Microstructural differences in the thalamus and thalamic radiations in the congenitally deaf

Rebecca C. Lyness [a,*], I. Alvarez [b], Martin I. Sereno [a,c], Mairéad MacSweeney [d,e]

[a] Cognitive and Perceptual Brain Sciences, 26 Bedford Way, University College London, London WC1H 0AP, UK
[b] Institute of Child Health, University College London, London WC1N 1EH, UK
[c] Birkbeck, University of London, Malet Street, Bloomsbury, London WC1E 7HX, UK
[d] Deafness, Cognition & Language Research Centre, 49 Gordon Square, University College London, London WC1H 0PD, UK
[e] Institute of Cognitive Neuroscience, 17 Queen Square, University College London, London WC1H 3AR, UK

ABSTRACT

There is evidence of both crossmodal and intermodal plasticity in the deaf brain. Here, we investigated whether sub-cortical plasticity, specifically of the thalamus, contributed to this reorganisation. We contrasted diffusion weighted magnetic resonance imaging data from 13 congenitally deaf and 13 hearing participants, all of whom had learnt British Sign Language after 10 years of age. Connectivity based segmentation of the thalamus revealed changes to mean and radial diffusivity in occipital and frontal regions, which may be linked to enhanced peripheral visual acuity, and differences in how visual attention is deployed in the deaf group. Using probabilistic tractography, tracts were traced between the thalamus and its cortical targets, and microstructural measurements were extracted from these tracts. Group differences were found in microstructural measurements of occipital, frontal, somatosensory, motor and parietal thalamo-cortical tracts. Our findings suggest that there is sub-cortical plasticity in the deaf brain, and that white matter alterations can be found throughout the deaf brain, rather than being restricted to, or focussed in the auditory cortex.

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Introduction

There is evidence of a number of different plastic processes in the deaf brain, which occur in response to, and to compensate for the atypical sensory environment. These include crossmodal (Fine et al., 2005; Finney et al., 2001; MacSweeney et al., 2004; Nishimura et al., 1999; Petitto et al., 2000), and intermodal plasticity (Bottari et al., 2011; Buckley et al., 2010; Codina et al., 2011), in addition to the dystrophic changes which occur in the auditory cortex (Emmorey et al., 2003; Li et al., 2012). The thalamus is an important structure for regulating both the flow of information into the cortex and between cortical areas. Whether this structure is altered in congenitally deaf humans has not yet been investigated.

Crossmodal plasticity is evident in the congenitally deaf brain. Activation in the secondary auditory cortices has been robustly demonstrated in fMRI studies in response to a wide range of visual stimuli, including sign language (MacSweeney et al., 2002; Petitto et al., 2000), biological motion (MacSweeney et al., 2004), as well as more simple visual stimuli such as dot motion (Finney et al., 2001). Controversy remains as to whether there is visual colonisation of Heschl's gyrus,

the typical site of primary auditory cortex. In deaf people, activation in response to visual stimuli has been reported in studies using spatial normalisation procedures (Finney et al., 2001), and in studies which do not contrast visual stimuli to a resting baseline (Karns et al., 2012, Scott et al., 2014). However, Cardin (2013) did not find activation in a cytoarchitectonically based definition of primary auditory cortex when visual stimuli were contrasted to a resting baseline in deaf participants.

Somatosensory processing has been shown to be enhanced (Levanen and Hamdorf, 2001), and reorganised into auditory cortex in deaf people (Auer et al., 2007; Karns et al., 2012; Levanen et al., 1998). The use of spatial normalisation to a common template for MRI data (Auer et al., 2007), and MEG data (Levanen et al., 1998) preclude confident anatomical localisation of this activation to primary auditory cortex. However, when anatomical definitions of the regions are used, there is strong evidence of somatosensory takeover of primary auditory cortex (Karns et al., 2012). Findings from the animal literature concur with this also (Allman et al., 2009; Meredith et al., 2012). Single unit recordings from the auditory cortex of early deafened ferrets (oto-toxic lesions) have demonstrated somatosensory afferents in auditory cortex (Meredith and Allman, 2012). Tracer injections to the auditory core of these deafened animals revealed the same auditory thalamo-cortical projection sources as the hearing ferrets, which the authors interpreted as indicating that rather than new or unmasked latent projections, reorganisation occurred at the level of the brainstem (Meredith and Allman, 2012).

In addition, there is evidence of intermodal plasticity in deafness. Deafness enhances detection of both static and motion targets in the visual periphery (Loke and Song, 1991; Neville and Lawson, 1987b). This behavioural advantage is thought to facilitate the orienting to targets in the absence of sound (Merabet and Pascual-Leone, 2010). These changes have been linked to increases in the area of neural rim within the optic nerve head, and thicker retinal nerve fibre layer in temporal (peripheral) retina (Codina et al., 2011), and changes in primary visual cortex (Lyness et al., 2013). Differences in visual event-related potentials (ERPs) have also been observed in early visual cortex in deaf groups, which in turn were correlated with improved performance in a visual target detection task (Bottari et al., 2011).

That the function of a brain region is tightly coupled with its extrinsic anatomical connections is a widely held assumption in neuroscience. It follows that the inputs to a region affect what information is available to a region, and where the outputs of a region terminate determines the influence that a region will have. Empirical tests of this hypothesis have supported this assumption (Passingham et al., 2002; Saygin et al., 2011), and indeed, anatomical connectivity data can be used to define functionally distinct regions (Behrens et al., 2003, 2006; Johansen-Berg et al., 2004; Rushworth et al., 2006). Thus we argue that functional imaging studies concerning plasticity as a result of deafness should be considered in the context of changes to anatomical connectivity patterns. This complimentary approach may elucidate why certain patterns of reorganisation are seen in one brain region or modality, but not others.

Plastic change in the deaf brain may occur via a number of different mechanisms, none of which are mutually exclusive, and are likely have a different impact depending on the brain region (Bavelier and Neville, 2002). For example, visual activation in secondary auditory cortices may occur through synaptic reweighting of these regions, which typically act as a site for audiovisual integration (Calvert et al., 2000; Lee and Noppeney, 2011; McGettigan et al., 2012). Alternatively, the 'brainstem theory of crossmodal reorganisation' proposes that neither new nor latent projections are responsible for reorganisation, but instead, somatosensory inputs are able to takeover dormant auditory inputs found in the typically developing auditory brainstem at several nodes (Meredith and Allman, 2012). Subcortical connectivity changes have been suggested to contribute to crossmodal reorganisation as a result of congenital deafness, however, research into this possibility has as yet been limited to animal studies (see Proksch and Bavelier, 2002).

Here, we investigate how congenital deafness affects the thalamus, and thalamo-cortical projections. The thalamus has a critical role in regulating the flow of information into the cortex, as a substantial amount of information coming into the cortex does so through the thalamus (Sherman, 2007). In addition, and perhaps more importantly, the thalamus mediates cortico-thalamo-cortical connections, which make it ideally positioned functionally and anatomically to modulate a variety of different cognitive functions, which include emotion, motivation and multimodal perception (Jones, 2009; Sherman, 2007). Based on the overlapping nature of projections from different sensory modalities, the thalamus has additionally been suggested as a site of multimodal interplay (Cappe et al., 2009a,b). This has led to recent interest in the functional consequences of thalamic stroke (Carrera and Bogousslavsky, 2006), and the role of the thalamus in neurodevelopmental disorders such as autism spectrum disorder (Nair et al., 2013). Therefore, it is possible that looking at changes to the anatomy of the thalamus and thalamo-cortical tracts may illuminate the functional consequences of auditory deprivation.

Diffusion weighted magnetic resonance imaging (DW-MRI) is currently the only method for characterising neural tissue microstructure and reconstructing white matter tracts in vivo. Magnetic field gradients are used to sensitise the MRI signal acquisition to the displacement of water molecules due to Brownian motion. The application of diffusion gradients along multiple geometric directions allows the estimation of directional molecule displacement in the tissue sampled (Johansen-Berg and Rushworth, 2009). These data can be summarised by a diffusion tensor model, which describes the magnitude of the three principal axes of molecule displacement at each voxel sampled. Diffusion of water molecules is hindered by tissue properties, and in the case of white matter these include (but are not specific to) axonal ordering, axonal density and the degree of myelination (Johansen-Berg and Behrens, 2006). These underlying tissue properties can be approximated using tensor-derived microstructural metrics. These include fractional anisotropy (degree to which the first eigenvector dominates the second two), mean diffusivity (overall water diffusion in the specific voxel), and radial diffusivity (diffusion perpendicular to the principal eigenvector of the diffusion tensor).

Tractography with DW-MRI involves reconstructing continuous long range trajectories from voxel-wise estimates of the fibre orientation (Jones et al., 2013). From a seed region, streamlines can be traced in a probabilistic iterative fashion to determine the most likely path of the white matter tract of interest (Behrens et al., 2003). Tractography can be used to determine whether tracts exist between regions, and also to compare tracts in terms of their microstructural properties between groups (Johansen-Berg and Rushworth, 2009). Additionally, connectivity based segmentations of anatomical structures can be completed, in which structures are segmented on the basis of the highest probability of connection with different anatomical targets (Behrens et al., 2003). Behrens et al., first demonstrated this by generating a connectivity based segmentation of the thalamus, which closely resembled those derived from both animal anatomical tract tracing studies (Jones, 1985), and histological analyses (Morel et al., 1997).

DW-MRI data only detects the axis of diffusion (Johansen-Berg and Rushworth, 2009), and so we cannot differentiate between anatomical connections carrying information from the thalamus to its cortical targets (thalamo-cortical feedforward connections) from those carrying information from cortical targets to the thalamus (cortico-thalamic feedback connections). For simplicity, and to indicate that we have traced from thalamus to cortex, throughout this paper we refer to these tracts as thalamo-cortical connections with the understanding that they are likely to incorporate both feedforward and feedback connections.

To investigate the possible influence of congenital deafness on the anatomy of the thalamus, we first parcellated the thalamus based on connectivity profiles with its primary cortical targets. We contrasted the scalar microstructural measures of fractional anisotropy (FA), mean diffusivity (MD), and radial diffusivity (RD) in each parcellation between deaf and hearing groups. Second, to investigate the possibility of altered thalamo-cortical connectivity in congenital deafness, we reconstructed the tracts between the thalamus and its primary cortical
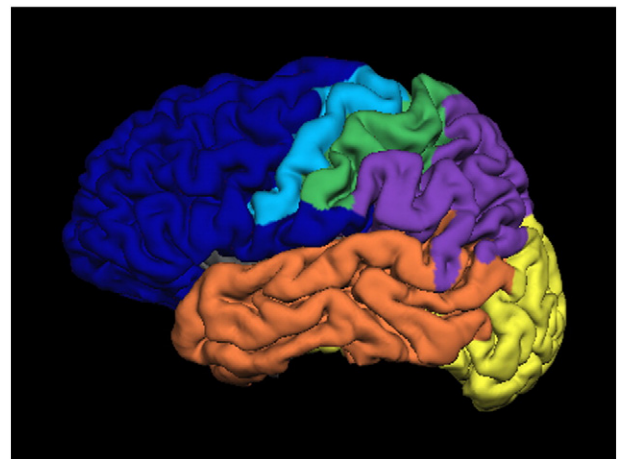

Fig. 1. Cortical target masks are demonstrated in a representative participant. The cortex has been divided into frontal (dark blue), motor (light blue), somatosensory (green), parietal (purple), temporal (orange) and occipital (yellow) regions.