beeps between prelingual and postlingual deaf recipients. There was however a main effect for number of beeps ( $F(2, 30) = 332$ ,  $p < 0.0001$ ), indicating that both groups were able to discriminate between 1, 2 and 3 beeps (see Figure 1).

In order to see to what extent the average responses given by the two groups were veridical, we performed one sample t-test against the actual number of presented beeps. Both groups overestimated the 1 beep stimulation ( $p = 0.004$ ) and

underestimated the 3 beeps stimulation ( $p < 0.0001$ ). In addition, a marginal tendency to overestimate the 2 beeps stimulation was also observed ( $p = 0.09$ ).

Figure 1



*Visual baseline*

The visual baseline was computed extracting responses from the unimodal condition (1, 2 or 3 flashes) presented during the test (i.e., unimodal visual events appeared intermingled among congruent and incongruent audio-visual trials). As for

the auditory baseline, visual responses were entered into an ANOVA with number of flashes (1, 2 and 3) as within-subjects factor and group (prelingual, postlingual and controls) as between-participants factor. We found a main effect of number of flashes ( $F(2, 46) = 522, p < 0.0001$ ), caused by participants being able to discriminate between 1, 2 and 3 flashes. Figure 2 shows performance on the visual baseline separately for group.

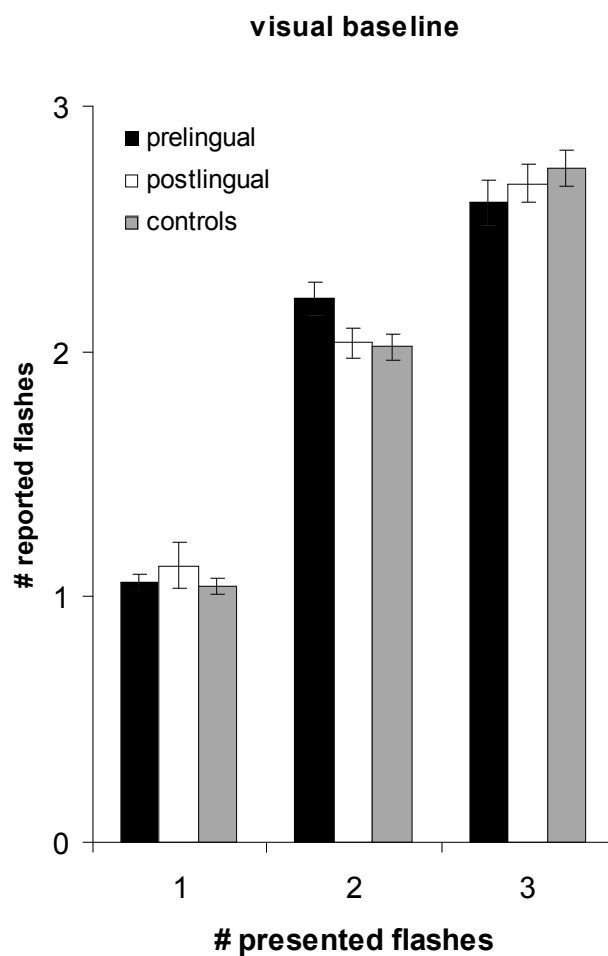


Figure 2



As for the auditory baseline, in order to see whether the average number of reported flashes was veridical we performed one sample t-test against the actual number of delivered flashes. All participants overestimated the 1 and 2 flash stimulation ( $p = 0.02$  on both comparisons) and underestimated the 3 flashes stimulation ( $p < 0.0001$ ).

### *Multisensory incongruent trials*

To test for the presence of illusory effects, we divided illusory trials into *fissions* (i.e., perception of more beeps than actually presented) and *fusions* (i.e., perception of fewer beeps than actually presented). Three combinations of audio-visual stimuli could give rise to fissions: 1 flash with 2 or 3 beeps, and 2 flashes with 3 beeps. Other three combinations of audio-visual stimuli could give rise to fusions: 2 flashes with 1 beep, and 3 flashes with 1 or 2 beeps.

We computed the illusory effect for fissions and fusions as the *absolute* difference between the reported and the actual number of flashes. Average illusory effects for each group are shown in Figure 3. Note that while for fissions any value above zero indicated the tendency to report a higher number of flashes than actually presented, for fusions any value above zero indicated the tendency to report less flashes than actually presented. These illusory effects were entered into an ANOVA with illusion type (fission or fusions) as within-participants variable, and group (prelingual, postlingual and controls) as between-participants variable. This analysis revealed a significant effect of the intercept ( $F(1,22) = 61.2$ ,  $p < 0.0001$ ), indicating that values were overall above zero (i.e., audio-visual illusions were indeed present). However, the main effect of group, the main effect of illusion type and the 2-way interaction were all far from significance (all  $F_s < 1$ ).

For completeness, we also analysed the un-signed error, without collapsing across the audio-visual conditions that produced fissions and fusions, but again no significant effect of group nor interactions involving this variable emerged.

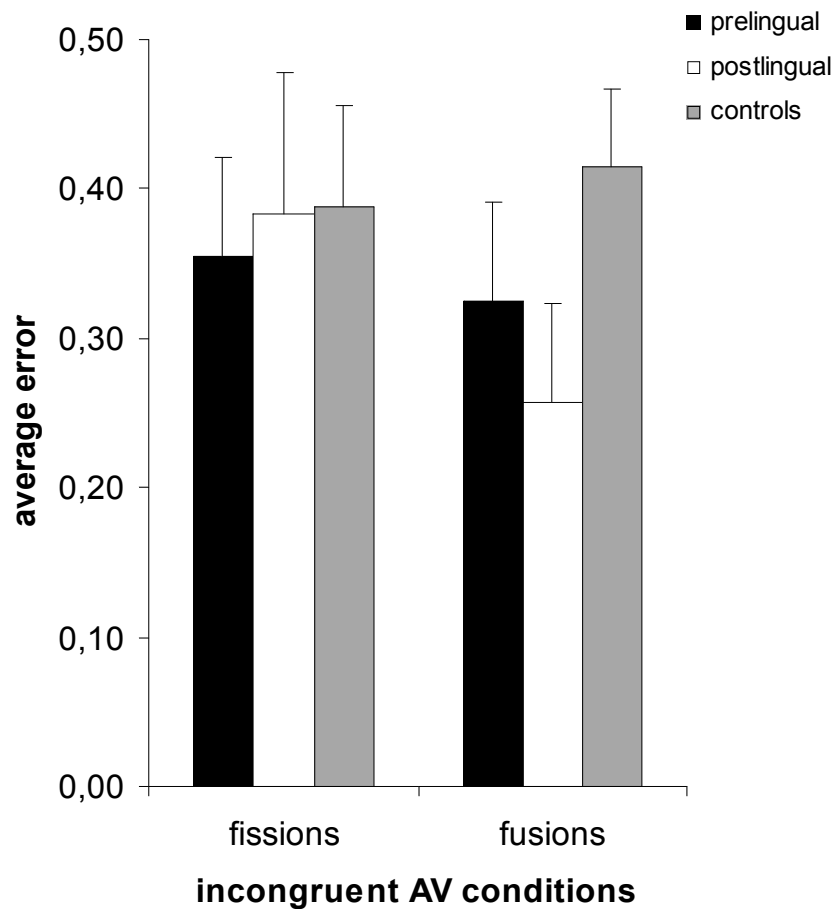
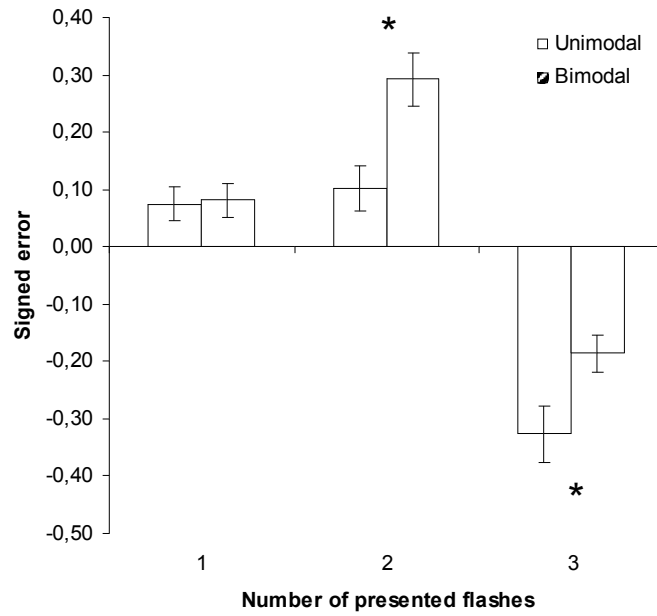


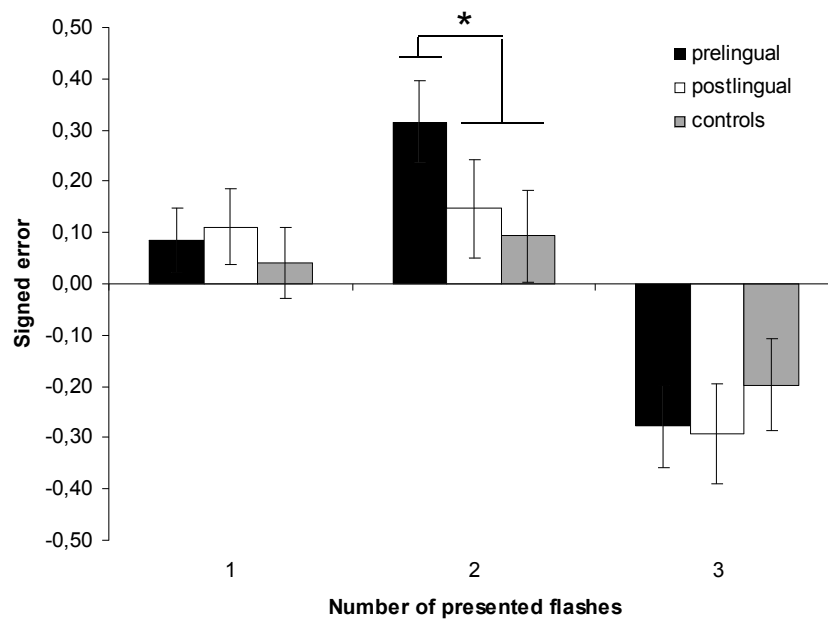
Figure 3

Figure 4

(a)



(b)



### *Multisensory congruent trials*

Having assessed that the three groups were equally affected by multisensory incongruent trials (reporting more flashes than actually presented in fission audio-visual trials, and less flashes than actually presented in fusion audio-visual trials), we investigated whether performance on reporting the number of flashes was modulated when audio-visual congruent trials were presented (e.g., 1 flash paired with 1 beep).

We run an ANOVA on the signed error with number of flashes (1, 2 or 3) and stimulation condition (unimodal or bimodal) as within-participants variables, and with group (prelingual, postlingual and controls) as between-participants variables. This analysis revealed a main effect of number of flashes ( $F(2,44) = 56.9$ ,  $p < 0.0001$ ), caused by a slight but significant overestimation when 1 flash was presented (mean = 0.08; t-test against zero,  $p = 0.008$ ), an even larger overestimation when 2 flashes were presented (mean = 0.2; t-test against zero,  $p < 0.0001$ ), but an underestimation when 3 flashes were presented (mean = -0.3; t-test against zero,  $p < 0.0001$ ). As shown in Figure 4a, this main effect was modulated as a function of stimulation condition ( $F(2,44) = 7.3$ ,  $p < 0.002$ ), selectively when 2 and 3 flashes were delivered. In addition, as shown in Figure 4b, there was an interaction between number of flashes and group ( $F(4,44) = 2.7$ ,  $p < 0.04$ ), with larger overestimation for the prelingual group, selectively when 2 flashes were delivered. Note that the three-way interaction between number of flashes, stimulation condition and group was far from significance ( $F < 1$ ).

## 8.5 Discussion

In the present study we investigated audio-visual interactions in prelingual and postlingual deaf individuals fitted with a cochlear implant late in life. As anticipated in the introduction, all previous studies that have examined perception of audio-visual stimuli in CI recipients used linguistic materials (i.e., seen and heard speech), leaving open the possibility that any observed interaction could be specific to communication stimuli. The novelty of this study consists in having tested cochlear implant recipients on audio-visual stimuli that were entirely non-linguistic.

While audio-visual conflict paradigms have commonly demonstrated how vision captures spatially the auditory component (e.g., the ventriloquist effect) or even modifies the final percept (e.g., the McGurk effect), the present study adopted the so-called ‘visual illusion induced by sound’, in which the sound alters the perception of visual stimulation. In adopting this paradigm, we reasoned that prelingual deaf recipients could be influenced to a larger extent than postlingual participants and hearing controls by the visual component. This because the early onset and prolonged auditory deprivation in the prelingual population could have resulted in enhanced visual abilities (as discussed in Chapter 2 and 7) as well as preferential processing of the visual input. Instead, we hypothesised that postlingual deaf recipients could have a pattern of result similar to hearing controls.

In the preliminary analyses, we examined whether the three groups were able to discriminate between the numbers of auditory beeps and visual flashes presented unimodally. Results on the auditory baseline showed that both prelingual and postlingual deaf recipients were able to discriminate between the numbers of presented beeps, although with overestimation for 1 beep stimulation and underestimation for 3 beeps stimulation. This finding indicates that despite any

temporal or gap distortion introduced by the cochlear implant, all recipients were able to perform this simple task. Also, it is worth noting that prelingual and postlingual recipients had different experience with their devices at testing. While prelingual deaf recipients had on average 4.4 years experience, the postlingual deaf only had 4 months experience when tested, which suggests that auditory temporal discrimination was recovered very soon after implantation in the postlingual group (see also Chapters 4 and 5 of the present thesis). The visual baseline showed that all participants were able to discriminate between the numbers of presented flashes, albeit with overestimation for 1 and 2 flashes and underestimation for 3 flashes.

When we turned to examine performance of the three groups in the multisensory trials results were clear cut. In incongruent audio-visual pairings, all participants experienced both types of illusory effects, with no difference whatsoever between groups. Participants reported more flashes than actually presented when the number of beeps exceeded the number of flashes (i.e., *fission* audio-visual conditions), and reported less flashes than actually presented when the number of beeps was lower than the number of flashes (i.e., *fusion* audio-visual conditions). In congruent audio-visual pairings, although performance differed for all groups between bimodal than unimodal trials, this difference could not be unambiguously interpreted as performance improvement. This is particularly evident if one considers the performance for 2 flashes presented in Figure 4a. During congruent audio-visual pairings, participants increased their overestimation for the number of presented flashes. This finding is at odds with the common notion that multisensory congruent stimuli can lead to enhanced performance, and may indicate that participants' responses reflected more a post-perceptual decision error, rather than a perceptual interaction between the stimuli. For instance, it could be speculated that when

exposed to 2 flashes and 2 beeps participants experienced some sort of increased overall numerosity of the events (i.e., 4 events perceived, in total), which in turn could have biased their numerosity judgement even further towards overestimation.

The latter possibility is compatible with the idea that the flash-beep effect described by Shams and colleagues (2002) likely includes a perceptual error (i.e., actually seeing more or less flashes than actually presented; e.g., Shams et al. 2006) and a response error (i.e., resulting from the conflict between the numerosity specified by vision and the numerosity specified by hearing). One important implication of this line of reasoning is that the emergence of illusion errors in all three groups may reflect the response error component rather than the perceptual component of this illusion. In other words, our findings would speak more about the multifaceted nature of this multisensory illusion, than about the changes in multisensory abilities of prelingual and postlingual CI recipients.

In conclusion, the present study has the merit of addressing for the first time the issue of multisensory integration in adult cochlear implant recipients with different deafness onset using non-linguistic stimuli. As stated above, we believe that a parsimonious explanation of our findings could be in terms of the response component that characterises the flash-beep illusion. Alternatively, one would have to conclude that the early deafness onset and the extensive auditory deprivation of the prelingually deaf cochlear implant recipients had no measurable effect on audio-visual integration. Future research should extend the novel approach of the present study to other types of audio-visual tasks with non-linguistic stimuli, for which perceptual interaction has been consistently documented (e.g., multisensory redundant signal effect, see Maravita et al., 2008).

# **CHAPTER 9**

## **General Discussion**



The present thesis investigated adult plasticity in an extended frame of reference, in that both the effects of sensory deafferentation and reafferentation were taken in consideration. The first part investigated plastic changes that lead to reorganisation of the remaining sensory modalities after *early* sensory deafferentation. In particular, Chapter 1 addressed the role of early sensory deprivation in leading to different types of plastic changes that occur at a neural and behavioural level in a compensatory fashion. In providing evidence of these changes, we focused on the specific case of early auditory deprivation in determining plastic reorganisation in the visual modality. In this respect, an issue that has lacked to be investigated in the deaf population is whether visual temporal information is processed differently after early sensory deafferentation. To this aim, we tested the ability of a group of profoundly deaf individuals to make temporal order judgments (TOJ) for pairs of visual stimuli presented at different eccentricities (Chapter 2). The reason why we placed stimuli at different spatial eccentricities is because one aspect of vision that seems to reorganise the most after auditory deafferentation is the response to visual stimuli presented in the periphery of the visual field (Loke & Song, 1991; Colmenero et al., 2004). In our study, participants were asked to determine which of two visual stimuli presented in rapid succession on either side of central fixation was presented first. Results from the profoundly deaf individuals were compared to results obtained from two different control groups (normal-hearing and auditory-deprived normal-hearing).

Our first main finding was that deaf individuals had comparable temporal abilities when confronted to hearing controls, as measured from their response accuracy. Our second finding was that deaf individuals were faster than hearing controls when judging the temporal order of visual stimuli under the shortest

intervals, and when the first stimulus appeared at peripheral than central locations. Taken together, our results show that temporal sensitivity in the deaf, as measured with judgments of visually presented stimuli in the millisecond range, is not impaired as a consequence of early auditory deprivation. In addition, the enhanced reactivity we found in the deaf adds evidence to the notion that reactivity may constitute one of the critical aspects of compensatory reorganisation following early auditory deafferentation.

The study we conducted supports the notion that compensatory plastic changes can occur after early sensory deprivation. Although behavioural studies cannot speak for the type of plastic mechanism underpinning enhanced functionality, our study may be linked to previous reports documenting modifications occurring in the dorsal visual pathway (Stevens & Neville, 2006), known for the fast and parallel processing of visual stimuli. In this view, future research should explore whether faster processing of visual stimuli as a consequence of auditory deprivation derives from higher reliance on the overused visual modality (intramodal change) or to more extensive cross-modal reorganisation that involves cortical functions of temporal areas (intermodal change).

One of the reasons that made us focus on auditory deprivation in the first part of the thesis is because deafness represents so far the only case of sensory loss for which reafferentation is possible through a device (the cochlear implant) that partially restores hearing. In the second part of the thesis we precisely address the question of the effects of auditory reafferentation on the ability of the adult auditory system to plastically adapt to the new input.

In Chapter 3, we explored some fundamental aspects characterising adult plasticity and the crucial role of experience in shaping and promoting plasticity in

adulthood. In particular, we reviewed some recent findings on perceptual abilities that are recovered through unilateral and bilateral implantation. Although unilateral implantation still represents the most common clinical practice, bilateral cochlear implants are rapidly growing, allowing to observe, for example, sound localisation abilities. The two studies we reported in Chapter 4 and 5, respectively, documented sound localisation abilities in two bilaterally late-implanted adults and in a group of unilaterally late-implanted adults. In the first study (Chapter 4) we observed the time course of the recovery of localisation abilities in two sequentially implanted adults. The two participants had similar characteristics in terms of age at testing and experience with single implant use prior to bilateral implantation, but were substantially different in their deafness onset, in that one became deaf early in life, the other in adulthood. This also means that they had different duration of deafness, since both were implanted in adulthood. The localisation task consisted in verbally reporting the loudspeaker from which the sound was perceived to have originated. The set-up comprised 8 loudspeakers positioned in circle around the participants. The two recipients were tested longitudinally on the day of activation of the second implant and at 3, 6 and 12 months follow-up. Results showed that the recipients who became deaf in adulthood recovered bilateral spatial hearing within a month from activation, and his abilities improved further throughout the following year. By contrast, the recipient who became deaf early in life took approximately 1 year to reach a performance with bilateral implants comparable to the other recipient. Since recipients were tested on each session with their two implants as well as with their first activated implant alone, we could observe the interplay between monaural and binaural hearing. Interestingly, testing of monaural abilities showed a different pattern of results for the two recipients. While the recipient who became deaf late in

life shifted almost all of his responses towards the first implanted ear after one month from activation (i.e., he immediately lost any monaural ability acquired prior to bilateral implantation), the other recipient maintained his monaural performance constant in every follow-up. Our results lead to different conclusions related to the single recipient. On the one side, the recipient who became deaf late in life suggests that recovery of spatial hearing abilities can occur in the shortest period even in adulthood. This fast recovery may possibly depend upon two factors: late deafness onset and short deafness duration. Although both factors may have played an important role, it is more likely that experience with typical auditory cues early in life may have promoted fast re-weighting of binaural cues later in life, as suggested by Knudsen et al. (1984). On the other side, the recipient who became deaf early in life suggests that recovery of spatial binaural hearing is possible even if atypical auditory cues were experienced early in life. However, the recovery appears to be very long compared to the fast recovery of the other recipient. Finally, monaural hearing for this recipient remained stable throughout binaural recovery. This result is particularly interesting and a hypothesis can be drawn out of it: since the recipient became progressively deaf early in life but in an asymmetrical fashion (one ear before the other), it is likely that his auditory cues were originally weighted on a single ear. If his associations between monaural cues and sound-source location developed and strengthened within the sensitive period for sound localisation, it may be the case that recovery of that experience later in life may be possible. Additionally, given that this recipient had at the end above-chance performances for both monaural and binaural hearing, it could be speculated that monaural and binaural cues are held in different representations if typical auditory cues are not experienced early in life.

The second study investigated sound localisation abilities in a group of prelingually deafened adults fitted with a single cochlear implant late in life. In addition, 4 postlingually deafened adults were also tested with the aim to investigate, as in Chapter 4, the role of auditory experience in determining the recovery of monaural spatial abilities. We adopted the same localisation task of the previous study, but, contrarily to the previous one, we tested our participants on a single session. Results showed that localisation performance for the prelingual deaf recipients was overall poor. However, some prelingual deaf recipient had localisation abilities that were above chance, and, interestingly, these recipients were also the ones who had a longer experience with their implant. This suggests that a long experience with the implant leads to some improvement in spatial abilities. By contrast, postlingually deafened adults reached a better performance compared to the prelingual deaf despite a much shorter experience with their implant.

Overall, the two studies conducted to investigate the effects of auditory reafferentation on spatial hearing abilities add evidence to the notion that some degree of plasticity can be observed in the adult brain. However, the extent and strength of this plasticity seems constraint to early experience. In this part of the thesis we have documented the effects of auditory reafferentation on the auditory system itself, and in comparing prelingually and postlingually deafened adults, we overall found an advantage for the postlingual deaf mainly due to the fact that they had restored a sensory modality that developed and strengthened its connections early in life. Postlingual deaf individuals strengthened their sensory modalities during typical development, which may lead to the claim that typical development may somehow be stronger than atypical development. The third part of the thesis challenges this view.

The final part of the thesis investigated the effects of auditory reafferentation on visual abilities and on audio-visual interactions. The general aim of this part was to observe if, and how, the new input arisen by the cochlear implant could lead to perceptual changes in the visual modality and in its interaction with the reafferented modality. In particular, given the compensatory changes that emerge after auditory deafferentation, as documented in the first part of the thesis, and that emerge particularly for the visual modality, our question was whether these changes would remain stable after auditory reafferentation.

In the first experiment (Chapter 7) we tested prelingually and postlingually deafened adults implanted late in life on a visual detection task, in which participants were asked to respond as quickly as possible to a rapid visual stimulus presented in different spatial locations on a computer monitor. We hypothesised that if compensatory changes had taken place before implantation in the prelingual group, this would show enhanced reactivity to visually presented stimuli. By contrast, we hypothesised that postlingually deafened adults would show a pattern of results similar to hearing controls. Results showed that, in line with our hypotheses, prelingual deaf recipients had an advantage in speed of response compared to postlingual deaf recipients for stimuli presented in the periphery of the visual speed. In addition, we found that this pattern of result remains stable even in prelingually deafened adults that had experienced auditory reafferentation up to 9 years. Overall, these findings suggest that atypical sensory experience achieved early in life leads to consistent compensatory changes that persist even if the deprived sensory modality is restored later in life. This means that any experience (be it from a developmental point of view typical or atypical) achieved during sensitive periods has a particular strength that cannot be reversed in adulthood.

In the second experiment we investigated how prelingual and postlingual deaf recipients implanted late in life integrate visual and auditory stimuli. To this aim, we tested the two groups on an audio-visual task that leads to illusory visual percepts. Commonly, hearing adults, when presented with an incongruent number of visual and auditory stimuli, tend to bias their responses towards the number of perceived auditory stimuli. We adopted this visual illusion induced by sounds with the rationale adopted for the previous study: prelingual deaf recipients would likely show less illusion compared to postlingual deaf recipients because of a higher reliance on the visual modality. Our results disconfirmed our initial hypotheses, in that we found comparable performance of prelingual and postlingual deaf recipients matched with a group of hearing controls. However, results obtained with that particular task speak more for the multifaceted nature of the illusion rather than for multisensory abilities in prelingual and postlingual cochlear implant recipients. Future research should extend research on multisensory integration in cochlear implant recipients by testing them on other types of audio-visual tasks, for which perceptual interaction has been consistently documented.

### *Conclusions*

The present thesis has added evidence to the notion that plasticity is present in the adult brain, and that early experience shapes and promotes plasticity in adulthood. In particular, we have shown that any early typical or atypical experience shapes brain with a particular strength, in line with the notion that experience during sensitive periods significantly alters behaviour. In this view, we have also shown that plasticity in adulthood is somehow limited by the stability achieved during these

periods. However, adult plasticity can be shaped by the effects of learning, in that individuals' behaviour can, to some extent, be changed through interaction with the environment. Lessons of these issues come from early auditory deprivation and late reafferentation through a cochlear implant. We have documented that early sensory loss leads to modifications in the remaining sensory modalities (Part I), and that these changes remain stable throughout life, even if a new sensory input is given in adulthood (Part III). Plasticity in adulthood is particularly shaped by early experience in sensory development, and whenever this experience is restored later in life, it will be re-established in the shortest period (Part II).



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*Francesco* – you know me – I couldn't bother less (under some circumstances) about other peoples' thoughts...

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