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VISUAL ABILITIES IN PROFOUND DEAFNESS: A WINDOW INTO THE MECHANISMS OF MULTISENSORY PERCEPTION

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TABLE OF CONTENTS

ABSTRACT

The present thesis addresses the cross-modal plasticity occurring in the visual modality due to profoundly deafness. In Chapter 1, we review the current perspective on the general mechanisms of cross-modal plasticity and, in particular, the changes occurring in visual modality in the case of profound deafness. Enhanced visual abilities in the deaf have typically been reported when in tasks that involve visual attention resources and processing of peripheral portions of the visual field. In this thesis, we present a series of four experimental studies aimed at specifying which visual attentional components display modulations in case of deafness. In Chapter 2 and 3, we contrasted the role of endogenous and exogenous capture of visual attention. The results showed that endogenous attention, when tested in a transient-free context, does not reveal compensations effects due to deafness (i.e., enhancement). By contrast, enhanced performance for peripheral portion of the visual field emerged when exogenous capture of selective attention was involved. We suggest that enhanced visual performance in the deaf is transients selective. In Chapter 4, we contrasted the ability to simply react to a visual event (simple detection task) and the ability to orient visual attention (shape discrimination task). The results showed that deaf posses marked enhanced reactivity compared to hearing controls, when detecting targets presented at both central and peripheral locations. Reactivity is thus an enhanced visual skill in the deaf that is not spatially selective, in the sense that it does not emerge solely at peripheral locations. In addition, RTs results support the hypothesis that deaf may display a different neural representation of the peripheral portion of the visual field. These effects were not paired by enhanced ability to discriminate between different shapes regardless of their relative position, suggesting that enhanced reactivity was not due to a better mechanism of

attention orienting. Finally, in Chapter 5, we present the electrophysiological data recorded during a simple visual detection task. The ERPs analysis revealed that deafness determines quantitative and qualitative modulations of visual processing already at the early stages (C1, P1). Finally, Chapter 6 resume and discuss the implications of the overall set of results.

CHAPTER 1

GENERAL INTRODUCTION

Cross-modal plasticity

In cognitive neuroscience, the term ‘brain plasticity’ refers to the ability of neurons and neuronal networks to change their functions in consequence of their previous activity (e.g. Wiesel and Hubel, 1963). This is one of the fundamental mechanisms that allow adaptation in the nervous systems, and occurs continuously in our lives. Brain plasticity characterises all level of cognition from the formation of new semantic memories to basic perceptual learning. Addressing brain plasticity thus implies probing a fundamental aspect of brain and cognition. When a multisensory frame of reference is adopted, the phenomenon of brain plasticity is termed ‘cross-modal plasticity’. In this respect, one powerful experience in driving cross-modal plasticity is the lack of one sensory modality. The studies that evaluated cross-modal plasticity following long-term sensory deprivation (e.g., blindness or deafness) have revealed not only behavioural changes in the remaining modalities, but also reorganization of cortical functions (see Bavelier & Neville, 2002 for a review).

Cross-modal plasticity, anatomical mechanisms

One first aspect of cross-modal plasticity following long-term sensory deprivation concerns changes occurring at the brain level. Anatomically cross-modal plasticity may occur at least in two main loci: polymodal association areas and primary sensory areas. On the one hand, polymodal association areas can show enhanced processing of the input from the remaining sensory modalities (e.g. Buchet et al 1998). The general assumption is that all the areas of the brain that process multisensory inputs are possible candidates to show cross-modal plasticity. The main mechanism is the activity-based competition between different inputs. Neurons that respond to different modalities and that do not receive the input form one of them will be then tuned preferentially to the remaining modalities. On the other hand, both animal and human studies indicate that <u>primary sensory areas</u> associated with the deprived sensory modality can be recruited by the remaining modalities (e.g. Cohen et al., 1997). In this respect, Ghazanfar and Schroeder (2006) recently challenged the idea that purely unisensory areas exist in neocortex, and reviewed a number of works showing that primary sensory cortices receive inputs from the other sensory modalities even in absence of sensory deprivation. For instance, animal studies showed that neurons in striate cortex receive visual but also auditory and somatosensory inputs. Both studies by Morrell (1972) and by Fishman and Michael (1973) showed that about 40% of neurons in striate and extra-striate cortices responded to both auditory and visual stimuli. Interestingly, these bimodal cells had coincident acoustic and visual receptive fields, thus representing the same portion of space and suggesting strong functional coupling. More recently Falchier and colleagues (Falchier, Clavagnier, Barone and Kennedy, 2002) showed that the portions of striate cortices that represent the peripheral visual field in the macaque monkey are closely linked to the auditory cortices. The interconnection between primary sensory cortices in absence of sensory deprivation could thus be one of the basis that allows recruitment of one primary sensory areas by the other modalities when the dominant input is absent. Obviously, there are enormous differences in the re-organization if the sensory deprivation occurs when the nervous system is still in development or when it is mature. As it can be supposed, it is generally reported that early deprivation determines more cortical re-organization than late deprivation (Kupers et al., 2006).

According to Bavelier and Neville (2002) four main mechanisms of cross-modal plasticity can be identified.

1. *Changes in local connectivity.* This type of plasticity can be observed in sensory maps after sensory stimulation or deafferentation, and can be observed in both developing and mature organisms (Kaas, 1995). Different mechanisms have been proposed for such local connectivity plasticity including dendritic and axon sprouting, unmasking of silent synapses and modulatory effect due to existing lateral connections.
2. *Changes in subcortical connectivity.* This form of plasticity seems to be limited to developing organisms and rely on the normally redundant pathways that are present at birth. Recently, for instance, it has been shown that deaf mice display aberrant projections originating from the retina to subcortical structures that are typically involved in auditory processing, including medial portion of the Superior Colliculus and the Medial Geniculate Nucleus in the Thalamus (Hunt et al., 2004).
3. *Changes in cortico-cortical feedback.* Another possible mechanism of plasticity relies on back projections from multimodal areas, such as the parietal cortex, to sensory specific areas. For instance, it has been show that enhanced functional connectivity can be found in deaf individuals between parietal cortex and earlier visual areas (Bavelier et al., 2000).
4. *Changes in long-range cortico-cortical connectivity.* This kind of plasticity is supposed to be based on the existing connections between different sensory modalities. As previously described there is evidence of pathways from the primary auditory cortex to areas that represent peripheral vision in primary visual cortex in adult monkeys (Falchier et al. 2002).

Cross-modal plasticity, functional changes

In addition to causing changes at the anatomical level, cross-modal plasticity also emerges functionally, often in the form of enhanced behavioural skills. For this reason functional manifestations of cross-modal plasticity are also termed cross-modal compensation phenomena.

Much of the studies that examined cross-modal plasticity as a consequence of long-term sensory deprivation have focused on the consequences of blindness (e.g., Amedi, Raz, Pianka, Malach & Zohary, 2003; Cohen, Celnik, Pascual-Leone, Corwell, Faiz et al., 1997; Röder, Stock, Bien, Neville, & Rösler, 2002; for reviews see Pascual-Leone, Amedi, Fregni, & Merabet, 2005; Röder & Rösler, 2004). For instance a number of studies have demonstrated that early blind individuals display better ability to discriminate features of auditory or tactile stimuli, such as spectrum (Doucet et al. 2004), pitch (Gougoux et al. 2004; Hamilton et al. 2004; Witkin et al., 1968), timing (Muchnik et al., 1991; Röder et al., 2004; Stevens and Weaver, 2005), intensity (Benesetti and Loeb, 1972; Sterr et al., 1998) or fine spatial cues (Ashmead et al., 1998; Goldreich and Kanics, 2003: Grant et al., 2000; Lessard et al., 1998; Muchnich et al., 1991; Van Boven et al., 2000; Voss et al., 2004). One representative example of this literature is the classical study conducted by Röder and colleagues (Röder, Teder-Sälejärvi, Sterr, Rösler, Hillyard and Neville, 1999) on the effect of blidness for auditory spatial perception.

Röder and colleagues evaluated behaviourally and electrophysiologically auditory spatial tuning for central and peripheral sounds in congenitally blind individuals and in blindfolded sighted, to test the hypothesis that blindness can result in enhanced processing of peripheral sounds. Auditory stimuli (noise bursts) were presented randomly from 4 central and 4 peripheral loudspeakers. Participants were asked to detect rare deviants sounds (change in pitch) originating from one loudspeaker, while ignoring deviants originating from adjacent speakers (placed at 6, 12, and 18 degrees at relative left from the target speaker). On half of the blocks participants attended to a central speaker (placed directly at fixation); on the remaining half they attended to a speaker placed 90° degrees on the periphery. In sum, the task was to recognise whether the deviant came from the attended speaker or not, thus it was a spatial discrimination task. Behaviourally, blind individuals outperform sighted at detecting the deviant sound only when this originated from peripheral locations. Moreover, the electrophysiological recordings revealed sharper tuning of early spatial attention in blind individuals, as evidence by an ampler N1 component, compared to hearing controls, in response to stimuli presented attended peripheral location.

In the last decade, the consequences on perception, language and cognition of long-term deprivation of auditory input due to profound deafness also became a fundamental topic in cross-modal plasticity research (for recent reviews and clinical implications see the recent book on deaf cognition edited by Marschark & Hauser, 2008). In particular, one aspect of deaf cognition that has received considerable attention in recent years concerns the functional and anatomical re-organization that occur within the visual modality when the auditory input is absent (for a review see Bavelier et al., 2006).

Cross-modal plasticity in deafness: effects on visual processing

A key observation of the literature on visual abilities in bilateral profound deafness is that not all aspects of visual processing are enhanced in this sensory-deprived population. This is a fundamental observation that may reveal functional dissociations within the cross-modal plasticity phenomena that occur after profound deafness. Understanding which cortical networks and/or functions are susceptible and which are instead unaffected by these re-organizations can shed light into the specific functionality of auditory cortex and its interactions with the other sensory modalities. In the present section, we will review some of the most relevant features of visual processing in the profoundly deaf.

Visual sensory thresholds

The literature on visual abilities of profoundly deaf individuals have typically reported that visual sensory thresholds are comparable between deaf and hearing controls. The lack of a cross-modal effect due to auditory deprivation has been documented in studies that evaluated thresholds for brightness discrimination, visual flicker frequency, contrast sensitivity, motion direction and motion velocity (Bross, et al., 1979, 1980; Stevens and Neville 2006; Finney and Dobkins, 2001; Bosworth and Dobkins, 1999; Bosworth and Dobkins, 2002; Brozinsky and Bavelier, 2004).

For instance, in series of three experiments Brozinsky and Bavelier (2004) tested whether deaf individuals process motion velocity information differently from hearing non-signers. All experiment used adaptive staircase procedures to reach the 79% threshold for each participant. In Experiment 1, participants watched radially moving dots and were asked to detect the quadrant in which the velocity of the dots had changed. The results showed that similar sensory thresholds were observed in the two populations. In Experiments 2 and 3, the authors evaluated peripheral and central thresholds separately, as previous studies suggested early deafness leads mainly to changes in the peripheral visual processing. The results did not show difference between the two groups for central or peripheral visual moving thresholds. The only difference between deaf and hearing controls that has been documented in the study by Brozinsky and Bavelier (2004) was a threshold asymmetry between the two visual hemi-fields. Deaf native-signers exhibited better thresholds in the right than left visual hemi-field, whereas the opposite pattern was observed in the hearing signers.

Interestingly, an absence of modulation due to deafness in threshold tasks was documented also in tactile modality. Levänen and Harmdorf (2001) showed that tactile-frequency discrimination thresholds are comparable between deaf and hearing controls, supporting the notion that the sensory thresholds do not display cross-modal modulations due to auditory modulations.

Spatial selectivity of enhanced visual abilities in the deaf

An empirical observation that has been repeatedly reported concerns the spatial selectivity of enhanced visual processing in the deaf. Namely, enhanced performance in the deaf have typically been described for visual stimuli occurring towards peripheral portions of the visual field than stimuli occurring towards the centre.

Deaf individuals show faster reaction times when detecting or discriminating single peripheral visual targets (e.g., Colmenero et al. 2004; Loke and Song 1991; Neville and Lawson, 1984). By contrast, reaction time differences between deaf and hearing controls do not emerge for single targets appearing at or near central fixation

(Neville and Lawson 1984; Poizner and Tallal 1987). For instance, Loke and Song (1991) evaluated the ability of deaf individuals and hearing controls to perform a simple detection task for static targets appearing at central (0.5°) or peripheral locations (25°). The results showed that deaf were faster than controls at detecting peripheral targets, while for central targets no differences emerged. Similarly, an earlier study by Neville and Lawson (1984) evaluated the ability to discriminate moving stimuli at central (above fixation) or at peripheral locations (18°). Deaf resulted on average 70 ms faster than hearing controls at discriminating targets at peripheral locations, whereas performance at central location was comparable. A somewhat similar conclusion has been reached by studies addressing the effect of central and peripheral distractors on the performance of deaf and hearing controls. In these studies, the performance was modulated by deafness when the tasks involved peripheral visual space. In particular when concurrent central and peripheral targets competed for attentional resources, deaf show enhanced processing at peripheral than central locations (Chen et al 2006; Proksch and Bavelier, 2002; Sladen et al. 2005).

Enhanced performance at peripheral location is compatible with the notion that, under normal conditions, the auditory system provides important information about the events that occur outside the field of view. In the absence of audition, visual processing may be recalibrated to favour rapid detection of events outside foveal regions of the retina, in the attempt to monitor the environment through peripheral vision instead of audition (Loke and Song 1991; Parasnis and Samar 1985). Evidence in support of this functional account come from a recent study by Stevens and colleagues (Stevens and Neville, 2006) that revealed enlarged useful field of view at the extreme periphery when detecting motion stimuli. In that study, deaf individuals and hearing controls were tested in a kinetic perimetry task to evaluate the extension of the visual field in which the presence of moving stimuli can be detected. Interestingly, animal studies have revealed that connections between visual and auditory cortices are stronger for peripheral than central portions of the visual filed (Falchier et al., 2002) thus offering a possible neural substrate for this spatially selective enhancement. Moreover, it is particularly intriguing the observation that in deafness and blindness there is a sort of mirrored cross-modal effect, the enhanced processing in the remaining modality occurs for peripheral space, in case of deafness is the peripheral vision in case of blindness is the peripheral auditory processing. This evidence highlights once again the adaptive role of the cross-modal plasticity.

The role of attention orienting in enhanced visual processing of the deaf

An important aspect that should be considered is the role of spatial selective attention in enhanced visual processing of the deaf. The notion that spatial selective attention plays a key role in modulating visual responses in the deaf has been recently advocated by Bavelier and colleagues (Bavelier et al., 2006; Dye et al., 2008) and originally stemmed from the empirical observation that differences between deaf and hearing controls at the neural level emerge specifically when attention is endogenously directed to the target (Bavelier et al., 2000; Neville and Lawson 1987).

The first study that suggested that the neural system that mediate attention to visual space could be modulated by deafness was conducted by Neville and Lawson (1987). In their EEG study deaf and hearing controls were evaluated in a discrimination task for moving targets placed at central or peripheral locations. In different blocks, participants were explicitly requested to attend and respond only to targets presented at one location a time, centrally or peripherally (right of left). Behaviourally, deaf resulted faster than hearing controls at discriminating peripheral targets while centrally no differences emerged. The Evoked Responses Potentials analysis on the N1 component revealed that the magnitude of the attention related increase was larger in deaf than hearings solely for peripheral targets. This results lead the authors conclude that auditory deprivation determines changes in the peripheral visual system and to the attentional peripheral engagement.

More recently, evidence showed that peripheral task-irrelevant distractors interfere with shape discrimination more than central distractors in the profoundly deaf, whereas the opposite pattern is observed in hearing controls (Proksch and Bavelier, 2002). In the study by Proksch and Bavelier (2002) deaf and hearing controls were evaluated in a flanker interference paradigm. Participants were asked to perform a shape discrimination task with different levels of perceptive load while central or peripheral distractors were presented. The results showed that deaf were more susceptible to peripheral than central distractors while hearing controls displayed the opposite pattern. This result lead the author conclude that deaf possess enhanced peripheral attention resources than hearing controls.

Finally, a role of spatial attention has been suggested in those studies that examined attention orienting and revealed faster disengagement and re-orienting to the target after an invalid cue (Bosworth and Dobkins, 2002; Chen et al., 2006; Colemenero et al., 2004; Parasnis and Samar, 1985). In the study by Colemenero and colleagues (2004) for instance, deaf and hearing controls were asked to perform the detection of a visual stimuli in a spatial cuing paradigm. Deaf resulted to be faster than hearings to detect target at un-cued location. Moreover contrarily to hearing controls, deaf did not show advantages at cued location, that coupled with the previous result suggested faster disengagement of spatial attention.

However, whether all aspects of visual enhancement in the deaf are necessarily linked to allocation of selective attention in space it is still a matter of debate. Under some circumstances enhanced visual performance in the deaf has been observed in the absence of attention orienting (Armstrong et al., 2002; Chen et al., 2006; Loke and Song, 1991). For instance the EEG study by Armstrong and colleagues (Armstrong, Hillyard, Neville and Mitchell, 2002) evaluated the visual evoked potentials of deaf and hearing controls in response to the presentation of moving stimuli. In particular stimuli were delivered from five spatial locations, one at fixation and the other four at peripheral locations (on the diagonals). At these five locations continuous moving gratings were presented. Randomly, one visual grating a time could accelerate its relative movement (standards) or turned in a black square (deviants). The task implied the detection of the deviant, that could appear at any of the five locations, thus participants were asked to diffuse their visual attention to the entire monitor. The results showed that the N1 component was ampler in deaf than hearing controls in response to both central and peripheral moving stimuli. Thus, this study revealed that to show enhanced cortical activation in response to moving stimuli in the deaf it is not necessary to ask participants to focus visual attention to peripheral locations.

Assessing the role of attention is fundamental to highlight at which stage of visual processing the performance benefit of the deaf could emerge. In particular, showing that enhanced processing emerge prior to orienting of attention would reveal that at least some components of enhanced processing of the deaf occurs at very early stages of visual processing in the brain.

Enhanced processing of visual features that activate the dorsal visual stream

Several authors have proposed that enhanced visual abilities in the deaf appear selectively for processing of visual features that are preferentially analysed within the visual-for-action pathway associated with the dorsal visual stream (Milner and Goodale, 1995). These include moving patterns (Armstrong et al., 2004; Bavelier et al., 2000, 2001; Bosworth and Dobkins, 2002) as well as peripheral vision (e.g. Stevens aet al., 2006; Chen et al., 2006; Colmenero et al. 2004; Loke and Song, 1991). In this respect, anatomical evidences indicate that both motion processing and peripheral vision are predominantly mediated through the dorsal visual pathway (Livingstone and Hubel, 1988). Moreover, in support of the dorsal stream hypothesis, the Magnocellular pathway, that dominate this visual stream, has been indicated as more susceptible to plasticity in general (see Stevens and Neville).

For what it concerns moving stimuli, with functional neuroimaging (fMRI) studies, Bavelier and colleagues (Bavelier, Tomann, Hutton, Mitchell, Corina, Liu and Neville, 2000, Bavelier, Brozinsky, Tommn, Mitchell, Neville and Liu, 2001) showed enhanced cortical activation in the MT+ complex of deaf than hearing controls when attending to motion stimuli at peripheral locations. For instance in the study by Bavelier and colleagues (Bavelier, Tomann, Hutton, Mitchell, Corina, Liu and Neville, 2000) participants were asked in different blocks to attend centrally, peripherally or the entire monitor to detect changes of luminance within a pattern of moving dots. The results showed enhanced activation of MT+ complex, Posterior Parietal cortex and Superior Temporal Sulcus in the deaf compared to hearings, when attending the peripheral portion of the moving pattern. These results showed for the first time that visual moving stimuli could activate polymodal areas as result of deafness. In addition, moving stimuli resulted also to activate right auditory cortex in the deaf (Fine et al., 2005; Finney et al., 2001). In the fMRI study by Fine and colleagues for instance (Fine, Finney, Boyton, and Dobkins, 2005) deaf and hearing controls were evaluated when attending or not peripheral moving stimuli. The results showed that moving stimuli were able to activate the right auditory cortex corresponding to Brodman areas 41,42 and 22 in the deaf. The auditory cortex activation was ampler for attended than un-attended conditions suggesting top-down processes. Interestingly this study did not replicate the enhanced activation of the MT+ complex observed in the previous study (Bavelier et al., 2000; 2001), even if the tasks were very similar. Finally, an event-related potential (ERP) study by Armstrong and colleagues (Armstrong, Hillyard, Neville and Mitchell, 2002) revealed enhanced cortical response (larger N1 components) in deaf than hearing controls in response to task irrelevant moving stimuli at both central and peripheral locations, even without specific attentional instructions. Importantly, when cortical activity was compared between groups for coloured stimuli (preferentially processed by the ventral visual stream), enhanced cortical responses for deaf than hearing participants no longer emerged. This specific observation is another evidence in support that cross-modal plasticity in the profoundly deaf could mainly involve a cortical re-organisations within the dorsal stream of visual processing (Armstrong et al., 2002; Bavelier et al., 2006; Bavelier and Neville, 2002). Although moving stimuli appear to be a preferential visual event to show cross-modal plasticity in the deaf, to our knowledge no studies tried to directly compare the cortical activation of static and moving stimuli. Other studies document that deaf signers outperform hearing.

Even if the dorsal stream hypothesis have some evidences in support, we want to remark that at least one typical ventral stream function appears to be enhanced in the deaf, face processing. Anatomically, faces are known to selectively activate a region of ventral cortex, specifically the Fusiform Gyrus, while objects and shapes activate a broad portion of the ventral visual cortex (Puce et al, 1995; Kanwisher et al, 1997). In this respect, when participants were required to perform a face-matching task in which two unfamiliar faces differed only in the identity of single features (e.g. eyes, mouth, nose), deaf signers resulted better than both hearing native signers and non-signers (McCullough & Emmorey,1997), particularly when the mouth differed. This result suggests that a rigid attribution to the cross-modal plasticity in deafness solely to the dorsal stream cannot be assumed.

Aim of the thesis

The overall aim of the present thesis was to expand the current knowledge of the cross-modal effects that profoundly deafness has on visual perception. In particular, we aimed to investigate further the notion that enhanced visual abilities in the deaf could reflect modulation in visual attention abilities (see paragraph above). Despite the famous statement of William James ("Every one knows what attention is"; James, 1890, p. 403) attention is a shifty concept, that represent a multi-component mechanisms of the cognitive system. Thus, the question as to the role of attention in the modified visual abilities of the profoundly deaf should be, at the very least, which attentional component show enhanced processing in deaf than hearings? The answer to this questions could give relevant information to comprehend what 'drives' the cross-modal effects due to auditory deprivation. For instance, the dissociation between automatic and voluntary attention encapsulate the distinction and the interaction between the external world and its events, and the internal world and its states. To study visual abilities in the deaf we adopted paradigms to contrast different visual attentional components, to be sure that the interpretation could be as much as possible straightforward.

Thesis outline

In Chapter 2, we present a study in which we addressed whether endogenous attentional resources are enhanced in the deaf. As reviews above, some studies showed that when deaf are requested to perform visual tasks while endogenously attending to peripheral location of the visual field, enhanced performances and neural activations differences with respect to hearing controls emerge. In the presented study, we adopted a paradigm (i.e., the change blindness task) that masks visual transients events that would normally attract visual attention exogenously, to evaluate selectively the spatial allocation of endogenous visual attention in deaf and hearing individuals. In Chapter 3, we present a work that build up on the conclusions of Chapter 2. We adopted again a paradigm that mask target related transients, but we added brief irrelevant spatial cues in a controlled manner to drive visual attention exogenously. This manipulation was adopted to evaluate specifically the effects of an irrelevant abrupt onset presented at different spatial location on the visual performance of deaf and hearing participants. This second study was thus designed to contrast the role of endogenous and exogenous capture of visual attention within the same paradigm. In Chapter 4, we present a study that was designed to compare the performance of profoundly deaf individuals and hearing controls in a simple detection task and in a shape discrimination task, adopting the same set of stimuli. These two tasks were contrasted to evaluate whether deafness leads to modulation in a task that evaluates reactivity in a distributed attention context (simple detection) as well as in a task that requires to orient selective spatial attention to a target to identify and discriminate it (discrimination task). In both tasks central and peripheral locations were evaluated and static stimuli were adopted. In Chapter 5, we present an electrophysiological study of a simple visual detection task were we examined in details whether early visual evoked potentials in response to central and peripheral static targets are modulated by deafness in a distributed attention context. Finally, Chapter 6 presents a summary of the results emerged from our series of experimental studies, with a discussion of their theoretical implication with respect to the existing literature on deafness.

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CHAPTER 2

CHANGE BLINDNESS IN PROFOUND DEAF INDIVIDUALS AND COCHLEAR IMPLANT RECIPIENTS

Bottari D., Turatto M., Bonfioli F., Abbadessa C., Selmi S., Beltrame M.A. and Pavani F. (2008). Change blindness in profoundly deaf individuals and cochlear implant recipients. Brain Res. May 26. PMID: 18597741

Abstract

We used a change blindness paradigm to examine visual abilities in the profoundly deaf when exogenous capture of attention is prevented and only endogenous attention shifts are possible. Nineteen profoundly deaf participants, 22 cochlear implant recipients and 18 hearing controls were asked to detect a change occurring between two consecutive visual scenes separated by a blank. Changes occurred on half of the trials, either at central or peripheral locations, and the task was performed under focused attention (at the centre or at the periphery) or under distributed attention. When allowed to focus attention, all groups showed comparable change sensitivity, with better performance for central than peripheral stimuli. However, in the distributed condition, only the

profoundly deaf participants remained reliably more sensitive to changes occurring at central than peripheral locations. This finding contradicts the well-known visual performance enhancement typically observed for peripheral regions of the visual field in the profoundly deaf. We suggest this discrepancy between our novel finding and the existing literature reflects the strictly endogenous nature of our change blindness paradigm. Our results point to a differential role of exogenous and endogenous attention components in the multisensory plasticity occurring after auditory deprivation and suggest that compensatory abilities in the deaf may be linked to exogenous capture of visual attention.

Introduction

One of the most intriguing findings of cognitive neuroscience is the demonstration that the brain can reorganise in response to sensory deprivation. Substantial changes in the processing of information from the intact sensory modalities has been extensively documented in the case of blindness (e.g., Amedi, Raz, Pianka, Malach & Zohary, 2003; Cohen, Celnik, Pascual-Leone, Corwell, Faiz et al., 1997; Röder, Stock, Bien, Neville, & Rösler, 2002; for reviews see Pascual-Leone, Amedi, Fregni, & Merabet, 2005; Röder & Rösler, 2004). In addition, a fast growing literature has now revealed that similar changes in the processing of inputs from the intact modalities can also emerge in the case of profound deafness (e.g., Bosworth & Dobkins, 2002; Chen, Zhang & Zhouet 2006; Fine, Finney, Boynton & Dobkins, 2005; Levanen & Hamdorf, 2001;

Loke & Song, 1991; Neville & Lawson, 1987; Proksch & Bavelier 2002;Stevens & Neville, 2006; see Bavelier, Dye & Hauser, 2006 for a review). In the present study we examined the effects of profound deafness on the ability to perceive changes in the visual modality, when exogenous capture of attention is prevented and only endogenous attention shifts are possible.

A recent review on visual abilities in the profoundly deaf (Bavelier et al., 2006) suggests that enhanced visual performance in this population emerges in visual tasks that involve selection processes mediated by attention. In addition, most of the existing evidence points to an advantage for visual targets appearing towards the periphery of the visual field. Deaf are faster than hearing controls at detecting the onset of peripheral visual targets (e.g. Chen et al., 2006; Colmenero, Catena, Fuentes & Ramos, 2004; Loke & Song, 1991) or at discriminating the direction of motion for visual targets presented at attended peripheral locations (Neville & Lawson, 1987; see also Baveleir, Tomann, Hutton, Mitchell, Corina, Liu and Neville 2000; Bavelier, Brozinsky, Tomann, Mitchell, Neville and Liu 2001; Bosworth & Dobkins, 2002). By contrast, no difference between deaf and hearing controls emerges when targets are presented at locations towards the centre of the visual field (Neville & Lawson, 1987) or directly at fixation (Poizner and Tallal, 1987). Similarly, when central and peripheral static stimuli compete for selective attention resources, visual attention resources in the deaf appear to be oriented more towards peripheral than central locations (Chen et al., 2006; Proksch & Bavelier, 2002; Sladen, Tharpe, Ashmead, Grantham & Chun, 2005). Finally, profoundly deaf individuals can be more efficient than hearing controls in visual search tasks (Stivalet, Moreno, Richard, Barraud & Raphael, 1998) and in tasks that require re-orienting of visual attention to the target when a wrong location in the visual field is cued first (Parasnis & Samar, 1985).

One common aspect of this previous literature is the presence of sudden luminance changes in the visual scene, often related to the target itself. Examples of these luminance changes are the abrupt onset of a target shapes (e.g., Parasnis & Samar, 1985; Proksch & Bavelier, 2002) or motion signals (e.g., Bosworth & Dobkins, 2002; Neville & Lawson, 1987) in the visual scene. Using a terminology of the visual attention literature, these were all ‘transients’ that could trigger involuntary (or exogenous) orienting of visual attention (Breitmeyer & Ganz 1976; Corbetta & Shulman 2002; Klein, Kingstone & Pontefract, 1992; Phillips & Singer, 1974; Turatto & Bridgman 2005). Cognitive psychologists have long distinguished between two components of attention orienting, an exogenous component (also termed involuntary or automatic), by which selective attention resources are summoned to an object or allocation because of its salience and an endogenous component (also termed voluntary), by which selective attention resources are summoned to an object or location voluntarily because it is relevant for the current behavioural goal (Jonides 1981; Posner 1980). By using tasks that involved visual transients that capture attention, the vast majority of previous studies addressing visual skills in the deaf inevitably examined the exogenous component of visual attention, or mixed exogenous and endogenous components of attentional orienting within the same paradigm. Even those studies that intended to manipulate endogenous attention alone could have in fact mixed endogenous and exogenous components, as the mere abrupt onset of target stimuli could have produced involuntary re-orienting of attention resources. For instance, in the classic study by Neville and Lawson (1987) participants were instructed to attend to one eccentricity at a time (i.e., to focus their attention endogenously to either the centre or the periphery) and respond only to targets at the attended locations. However, targets appearing abruptly at fixation or in the periphery of the visual field surely triggered exogenous orienting of attention. Thus, the faster discrimination responses in deaf than hearing controls observed by Neville and Lawson (1987), could reflect both the endogenous attention shift determined by the instructions, and the exogenous attention shift determined by target onset. Similarly, in a study by Bosworth and Dobkins (2002) participants were endogenously cued to the upcoming target location beforehand. However, the abrupt onset of a patch of moving dots (i.e., the target stimulus in their study) could have introduced an (additional) involuntary attention component in their paradigm (note that this could have been especially true in their ‘multiple display condition’ in which the patch of moving stimuli containing the target was accompanied by three concurrent patches of random moving dots; see Bosworth & Dobkins, 2002). In sum, we argue that whenever exogenous attention capture (i.e. abrupt stimulus onset) and endogenous attention (i.e. focus attention) are combined any observed visual enhancement can be attributed to one or the other component of attentional selection. To our knowledge, this ambiguity as to which exact attentional component determines enhanced visual abilities in the profoundly deaf characterises most of the existing studies (e.g. Bavelier et al., 2000; Bosworth & Dobkins, 2002; Chen et al., 2006; Neville & Lawson, 1987; Proksch & Bavelier, 2002).

The aim of the present study was to examine visual abilities in profoundly deaf individuals using a paradigm that completely prevents any exogenous capture of attention and therefore evaluates, for the first time, only the endogenous component of attention orienting. To this aim, we adapted the so-called flicker version of the 'change blindness' paradigm (O'Regan, Rensink & Clark, 2000; Rensink, 2001; Turatto & Bridgeman, 2005). The rationale behind this paradigm is the following. When comparing two alternating visual scenes, any occasional change is usually detected without effort because it constitutes a local transient that readily attracts exogenous attention precisely to the location of the image where the change has occurred (O'Regan et al., 2000). However, if a blank image is interposed between the two alternating scenes, any single part of the new scene changes with respect to the previous blank image, resulting in a global rather than local transient. As a consequence, attention can no longer be summoned exogenously to the location of change, and the change is noticed only through a strategic (endogenous) scan of the visual scene (Rensink, 2001).

When considering these peculiar aspects of the change blindness paradigm the following predictions can be put forward. If enhanced visual attentional abilities observed in the existing literature rely specifically upon exogenous capture of visual attention, deaf individuals should perform in a similar way to hearing controls in a change blindness paradigm that prevents exogenous attentional capture. Alternatively, if compensatory visual skills in profound deafness are associated with a different distribution of endogenous attention profound deaf participants should perform better than hearing controls, particularly in the peripheral portions of the visual field.

The version of the change blindness paradigm we have adopted in the current study is the so-called ‘one-shot’ procedure (for a review see Rensink, 2002), in which two visual scenes are presented one after the other in each experimental trial, separated by a single blank. Each visual scene in our task comprised 4 or 8 line-drawing images, half of which were arranged at 3 degrees from central fixation (central stimuli) and the other half were arranged at 8 degrees from central fixation (peripheral stimuli). A schematic example of one experimental trial comprising 4 items is shown in Figure 1. On 50% of the trials, the two scenes repeated identical (no-change condition), whereas on the other 50% of the trials one drawing in the first scene changed into a different one in the second scene (as shown in the example trial depicted in Figure 1). The participant's task was to detect whether the change was present or absent, by pressing one of two buttons on the computer mouse. In the present study, we also manipulated endogenous attention between blocks by asking participants to either attend to specific regions of the visual field (centre or periphery; focused attention conditions) or to distribute spatial attention across to the whole visual scene (distribute attention condition). Focused attention conditions examined the participant's ability to allocate attentional resources on request, whereas the distributed attention condition evaluated the spontaneous allocation of endogenous attention across the visual field. Note that several previous studies have suggested that endogenous focused attention is critical for observing enhanced visual abilities in the deaf (e.g. Bavelier et al. 2000, 2001; Neville & Lawson, 1987).

Figure 1

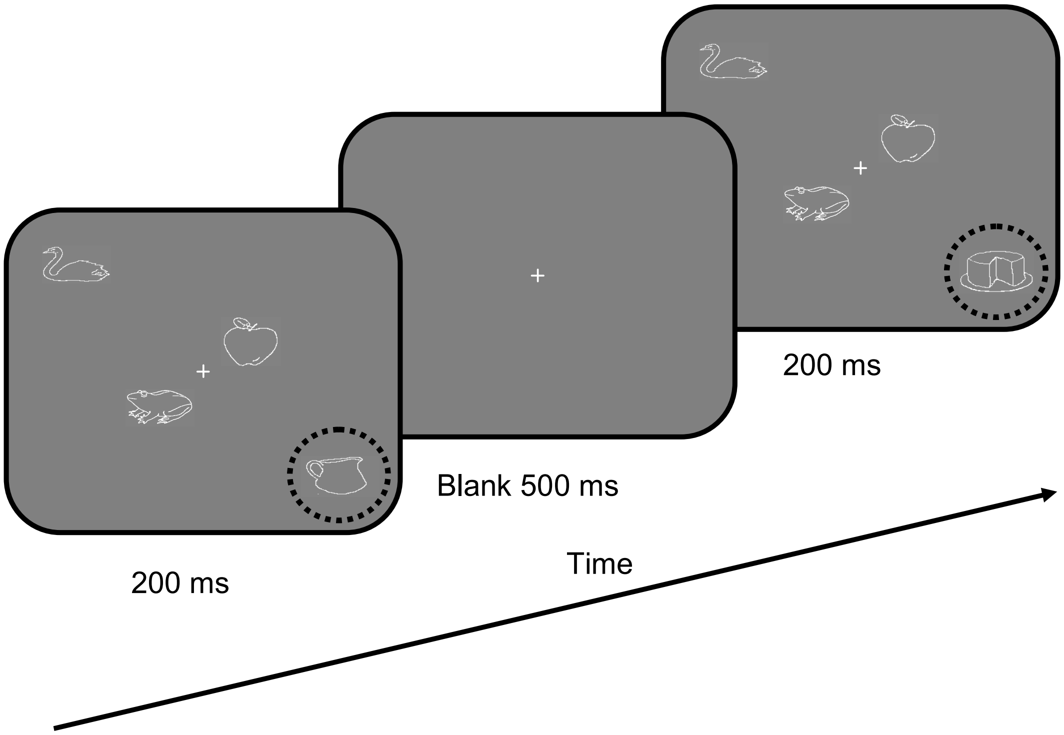


Figure 1. Example of a change trials in a 4 drawings display. Trial sequence is illustrated from the onset of first configuration of drawings. In this example, the peripheral picture on the bottom right corner changes identity. Note that dotted circle is introduced here only for descriptive purposes and was not visible in the actual experimental task.

Nineteen profoundly deaf participants and 18 hearing controls were tested in this version of the change blindness paradigm. In addition, we had the opportunity to recruit a group of 22 cochlear implant recipients (see Experimental Procedure for a detailed description of the participants). Deafness is currently the only condition of sensory deprivation for which neuroprosthetic devices are routinely implanted in the clinical practice. Under the circumstances in which deafness results from a damage to structures of the inner ear with spared auditory nerve functions, functional hearing can be restored by using a prosthetic device known as cochlear implant (Rauschecker & Shannon, 2002). A cochlear implant (CI) is an electronic device which comprises a microphone, located next to the outer ear, a sound processor that transforms auditory stimuli of the environment into electrical pulses, and a microelectrode array that directly stimulates the nerve fibres of the cochlea. Deaf individuals with cochlear implants represent a unique chance to study the effects of sensory reafferentation after years of deprivation (e.g., Rouger, Lagleyre, Fraysse, Deneve, Deguine & Barone, 2007; Desai, Stickney and Zeng, 2008). Our additional aim was to examine whether visual attention in deaf individuals may change after partial auditory reafferentation with CI.

Results

For each participant we computed sensitivity (d') to changes using standard signal detection procedures (Macmillan & Creelman, 1991) to combine hits (i.e., correct 'change present' responses when a change was indeed present) and false alarms (i.e., erroneous 'change present' responses when no change occurred). Mean d' values (with standard errors in parenthesis) for change detection are reported in Table 1, as a function of experimental group (deaf, CI recipients or hearing controls), endogenous attention condition (focused or distributed), position of the change (centre or periphery) and number of drawings in the visual scene (4 or 8).

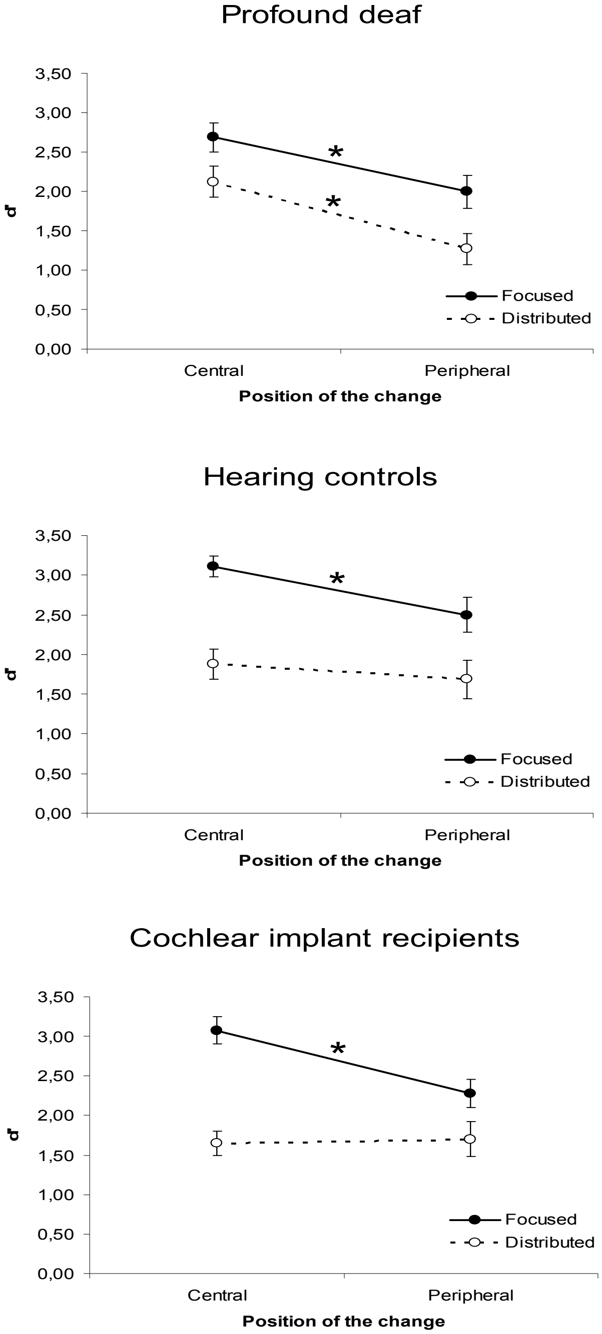
	4 drawings display				8 drawings display			
	Focused		Distributed		Focused		Distributed	
	d'	SE	d'	SE	d'	SE	d'	SE
Profound deaf								
Central	2,69	(0,19)	2,12	(0,19)	1,56	(0,15)	1,02	(0,14)
Peripheral	2,00	(0,21)	1,27	(0,20)	0,99	(0,18)	0,64	(0,19)
CI recipients								
Central	3,08	(0,17)	1,65	(0,15)	1,59	(0,14)	0,86	(0,15)
Peripheral	2,28	(0,18)	1,70	(0,21)	1,43	(0,17)	0,60	(0,11)
Hearing controls								
Central	3,11	(0,13)	1,88	(0,18)	1,83	(0,12)	1,05	(0,18)
Peripheral	2,50	(0,22)	1,69	(0,24)	1,30	(0,16)	0,65	(0,21)

Table 1: Mean sensitivity (d') in the change detection task (with standard error in parenthesis) as a function of group, attention condition, position of the change and number of elements in the visual scene.

Mean d' values for each participant were entered into a mixed Analysis of Variance (ANOVA), with attention condition, position of the change and number of drawings as within-participants factors, and group as between-participants factor. This analysis revealed a significant main effect of attention condition (F(1,56) = 79.0, $p < 0.0001$), position of the change (F(1,56) = 30.6, $p < 0.0001$), and number of elements (F(1,56) = 367.9, $p < 0.0001$). These main effects reflect higher sensitivity to changes during focused (mean d' = 2.03, SE = 0.08) than distributed attention (mean d' = 1.26, SE = 0.07), at central (mean d' = 1.86, SE = 0.06) than peripheral locations of the visual display (mean d' = 1.42, SE = 0.08), and for configurations of 4 (mean d' = 2.16, SE = 0.07) than 8 drawings (mean d' = 1.13, SE = 0.05). The analysis also revealed a significant interaction between attention condition and number of drawings (F(1,56) = 5.2, $p < 0.03$), caused by larger sensitivity differences in the two attention conditions (focused minus distributed) with the 4 drawings display (mean difference = 0.54, SE = 0.07) than the 8 drawings display (mean difference = 0.34, SE = 0.06). Finally, the 4-way interaction involving the group factor was also significant (F(2,56) = 4.187, $p < 0.02$). To understand this high-order interaction, we separated our data set as a function of the number of drawings in the scene (4 or 8) and analysed each set separately using an ANOVA with attention condition and position of the change as within-participants factors, and group as between-participants factor. The analysis on the 4 drawings display, revealed a significant interaction between attention condition, position of the change and group (F(2,56) = 3.3, $p < 0.05$). This three-way interaction is illustrated in Figure 2. By contrast, no interaction involving the group factor emerged when the 8 drawings display was considered (F(2,56) = 0.3, n.s.). We believe this null effect with the 8 drawings condition likely reflects a floor effect that masked any between-group difference (recall that mean d' in this condition was approximately half of that observed with the 4 drawings display; see main effect described above). This is not surprising given that change detection relies on visual short-term memory (Turatto & Bridgeman, 2005) which is a storage system with limited capacity (4/5 visual elements according to Luck & Vogel, 1997). Given these considerations, all subsequent analyses only focused on the 4-drawings conditions. Visual inspection of Figure 2 suggests that the interaction involving the group factor, observed in the 4 drawings display, was driven by the different performance of the three groups as a function of position of the change in the distributed attention condition. Under distributed attention, deaf participants were more sensitive to changes occurring at central (mean d' = 2.12, SE = 0.2) than peripheral locations (mean d' = 1.27, SE = 0.2; t(8) = 2.9, p = 0.009). By contrast, change sensitivity was equally accurate at central and peripheral locations for both hearing controls (mean d’ = 1.88 and 1.69, respectively; t(17) = 0.8, n.s) and CI recipients (mean d’ = 1.65 and 1.70, respectively; t(21) = 0.2, n.s.). Under focused attention, deaf showed again better change sensitivity at central than peripheral locations, however this advantage for central locations emerged for the other groups of participants as well (F(2,56) = 0.3, n.s.). In sum, unlike most of the previous literature on visual abilities in the profoundly deaf, our deaf participants were systematically better at responding to central than peripheral targets, regardless of attention conditions. In addition, a between-group difference emerged only in the distributed attention condition. Surprisingly, though, the only participants that (on average) remained more sensitive to changes occurring at central than peripheral locations under distributed attention were the deaf. We have also documented an overall performance difference between focus vs. distributed attention. This can reflect, at least to some extent, the fact that all participants inevitably attended to fewer elements in the focused condition as compared to the distributed one. However, it is worth noting that this potential confound does not undermine the advantage for the central locations consistently observed in the deaf regardless of attention condition, nor the observed difference between the three groups (that emerged selectively in the distributed attention condition; i.e., when all groups processed exactly the same number of visual targets).

Figure 2. The plot illustrate change sensitivity in the 4 drawings display, as a function of group, attention condition and position of the change. Note that asterisks indicate significant differences between performance at central and peripheral locations ($p < 0.01$). In the distributed attention condition deaf participants performed better at central than peripheral location (t(18) = 2.9, p<0,009), whereas no such difference emerged in hearing controls and CI recipients. Error bars show the standard error of the mean.

Figure 2


Profound deaf
3,50
3,00
2,50
2,00
1,50
1,00
0,50
0,00
d'
*
*
Focused
Distributed
Central
Peripheral
Position of the change
Hearing controls
3,50
3,00
2,50
2,00
1,50
1,00
0,50
0,00
d'
*
Focused
Distributed
Central
Peripheral
Position of the change
Cochlear implant recipients
3,50
3,00
2,50
2,00
1,50
1,00
0,50
0,00
d'
*
Focused
Distributed
Central
Peripheral
Position of the change

Role of anamnestic variables

Having assessed the overall performance of our three groups of participants in the change detection task, we turned to examine whether age of the participants (adolescent or adult), deafness onset (congenital, pre-verbal and post-verbal) and preferential communication strategy (oral or sign-language) played a role in modulating the observed performance. For the CI recipients, we also examined whether time from CI surgery influenced performance. Age of participants. One distinguishing aspect of our sample is the age heterogeneity. Age of the deaf and of the CI recipients ranged between 10 and 38 years old (see Experimental Procedure for details). Hearing controls were recruited accordingly, to match this age range (i.e., age of the hearing controls also ranged between 10 and 37 years old). To evaluate the role of age, we divided each experimental group into two sub-groups using the mean age of the overall distribution (i.e., 22.6 years old) as cut-off point. While this cut-off point is somewhat arbitrary, it captured best the binomial age distributions in our sample (young participants: mean age = 15 years, SD = 4; adult participants: mean age = 30 years, SD = 5). More specifically, applying the cut-off criterion resulted in 25 participants younger than 22 years (deaf: N = 5, mean age = 15 years old, SD = 1.8; CI recipients; N = 12, mean age = 15 years old, SD = 3.4; hearing controls: N = 8, mean age = 13 years old, SD = 3.2) and 34 participants with 22 years or more (deaf: N=14, mean age = 33 years old, SD = 4.3; CI recipients: N = 10, mean age = 28 years old, SD = 3.3; hearing controls: N = 10, mean age = 25, SD = 5). After this re-organization of the data set, mean d' were entered into an ANOVA with two within-group factors (attention condition and position of the change) and two between-group factors (group and age). This analysis revealed no significant main effect or interaction involving the age factor (all Fs < 2.5), suggesting that differences between the deaf and the other two groups in the distributed attention conditions documented above did not depend on the age of participants. Because the number of deaf participants in the younger age group was rather limited (N=5), we also ran an analysis that focused exclusively on the performance of adult participants. This additional analysis is of particular importance for comparison with the existing literature, given that all previous findings of enhanced visual performance in deaf have typically been conducted in the adult population. A similar ANOVA to the one conducted above, this time on adult participants only, confirmed the main effects of attention condition ($F(1,31) = 54.6$, $p < 0.0001$) and position of the change ($F(1,31) = 17$, $p < 0.0001$). However, unlike the main analysis reported above (i.e. the analysis including all participants regardless of age), the interaction between attention condition, position of the change and group only approached significance ($F(2,31) = 2.0$, $p = 0.15$). No other main effect or interaction was significant (all Fs < 1). While this further analysis constraints the interpretation of the between-group difference reported above (see Figure 2), it emphasises once again that deaf performed very similarly to the other groups and, most important, that change detection was systematically better for central than peripheral locations overall (as documented by the main effect of position of change, which was again driven by better change detection sensitivity for central than peripheral items). This pattern of result also emerges if performance of adult deaf participants and hearing controls is compared in terms of reaction time (see Footnote 1).

Role of deafness onset. As recently argued by Bavelier et al. (2006) deafness onset might be a relevant factor to take into account when studying the compensatory abilities in this population. In particular, Bavelier and colleagues emphasised the distinction between congenital and acquired deafness. The term 'congenital deafness' characterises individuals born or suspected to be born deaf, whereas the term 'acquired deafness' characterises individual that acquired deafness either before the acquisition of language (i.e., before 18 months of age, approximately; pre-verbal onset) or after the acquisition of language (post-verbal, i.e., after the 18 months of age). Accordingly, we divided the deaf participants in three sub-groups: congenital deafness (N = 5, mean age = 30 years old, range 17-39), pre-verbal acquired deafness (N = 4, mean age = 32 years old, range 15-38) and post-verbal acquired deafness (N = 10, mean age = 26 years old, range 12-38). Mean change sensitivity for the deaf was then analyzed using a similar ANOVA to the one reported above, but this time deafness onset was the only between-participants factor. This analysis revealed no significant main effect or interaction involving deafness onset (all Fs < 0.7). Role of communication strategy. Profoundly deaf participants in our study adopted two different communication strategies. Eight deaf participants used oral communication and lip-reading as preferential communication strategy (the so-called 'oralist' communication approach), whereas the remaining 11 deaf participants used the Italian sign-language as prevalent communication strategy (see Footnote 2). An ANOVA similar to the one reported above, but this time with communication strategy as the only between-participants factor revealed better sensitivity to changes in the deaf using sign-language (mean d'= 2.2, SE = 0.1) than in the deaf individuals using oral communication (mean d' = 1.7, SE = 0.2), resulting in a significant main effect of communication strategy (F(1,17) = 5.0, p = 0.04). No other interaction involving this between-participants factor approached significance (all Fs < 1.2). Note that the absence of an interaction between attention condition, position of the change andcommunication strategy (F(1,17) = 0.7, p < 0.4) indicates that the advantage for changes occurring at central than peripheral locations in the deaf under distribute attention is not the mere consequence of a visual bias related to lip-reading strategies.

Role of time from CI surgery.

Finally, we examined whether change sensitivity in CI recipients was modulated by the time (in month) from surgery. Recall that the only difference we observed with the present paradigm between deaf and hearing controls emerged in the 4 drawings display, under distributed attention, when all age groups were pooled together. Namely, deaf participants were more sensitive to changes at central than peripheral locations, whereas hearing controls were equally sensitive to changes regardless of their eccentricity. If this performance characterises the deaf population, participants who received a CI from less time should show larger sensitivity difference between central and peripheral locations than participants who received a CI from longer time. We thus ran a correlation analysis between sensitivity difference at the two eccentricities (i.e., d' for peripheral changes minus d' for central changes) in the distributed attention condition and the time from CI surgery (in months). This correlation analysis is shown in Figure 3. Positive values on the y-axis indicate better performance for central than peripheral locations (as observed in the deaf). Values

around zero on the y-axis indicate equal performance for central and peripheral locations (as observed in the hearing controls). If CI recipients gradually change their performance in the distributed attention condition as a function of time from the surgery, data points should distribute along a negative slope (i.e., from positive values to negative or zero values). However, as can be seen from Figure 3 this was clearly not the case (Rsq =0.03; p = 0.8).

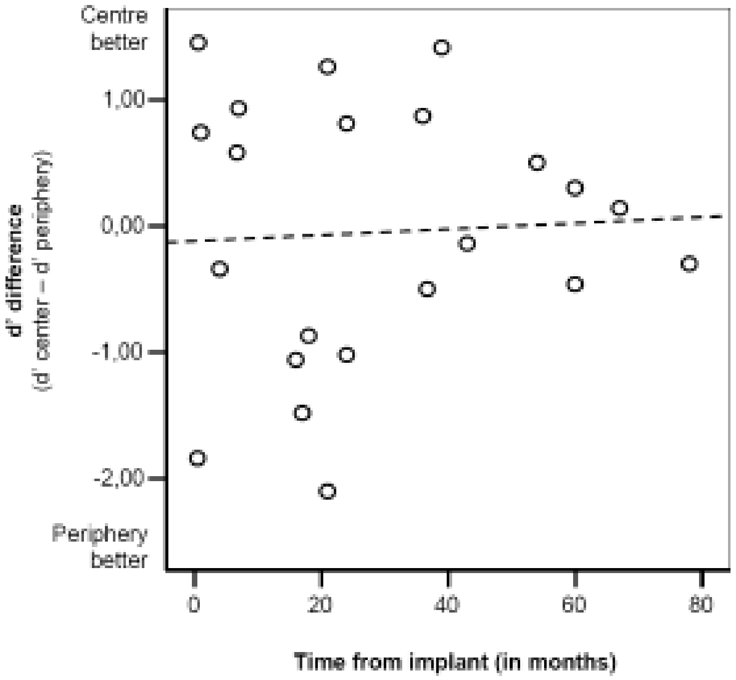


Figure 3. The plot depicts the relation between the change sensitivity difference between peripheral and central locations under distributed attention, and the time (in months) from CI surgery. No significant correlation emerged.

Discussion

Enhanced visual performance in the profoundly deaf has typically been documented as an advantage for processing stimuli occurring towards peripheral than central locations of the visual field (Baveleir et al., 2000; Bavelier et al., 2001; Bosworth & Dobkins, 2002; Chen et al., 2006; Colmenero et., 2004; Loke & Song, 1991; Neville & Lawson, 1987; Proksch & Bavelier, 2002; Sladen et al., 2005). One current influential view suggests that such compensatory ability of the deaf may be the consequence of different distribution of attentional resources across the visual field in this population (see Bavelier et al., 2006 for review). However, the question of whether this visual ability of the deaf relies upon endogenous or exogenous components of selective attention has been overlooked so far. In the present study, we adopted a task explicity designed to avoid abrupt visual onsets to examine for the first time compensatory visual ability of the deaf in a context in which exogenous capture is prevented and only endogenous shifts of attention are possible. Our findings reveal that making all local transients ineffective for exogenous attention capture results in remarkably similar change sensitivity in deaf individuals, hearing controls and CI recipients. All participants were more accurate under focused than distributed attention and equally affected by the numerosity of the visual displays. Most important, deaf participants always proved more sensitive to central than peripheral items, regardless of whether they were instructed to focus or distribute their attention resources in the visual field. As can be seen from Table 2, the very small proportion of deaf participants showing an advantage for peripheral locations in change detection does not appear to be dependant upon different deafness onset (pre-verbal or post-verbal) or preferential communication strategy ('oralist' or signers). This observation is in agreement with the results of the statistical analyses that excluded a modulation of change detection abilities as a function of these two anamnestic variables in the deaf. Thus, unlike the typical evidence in the literature on visual abilities in the deaf, no better performance at peripheral than central location emerged in the current study. The only difference between the three groups we have observed emerged under distributed attention. When all age groups were pooled together, hearing controls and CI recipients distributed their attention resources equally well between central and peripheral locations, whereas deaf participants remained systematically more sensitive to changes at central than peripheral locations. In other words, when asked to distribute visual attention across the entire visual scene, profoundly deaf participants were more likely to process stimuli occurring towards the centre than stimuli occurring towards the periphery. This between group difference could raise some intriguing speculations as to possible endogenous attention biases in the profoundly deaf (see Footnote 3), however it should be taken with caution since the three-way interaction between attention condition, position of change and group was no longer present when the statistical analysis was restricted to the adult participants alone. The first implication of the current findings is that enhanced visual performance at peripheral locations in the deaf may be critically dependent upon the exogenous component of attention. When exogenous components of visual attention are removed deaf participants do not show a preference for processing items at the periphery of the visual field. In fact, deaf individuals in the current study processed central items better than peripheral ones, both when they were instructed to attend specific regions of the visual field (focused attention condition) and when they were free to distribute attention resources across the visual scene (distributed attention condition). This suggests that the visual advantage for peripheral locations typically observed in previous studies could reflect capturing of participant's attention by local transients (mostly related to target onset), rather than endogenous strategies. In addition, our findings points to the conclusion that exogenous capture by visual transients may be a critical aspect of the compensatory visual mechanisms occurring in profound deafness. As anticipated in the Introduction, differential effects between deaf and hearing controls were obtained, to our knowledge, mostly in the presence of events capturing attention (e.g., Chen et al., 2006; Neville & Lawson, 1987; Proksch & Bavelier, 2002). In this respect, it is interesting to note that enhanced visual performance in the deaf failed to emerge in those studies in which complex visual scenes were abruptly presented (e.g., Brozinsky and Bavelier, 2004; Dye et al., 2006; Proksch & Bavelier, 2002). We argue that in such complex scenes multiple visual elements could have competed with one another, making attention orienting to local transient more difficult. In other words, these paradigms could have inadvertently produced an analogue of the so-called 'mud-splashes' effect (a change blindness paradigm alternative to the one adopted here; see O'Regan, Rensink & Clark, 1999), in which visual transients related to the change are masked by the simultaneous appearance in the scene of many other unrelated transients. In the study by Proksch and Bavelier (2002), for instance, participants performed a shape discrimination task with congruent or incongruent distracting shapes appearing at central and peripheral locations with respect to the targets. They showed that deaf individuals are affected by peripheral distractors more than hearing controls. However, such between-group difference disappeared when the number of concurrent visual stimuli appearing on the screen increased from 5 to 7 (i.e., from 4 to 6 shapes in the target array, plus 1 distractor; Proksch & Bavelier 2002, Exp.1). Similarly, Brozinsky and Bavelier (2004), did not show a difference between deaf and hearing individuals in a task in which participants were asked to observe a complex configuration of multiple moving dots and detect in which region of this configuration a velocity change occurred. In such a task, velocity changes occurred rapidly and near-threshold. Most importantly for the current purposes, the (relevant) transients related to the velocity change competed with the simultaneous (irrelevant) transients related to the other moving dots in the configuration. Finally, a recent study by Dye et al. (2007) showed that deaf and hearing individuals display similar alerting and attention orienting abilities, when asked to decide whether an arrow flanked by 4 distracting arrows is pointing left or right. Interestingly, a between-groups difference in this study emerged when the number of flanker elements was reduced to 2, suggesting again that the presence of several competing items in the scenes can prevent exogenous attention capture to the target, leading to no enhanced performance in the deaf. The second implication of the current findings is that endogenous allocation of focused attention is not sufficient to reveal differences between profoundly deaf individuals and hearing controls. In our study, no performance difference between deaf individuals and hearing controls emerged under the condition of focused endogenous attention. This finding contradicts previous suggestions that changes in visual processing after auditory deprivation are best revealed under conditions of focused attention (e.g., Bavelier et al., 2006, p. 513; see also Neville & Lawson, 1987). This proposal originated from fMRI studies that documented enhanced activity in the MT/MST complex when peripheral motion stimuli were attended, but not when they were perceived under passive viewing (Bavelier et al., 2000; see also Fine et al. 2005).

However, note that several other studies have now shown that enhancement of visual abilities in the deaf can decouple from focused attention. For instance, Armstrong and colleagues (Armstrong, Hillyard, Neville & Mitchell, 2002) conducted an ERP study in which deaf participants were asked to observe moving gratings to detect the occurrence of a rare target. Larger and more anteriorly distributed N1 components emerged despite the fact that the task was always performed under distributed attention. Similarly, two studies have shown that enhanced detection for peripheral targets can emerge in the deaf irrespective of attentional manipulations. Chen et al. (2006) have shown that deaf are faster than hearing controls (56 ms on average) at detecting a transient light at 3 degrees from visual fixation, regardless of whether attention was focused on the target or attracted away from it by an invalid cue. Similarly, Colmenero et al. (2004) showed that deaf were faster at detecting peripheral targets regardless of whether the preceding visual cue was invalid or neutral. Thus, enhancement of motion processing and target detection can emerge in the deaf even when attention is not previously focused on the target. We expand this conclusion by showing that explicit instructions to focus attention in a region of space (either central or peripheral) do not result in enhanced change detection performance in the deaf when all local transients related to the target are removed. The third implication of our results is that compensatory visual mechanisms in the profoundly deaf cannot be described as a generalised enhancement of attentional resources. Deaf participants did not show overall enhanced sensitivity with respect to hearing controls or CI recipients in any of our experimental conditions. This conclusion is in agreement with recent works that suggest that not all aspects of visual attention are modified by deafness (e.g., Dye, Baril & Bavelier, 2007, Hauser, Dye, Boutla, Green & Bavelier, 2007). For instance, Hauser and colleagues (2007) have shown that deaf and hearing controls have similar abilities when attending and monitoring multiple objects simultaneously. Our novel findings suggest that the distinction between endogenous and exogenous attention components may be critical for understanding the context in which compensatory visual abilities in the deaf can emerge. In conclusion, our findings provide further understanding into the specificity of multisensory plastic changes occurring after auditory deprivation (e.g., Armstrong et al., 2006; Dye et al., 2007; Hauser, Dye, Boutla, Green and Bavelier, 2007) by showing that endogenous attention shifts alone may not be responsible for the enhanced visual abilities in the profoundly deaf. Our findings raise the possibility that previous evidence showing enhanced visual performance in the deaf at the periphery of the visual field reflects preferential processing of peripheral exogenous transients in this population, rather than general enhancement of endogenous attentional resources towards this region of space.

Experimental Procedure

Participants

Nineteen bilateral profoundly deaf (mean age = 28.2 years, SD = 9.1, range 12- 38 years old; 10 males and 9 female) gave their informed consent to participate in the study. Eleven were recruited at the National Association for Deaf (Ente Nazionale per la protezione e assistenza dei Sordi di Trento, Italy), eight were consecutive candidates to receive a cochlear implant at the Hospital “Santa Maria del Carmine” (Rovereto, Italy).

All participants had uncorrected bilateral profound hearing loss (>80 dB). Among the deaf participants, 9 became deaf before of acquisition of language within the first 18 months of age (i.e. pre-verbal onset), 9 became deaf after the acquisition of language (i.e., post-verbal onset) and 1 had unknown deafness onset.

Twenty-two individuals with unilateral cochlear implant (mean age = 20.5 years, SD = 7.4, range 10-33 years old; 8 males, 14 females; average time from CI surgery 28.8 months, SD = 23.3) were also recruited at the local hospital to take part in the study. Among CI recipients, 18 were deaf with pre-verbal onset, and 4 were deaf with post-verbal onset. Note that all post-verbal deaf participants and CI recipients acquired deafness before 6 years of age. Eighteen hearing controls (mean age = 19.4 years, SD = 7.5, range 10-37 years old; 9 males, 9 females) also took part in the study. They were selected to match the age of deaf individuals and CI recipients. All participants in the study reported normal hearing abilities, normal or corrected-to-normal vision, and were right-handed by self report. The study was approved by the ethical committee of the

Hospital “Santa Maria del Carmine” (Rovereto, Italy). Stimuli and apparatus Stimuli were 14 line-drawings depicting common objects, either living or nonliving (e.g., an animal, a fruit, a piece of furniture, etc.) selected form the Snoodgrass and Vanderbilt (1980) stimulus-library. All were drawn in white on a uniform grey background. All drawings had their main axis along the horizontal dimension, and covered a visual area of 2.7 by 3.5 degrees of visual angle. Visual luminance was equated for all stimuli in a previous pilot study. Each visual scene comprised 4 or 8 drawings, all different and randomly selected from the experimental set. Selected drawings were arranged on two invisible concentric circles centred on visual fixation, with a radius of 3 degree (inner circle) or 8 degree (outer circle, see Figure 1). From now on we refer to locations and drawings on the inner circle as central, and locations and drawings on the outer circle as peripheral. In the 4 drawings configurations, 2 drawings were arranged on the inner circle along one of the diagonals of the display (e.g., +45° diagonal), and the other 2 drawings were arranged on the outer circle along the other (orthogonal) diagonal of the display (e.g., - 45° diagonal; see Figure 1). In the 8 elements configuration, 4 drawing appeared on each circle, arranged on both diagonals in each circle. The fixation point was a white cross at the centre of the screen.

Stimuli were presented on a standard 17 inches monitor, with 1024 X 768 pixel resolution. Participants sat at approximately 60 cm from the monitor and were instructed to keep their head and eyes oriented towards fixation throughout the experiment. Responses were recorded using the two mouse buttons (the left mouse button was used to indicate ‘change present’ responses, the right mouse button was used to indicate ‘change absent’ responses). The experiment was programmed with E-Studio

1.1.4.1, presented and controlled with E-Prime 1.1.4.1 (www.pstnet.com/products/eprime).

Eye position was not monitored in the present study. However, the experimenter remained in the room throughout testing, and checked that participants complied with the posture instructions given at the beginning of each block. Note that we have introduced flickering fixation precisely with the purpose of attracting the participant's attention to the centre of the visual scene at the beginning of each trial. In addition, because our paradigm entirely removed all local visual transients, there was no peripheral event capturing the eyes (and attention) during the trial. Finally, any systematic failure to maintain fixation during the task would have inevitably resulted in a considerable drop of performance. Participants were reminded of this specific information at the beginning of each block (and received an overall feedback on their performance at the end of each block).

Procedure

Before starting the experiment each participant received detailed instructions about the task directly on the computer screen. Instructions comprised text and images and were carefully designed to be self-explanatory and comprehensible to all participants (i.e., regardless of hearing abilities or age). In addition, an interpreter of the Italian Sign Language always accompanied participants that used sign language as primary way to communicate.

Each trial began with the fixation cross flickering at 5 Hz in the centre of the empty display for 600 ms, to capture the participant's attention and gaze at the centre of the screen and provide an alert signal. Fixation remained visible throughout the trial, until the participant's response. As soon as fixation flickering ended, the two configurations of drawings appeared in sequence, for 200 ms each, separated by an empty grey screen lasting 500 ms. In 50% of trials, one of the drawings of the first scene changed to a different drawing in the second scene, thus producing a 'change trial'. In the other 50% of trials, the two scenes were completely identical, thus producing a 'no-change trial'.

Each participant completed three experimental blocks, which differed in terms of the attentional instructions. Participants were instructed to either focus their attention endogenously towards central locations (central focused attention), focus their attention endogenously towards peripheral locations (peripheral focused attention) or distribute attention across the whole screen (distributed attention). n focused attention conditions, all changes occurred within the attended area (central or peripheral), with equal probability for each of the 4 possible locations within a circle. In the distributed attention condition, changes were equally likely to occur at any of the 8 possible locations on the screen (i.e. 4 central and 4 peripheral). At the beginning of each experimental block a verbal instruction (e.g. "attend to peripheral locations") and a pictorial cue (e.g. a visible red circle of 8° radius printed on the screen, also indicating peripheral target locations) clearly identified which eccentricity had to be attended throughout the block of trials. A short practice block of 16 trials was run before each experimental block to familiarise participants with the specific attentional set. At the end of the practice block percentage of correct responses was displayed. Participants were instructed to follow attentional instructions and detect whether one of the drawings in the second scene had changed by pressing the left or the right buttons of the mouse (to indicate 'change present' or 'change absent' responses respectively). At the end of each experimental block the overall percentage of correct responses was shown on the screen to provide average feedback. All sessions were completed within the same day and the whole experiment lasted approximately 1 hour. The experiment comprised of 300 trials in total, equally distributed among the three experimental blocks. Order of blocks, varied pseudo-randomly between participants.

Footnotes

1. Although our task stressed accuracy over response speed (as most change blindness paradigm in the literature) we examined reaction times (RTs) for the adult deaf and hearing controls. This analysis was not possible on young participants and most CI recipients because RTs for these groups were considerably more variable and unreliable. Medians RTs for adult deaf (N = 10) and adult hearing controls (N = 11) were entered into an ANOVA with attention condition and position of the change as within-participants factors, and group as between-participants factor. This analysis revealed only a main effect of position of the change ($F(1,19) = 8.4$, $p < 0.01$; center: mean = 506 ms, SE = 23; periphery: mean = 575 ms, SE = 35). No other main effect or interaction reached significance (all Fs < 2.2). Note that this result is in support of the sensitivity pattern, i.e., adult deaf participants are systematically faster at central than peripheral locations, but overall not different from hearing control. 2. The role of communication strategy was not addressed in CI recipients because all participants in this group used oral communication and lip-reading as preferential communication strategy (the so-called 'oralist' communication approach). This was true also for those CI recipients who were deaf with pre-verbal onset. This unusual homogeneity of communication strategy in the CI recipient group reflects two facts that are peculiar to

the Italian context. First, in Italy (unlike the UK or USA) the oralist approach is still prevalent over the sign-language approach (Fischer & Lane, 1993; Porcari Li Destri & Volterra, 1995). Second, in the Italian context, it is far more likely that deaf requesting a CI surgery have been trained to use oral-comunication strategies.

3. The difference between the three groups under distributed attention could reflect an adaptive behavior of the deaf participants that comes into play when the task requires monitoring of the entire visual field. Specifically, we speculate that the most adaptive attention strategy for the deaf could be to focus their endogenous attention centrally, given that the periphery would anyway rely on exogenous attentional capture. Clearly, while such a strategy could lead to balanced attention distribution in everyday life, it proved inefficient in our task due to the complete removal of central and peripheral local transients that could capture attention to the change location. This resulted in the uneven change detection performance of the deaf and a persistent advantage for central than peripheral locations under distributed attention.

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Interim conclusions

The main result of the previous study showed that adult deaf individuals do not display enhanced endogenous attention in a task that prevents exogenous capture. The present result contrast with previous studies that linked enhanced visual performances in deaf than hearing controls specifically to in the deployment of endogenous selective attention resources in the visual field. The discrepancy between the present finding and the previous literature could suggest that exogenous than endogenous attention plays a key role in enhanced visual abilities in the deaf. This hypothesis was tested further and more directly in the second study.

CHAPTER 3

COMPENSATORY VISUAL ABILITIES IN PROFOUND DEAFNESS: THE CONTRASTING ROLE OF EXOGENOUS AND ENDOGENOUS ATTENTION

Bottari D., Turatto M. and Pavani F. (under review). Compensatory visual abilities in profound deafness: the contrasting role of exogenous and endogenous attention. Submitted to Neuropsychologia.

Abstract

We used a modified version of the change-blindness paradigm to assess the relative contribution of endogenous and exogenous components of visual attention in the compensatory visual abilities due to deafness. Ten deaf individuals and 12 hearing controls were asked to detect a change between two consecutive visual scenes comprising stimuli at central and peripheral locations. In half of the trials, a blank screen was interposed between the scenes to prevent any exogenous capture of attention from change-related transients. This produced an entirely endogenous attention setting. In the remaining trials, a visual cue appeared on the otherwise blank screen interposed between the scenes, at either valid or invalid locations with respect to the change. This produced an exogenous attention setting. Participants also completed a simple-detection task for central or peripheral visual stimuli. The change blindness task showed that visual compensatory mechanism of deafness dissociate as a function of which attention component is involved. When captured by valid exogenous events, deaf showed enhanced reactivity to peripheral targets, unlike hearing controls. By contrast, when relying on endogenous attention alone, deaf attended more to central than peripheral locations. Finally, in the simple-detection task, deaf performed 56 ms faster than controls, regardless of stimulus location. These findings suggest a key role of attention in the visual abilities observed in deafness, but point to a contrasting role of exogenous and endogenous attention components on this adaptive compensatory mechanism. In addition, they suggest that visual abilities in the deaf characterise as enhanced reactivity to the visual events.

Introduction

In everyday life, hearing plays a key role that extend well beyond language and communication, being critically important for monitoring the external environment in which we live (e.g., Näätänen, Tervaniemi, Sussman, Paavilainen & Winkler, 2001; Heffner & Heffner, 1992). The last decade has witnessed an increase interest in the perceptual and attentional abilities of individuals with profound deafness (e.g., Armstrong, Hillyard, Neville, Mitchell, 2002; Bosworth & Dobkins, 2002; Chen, Zhang & Zhou 2006; Dye, Baril & Bavelier, 2007; Fine, Finney, Boynton & Dobkins, 2005; Levanen & Hamdorf, 2001; Proksch & Bavelier 2002; Stevens & Neville, 2006). Several studies have shown that the brain of deaf individuals can re-organise to compensate for this sensory deprivation, adjusting its responses to the remaining sensory modalities and in particular to vision (e.g., Armstrong et al. 2002; Bavelier, Tomann, Hutton, Mitchell, Corina, Liu, Neville, 2000; Neville & Lawson, 1987; see Bavelier, Dye & Hauser, 2006 and Mitchell & Maslin, 2007 for reviews). However, the exact nature of these compensatory effects, as well as their interplay with voluntary and involuntary behaviour, remains poorly understood.

The current perspective on compensatory visual abilities in the deaf is that enhanced visual responses in this population predominantly emerges for visual targets appearing towards the periphery of the visual field (see Bavelier et al., 2006 for a review). For instance, deaf individuals can be faster than hearing controls at detecting the onset of peripheral visual targets (e.g. Chen et al., 2006; Colmenero, Catena, Fuentes & Ramos, 2004; Loke & Song, 1991) or at discriminating the direction of visual motion at attended peripheral locations (Neville & Lawson, 1987; see also Baveleir et al., 2000; Bavelier, Brozinsky, Tomann, Mitchell, Neville & Liu, 2001).

Similarly, when central and peripheral static stimuli compete for selective attention resources, deaf participants are more likely to orient visual attention towards peripheral than central locations (Chen et al., 2006; Proksch & Bavelier, 2002; Sladen, Tharpe, Ashmead, Grantham & Chun, 2005). Finally, deaf individuals have been shown to possess a field of view that extends further towards the periphery than hearing controls (Stevens & Neville, 2002). By contrast, no difference between deaf and hearing controls have typically been documented when processing targets presented towards the centre of the visual field (Loke & Song, 1991; Neville & Lawson, 1987) or directly at fixation (Poizner & Tallal, 1987).

Several authors have suggested that enhanced peripheral performance in the deaf may reflect a different distribution of attentional resources in this population (e.g., Bavelier et al., 2000, 2001; Neville & Lawson, 1987; but see Armstrong, Hilliard, Neville & Mitchell, 2002). In particular, Bavelier and colleagues (2006) have recently proposed that enhanced modulations of spatial attention in the remaining sensory modalities could be “a core compensatory mechanism of cross-modal plasticity” in the profoundly deaf (p. 515). Despite this strong assumption, to date there have been little attempts to examine exactly which aspect of selective attention plays a role in these compensatory visual abilities of the deaf. Classically, two distinct mechanisms of spatial attention have been identified, which are both functionally (Posner, 1980; Jonides, 1981) and anatomically distinct (Corbetta & Shulman, 2002; Mayer, Dorflinger, Rao & Seideberg, 2004). On the one hand, visual attention can be oriented to an object or a location because an abrupt change in visual luminance at the retinal level (i.e., a visual transient) has occurred for that specific region of the visual field. This type of bottom-up attention orienting is entirely automatic and has typically been referred to as exogenous orienting. On the other hands, visual attention can be summoned to an object or a location because of it is relevance for the behavioural goal of the individual. This type of top-down attention orienting is voluntary and strategic and has typically been referred to as endogenous orienting. Exogenous orienting is thought to be mediated by ventral fronto-parietal cortices predominantly lateralised in the right-hemisphere (including temporo-parietal junction and inferior frontal cortices), plus subcortical structures including the superior colliculus (e.g., Rafal, Henik,, & Smith, 1991). By contrast, endogenous orienting is though to be mediated by more dorsal fronto-parietal cortices in both emispheres (including regions such as the Inferior Parietal Sulcus and the Frontal Eye Field; e.g., Corbetta & Shulman, 2002). Although these two functions are not entirely segregated and are known to interact (Corbetta & Shulman, 2002), it is crucial to define to what extent each of them (or both) could contribute to the compensatory cross-modal plasticity in the deaf.

To our knowledge, no study in the literature on visual abilities in the deaf has tried to disentangle the contribution of the two selective attention components within the same experimental paradigm. In fact, even those studies that intended to manipulate endogenous attention alone (e.g., Bosworth & Dobkins, 2002; Neville & Lawson 1987; Parasnis & Samar, 1985) could have in fact mixed endogenous and exogenous attention orienting. This because the mere abrupt onset of target stimuli in the scene could have produced involuntary re-orienting of attention resources towards that region of visual space (for a detailed discussion of this point see Bottari, Turatto, Bonfioli, Abbadessa, Selmi, Beltrame & Pavani, 2008). For instance, in the classic study by Neville & Lawson (1987) participants were instructed to attend to one eccentricity (centre or periphery) at a time and to respond only to targets at the attended locations. Although this task apparently engaged endogenous attention alone, the visual targets appearing abruptly at fixation or in the periphery of the visual field surely triggered exogenous orienting of attention. Similarly, in a study by Bosworth and Dobkins (2002) participants were endogenously cued to the upcoming target location beforehand. However, the abrupt onset of a patch of moving dots (i.e., the target stimulus in their study) likely introduced an (additional) exogenous attention component in their paradigm. To our knowledge, this ambiguity as to which exact attentional component determines enhanced visual abilities in the profoundly deaf characterises most of the existing studies (e.g. Bavelier et al., 2000; Bosworth & Dobkins, 2002; Chen et al., 2006; Neville & Lawson, 1987; Proksch & Bavelier, 2002; Stevens & Neville, 2006).

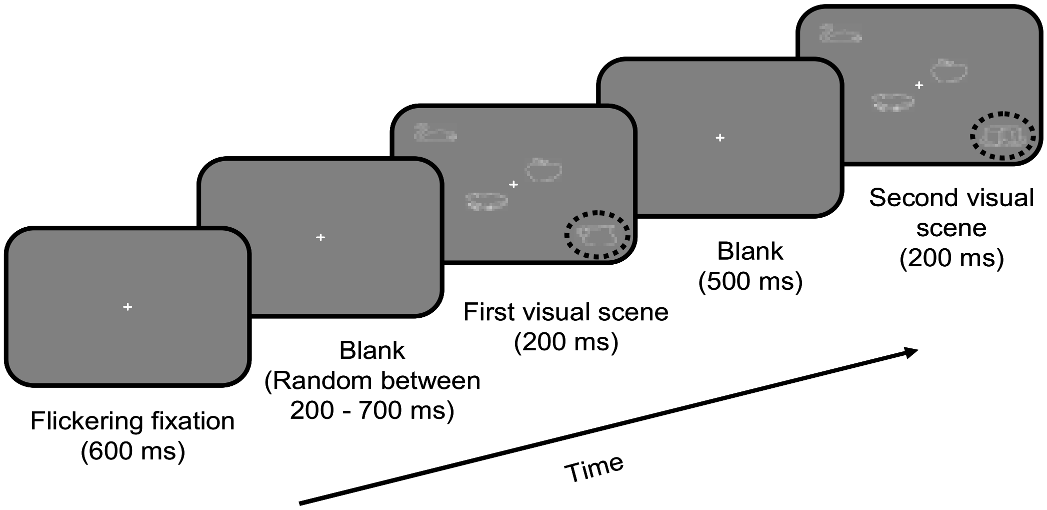
The aim of the current study was to assess visual abilities in the profoundly deaf in a paradigm that clearly disentangle endogenous and exogenous components of selective attention. To this aim, we adapted a change detection paradigm that we recently used to investigate endogenous attention in the deaf (Bottari et al., 2008). The paradigm consists in the sequential presentation of two visual scenes, each comprising four line-drawings object (see Figure 1). In half of the trials one of the drawings changes into a different one (in the example shown in Figure 1, the 'jug' on the bottom right corner of the first scene changes into a 'cake' in the second scene), and the participant's task is to decide in each trial whether a change was present or absent. Importantly, a 500 ms blank-screen is introduced between the two scenes in all trials. This creates a global visual transient in the sequence (i.e., any single pixel in the second scene containing the drawings will inevitably change its luminance with respect to the preceding blank-screen) that consequently masks the local visual transients related to the possible line-drawing change. This experimental procedure, originally developed by

Phillips in 1974, more recently became known as the one-shot version of the 'change blindness paradigm' (O'Regan, Rensink & Clark, 2000; Rensink, 2002; Turatto & Bridgeman, 2005). The complete masking of local transients obtained using this procedure, lead to the inability to orient attention exogenously to the relevant change location, and results in substantial blindness to the change.

In the present study, we took advantage of this distinctive aspect of the change blindness paradigm to create two types of trials, intermingled during the experiment. In endogenous trials, the trial sequence was exactly as described above, thus preventing any exogenous capture of visual attention and allowing to assess the endogenous component of visual attention alone (Figure 1a). In exogenous trials, we introduced a spatial cue (a white dot) before each of the visual scene containing the line-drawings (see Tse, 2003 for a similar procedure) at one of the four possible change locations. The example shown in Figure 1b illustrate a trial in which the cue appeared exactly at the change location. However note that during the experiment the cue was entirely non-predictive of change location (i.e., occurred at the change location in ¼ of exogenous trials, and at the no-change locations in the remaining ¾ of exogenous trials). Finally, to probe central as well as peripheral locations of the visual field, the four line-drawings in each visual scene were equally distributed at two eccentricities (3° and 8° from central fixation).

Figure 1

(a) Cue absent trial



(b) Cue valid trial

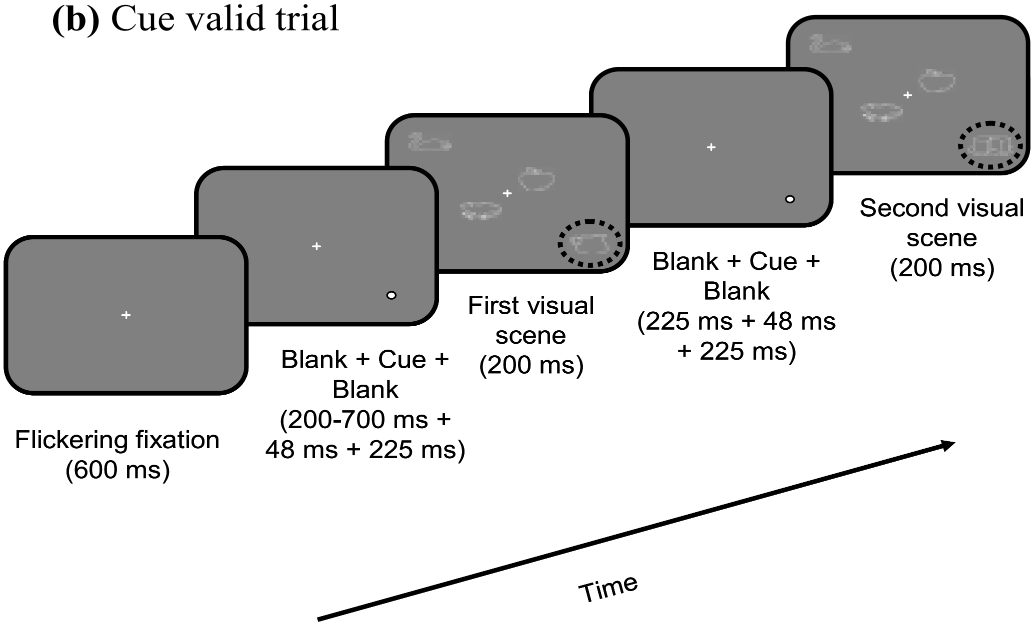


Figure 1. Time sequence in the change detection paradigm for a) cue-absent trials; b) cue-valid trials, the cue precedes each visual display and correctly indicate the change location. Cue-invalid trial (not shown in figure) were entirely identical to cue-valid trials, with the sole exception that the cue location did not correspond to the change location. Both examples depict a change present trial. The dashed circle in the second visual display indicates the changed drawing for illustrative purposes only (i.e., no circle was present in the actual experiment).

Based on past literature on enhanced visual performance in the deaf, we expected any difference between deaf and hearing controls to emerge as a different performance for central and peripheral locations (e.g., Bavelier et al., 2000; Neville & Lawson, 1987; Proksch & Bavelier, 2002). Moreover, because our previous study using the change blindness paradigm (with endogenous trials only, unlike here) suggested that deaf individuals do not outperform hearings controls in a visual task that prevents exogenous capture of visual attention (Bottari et al., 2008), we expected a difference between the two groups to emerge selectively for exogenous than endogenous trials. With this prediction in mind, and also to further establish how deaf participants and hearing controls reacted to the exogenous spatial cue introduced in the change detection task, we also ran a parallel experiment in which the visual cue was presented alone (at the exact same locations as in the change detection task) but this time it was the imperative stimulus for the response (instead of a task-irrelevant item). Note that such a basic detection task, despite its obvious simplicity, has rarely been used in the literature on visual abilities in the profound deaf (see Loke & Song, 1991).

Methods

Participants

Ten profoundly deaf individuals (mean age = 33 years, SD = 7.4, range 20-41 years old; 5 males and 5 female) were recruited at the National Association for Deaf (Ente Nazionale per la protezione e assistenza dei Sordi, Trento, Italy) and gave their informed consent to participate in the study. All participants had uncorrected bilateral profound hearing loss (>80 dB). All acquired deafness within the first 2 years of age, except one participant who was diagnosed deaf at the age of 5 years-old. Four had congenital deafness. All deaf participants were proficient sign-language users.

Twelve hearing controls (mean age = 30 years, SD = 7.7 range 22-45 years old; 3 males, 9 females) were recruited among the students at the Faculty of Cognitive Science of the University of Trento to take part in the study. All participants had normal or corrected-to-normal vision and were right-handed by self-report. The study was approved by the ethical committee at the University of Trento (Italy).

Stimuli and apparatus

The change detection task required the comparison of two visual scenes presented one after the other. Each visual scene comprised 4 different line-drawings, randomly selected in each experimental trial from a pre-determined set of 14 stimuli of the Snodgrass and Vanderwart (1980) line-drawing library. Each line-drawing depicted a common object, either living or non-living (e.g., an animal, a piece of fruit or a piece of furniture), and was drawn in white on a grey background. All drawings had their main axis along the horizontal dimension and covered a visual area of 2.7 by 3.5 degrees of visual angle. Subjective equation of visual luminance was determined for all stimuli in a pilot study.

In the change detection task, the four selected drawings in each of the visual scenes were presented simultaneously and arranged on two invisible concentric circles centred on visual fixation. The radius of the inner circle was 3 degrees of visual angle, the radius of the outer circle was 8 degrees of visual angle. The two drawings on the inner circle were placed along one of the two diagonals of the display (e.g., the diagonal oriented 45° to the right), while the two drawings on the outer circle were placed along the orthogonal diagonal (e.g., the diagonal oriented 45° to the left; see Figure 1 for an example). The combination of stimulus eccentricity (center or peripheral) and diagonal (45° right or 45° left) changed every block of trials. From now on we refer to locations on the inner circle as central, and locations on the outer circle as peripheral. In addition to the line-drawings, a small white dots of 0.5 degrees of visual angle could be presented on screen during the exogenous trials, shortly before each of the visual scenes. The dot could appear at any of the 8 possible locations occupied by the line-drawings (i.e., four central locations and four peripheral locations, across all blocks), lasted 48 ms and always disappeared before the line-drawing were presented. This visual stimulus was used in exogenous trials only (see procedure) as task-irrelevant transient for automatic attention capture in the change detection task. In addition, it was used as the imperative visual target in the simple detection task that participants also completed during the experimental session. Visual fixation was a white cross, present at the centre of screen throughout the trial.

All stimuli were presented on a standard 17 inches monitor, with 1024 X 768 pixel resolution. Responses were recorded using the right and left mouse keys. 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).

Procedure and design

Participants sat at approximately 60 cm from the computer monitor and were instructed to keep their head and eyes oriented towards fixation throughout testing (see Footnote 1). The experimental session always comprised two parts. The first part, consisted in a change detection task and lasted approximately 50 minutes. Participants were required to decide whether a visual change occurred between the two visual scenes presented in rapid succession. The second part of the experimental session consisted in a simple detection task and lasted approximately 20 minutes. Participants were required to respond as quickly as possible to the sudden onset of a simple visual target. All participants except one hearing control completed both task. Procedure and design of these tasks will be described separately in the following paragraphs.

Change detection task

Each trial of the change detection task began with visual fixation flickering at 0.5 Hz for 600 ms. This had the purpose of capturing participant's attention and gaze towards the centre of the screen. After flickering, fixation remained still on a uniformly gray screen for a random interval ranging between 200 and 700 ms before the first visual scene was presented. This first scene remained visible for 200 ms, and was followed by a uniformly grey screen lasting 500 ms and finally by a second visual scene lasting 200 ms. In 50% of trials, one of the drawings of the first visual scene changed to a different drawing in the second visual scene, thus producing a 'change trial'. In the other 50% of trials, the two scenes were completely identical, thus producing a 'no-change trial'.

Orthogonal to the change/no-change trials, two additional types of trials were possible: endogenous and exogenous trials. In endogenous trials, the gray screens appearing before the first and the second scene only contained visual fixation. In exogenous trials, the gray screens contained instead a small white dot, arranged at one of the 8 possible drawing locations, and delivered for 48 ms at 225 ms before each of the visual scenes. The dot appeared with equal probability across all drawing locations, and was not-predictive of change presence or absence, nor of change location. Note that the cue appearing before the first scene, and the cue appearing before the second scene always occupied the same spatial location within each trial (see Figure 1). Endogenous trials were also identified as ‘cue absent trials’. Exogenous trials were identified as ‘cue valid trials’, when the cue appeared at the exact change location or as a ‘cue invalid trials’, when the cue appeared at different location with respect to the change. Among all cue trials, 25% of trials were cue valid, and 75% of trials were cue invalid.

Before starting each of the two tasks participants received detailed instructions directly on the computer screen. Instructions comprised text and images and were carefully devised to be self-explanatory and comprehensible to all participants (i.e., regardless of their hearing abilities). In addition, a hearing interpreter of the Italian Sign Language always accompanied deaf participants. Participants were instructed to respond in each trial using the left mouse key to indicate the presence of a change, and the right mouse key to indicate the absence of a change. They were informed that the occasional dots appearing before the visual scenes were completely task-irrelevant and could be ignored. Finally, they were instructed to be as accurate as possible.

The change detection experiment was divided in two blocks. In one block, central line-drawings were placed along the diagonal oriented 45° to the right, while peripheral line-drawings were placed along the orthogonal diagonal oriented 45° to the left. In the other block, the arrangement of central and peripheral line-drawings along the diagonals was reversed. The order of blocks was counterbalanced across participants. This manipulation avoided the possible confound that cue-trials could inform participants as to the subsequent configuration of drawings, unlike the cue-absent trials (recall that, when present, the cue was un-predictive of change location, but always appeared at one location in which a subsequent drawing would be presented within each trial). The change detection task comprised 384 trials in total, equally distributed between the two blocks. In addition, participants completed 16 practice trials.

The experiment was a 2 by 3 factorial design, with change location (central or peripheral) and cueing condition (cue absent, cue valid or cue invalid) as within-participants factors, and group (deaf or hearing controls) as between-participants factor. Dependent variables were change detection sensitivity (d') and response times (in milliseconds). Sensitivity was computed using standard Signal Detection Theory to combine the proportion of hits and false alarms for each participant in each experimental condition (Macmillan & Creelman, 1991). Response times (RTs) were computed as the median RT of correct responses for each participant in each trial. Our instructions to participants favoured accuracy over speed of response, as is typically done in change detection studies and in the change blindness literature. However, we also considered RTs as dependent measure because a large part of the literature on visual abilities in the profoundly deaf found differences between this population and hearing participants specifically when readiness of response is considered (e.g., Bavelier et al., 2000; Colmenero et al., 2004; Loke & Song, 1991; Nava, Bottari, Zampini & Pavani, 2008; Neville & Lawson, 1987; Parasnis & Samar, 1985; Proksch & Bavelier, 2002; Sladen et al., 2005).

Simple detection task

Each trial of the simple detection task began with visual fixation flickering at 5 Hz for 600 ms. As before, this manipulation had the purpose of capturing participant's attention and gaze towards the centre of the screen. After flickering, fixation remained still for a random interval (ranging between 200 and 700 ms) before the imperative visual target appeared at any of the 8 possible locations (i.e., 4 central and 4 peripheral) used also in the change detection task. The visual target was the small white dot presented in exogenous trials of the change detection experiment, presented for 48 ms as before. Participant's response terminated the trial, and a random inter-trial interval ranging between 1250 and 1750 ms was introduced before the beginning of the subsequent trial. In case of anticipation responses a visual warning signal was delivered.

Participants were instructed to press the space bar of a computer keyboard as fast as possible upon the appearance of the visual target, regardless of its location. The experiment comprised of 60 trials in total. The first 12 trials were used as practice and removed from subsequent analyses. The experiment was a 2 by 2 factorial design, with target location (central or peripheral) as within-participants factor and group (deaf or hearing controls) as between-participant factors. The only dependent variable was RT.

Results

Change detection task: Sensitivity

Mean sensitivity measures (d') with standard errors for each experimental group are reported in Table 1, as a function of change location and cueing condition. Sensitivity for each participant was entered into a mixed Analysis of Variance (ANOVA), with change location (central or peripheral) and cueing condition (cue absent, cue valid or cue invalid) as within-participants factors, and group (deaf or hearing controls) as between-participants factor. When appropriate the Greenhouse-Gaisser method was adopted to correct for sphericity violations in the ANOVA.

This analysis revealed a significant main effects of change location (F(1,20) = 22.7, $p < 0.0001$) caused by higher sensitivity for changes occurring at central (d' = 2.0, SE = 0.1) than peripheral locations (d' = 1.6, SE = 0.1). There was also a main effect of cueing condition (F(2,19) = 18.4, $p < 0.0001$) caused by worse sensitivity for changes in the cue invalid condition (d' = 1.5, SE = 0.1), than cue valid (d' = 2.0, SE = 0.2) and cue absent conditions (d' = 1.9, SE = 0.1; $p < 0.0001$ for both comparisons on paired t-tests). By contrast, sensitivity did not differ between cue valid and cue absent conditions (t(21) < 1, n.s.). No other main effect or interaction emerged from this analysis (all Fs < 1.2). Importantly, there was no main effect or interaction involving the group factor, indicating that sensitivity did not differ between groups as a function of visual change eccentricity. In fact, both groups performed worse for changes occurring at peripheral than central locations. In addition, both groups performed worse when a task-irrelevant visual cue exogenously attracted attention away from the actual change location.

	Endogenous attention	Exogenous attention	
	Cue absent trials	Cue valid trials	Cue invalid trials
Deaf			
Central change	2,19 (0,12)	2,23 (0,10)	1,61 (0,15)
Peripheral change	1,71 (0,16)	1,72 (0,28)	1,20 (0,14)
*Mean difference**	*0,48*	*0,51*	*0,42*
Hearing controls			
Central change	1,98 (0,14)	2,08 (0,24)	1,68 (0,16)
Peripheral change	1,70 (0,24)	1,79 (0,26)	1,37 (0,20)
*Mean difference**	*0,28*	*0,29*	*0,31*

** Positive mean differences indicate better performance for changes at central than peripheral locations*

Table 1. Mean change sensitivity (d') with standard errors in parenthesis for each experimental group as a function of cueing condition and change location.

Change detection task: Response Times

Inter-participant mean RTs for correct responses in the change detection task are reported in Table 2 as a function of group, change location and cueing condition. Median RTs for each participant were entered into an ANOVA similar to the one used above for sensitivity data. This analysis revealed a main effect of change location ($F(1,20) = 15.9$; $p < 0.001$) caused by faster change detection at central (mean = 580 ms, SE = 21) than peripheral locations (mean = 635 ms, SE = 23). In addition, there was a significant three-way interaction between change location, cueing condition and group ($F(2,19) = 3.9$; $p < 0.03$). No other main effect or interaction was significant.

	Endogenous attention	Exogenous attention	
	Cue absent trials	Cue valid trials	Cue invalid trials
Deaf			
Central change	548 (44)	573 (30)	586 (57)
Peripheral change	644 (57)	571 (45)	638 (73)
*Mean difference**	*96*	*-2*	*52*
Hearing controls			
Central change	586 (54)	583 (63)	601 (57)
Peripheral change	609 (52)	664 (49)	673 (66)
*Mean difference**	*23*	*81*	*72*

** Positive mean differences indicate better performance for changes at central than peripheral locations*

Table 2. Median Response Times with standard errors in parenthesis for each experimental group as a function of cueing condition and change location.

Figure 2

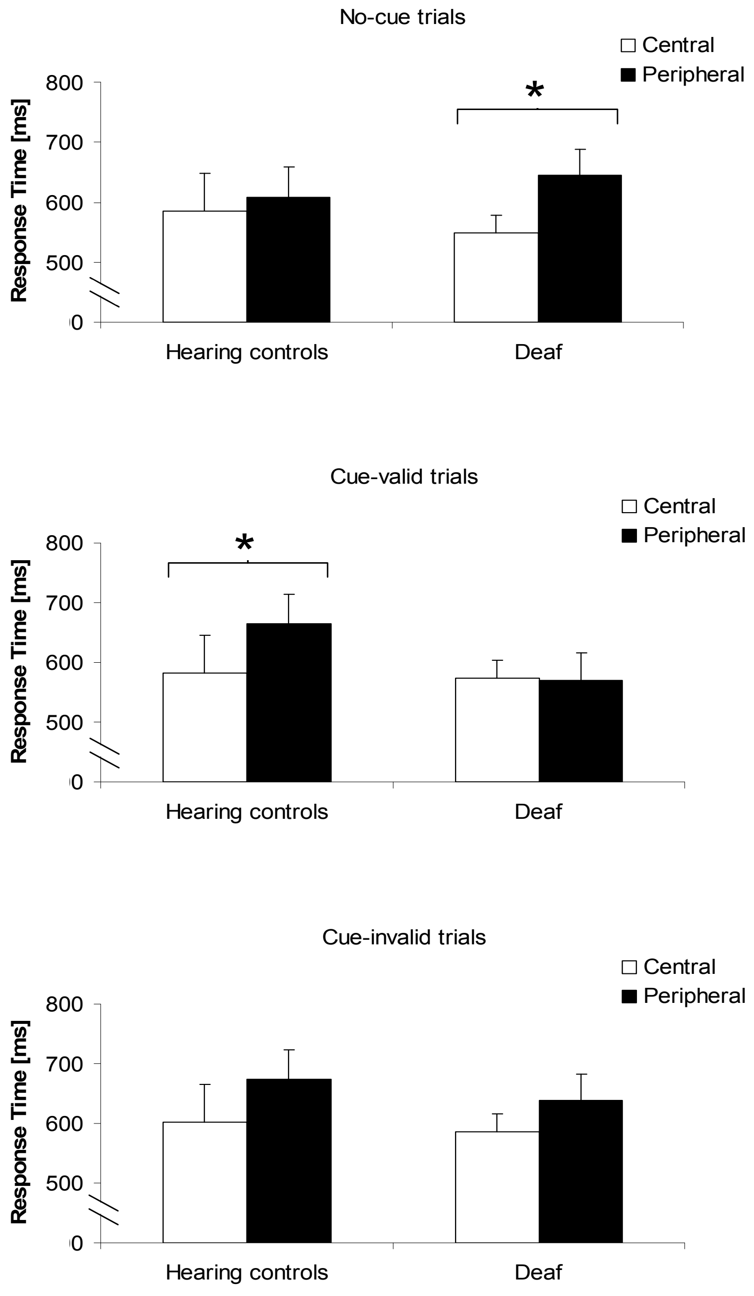


Figure 2. Mean RT data for correct responses in 'change trials' of the change detection task. The plot depicts the three-way interaction between change location, cueing condition and group (see text for details): a) cue-absent condition; b) cue-valid condition; c) cue-invalid condition. Asterisks indicate significant RT differences ($p < 0.05$) between detected changes at central vs. peripheral locations. Error bars indicate the standard error of the mean.

The three-way interaction involving the group factor is illustrated in Figure 2 (see also Table 2). RTs for changes occurring at central versus peripheral locations in deaf and hearing controls clearly differed as function of the cueing condition. In the cue absent condition (i.e., in which no exogenous capture was present and the task reflected the spontaneous distribution of endogenous attention across visual locations), deaf were slower at detecting changes at peripheral than central locations (t(9) = 4.3, $p < 0.002$), whereas hearing controls showed comparable change detection speed regardless of change location (t(11) = 1.3, n.s.). In the cue-valid condition (i.e. exogenous trials in which the spatial cue attracted attention to the correct change location), the pattern reversed. Profound deaf had comparable change detection speed regardless of change location (t(9) = 0.1, n.s.), whereas hearing controls were slower at detecting changes occurring at peripheral than central locations (t(11) = 2.7; $p < 0.02$). Finally, in the cue-invalid condition (i.e. exogenous trial in which the cue exogenously attracted attention away from the correct change location), no statistically significant difference emerged between central and peripheral locations, for both deaf participants (t(9) = 1.3, n.s.) and hearing control (t(11) = 2.0, n.s.).

These RTs results clearly show a dissociation between groups depending on which attentional component was involved in the task. When attention was correctly captured exogenously to the change location, hearing controls showed longer RTs for changes occurring at peripheral than central locations, whereas deaf participants showed comparable RTs regardless of change location – i.e., no cost for peripheral items. By contrast, when the cue was absent and attention could only be moved endogenously in the visual scene, hearing controls became comparably accurate regardless of change location, whereas deaf participants responded faster to central than peripheral changes.

Finally, when the cue was invalid the two groups performed in a similar way (if anything with a numerical trend for faster responses to central than peripheral locations). One possible interpretation of this finding is that whenever the change was not found at the cued location participants had to start a strategic scanning of their visual memory of the scenes to determine whether the change had been present or not. Thus, correct change detection after an invalid cue is more the consequence of endogenous re-orienting of attention than the consequence of exogenous capture. Intriguingly, the RT performance of the deaf in this condition was more akin to that observed in the cue-absent (endogenous) condition than the cue-valid (exogenous) one.

Detection of cue onset: Response Times

In addition to the main experimental task (i.e., change detection), all participants (except one hearing control) also completed a control study in which they were required to respond as fast as possible to the appearance of a dot. Recall that this visual target was exactly the spatial cue that appeared before each of the visual scenes in the exogenous trials of the change detection task. However, this time the dot was presented alone and was the imperative stimulus for the participant.

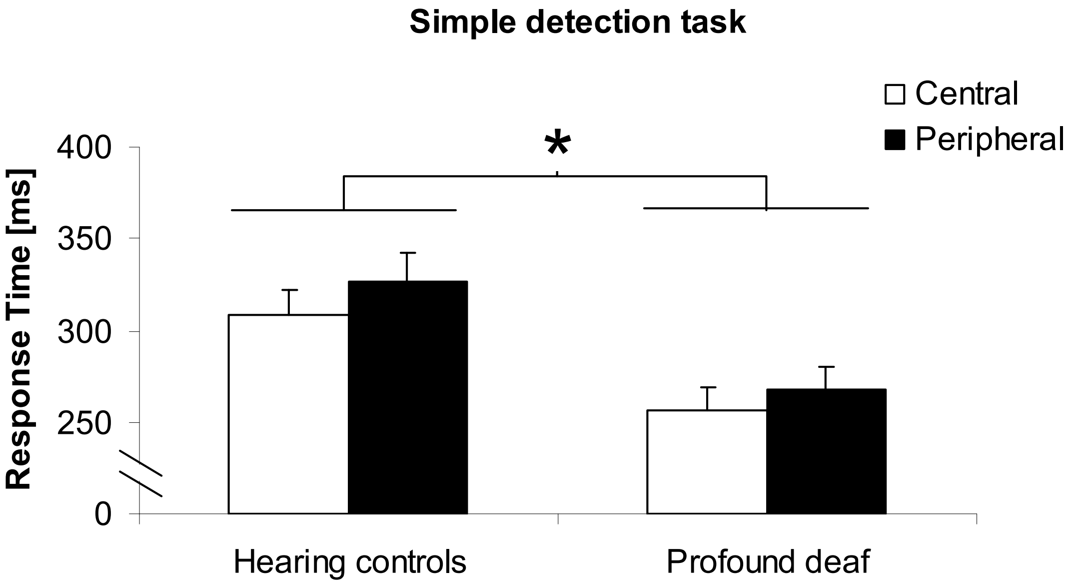


Figure 3. Mean RT data for the simple detection task, as a function of group and change location. Profound deaf were on average 56 ms faster than hearing controls, regardless of the eccentricity of the visual target. The asterisk indicate this overall difference between groups ($p < 0.01$). Error bars indicate the standard error of the mean.

Simple median RTs in response to this visual target were entered into a mixed ANOVA with visual target location (central or peripheral) as within-participants factor and group (deaf or hearing controls) as between-participant factors. This analysis revealed a main effect of target location ($F(1,19) = 18.5$, $p < 0.0001$), indicating that all participants were faster at reacting to central (mean = 284 ms, SE = 11) than peripheral targets (mean = 298 ms, SE = 12). More importantly for the purpose of the present study, a main effect of group was also present ($F(1,19) = 8.2$, $p < 0.01$). Deaf participants were on average 56 ms faster than hearings controls at detecting the visual targets (mean = 262 ms, SE = 9; vs. mean = 318 ms, SE = 9; respectively). No other main effect or interaction was significant. In particular the interaction between target location and group did not reached the level of significance ($F(1,19) = 1.3$, n.s.), indicating that faster detection responses in the deaf emerged regardless of target location in the visual field (see Figure 3). In sum, when asked to make a simple detection to abrupt visual targets (attracting attention exogenously) deaf participants were substantially faster than hearing controls, both when the visual stimulus appeared at central and peripheral locations.

Discussion

In the present study we examined visual abilities in deaf and hearing controls in a paradigm that disentangles endogenous and exogenous components of visual attention. The results clearly revealed a dissociation of performance between the two groups as a function of which attentional component was involved, that in addition emerged selectively when RTs were considered. In the cue valid condition (i.e., valid exogenous orienting), when the non-predictive spatial cue was delivered at the exact location of the change, a cost for responding to changes at peripheral than central locations emerged for hearing controls but not deaf participants. By contrast, in the cue-absent condition (i.e., strictly endogenous orienting), when the global change introduced by the blank screen prevented any attention capture, deaf individuals were – somewhat paradoxically – slower at detecting changes at peripheral than central location, whereas hearing controls showed comparable performance across the two change locations. These findings reveal that the peripheral advantage for processing visual stimuli towards the periphery, a critical aspect of the compensatory visual ability in the deaf, is tightly linked with exogenous capture of visual attention.

In one previous study (Bottari et al., 2008), we used the change blindness paradigm to examine visual abilities in the deaf when all visual transients were removed from the scene. In that task, involving only endogenous attention, deaf were systematically better at detecting changes at central than peripheral locations. The current study considerably extend this previous observation by directly contrasting, for the first time, the contribution of endogenous and exogenous components of attentional orienting within the same experiment. Our novel findings reveal a dissociation in the visual compensatory mechanisms of deafness as a function of the attention component involved. On the one hand, when captured by exogenous transient events, deaf show enhanced reactivity to peripheral targets, unlike hearing controls. On the other hand, when relying on the endogenous component of visual attention alone, deaf appeared to strategically attend more to central than peripheral portion of the visual field. We will discuss each of these results and their implications in turn.

Enhanced reactivity in response to exogenous attention capture

In addition to the current empirical report, two aspects of the existing literature strengthen our conclusion that compensatory visual abilities in the deaf (and particularly the peripheral advantage for targets towards the visual periphery) are closely linked to exogenous capture of attention.

A first striking aspect to note is that the advantage for peripheral items in the present study and in many previous reports has been described when RT measures were considered (e.g., Bosworth & Dobkins, 2002; Chen et al., 2006; Colmenero et al., 2004; Loke & Song, 1991; Nava et al., 2008; Parasnis & Samar, 1985; Proksch & Bavelier, 2002; Sladen et al., 2005; Stivalet et al., 1998). By contrast, less consistent advantages for deaf than hearing controls emerged whenever the task was designed around accuracy (e.g., Bavelier et al., 2000; Bosworth & Dobkins, 2002) or perceptual thresholds (e.g., Brozinsky & Bavelier, 2004). We suggest that this discrepancy between the results of tasks involving RT measures and task that focused on accuracy could reflect the different contribution of exogenous and endogenous visual attention. As recently argued by Prinzmetal and colleagues (e.g., Prinzmetal, McCool & Park, 2005; Prinzmetal, Zvinyatskovskiy, Gutierrez & Dilem, 2008) endogenous and exogenous attention influence RTs and accuracy measures differently. Endogenous attention can affect performance both in experiments designed to measure accuracy alone (i.e., that stress participants to respond as accurately as possible, without any time limitation) and experiments that measure RTs (i.e., in which accuracy is not stressed, and participants instead favour speed of response). By contrast, exogenous capture of attention can affect performance in experiments that measure RTs but not experiment designed around accuracy alone. According to Prinzmetal et al. (2005) this might occur because endogenous attention enhances the perceptual representation of the stimulus at the attended location, relative to other locations (resulting in beneficial performance effects whatever the task), whereas exogenous attention only affect post-perceptual decisions as to which location should be responded to, without changing the perceptual representation of the stimulus (resulting in beneficial performance effects only in terms of response speed; see Prinzmetal et al., 2005, 2008). The intriguing theoretical implication for the research on visual abilities in the deaf is that the underlying compensatory mechanism exhibited by this sensory-deprived population could entail post-perceptual processing (e.g., response decision, response selection or access to visual working memory of visual input) rather than perceptual representation enhancement (e.g., change in signal to noise ratio for the visual stimulus; Lu & Dosher, 2004).

A second aspect of the literature in support of our claim that enhanced visual performance in the deaf is closely linked to exogenous attention capture, is the observation that such enhanced performance has not typically been observed when visual scenes comprised many simultaneous elements (e.g., Brozinsky & Bavelier, 2004; Dye et al., 2006; Proksch & Bavelier, 2002). One such example can be found in the study of Dye and colleagues (2007). Participants judged the direction of a central arrow (pointing left or right) flanked by peripheral distractors (other arrows with congruent or incongruent pointing directions). When 4 peripheral distracting arrows were used, deaf displayed similar performance to hearings controls. By contrast, a between-group difference emerged when the number of flanker arrows was reduced to 2, suggesting that the presence of several competing elements in the scene can lead to no differences in the performance between deaf and hearing controls (see Bottari et al., 2008 for a detailed discussion of further examples in the literature, i.e., Brozinsky & Bavelier, 2004; Proksch & Bavelier 2002). We suggest that whenever the scene complexity increases the multiple visual elements compete with one another, making exogenous attention orienting to the task-relevant target more difficult. This is exactly the mechanism behind the so-called ‘mud-splashes’ effect: a change blindness paradigm alternative to the one adopted here (see O'Regan, Rensink & Clark, 1999). In the ‘mud-splash’ paradigm the visual transients related to the change (the element to detect) are masked by the simultaneous appearance in the scene of many other unrelated transients. In other words, we argue that those context in which multiple elements compete could be substantially akin to the endogenous condition described in the present study.

An important role of reactivity in the visual abilities of the deaf is also highlighted by our simple target detection experiment. The result of this additional experiment show that deaf are overall faster (56 ms on average) than hearings controls at detecting the onset of a visual target, regardless of whether it appears at central or peripheral locations. Loke and Song (1991) conducted a similar study evaluating the ability of hearing controls and deaf individuals to react to the onset of a static visual stimulus. In that study participants reacted as fast as possible to the presentation of a visual target (an asterisk), placed at central or peripheral locations of the visual field (at 0.5° or 25° of visual angle respectively). The results, based on 10 trials for each target location, revealed statistically faster responses for deaf than hearing controls only for peripheral targets. However, a similar between group difference was also numerically evident for central locations (38 ms on average; Loke & Song, 1991, p. 439). The current results confirm and expand this earlier observation by showing that enhanced reactivity to abrupt visual events in deaf than hearing controls can occur regardless of target position in the visual field. This provides initial evidence that enhanced reactivity in the deaf can emerge regardless of stimulus eccentricity (see also Nava et al., 2008). More recent results from our lab, using the same simple-detection paradigm but increasing statistical power with more trials, confirm the overall enhanced reactivity of deaf than hearing controls (that persist even when hearing controls perform the visual task while all auditory input from the environment is suppressed by means of sound-attenuation methods and continuous white noise). Nonetheless the most pronounced reactivity advantage in the deaf emerged for peripheral than central locations (Bottari, Nava, Ley & Pavani, 2008).

Central bias during endogenous attention

In the cue-absent condition of the change detection task, responses of deaf participants were slower for peripheral than central locations. By contrast, hearing controls showed comparable RTs regardless of change location. This decrement in RT performance in the deaf when detecting changes at peripheral than central locations appears somewhat paradoxical, as it is the exact opposite of the peripheral advantage typically observed in deaf participants and described here for cue-valid trials. We speculate that this endogenous bias may be the consequence of an adaptive behavior that profound deaf participants implement to balance out their enhanced reactivity to events occurring towards the periphery of the visual field, and possibly avoid distractibility (see also Bottari et al., 2008 for a similar finding). This is compatible with the observation that changes in the level of endogenous engagement of visual attention can modulate the response to irrelevant distractor that could capture attention exogenously (e.g., Rees, Frith & Lavie, 1997).

Candidate neural substrates for enhanced reactivity to visual events

The prominent view as to the neural basis underlying compensatory visual abilities in the deaf focuses on changes occurring at the cortical level. Neville and colleagues in particular (e.g., Bavelier & Neville, 2002; Stevens & Neville, 2006), have hypothesized that auditory deprivation may have more pronounced effects on dorsal than ventral visual stream functions. This account is based on the observation that in auditory deprivation studies in adult humans enhanced processing typically involve stimuli in the visual periphery (e.g., Armstrong et al. 2002; Bavelier et al., 2000; Neville & Lawson, 1987; Proksch & Bavelier, 2002; Stevens & Neville, 2006), which is preferentially processed along the dorsal visual pathway (e.g. Ungerleider & Haxby, 1994; Aizer, Ungerleider & Desimone, 1991). This cortical account matches well with the current observation that enhanced visual abilities in the deaf emerge for RTs rather than accuracy, as the dorsal visual pathway is known for fast and parallel processing of visual stimuli (e.g., Paradiso, 2002). Neurophysiological investigations in the macaque monkey show that areas reaching from V1 to MST and the frontal eye-fields (FEF) are almost simultaneously activated within the first 50 milliseconds from stimulus presentation (Lamme & Roelfsema, 2000).

However a sub-cortical account of the observed visual compensatory effects should also be considered. Neuroanatomical studies in deaf mice, for example, have revealed aberrant projection from the retina to the auditory thalamus (Medial Geniculate Nucleus) and to the intermediate auditory layers of the Superior Colliculus (Hunt, King, Kahn, Yamoah, Shull & Krubitzer, 2004). Extrapolating this findings to deaf humans, a redundancy of neurons dedicated to the analysis of visual information in subcortical auditory structures can also be hypothesised. The superior colliculus is particular known to play a key role in fast detection of unisensory and multisensory stimuli (e.g., Carlsen, Chua, Inglis, Sanderson & Franks, 2004; Maravita, Bolognini, Bricolo, Marzi & Savazzi, 2008). In addition, it has been involved in overt and covert exogenous orienting (e.g., Ignashchenkova, Dicke, Haarmeier & Their, 2004; Posner, Cohen & Rafal, 1982; Rafal et al., 1991). In this respect, these subcortical structures are well-suited for the processing advantage we have reported in profoundly deaf participants in the cue-valid exogenous trials and in the simple detection task.

Conclusions

In keeping with the original proposal of Bavelier and colleagues (2006) our findings highlight that visual abilities in the deaf may be tightly linked to modulations of spatial attention. In addition they point to a distinction between endogenous and exogenous attention components that may be critical for understanding the context in which compensatory visual abilities in the deaf can emerge. Namely, preventing exogenous capture of attention eliminates the advantage for processing stimuli towards the periphery in the deaf, and instead reveal a possible endogenous bias for central regions of the visual field. Finally our results reveal a key role of reactivity in this sensory-deprived population, which may serve well for adaptive fast re-orienting towards regions of extrapersonal space outside the focus of vision.

Footnotes

1. Eye-position was not monitored in the present study. However, the experimenter remained in the room throughout testing, and checked that participants complied with the eye-head posture instructions given at the beginning of each block. The flickering fixation was introduced (see Procedure section) precisely with the purpose of attracting the participant's attention to the centre of the visual scene at the beginning of each trial. In addition, note that any systematic failure to maintain fixation during the task would have inevitably resulted in a considerable drop of performance. Participants were reminded of this specific information at the beginning of each block (and received an overall feedback on their performance at the end of each block).

Acknowledgements

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Interim conclusions

The results of the studies presented in Chapters 3 and 4 suggest that in the absence of transient elements (due to masking) enhanced performance in the deaf for peripheral locations no longer emerge. In this respect, the endogenous and strategic allocation of attention resources required to scan visual working memory and perform the perceptual comparison between the two visual scene did not result in any enhanced performance in the deaf. By contrast, when a visual transient was presented at peripheral locations deaf outperform hearing individuals. Taken together these results suggest that a key factor in enhanced visual abilities in the deaf is the presence of transient elements capable of attracting visual attention exogenously. In sum, the results of the present study suggests that the exogenous capture of visual attention may be responsible for the enhanced peripheral visual abilities in the deaf.

CHAPTER 4

ENHANCED REACTIVITY TO VISUAL STIMULI IN THE PROFOUNDLY DEAF

Bottari D., Nava E., Ley P. and Pavani F. (under review). Enhanced reactivity to visual stimuli in profoundly deaf (submitted to Restorative Neurology and Neuroscience).

Abstract

Several works have reported faster response time to visual stimuli in the profoundly deaf. This result is often linked to processing of peripheral targets, and occurs in relation attention orienting. Here we examined 11 deaf individuals and 11 hearing controls, in a simple detection task and in a shape discrimination task. While simple detection can be performed under distributed attention, shape discrimination requires orienting of spatial attention to the target. The same visual targets served for both tasks, presented at central or peripheral locations and corrected for cortical magnification. The simple detection task revealed faster RTs in deaf than hearing controls, regardless of target location. Moreover, while hearing controls paid a cost in responding to peripheral than central targets, deaf participants performed equally well regardless of target eccentricity. In the shape discrimination task deaf never outperformed hearing controls. These findings reveal that enhanced reactivity to visual stimuli in the deaf cannot be explained by faster orienting of attention alone, and can emerge for central as well as peripheral eccentricities. Moreover, the persisting advantage for peripheral locations in the deaf, observed here under distributed attention, suggests that this spatially-selective effect could result from reorganised sensory processing rather than different attentional gradients.

Introduction

The consequences on perception, language and cognition of long-term deprivation of auditory input due to profound deafness are a fundamental topic in cross-modal plasticity research (for recent reviews and clinical implications see Marschark and Hauser, 2008). In particular, one aspect of deaf cognition that has received considerable attention in recent years concerns the functional and anatomical re-organization that occur within the visual modality when auditory input is absent (e.g. Bavelier et al., 2006; Dye et al., 2008; Mitchell and Maslin, 2007). A key observation of this recent literature is that not all aspects of visual processing are enhanced in the deaf, thus revealing functional dissociations that can shed light into the mechanisms of cross-modal plasticity that occur in profound deafness. In the present work, we will start by briefly reviewing some of the most relevant features of visual processing in the profoundly deaf, and then we will report an experimental investigation on the functional mechanisms that could subtend the enhancement of response speed observed in this population.

Spatial selectivity of enhanced visual abilities in the deaf

An empirical observation that has been repeatedly reported concerns the spatial selectivity of enhanced visual processing in the deaf. Namely, enhanced performance in the deaf have typically been described for visual stimuli occurring towards peripheral portions of the visual field than stimuli occurring towards the centre1.

Deaf individuals show faster reaction times when detecting or discriminating single peripheral visual targets (e.g., Colemenero et al., 2004; Loke and Song, 1991; Neville and Lawson, 1987, see also Bavelier et al., 2001; Bavelier et al., 2000; Bosworth and Dobkins, 2002). By contrast, reaction time differences between deaf and hearing controls do not emerge for single targets appearing at or near central fixation (Neville and Lawson, 1987; Poizner and Tallal, 1987). Similarly, when concurrent central and peripheral targets compete for attentional resources, deaf preferentially orient visual attention towards peripheral than central locations (Chen et al., 2006; Proksch and Bavelier, 2002; Sladen et al., 2005).

Enhanced performance at peripheral location is compatible with the notion that, under normal conditions, the auditory system provides important information about the events that occur outside the field of view. In the absence of audition, visual processing may be recalibrated to favour rapid detection of events outside foveal regions of the retina, in the attempt to monitor the environment through peripheral vision instead of audition (Loke and Song, 1991; Parasnis and Samar, 1985). Evidence in support of this functional account come from a recent study by Stevens and Neville (2006) that revealed enlarged useful field of view at the extreme periphery when detecting motion stimuli. In that study, deaf individuals and hearing controls were tested in a kinetic perimetry task to evaluate the extension of the visual field in which the presence of moving stimuli can be detected. Interestingly, animal studies have revealed that connections between visual and auditory cortices are stronger for peripheral than central portions of the visual filed (Falchier et al., 2002)], thus offering a possible neural substrate for this spatially selective enhancement.

Enhanced response speed rather than sensitivity

A further general observation concerning visual processing in the deaf is that enhanced abilities at the behavioural level have mainly emerged in tasks measuring speed rather sensitivity responses. Systematic enhanced visual abilities have been reported in studies adopting speeded tasks (e.g., Chen et al., 2006; Colmenero et al., 2004; Loke and Song, 1991), with an overall response time (RT) benefit for the profoundly deaf of over 40 ms. By contrast, studies that examined accuracy measures for near-thresholds or above-threshold visual stimuli often failed to show enhanced abilities in the deaf with respect to hearing controls (e.g., Bosworth and Dobkins, 2002; Brozinsky and Bavelier, 2004; Finney and Dobkins., 2001; Nava et al., 2008; Nevilel and Lawson, 1987; see also Levänen et al., 2001 for similar results in frequency discrimination task for vibrotactile stimuli).

No accuracy between deaf and hearing controls emerged for visual contrast sensitivity (Finney and Dobkins, 2001) or luminance change detection (Bavelier et al., 2001; 2000;). Similarly, perceptual thresholds for motion velocity (Brozinsky and Bavelier, 2004) or motion direction changes (Bosworth and Dobkins, 2002) appear to be comparable in the two groups. Intriguingly, upon closer examination, the latter study on motion direction sensitivity reveals a slight speed-accuracy trade-off in the performance of the profoundly deaf: their sensitivity performance is slightly worse than hearing controls, but their response speed is numerically faster (see Bosworth and Dobkins, 2002 p. 160). Further evidence for comparable sensitivity of deaf and hearing controls accompanied by faster RTs in the deaf have also been documented by Neville and Lawson (1987) who showed that discrimination accuracy of motion direction at peripheral locations is comparable in deaf and controls to hearings, but deaf perform significantly faster (70 ms on average). In addition, Nava and colleagues (Nava, Bottari, Zampini and Pavani, 2008) showed that in spite of comparable temporal sensitivity, deaf participants were on average 100 ms faster than hearing controls when judging the temporal order of visual stimuli under the most demanding (i.e., shortest) asynchronies. Finally, in a flanker interference study (Proksch and Bavelier, 2002) deaf showed more interference from peripheral than central distractors than hearing controls, but this finding emerged only in terms of RTs and not for the accuracy measure.

The observation that better visual abilities in the deaf emerge mainly for reactivity than accuracy or sensitivity measures argues against the hypothesis that profound deafness results in enhanced perceptual representation of the visual events. By contrast, it suggests modifications that occur in visual processing either at the level of processing speed, or at the level response selection/generation or at both these stages. The latter distinction maps nicely on two types of performance enhancements recently proposed by Prinzmetal and colleagues (Prinzmetal et al., 2005a, 2008): perceptual channel enhancement vs. perceptual channel selection. While channel enhancement would result in better sensory threshold for the perceptual event (and has been associated with endogenous attention selection), channel selection would only result in faster processing of the sensory event (and has been associated with exogenous attention capture).

Enhanced processing of visual features that activate the dorsal visual stream

Several authors have proposed that enhanced visual abilities in the deaf appear selectively for processing of visual features that are preferentially processed within the visual-for-action pathway associated with the dorsal visual stream (Milner and Goodale, 1995). These include moving patterns (Armstrong et al., 2002; Bavelier et al., 2000, 2001; Bosworth and Dobkins, 2002) as well as abrupt onsets in the scene (Bottari et al., under review; Chen et al., 2006; Colemenero et al., 2004; Loke and Song, 1991).

For instance, in two functional neuroimaging (fMRI) studies, Bavelier and colleagues (Bavelier et al., 2000; 2001) showed enhanced cortical activation in the MT+ complex of deaf than hearing controls when attending to motion stimuli at peripheral locations. Motion stimuli were also shown to activate right auditory cortex in the deaf

Finney et al., 2001; Fine et al., 2005). Finally, an event-related potential (ERP) study by Armstrong and colleagues (Armstrong Hillyard, Neville and Mitchell, 2002, see also Neville and Bavelier, 2002) revealed enhanced cortical response (larger N1 components) in deaf than hearing controls in response to task irrelevant moving stimuli at peripheral locations, even without specific attentional instructions. Importantly, when cortical activity was compared between groups for coloured stimuli (preferentially processed by the ventral visual stream), enhanced cortical responses for deaf than hearing participants no longer emerged. This specific observation led to the suggestion that cross-modal plasticity in the profoundly deaf could mainly involve a cortical re-organisations within the dorsal stream of visual processing (Armstrong et al., 2002; Bavelier et al., 2006; Neville and Bavelier, 2002).

Further evidence in support of the notion that enhanced visual processing may depend upon processing transient visual events that tap onto the dorsal visual stream also comes from two recent studies of our group Botttari et al., 2008; Botttari et al., under review). We used a behavioural paradigm known as the ‘flicker task’ (Phillips and Singer, 1974; Rensink, 2002), to systematically manipulate the presence or absence of transient events that could capture the observer’s visual attention to the target. The general experimental procedure consisted of two alternating visual scenes composed of different drawings, separated by a blank display. In half of the trials, one of the drawings changed into a different one in the second scene, and participants were required to detect whether a changed had occurred or not. Critically, with such a paradigm any local transient related to the occasional change is masked by the fact that the entire visual scene is a global change with respect to the interposed blank display (a procedure known as the flicker version of the change blindness task ; Rensink, 2002).

We showed that when all visual transients related to target onset are masked, no performance difference between deaf and hearing controls emerge in response to visual events Bottari et al., 2008; Bottari et al., under review). By contrast, when transient elements were reintroduced a performance advantage in terms of RTs emerged for deaf than hearing controls, selectively for peripheral changes (Bottari et al., under review). The results of these studies highlight the possibility that visual compensations in deafness may be strictly connected to the presence of sudden onsets, a visual feature that strongly characterise responses of the dorsal visual stream.

The role of attention orienting in enhanced visual processing of the deaf

A final aspect that should be considered is the role of spatial selective attention in enhanced visual processing of the deaf. The notion that spatial selective attention plays a key role in modulating visual responses in the deaf has been recently advocated by Bavelier and colleagues (Bavelier and Hauser, 2006; Dye et al., 2008) and originally stemmed from the empirical observation that differences between deaf and hearing controls at the neural level emerge specifically when attention is endogenously directed to the target (Bavelier et al., 2000; Neville and Lawson, 1987). In addition, it has been supported by evidence showing that peripheral task-irrelevant distractors interfere with shape discrimination more than central distractors in the profoundly deaf, whereas the opposite pattern is observed in hearing controls (Proksch and Bavelier, 2002). Finally, a role of spatial attention has been suggested in those studies that examined attention orienting and revealed faster disengagement and re-orienting to the target after an invalid cue (Bosworth and Dobkins, 2002; Chen et al., 2006; Colemenero et al., 2004; Parasnis and Samar, 1985).

However, whether all aspects of visual enhancement in the deaf are necessarily linked to allocation of selective attention in space it is still a matter of debate. First, at least under some circumstances enhanced visual performance in the deaf has been observed in the absence of attention orienting (Armstrong et al., 2002; Chen et al., 2006; Loke and Song, 1991). Assessing the role of attention is fundamental to highlight at which stage of visual processing the performance benefit of the deaf could emerge. In particular, showing that enhanced processing emerge prior to orienting of attention would reveal that at least some components of enhanced processing of the deaf occurs at very early stages of visual processing in the brain.

The present study

In the present study, we adopted two speeded visual tasks, to briefly flashed targets occurring at central vs. peripheral locations, to examine directly whether orienting of spatial attention is responsible of the enhanced visual processing in the deaf. Specifically, we tested a group of profoundly deaf individuals and a group of hearing controls in a simple detection task and in a shape discrimination task, performed exactly on the same visual stimuli. The critical difference between these two tasks is that simple detection can be solved under distributed attention (i.e., without any orienting of spatial attention), whereas shape discrimination necessarily requires orienting of visual attention to the target, for localisation and identification (e.g., Bravo and Nakayama, 1992; Turatto et al., 2007).

If enhanced reactivity to visual events in the deaf specifically reflects more efficient and fast orienting of selective attention to the target, faster responses in deaf than hearing controls should emerge more strongly in the shape discrimination task than the simple detection task. By contrast, if enhanced reactivity to visual events in the deaf is not critically dependent upon orienting of spatial attention, it should emerge in the simple detection task as well. It should be emphasised that a direct contrast of these two simple visual paradigms, with targets occurring both at central and peripheral locations, has never been conducted in the literature on visual abilities in the deaf. In fact, to our knowledge, only one study in this literature has ever adopted a simple visual detection task, performed in the absence of any previous cue orienting the participant's spatial attention (Loke and Song, 1991; we will return to this pioneering study in detail in the Discussion).

Intriguingly, one simple detection study in the deaf conducted in the tactile modality (Levänen et al., 2001) have suggested that deaf can outperform hearing controls when the task requires a response to rare tactile-frequency changes (i.e., deviants), embedded into a stream of stimuli of homogenous tactile frequency (i.e., standards). Thus, as a side aim, we explored whether any difference between deaf and hearing controls could also emerge in relation to the probability of occurrence of visual stimuli. Similar to a study conducted by Neville and colleagues (Neville Schmidt and Kutas, 1983), we manipulated the probability of temporal onset of our visual targets. Most visual targets (84%) were delivered between 400 and 800 ms after the warning signal at trial onset (standards), whereas a minority of targets (16%) was delivered 1800 ms after the warning signal (deviants).

Methods

Participants

Eleven profoundly deaf individuals (mean age = 26 years, SE = 1, range 21-34 years old; 8 males and 3 female) were recruited at the Italian national association for deaf (Ente Nazionale per la protezione e assistenza dei Sordi, Verona, Italy) and gave their informed consent to participate in the study. All participants had uncorrected bilateral profound hearing loss (>80 dB). Two acquired deafness around the age of 4, 7 acquired deafness before the age of 3, and 2 had congenital deafness. All deaf participants were proficient sign-language users.

Eleven hearing controls (mean age = 28 years, SE = 1, range 24-32 years old; 5 males, 6 females) were also recruited to take part in the study. All hearing controls were recruited among the students at the Faculty of Cognitive Science (University of Trento). All participants had normal or corrected-to-normal vision and were right-handed by self-report. The study was approved by the ethical committee at the University of Trento (Italy).

Stimuli and apparatus

All stimuli were presented on a standard 17 inches monitor, with 1024 X 768 pixel resolution. 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. The target was always a circle, opened on the left or right side, that could be presented at one of 8 possible locations arranged on two invisible concentric circles centred on visual fixation. The radius of the inner circle was 3 degrees of visual angle, the radius of the outer circle was 8 degrees of visual angle. There were 4 possible target locations on the inner circle and 4 possible target locations on the outer circle, placed along the two diagonals of the display. From now on we will refer to locations on the inner circle as central, and locations on the outer circle as peripheral. Target appearing at peripheral locations were corrected for the cortical magnification factor (Saarinen, Rovamo and Visnu, 1989). Central targets covered a visual angle of 1.5 degrees and peripheral target of 2.6 degrees.

All possible target locations are indicated by dotted circles in Figure 1 for descriptive purpose only (i.e., no circle was present on the actual experimental display). This figure also shows one representative central target (circle open on the left side) and one representative peripheral target (circle open on the right side). Again, this is only for descriptive purposes, as a single target was presented in every trial.

Figure 1

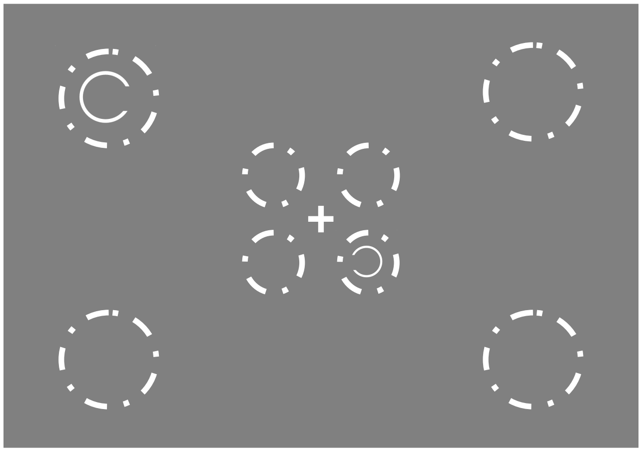


Figure 1. All possible target locations are indicated by dotted circles; this serves only descriptive purpose as no circle was present on the actual experimental display. The figure also shows one representative central target (circle open on the left side) and one representative peripheral target (circle open on the right side). Again, this is only for descriptive purposes, as a single target was presented in every trial (see text).

Procedure and design

Participants sat at approximately 60 cm from the computer monitor, resting their chest on the edge of the table, and were instructed to keep their head and eyes oriented towards fixation throughout testing. These instructions were repeated at the beginning of each experimental block, in addition the experimenter always remained in the room during testing to check that participants complied with the eye-head posture instructions. The flickering fixation was introduced precisely with the purpose of attracting the participant's attention to the centre of the visual scene at the beginning of each trial.

The experimental session always comprised two parts: a simple detection task (lasting approximately 20 minutes) and a shape discrimination task (lasting approximately 30 minutes). In the simple detection task, participants were asked to respond as fast as possible to the sudden onset of the visual target, by pressing the space bar on the computer keyboard. In the shape discrimination task, participants were asked to make speeded discrimination of the target shape. Namely, they were instructed to press the 'B' key when the target circle was opened on the left side, and the 'N' key when the target circle was opened on the right side.

Each trial began with visual fixation flickering at 5Hz for 600 ms. This manipulation had the purpose of capturing the participant's attention and gaze towards the centre of the screen. After flickering, fixation remained still for a random interval ranging between 400 and 2200 ms, before that the visual target appeared at any of the 8 possible locations (i.e., 4 central and 4 peripheral) for 48 ms. As anticipated in the Introduction, one side aim of the present study was to assess whether reactivity of response could differ between deaf and hearing controls as a function of whether some aspect of the target is frequent or infrequent. To this aim, on 84% of the trials the target stimulus appeared between 400 and 800 ms after fixation stop flickering (short ISI); whereas on the remaining 16% of the trials the target appeared exactly 1800 ms after the end of fixation flickering (long ISI; see Neville Schmidt and Kutas, 1983 for a similar manipulation). From now on we will refer to short ISI trials as 'standards' and to long ISI trials as 'deviants'. Deviant trials could be delivered only after three consecutive standards trials. The participant's response terminated the trial, and a random inter-trial interval ranging between 1250 and 1750 ms was introduced before the beginning of the subsequent trial. In case of anticipation responses or errors in the shape discrimination task, a warning sentence was delivered at fixation ('Early response' or 'Wrong response', respectively).

Each experimental block comprised 112 trial, evenly distributed across the 8 possible target locations. This resulted in 56 central trials, and 56 peripheral trials. Also, within each block 96 trials were standards and 16 were deviants. A practice block of 12 trials preceded each experimental block; this was not analysed. The experiment was a 2 by 2 by 2 factorial design, with target location (central or peripheral) and trial type (standard or deviant) as within-participants factors, and group (deaf or hearing controls) as between-participant factor. In the simple detection task, the only dependent variable was the response time (RT). In the discrimination task, both RTs and accuracy were examined.

Results

Simple detection task

The data of one deaf participants were eliminated by the analysis of this simple detection task because his mean response times were more than three standard deviations away form the deaf population mean .

Median simple RTs in response to visual targets were computed for each participant and entered into a mixed Analysis of Variance (ANOVA) with target location (central or peripheral) and trial type (standard and deviant) as within-participants factor, as well as group (deaf or hearing controls) as between-participant factor.

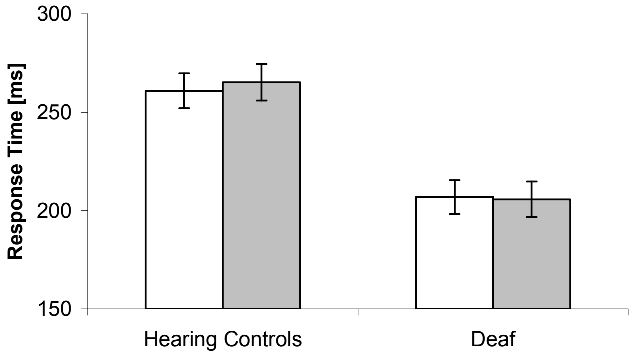
This analysis revealed a significant main effect of target location ($F(1,19) = 10.3$, $p < 0.005$), caused by faster responses to central (mean = 240 ms, SE = 5) than peripheral targets (mean = 244 ms, SE = 5) overall. In addition, there was a main effect of trial type ($F(1,19) = 8.7$, $p < 0.008$), caused by faster responses to standard (mean = 235, SE = 7) than deviant targets (mean = 249, SE = 5). More importantly for the purpose of the present study, there was also a main effect of group ($F(1,19) = 17.3$, $p < 0.001$). Deaf participants were on average 44 ms faster than hearing controls at detecting the visual targets (mean = 220 ms, SE = 7; vs. mean = 264 ms, SE = 8, respectively; see Figure 2a). The interaction between group and trial type was also significant ($F(1,19) = 7.1$, $p<0.015$). Although deaf participants were faster than hearing controls regardless of trial type ($p < 0.008$), RTs in the deaf were faster for standard than deviant targets (206 ms vs. 233 ms, respectively; $p<0.001$) unlike hearing controls (263 ms vs. 264 ms; $t(10) = 0.2$, n.s.). Finally, the interaction between group and target location also approached significance (F(2,19) = 3.5, $p<0.08$). No other interaction reached significance ($F < 2.1$).

To further evaluate the interaction between group and target location we run an additional analysis on RTs in standard trials only. This was motivated by the large trial difference between standard and deviant conditions: with 48 trials for each target locations in standard trials and only 8 trials for target location in deviant trials. Median simple RTs in response to the standard target alone were entered into a mixed ANOVA with target location (central or peripheral) and group (deaf, hearing controls) as factors. This analysis confirmed a main effect of group (F(1,19) = 9.8, $p < 0.001$), caused by deaf participants responding on average 57 ms faster than hearing controls (mean = 206 ms, SE = 9; vs. mean = 263 ms, SE = 9, respectively). In addition, the interaction between the group and target location was now significant (F(2,19) = 4.5, $p<0.05$). Although deaf were faster than hearing controls regardless of target location ($p < 0.0001$), a significant cost of responding to peripheral than central targets emerged for hearing controls (central: mean = 261, SE = 9; peripheral: 265, SE = 8.6; t(10) = 2.3, $p < 0.05$), but not for deaf participants (central: mean = 207 ms, SE = 9; peripheral: mean = 206, SE = 9; t(9) = 0.7, n.s.).

In sum, when standard trial are analysed separately, it becomes evident that unlike hearing controls, deaf participants do not pay any cost in terms of RTs when reacting to peripheral than central targets. Perhaps more strikingly, in both analyses deaf proved substantially faster than hearing controls overall, revealing an enhancement of visual processing which does not selectively emerge for targets presented at the periphery of the visual field.

Figure 2

(a) Simple detection



(b) Shape discrimination

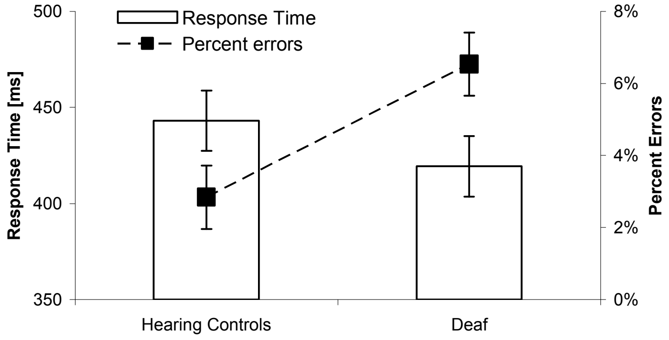


Figure 2. Performance of deaf participants and hearing controls (a) in the simple detection task, as a function of target locations; (b) in the shape discrimination task, both in terms of response time and percent errors. See text for details.

Discrimination task

Median RTs for correct discrimination trials were entered into a mixed ANOVA with target location (central or peripheral) and trial type (standard or deviant) as within-participants factors, as well as group (deaf or hearing controls) as between-participant factor. This analysis revealed a main effect of target location (F(1,20) = 15.02, $p < 0.001$), indicating that all participants were faster at discriminating central (mean = 423 ms, SE = 11) than peripheral targets (mean = 439 ms, SE = 12). The main effect trial type was also significant (F(1,20) = 39.8, $p < 0.0001$), caused by faster discriminations for standard (mean = 421 ms, SE = 11) than deviant targets (mean = 442 ms, SE = 12). Importantly, the main effect of group did not reach the level of significance (F(1,19) = 1.1, $p < 0.3$; see Figure 2b). No other interaction was significant (all Fs < 1.3).

A similar analysis was conducted on the percentage of errors in shape discrimination. This analysis did reveal a main effect of group (F(1,19) = 4.8, $p < 0.05$); surprisingly, however, this main effect revealed that deaf participants performed worse than hearing controls (mean = 6%, SE = 1%; mean = 3%, SE = 1%, respectively; see Figure 2b). No other main effect or interaction was significant (all Fs < 1.6).

As for the simple detection task, we repeated all analyses on standard trials considered alone using mixed ANOVA design with target location (central or peripheral) and group (deaf, hearing controls) as factors. The analysis on RTs confirmed a main effect of target location (F(1,20) = 11.6, $p<0.003$), caused by faster discrimination responses for central (mean = 413 ms, SE = 10) than peripheral targets (mean = 428 ms, SE = 12). No other main effect or interaction reached significance (all Fs <1.5). The analysis on percent errors confirmed main effect of group (F(2) = 8.9, $p < 0.01$) caused by deaf participants performing worst than hearing controls overall (mean = 7%, SE = 1%; mean = 2%, SE = 1%, respectively). No other main effect or interaction was significant (all Fs < 1.6).

In sum, the results of the discrimination task revealed no between-group differences in terms of RTs. In fact, discrimination performance was significantly worse in deaf individuals than hearing controls.

Discussion

The aim of the present study was to assess whether faster reactivity to visual events in the profoundly deaf is strictly dependent upon orienting of selective spatial attention. To this aim we compared reactivity in deaf and hearing controls to identical visual stimuli appearing at central or peripheral locations, when the task requires simple detection or shape discrimination of a single visual target. Because simple detection does not need target localisation and identification it is usually assumed to occur without orienting of spatial attention (i.e., under distributed attention, Bravo and Nakayama, 1992; Turatto et al., 2007). By contrast, shape discrimination can only be performed after attention has been oriented to the stimulus.

The results of the present study clearly revealed a response time advantage in deaf than hearing participants, which emerged selectively for simple detection but not for shape discrimination. While in the simple detection task deaf outperformed hearing controls by 44 ms (i.e., a 17% reduction of response time, when compared with the average RT of hearing controls; mean = 264 ms), in the shape discrimination task neither response time nor accuracy was better in deaf than hearing participants. In fact, deaf participants made significantly more errors than hearing controls. Notably, faster responses in the deaf during the simple detection task were not spatially selective, i.e., they emerged regardless of target location, instead of appearing only for peripheral targets (Loke and Song, 1991). This finding is even more striking when considered within the context of differential response time ratios in the two groups as a function of target location. Hearing controls paid a significant RT cost for peripheral than central target, whereas deaf individuals performed comparably well across the two target locations. Thus, in addition to replicating the well-known enhancement of peripheral processing in the deaf, our finding reveal that the reactivity enhancement in the deaf advantage cannot be reduced to peripheral processing alone.

These findings raise the possibility of two functionally distinct aspects in the re-organisation plasticity occurring in the visual system of the profoundly deaf. One the one hand, the observation that deaf were faster than hearing controls in a task that does not require any orienting of attention prior to the response (i.e., simple detection) implies a functional enhancement which is not dependent upon movements of visual attention in external space. Importantly, this aspect of compensatory plasticity extends to central as well as peripheral locations of the visual field, instead of emerging selectively for peripheral items. One the other hand, the observation that the profoundly deaf show no RT cost when processing peripheral items even in a simple detection task that can be solved under distributed attention, implies a functional enhancement for peripheral portions of the visual field that cannot be reduced to differential allocation of attentional resources alone (see also Stevens and Neville, 2006 for related evidence). Because the cost for processing peripheral than central targets in hearing controls likely reflects the amount of visual neurons devoted to the analysis of central than peripheral portion of the visual field (which would result in shorter RTs according to a horse-race model of response release Marzi and Di Stefano, 1981; Chelazzi et al., 1988), we speculate that profound deafness can modify the relative proportion of neurons devoted to peripheral processing.

Before discussing further the possible mechanisms that led to enhanced reactivity in the deaf in the simple detection task, we will examine in more details the previous evidence on speeded detection and speeded discrimination in the profoundly deaf.

Speeded detection to visual targets

The evidence that deaf show faster detection response time to static visual targets regardless of attentional instructions, was documented by Chen and colleagues (Chen, Zhang and Zhou, 2006) for targets appearing at para-foveal eccentricities (i.e., 3 degrees; the same eccentricity used in the present study for central visual targets). In their study, regardless of whether the target appeared at spatially valid or invalid cued locations, deaf responded on average 59 ms faster than hearing controls (but see Parasnis and Samar, 1985). Similarly, speeded responses to static targets at peripheral eccentricities (i.e., 20 degrees) were examined by Colmenero and colleagues (Colmenero, Catena, Fuentes and Ramos, 2004), in a task in which targets were always preceded by a cue that was either spatially valid, invalid or neutral. Regardless of cue validity, deaf resulted on average 43 ms faster than hearing controls. Remarkably, only one study (Loke and Song, 1991) has contrasted directly central and peripheral locations (at 0.5° or 25° of visual angle respectively), during a speeded detection task performed in the absence of attention orienting cues. Based on the average of only 10 trials for each target location, they documented statistically faster responses for deaf than hearing controls for peripheral targets. Intriguingly, a similar between-group difference was also numerically evident for central locations (38 ms on average Loke and Song, 1991, see p. 439).

The latter study particularly contributed to the shared assumption that speeded responses in the profoundly deaf are faster only for peripheral locations (e.g., Bavelier, Dye and Hauser, 2006). However, the novel empirical evidence of the present study, as well as other existing evidence from previous works on speeded detection (Bottari et al., under review; Chen et al., 2006; Colmenero et al., 2004), call for a re-definition of this general assumption. First, deaf enhanced reactivity to static visual targets can occur regardless of target eccentricity. Second, it does not depend entirely upon allocation of attentional resources in the visual field.

Speeded discrimination to visual targets

To our knowledge, the only study that adopted a discrimination paradigm somewhat similar to ours is the pioneering work of Neville and Lawson (Neville and Lawson, 1987), in which deaf participants were asked to make a trial-by-trial motion-direction discrimination for single supra-threshold stimuli presented at central or peripheral locations (just above fixation vs. 18 degrees from fixation, respectively). In their study, deaf were faster than hearing controls at discriminating the direction of motion of peripheral targets (in the absence of accuracy differences between groups). This result is clearly at odds with the present observation of worse performance in the deaf regardless of target eccentricity, as measured by accuracy. Two discrepancies could however account for the present finding. First, our peripheral targets appeared at much less eccentric locations than those of Neville and Lawson (8 degrees vs. 18 degrees, respectively). This raise the possibility that speed benefits in the deaf related to attention shifts (always needed in discrimination tasks) are more likely to be detected the larger the spatial attention shift in the visual scene. Second, all our stimuli were static whereas stimuli in Neville and Lawson's study were moving. This raise the possibility that motion and static stimuli have a different status in plasticity phenomena occurring in the deaf.

Which mechanisms can lead to enhanced reactivity in the simple detection task?

One first possibility is that faster responses to visual targets reflect sensory enhancement occurring in sub-cortical structures. Neuroanatomical studies have shown that several sub-cortical structures which are normally part of the auditory pathway can be recruited for visual processing in deaf mice. For example, aberrant projection from the retina have been found in the dorsal and ventral portion of the medial geniculate nucleus (MGL) of the thalamus and in the intermediate layers of the superior colliculus (SC, Hunt et al., 2005). If similar phenomena of sub-cortical plasticity occur in humans, this would lead to a redundancy of neurons dedicated to visual processing within subcortical neural structures known to enhance speed of response. For instance, it is now well-documented that faster detection responses occur with two concurrent sensory signals than one (the so-called 'Redundant Target Effect'). This effect is mediated by neural summation occurring in the SC (Savazzi and Marzi 2002), particularly in the magnocellular layers (Turatto et al., 2004). Intriguingly, this phenomenon has recently been documented also with audio-visual pairings (Leo, et al., 2008; Maravita et al., 2008). Thus, it would be tempting to link speeded responses in our detection task with the recruitment for visual processing of sub-cortical structures originally devoted to auditory processing.

A second possibility that should be considered is that faster responses in the deaf reflect some aspect of response preparation or release. Simple detection tasks allow response selection and response programming before target presentation. Therefore, only a response release is needed following the target stimulus. This is clearly illustrated by the fact that response times in simple detection tasks do not increase when response complexity increases (Klapp, 1995), unlike in choice RT tasks. Interestingly, there is evidence to suggest that response release in simple detection tasks may be mediated by sub-cortical structures (Calsen et al., 2004). Thus, it could be hypothesised that reactivity effects observed in the profoundly deaf may reflect to some extent a facilitated release of pre-programmed motor responses. This interpretation of our findings would account well for the speed-accuracy trade-offs occasionally noted in the profoundly deaf (Bosworth and Dobkins, 2002), as facilitated response release could lead to delivery of the wrong response.

Finally, it can be hypothesised that enhanced response speed in the deaf reflect changes occurring at the cortical level. In this respect, it is known from EEG studies that latencies in the response to visual targets co-varies with latencies in peaks recorded from occipital electrodes (Fort et al., 2005; Hartwell and Cowan, 1994). This lead to the strong prediction that fast RTs in the deaf should correspond to early activation peaks in cortical responses of the deaf than hearing controls. To date, however, such evidence have never been reported. The ERP study by Neville and Lawson (Neville and Lawson, 1987), that showed a 70 ms RT difference between deaf and hearing controls at the behavioural level, showed no difference between the two groups in terms of neural latencies (see also Neville et al., 1983). Instead, between-group differences have been documented on the amplitude of the N1 component (Armstrong et al., 2002; Neville and

Lawson, 1987). Although this negative finding should be taken with caution, it argues against a cortical origin of the substantial reactivity effect we have observed.

Different performance for standard and deviant targets

One secondary aim of the present study was to assess whether any difference between deaf and hearing controls could also emerge in relation to the probability of occurrence of visual stimuli. We remind that we manipulated the probability of temporal onset of our visual targets (i.e., standard targets were delivered between 400 and 800 ms after warning at fixation, whereas deviant targets were delivered 1800 ms after warning at fixation). The results showed that deaf participants were slower at detecting deviant than standard targets, unlike hearing controls who did not show a different performance for standard and deviant targets. We briefly discuss this finding for completeness. However, because the target probability manipulation was confounded with different timing of stimuli, we believe any standard/deviant comparison is problematic and inconclusive. Namely, deaf participants could have been slower at detecting deviants targets because of their minor probability or because of their long timing. Based on previous evidence by Levänen and Hamdorf (2001), which showed better ability to detect tactile deviants in the deaf, the interpretation based on stimulus timing seems however more likely.

Conclusions

Taken together the results of the present study provide clear evidence that enhanced reactivity to visual stimuli in the deaf cannot be explained by faster orienting of attention alone. Moreover, we show that this performance enhancement can emerge for central as well as peripheral eccentricities. However, we also show that while hearing controls paid a cost in responding to peripheral than central targets, deaf participants performed equally well at both target locations. This peripheral advantage, observed here under distributed attention in the simple detection task, suggests that the spatially-selective effect in the deaf could result from reorganised sensory processing rather than different attentional gradients.

Footnotes

1.The actual eccentricities associated with the terms ‘central’ and, particularly, ‘peripheral’ locations varied considerably across the different studies. Researchers referred to central locations both when the stimulus was presented directly at fixation (Poizner and Tallal, 1987) or peri-foveally (Neville and Lawson, 1987). Instead, peripheral locations in the visual field ranged from eccentricities of 3 degrees (Chen et al., 2006) to eccentricities of 20 degrees or more (Colmenero et al., 2004; Loke and Song, 1991; Stevens and Neville, 2006).

2.As can be noted from Figure 2b the worse performance of deaf participants was accompanied by a numerical trend for longer RTs in deaf than hearing controls. This difference was statistically not significant and therefore will not be discussed further in the manuscript. However, it should noted that a tendency towards speed accuracy trade-off has already been documented in the literature on visual abilities of the deaf (e.g., Bosworth and Dobkins, 2002).

Acknowledgements

We are grateful to the deaf at the Ente Nazionale Sordi (Verona) who generously volunteered their time in this study. F.P. was supported by a PRIN 2006 grant (Prot. 2006118540_004) from MIUR (Italy), a grant from Comune di Rovereto (Italy) and a PAT-CRS grant from University of Trento (Italy).

Interim conclusions

The present study showed that reactivity is a critical aspect of enhanced visual abilities in the deaf. Such functional cross-modal effect is not spatially selective, in the sense that it does not emerge solely for visual events at peripheral locations. Moreover, the study revealed a different ratio between the two groups in the RT measure, when detecting central vs. peripheral targets. Contrarily to hearing controls, deaf do not show any cost at reacting to stimuli presented at peripheral than central locations. This modulations seems not to be driven by a different ability of attention orienting, because the discrimination task did not reveal a better ability in the deaf. Different mechanisms could account for this enhanced reactivity in the deaf, which can relate to cross-modal plastic changes occurring in sub-cortical as well as cortical structures. In the next chapter an EEG study will be presented to examine further the cortical aspects of this enhanced reactivity in the deaf.

CHAPTER 5

MODULATIONS OF EARLY VISUAL EVOKED POTENTIAL IN THE PROFOUNDLY DEAF

Bottari D., Caclin A., Giard M.H. and Pavani F. (in preparation). Modulations of early visual evoked potentials in the profoundly deaf

Introduction

The results of the two studies describer in Chapter 3 and 4 provide strong behavioral support to the notion that abrupt events capturing attention can lead to faster reactivity in deaf than hearing individuals. In both studies, deaf responded to visual target with a speed advantage of 50 ms on average with respect to hearing controls. As discussed in Chapter 4, several interpretations of this finding are possible and currently open. In this respect, it would be extremely interesting to address at what stage of visual processing the performance of deaf and hearing controls start to diverge. To this aim, we conducted a further study, using exactly the simple detection task adopted in Chapter 4 but recording electrophysiological activity (event-related potentials, ERPs) in addition to behavioral responses.

Similar to the study reported in Chapter 4 (Bottari et al., submitted b), a simple visual target was presented at central or peripheral locations, in upper or lower sectors of the visual field. However, two differences were introduced. First, the alerting signal appearing at fixation prior to target onset was a static red square lasting for 500 ms, instead of a flickering patter of the fixation point. This first methodological change was introduced to avoid possible artifacts in the EEG recording due to a flickering visual stimulus, such as the repetition and the possible superposition of the visual evoked potential due to the alternating onsets and offsets responses. Second, the time interval between alert at fixation (i.e., the red square) and target was fixed to 500 or 1800 ms and, unlike our previous study, the percentage of occurrence of the two possible ISIs was comparable (i.e., 50% of targets appeared after a short ISI and 50% of targets with appeared after a long ISI). This second methodological change was introduced following a series of pilot study that clarified one of the results that emerged in the simple detection study that we showed in Chapter 4 (Bottari et al., submitted b). In this respect, that study (Bottari et al., submitted b) revealed a different modulation in terms of RTs between deaf and hearing controls at reacting to standard and deviant trials that could have at least two alternative explanations. From one side the modulation could be due to the fact that standard and deviant trials had different ISIs (700 ± 200 ms and 1800 ms respectively). Alternatively to the fact that standard and deviant were different in terms of percentage of occurrence (84% and 16% respectively), thus the deviant was a rare change in the target features (timing). In a pilot study we used analogues ISIs as the previous simple detection experiment but with the same percentage of occurrence (50% each). The result revealed that presenting targets with two different ISI was sufficient to modulate the performance differently between deaf and hearing controls and congruently with the previous result (see bottari et al., submitted b). For this reason in the present simple detection study we adopted two ISIs equally represented, 50% each. Nonetheless, the possibility that the ability to react to visual targets is also modulated by a rare change of the target feature, remain still open. Further studies are needed to clarify this interesting possibility.

Previous electrophysiological studies on visual responses in the deaf

Despite the many studies that characterised the response to visual stimuli in the profoundly deaf behaviourally and more recently using functional neuroimaging, only few works have examined this compensatory ability of the deaf using electroencephalography. Here we briefly review the existing literature, before presenting our own EEG study.

The first electrophysiological study that evaluated the cortical response to visual stimuli in deaf and hearing people was the pioneering work by Neville, Shmidt and Kutas (1983). In that study, the two groups of participants were evaluated during passive viewing of visual stimuli, presented randomly at fixation or at peripheral locations (8° of eccentricity). The stimuli were presented either 0.5, 1 or 3 seconds after trial onset, with these different ISIs intermixed randomly and occurring with different probability (50%, 33% or 17 % of the trials, respectively). The comparison of visual evoked potentials (VEPs) for deaf and hearing controls showed differences in terms of components amplitude. In particular, over the anterior scalp region the negative component measured at Cz and peaking at about 150 ms (termed N150 in the paper) was 1.5 to 3 times larger in deaf than hearing controls for stimuli presented at peripheral location. Contrarily, no differences emerged for stimuli occurring at fixation. Moreover, while the N150 was larger for central than peripheral stimuli in hearing individuals, no such difference emerged in the profoundly deaf. Based on these results, Neville and colleagues (1983) suggested a specific modulation to the peripheral representation of visual space due to deafness. In addition, over the posterior electrodes the positive component peaking at about 230 ms (P230) resulted ampler for deaf than hearing controls for both central and peripheral stimuli. No specific interpretation was proposed for this difference emerging in this later visual component. Finally, all amplitude differences (i.e., both in the N150 and P230) between deaf and hearings were particularly evident for VEPs in response to stimuli presented at the 3 seconds intervals. This results lead the Authors conclude that the slowly recovering neural responses are less refractory in deaf than hearing individuals. However, a possible alternative explanation of this result could related to the rare and deviant nature of the stimuli occurring at the longest ISI (see Levanen et al., 2004, for a related finding on the tactile modality). The 3 seconds ISI was both the timing condition less likely to occur (17% of trials), as well as the most diverse ISI among the three (6 and 3 times slower, with respect to the 0.5 seconds and the 1 second ISI respectively). To sum up, this pioneering study by Neville and colleagues was the first to reveal that the dynamic of VEPs in response to stimuli occurring at peripheral locations can be modulated by deafness.

The second ERPs study comparing deaf and hearing controls that appeared in the literature was again conducted by Neville and colleagues (Neville & Lawson, 1987). Unlike the study described above, VEPs of deaf and hearing controls were compared in an active discrimination task. Stimuli were white squares presented at central or peripheral locations (just above fixation, 18° to the right or 18° to the left of fixation), with an ISI from trial onset ranging randomly between 280 to 480 ms. On 80% of the trials (termed ‘standards’), a single square appeared one of these predetermined locations for 33 ms. On the remaining 20% of the trials (termed ‘deviants’), the square jumped slightly after the first 33 ms to one of 8 possible immediately adjacent locations. The participant’s task consisted in discriminating the direction of the moving square in deviant trials. Importantly, although participants fixated centrally throughout the experimental session, they were also requested to orient their attention to one of the three possible target locations (central or right/left peripheral) across blocks.

In terms of behavioural performance, deaf resulted faster than hearing controls (on average 70 ms) at discriminating visual moving targets at peripheral locations. By contrast, no between-group difference emerged for targets occurring at central locations. In terms of EEG response, three main findings were reported. First, the visual evoked component termed P1 (i.e., positivity peaking at about 100 ms after the stimulus presentation), was comparable between groups regardless of stimulus (standard or deviant) location and attention condition. Second, a larger amplitude in the N1 component emerged in deaf than hearing controls when standard or deviant target appeared at peripheral attended locations. These greater increase in cortical response due to attentional engagement in deaf than hearing controls was recorded over the occipital electrodes and in left parietal and temporal regions. Third, the overall amplitude of the N1 was larger over the right than left hemisphere in hearing controls, but larger over the left than right hemisphere in deaf individuals. Contrarily, the VEPs in response to central standards and targets did not differ between groups. In summary, the result of the study by Neville and Lawson (1987) suggested one main finding. Deafness seemed to modulate the neural system that mediates spatial attention. Indeed the main differences in the VEPs in response to both static and moving stimuli (standard and targets respectively) were elicited in the condition of attentional engagement to peripheral locations of space.

More recently, Armstrong and colleagues (Armstrong, Hillyard, Neville and Mitchell, 2002) conducted an EEG study on visual abilities of the deaf to test the hypothesis that cross-modal plasticity due to deafness could be prevalently occur for stimuli processed with the dorsal visual pathway, than the ventral one (Goodale and Milner, 1992). Accordingly, their study used stimuli designed to activate preferentially the ventral and the dorsal stream of visual processing. Namely, ERPs were recorded in response to <u>colour</u> changes of isoluminant high-spatial frequency gratings, and in response to <u>motion</u> gray-scale low-spatial frequency gratings. Colour and moving stimuli were presented in different blocks. Stimuli were delivered at five locations: directly at fixation or along the two diagonals of the screen at 8° from the fixation point.

Stimuli were continuously visible at all five locations and, after a time interval varying randomly between 150 and 450 ms, one of the stimuli would change. ERPs were time-locked to this change called ‘standard’. Colour standard consisted of a colour change, whereas motion standard consisted of an acceleration of the moving grating. Across both colour and motion blocks, infrequent (10%) ‘targets’ were also randomly presented. These targets consisted of any one of the five stimuli being replaced with a static black square lasting 100 ms. Participants were asked to detect any infrequent target presented by pressing a response key. Asking participants to detect any presented target at both central or peripheral locations determined the distribution of visual attention across all five locations during stimulation.

The study was designed to compare VEPs in response to color and motion changes between groups, thus behavioural responses to targets were not analyzed. The result were quite straightforward. No VEPs differences between deaf and hearing controls emerged in response to colour changes. By contrast, deaf displayed significantly larger N1 amplitudes than hearing controls in response to peripheral motion changes. Intriguingly, a similar tendency was also present for motion stimuli occurring centrally, directly at fixation. Finally, the N1 component was distributed more medial and anterior on the scalp in deaf than hearing participants, suggesting a reorganization of its cortical generators due to deafness. In sum, the main result of the study by Armstrong and colleagues (2002) is that deafness alters specifically motion processing and not colour processing in agreement with the hypothesis of a preferential modulation within the dorsal pathway. This study extended previous evidence showing that deaf posses enhanced motion processing (Neville and Lawson, 1987) and demonstrate that this can occur even when participants do not attend specifically to that feature or that location. Intriguingly, it provides initial evidence that this difference between deaf and hearing individuals can be observed for peripheral as well as central locations. Finally, it should be noted that evoked potentials components that occur earlier than the N1 (e.g., P1) did not appear to differ between groups, leading to the suggestion that auditory deprivation may not alter significantly the initial stages of visual cortical processing.

Taken together these three EEG studies showed that enhanced cortical response to motion stimuli can occur for peripheral as well as central locations in the visual field. Nonetheless this effect is greater for stimuli occurring at peripheral than central locations. For what concerns the role of visual attention in modulating the EEG response, the results appear controversial. While the early study by Neville and Lawson (1987) showed larger N1 in deaf than hearing controls under condition of focused endogenous attention (see also Bavalier et al. 2000, 2001), a more recent work by Armstrong and colleagues (2002) indicates that an endogenous allocation of selective attention to the target may not necessary to show the enhancement of ERP component in the deaf. Finally, the visual processing of colour does not appear to be modulated by deafness, strengthening the account that propose a specificity of the dorsal pathway in the cros-smodal plasticity phenoman occurring after long-term auditory deprivation.

The present study

The principal questions that arise from the behavioural data are: when in the processing chain, where in the brain, and by which neural mechanisms deaf individuals get the reactivity advantage at detecting a visual target compared to hearings? As discussed in the Chapter 4 different mechanisms could account for the reactivity advantage in the deaf, from subcortical to cortical structures that are implied in the visual processing as well as in the motor planning. We decided to run the present study to start by an electrophysiological point of view to answer to the question of where and how the reactivity advantage emerge. The EEG technique could allow to evaluate in detail the dynamic of the visual processing and part of the motor preparation and release.

In particular, one of the specific aims of the present study, was to evaluate in detail the early visual evoked potentials (VEP) at this detection task, in deaf and hearing controls.

Methods

Participants

Ten profoundly deaf individuals (mean age = 33 years, SD = 4, range 18-50 years old; 6 female) were recruited at the National Association for Deaf (Ente Nazionale per la protezione e assistenza dei Sordi, Trento, Italy) and gave their informed consent to participate in the study. All participants had uncorrected bilateral profound hearing loss (>80 dB). All acquired deafness within the first 3 years of age, 8 had congenital deafness. All deaf participants were proficient sign-language users.

Ten hearing age-matched controls (mean age = 29 years, SD = 2.5, range 23-50 years old; 5 females) were also recruited to take part in the study. All participants had normal or corrected-to-normal vision and were right-handed by self-report. The study was approved by the ethical committee at the University of Trento (Italy).

Stimuli and apparatus

Visual fixation was a white cross, presented at the centre of the screen throughout the trial. The target was a circle opened at left or right side that could be presented at 8 possible locations arranged on two invisible concentric circles centred on visual fixation. The radius of the inner circle was 3 degrees of visual angle, the radius of the outer circle was 8 degrees of visual angle. Four possible target location were on the inner circle and four were on the outer (see Figure 1 on page Chapter 4). Each location was placed along the two diagonals of the display, thus resulting in 4 possible stimulus locations in the upper portion of the visual field, and 4 possible stimulus locations in the lower portion of the visual field. From now on we will refer to locations on the inner circle as central, and locations on the outer circle as peripheral. Targets appearing at peripheral locations were corrected for the cortical magnification factor (see Saarinen et al., 1989). Central target covered a visual angle of 1.5° and peripheral target of 2.6°. Participants were required to press as fast as possible the space bar of a computer as soon as the target was presented. All stimuli were presented on a standard 17 inches monitor, with 1024 X 768 pixel resolution, refresh frequency was 75Hz. 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).

Procedure and design

Participants sat at approximately 60 cm from the computer monitor and were instructed to keep their head and eyes oriented towards fixation throughout testing. The experimental session lasted approximately 60 min.

A cross centred at fixation was present throughout the experimental session. Each trial began with an alerting stimulus consisting in a red square covering 1.5 ° of visual angle and presented for 500 ms (note that visual fixation was nonetheless presented on top of the red square). This manipulation had the purpose of capturing participant's attention and gaze towards the centre of the screen and alert participant that the target was about to arrive. After the red square disappeared, two possible intervals of time (see further) were randomly selected before that the imperative visual target appeared at any of the 8 possible locations (i.e., 4 central and 4 peripheral). All target positions were equiprobabile and randomly selected. The ISI between the warning signal (red square) and the target could be either 500 ms (short ISI) or 1800 ms (long ISI). These two possible ISIs were equiprobabile.

The visual target was a circle opened at left or right side presented for 48 ms. Participant's response terminated the trial, and a random inter-trial interval ranging between 1250 and 1750 ms was introduced before the beginning of the subsequent trial. In case of anticipation responses a visual warning signal was delivered. Before the beginning of data recording participants completed a practice block of 24 trials. The experimental session was divided into 10 blocks. Each block comprised 98 trials and lasted approximately 5 minutes. Between blocks we gave participants the possibility to take rests. The experiment was a 2 by 4 factorial design, with target location (central or peripheral) and timing (Short or Long ISI) as within-participants factor, and group (deaf or hearing controls) as between-participant factors.

Electrophysiological recording and Data Analysis

The EEG was recorded (analog bandwidth: 0.1-200 Hz, sampling rate:1 kHz) from 34 scalp sites using the international 10-20 System extended montage (documentation in http://www.easycap.de). Standard 10-20 sites were FP1, Fp2, F7, F3, Fz, F4, F8, T7, C3, Cz, C4, T8, T5 (P7), P3, Pz, P4, T6 (P8), O1 and O2. Additional intermediate sites were FC5, FC1, FC2, Fc6, TP9 (M1), CP5, CP1, CP2, TP10 (M2), PO3, PO4, PO9, Iz and PO10 (see Fig 1) .

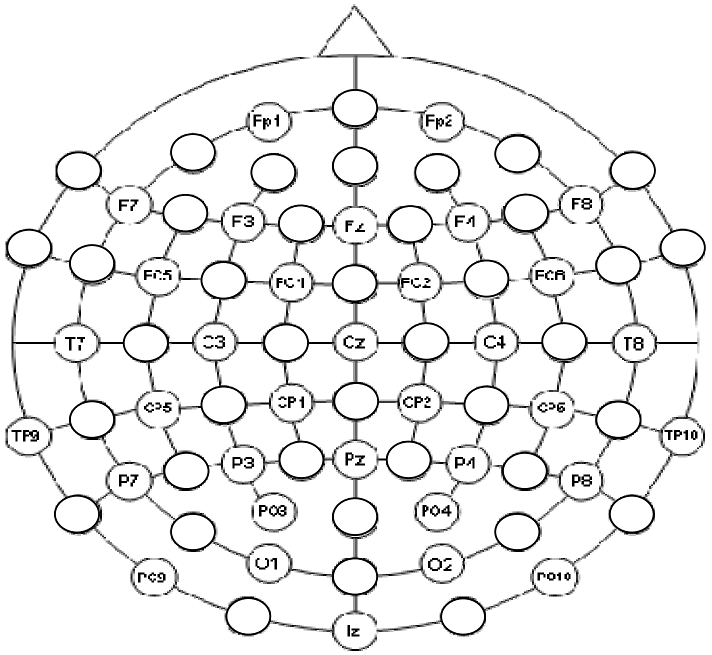


Figure 1.

All scalp channels were referenced to the nose. Horizontal eye-movements were monitored with a bipolar recording from electrodes at left and right outer canthi. Here we want to emphasize that the choice of the reference electrode is an important difference with all previous EEG experiment that evaluated visual abilities in the deaf. The reference to the nose was selected to maximize the acquisition of activity at occipito-temporal sites. To eliminate the artefacts due to blinks in the EEG signal, we used an Independent Component Analysis (ICA, Comon, 1994) implemented in a custom made program (EEGLAB) running in MATLAB (http://www.mathworks.com/). After the removal of blink effects, signals including incorrect responses (anticipations) or exceeding 100 μV were excluded from averaging. ERPs were computed from 300 ms before the warning signal onset to 350 ms after the target onset. Finally, the ERPs were digitally filtered (0-30 Hz). Scalp potential and current density maps were generated using spherical spline interpolation (Perrin et al., 1987, 1989). All EEG data were analysed with the ELAN-pack software developed at INSERM U821 (Lyon).

Results

Behavioural responses

Simple median RTs in response to the visual target were entered into a mixed ANOVA with visual target location (central or peripheral) and timing (Short or Long ISI) as within-participants factor and group (deaf or hearing controls) as between-participant factor. This analysis revealed that both main effects of target location ($F(1,18) = 4.85$, $p < 0.05$) and timing ($F(1,18) = 44.4$, $p < 0.0001$) were significant. The main effect of target location revealed that all participants were faster at reacting to central (mean = 286 ms, SE = 7) than peripheral targets (mean = 288 ms, SE = 7). The main effect of timing revealed that all participants reacted faster to Long ISI than Short ISI (mean = 273 ms, SE = 6 and mean = 300 ms, SE = 8, respectively). More importantly for the purpose of the present study, a main effect of group was also present ($F(1) = 6.7$, $p < 0.02$). Deaf participants were on average 36 ms faster than hearings controls at detecting the visual targets (mean = 269 ms, SE = 10; vs. mean = 305 ms, SE = 10, respectively), regardless of target location and timing. The analysis revealed also that the interaction between the factor location and group was approaching to significance (F(2,18) = 3.3, p<0.08); this tendency indicates a possible different ratio between the RTs at central and at peripheral target locations within the two groups of participants (see Chapter 4 for a similar result). While hearings controls paid a slight RT cost (4 ms) when responding to peripheral than central targets (mean = 307, SE = 10 vs. mean = 303 ms, SE = 10), in deaf participants this cost was negligible (0.4 ms; central: mean = 269 ms, SE = 10; peripheral: mean = 269 ms, SE = 10; .

The analysis also revealed that the interaction between the factor group and timing was significant (F(1,18) = 8.8, p<0.008). While deaf individuals displayed no difference in terms of RTs at detecting targets at Short or Long ISI (t(9) = 0.3, n.s.; mean = 276 ms, SE = 11 and mean = 261 ms, SE = 9, respectively) hearing controls showed slower RTs at detecting Short ISI than Long ISI targets (t(9) = 2.6; p<0.03; mean = 324 ms, SE = 11 and mean = 285 ms, SE = 9, respectively; see Figure 2).

Figure 2

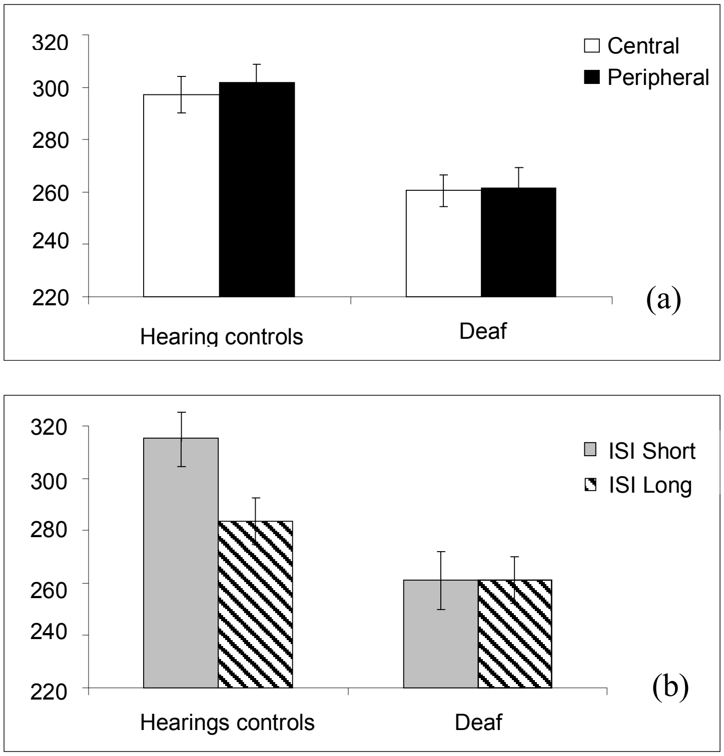


Figure2. Performance of deaf participants and hearing controls (a) in the simple detection task, as a function of target locations, (b) as a function of the short or long ISI, both in terms of response time. See text for details.

Faster detection for targets at Long ISI than Short ISI (mean difference = 40 ms) in the hearing controls can be accounted by the fact that posterior probability reaches the value of 1 after the target at Short ISI did not appear (see Trillenberg et al., 2000). In other words, if the target does not appear at Short ISI participants are sure that it will appear at Long ISI. Intriguingly, however, deaf participants do not show this well documented difference between the two ISI conditions (mean difference = 15 ms). As in the previous visual detection experiment deaf resulted particularly faster than hearing controls at detecting a target presented at Short ISI. Notably, the between-groups difference was 48 ms at Short ISI, but only 15 ms at Long ISI.

This latter finding indicates for the first time that timing itself is a condition that can modulate differently the RTs in response to a visual target in deaf and hearing individuals. Moreover, as the previous experiment showed, this study confirm that deaf are faster than hearings regardless of target location and timing. Finally, in the present study the interaction between the target location and group was only approaching significance. As we showed in the previous visual detection experiment (Bottari et al. 2008, submitted b) this effect appears to be rather small in simple detection and emerges only when the variability of data is very limited. In this experiment participants performed the detection task for one hour long and this could have introduced fatigue and variability in the data.

Electroencephalography

Before comparing the cortical activity between groups, we first evaluated the emergence of visual evoked responses within each group. For that, we run a series of Wilcoxon tests separately for each group, comparing to zero the activity recorded at each time sample. These tests gave us the opportunity to show the emerging of evoked potentials without assumptions. We used these results to select the time window for classical between-groups comparisons.

Responses to the warning stimulus (red square)

We started by analysing the electrical activity due to the appearance of the red square, to evaluate the cortical response to a visual object that was not the target of the task. In addition, this gave us the opportunity to evaluate the whole epoch of the trial, from the warning signal (the red square) to the target. Averaged potentials were referred to a baseline fixed at -100 ms to 0 before the appearance of the red square.

The first VEP component that we could take into account was the so called C1. This component is typically described with an onset latency between 40 and 70 ms and peak latency between 60 and 100 ms (Di Russo et al., 2001). Considered that the red square stimulus was placed at the fixation point, it was not possible to show a reverse in polarity for upper vs. lower visual field as previously shown (e.g., Di Russo et al. 2001). In our experiment, the C1 was indeed characterized as a negative wave at all posterior electrodes. We decided to compare between groups the activity at Iz because this central electrode could better capture this VEP component. C1 was analyzed in the 60-95 ms latency window to cover the responses of all participants. The peak amplitude, peak latency and mean amplitude values of each participant were entered into a Kruskal-

Wallis test with group as between-participant factor. The analysis showed a significant effect of peak latency (H = 4.7, d = 1, $p<0.03$) revealing that C1 peaked earlier for the deaf group than hearing controls (mean = 78 ms, SE = 10 vs. mean = 87 ms, SE = 6, respectively). Deaf individuals showed C1 peak latency 8.5 ms before the hearing group, indicating a speed advantage of about 10% on this component (see Figure 1). No other interaction was significant (all Hs < 2.8). A first novel result was thus that the visual C1 component of profoundly deaf peaks earlier than that of hearing controls, even for a stimulus that is <u>not</u> the target of the task. The C1 is supposed to index the activity of the primary visual cortex (Bodmann's area 17, striate cortex; e.g. see Di Russo et al., 2001).

Both the Wilcoxon test for VEP emergence and visual inspection of averaged response indicated that deaf activity at parietal-occipital electrodes (Pz, PO3, PO4) was already present before the appearance of C1 component. For explorative purpose we run a Kruskal-Wallis test between the two groups comparing the activity recorded at each time sample. This multi-comparison test revealed that activity recorded at parieto-occipital sites was greater in deaf than hearing individuals already 25 ms after the appearance of the red square. This early and sustained activity suggested a stronger anticipatory activity of visual cortices in deaf than hearing controls. To test this hypothesis we calculated the averaged potential relative to a baseline taken over the 300-200 ms period before the red square appearance. First, we entered into a Kruskal-Wallis test the mean amplitude and peak amplitude of potential at parieto-occipital electrodes (PO3, PO4, Pz) with group as between subjects factor. The analysis revealed that deaf displayed greater sustained activity than hearing controls (H = 3.9, d =1, $p< 0.5$) at those electrodes for the whole 200 ms period before the appearance of the red square (while the peak amplitude did not differ, H = 1.5, n.s., see Fig. 2). With this procedure, the same result was obtained over the 0-45 ms period after stimulus onset, well before the C1 wave was elicited: deaf presented greater mean amplitude at the electrodes PO3, PO4 and Pz compared to hearing controls ($H = 4.8$, $d = 1$, $p< 0.03$), and also enhanced peak amplitude ($H = 6.2$, $d = 1$, $p< 0.02$; see Fig. 2). This anticipatory sustained parieto-occipital activity could be one element that contributed to the C1 earlier peak latency displayed by deaf individuals compared to hearing controls. Note that the sustained activity was more parietally centred while the C1 peak was more occipital, at O1-O2-Iz.

To sum up, these analyses revealed an interesting difference between the two groups of participants, deaf display enhanced pre-activation of the parieto-occipital sites compared to hearing controls. Interestingly, the anticipation of cortical activity was present before the red square stimulus appearance, that represented in the present task the warning signal that announced the beginning of the trial. Thus, the red square was an element that should induce attentional engagement and then eventually anticipation. Surprisingly, deaf showed anticipation already 200 ms before the red square, in a time window that should be of rest (this is the time after the detection of the previous target). In this respect it would be interesting evaluating if this pre-activation of the visual cortices is a steady state or not.

Figure 3

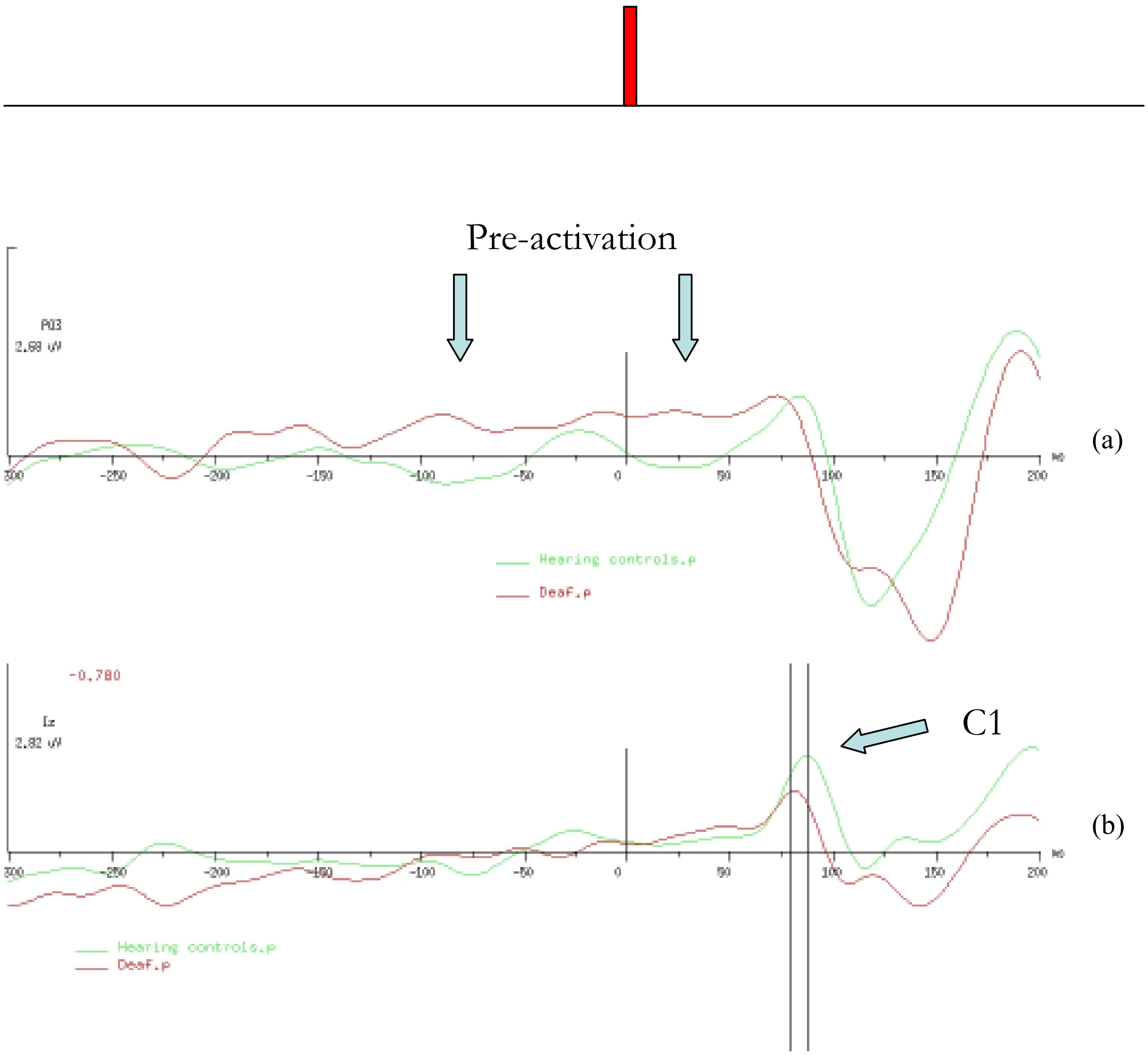


Fig 3. (a) Anticipatory activation in visual sites (PO3 electrode). The cursor indicates the onset of the warning stimulus (red square). Compared to hearing controls (green curve), deaf subjects (red curve) display a sustained cortical activity of significant amplitude from 200 ms *before* the stimulus onset to 45 ms after at parieto-occipital sites (PO3-PO4-Pz). (b) Peak latency of the C1 component generated by the warning signal (red square). The two cursors indicate the peak latency of C1 at Iz. C1 peaks earlier in deaf subjects (red curve) than in hearing controls (green curve).

The second VEP component observed is a positivity termed P1, typically described with an onset latency between 65 and 80 ms and a peak latency around 100 and 130 ms. There is evidence that this early component is mainly generated in extrastriate cortices (Di Russo et al. 2001). As shown in Figure 3, the main difference between the two groups seems to be the late phase of the P1 component at occipito-temporo-parietal sites (T5-T6-PO3-PO4-Pz; Figure 3 shows the representative profile recorded at T5). While the early phase of this component display similar peak amplitudes and latencies in both groups, the second phase clearly appear to different in magnitude. First, we analysed the whole P1 epoch, selecting a window between 80 and 170 ms at T5 and T6, the peak sites of this component. The peak amplitudes, mean amplitudes and peak latencies of P1 were entered in a Kruskal Wallis test with group as between-participant factor. The analysis revealed that deaf display enhanced peak amplitude ($H = 4.2$, $d = 1$, $p<0.05$) compared to hearings, and tendency of enhanced mean amplitude ($H = 3.02$, $d = 1$, $p=0.08$). We run the same analysis over the 80-130 ms time window trying to isolate the first phase of the P1 component. This analysis did not reveal any significant effect (All Hs < 2.06). Then, we evaluated the second phase of the P1 component over 130-170 ms. The analysis revealed a significant effect at T5-T6 of peak amplitude ($H = 4.2$, $d = 1$, $p<0.05$) and a tendency of enhanced mean amplitude ($H = 3.02$, $d = 1$, $p=0.08$). Thus, deaf displayed enhanced peak amplitude at T5-T6 and a tendency of enhanced mean amplitude compared to hearing controls. This result emerged in the whole epoch of the P1 (80-170) and in the second phase of the P1 component (130-170) while it did not emerged in the first phase.

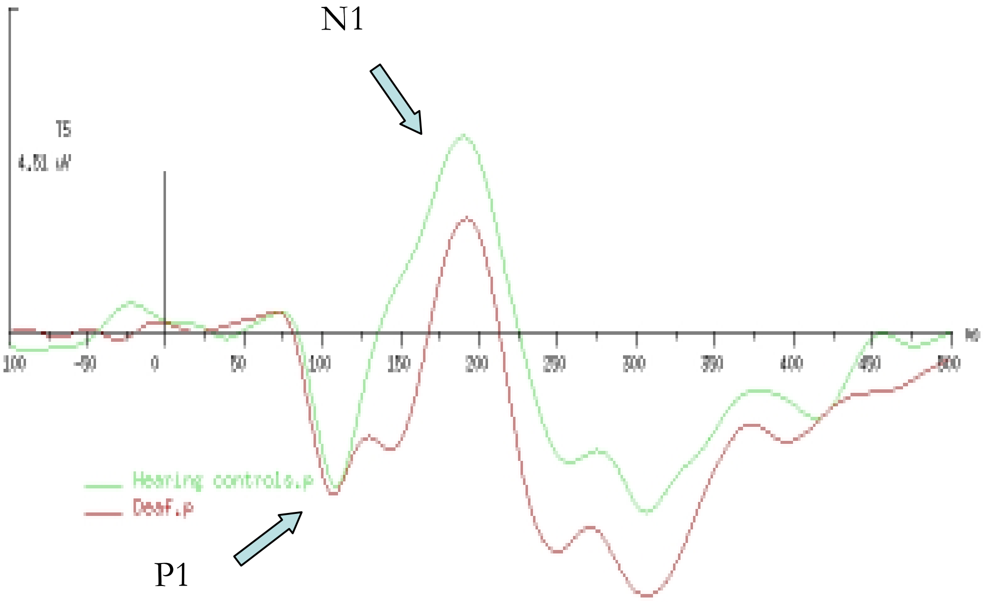


Fig 4. Visual responses to the warning stimulus at a temporo-occipital electrode (T5) in hearing controls and in deaf subjects. Negativity is up. The responses are characterized by a positive P1 complex peaking between 80 and 170 ms, followed by a negative deflection of large amplltude peaking around 200 ms (N1). In deaf subjects (red curve), P1 is composed of two successive deflections. The second deflection present only in deaf subjects results in a delayed N1 onset and a smaller N1 peak amplitude for deaf people compared to hearing controls (green curve).

Because of the difference in the second phase of P1, one also observed differences in the onset latency of the subsequent VEP, the so-called N1 component (also visible in Figure 4). As can be shown in the sequence of potential maps (Figure 5), the two groups of participants show clearly a different dynamic between 120 and 150 ms. To test this different pattern of activation, we measured for each participant the point in time at which the averaged potential crossed the line of 0 µV of activation. This was calculated to compare the onset of the N1 component, peaking over occipito-temporal electrodes (around T5 and T6) . With an analogous procedure, we measured the offset of the N1 component. We run a Kruskal-Wallis test comparing the onset time and the offset time of the N1 component at T5 and T6 between groups. We run this comparison at the two electrode sites separately because, as shown by the maps in Figure 5, the main difference in the dynamic of the late P1 component seems to be more left lateralized. The analysis revealed that at T5, the N1 onset between groups differed significantly ($H = 3.9$, $d = 1$, $p < 0.05$); while hearing controls N1 onset was at 145.2 ms after the red square appearance, deaf N1 onset appeared at 159 ms, with a delay of 13.8 ms. Contrarily at T6 the onset difference was not significant ($H = 2.01$, n.s). More importantly for the present analysis, the offset of the N1 component did not differ between groups at either electrode sites (All $Hs = 0.12$). This result shows that the different dynamics of the second phase of P1 result in different N1 latency onsets for the two groups. The parieto-occipital activity related to the second phase of the P1 is longer in time (as can be seen also by the maps in Figure 5) and larger in amplitude for deaf than hearing controls.

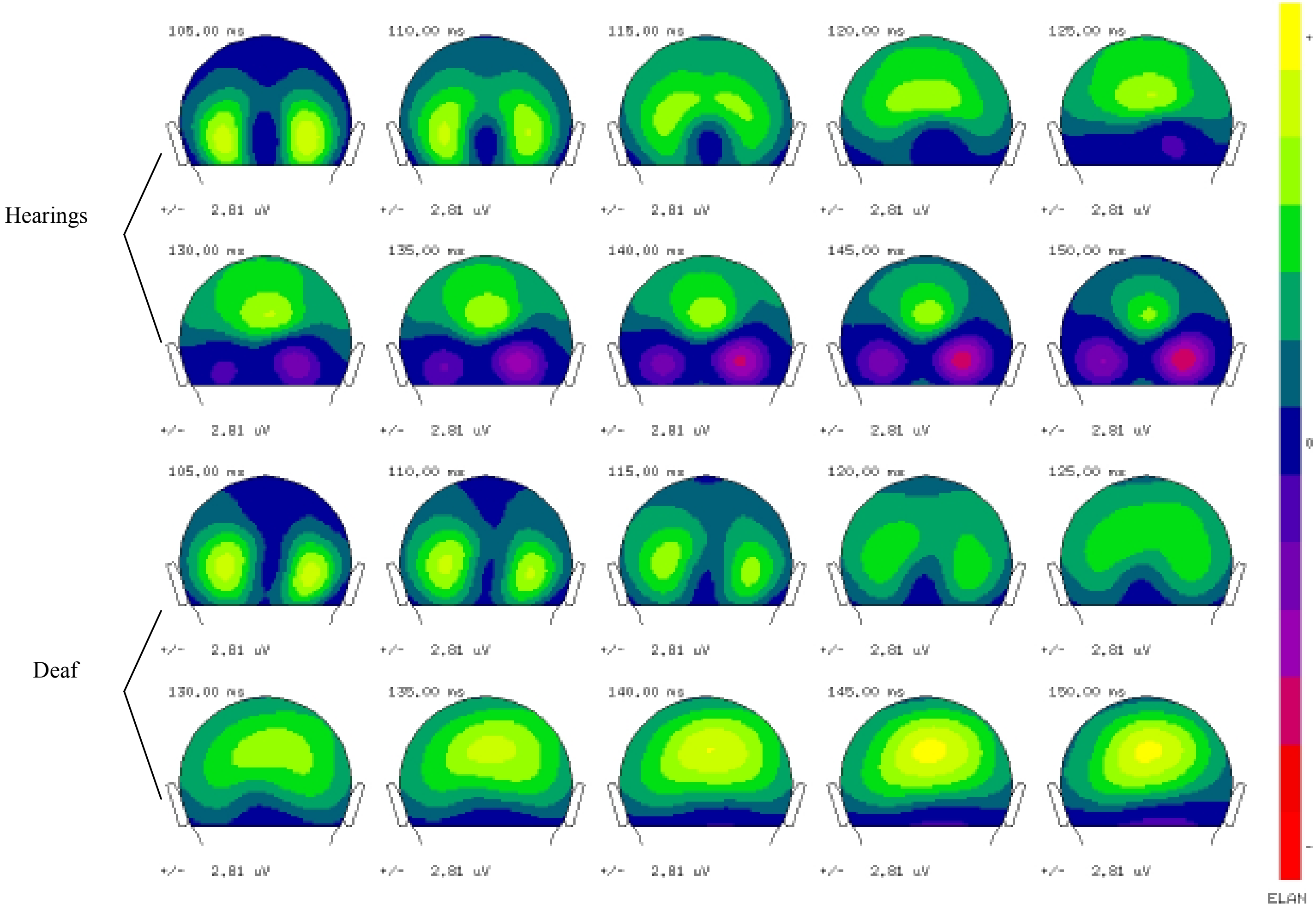


Figure 5. Topography of the visual responses (potential maps) between 105 ms and 150 ms after the warning stimulus onset at posterior sites. The first two rows depict the responses of the hearing control group, the last two rows the deaf group potentials. As can be seen, the activity at 105 ms is comparable between the two groups. Contrarily ~~at~~ around 120 ms, while the control group shows a positivity at parietal sites (referred to as the second phase of P1 in the text), deaf group activity remains in occipital sites and evolves towards the parietal sites only later. Moreover as can be seen in the second row of both groups, between 120 and 150 ms the positivity at parietal sites is ampler and longer for deaf than for hearing controls.

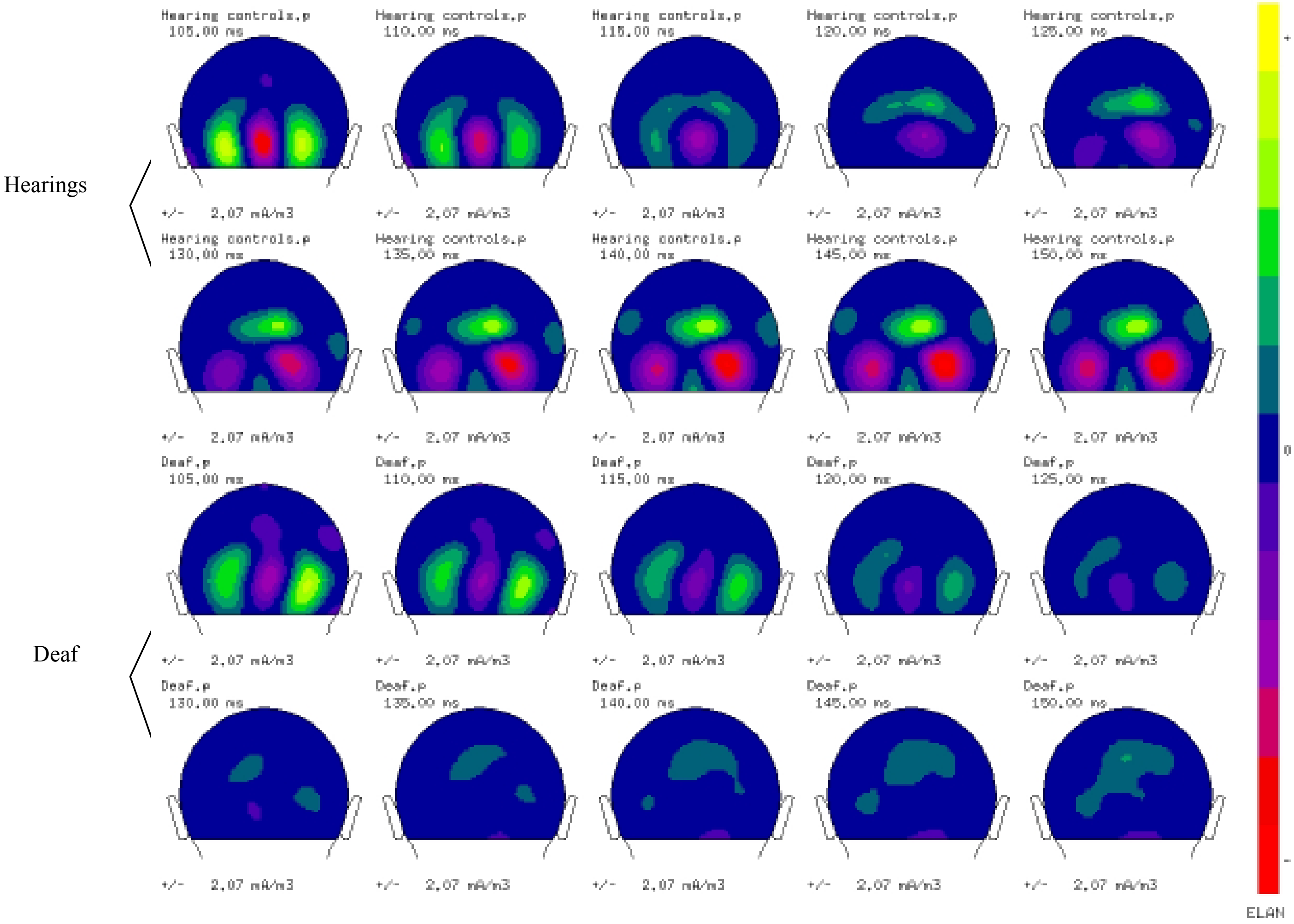


Figure 6. Scalp current density maps in response to the red square between 105 and 150 ms latency. The first two rows depict the responses of the hearing control group, the last two rows the deaf group. Interestingly, numerically the second phase of the P1, between 130 and 150 ms is less ample in deaf than hearings. Considered that the maps of potentials depicted in Figure 4 have the opposite trend, we can conclude that the generators of this late P1 component are multiple (Pernier et al. 1988) and differently activated in the two groups.

We also analysed the mean amplitude, peak amplitude and peak latency of the N1 component over the 130-250 ms latency range. Hearing controls showed enhanced N1 mean amplitude compared to deaf individuals at left occipito-temporal sites T5-TP9-T3 ($H = 3.9$, $d = 1$, $p<0.05$; see Fig. 3). This difference could again be due to the second phase of the P1: the strong positivity peaking prominently at parietal electrodes in the deaf group reduces subsequent negative response (N1) compared to controls. On the other hand, it is possible that deaf simply display a less prominent N1 at left occipito-temporal sites.

Delay between the warning signal and the target: the CNV

Between the warning signal and the target, all subjects presented a slow negative shift of the evoked potentials at central sites. This slow potential, called Contingent Negative Variation (CNV) component, is associated with an anticipated response and a motor preparation to an expected stimulus. As shown in Figure 7, that represents the whole epoch of a trial, the first part of the slow central potential seems to differ between groups. We compared the mean amplitude, peak amplitude and amplitude range (the interval of amplitude between the lowest and the highest potential values) between groups, at Cz over the 500-1000 ms time window. This time window covers the time between the offset of the red square and the appearance of the target in the Short ISI condition. A Kruskal Wallis test on these measures with group as between-participants factor revealed a significant effect of the amplitude range ($H = 4.5$, $d = 1$, $p<0.04$). This analysis showed that the CNV in the deaf group had a ampler range than in hearing controls (mean = 5.3 μV v.s mean = 3.9 μV; see Fisure 7). No other effect was significant (all $Hs < 1.7$). We also run a similar analysis over the 1300-2300 ms time window to evaluate the late part of the CNV. This analysis did not reveal any between groups differences (all $Hs < 1$).

Figure 7

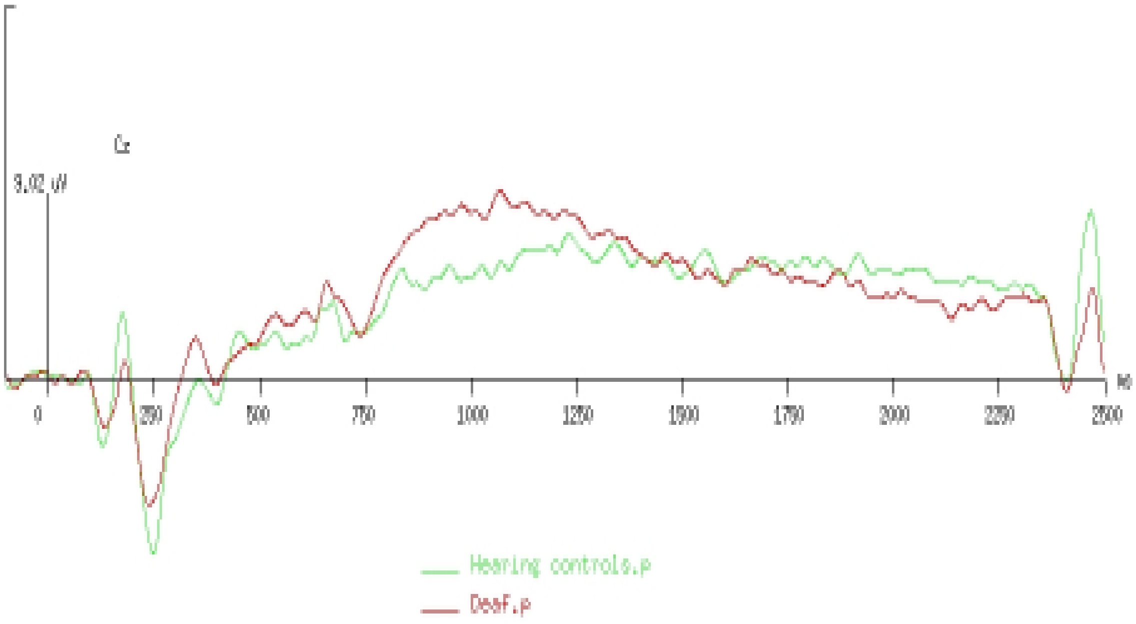


Figure 7. Responses at a central electrode (Cz) from the warning signal onset (cursor) until the visual response to the target in the long ISI condition. The responses are characterized by the Contingent Negative Variation (CNV), a component associated with an imperative stimulus expectancy (anticipated response and motor preparation). Between 500 and 1000 m, the CNV presents a wider amplitude range (difference between minimum and maximum value) in deaf than in hearings.

In sum, this analysis revealed that the earlier part of the CNV between 500 and 1000 ms had a different dynamic between the two groups. Deaf group showed a wider variation of potential amplitudes compared to hearing controls; this slow component started at the same amplitude in the two groups, but had a stronger amplitude range in the deaf group. This result is particularly interesting if compared to the behavioural data. Deaf are always faster than hearing controls, but in particular when the target appears at the Short ISI, that is, in the condition when the two groups display a different activation in the CNV.

Responses to Targets

As in the analysis of the responses to the warning signal, we first examined the C1 component to the target. As previously evidenced in several studies (e.g. Jeffrey and Axford, 1972a,b; Butler et al., 1987; Clarck et al. 1995; Mangun, 1995) we found responses of inverse polarity for upper vs. lower visual field stimulation (compare panel a and b in Figure 8). This reversal of polarity corresponds to the retinotopic organization of the striate cortex, in which the lower and upper visual hemifields are represented in upper and lower banks of calcarine fissure, respectively. Thus, stimulations above and below the horizontal meridian of the visual field should activate neural populations with geometrically opposite orientations determining opposite polarity in the evoked potentials. Unfortunately, we could not compare the C1 activity between groups in response to the target because it was not clearly evident in all participants. At least two reasons may explain the lack of a clear C1 in response to the target. First, the target was a stimulus of much less visual energy than the red square, thus it elicited a C1 component of smaller amplitude. Second, the signal-to-noise ratio of the VEPs to each target type (e.g. upper central) (about 120 trials) was much lower than that to the warning signal (averaged over about 980 trials). For these reasons, the first statistical analysis on VEPs to the targets were performed on the P1 component. We averaged the VEPs to targets presented at central locations and separately we averaged VEPs to targets presented at peripheral locations.

Figure 8

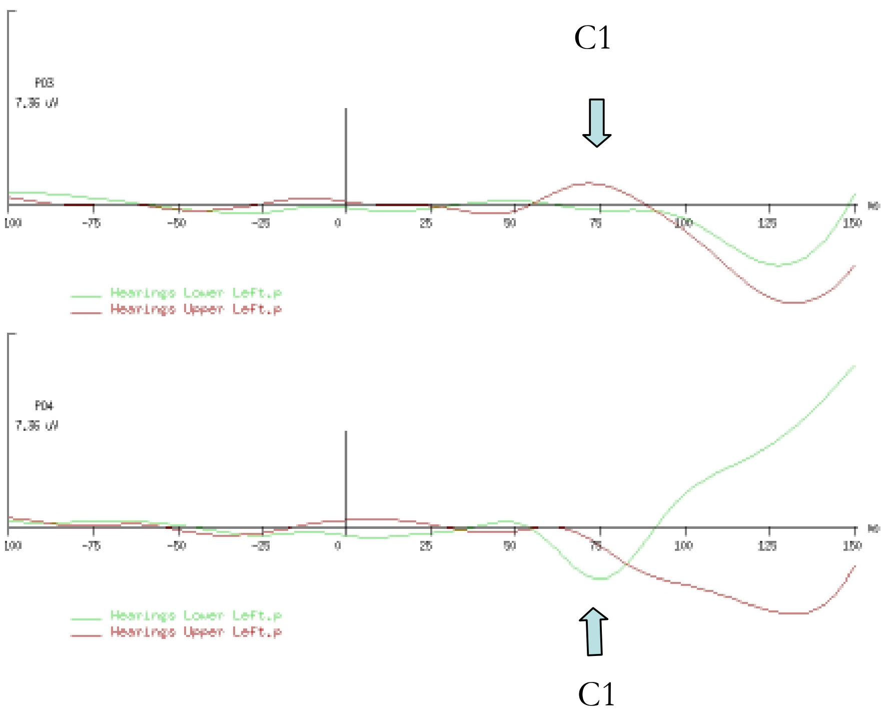


Figure 8. C1 for the hearing control group at PO3 and PO4 for the target at left central upper (green line) and left central lower visual field (red line). As typically described, the C1 is negative and ipsilateral for the upper visual stimulus as can be seen at PO3. Contrarily C1 is positive and contralateral for lower visual stimulus as can be seen at PO4.

<u>Central targets</u>

Visual inspection of the P1 component in both groups suggested again that the second phase of P1 was different between the two groups. For the P1 analysis we selected a window between 60 and 180 ms latency. The mean amplitude, peak latency and peak amplitude were entered into a Kruskal Wallis test with group as between participant factor. The analysis revealed that at T5-T6, the peak latency was earlier for hearing than for deaf (H = 5.3, d = 1, p<0.03; mean = 101.7 ms vs. mean = 117.6, respectively; see Fig. 8a). Moreover, the mean amplitude at parieto-occipital electrodes (Pz-PO3-P4) was enhanced in deaf compared to hearing group (H = 4.5, d = 1, p< 0.04;

mean = 4.2 vs. 3.2 µV, respectively; see Fig. 9a). These results show again that the parieto-occipital component of the P1, the second P1 phase, is enhanced, and that the peak latency is delayed in the deaf compared to hearings, a result similar to what was observed in the responses to the warning signal. We then analyzed the N1 component between 100 and 260 ms latency. The mean amplitude, peak latency and peak amplitude were entered in a Kruskal Wallis test with group as between participant factor. The analysis revealed that the mean amplitude of N1 at occipito-temporo-parietal sites (T5-T6-PO3-PO4-O1-O2) was reduced in deaf individuals compared to hearings ($H = 7.4$, $d = 1$; $p<0.01$; see Fig. 9a).

Figure 9

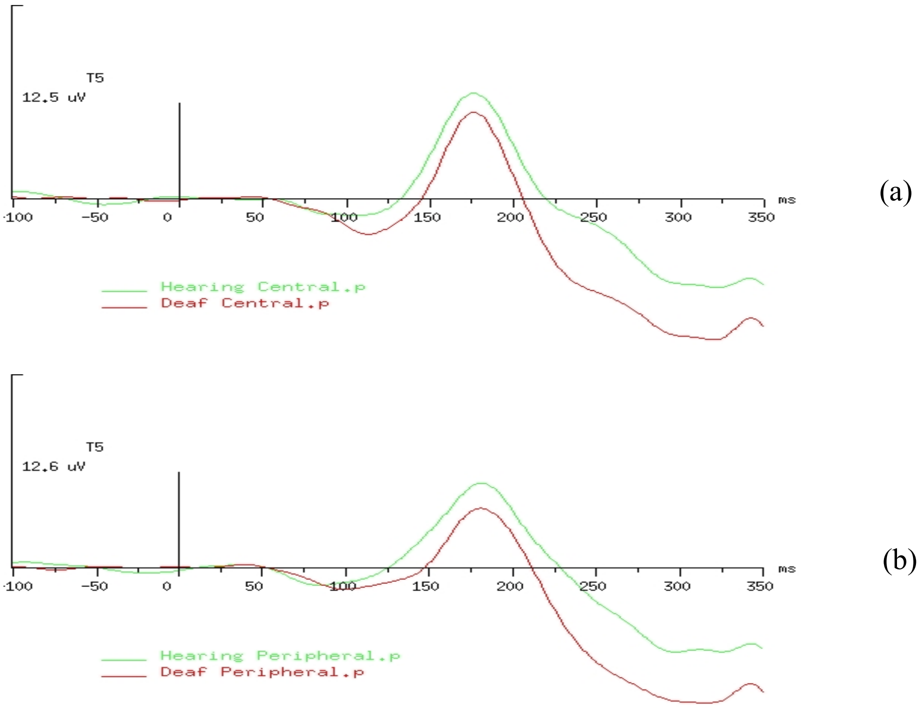


Figure 9.
(a) VEPs for central targets. The P1 component has a larger mean amplitude and a later peak latency in deaf than in hearing. The mean amplitude of N1 is reduced in deaf compared to hearings. (b)VEPs for peripheral targets.The peak latency of P1 is earlier in hearing than in deaf. The mean amplitude of N1 is smaller in deaf than in hearing controls.

Peripheral targets

For the P1 analysis we selected the same time window as for central targets, between 60 and 180 ms. The mean amplitude, peak latency and peak amplitude were entered in a Kruskal Wallis test with group as between participant factor. No significant difference was found on the mean amplitude or peak amplitude (all Hs < 2.8). However, the P1 peak latency was shorter for hearings (98.9 ms) than for deaf individuals (123.8 ms) at all temporo-parietal electrodes T5-T6-Pz-PO3-PO4 ($H = 6.2$, $d = 1$, $p< 0.01$; see Fig. 9b). To sum up, unlike for the P1 component to central targets, deaf did not display enhanced mean amplitude of the second phase of P1. But in agreement with the results for central targets, the peak latency was earlier for hearings than for deaf, suggesting again that the temporal dynamics of this P1 complex is different between the two groups.

The N1 component was analyzed over the 100-200 ms time window similarly to the N1 to the central targets. The mean amplitude of N1 at occipito-temporo-parietal sites (T5-T6-PO3-PO4-O1-O2) was found reduced in deaf individuals compared to hearings ($H = 4,8$ $d =1$; $p<0.03$; see Fig. 9b).

Central Vs. Peripheral targets

In this section we will compare the VEPs for central and peripheral targets within each group. This analysis could be helpful to understand the possible differences the two groups process central and peripheral targets. As previously mentioned, while hearing controls detected faster central than peripheral targets, deaf showed comparable performance for the two types of targets. Here we will use the same time window used previously to evaluate P1 and N1 components (60-180 ms and 100-260 ms respectively).

Controls. Mean amplitude, peak amplitude and peak latency measures of the P1 component were entered in a Wilcoxon test for paired samples. The analysis revealed that P1 peaked significantly earlier for peripheral (99.7 ms) than central (110.4 ms) targets ($Z = 2.5$, $p < 0.2$) at posterior sites (T5-T6-Pz-PO3-PO4-O1-O2). No other effects were significant (all $Zs<1.3$).

The same analyses performed on the N1 component revealed that mean amplitude at Pz was enhanced for central compared to peripheral targets ($Z = 2$, $d =1$, $p<0.05$).

Deaf. The same analyses performed in the deaf group did not reveal any difference in the peak latency of P1 between central and peripheral targets (all $Zs< 1.3$), a results therefore different of what was observed for hearing subjects. On the other hand, the mean amplitude of N1 at T5-T6 was enhanced for central compared to peripheral targets ($Z = 2.7$, $d =1$, $p<0.01$).

In sum, hearing subjects elicited a P1 component with a shorter peak latency for peripheral than for central targets, whereas the deaf group did not present significant differences between the two types of targets. On the other hand, the N1 component displayed a similar trend in both groups, with an enhanced peak for central than for peripheral targets. Hearing controls showed this pattern solely at Pz while deaf showed it at both T5 and T6 sites.

Discussion

Analysis of the early evoked potentials in a simple detection task revealed that the visual responses of deaf subjects and hearing controls present both quantitative and qualitative differences.

First of all, we showed that deaf individuals display activation at occipito-parietal sites before any visual stimulation. This pre-activation of the visual sites could manifest a stronger visual attention and preparation to the upcoming stimulus. An interesting further direction of investigation could be to evaluate the resting state of deaf individuals to evaluate if the occipital cortex display such activation even when no visual tasks are requested. Indeed our explanation of the activation at occipital electrodes before any visual stimulation is the most conservative. An alternative explanation could be that the visual cortex in the deaf display a more excited state also at rest.

Moreover, the first C1 component of VEP, known to be generated in the primary visual cortex (Di Russo et al.), peaks earlier in deaf than in hearings. This result is particularly interesting because it has been shown recently that the C1 component represents mainly the Parvocellular activity (Foxe et al., 2008). Interestingly, up to now all the differences between deaf and hearings have been more related to the Magnocellular and then dorsal pathways (see Armstrong et al. 2002). In addition, it is important to remark that the C1 component is considered a VEP that is not modulated by selective attention (e.g. Clark and Hillyard, 1996; Hopfinger and West, 2005). If this is true, we could conclude that the pathway that brings visual information to primary visual cortex is faster in deaf than hearings, or alternatively that the processing within this cortex is faster and leads earlier latency peak in the deaf.

Another interesting finding that emerged from the present study was the different dynamic of the VEPs to both the warning stimulus and the target between the two groups, with a prolonged and ampler visual analysis at the level of the P1 complex in deaf compared to hearings. The amplitude and the timing of the P1 complex are so different between the two groups that they modulated differently the onset of the N1 component: deaf showed a delayed N1 onset compared to the hearing (while the offsets were comparable). We would like to emphasize that here, for the first time, we show not only a difference in terms of amplitude in a visual component between deaf and hearings. We show that the dynamic within the P1 complex is modulated by deafness. As can be seen in Fig. 4, when the N1 component is already present in hearing controls at occipito-temporal sites, deaf are still in a late P1 phase. This result suggests a deepen evaluation of this second phase of the P1 in the deaf. An interesting consideration emerges when we analyze the scalp current density (SCD) topographies in deaf and hearings during the P1 component. As can be seen in Figure 6, deaf display numerically less current amplitude than hearings during the second phase of the P1. This simple visual evaluation has important implications. Indeed, SCD amplitudes attenuates much more than potential amplitudes when the neural sources are deeper in the brain (that is, SCDs are sensitive to superficial generators and "blind" to deep generators). Considered that the potential at these latencies is higher in deaf than in hearing, and that the opposite is true for SCD, we can conclude that the second phase of the P1 component in the deaf could be deeper than in hearing controls. This could thus suggest that the two subjects' groups activate differently the generators of this sub-component of P1.

Comparing the N1 responses between groups, we also observed that this component is reduced in amplitude in deaf compared to hearings, in response to both the warning stimulus and the target. This result opens interesting considerations. Most of the studies that evaluated the visual abilities in deaf and hearings using EEG found enhanced amplitudes of the N1 component in the deaf (Neville et al., 1984; Armstrong et al., 2002). These studies used moving stimuli and required a visual discrimination task between different targets. Interestingly, it has been shown that the N1 component is particularly involved in attentional visual discrimination processes (Clark and Hillyard, 1996). In our case, the task (simple detection) required more superficial visual analysis, at least concerning the processes reflected in the visual N1 component. The smaller N1 response for deaf than for hearings in our paradigm could indicate that deaf engage less visual energy at this processing stage, perhaps because the stimuli have been evaluated more deeply at earlier latencies.

Finally we found that the CNV component in the deaf varied on a wider range of amplitude between 500 and 1000 ms latency. This result fits very well with the behavioral data that showed how deaf are much faster than hearing when the target is presented at Short ISI, that is at 1000 ms from the onset of the warning stimulus. From this result we could conclude that deaf have a better ability to prepare a (perceptual and motor) response to an expected stimulus presented at a short latency from a warning signal.

Although the analysis on the recorded electrophysiological data are not concluded, they suggest that the cross-modal plasticity in the deaf takes place at the very early stages of cortical visual analysis.

CHAPTER 6

GENERAL DISCUSSION

The general aim of the present thesis was to study the mechanisms underlying the changes in visual abilities observed after profound deafness. In particular, the research aimed at clarifying the role of selective visual attention in the cross-modal plasticity determined by long-term auditory deprivation. Using different behavioural paradigms we contrasted the role of endogenous and exogenous orienting of visual selective attention between profoundly deaf individuals and hearing controls (Chapter 2 and 3) and we evaluated the role played by visual attention in the enhanced reactivity of the deaf (Chapter 4 and 5). The following sections will summarise and discuss the implications of these two set of results in turns, and then we will conclude by combining our results within the overall framework of cross-modal plasticity due to deafness.

The role of endogenous and exogenous visual attention in deafness

The study reported in Chapter 2 (Bottari et al., 2008) addressed directly the hypothesis that enhanced visual abilities for the periphery of the visual field documented in the deaf reflect an enhancement of endogenous visual attention for peripheral visual locations (Bavelier et al., 2006; see also Chapter 1). To test this hypothesis we adopted a change blindness paradigm, which has the peculiarity of masking transient elements in the scene, and thus prevent any <u>exogenous</u> capture of visual attention. The paradigm consists in the presentation of two alternating scenes and the interposition between them of a blank display. When the second scene appears after the blank it constitutes a global transient for our visual system, that masks any local transient that would normally attract visual attention exogenously. The consequence of this transient masking procedure is that detection of changes in the scene becomes difficult (hence the term ‘change blindness’), and is successful only when endogenous selective attention is allocated on the spatial position (or object) where the change occurs (Rensink, 2001).

In our first study (Chapter 2; Bottari et al., 2008) we briefly presented two scenes composed of 4 or 8 drawings placed at central and peripheral locations, interleaved by a blank. In 50% of the trials one of the drawings of the first scene could be substituted by a different one in the second. Deaf individuals, hearing controls and a group of coclhear implant recipients were asked to compare the first and the second scene and to decide whether a change occurred or not. Moreover, we asked participants in different blocks to selectively attend to a specific portion of the scene (centre, periphery or to the entire scene). These attentional instruction were given to address the spontaneous allocation of endogenous attention (distributed attention condition), as well as the consequences of specifically attending to a location of space (attend centre, attend periphery) for the three experimental groups. The result of this change blindness study revealed no differences in terms of sensitivity (d’) or in terms of RTs between the three groups. In particular, in the distributed attention condition deaf did not show better performance for peripheral locations than hearing controls (as could have been expected if deafness led to more endogenous attention resources being allocated to the periphery of the visual field). Moreover, the performance was comparable between groups even when participants were asked to actively attend peripheral locations of the scene, suggesting that the endogenous allocation of attention was comparable in deaf and hearing controls.

The results of this first study are contrast with previous evidence in literature that suggested that enhanced visual performances in the deaf at peripheral locations occurs especially when they are asked to monitor the relative periphery of the visual field. We believe this finding does not reflect a lack of sensitivity of our experimental paradigm, because performance modulations as a function of attentional instructions, spatial locations of the targets and task difficulty did emerged within each group of participants (see Chapter 2 page 26). Instead, we suggest that a possible explanation for the discrepancy between our own findings and previous results in the literature is related to our experimental choice of preventing exogenous capture of attention through masking of transients. The implication of this hypothesis is that enhanced visual performance in deaf that hearing individuals would emerge specifically when visual transient are present in the scene and can capture visual attention exogenously. To test specifically this hypothesis we run the second study, reported in Chapter 3 (Bottari et al., submitted a).

In our second study, we adopted again the change blindness task to evaluate the performance of deaf individuals and hearing controls in a context which prevented transient events and exogenous capture of attention. The adopted stimuli and procedure were analogue to our the first study (Bottari et al., 2008), however we now also introduced a controlled transient element (a spatial cue that could attract visual attention exogenously) in a proportion of trials. When the spatial cue was presented, it appeared before each of the two scenes containing the drawings (see Figure 1 on page 63). Importantly, the cue was entirely non-predictive of change location (i.e., it occurred at the change location only in ¼ of the exogenous trials, and at no-change locations in the remaining ¾ of the exogenous trials). The result were straightforward. Overall, the cue was effective in driving exogenously visual attention, as revealed by worst sensitivity for congruent or absent cue trials than incongruent cue trials. Moreover, when comparing the performance between groups, no difference emerged in terms of sensitivity (d’). However, the analysis of RTs revealed a striking dissociation between deaf individuals and hearing controls. When the cue was absent (i.e. in a purely endogenous attention context, similar to that tested in Chapter 2) hearing controls displayed comparable RTs at detecting the change at central and peripheral locations whereas deaf displayed a cost at detecting peripheral than central changes. By contrast, when the cue was present and congruent with the position of change, hearing controls showed a cost in terms of RTs at detecting peripheral than central changes, whereas deaf displayed comparable RTs at central and peripheral locations (see Figure 2 on page 73). This results show an interesting modulation in the performance that clearly differed between groups depending on the presence or absence of a transient element on the scene. In this respect, the purely endogenous attention context confirmed the results of the previous change blindness study (Bottari et al., 2008), revealing that without a visual transient element on the scene deaf do not outperform hearing individuals performance. Instead, enhanced performance for deaf individuals at peripheral locations emerged when the spatial cue was presented and when it was spatially congruent with the change to detect. Taken together these results suggest that transient elements capable of attracting visual attention exogenously could play a key role in enhanced visual abilities of the deaf. In addition, they point to a fundamental role of <u>exogenous</u> attention capture, instead of the endogenous attention component.

Another interesting aspect of the change blindness study reported in Chapter 3 (Bottari et al., submitted a) emerged from the comparison of sensitivity and RTs measures. Enhanced performance at peripheral location in deaf than hearing controls emerged only in the <u>reactivity</u> measure, while the sensitivity was comparable between groups. This result suggested us to re-examine which measures characterised enhanced visual performances in deafness. A retrospective analysis of the literature, revealed that in most of the studies that showed enhanced visual abilities in profoundly deaf the between-group difference emerged in terms of response time (e.g. Colemenero et al., 2004; Chen et al., 2006; Loke and Song, 1991; Nava et al., 2008; Parasnis and Samar, 1985). By contrast, less consistent advantages for deaf than hearing controls emerged whenever the task was designed around accuracy (e.g., Bavelier et al., 2000; Bosworth & Dobkins, 2002) or perceptual thresholds (e.g., Brozinsky & Bavelier, 2004). Interestingly, this discrepancy between the results of tasks involving RT measures and task that focused on accuracy could reflect the different contribution of exogenous and endogenous visual attention to performance. As recently argued by Prinzmetal and colleagues (e.g., Prinzmetal, McCool & Park, 2005; Prinzmetal, Zvinyatskovskiy, Gutierrez & Dilem, 2008) endogenous attention and exogenous attentional capture influence RTs and accuracy measures differently. Endogenous attention affects performance both in experiments designed to measure accuracy alone and experiments that measure RTs (i.e., in which accuracy is not stressed, and participants instead favour speed of response). Contrarily, exogenous capture of attention affects performance in experiments that measure RTs but not experiment designed around accuracy alone. According to Prinzmetal et al. (2005) this might occur because endogenous attention enhances the perceptual representation of the stimulus at the attended location, relative to other locations (resulting in beneficial performance effects whatever the task). On the other hand, exogenous attention might only affect post-perceptual decisions as to which location should be responded to, without changing the perceptual representation of the stimulus (resulting in beneficial performance effects only in terms of response speed; see Prinzmetal et al., 2005, 2008). This dissociation between the measures affected by endogenous and exogenous capture of visual attention support the results of these two change blindness studies. In conclusion, all these findings support the notion of a selective enhancement of the exogenous capture by visual abrupt events in case of profoundly deafness. This conclusion changes the current perspective on visual abilities in deafness by specifying that cross-modal plasticity due to auditory deprivation may critically modulate specific aspects of visual attention (e.g., exogenous attention capture).

Enhanced reactivity in the profoundly deaf

The study presented in Chapter 3 also comprised a control experiment that we adopted to evaluate the reactivity of deaf and hearing controls in a simple visual detection task. Each trial began with a flickering cross at fixation for 500 ms that indicated the begin of the trial. After a variable delay a visual target was presented at central (3°) or at peripheral locations (8°). Participants were asked to react as fast as possible to the appearance of the visual target independently by its position. Before resuming the results, we want to remind that the only previous study that evaluated the ability to react to visual events placed at central and peripheral location was performed by Loke and Song (1991). In that study, deaf resulted faster than hearings at detecting targets presented at peripheral locations while comparable performance between groups emerged at central location. This simple result is reported in most (if not all) review paper or introduction as strong evidence that deaf are faster at detecting peripheral targets than hearing controls, while at central locations this advantage no longer emerge. The results of the simple detection experiment we report in Chapter 3 show that deaf can outperformed hearing controls both at central and peripheral locations, by 56 ms on average. This enhanced reactivity regardless of target location challenges the notion of strict spatial selectivity of visual abilities in the deaf that has repeatedly put forward in the literature (see Chapter 1).

The result of this simple detection study could not specify which functional mechanism could have generated this RT advantage in the deaf. At least two alternative explanations were plausible. Reactivity could either reflect the enhancement of some pre-attentive process (e.g., enhanced motor reactivity or faster visual processing), or could relate to faster orienting of visual attention to the target. To further investigate the substantial reactivity advantage of deaf individuals we run a further study, reported in Chapter 4 (Bottari et al. submitted b), in which we decided to adopt two speeded visual tasks: a simple detection task and a shape discrimination task, performed exactly on the same visual stimuli. The direct comparison of a detection and discrimination task could allow us to examine directly whether orienting of spatial attention plays a role in enhanced reactivity in the deaf. The critical difference between these two tasks is that simple detection can be solved under distributed attention (i.e., without any orienting of spatial attention), whereas shape discrimination necessarily requires orienting of visual attention to the target, for localisation and identification (e.g., Bravo and Nakayama, 1991; Turatto et al., 2007). If enhanced reactivity to visual events in the deaf specifically reflects more efficient and fast orienting of selective attention to the target, faster responses in deaf than hearing controls should emerge more strongly in the shape discrimination task than the simple detection task. By contrast, if enhanced reactivity to visual events in the deaf is not critically dependent upon orienting of spatial attention, it should emerge in the simple detection task as well. It should be emphasised that a direct contrast of these two simple visual paradigms, with targets occurring both at central and peripheral locations, had never been conducted in the literature on visual abilities in the deaf. For this study, we tested a group of profoundly deaf individuals and a group of hearing controls.

The results for the simple detection task, confirmed that deaf react substantially faster than hearing individuals (on average 44 ms), both for targets occurring at central and peripheral locations. In addition, it revealed a between group difference which was modulated by target location). While hearing controls reacted faster to central than peripheral targets, deaf showed comparable performance regardless of target location. These two result add important specifications on the notion of enhanced reactivity to visual events in deafness. First, they confirm that reactivity cannot be accounted exclusively as a spatially selective advantage, because it does not only emerge for peripheral locations. Second, they reveal an advantage for peripheral targets in the deaf, thus suggesting that spatially selective modification can indeed occur, parallel to the overall speed enhancement (note that this spatially selective result did not emerge in the control experiment reported in Chapter 3, in which a more limited number of trials was used).

The effect of slower RTs when reacting to peripheral than central targets in hearing controls is well known in literature (see Chapter 1). Generally, it is considered to reflect the different number of ganglion cells that represent central and peripheral portion of visual space (e.g., Marzi, Di Stefano, 1981; Chelazzi et al., 1988). Which mechanism could account for the deaf comparable performance in terms of RTs at detecting central and peripheral targets? To answer this question it is striking to consider the results that emerged from the shape discrimination task. If orienting of attention is enhanced in the deaf we should at least find faster reaction times in deaf than hearing controls at discriminating peripheral targets. In contrast to this possibility, the results of the shape discrimination task showed that the RTs were comparable between deaf and hearing controls and in addition deaf resulted overall in a worst accuracy performance. Thus, if faster orienting seems not to be the cause of the comparable RTs for central and peripheral targets locations, an alternative possibility is that the neural representation of visual peripheral space is different in the deaf, in the sense that peripheral representation at 8° is comparable to the central one. In this respect, the study by Stevens and Neville showed that deaf individuals posses enlarged filed of view to detect moving stimuli at the extreme periphery of the visual field, suggesting a neural re-organization of the representation of the visual field. In future studies it would be interesting to perform a simple detection task considering the entire visual field, to evaluate in detail the gradient of relation eccentricity-reactivity in the deaf.

To summarize, the result of the study presented in Chapter 4 (Bottari et al., submitted b) suggest that the enhanced reactivity to visual events in the deaf is likely not due to a faster orienting of visual attention. In addition, although they confirm the existence of enhanced processing in the deaf for stimuli occurring towards the periphery of the visual field, clearly this spatially-selective phenomenon alone does not account for the overall increase in the response speed that we also documented. Which mechanisms of cross-modal plasticity could account for this overall enhanced reactivity in the deaf? Here we will briefly present a few speculations, for a detailed discussion see the study in Chapter 4 (Bottari et al., submitted b).

One first possibility is that faster responses to visual targets reflects cross-modal plasticity occurring in sub-cortical structures. In this respect, animal studies have shown that several sub-cortical structures which are normally part of the auditory pathway can be recruited for visual processing in deaf mice such as the medial geniculate nucleus (MGL) of the thalamus and in the intermediate layers of the superior colliculus (SC; Hunt et al., 2004). If similar phenomena of sub-cortical plasticity occur in humans, this would lead to a redundancy of neurons dedicated to visual processing within subcortical neural structures known to enhance speed of response (e.g. redundant target effect). A second possibility that should be considered is that faster responses in the deaf reflect some aspect of response preparation or release. It is known that simple detection tasks allow response selection and response programming before target presentation. Thus, it could be hypothesised that reactivity effects observed in the profoundly deaf may reflect to some extent a facilitated release of pre-programmed motor responses. Finally, enhanced response speed in the deaf reflect changes occurring at the cortical level, such as faster visual processing. Nonetheless this last hypothesis seems hardly likely if we consider that all the previous EEG and MEG studies (EEG and MEG are the methods with best time resolution) never showed differences between deaf and hearings in terms of latency of visual processing (Neville and Lawonon, 1987; Armstrong et al., 2002; Fine et al., 2005). Indeed, considered that reaction times and VEPs covariates (e.g. Osaka and Yamamoto 1978; Wolf, Baedeker and Appel, 1988) if at least a part of the reactivity advantage in the deaf reflects faster visual processing at cortical level we should observe significant difference of latencies in the measure of the visual processing.

Given the last strong prediction we run a similar version of the speeded simple-detection task described in Chapter 4 while recording the elettroecephalographical (EEG) activity, using a 34 electrodes setup (Chapter 5). The paradigm that we adopted presented two main differences with respect to the simple detection experiment described in Chapter 4 (Bottari et al. submitted b). First, we changed the warning signal that indicated the beginning of the trial, replacing the flickering fixation with a static red square lasting 500 ms. Secondly, we adopted two ISIs between the warning signal and the target presentation, a short ISI of 500 ms and a long ISI of 1800 ms. These two timings were randomly selected and equiprobabile (50% each).

The behavioural result of the EEG study confirmed the observations of our previous experiments (Bottari et al., submitted a; Bottari et al., submitted b; see Chapters 3 and 4, respectively). In particular, deaf resulted faster than hearing controls at both central and peripheral locations. In addition, a different ratio between groups for target presented at central and peripheral locations emerged again in the RT pattern. While hearing controls paid a cost at reacting to peripheral than central targets, deaf showed comparable performance. Finally, the ISI modulation affected RTs differently in the two groups. Hearing controls displayed faster RTs when detecting target presented at long than short ISI from trial on-set, whereas deaf showed a comparable performance regardless of ISI. The modulation of RTs as a function of ISI in the hearing controls reveals the well-known effect of posterior probability: if the target does not appear at the first ISI its probability of arrival at the second ISI is maximal, resulting in a substantial decrement of RTs in detection tasks (Trillenberg et al., 2000). We will discuss further this point when evaluating the visual evoked potentials (VEPs).

Although the analysis of VEPs in this simple visual detection task is still a work in progress, a number of important novel findings are already clear. First, deaf individuals showed pre-activation at occipito-parietal sites before any visual stimulation, unlike hearing controls. This activity was evident before the appearance of the warning signal, that indicated the begin of the trial. At the present stage, this pre-activation could reflect a task-related attention engagement or alertness in anticipation of the upcoming stimulus, or a resting state difference (unrelated to the task) between deaf and controls. In this respect, recent evidence have shown that in the early blind the occipital cortex is pre-activated when an upcoming auditory stimulus is attended (Stevens et al., 2007). Clarification of pre-activation in deaf individuals would require new ad-hoc studies that compare brain responses before stimulus arrival during a rest condition, during a condition of passive looking and during active conditions in which task-relevant stimuli are presented.

The second novel finding of the EEG data is that the C1 component in response to the red square (i.e., the alerting stimulus at the beginning of the trial, which represented a 'non-target' for the participants) peaks earlier in deaf than hearing individuals (see Figure 3b on page 131). Because the C1 component has been associated with the first response of the striate cortex (V1 and, possibly, V2), such modulation in latency peak is particularly surprising. Interestingly, the C1 component is thought to be impermeable to attention in terms of amplitude and latency (Clark and Hillyard, 1996; Hopfinger and West, 2005). Thus, the difference in latency that we observed could be linked to a different speed of processing of the sub-cortical pathways that send visual information to the striate cortex rather than the consequence of a modulation resulting from selective attention. Alternatively, because the difference between deaf and hearing controls in the C1 component is in peak-latency and not in peak-onset, we could speculate that the processing within the striate cortex reach the peak of activity earlier in deaf than controls. Finally, this cross-modal effect due to auditory deprivation is particularly interesting because it has been recently shown that the C1 component represents mainly the parvocellular activity (Foxe et al., 2008). This results is intriguing because, as discussed in Chapter 1, differences between deaf and hearing individuals have typically been associated with cross-modal changes occurring within the dorsal pathway, which mostly captures magnocellular activity (see Armstrong et al. 2002).

Another early visual evoked potential that showed a modulation due to deafness is the P1 complex. This modulation occurred in response to both the red square and target. This positivity peaking at about 100 ms is thought to represents the activity of extra-striate cortices (Di Russo et al.2005; 2007). In particular, the second phase of the P1 complex (in response to the red square) was ampler and prolonged in deaf than hearing controls. This late P1 phase was so different between groups that it also produced substantial modulations of the N1 component onset: deaf showed a delayed N1 onset than the hearing controls (while the offsets were comparable). Moreover, a comparison between the potential maps and scalp current density maps, also suggest that the second phase of the P1 component has different generators between deaf and controls, or – at least – that these generators are differently activated. Further statistical analysis will clarify this specific point, nonetheless we want to emphasise that the this is the first study in the literature that show important changes in the dynamic of the early VEPs in the deaf. Previous research have typically showed ampler N1 component in deaf than hearing controls in response to moving stimuli (Armstrong et al., 2002; Neville and Lawson, 1987). Here we show differences in terms of latency at the level of the C1 and P1, suggesting that even the first sensory visual evoked components can be modulated by deafness.

The second (late) phase of the P1 component (which we documented ampler in deaf than controls) has recently been linked to the exogenous capture of visual attention

(Hopfinger and West, 2005). This result was obtained in a paradigm that involved simultaneously endogenous and exogenous capture of attention. The relative contribution of these two attentional components was measured separating spatially the endogenous attention and the exogenous capture, when the endogenous attention was allocated at the right hemifield, the exogenous capture effect was measured presenting an exogenous irrelevant transient in the opposite hemifield. While endogenous attention modulated the N1 component (a well-known finding in the EEG literature; e.g. Clark and Hillyard, 1996), the exogenous capture determined an ampler and prolonged late P1 component. This evidence fits well with our previous observation of selective enhancement of exogenous capture in the deaf (see Chapter 3; Bottari et al., submitted a). The analysis on the N1 showed in this respect another novel finding. While previous study that adopted moving stimuli showed ampler N1 in deaf than hearing controls (Neville and Lawson, 1987; Armstrong et al., 2002), here we showed that the N1 in response to both the red square and the targets was reduced in deaf than hearing controls. The main difference with respect to previous tasks is the type of stimuli. While enhanced N1 was evident in response to moving stimuli even in case of a detection task that requested distributed attention as here (e.g., Armstrong et al., 2002), the present study adopting static stimuli determined the reversed pattern. This discrepancy would reveal an interesting element, namely that the N1 component modulations could reveal different type of cross-modal effects due to deafness. In case of moving stimuli an ampler activity, in case of static stimuli a reduced activity. In this respect, we remind that fMRI studies showed that moving stimuli induced enhanced activation in MT+ complex in deaf than hearing controls (e.g. Bavelier et al., 2000). Finally, because the N1 component has been associated to visual discrimination processes that require attention (e.g. Clark and Hillyard, 1996), the smaller N1 response for deaf than hearings that emerged in our simple detection paradigm could reflect a more superficial processing of the stimuli in the deaf, possibly because the stimuli have been evaluated more deeply at earlier latencies, like the P1.

A final result that emerged from the EEG study concerns the slow potential called Contingent Negative Variation (CNV). The CNV is considered a multi-componential activity linked to the motor preparation and the expectancy with an up-coming event. Its amplitude covariates with the RTs in detection tasks (Trillenberg et al., 2000). This slow potential complex varied over a wider amplitude range in deaf than hearing controls in the 500 to 1000 ms latency period. This result fits very well with the behavioral data that showed ampler difference in terms of response times between deaf and controls when the target is presented at Short ISI, that is at 1000 ms from the onset of the warning stimulus. This result suggests that deaf have a better ability to prepare a (perceptual and/or motor) response to an expected stimulus presented at a short latency from a warning signal.

To summarize, the findings reported in Chapter 5 show for the first time a modulation of early visual evoked components C1, P1 and N1 in the deaf. Moreover, beside quantitative changes in terms of amplitude variations, we also documented qualitative changes in the component dynamic that suggest a reorganization of the generators that subtend the electrophysiological activity. Future analyses on these recordings data will be needed to clarify other interesting aspects like motor preparation and release, the activity expressed by temporal sites, and the activity in frequency bands.

Conclusions

Taken together the results of the experimental investigations reported in this thesis expand the existing knowledge on visual abilities in the deaf in at least four main directions.

First, they clearly show that not all aspects of visual attention play a role in the cross-modal reorganization of visual abilities that occurs in profound deafness. We did not find evidence of modulations occurring in the visual endogenous attention. Instead, we found convergent evidence from behavioural and EEG data that exogenous capture by visual transient plays a critical role. We refer to this new type of selectivity of the enhanced visual abilities in the deaf as <u>selectively for transient events</u>.

Second, we provided new evidence showing that enhanced reactivity in the deaf occurs regardless of stimulus location in the scene (i.e., no spatial selectivity). Faster reactivity is the first reported aspect of enhanced visual skill due to deafness that does not emerge exclusively for peripheral portion of the visual field. In addition, we showed that such reactivity advantage does not reflect faster orienting of attention, as evidenced by the fact that discrimination of the same stimuli did not resulted enhanced in the profoundly deaf.

Third, we showed (Chapter 3) a dissociation between reactivity and sensitivity. In particular, enhanced performance at peripheral locations in a complex task (change blindness associated to an irrelevant spatial cue) emerged in the deaf only in terms of reactivity and not for sensitivity measures. A review of the existing literature confirm this observation. Most of the studies that reported enhanced visual performances in deaf than hearing controls documented this effect in response times, rather than sensitivity or accuracy. Interestingly, this dissociation between accuracy and reaction times could related to some extent to the dissociation between endogenous vs. exogenous capture of visual attention (see Prinzmetal et al., 2008).

Fourth, we provided for the first time evidences that deafness modulates all the early stages of visual processing, both quantitatively and qualitatively. This difference between deaf and hearing controls in visual processing could reflect cross-modal changes starting in subcortical structures and spreading to cortical areas.

Future directions

Understanding cross-modal plasticity has several theoretical and clinical implications.

First, <u>it may help delineate cortical functional specificity</u>. Pascual-Leone and Hamilton (2001) have proposed that what would be specific of a sensory cortex is not the sensory modality which is typically processed, but rather the functional specificity that it can express. For instance, they argued that the visual cortex could be a metamodal structure that receives visual, auditory and tactile inputs, and is critical for spatial discrimination. In normal conditions, this cortex processes preferentially the visual inputs because vision is the sense that carries the richest spatial information. In this respect the evidences that showed how blind individuals and blindfolded sighted activate the occipital cortex to perform tactile spatial discrimination tasks support this innovative vision of the brain (Cohen et al., 1997). In this respect understanding the cross-modal plasticity in case of auditory deprivation could provide information on the functional specificity of the auditory cortices. As previously reported in the present thesis, it has been shown that visual stimuli can activate the auditory cortex (e.g. Finney et al., 2001), nonetheless it is still to clarify at which level these the visual information are processed. This, is in our opinion, could be a relevant aspect to define that could help to reveal why the temporal lobe is recruited for the visual analysis. In this respect, the functional reasons of this cross-modal recruitment are still an open issue. Possible functions that could be specifically evaluated within the deaf auditory cortex for instance are the temporal processing and alertness, considered that the auditory system results particularly specialized in these functions.

Second, further studies to specify the cross-modal plasticity may shed light on the actual constraints of this mechanism. Do sensory plasticity occur throughout life? Can it be reversed? For instance as we speculated, some of the finding of the present thesis could be related to sub-cortical plasticity. If this occurs, it would be important to evaluate if there are sensitive periods that characterize its occurrence and if the reafferentation of the auditory modality can reverse this re-organization. In this respect, understanding the characteristics of the functional and anatomical re-organization of the brain can also give <u>predictions about the effect of sensory implants in humans</u>. For instance recent studies showed in the deaf that the recruitment of the auditory cortex due to cross-modal plasticity can be used as predictor of the efficacy of a cochlear implant. the strongest is the re-organization the less is successful the implant (Giraud and Leee, 2007; Lee et al. 2007). These studies measured at rest the metabolic activity of the auditory cortex, again without addressing which processing are performed by the recruited cortices. This leaves open the possibility that not all the functional recruitment of the auditory cortices by vision interfere with the cochlear implant.

Third, the comprehension of the functional changes occurring in case of sensory deprivation can help to <u>improve the strategies adopted in education</u>. The plasticity due to re-organization in case of sensory deprivation determines different functional modulations. These changes in the behaviour must be taken into account to propose the correct approach in schools and in the developing of the aid technologies. For instance the evidences that suggest enhanced exogenous capture of attention are well coupled with the typical observation in clinical practice that deaf individuals are highly distractible. This could be interpreted as a behavioural difficulty, while it could represent an adaptive visual processing to detect relevant visual information that are outside of fixation. If these phenomena occur, it would be relevant to study educational strategies to limit the visual sudden events that attract deaf visual attention automatically.

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