



Adaptation to sensory loss

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The human brain has the remarkable ability to adapt to changes in its environment by benefiting from its 'plastic' properties. Following brain injury, the amputation of a limb, or the loss of a sensory input such as peripheral blindness, brain circuitry often seems to be able to reorganize itself in order to compensate for the handicap by being recruited to carry out tasks not associated with their prior 'default' functioning. The purpose of this review is to illustrate the brain's remarkable ability to adapt to changes in its environment, particularly when it is faced with a sensory loss. Two excellent models to study this phenomenon are provided by blind and deaf individuals. In both cases, studies have shown that they appear to compensate for the loss of sensory input with enhanced abilities in their remaining senses. These behavioral modifications are often coupled with changes in cerebral processing, generally in the form of crossmodal recruitment of deafferented primary and secondary sensory areas. We will also discuss the possible mechanisms underlying these changes and whether the functional topography of these regions present in unimpaired individuals is preserved in blindness and deafness. The notion of a critical period for plastic changes will also be discussed and its importance will be shown to be twofold. On the one hand, the functional relevance of crossmodal processing appears to decrease as a function of the age of onset of the deficiency. On the other hand, the more cortical reorganization takes place, the less likely brain areas will be able to process input from its original sensory modality. This is especially important for deaf individuals as auditory input can now be restored thanks to cochlear implants. © 2010 John Wiley & Sons, Ltd. *WIREs Cogn Sci* 2010 1 308–328
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INTRODUCTION

Our experiences are constantly shaped by our interactions with our surrounding environment. Such interactions are possible due to the evolutionary processes that have enabled the development of specific sensory organs designed to capture different exterior energies in order to obtain information on and from the outside world. The human body is equipped with five such organs, thus allowing us to perceive and sense the outside world via five different sensory modalities. In humans, the senses with the longest 'reach' are no doubt those of vision

and hearing (audition), made available to us by our eyes and ears, respectively. These senses are well equipped to acquire large amounts of information in a simultaneous manner. Many would indeed argue that they are perhaps the most important senses, especially with regards to our ability to properly function and navigate within our environment. For those of us benefiting of all our five senses, simple daily activities seem quite trivially accomplished. But crossing the street without vision or communicating with peers without hearing don't seem so trivial. Remarkably, however, blind and deaf individuals do not seem as handicapped as we might expect them to be. To the contrary, in fact, many seem to develop special skills in their remaining senses, which constitutes a form of compensation to balance the loss of sight or hearing.

The advent of precise neuroimaging techniques have allowed researchers to observe impressive plastic changes in the brains of the sensory deprived and have shown that these changes are closely linked to the marked behavioral changes observed in them. The purpose of this paper is therefore to take a closer

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look at the consequences of sensory deficits and how individuals, and their brains, adapt to these challenges.

BLINDNESS AND ASSOCIATED BEHAVIORAL COMPENSATIONS

Studying blind individuals presents a unique opportunity to see how important vision is in shaping our other senses. In fact, many have argued that in the absence of vision, individuals would be severely handicapped as their remaining senses (especially those with spatial components—such as auditory and tactile modalities) are expected to benefit from visual calibration.^{1,2} This has often been referred to as the perceptual deficiency hypothesis, which proposes that an impairment of one sensory modality has adverse effects across other perceptual systems. In fact, a large body of animal studies has shown that visual feedback plays an important role in auditory spatial learning^{3–7} (Also, the early loss of vision prevents the normal development of an orderly acoustic spatial map in the superior colliculus^{8–10}). In the same vein, some studies carried out in blind humans have shown them to be less accurate when having to localize sounds compared to sighted controls.^{11,12} However, an opposing point of view has also emerged. Many researchers have suggested that not only are blind individuals not severely handicapped but that they actually develop exceptional abilities within their remaining sensory modalities.¹³ In fact, throughout history there have been numerous anecdotal reports that blind individuals can develop heightened acuity in their remaining senses to compensate for their visual handicap. Diderot,¹⁴ in his *Lettre sur les aveugles*, reported the famous case of a blind mathematician who could recognize fake from real money coins just by touching them. Diderot went on to suggest that individuals who are blind from birth can develop exceptional hearing and tactile abilities to compensate for the lack of visual input.

More recently, a vast number of experimental studies support the latter notion that blind individuals possess enhanced abilities in their remaining tactile and auditory modalities (see Théoret et al.¹⁵). Many of these studies revolve around spatial concepts, given the important role the visual modality plays in spatial perception in sighted individuals. How do the blind perceive space? The great theorist William James actually had a chapter dedicated to this question in his 19th century essay ‘The principles of psychology’.¹⁶ He brought forth the notion of facial perception (i.e. ‘seeing’ with the face), as described to him by a blind colleague. This so-called sixth sense seemingly resulted from sensitivity to air pressure changes induced by near object surfaces, perhaps similar to the

shark’s lateral line system, allowing them to ‘feel’ their surroundings without actually seeing them. As such, blind individuals would be able to create a mental image of where objects are in their environment based on these facial feelings. However, lack of experimental support has somewhat led to the fading of this theory. A more empirically based explanation of this sixth sense is an enhanced ability of the blind to use echo cues, a process known as echolocation. Several studies have shown that both blind and blindfolded individuals can locomote without collisions through space containing large objects,^{17–19} and that blind individuals are more efficient at using echo cues to achieve this.^{20–23} Such echo cues are indeed instrumental for blind individuals when navigating; they often use them either by tapping their canes or by making clicking noises with their mouths in order to receive reverberations following the contact of the sound waves with neighboring objects.

Another measure of spatial auditory acuity can be obtained via sound localization tasks, which is an important skill to have when blind; hearing oncoming vehicles and detecting the sound alerts for street crossings is evidently essential to their well-being. Initial reports have brought forth conflicting results, with some papers citing better sound localization skills in blind individuals,^{24,25} whereas others report no difference compared to sighted individuals.^{2,26–31} Despite the apparent discrepancies, subsequent studies approached the problem in a more systematic manner attempting to clearly identify under which circumstances blind individuals show enhanced localization abilities³². In an influential paper last decade, Lessard et al.³³ showed that although no differences were observed between sighted and blind participants in a typical azimuthal sound localization task, half of the blind subjects significantly outperformed the sighted ones when they had to localize the sounds with one ear occluded (monaural localization) (see Figure 1). Although this was only true for half of the blind subjects, the difference was so marked that it strongly suggests differential mechanisms in the processing of the sounds between those blind individuals and the rest of the subjects. Since then, we have replicated this result on several occasions in our laboratory.^{34–36}

Another consistent finding is that blind individuals typically outperform sighted ones in binaural localization tasks when the sound sources are located in more peripheral positions as opposed to when they are presented centrally.^{37–39} In the latter study, we evaluated sound localization in far space, a region of space where sensorimotor feedback could not contribute to the calibration of auditory spatial maps. We showed not only that blind individuals properly

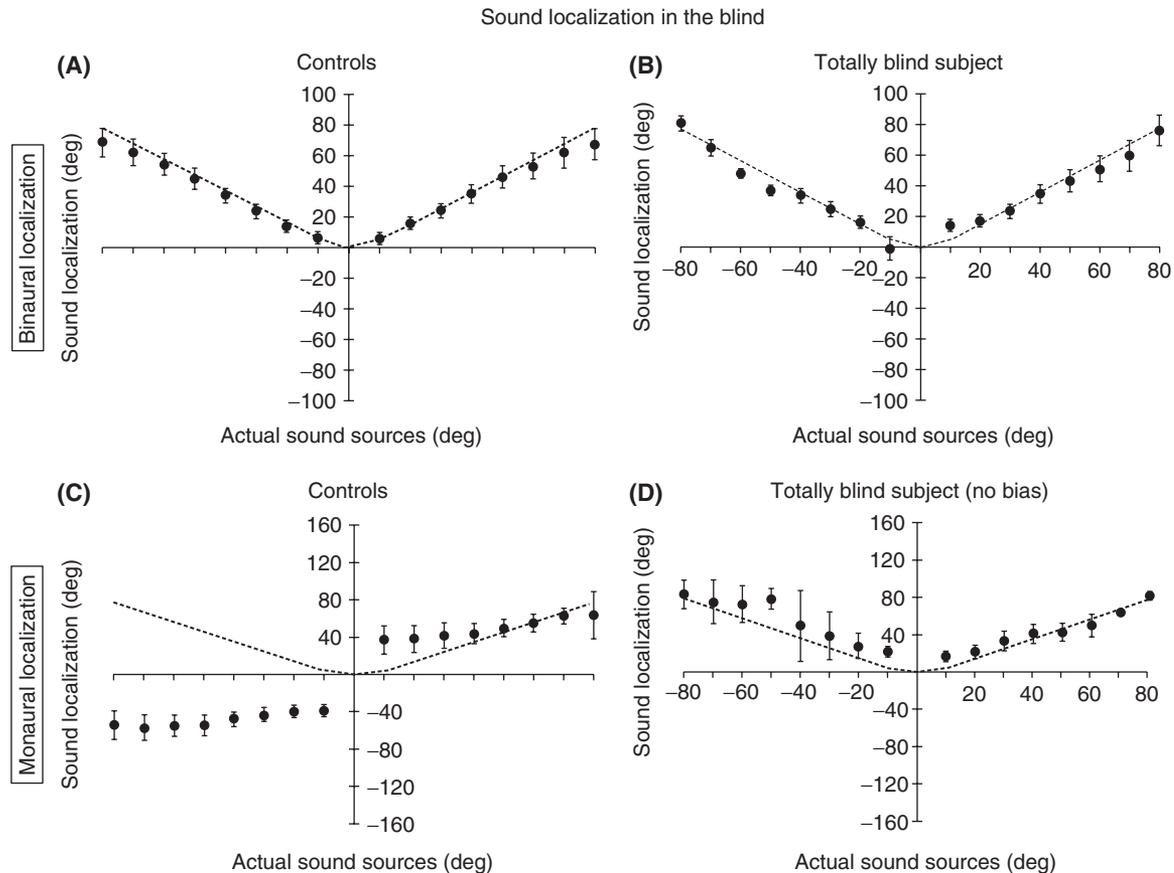


FIGURE 1 | Sound localization performances: (A) Sighted control subjects in the binaural condition of listening; (B) one representative totally blind subject in the binaural condition of listening; (C) sighted control subjects in the monaural condition of listening; (D) one totally blind subject who correctly localized the sound with no directional bias. The *dashed lines* indicate the actual sound sources locations, whereas the black dots refer to the perceived target locations with their respective standard deviations. (Adapted with permission from Ref 33. Copyright 1985 Nature Publishing Group).

mapped their auditory distant space, but actually outperformed their sighted counterparts under specific conditions.³⁹ Moreover, we also showed blind individuals to be more accurate in evaluating the distance of presented sounds.³⁹ The conclusion that seems to emerge from these studies is that it is essentially when tasks are difficult (i.e. the sighted subjects are not performing at near perfect levels) that blind individuals are able to show superior abilities.

Indeed, several studies have shown that differences between both groups are generally not found for basic sensory threshold paradigms such as loudness discrimination,⁴⁰ auditory temporal acuity,⁴¹ and white noise detection.⁴² One noteworthy exception is the fact that there is an impressively higher proportion of blind musicians who possess absolute pitch compared to sighted musicians.⁴³ Generally, differences rather seem to emerge when higher-order functions are involved, such as speech perception,^{24,25,44,45} voice recognition,⁴⁶ auditory attention,⁴⁷ bimodal divided attention,^{48,49} auditory

memory,⁵⁰ verbal memory,^{51–53} temporal order judgment, auditory perceptual consolidation,⁵⁴ and complex pitch discriminations.⁵⁵

The tactile modality has also been quite extensively studied in blind individuals and is especially interesting given its importance in Braille reading. While earlier reports lead to conflicting results,^{1,56,57} more recent ones are unfortunately not much more conclusive. Although Grant and collaborators⁵⁸ showed blind persons to have lower thresholds for the discrimination of Braille-like stimuli, this effect disappeared after additional training sessions, suggesting that the initial result was rather the consequence of familiarity and practice than that of heightened acuity. No effect of blindness was found, moreover, when using a two-point discrimination task.⁵⁹ However, many have critiqued the use of the two-point threshold paradigm as an accurate measure of tactile spatial resolution (see Craig and Johnson^{60,61}), and have rather suggested the use of an alternative method consisting

of sensitivity to grating orientations.⁶² In essence, subjects have to discern the orientation of grooved surfaces pressed against a fingertip. Even with this new method, inconsistent results have been obtained, with some finding superior acuity in the blind^{63–65} whereas others did not.^{58,66} Several methodological differences could account for these inconsistencies, such as type of stimulation (active or passive) and improper matching of sex and age with the sighted control group. In fact, when age and sex are properly controlled, the difference between blind individuals and sighted ones is quite impressive: the average blind subject had the acuity of an average sighted person of the same gender but 23 years younger.⁶³ Moreover, the tactile thresholds are not correlated with the age of onset of blindness or with the level of Braille expertise.⁶³ This strongly suggests that the heightened acuity is a direct consequence of the loss of sight irrespective of the onset and quantity of tactile activity. Unfortunately, we were not able to replicate the latter finding.⁶⁶ Although on average our blind subjects had lower discrimination thresholds than the sighted, the difference failed to reach statistical significance. This may be the result of having a slightly younger control group than our blind group because performance on grating discrimination rapidly decreases with age.⁶³ Grating perception is presumed to rely only on slowly adapting receptors in the skin. We also examined this problem using different types of stimuli that allowed us to assess more rapidly adapting receptors in the blind. In doing so, we compared the performance of blind and sighted individuals in a texture discrimination task and a vibrotactile discrimination task and found no difference between groups in either task.⁶⁶ However, when subjects were asked to actively explore two-dimensional (2-D) angles with their index finger, we showed that blind persons were significantly more accurate than sighted ones in discriminating between pairs of angles with slight angular differences (see Figure 2), suggesting that the blind may have heightened abilities in processing haptic inputs.⁶⁷

Taken together, the aforementioned results suggest that adaptive mechanisms are at play in blind people which allow them to use their remaining senses in a more efficient, and sometimes supranormal, manner. However, the exact cerebral mechanisms responsible for such crossmodal compensation remained somewhat elusive until the advent of new technology enabling researchers to evaluate brain function *in vivo*. Indeed the rapid development of neuroimaging tools over the past few decades has allowed us to probe the brain's functioning and anatomy in a noninvasive manner. As a whole, the results clearly indicate that the normally 'visual' occipital cortex does not become

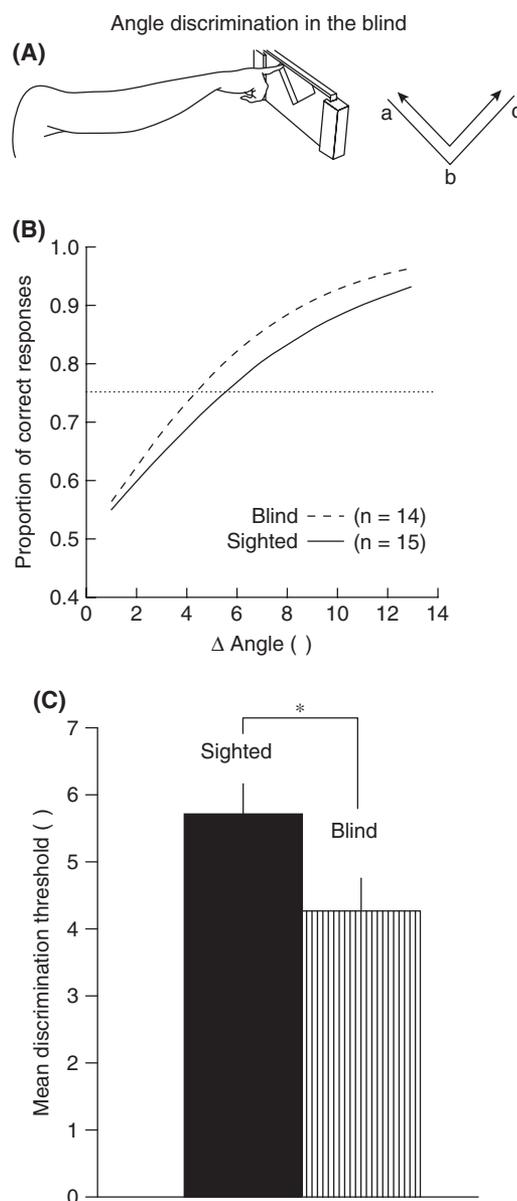


FIGURE 2 | Angle discrimination in the blind. (A) Position of the arm of the subject during haptic discrimination, relative to the angles (90° angle shown here). Angles were explored with the arm outstretched using the distal phalanx of the index finger for exploration. A single continuous to and fro movement was used to explore the angles, following the sequence *abcba* (digit shown in the start position *a* here). (B) Comparison of the performance of blind ($n = 14$) and sighted subjects ($n = 15$) in the 2-D angle discrimination task. Logistic functions fitted to the pooled data are shown here, with proportion of correct responses versus Δ angle. (C) Mean discrimination threshold (\pm SEM) in sighted (black) and blind subjects (striped). (Adapted with permission from Ref 67. Copyright 2008 Springer).

dormant and inoperative, but is rather functionally engaged by stimuli not restricted to the original default modality (see Pascual-Leone et al.,⁶⁸). This will be discussed more thoroughly in the following section.

THE PLASTIC—OR MULTIMODAL—OCCIPITAL CORTEX

The recent advent of brain imaging tools gave rise to the first studies investigating brain function in the blind. The first published results revealed elevated resting metabolism levels in the occipital cortex of the blind, compared to the sighted,^{69,70} thus raising questions about the functionality of their visual cortex. Subsequently, Uhl and collaborators^{71,72} were among the first to show task-related activations via tactile stimulation in the occipital cortex of blind individuals. By, numerous neuroimaging studies evaluating Braille^{73–79} and non-Braille^{73,74,80,81}; touch were shown to elicit occipital responses in blind individuals in a task-dependent manner. Although in some experiments it might be difficult to dissociate activations as a result of blindness-induced reorganization and those that are occasionally observed in sighted individuals,^{82,83} it is clear that there are differences in the activation patterns between these groups (see Sathian et al.,⁸⁴ for a review). These data indicate that blindness does indeed alter the already existing processing of tactile stimuli in the occipital cortex.

Similar task-related activations have been observed in the auditory modality as well. Event-related potentials (ERPs) studies showed posterior shifts in the cortical responses to various auditory stimuli.^{38,49,85,86} Similarly, we found a posterior shift of the scalp recordings during monaural sound localization in the same blind individuals from the Lessard et al.³³ study who showed significantly better abilities than the sighted individuals.³⁶ Brain imaging techniques tracking blood flow have also found significant occipital activations in blind individuals during sound localization tasks (binaural⁸⁷; monaural³⁵).

Perhaps more surprising was the presence of activation in the occipital cortex, normally driven by low-level inputs, by higher-order cognitive tasks. Amedi and collaborators⁵³ showed that an auditory verbal memory task evoked significant occipital responses. Several other studies have recently published results showing occipital activation in a variety of memory and language-related tasks such as verb generation and semantic processing,^{88–90} and episodic memory retrieval.⁹¹ Büchel⁹² proposed that the normal hierarchy observed in the occipital cortex of sighted individuals is most likely not set in stone, and that in the blind the occipital cortex becomes a higher-tier area, likely able to participate in more demanding cognitive processes.

But what do these occipital activations mean? Are they truly task-related or simply an epiphenomenon related to the absence of visual input? Several indications now seem to indicate that the former is in fact true. Essentially, these were achieved through three different avenues: (1) correlations between activity and performance, (2) virtual lesion studies with transcranial magnetic stimulation (TMS) or neuropsychological assessments of actually lesioned patients, and (3) the demonstration of functional correspondence between occipital recruitment in sighted and blind subjects. Indeed, the visual cortex has been shown to be functionally engaged in nonvisual processing through correlations between level of occipital activity and behavioral performance under numerous conditions including verbal memory,⁵³ episodic retrieval,⁹¹ and semantic/syntactic processing.⁹² We also recently showed a similar relationship between occipital activation of blind participants and their performance in a monaural sound localization task,³⁵ with the activity in the right dorsal extrastriate cortex explaining nearly 60% of the performance variance (see Figure 3). Similarly, Stevens et al.⁹³ showed that preparatory activity in the occipital cortex of blind individuals in response to an attention cue predicted performance in an auditory discrimination task.

An additional tool to assess the functional role of the occipital cortex in nonvisual processing in the blind is the use of repetitive TMS (rTMS) to cause temporary and reversible virtual lesions. Using this method, we showed that disrupting the occipital cortex of blind individuals significantly impaired their ability to monaurally localize sounds, while having no effect on the performance of sighted subjects, further confirming its functionally relevant recruitment during nonvisual events.⁹⁴ Similar protocols by other groups also showed that magnetic stimulation of the occipital cortex of blind individuals significantly increases error rates in verbal memory⁹⁵ and Braille identification tasks.⁹⁶ Perhaps one of the more spectacular forms of evidence comes from a blind expert Braille reader, who completely lost her ability following an ischemic stroke which caused bilateral lesions to her occipital cortex.⁹⁷ Finally, there are several lines of evidence showing that specialized visual areas (e.g. face processing and motion processing) process equivalent auditory stimuli in the blind, suggesting that the occipital cortex may conserve its basic functional properties.^{98,99}

Given this general consensus that the occipital cortex is functionally recruited by a substantial amount of nonvisual stimuli and tasks, several questions remain unanswered regarding this recruitment. Among the first to come to mind are how, where,

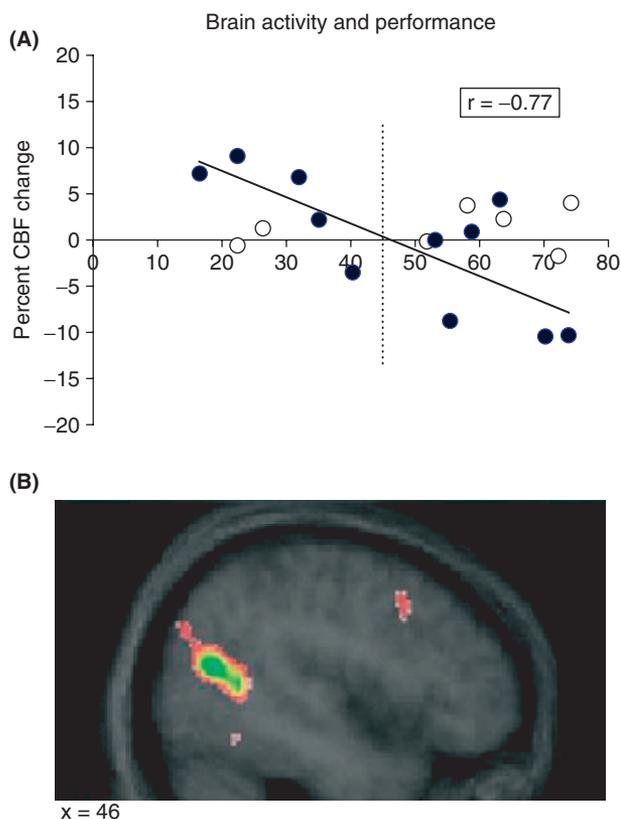


FIGURE 3 | Correlation of brain activity with performance. (A) The scattergram shows the individual values extracted for performance in the monaural localization task and CBF values in dorsal extrastriate cortex (closed circles indicate blind subjects; open circles indicate sighted ones). (B) An illustration of the statistical parametric map of the correlation with one of its maximal points (two other occipital foci were found but are not shown here). X coordinate is in standardized stereotaxic space. (Adapted with permission from Ref 35. Copyright 2009 PLoS Biology).

and when does this recruitment take place. More specifically, how is the occipital cortex recruited by nonvisual stimulations, where does the information travel to get there, and is there a critical period for this adaptation to take place? The following sections will attempt to address these questions.

Occipital Recruitment—The How

An important question raised by the issue of crossmodal reorganization is how the visual cortex processes the nonvisual information it receives. Does it code information the same way as for visual inputs? Are the functional properties of the occipital cortex preserved in the processing of nonvisual information? For instance, it is well known that the visual cortex is organized topographically, following a retinotopic organization.¹⁰⁰ Does such a relation exist between the other modalities and the spatial coordinates of

the outside world within the occipital cortex? Or, to the contrary, would the occipital cortex process auditory information as it is processed in the auditory cortex, following a tonotopic topography.¹⁰¹ Early indications would rather suggest that the initial properties of the occipital cortex are preserved when processing other modalities in blindness. For instance, moving auditory stimuli⁹⁹ and tactile flow stimuli¹⁰² have been shown to activate visual motion areas in the blind. Similarly, we have recently shown that voice stimuli, which are for some the auditory analogue of face stimuli,¹⁰³ not only activate voice-sensitive areas but also activate the face fusiform area in the blind.¹⁰⁴ Also, current data support the conservation of the dual-stream organization of the occipital cortex, containing the ‘where’ dorsal pathway and the ‘what’ ventral pathway.¹⁰⁵ Functional imaging of sound localization in the blind, clearly a ‘where’ task, has shown activations primarily in the dorsal portion of the occipital cortex.^{35,87} Moreover, rTMS over dorsal occipital cortex interfered with the performance of blind individuals during sound localization but not during pitch or intensity discriminations.⁹⁴ The latter rely more on ventral occipital processing in the blind.^{47,106} Similarly, nonspatial, object-related, task-specific activations typically engage more ventral regions of the occipital cortex^{73,76,81}. Although these data do not provide a clear double dissociation, they do hint toward a preserved dual-stream organization of the occipital cortex.

Occipital Recruitment—The Where

How does the nonvisual information make its way to the occipital cortex? Two obvious answers are either via already existing connections or through the establishment of new connections not present in sighted individuals. The former could result from the unmasking/strengthening of latent preexisting pathways between sensory-specific cortices and between multisensory areas and the occipital cortex.

There are several pathway(s) via which the nonvisual information could travel to reach the occipital areas of the brain, many of which mediate multisensory interactions involving vision. One possible mechanism that could account for these changes would be a reorganization of subcortical structures (such as the colliculi) that contain representations of different modalities in a small neural space, which would then redirect nonvisual input toward occipital areas. Similarly, plasticity at the thalamic level could account for the occipital recruitment by nonvisual stimulations. However, several recent anatomical studies using diffusion tensor tractography methods and voxel-based morphometry provide evidence against the use

of visual thalamo-cortical paths in the crossmodal processing by revealing atrophied optic radiations in the blind.^{107–111} However, one must keep in mind that atrophy does not necessarily imply a total absence of use. For instance, studies with blind animals have shown connections between the inferior colliculus (an important auditory relay) and the lateral geniculate nucleus (LGN—an important visual relay),^{112,113} suggesting that auditory information may still reach the occipital cortex via the optic radiations ascending from the LGN. However, this step could be bypassed via connections between the median geniculate nucleus (MGN—an important auditory relay) and the occipital cortex or between the inferior colliculus and the occipital cortex.¹¹⁴ Karlen and collaborators¹¹⁵ have in fact shown that the occipital cortex of congenitally blind opossums receives projections from the somatosensory (ventral posterior nucleus of the thalamus), auditory (MGN), and motor systems (dorsal and ventral anterior nucleus of the thalamus). Moreover, the primary visual area (Brodmann area 17) was shown to receive projections from the primary somatosensory and auditory cortices, consistent with previous findings suggesting that cortico-cortical connections could mediate crossmodal plasticity in blind individuals.^{116–118} Although it is hard to rule out any of the abovementioned potential pathways, the front-runner currently appears to be cortico-cortical projections in enabling nonvisual input to be processed in the visual cortices. Indeed, a recent TMS study brought forth evidence that strongly suggests increased connectivity between the parietal and occipital cortices,¹¹⁹ perhaps via already existing pathways.¹¹⁸

Perhaps these connections are already used in normal sighted individuals in multisensory interaction and integration. It is also likely that multiple different pathways are used to convey the information to the more posterior regions of the brain, given the large variety of different inputs that can activate the visual areas, ranging from sound localization to language processing and from tactile discriminations to episodic memory retrieval. Consequently, several of the aforementioned pathways are likely to be concomitantly functional to allow such versatile processing in the occipital cortex.

Occipital Recruitment—The When

When do these changes take place? Or perhaps even more importantly, is there a limited time window in which these plastic changes can occur? Indeed one matter of debate surrounding the concept of plasticity is the notion of a critical period. Until this point, the present paper has focused exclusively on early blind

individuals. Such individuals were either born blind or lost the use of their sight within the first few years of life. In contrast, individuals referred to as being late-blind have generally benefited from vision for a substantial amount of time and lost their sight in their late teens or early adulthood.

There is a general agreement that the extent of reorganization depends upon the timing of the onset of blindness. Accordingly, puberty has been found to be an important milestone for visual cortex reorganization, as illustrated by early positron emission tomography (PET) studies demonstrating elevated glucose metabolism in the visual cortex of early onset blind individuals, but decreased levels (with respect to sighted individuals) in late-onset blind ones.⁷⁰ More recent studies have also shown a strict critical period for plasticity of the occipital cortex (14 years of age: Cohen et al.⁷⁸; 16 years of age: Sadato et al.⁷⁵) after which no reorganization was observed if the onset of blindness occurred beyond this period. However, a number of other studies have demonstrated that restructuring might in fact occur in the mature brain. One, involving PET imaging, revealed activation of visual cortex, albeit manifesting somewhat different patterns, during Braille reading and auditory word processing in both early and late-blind subjects.⁷⁶ Similarly, ERP studies have shown activation in posterior brain regions during sound-change detection in both early and late-blind subjects.⁸⁶ Furthermore, Burton and collaborators have observed occipital activations in late-onset blind individuals on numerous tactile and auditory tasks.^{77,80,81,88,120,121}

Having previously shown that late-blind individuals could show similar exceptional abilities as the early blind in several sound localization tasks,³⁹ we asked whether or not they would show similar activation patterns as well. Although the late-blind did recruit occipital regions,^{39,122} it was not accompanied by improved performance in the monaural sound localization task. This is perhaps because despite the fact the late-blind showed crossmodal recruitment, it was not as extensive as was observed in the early blind, as evidenced by a significant correlation between the age of onset of blindness and occipital activity (see Figure 4A). Surprisingly, the late-blind also recruited regions in the ventral visual pathway that correlated negatively with their performance, suggesting not only that not all crossmodal recruitment is beneficial, but that it may also on occasion be detrimental to the task (see Figure 4B).

Fieger and colleagues¹²³ also showed that late-blind individuals can excel in an auditory spatial task, just as did their early blind counterparts using the

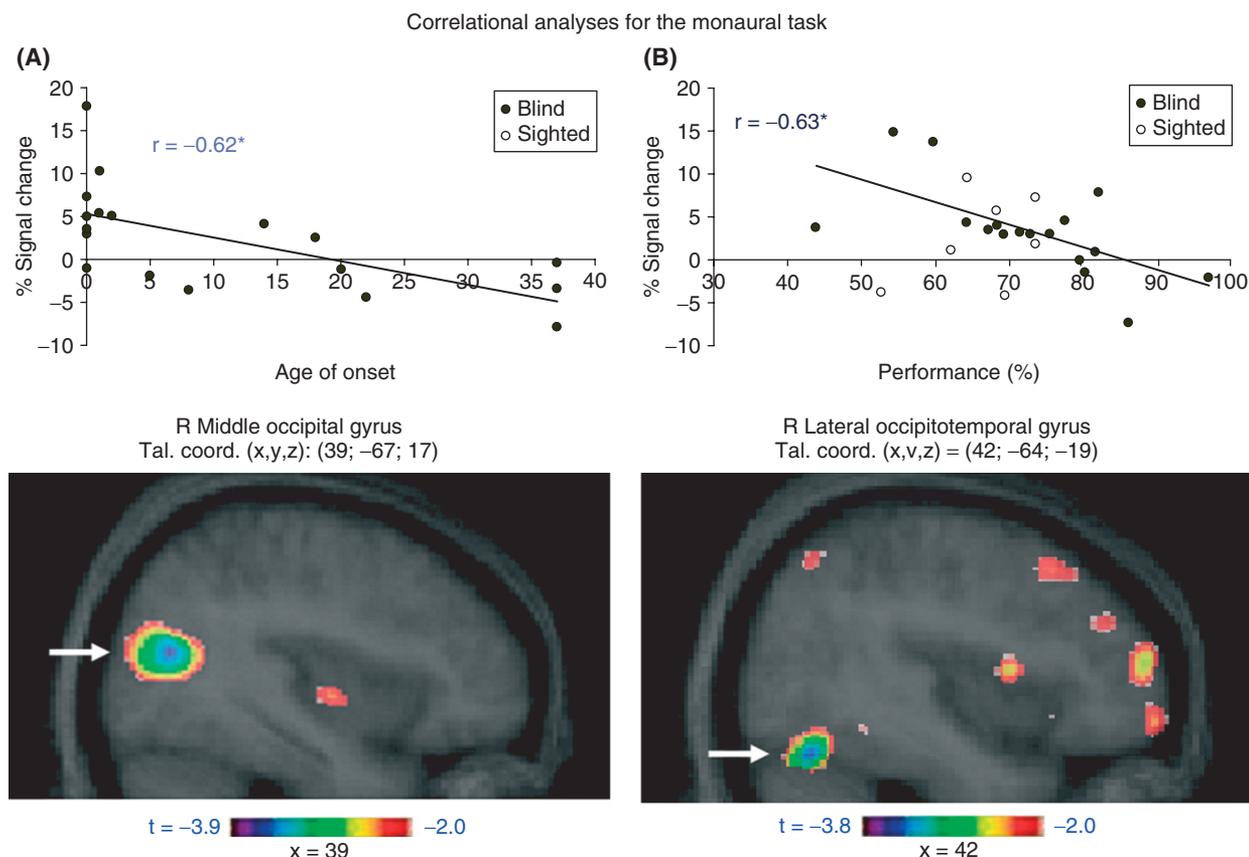


FIGURE 4 | Correlational analyses for the monaural task. In the left panel (A) are shown the scattergram plotting CBF change against age of onset of blindness (top) and the statistical parametric map of the correlation with a maximal point in the right extrastriate cortex (bottom). The negative relationship between the two variables indicates that the earlier a blind person loses his/her sight, the more the occipital is recruited by the task. Similarly, in the right panel (B) are shown the scattergram plotting CBF change against performance (top) and the statistical parametric map of the correlation with a maximal point in the right lateral occipito-temporal cortex (bottom). The negative relationship between the variables implies the less this region is recruited, the better the performance of the blind person. (Adapted with permission from Ref 122. Copyright 2006 MIT Press).

same protocol.³⁸ They showed however, using ERPs, that the late- and early blind achieved their respective performances via different mechanisms: whereas congenitally blind persons demonstrated a more sharply tuned early attentional filtering, manifested in the N1 component, late-blind individuals benefited from a later processing stage of target discrimination and recognition, indexed by the P3. This result supports the notion that adult crossmodal plasticity may be supported by different mechanisms than for individuals who lost their sight during childhood.

Despite the mixed evidence for cortical plasticity in the late blind, few studies actually evaluated these plastic changes with regards to their functional relevance to specific tasks. Using TMS, Cohen et al.⁷⁸ showed that stimulating the occipital cortex only affected the performance of the early—and not the late—blind during Braille reading, thus strongly suggesting the absence of any functional role of the

occipital cortex for Braille reading in the late blind. This was not so surprising, however, given the fact that no occipital activity was observed in their late-blind subjects with PET.⁷⁸ Goyal and collaborators,⁹⁸ on the other hand, showed that tactile exploration of faces activated the fusiform face area in late-blind subjects, and that moving objects on their skin activated the MT/V5 region, suggesting a functional role in the activations, given the parallels between the tasks and the visual equivalents known to activate these regions.

A strong argument supporting the existence of adult crossmodal plasticity can be seen when blindfolding sighted subjects for short periods of time. Studies have shown that sighted subjects not only recruit occipital cortices while performing tactile tasks after a short period of visual deprivation,^{124–126} but also show enhanced perceptual acuity.^{127–129}

Furthermore, Boroojerdi et al.¹³⁰ showed that short-term visual deprivation (ranging from a few minutes to a few hours) can induce changes in the visual cortex excitability (as measured by the minimum intensity of stimulation required to elicit phosphenes). Pitskel et al.¹³¹ followed up by showing that this change in excitability quickly reverses and returns to baseline levels following as little as 2 h of light exposure, suggesting that plastic changes occurring in the adult brain might be limited to the period of deprivation and be reversible.

Knowing whether changes are reversible is crucial to the development of neuroprostheses designed to restore vision in blind individuals. Although significant progress has been made toward achieving such a goal, future research is extremely dependent on our understanding of how blindness affects the brain. Knowing how the optic tracts and radiations are atrophied in the early blind^{107–111} raises serious questions about the integrity of these visual pathways and whether or not they could convey electrical information stemming from retinal, subretinal, or epiretinal implants (see Merabet et al.,¹³²). Such implants would be connected to a digital camera and signal processor mounted on a pair of glasses that would convert patterns of light into electrical signals.

There are reasons to believe however that such devices might still work with late-blind individuals. Pan and colleagues¹⁰⁸ showed that white matter (WM) loss in the optic tract and radiation of early blind individuals was modulated by the age of onset of blindness, suggesting that a later onset would have less of an adverse effect on the anatomical integrity of the pathways. Moreover, Schoth et al.,¹³³ found no evidence of WM loss in either the visual cortex or in the visual tracts between late-blind (with a mean age of onset of blindness of 12) and sighted subjects, suggesting that the visual pathways may still be able to communicate signals to the occipital cortex.

Since the literature clearly shows that occipital cortex of the blind is now responsive to auditory and tactile sensations, would direct or indirect electrical stimulation of the occipital cortex of blind individuals elicit visual sensations? Gothe and colleagues¹³⁴ have shown a dramatic reduction in the visual properties of the occipital cortex of the blind (as assessed by the capacity to produce phosphenes with TMS). Moreover, regardless of all the theoretical uncertainties, there still are numerous technical challenges that need to be resolved to achieve a clinically viable visual prosthesis.^{132,135} But in the meantime, we can perhaps turn our attention to the research done with deaf individuals. Technological advances in restoring hearing in profoundly deaf individuals have achieved

a fair deal of success in the past few years with the development of sophisticated cochlear implants (CI). Such progress has allowed researchers to ascertain the consequences of crossmodal plasticity in the deaf population on the success rate of CIs. The following sections will take a closer look at the crossmodal plasticity of the auditory cortex and how it impacts our ability to restore hearing in deaf individuals.

DEAFNESS: CROSSMODAL PLASTICITY AND COMPENSATION

As with blind individuals, deaf people must rely more heavily on their remaining senses to carry out their everyday activities. Although to many they may seem less handicapped than blind people, the input received from the outside world is essentially limited to the binocular visual field, whereas precious information obtained from the auditory system can capture percepts from all directions in space covering 360° along any axis. Given this loss of information, do deaf individuals also compensate for their deficit via heightened perceptual abilities? One of the first questions to come to mind is probably whether or not deaf individuals 'see better' than normal hearing individuals. The answer is not straightforward as there are several discrepancies in the literature, with some indicating improved visual abilities and others worse. One of the reasons underlying these differences is the disparity in the composition of the deaf groups used in the different studies. In fact, Bavelier and coauthors¹³⁶ note that most studies reporting visual deficits include deaf subjects with heterogeneous backgrounds, whereas those reporting enhanced abilities contain much more homogenous groups of deaf subjects. The latter set of groups is often composed of *deaf native signers*, a subsample of the deaf population known to not suffer from comorbidity confounds related to language and communication deficits often associated with deafness.¹³⁷

The improvements observed in deaf native signers are however not generalized and widespread, but rather are limited to specific areas of visual cognition. Similar to the blind, basic sensory thresholds do not appear to be enhanced in the unaffected modality. In fact, deaf and hearing subjects have been shown to be comparable for contrast sensitivity,¹³⁸ motion velocity,¹³⁹ motion sensitivity,¹⁴⁰ brightness discrimination,¹⁴¹ temporal discrimination,¹⁴² and temporal resolution.^{143,144} Enhanced visual skills have rather been limited to more complex tasks, where visual attention and/or processing of the peripheral visual field are manipulated. Neville and Lawson¹⁴⁵ showed that deaf individuals were more accurate and

faster than hearing subjects for the detection of motion of attended peripheral targets. Similarly, Loke and Song¹⁴⁶ showed that the deaf were faster and more accurate at detecting the onset of a peripheral target. Deaf individuals were also reported to be better at detecting moving lights presented in the periphery, and not when presented foveally.¹⁴⁷ Additional evidence of enhanced processing of peripheral stimuli stems from several studies showing that peripheral distractors disrupt the processing of centrally presented targets significantly more in the deaf than in the hearing.^{148–150} Electrophysiological recordings have also supported the notion of improvements being related to attentional mechanisms. The faster and more accurate performance of deaf individuals in the detection of the direction of motion of attended stimuli was coupled with an increased N1 component, which is often associated to a modulation of visual attention.¹⁴⁵ In addition, these N1 enhancements have been shown to be more pronounced for peripheral than central stimuli on several occasions.^{145,151,152}

The aforementioned results suggest two primary hypotheses. The first suggests simply that deafness leads to better peripheral vision, possibly through expansion of the cortical areas of the peripheral visual field. The second states that deafness leads rather to the reallocation of attention toward the peripheral visual field given the absence of audition to orient to their extrapersonal space. Although neither of these hypotheses has received more support than the other, it is important to keep in mind that they might not be mutually exclusive, perhaps explaining the lack of a front-runner.

As in the study of blind individuals, the perceptual changes in visual function in the deaf have led many to search for any associated neuronal changes. Several studies have focused their attention on the middle temporal (MT) and middle superior temporal (MST) areas known to be not only involved in visual motion processing, but also heavily modulated by attentional processes. Consistent with the behavioral data, neuroimaging has revealed that differences in MT/MST between deaf and hearing individuals in response to motion stimuli only emerge when they are attended to in the peripheral field.^{153,154} However, given the substantial role of motion in sign language, one can wonder if this difference could be due to the acquisition of this visuospatial language rather than to auditory deprivation *per se*. Bavelier and collaborators¹⁵³ attempted to address this issue by including a third group in their study, one composed of hearing native signers, and this yielded several interesting results. For instance, being a signer only affects the lateralization of MT/MST activation, with

a leftward bias, as compared to non-signers, probably reflecting a shift of motion processing toward the language dominant hemisphere. Early deafness however, and not early exposure to sign language, was responsible for an increase of MT/MST activation under peripheral rather than central attention (the opposite finding occurred in the two hearing groups).

Given the multimodal nature of the temporal cortex, is it also possible that the now deafferented auditory cortex becomes more responsive to non-auditory inputs compared to hearing controls? Earlier animal studies showed that this was indeed possible by demonstrating that neurons in the primary auditory cortex could reorganize themselves to process visual information in the absence of auditory input.^{155,156} More recently, several groups have shown BOLD changes in the auditory cortex of deaf individuals in response to visual motion.^{157–160} We have also recently investigated the deafferented temporal cortex sensitivity to visual motion. We recorded BOLD signal changes in both deaf and hearing individuals using global motion and forms defined by motion stimuli previously validated in healthy hearing individuals.¹⁶¹ Our preliminary results with deaf individuals are consistent with the current literature and show the involvement of higher-order auditory areas in the processing of the stimuli, most notably the right supratemporal gyrus.¹⁶²

Similarly, several other groups have shown recruitment of the auditory cortex by visually presented sign language in deaf subjects.^{163,164} Importantly, it was also shown that this crossmodal recruitment is not a by-product of signing, but rather of being auditorily deafferented.¹⁵⁴ What remains unclear is whether the activation patterns actually reflect linguistic or visual processing when observing sign language. Again, these are not mutually exclusive, especially because several studies have shown that the visual cortex of blind individuals appears to be involved in semantic processing.^{88–90}

Anatomical support for visual processing in the auditory cortex comes from animal studies showing direct connections between both primary cortices.^{117,118} Unfortunately, the literature on the anatomical integrity of WM pathways in deaf humans is currently lacking, as DTI and tractography studies are lacking. One study did however report an absence of morphometric differences of the corpus callosum between deaf and hearing individuals.¹⁶⁵ Other anatomical findings have focused on the auditory cortex and the superior temporal gyrus, where morphometry studies have shown a reduction in WM in deaf individuals compared to hearing.^{166,167} While finding no differences within the auditory cortices,

Penhune and colleagues¹⁶⁸ did reveal an increase in gray matter (GM) density within the left motor hand area, possibly related to more active use of the dominant hand in signed languages.

The notion of the age of onset is at least equally lacking in the literature on deafness. The studies on blind individuals have clearly shown how the age of acquisition of blindness modulates and determines the type and amount of crossmodal plasticity available to them. Only one study, to our knowledge, specifically attempted to address this important research query.¹⁶⁰ Both groups showed similar activation of the planum temporale, but differed with respect to the activation in the middle superior temporal sulcus (STS), which was more prominent in the early deaf. With the middle STS corresponding to the main voice-sensitive area, the authors argued that exposure to voices had hindered the region's ability to ultimately process sign language.

Finally, it is also worth noting that the auditory cortex of deaf individuals is differentially modulated not only by visual stimuli, but also by tactile ones. Although such somatosensory-sensitive auditory regions are known to exist in the hearing,^{169,170} it was recently shown that vibrotactile stimulation elicited higher and more widespread activity in the auditory cortices of deaf compared to hearing individuals.¹⁷¹ This crossmodal benefit might underlie the previously observed enhanced sensitivity to vibrotactile stimuli in congenitally deaf persons.¹⁷²

THE CI: CROSSMODAL PLASTICITY AS AN INDICATOR FOR POTENTIAL RECOVERY

The relevance of crossmodal plasticity for the implementation of neuroprosthetic devices was elaborated earlier in relation to blind individuals. Importantly, the same rationale applies to deaf individuals as well. Once responsive to a new input modality, can the auditory cortices respond to their original auditory input? This question bears special importance given that profound deafness can sometimes be reversed by auditory stimulation via a CI.¹⁷³ Put simply, the device replaces normal cochlear function by converting auditory signals into electrical impulses delivered to the auditory nerve (see Mens,¹⁷⁴). The purpose here, however, is not to explore the efficacy of the CI and how performances on auditory and audiovisual tasks are comparable to those of normally hearing individuals (see Fallon et al.,¹⁷⁵ for a review), but rather to demonstrate how early experience and the brain's plastic nature can alter the success rate of the prosthesis.

Studies have shown the existence of a critical period that cannot be exceeded for recovery of auditory functions following deprivation.^{176,177} This time window is generally limited to the first few years of life, with the chances of recovery rapidly decreasing afterward. Several studies have shown that if implanted before the age of 2, initially deaf children can acquire spoken language in a comparable time frame to normal hearing children.^{178,179}

Although it was initially thought that the duration of auditory deprivation should account for most of the variance of the implantation outcome, several studies clearly show that other factors modulate it.^{180–182} In fact, in a retrospective case review, Green et al.¹⁸³ showed that duration of deprivation accounted for only 9% of the variability in implant outcome, which is substantially less than first thought. An alternate predictor can be found in preoperative measures of cerebral metabolism. For instance, Lee et al.¹⁸⁴ found that the temporal cortex becomes hypometabolic following auditory deprivation. Moreover, the level of hypometabolism is inversely correlated to the duration of deafness and positively correlated to speech comprehension scores obtained postimplantation. In other words, the longer a person has been deaf, the less likely it is that their temporal cortex will be hypometabolic and the more likely their speech perception capacity will be compromised. Given that the amount of temporal hypometabolism mostly reflects age-related changes, the results confirmed that there is still considerable variability between individuals with similar deprivation durations, suggesting that other processes may be at play, such as the level of crossmodal reorganization of the auditory cortex (see Giraud and Lee,¹⁸⁵). In follow-up studies, it was shown that speech perception performance was positively associated with preoperative activity in fronto-parietal networks and negatively associated with activity in occipito-temporal networks,¹⁸⁶ even when factoring out the confounding effect of age of implantation.¹⁸⁷ Indeed the hindering effect of preoperative activity in occipito-temporal areas might be a sign that auditory areas may have been taken over by the visual modality, suggesting that crossmodal recruitment can serve as a predictor of the outcome of implantation.

To examine this issue, we recently compared evoked potentials involved in the processing of visual stimuli between implanted (at least 1 year postoperative) and hearing subjects.¹⁸⁸ We also examined the speech perception of the implanted subjects and subsequently divided them into two groups based on their performance. The results showed that implanted individuals with broader and more anterior scalp

distributions (i.e. showing signs of visual processing in the temporal cortices) in response to visual stimuli were those who performed more poorly in the speech perception task and vice-versa (see Figure 5). Similarly, Green and collaborators¹⁸⁹ showed that speech perception was positively correlated with auditory cortex activation, which in turn was negatively correlated with duration of deafness. Taken together, these studies point to useful tools that can be used to assess the potential of success for implantation on an individual basis and show the importance and influence of prior experience in the successful outcome of implantation in deaf individuals.

Given the possibility that visual input might hinder hearing in CI users, one may wonder how the two modalities would interact during multisensory perception, especially in nonproficient CI users. Recent evidence suggests that they are able to properly integrate congruent audiovisual stimuli.^{190,191} Multisensory perception in children with a CI is visually dominated when presented with tasks eliciting the McGurk effect, where incongruent lip movements can induce the misperception of spoken syllables.^{192,193} However, the ability to segregate conflicting auditory and visual inputs had not been properly ascertained in this population. Consequently, along with collaborators at our lab, we designed a study aiming to determine the effect of visual stimulation on auditory performance in CI users.¹⁹⁴ An auditory speech recognition task was used in the presence of three different incongruent visual stimuli (color-shift, random-dot motion, and lip movement) with CI users and matched hearing controls. The results showed that the presentation of visual stimuli significantly impairs word recognition in nonproficient CI users (individuals with poor performance in the speech task without any concurrent visual presentation) while not affecting the performance of proficient CI users and normal hearing subjects. Moreover, this effect was not specific to the presence of linguistic cues (lip movement condition), but also present during the random-dot motion stimuli (see Figure 6). These findings strongly suggest adapting speech training programs on an individual basis, such that individuals with a substantial amount of crossmodal processing in their auditory cortices might benefit from different types of training than those that are more adapted to proficient CI users.

CONCLUSION

The study of sensory deficits has allowed us to better understand the nature of brain functioning and has

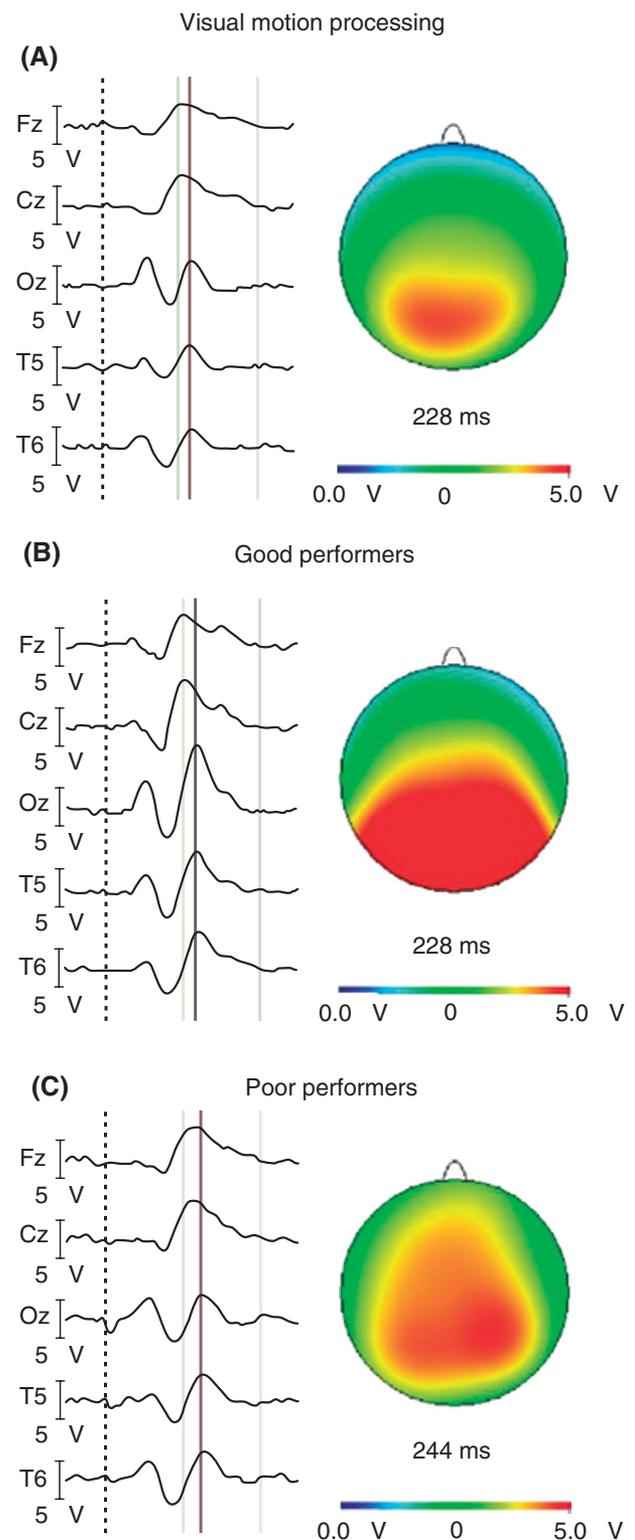


FIGURE 5 | Scalp distributions and waveforms at the maximum amplitude of the Oz P2 component in response to visual motion stimuli in controls (A), good performers (B), and poor performers (C). (Adapted with permission from Ref 188. Copyright 2006 Oxford University Press).

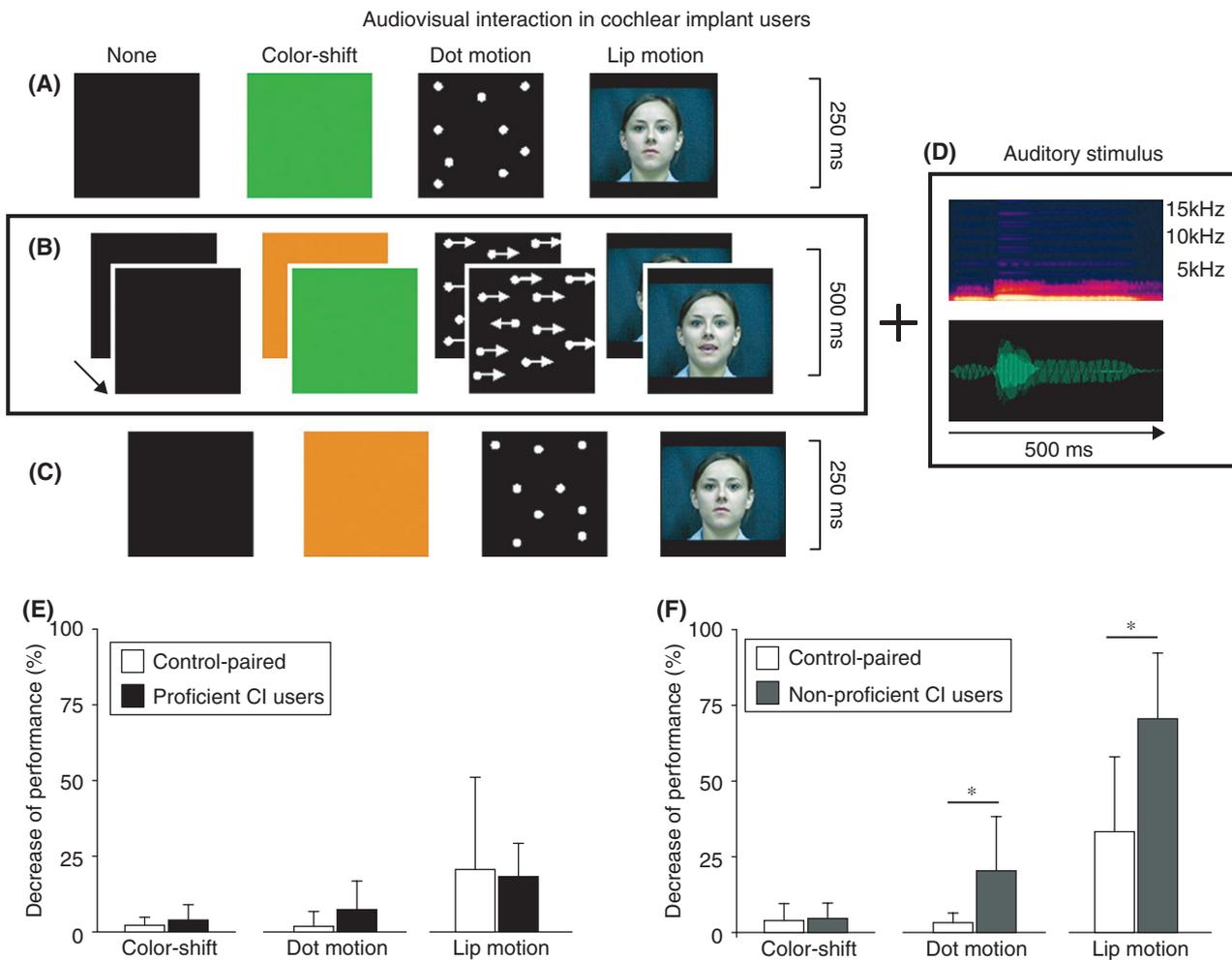


FIGURE 6 | Audiovisual interaction in CI users. In the top panel is the illustration of the experimental procedure. Each condition began (A) and ended (C) in a static neutral position. In all audiovisual conditions (B), auditory stimuli (D) were simultaneously presented with a visual stimulus change (color, movement, or video sequence). In the bottom panel are plotted the decreases in performance (%) for each audiovisual condition for both proficient (E) and nonproficient (F) CI users. (Adapted with permission from Ref 194. Copyright 2007 Elsevier).

served as a window into how the brain is wired. Although the purpose here was not to show how the brain is not as unimodally organized as once thought, the study of crossmodal plasticity in the deaf and in the blind has nonetheless revealed a lot in this respect. The cortical flexibility observed in these individuals simply seems to be a reflection of the brain's natural predisposition for multimodality; when a cortical region no longer receives its preferred input, it will

adapt in order to process its most suited successor. From a more clinical standpoint, the study of cross-modal plasticity is crucial for the development of neuroprostheses intended to restore input from the absent modality. Although much work remains to be done for the blind, a great deal of success has been achieved for the deaf with the CI. This is obviously encouraging for the general population as the fight against deafness is proving fruitful.

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