What and How the Deaf Brain Sees

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Abstract

■ Over the past decade, there has been an unprecedented level of interest and progress into understanding visual processing in the brain of the deaf. Specifically, when the brain is deprived of input from one sensory modality (such as hearing), it often compensates with supranormal performance in one or more of the intact sensory systems (such as vision). Recent psychophysical, functional imaging, and reversible deactivation studies have converged to define the specific visual abilities that are enhanced in the deaf, as well as the cortical loci that undergo crossmodal plasticity in the deaf and are responsible for mediating these superior visual functions. Examination of these investigations reveals that central visual functions, such as object and facial discrimination, and peripheral visual functions, such as motion detection, visual localization, visuomotor synchronization, and Vernier acuity (measured in the periphery), are specifically enhanced in the deaf, compared with hearing participants. Furthermore, the cortical loci identified to mediate these functions reside in deaf auditory cortex: BA 41, BA 42, and BA 22, in addition to the rostral area, planum temporale, Te3, and temporal voice area in humans; primary auditory cortex, anterior auditory field, dorsal zone of auditory cortex, auditory field of the anterior ectosylvian sulcus, and posterior auditory field in cats; and primary auditory cortex and anterior auditory field in both ferrets and mice. Overall, the findings from these studies show that crossmodal reorganization in auditory cortex of the deaf is responsible for the superior visual abilities of the deaf. ■

INTRODUCTION

The loss of a sensory modality can cause an increase in the abilities of other intact sensory systems coinciding with adaptive and compensatory reorganization of neural structures to integrate functions of two or more sensory systems (Merabet & Pascual-Leone, 2010; Bavelier & Neville, 2002; Neville & Bavelier, 2002; Rauschecker, 1995). Visual crossmodal plasticity occurs following deafness, whereby the auditory system reorganizes to process visual input (Kim et al., 2016; Bavelier & Neville, 2002). This reorganization, as well as the subsequent enhancement of visual perception, is typically considered compensatory, as it can provide some substitute for the lost modality (Heimler, Weisz, & Collignon, 2014). Thus, it is important to understand what and how the deaf brain sees, as sensory perception plays a critical role in information processing underlying cognitive processes (Gilbert, 2013). This is of particular importance, because (1) deaf individuals rely to a greater extent on visual perception to encode their environment in the absence of sound information and (2) understanding the nature of visual crossmodal reorganization will inform the degree to which these changes may impede hearing restoration.

The objective of the present review is to elucidate how visual crossmodal plasticity occurs in the deaf by converging behavioral, physiological, and anatomical descriptions. Importantly, it attempts to focus on the open question of whether visual sensory abilities are enhanced in the absence of confounding cognitive influences, such as attention. This is in contrast to improvements in performance on aspects of vision that are attentionally demanding, such as when an individual cannot predict where or when the stimulus will appear or when selecting a stimulus from among distractors, which have been repeatedly shown to be enhanced in the deaf (for a review, see Pavani & Bottari, 2012; Mitchell & Maslin, 2007; Bavelier, Dye, & Hauser, 2006).

Except for a handful of studies examining crossmodal plasticity in the auditory cortex of deaf mice (Hunt, Yamoah, & Krubitzer, 2006) or ferrets (Meredith & Allman, 2012; Meredith, Keniston, & Allman, 2012), most assessments of visual enhancement following deafness have been performed in either humans or cats (for a lateral view of the auditory cortex by species, see Figure 1). It is important to consider when choosing animal models (for a review, see Butler & Lomber, 2013) that rodents and nonrodents may exhibit crossmodal plasticity distinctions, as the pattern of connections between primary sensory cortices seems to be species-specific (Meredith & Lomber, 2017).

Collectively, studies investigating visual crossmodal plasticity have done so in deaf populations with different deafness onsets (congenital, early, late or mixed), magnitudes (e.g., severe, complete, unilateral), and etiology (e.g., pre- or postnatal impairment, ototoxically induced). The age of human participants ranges from infants (Xia et al., 2017) to adults. However, although approximately
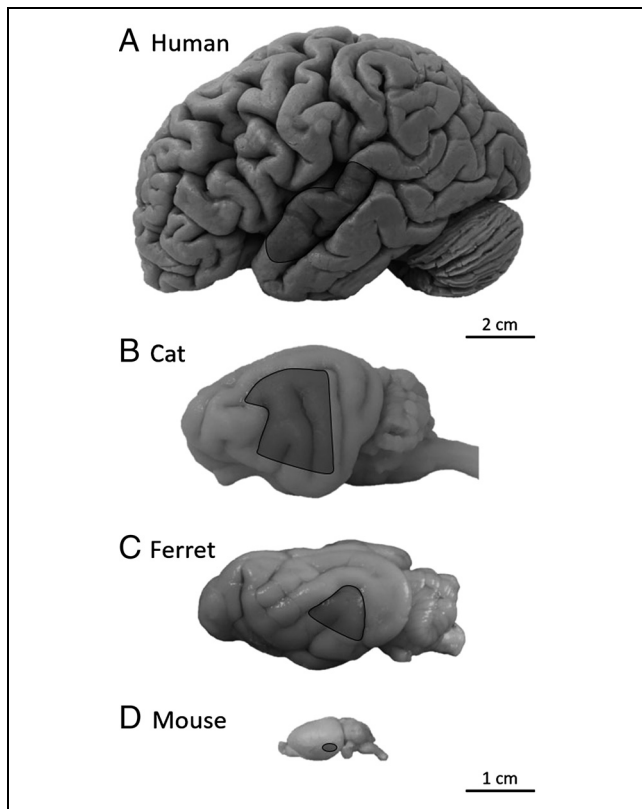
Figure 1. Shadow showing a lateral view of the left auditory cortex in (A) human, (B) cat, (C) ferret, and (D) mouse. The scale represents 2 cm for the human brain and 1 cm for the other brains.

one third of people over 65 years are affected by disabling hearing loss (World Health Organization [WHO], 2013), no study has investigated visual cross-modal plasticity following hearing loss in older adults. The studies considered in this review employed methodologies including psychophysics, neuroimaging, and electrophysiology.

IMPORTANCE OF UNDERSTANDING HEARING LOSS

Hearing loss is the most prevalent sensory disability in humans and represents one of the most common neurological disorders (WHO, 2013). There are approximately 360 million people in the world with disabling to profound hearing loss (i.e., 5.3% of the world's population), including 32 million children (WHO, 2017). Disabling hearing loss refers to hearing loss greater than 40 dB in the better hearing ear (WHO, 2013), whereas profound hearing loss or deafness refers to deficit of more than 81 dB in both ears (Morton, 1991). In addition, unaddressed hearing loss poses an annual global cost of 750 billion international dollars[1] (WHO, 2017). In addition to the staggering socioeconomic impact of deafness (Berryman et al., 2006), studies have also revealed very

interesting consequences of the neural reorganization that arises as a result of profound deafness.

WHAT VISUAL ABILITIES ARE ENHANCED IN THE DEAF?

Human Psychophysics

In 2006, Bavelier and colleagues published an examination of all the human psychophysical studies that considered the visual abilities of the deaf (Bavelier et al., 2006). This exciting meta-analysis of the literature revealed that the deaf do not have a general visual enhancement, as they were similar to those with normal hearing with regard to motion direction discrimination (Bosworth & Dobkins, 1999, 2002), motion velocity detection (Brozinsky & Bavelier, 2004), visual temporal discrimination in the central visual field (Poizner & Tallal, 1987; Mills, 1985; Bross & Sauerwein, 1980), brightness discrimination (Bross, 1979), and contrast sensitivity both in the central (Finney & Dobkins, 2001; Stevens & Neville, 2006) and peripheral visual fields (Finney & Dobkins, 2001). In addition to the studies reviewed, it has been confirmed that deaf and hearing individuals also have similar abilities to discriminate direction of motion (Hauthal, Sandmann, Debener, & Thorne, 2013) and that they show similar performance in orientation and facial discrimination tasks (Parasnis, Samar, Bettger, & Sathe, 1996). Rather than a general effect, Bavelier et al. (2006) concluded that the deaf have supranormal visual abilities only under conditions of attentional demand, as when asked to detect the direction of motion of a peripheral target at an attended location or to detect peripheral or moving stimuli that require attentional selection. The deaf also outperform those with normal hearing on visuomotor synchronization tasks where individuals are instructed to tap in synchrony with visual flashes (Iversen, Patel, Nicodemus, & Emmorey, 2015). The review of Bavelier et al. (2006) directed a spotlight on the visual abilities of the deaf; however, in the last decade, several studies contradicting their viewpoint have shown enhancements of visual sensory ability without attentional modulation in the deaf (Megreya & Bindemann, 2017; Smittenaar, MacSweeney, Sereno, & Schwarzkopf, 2016; Shiell, Champoux, & Zatorre, 2014; Codina, Buckley, Port, & Pascalis, 2011; Stevens & Neville, 2006; see Table 1).

Deaf adults routinely show enhanced visual performance compared with age-matched hearing controls for the localization of stimuli presented in the periphery of the visual field (Smittenaar et al., 2016; Codina et al., 2011; Stevens & Neville, 2006; Brozinsky & Bavelier, 2004; Bosworth & Dobkins, 2002; Bavelier et al., 2001). Interestingly, whereas deaf individuals display a bias for better performance in the peripheral field than the central field, hearing controls and hearing signers (hearing participants who are fluent in sign language) display the opposite trend (Bavelier et al., 2001). These localization paradigms suggest that the deaf have better visual

Table 1. Summary of Psychophysical Studies Investigating Crossmodal Visual Plasticity in the Deaf

Tasks	Species	Sample	Deafness Onset	Results p < .05	Author(s)
Motion detection	Human	16 Deaf and 20 hearing adults	Mixed	The deaf were better than the controls	Stevens and Neville (2014)
	Human	13 Deaf and 13 hearing adults	Not informed	The deaf were better than controls	Stevens et al. (2006)
	Cat	3 Deaf and 3 hearing	Congenital	The deaf were better than the controls	Lomber et al. (2010)
	Cat	3 Deaf and 3 hearing	Congenital	The deaf were better than the controls	Lomber et al. (2011)
Motion direction	Human	9 Deaf and 15 hearing adults	Mixed	The deaf showed right visual field advantage	Bosworth and Dobkins (1999)
	Human	16 Deaf and 25 hearing adults	Mixed	The deaf showed right visual field and peripheral advantages. The hearing showed left visual field advantage	Bosworth and Dobkins (2002)
	Human	19 Deaf and 19 hearing adults	Mixed		Hauthal et al. (2013)
	Cat	3 Deaf and 3 hearing	Congenital		Lomber et al. (2010)
Motion velocity	Human	12 Deaf and 12 hearing adults	Not Informed	The deaf showed right visual field and peripheral advantages	Brozinsky and Bavelier (2004)
	Cat	3 Deaf and 3 hearing	Congenital		Lomber et al. (2010)
Visual localization	Human	25 Deaf and 64 hearing children; 17 deaf and 18 hearing adults	Mixed	Deaf children (5–10 years) were worse the controls in the periphery. Deaf adolescents (13–15 years) were better than the controls in the periphery. Deaf adults were better than the controls in the periphery	Codina et al. (2011)
	Cat	3 Deaf and 3 hearing	Congenital	The deaf were better than the controls in the periphery	Lomber et al. (2010)
	Cat	3 Deaf and 3 hearing	Congenital	The deaf were better than the controls in the periphery	Lomber et al. (2011)

Table 1. (*continued*)

Tasks	Species	Sample	Deafness Onset	Results p < .05	Author(s)
Visuomotor synchronization	Human	23 Deaf and 22 hearing adults	Mixed	The deaf were better than the controls	Iversen et al. (2015)
Orientation discrimination	Human	12 Deaf and 12 hearing children	Congenital		Parasnis et al. (1996)
	Cat	3 Deaf and 3 hearing	Congenital		Lomber et al. (2010)
Temporal discrimination	Human	6 Deaf and 6 hearing adults	Congenital		Bross and Sauerwein (1980)
	Human	44 Deaf and 50 hearing adults	Mixed		Mills (1985)
	Human	10 Deaf and 12 hearing adults	Congenital		Poizner and Tallal (1987)
Object discrimination	Human	40 Deaf and 40 hearing adolescents	Mixed	Deaf adolescents were better than the controls	Megreya and Bindemann (2017)
Brightness discrimination	Human	6 Deaf and 6 hearing children	Not informed		Bross (1979)
Contrast sensitivity	Human	13 Deaf and 21 hearing adults	Mixed		Finney et al. (2001)
	Human	13 Deaf and 13 hearing adults	Not informed		Stevens and Neville (2006)
Grating acuity	Cat	3 Deaf and 3 hearing	Congenital		Lomber et al. (2010)
Vernier acuity	Human	14 Deaf and 15 hearing adults	Congenital	The deaf were better than the controls in the periphery	Smittenaar et al. (2016)
	Cat	3 Deaf and 3 hearing	Congenital		Lomber et al. (2010)
Facial discrimination	Human	40 Deaf and 40 hearing adolescents	Mixed	Deaf adolescents were better than the controls	Megreya and Bindemann (2017)
	Human	12 Deaf and 12 hearing children	Congenital		Parasnis et al. (1996)

sensitivity in the periphery than hearing controls, providing a larger useable field of view than hearing participants (Stevens & Neville, 2006). Indeed, studies have shown that the deaf have lower motion detection thresholds (Shiell et al., 2014) and a significantly larger field of view for detecting motion, as evidenced by superior detection of moving light points in the periphery than hearing controls (Stevens & Neville, 2006). Deaf individuals also outperform hearing controls in a Vernier acuity task with misaligned dots presented in the peripheral visual field (Smittenaar et al., 2016). It is important to note that no published study has shown visual sensory impairment related to deafness in adult humans or mature animals (Table 2).

Laterality of Visual Enhancement

Deaf participants often exhibit a strong laterality effect, performing better when stimuli are presented in the right than in the left visual field (Brozinsky & Bavelier, 2004; Bosworth & Dobkins, 1999, 2002). Conversely, normal hearing participants typically show either equivalence between left and right visual fields or a bias toward stimuli in the left visual field (Brozinsky & Bavelier, 2004). However, it is possible that this difference in laterality is the result of sign language use rather than hearing loss per se as a right visual field advantage has been demon-

strated in both deaf and hearing signers (Bosworth & Dobkins, 2002). Unfortunately, this is not easily resolved, as deaf nonsigners are a difficult population to locate (Table 1).

Visual Performance Development in Deaf Humans

Behavioral measures have revealed an interesting pattern of performance during development in the deaf (see Figure 2). Deaf children perform worse on measures of visual perception than normal hearing, age-matched controls until an age of approximately 10 years, similar to normal hearing controls between the ages of 10 and 12 years, and better than controls from age 13 to adulthood (Megreya & Bindemann, 2017; Codina et al., 2011; Parasnis et al., 1996; Bross, 1979).

For example, deaf children aged 5–10 years old are worse at detecting dim stimuli in the far periphery than age-matched controls but reach equivalent performance at 11–12 years of age (Codina et al., 2011). Normal performance by 10–12 years of age is not restricted to peripheral vision; Bross (1979) found no difference in brightness discrimination between hearing and deaf children in the central visual field in this same age range (mean age = 11.3 years). Additionally, congenitally deaf children aged 10–12 years perform similarly to age-matched hearing children for central field tasks involving

Table 2. Summary of the Results from Psychophysical Visual Tasks

| Visual Measure/Task	References
D > H, Deaf Performed Better than Hearing	
Motion detection	Shiell et al. (2014), Lomber et al. (2010, 2011), Stevens and Neville (2006)
Visual localization	Codina et al. (2011), Lomber et al. (2010, 2011)
Visuomotor synchronization	Iversen et al. (2015)
Vernier acuity (on the periphery)	Smittenaar et al. (2016)
Object discrimination	Megreya and Bindemann (2017)
Facial discrimination	Megreya and Bindemann (2017)
D = H, Deaf Performed Similarly to Hearing	
Motion direction	Hauthal et al. (2013), Lomber et al. (2010), Bosworth and Dobkins (1999, 2002)
Motion velocity	Lomber et al. (2010), Brozinsky and Bavelier (2004)
Orientation discrimination	Lomber et al. (2010), Parasnis et al. (1996)
Temporal discrimination	Poizner and Tallal (1987), Mills (1985), Bross and Sauerwein (1980)
Brightness discrimination	Bross (1979)
Contrast sensitivity	Stevens and Neville (2006), Finney et al. (2001)
Grating acuity	Lomber et al. (2010)
Vernier acuity	Lomber et al. (2010)
Facial discrimination	Parasnis et al. (1996)
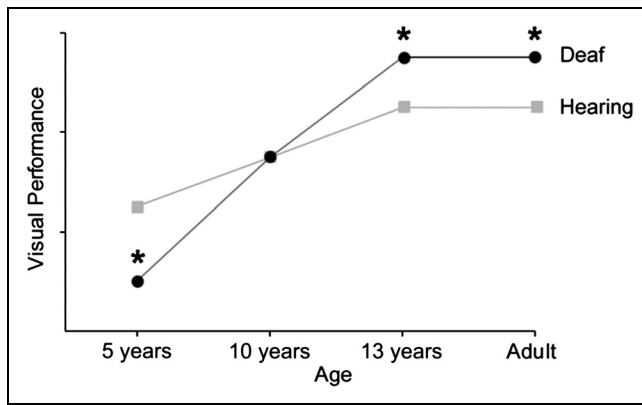
Figure 2. Summary of the visual performance development of deaf and hearing participants measured behaviorally (Megreya & Bindemann, 2017; Codina et al., 2011; Parasnis et al., 1996; Bross, 1979). Asterisks indicate statistical significance. Square gray markers (■) represent the hearing, and black round markers (●) represent the deaf.

facial recognition and judgments of the orientation of partially drawn lines (Parasnis et al., 1996).

By age 13–15 years, however, deaf children show enhanced performance relative to hearing adolescents and hearing adults on peripheral visual tasks (Codina et al., 2011), visual object-matching tasks, and face-matching tasks in both upright and inverted conditions, where the deaf show significantly better rates of correct identifications and correct rejections, fewer misidentifications, and greater overall accuracy (Megreya & Bindemann, 2017).

An important caveat for studies seeking to examine the visual abilities of children with hearing loss is to ensure that participants have normal or corrected-to-normal visual acuity. Some epidemiological studies have shown that the prevalence of refractive and binocular abnormalities is higher in children with hearing loss than in comparative groups of normal hearing individuals (for a review, see Hollingsworth, Ludlow, Wilkins, Calver, & Allen, 2014).

Animal Psychophysics

Psychophysical evaluations in animals provide us with a means of evaluating the mechanisms that underlie functional reorganization following deafness. For example,
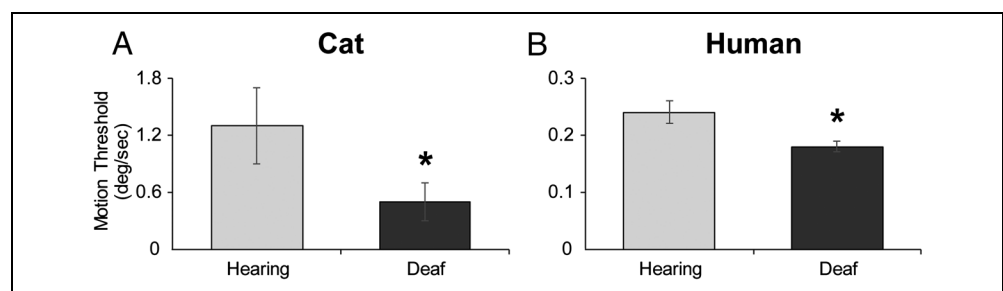
studies in cats have combined behavioral approaches with reversible cortical deactivation to identify the neural substrates of enhanced visual abilities in the deaf and to evaluate the relationship between different areas of the deaf auditory cortex and visual performance (Tables 1 and 2).

Psychophysical studies have measured visual performance in deaf cats before and after cooling specific cortical areas to understand their functional contribution to enhanced visual functions in the deaf (Lomber, Meredith, & Kral, 2010, 2011). For example, visual localization was tested by placing the cats in the center of an arena and measuring how accurately animals localized briefly illuminated LEDs presented at different eccentricities ranging from 0° to 90°. Congenitally deaf cats show enhanced visual localization in the peripheral field, outperforming hearing controls for targets presented between 60° and 90° from the point of fixation (Lomber et al., 2010, 2011). Using a two-alternative forced-choice method with a staircase procedure, motion detection thresholds (see Figure 3) for deaf cats were also shown to be lower than for hearing cats (better performance; Lomber et al., 2010, 2011), an effect that has since been replicated in humans (Shiell et al., 2014).

Although these animal studies provide a detailed measure of specific visual advantages in the deaf, they also highlight the fact that visual enhancement is not universal across stimulus features. For example, using the previously described methods, Lomber et al. (2010, 2011) did not find evidence of differences in other visual tasks including direction of motion discrimination, velocity discrimination, orientation discrimination, grating acuity, and Vernier acuity.

When deactivating specific auditory cortical areas, Lomber et al. (2010) revealed that the posterior auditory field (PAF) mediates enhanced visual peripheral localization in deaf cats, whereas the dorsal zone of auditory cortex (DZ) mediates enhanced movement detection (see Figure 4). This cooling technique allowed for the establishment of a causal link that would not be possible in human studies.

Lomber et al. (2010) convincingly demonstrated that, although auditory cortex in the deaf is involved in visual perception, crossmodal reorganization respects the function of the affected area. For example, both PAF (Malhotra, Hall, & Lomber, 2004) and the auditory field

Figure 3. Mean motion detection threshold ± *SEM* for hearing (light gray) and deaf (dark gray) (A) cats (Lomber et al., 2010, 2011) and (B) humans (Shiell et al., 2014). Asterisks indicate statistical significance.

Figure 4. Colored regions of auditory cortex are areas known to undergo visual crossmodal plasticity in (A) human: BA 41 (Almeida et al., 2015; Fine et al., 2005; Finney et al., 2001), BA 42 (Twomey et al., 2017; Cardin et al., 2013; Vachon et al., 2013; Fine et al., 2005; Finney et al., 2001), and BA 22 (Twomey et al., 2017; Cardin et al., 2013; Vachon et al., 2013; Fine et al., 2005; Finney et al., 2001), R (Scott et al., 2014; Karns et al., 2012), PT (Sadato et al., 2004; Finney et al., 2001), Te3 (Bola et al., 2017; Twomey et al., 2017), and TVA (Benetti et al., 2017); in (B) cat: A1 (Rebillard et al., 1977, 1980), AAF (Meredith & Lomber, 2011), DZ (Land et al., 2016; Lomber et al., 2010), FAES (Meredith et al., 2011), and PAF (Lomber et al., 2010); in (C) ferret: A1 (Meredith et al., 2012) and AAF (Meredith et al., 2012); and in (D) mouse: A1 (Hunt et al., 2006) and AAF (Hunt et al., 2006). Red areas are from imaging studies, yellow areas are from electrophysiological studies, blue areas are from reversible deactivation studies, and the green area is from a study that used both electrophysiology and reversible deactivation.
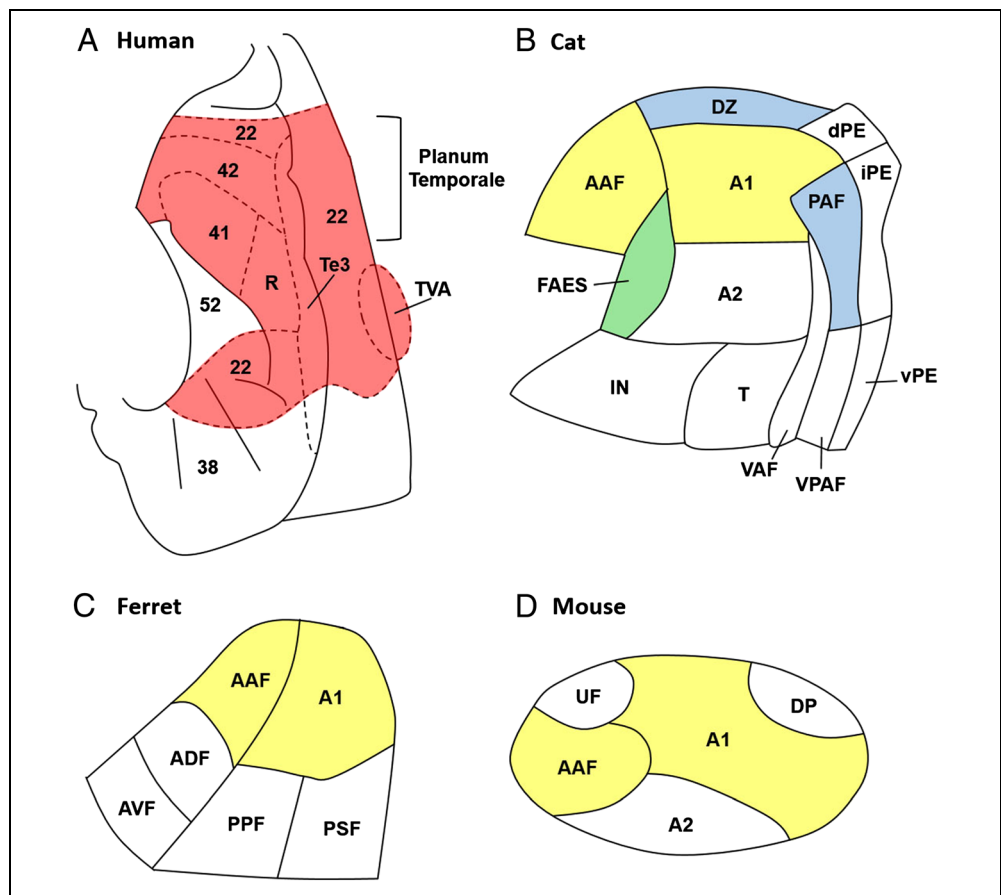
of the anterior ectosylvian sulcus (FAES; Meredith et al., 2011) are involved in auditory localization in normally developed animals and are reorganized to support visual localization in the deaf.

It is important to note that deactivating subregions of the auditory cortex does not always affect visual behavior. For example, deactivation of the primary auditory cortex (A1) and/or the anterior auditory field (AAF), the core auditory areas in cats, does not have any effect on visual performance in either deaf or hearing animals. Thus, the adoption of visual function is specific to particular regions of the auditory cortex and may be limited to those regions that have functional analogues across sensory systems.

WHAT CORTICAL REGIONS CONTRIBUTE TO ENHANCED VISUAL ABILITIES?

Human Electrophysiology

It is possible to examine crossmodal cortical plasticity in the deaf by measuring the electrical activity of the brain using electrodes placed on the scalp. For example, visual evoked potentials (VEPs) are well characterized

electrophysiological measures elicited by visual stimulation (Campbell & Sharma, 2016). Moreover, statistical procedures, like independent component analysis, identify individual components that underlie the visually evoked potential and can be utilized to estimate the location of cortical generators that contribute to the response (Makeig, Jung, Bell, Ghahremani, & Sejnowski, 1997). In the typically developed brain, visual cortical regions are the underlying sources of the VEP (Campbell & Sharma, 2016). Measurements of VEPs in children (mean age = 9.4 years) show that, in response to simple, static visual stimuli such as flashes of light, the activation patterns recorded from both deaf and age-matched hearing children are similar, showing a characteristic pattern over the occipital region with no evidence of generators beyond visual cortex (Charroó-Ruíz et al., 2013; see Table 3).

However, in support of behavioral data suggesting a visual advantage specific to the peripheral field, Neville, Schmidt, and Kutas (1983) found that VEPs recorded from congenitally deaf adults in response to peripherally and foveally presented stimuli differed from those recorded in adults with normal hearing in a manner consistent with compensatory cortical reorganization. The

Table 3. Summary of Electrophysiological Studies Examining Crossmodal Visual Plasticity in the Deaf

Author(s)	Species	Sample	Deafness Onset	Technique/Stimuli	Results p < .05
Charró-Ruíz et al. (2013)	Human	14 Deaf and 28 hearing children	Mixed	VEP/flashes of light	
Armstrong et al. (2002)	Human	11 Deaf and 11 hearing adults	Congenital	VEP/apparent motion	The deaf showed larger amplitude (N1) than the age-matched hearing
Bottari et al. (2014)	Human	12 Deaf and 12 hearing adults	Mixed	VEP/apparent motion	The deaf showed neuronal response in the auditory cortex
Chlubnová et al. (2005)	Human	6 Deaf and 6 hearing adults	Congenital	VEP/reversing checkboard pattern and apparent motion	The deaf showed smaller N1 in occipital regions than the hearing
Hauthal et al. (2014)	Human	11 Deaf and 11 hearing adults	Congenital	VEP/reversing checkboard pattern	Deaf participants showed shorter N1 latency and larger P1 amplitude than the age-matched hearing
Neville et al. (1983)	Human	8 Deaf and 13 hearing adults	Congenital	VEP/intermittent rectangle	The deaf showed larger N1 amplitude over the auditory cortex and larger P2 amplitude over VC than the age-matched hearing
Kral et al. (2003)	Cat	2 Deaf and 2 hearing	Congenital	Multi-unit/phase reversal gratings	
Land et al. (2016)	Cat	4 Deaf and 4 hearing	Congenital	Multi-unit/flashes of light and apparent motion	The deaf showed neuronal response in DZ
Meredith and Lomber (2011)	Cat	3 Deaf and 3 hearing	Early onset	Single unit/flashed or moving spots or bars of light	The deaf showed neuronal response in AAF
Meredith et al. (2011)	Cat	3 Deaf and 3 hearing	Early onset	Single unit/moving bar of light	The deaf showed neuronal response in FAES
Rebillard et al. (1977)	Cat	18 Deaf and 6 hearing	Mixed	VEP/flashes of light	The deaf with complete and early deafness showed neuronal response in the auditory cortex
Rebillard et al. (1980)	Cat	26 Deaf	Mixed	VEP/flashes of light	The deaf with complete and early deafness showed neuronal response in the auditory cortex
Stewart and Starr (1970)	Cat	1 Deaf and 3 hearing	Congenital	Multi-unit/flashes of light	
Meredith et al. (2012)	Ferret	5 Hearing-impaired and 5 hearing	Late onset	Flashed or moving light or dark stimuli	The deaf showed neuronal response in A1/AAF
Meredith and Allman (2012)	Ferret	3 Hearing-impaired	Late onset	Flashed or moving light or dark stimuli	
Hunt et al. (2006)	Mouse	8 Deaf and 9 hearing	Congenital	Single unit/flashes of light, bars and moving circles	The deaf showed neuronal response in A1 + AFF; The deaf V1 had significantly increased in size

amplitude of the first negative peak (N1) recorded over the auditory cortex was 1.5–3 times larger in the deaf than in the hearing for visual stimuli presented to the periphery, but not to the central visual field, whereas the amplitude of the second positive peak (P2) measured over the visual cortex was much larger in the deaf for both peripheral and foveal stimuli. Other studies have used dynamic visual stimuli to examine which brain regions underlie the apparent specificity of functional reorganization for moving stimuli. For example, congenitally deaf adults have larger N1 amplitudes than age-matched hearing controls in response to apparent visual motion in either the central or peripheral visual fields (Armstrong, Neville, Hillyard, & Mitchell, 2002). No difference is observed for color discrimination, suggesting that the deaf advantage may be specific for dorsal visual pathway functions (Stevens & Neville, 2006; Armstrong et al., 2002; Bavelier & Neville, 2002; Bavelier et al., 2001). However, another pilot study examining six congenitally deaf young adults from 16 to 18 years of age found that the onset of motion evokes a smaller N1 amplitude from occipital regions in the deaf than in age-matched controls (Chlubnová, Kremláček, Kubová, & Kuba, 2005). Indeed, a reduction in visually evoked responses from the visual cortex may reflect the recruitment of the auditory cortex during the processing of visual motion (Bottari et al., 2014).

Hauthal, Thorne, Debener, and Sandmann (2014) have also described differences between congenitally deaf and normal hearing participants in N1 and the first positive peak (P1) of the VEP. Deaf participants showed shorter latency of the N1 component and higher P1 amplitude than normal hearing adults when evaluating the direction of movement of a reversing checkboard pattern. VEP cortical sources were the visual cortex and posterior parietal cortex (PPC) for deaf and hearing participants. Additionally, there was greater activation over PPC in deaf individuals. These findings are an indication that early auditory deprivation may affect the neural processing of visual information.

Animal Electrophysiology

Electrophysiological studies have investigated visual crossmodal plasticity in deaf cats (Land et al., 2016; Meredith et al., 2011; Meredith & Lomber, 2011; Kral, Schröder, Klinke, & Engel, 2003; Rebillard, Rebillard, & Pujol, 1980; Rebillard, Carlier, Rebillard, & Pujol, 1977), deaf mice (Hunt et al., 2006), and hearing-impaired ferrets (Meredith et al., 2012). Early studies (Rebillard et al., 1977, 1980) used bipolar (transcortical) electrodes to record VEPs in deaf cats and compared them to normal hearing animals. Those experiments determined that VEP components originating in A1 are elicited by flashes of light in congenitally deaf animals as well as those completely deafened via bilateral cochlear destruction during the first three postnatal weeks (Rebillard et al.,

1980). However, no VEP component arises from A1 in cats with incomplete deafness, late-onset deafness (4 weeks or more of age), a unilateral cochlear lesion, or hearing controls (Rebillard et al., 1977, 1980; see Table 3).

Single-Unit Studies

Single-unit studies of crossmodal plasticity provide the most direct measure of function at the neuronal level and provide a mechanistic understanding of the changes that occur subsequent to hearing loss onset. Investigations across species find that an overwhelming proportion of units in the auditory cortex of hearing animals are unimodal, responding only to auditory stimuli (Meredith & Allman, 2009, 2012, 2015; Meredith et al., 2011; Meredith & Lomber, 2011; Allman, Keniston, & Meredith, 2009; Las, Shapira, & Nelken, 2008; Carriere et al., 2007; Hunt et al., 2006; Wallace, Carriere, Perrault, Vaughan, & Stein, 2006; Rauschecker, 1995; Rauschecker & Korte, 1993). However, within the normally developed auditory cortex, there are also neurons that respond to tactile (Meredith & Allman, 2012, 2015; Meredith et al., 2011; Hunt et al., 2006) or visual stimulation (Meredith & Allman, 2009, 2015; Meredith et al., 2011). Furthermore, neurons can also be identified as bimodal, responding to both acoustic and nonacoustic stimuli (Meredith & Allman, 2009, 2012, 2015; Meredith et al., 2011; Hunt et al., 2006).

Core auditory cortex. In the deaf, compared with hearing animals, the relative number of neurons in the auditory cortex that respond to tactile and visual stimuli increases. Single-unit recordings in the core auditory cortex (A1 and AAF) of ferrets with late onset, partial deafness (6–8 months of age; ~32 dB deficit) show an average of 165% response increase to visual stimulation (flashed or moving light or dark stimuli) when compared with hearing controls (Meredith et al., 2012). Moreover, these deaf animals show a dramatic decrease in the number of unimodal auditory neurons compared with normal hearing animals (31% vs. 65%) and a subsequent increase in the number of multisensory (bimodal or trimodal) neurons that respond to visual and/or somatosensory stimuli in addition to sound (68% vs. 34%; Meredith et al., 2012). A similar shift has been observed in core auditory areas of congenitally deaf mice. Hunt et al. (2006) observed that whereas 91% of neurons in A1 and AAF of intact animals are unimodal auditory units, in deaf animals the neurons in these regions respond predominantly to somatosensory stimuli (50–68%) or to somatosensory and visual stimuli (18–40%). These same deaf animals also show an increase in the cortical volume occupied by the primary visual cortex (V1) relative to controls. However, Meredith and Allman (2012) did not find neuronal responses to visual stimulation (flashed or moving light or dark stimuli) within the auditory cortex of

hearing-impaired young ferrets that were ototoxically lesioned before maturation of the A1.

Similarly, the AAF of normal hearing cats consists of 93% unimodal auditory neurons, with the remaining 7% being nonresponsive to sensory stimulation (Meredith & Lomber, 2011). In stark contrast, 83% of the neurons in early-deaf AAF respond to somatosensory cues, and 47% are driven by visual stimulation such as flashed or moving spots or bars of light (values include unisensory and bimodal neurons; Meredith & Lomber, 2011). Interestingly, neither A1 (Kral et al., 2003; Stewart & Starr, 1970) nor the second auditory cortex (A2; Stewart & Starr, 1970) in the cat respond to visual stimuli, following deafness, suggesting a lack of crossmodal reorganization. However, commentaries of this work (Butler & Lomber, 2013) have raised the possibility that visually evoked activity may have been obscured by the anesthetic regimen used in those particular studies (halothane) and the small sample size (e.g., $n = 1$; Stewart & Starr, 1970).

Noncore auditory cortex. In the cat, crossmodal plasticity has also been observed in nonprimary regions; in area FAES of the normal hearing brain, the majority of neurons are unimodal auditory units, whereas a small proportion are responsive to a combination of auditory and visual inputs or are unresponsive (Meredith et al., 2011). This is in contrast to the brain of the deaf, in which 68% of the neurons are driven by visual stimulation whereas 33% respond to somatosensory stimulation (values do not sum to 100% because of bimodal neurons that respond to visual <u>and</u> somatosensory stimulation; Meredith et al., 2011). Area DZ of deaf cats also contains more units responsive to flashes of light and apparent visual motion than in hearing cats (Land et al., 2016).

Human Neuroimaging

Noninvasive neuroimaging techniques allow for examination of brain regions underlying sensory processing through real-time recording of patterns of brain activation in response to different stimuli (Lu et al., 2012). For example, following normal development, visual stimulation elicits activity within well-studied brain networks, including regions of visual and associative cortex.

Auditory Cortex Activation

Studies using fMRI and magnetoencephalography (MEG) have shown activity within presumptive auditory cortical regions in response to visual stimulation in deaf humans (Benetti et al., 2017; Bola et al., 2017; Almeida et al., 2015; Scott, Karns, Dow, Stevens, & Neville, 2014; Cardin et al., 2013; Vachon et al., 2013; Karns, Dow, & Neville, 2012; Fine, Finney, Boynton, & Dobkins, 2005; Sadato et al., 2004; Finney, Clementz, Hickok, & Dobkins, 2003; Finney, Fine, & Dobkins, 2001; but see

Hickok et al., 1997). Critically, activation in the auditory cortex during visual stimulation seems to be related to deafness itself and not to sign language experience. For example, increased activation in the superior temporal gyrus (STG) is present in response to pictures of objects in humans who were deaf from birth, but not in hearing signers (Twomey, Waters, Price, Evans, & MacSweeney, 2017). This is an important distinction to make, as the use of sign language by the deaf has been shown to drive plasticity in the left superior temporal cortex (STC). Cardin et al. (2013) showed that when presented with sign-based visual stimuli, both deaf signers and deaf non-signers show activity within the right STC whereas only the deaf signers show activity within the left STC. This suggests that language-related activity commonly observed in the left STC of normally developed cortex maintains its function in the deaf but is tuned to visual inputs (Table 4).

Many of the visual stimulus features shown to be represented in reorganized auditory cortex of animal models of deafness are also encoded in the auditory cortex of deaf humans. For example, the auditory cortices of congenitally deaf individuals represent the visual field location of a stimulus—information that is typically represented in early visual areas. In fact, it is possible to decode the location of a stimulus in the visual field from neural activity patterns in the auditory cortex of congenitally deaf but not hearing individuals (Almeida et al., 2015).

Auditory Regions Activated by Visual Stimulation

Auditory areas showing visually evoked activity in the deaf include BA 41 (Almeida et al., 2015; Fine et al., 2005; Finney et al., 2001), BA 42 (Twomey et al., 2017; Cardin et al., 2013; Vachon et al., 2013; Fine et al., 2005; Finney et al., 2001), and BA 22 (Twomey et al., 2017; Cardin et al., 2013; Vachon et al., 2013; Fine et al., 2005; Finney et al., 2001), which correspond to primary, secondary, and associative auditory cortex, respectively; the rostral area (R; Scott et al., 2014; Karns et al., 2012), one of the primary-like auditory areas in humans located along the posterior aspect of Heschl's gyrus (Da Costa et al., 2011); the planum temporale (PT; Sadato et al., 2004; Finney et al., 2001), an area related to auditory and language processing on the left hemisphere and motion on the right hemisphere; Te3 (Bola et al., 2017; Twomey et al., 2017), a high level auditory cortex area in humans (Morosan, Schleicher, Amunts, & Zilles, 2005); and the temporal voice-selective area (TVA; Benetti et al., 2017).

Deaf participants also show activation of the right PT when exposed to apparent visual motion (Finney et al., 2001), whereas hearing participants do not. Moreover, visually evoked activity in PT was greater in the right hemisphere of deaf participants during a dot-motion matching task and greater in the left hemisphere during

Table 4. Summary of Neuroimaging Studies Investigating Crossmodal Visual Plasticity in the Deaf

Author(s)	Species	Sample	Deafness Onset	Technique/Stimuli	Results p < .05
Allen et al. (2013)	Human	25 Deaf and 41 hearing adults	Congenital	MRI	The deaf showed increased V1 total volume than the age-matched hearing
Almeida et al. (2015)	Human	10 Deaf and 10 hearing adults	Congenital	fMRI/counterphase flickering checkerboard	The deaf showed auditory cortex (BA 41) activation
Bavelier et al. (2000)	Human	11 Deaf and 11 hearing adults	Congenital	fMRI/ apparent motion	The deaf showed greater recruitment of the MT/MST and more effective connectivity between the MT/MST and the PPC when attending the periphery than age-matched hearing
Benetti et al. (2017)	Human	15 Deaf and 16 hearing adults	Early onset	fMRI and MEG/faces and houses	The deaf showed greater recruitment of the TVA
Bavelier et al. (2001)	Human	9 Deaf and 16 hearing adults	Congenital	fMRI/apparent motion	The deaf showed greater recruitment of the MT/MST when attending to periphery than age-matched hearing. The deaf showed greater recruitment of the PPC and the pSTS than age-matched hearing
					The deaf and the hearing signers showed stronger left hemisphere activation in V3a and MT-MST. The hearing nonsigners showed stronger right hemisphere activation in V3a and MT-MST
Bola et al. (2017)	Human	15 Deaf and 15 hearing adults	Congenital	fMRI/visual flashes	The deaf showed high-level auditory cortex Te3 (overlapped marginally with A1) activation
Cardin et al. (2013)	Human	26 Deaf and 18 hearing adults	Early onset	fMRI/Sign based visual stimuli	The deaf showed STC activation
Fine et al. (2005)	Human	6 Deaf and 12 hearing adults	Mixed	fMRI/apparent motion	The deaf showed auditory cortex activation (BA 41, BA 42, and BA 22)
Finney et al. (2001)	Human	6 Deaf and 6 hearing adults	Not informed	fMRI/apparent motion	The deaf showed right hemisphere auditory cortex activation (BA 41, BA 42, and BA 22, including the PT)
Finney et al. (2003)	Human	5 Deaf and 5 hearing adults	Congenital	MEG/a sinusoidal luminance grating	The deaf showed right auditory cortex activation
Hickok et al. (1997)	Human	1 Deaf adult	Congenital	MEG and fMRI/reversing checkboards	

Table 4. (*continued*)

Author(s)	Species	Sample	Deafness Onset	Technique/Stimuli	Results $p < .05$
Karns et al. (2012)	Human	13 Deaf and 12 hearing adults	Congenital	fMRI/light	The deaf showed greater recruitment of the R than age-matched hearing
Shiell et al. (2016)	Human	11 Deaf adults	Mixed	MRI	The deaf showed correlation between greater cortical thickness of the right PT with enhanced visual motion detection
Shiell and Zatorre (2017)	Human	11 Deaf adults	Mixed	MRI	The deaf showed correlation between white matter structure (high FA and low MD and RD) of the right PT with enhanced visual motion detection
Sadato et al. (2004)	Human	7 Deaf and 19 hearing adults	Mixed	fMRI/dot-motion, signed-word related stimuli	The deaf showed greater recruitment of the right PT during a dot-motion task, but showed greater recruitment of the left PT during signed-word related tasks than age-matched hearing
Scott et al. (2014)	Human	9 Deaf and 7 hearing adults	Congenital	fMRI/visual flashes	The deaf showed auditory cortex activation (R area). The deaf showed increased signal change for more peripheral stimuli than perifoveal in A1, MT, STG, and PPC
Shibata et al. (2001)	Human	6 Deaf and 6 hearing adults	Mixed	fMRI/apparent motion	The deaf showed greater recruitment of the right STG and MTG
Smittenaar et al. (2016)	Human	14 Deaf and 15 hearing adults	Congenital	fMRI/apparent motion	The deaf showed larger V1 population receptive field and decreased V1 thickness than age-matched hearing
Twomey et al. (2017)	Human	23 Deaf and 25 hearing adults	Congenital	fMRI	The deaf showed enhanced (BA 42 and BA 22) and Te3 activation
Vachon et al. (2013)	Human	15 Deaf and 16 hearing adults	Mixed	fMRI/apparent motion	The deaf showed increased right auditory cortex (BA 42 and BA 22)
Xia et al. (2017)	Human	23 Deaf and 17 hearing infants	Congenital	Resting-state fMRI	The deaf showed increased ALFF and ReHo in the occipital cortex, but showed decreased ALFF and ReHo in the auditory and language-related brain areas

language-related tasks, such as lip movement discrimination and sign-related motion tasks when compared with age-matched hearing signers and nonsigners (Sadato et al., 2004). This hemispheric asymmetry may reflect a predisposition for basic motion processing in the right PT and language processing in the left PT. This hypothesis is supported by the finding that, in hearing adults, the right PT is specialized for processing auditory motion (Baumgart, Gaschler-Markefski, Woldorff, Heinze, & Scheich, 1999), whereas the left PT is specialized in auditory language processing (Galaburda, LeMay, Kemper, & Geschwind, 1978). Thus, although both the right and left PT switch from auditory to visual responsivity in the deaf, the nature of the computation performed by these regions remains the same as in hearing participants. In response to apparent motion, the deaf also show greater recruitment of the PPC and the posterior superior temporal sulcus (STS), a multisensory area activated by motion, than age-matched hearing controls (Bavelier et al., 2001). Collectively, these imaging results support behavioral studies demonstrating that deaf individuals have superior motion perception when compared with those with normal hearing (Shiell et al., 2014).

Consistency of function across modalities in reorganized auditory cortex is not limited to simple stimulus features. Early-deaf individuals show enhanced responses to faces in a region of the auditory cortex known as TVA, which is located on the upper bank of the central portion of the STG (Benetti et al., 2017). Both voices and faces are used in identification, such that crossmodal plasticity in the TVA also maintains the original function of the region, even in the case of complex sensory stimuli (Benetti et al., 2017).

fMRI signal change for peripherally presented stimuli is greater than for perifoveal stimuli in the deaf, but not in hearing participants, for both A1 and the rostral subdivision of Heschl's gyrus (area R; Scott et al., 2014). This pattern is also found in the middle temporal area (MT), along the STG, and in multisensory and/or supramodal regions, such as PPC. These findings are in accordance with behavioral data that show a bias for better performance in the peripheral visual field in deaf individuals (Smittenaar et al., 2016; Codina et al., 2011; Stevens & Neville, 2006; Brozinsky & Bavelier, 2004; Bosworth & Dobkins, 2002; Bavelier et al., 2001).

Importantly, human imaging studies allow for whole-brain analysis and, as such, are sensitive to neuroplastic consequences of deafness beyond the auditory cortex (which is typically the point of focus in more directed electrophysiological studies). For example, when attending to apparent motion in the periphery, the deaf show greater recruitment of motion-selective visual areas, including the MT and medial superior temporal (MST) areas (Bavelier et al., 2000, 2001), and show more effective connectivity between the MT/MST and PPC, an area involved in the direction and maintenance of attention (Bavelier et al., 2000).

It is also important to note that imaging studies typically use auditory stimulation to localize auditory ROIs in normal hearing listeners and use these areas to form ROIs across all participants, assuming homology in the deaf (Benetti et al., 2017; Bola et al., 2017; Almeida et al., 2015; Scott et al., 2014; Vachon et al., 2013; Karns et al., 2012; Fine et al., 2005; Sadato et al., 2004; Finney et al., 2003, 2001). However, the validity of this methodology is cause for concern, as anatomical investigations in at least one animal model have shown that the size and shape of auditory cortical regions are modified following deafness (Wong, Chabot, Kok, & Lomber, 2014).

HUMAN RESTING STATE

The effects of congenital hearing loss on brain function are evident early in life. Using resting-state fMRI under sedation, Xia et al. (2017) compared the amplitude of low-frequency fluctuations (ALFFs; a marker of the strength of spontaneous activity within a brain region) and the regional homogeneity (ReHo; a measure of the degree to which activity in a voxel is correlated to activity in surrounding voxels) in auditory-, language-, and vision-related brain areas between very young deaf and hearing children (mean age = 24 ± 14 months). ALFF and ReHo values in deaf children were decreased in the areas responsible for auditory processing and language perception and were increased in the visual cortex. This suggests that hearing, language, and visual functions are affected at this early age as a consequence of congenital hearing loss (Xia et al., 2017).

ANIMAL RESTING STATE

Resting-state functional brain network connectivity has also been examined in lightly anesthetized hearing and early-deaf cats. Five of the six brain networks found to have altered connectivity to presumptive auditory networks involved the dorsoposterior auditory network, an area mainly involved in spatial localization functions. The majority of the areas involved in this dorsoposterior network showed larger amplitude correlations with non-auditory networks in the deaf than in the hearing. These results may indicate that both compensatory plasticity and a general loss of function likely coexist between various networks in the brain of the deaf (Stolzberg, Butler, & Lomber, 2018).

LATERALIZATION

As is the case in normally developed sensory cortex, the brain of the deaf has also been shown to exhibit significant lateralization of activity. For example, Finney et al. (2003) used MEG to determine that the right auditory cortex shows a greater level of visually evoked activity

in response to a sinusoidal luminance grating than the left hemisphere in the deaf. Similar laterality effects have been documented using fMRI in the superior (Vachon et al., 2013; Shibata, Kwok, Zhong, Shrier, & Numaguchi, 2001) and middle temporal gyrus (MTG; Shibata et al., 2001) and in the STS (Vachon et al., 2013) in response to apparent motion. Conversely, the congenitally deaf show greater activity in V3a, MT, and MST of the left hemisphere than the right, whereas normal hearing participants show the opposite asymmetry (Bavelier et al., 2001). Critically, normal hearing signers born to deaf parents are more similar to deaf participants than hearing non-signers, suggesting that this particular laterality effect was the result of sign language learning and not of deafness per se (Bavelier et al., 2001).

ANATOMICAL CHANGES

The cortical mantle is a laminar structure that consists of layers with specific inputs, outputs, and intrinsic connectivity. The thickness of the gray matter has been hypothesized to relate to the neural density and complexity of dendritic arborization within these layers—measures that are affected by experience. In this way, differences in cortical structure in the deaf may relate to enhancement or loss of function. For example, the right PT undergoes visual crossmodal plasticity in the deaf and begins responding to visual motion (Sadato et al., 2004; Finney et al., 2001). Accordingly, a correlation is observed between increased cortical thickness of the right PT as measured by magnetic resonance imaging (MRI) and enhanced visual motion detection in the deaf (Shiell, Champoux, & Zatorre, 2016). This correlation was not found in other brain regions, including the left PT, Heschl's gyrus, MT, and V1. In addition to gray matter changes, the white matter structure in the right PT also correlates with motion detection threshold in the deaf; better visual motion detection is associated with measures that suggest increased myelination and axon density, including increased fractional anisotropy, decreased mean diffusivity, and decreased radial diffusivity (Shiell & Zatorre, 2017). These findings support the idea that the right PT, in the absence of auditory input, subserves visual motion processing, mediating the enhanced motion detection performance in the deaf (Shiell et al., 2014).

In addition to changes in auditory brain regions, complementary changes are observed in the visual cortex. For example, the deaf show increased V1 total volume (Allen, Emmorey, Bruss, & Damasio, 2013), a larger V1 population receptive field encoding the peripheral visual field, and decreased V1 thickness (Smittenaar et al., 2016) when compared with age-matched hearing controls.

Detailed comparisons of neural connectivity to a number of auditory cortical regions in the cat show varying degrees of functional reorganization following deafness.

Retrograde neuronal tracer deposits in AAF reveal an increase in visual projections in both early- and late-deaf cats compared with those with normal hearing. Specifically, projections arising from the visual cortical regions, as the anterior ectosylvian visual area (AEV) and the anterolateral lateral suprasylvian area (ALLS) are substantially increased (Wong, Chabot, Kok, & Lomber, 2015). These increases are accompanied by decreases in the proportion of projections to AAF arising from other regions of auditory cortex, particularly from A1, DZ, and FAES (Wong et al., 2015). These changes are in contrast to the other core auditory area, A1, which shows very little evidence of reorganization following hearing loss onset (Chabot, Butler, & Lomber, 2015).

Following similar tracer injections in DZ, the region that mediates enhanced movement detection in the deaf (Lomber et al., 2010), projections arising from visual areas are observed in congenitally deaf cats that are not present in normal hearing cats; the visual areas of the ventral posterior ectosylvian (vPE) gyrus constitute the main source of these novel projections (Barone, Lacassagne, & Kral, 2013). Both early- and late-deafened cats also show larger proportions of projections to DZ from visual cortical areas compared with hearing animals (Kok, Chabot, & Lomber, 2014). Conversely, PAF, the region that mediates enhanced localization in the visual periphery (Lomber et al., 2011), shows no evidence of a significant change in the proportion of neurons projecting from nonauditory areas in either early- or late-deaf animals (Butler, Chabot, & Lomber, 2016). Similarly, FAES also shows functional crossmodal reorganization following deafness, but the patterns and proportion of cortical and thalamic afferents to FAES of early-deaf animals are largely the same as observed in hearing animals Meredith, Clemo, Corley, Chabot, & Lomber 2016). These latter studies suggests that crossmodal plasticity may be synaptically based, evidence for which can be seen in the average spine head diameter and spine density of FAES supragranular neurons, which were found to be significantly larger in early-deaf animals than in hearing controls (Clemo, Lomber, & Meredith, 2016), a pattern that was also mirrored for synapses in A1 (Clemo, Lomber, & Meredith, 2017).

CONCLUSION

How and what does the deaf brain see? It is a question that has been asked for the last half century but which remains not fully answered. However, the studies examined here help reach important conclusions. Behavioral studies point to a visual advantage in the deaf that is acquired around 13 years of age and which is particularly evident for stimuli presented in the visual periphery (Megreya & Bindemann, 2017; Smittenaar et al., 2016; Codina et al., 2011; Stevens & Neville, 2006; Brozinsky & Bavelier, 2004; Bosworth & Dobkins, 1999, 2002; Bavelier et al., 2001). Although this advantage does not

universally enhance perception of all visual stimulus features, the deaf are at least as good as normal hearing individuals across all paradigms tested to date (Table 2). Overall, no visual decrements have been identified in the deaf, whereas many investigations have identified specific visual advantages. Although the deaf do not possess visual superpowers, like seeing through walls, they do have particular enhanced visual functions, such as object and facial discrimination, and peripheral visual functions, such as motion detection, visual localization, visuomotor synchronization, and Vernier acuity that are specifically enhanced compared with hearing subjects.

There is also strong evidence that recruitment of the sensory-deprived auditory cortex underlies enhancement of the remaining sensory modalities (Benetti et al., 2017; Bola et al., 2017; Twomey et al., 2017; Land et al., 2016; Almeida et al., 2015; Scott et al., 2014; Vachon et al., 2013; Karns et al., 2012; Meredith et al., 2011, 2012; Meredith & Lomber, 2011; Lomber et al., 2010; Hunt et al., 2006; Fine et al., 2005; Sadato et al., 2004; Finney et al., 2001; Rebillard et al., 1977, 1980). In contrast to the largely separable auditory and visual brain regions which arise through normal development, studies show activation of the deaf auditory cortex during visual stimulation in humans (Bola et al., 2017; Corina, Blau, LaMarr, Lawyer, & Coffey-Corina, 2017; Campbell & Sharma, 2016; Almeida et al., 2015; Bottari et al., 2014; Scott et al., 2014; Vachon et al., 2013; Karns et al., 2012; Fine et al., 2005; Sadato et al., 2004; Finney et al., 2001, 2003; Neville et al., 1983) and animal models of hearing loss (Land et al., 2016; Meredith et al., 2011, 2012; Meredith & Lomber, 2011; Hunt et al., 2006; Kral et al., 2003; Rebillard et al., 1977, 1980). These findings should not be too surprising as a multitude of studies have revealed that primary sensory cortices actually encode, or are influenced by, the presence of inputs from different sensory modalities (e.g., Karns et al., 2012; Kayser & Logothetis, 2007; Ghazanfar & Schroeder, 2006). Crossmodal plasticity exhibits region-dependent differences based on differences on their underlying connectivity. Among the potential connectional sources for primary sensory cortex are other primary sensory areas. Although primary-to-primary connectivity has received a great deal of attention recently, the literature clearly shows that primary-to-primary cortical connectivity occurs in rodents,

but there is little consistent evidence for this in nonrodents such as carnivores and nonhuman primates (Meredith & Lomber, 2017).

In some cases, visual enhancements in the deaf can be attributed to specific fields of the presumptive auditory cortex. The cortical loci identified to mediate these functions reside in deaf auditory cortex: BA 41, BA 42, and BA 22, in addition to areas R, PT, Te3 and TVA in humans; A1, AAF, DZ, FAES and PAF in cats; and A1 and AAF in both ferrets and mice. For example, using a combination of a behavioral approach and reversible deactivation, the auditory cortical area PAF has been shown to mediate enhanced visual peripheral localization, whereas area DZ mediates enhanced movement detection in congenital deaf cats (Lomber et al., 2010). In each case, the region being reorganized adopts a similar function to that which it performs in the normally developed brain, albeit contributing to a novel sensory modality. A similar conservation of function is beginning to emerge in studies of human reorganization following hearing loss.

Although a major restructuring of the neural projections between sensory brain regions was long thought to underlie functional reorganization following sensory loss, recent results from studies using retrograde tracers to quantify crossmodal projections in normal hearing and deaf animals show limited or no changes in the patterns of projections (Butler, de la Rua, Ward-Able, & Lomber, 2018; Butler, Chabot, Kral, & Lomber, 2017; Butler et al., 2016; Meredith et al., 2016; Chabot et al., 2015; Wong et al., 2015; Kok et al., 2014). Thus, future studies should consider alternate hypotheses, including the idea evidenced by Clemo et al. (2016, 2017) that synaptic level changes on projections that exist during development might give rise to functional differences in auditory cortex.

Overall, the findings from these studies show that crossmodal reorganization in auditory cortex of the deaf is responsible for the superior visual abilities of the deaf. Thus, although deafness may cause a general sensory impairment very early in life, behavioral advantages in the remaining sensory modalities emerge in adolescence and persist through adulthood. That visual perception is particularly enhanced for peripheral stimulation and stimuli in motion suggests compensatory function is related to optimizing survival in the absence of sound, a critical source of information about the world around us.

List of Abbreviations

AAF	anterior auditory field
ADF	anterior dorsal field
AEV	anterior ectosylvian visual area
ALFF	amplitude of low-frequency fluctuations
ALLS	anterolateral lateral suprasylvian area
AVF	anterior ventral field
A1	primary auditory cortex
A2	second auditory cortex
CI	cochlear implants
dB	decibels
DP	dorsoposterior field
dPE	dorsal posterior ectosylvian gyrus
DZ	dorsal zone of auditory cortex
FAES	auditory field of the anterior ectosylvian sulcus
fMRI	functional magnetic resonance imaging
IN	insular area
IPE	inferior posterior ectosylvian gyrus
MEG	magnetoencephalography
MRI	magnetic resonance imaging
MST	medial superior temporal area
MT	middle temporal area
MTG	middle temporal gyrus
MZ	multisensory zone
N1	first negative peak
PAF	posterior auditory field
PPC	posterior parietal cortex
PPF	posterior pseudosylvian field
PSF	posterior suprasylvian field
pSTS	posterior superior temporal sulcus
PT	planum temporale
P1	first positive peak
P2	second positive peak
R	rostral area
ReHo	regional homogeneity
STC	superior temporal cortex
STG	superior temporal gyrus
STS	superior temporal sulcus
T	temporal area
Te 3	temporal area 3
TVA	temporal voice area
UF	ultrasonic field
VAF	ventral auditory field
VC	visual cortex
VEP	visual evoked potential
VPAF	ventral posterior auditory field
vPE	ventral posterior ectosylvian
V1	primary visual cortex
V3a	third visual cortex accessory

Note

1. An international dollar is a currency unit defined by the World Bank as the amount that would buy in the cited country a comparable number of goods and services a U.S. dollar would buy in the United States (World Bank, 2017).

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