



Evidence of multisensory plasticity: Asymmetrical medial geniculate body in people with one eye



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ABSTRACT

The medial geniculate body (MGB) plays a central role in auditory processing with both efferent and afferent tracts to primary auditory cortex. People who have lost one eye early in life have enhanced sound localization, lack visual over auditory dominance and integrate auditory and visual information optimally, similar to controls, despite taking longer to localize unimodal visual stimuli. Compared to controls, people with one eye have decreased lateral geniculate nuclei (LGN) volume as expected given the 50% deafferentation of the visual system. However, LGN volume is larger than predicted contralateral to the remaining eye, indicating altered structural development likely through recruitment of deafferented LGN cells.

Purpose: the current study investigated whether structural MGB changes are also present in this group given the changes they exhibit in auditory processing.

Methods: MGB volumes were measured in adults who had undergone early unilateral eye enucleation and were compared to binocularly intact controls.

Results: unlike controls, people with one eye had a significant asymmetry with a larger left compared to right MGB, independent of eye of enucleation. MGB volume correlated positively with LGN volume in people with one eye.

Conclusions: volume asymmetry in the MGB in people with one eye may represent increased interactions between the left MGB and primary auditory cortex. This interaction could contribute to increased auditory and other left hemisphere-dominant processing, including language, as compensation for the loss of one half of visual inputs early in life. The positive correlation between MGB and LGN volume is not due to space constraints but rather indicates increased plasticity in both auditory and visual sensory systems following early eye enucleation.

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1. Introduction

Every day, as we interact with the world, we take in important information from the environment through our sensory systems. Sensory information, with the exception of olfaction, is first processed subcortically by the thalamus, which then projects information to the cortex for further processing (Bartlett, 2013). There is evidence that when one sense is compromised, as in the case of complete blindness, brain regions associated with the lost sense (i.e., visual cortex) can be reorganized for use by the other senses (e.g., Röder et al., 2002). We have recently shown that structural reorganization at the subcortical

level in the lateral geniculate nucleus (LGN) of the thalamus occurs in cases of sensory deprivation (Kelly et al., 2014).

The medial geniculate body (MGB) of the thalamus plays a central role in auditory processing (Devlin, 2006; Bartlett, 2013). It relays auditory information for higher order processing in primary auditory cortex, however, substantial reciprocal connections from the primary auditory cortex back to the MGB also exist (Bartlett, 2013; Lee et al., 2004; Lee, 2013). This combination of ascending/descending sensory connections allows for the complex perception of sounds (Bartlett, 2013). In humans, functional magnetic resonance imaging (fMRI) has shown activation in the MGB during sound localization and sound recognition (Maeder et al., 2001), as well as speech and emotional voice discrimination (von Kriegstein et al., 2008; Ethofer et al., 2012). Cortical feedback can alter MGB responses and provide dynamic gain enhancement or suppression through direct excitatory (corticothalamic feedback) or indirect inhibitory (corticothalamic influence on the thalamic reticular

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nucleus (TRN)) signals (Zhang et al., 1997; Bartlett, 2013). This gain control may contribute to enhancing auditory attention and context memory, important for predicting words in a spoken sentence (Bartlett, 2013).

Extensive investigation of the mammalian MGB, typically in the cat, has revealed three major subdivisions: ventral (vMGB), medial (mMGB) and dorsal (dMGB) (Devlin, 2006). The ventral division is sensitive to pure tone stimulation of the contralateral ear, whereas both the medial and dorsal divisions are more sensitive to complex and multi-sensory stimuli (see De Ribaupierre, 1997; Rouiller, 1997 for review). In addition, non-auditory stimuli also activate the MGB. The rat MGB responds to light flashes or rewards indicating that it plays a role in integrating multisensory stimuli to provide an enhanced contextual response (Komura et al., 2001, 2005; Bartlett, 2013). Congenitally deaf mice show reorganization at the level of the thalamus through the activation of the MGB (Hunt et al., 2005). Together, these findings indicate that it is possible for primary sensory afferents, such as retinal projections, to rewire and claim unused subcortical structures, resulting in anatomical re-modelling (Hunt et al., 2005; Karlen, 2006). Reorganization of the MGB following sensory loss, however, has not been studied extensively in humans.

Monocular enucleation, the surgical removal of one eye early in life, is a unique form of visual deprivation that provides a useful model for studying and quantifying the underlying neural consequences of the loss of binocularity during development. Monocular enucleation differs from other more common forms of monocular deprivation, such as strabismus and amblyopia, by providing a clean model of total monocular deprivation. This is unlike strabismus and amblyopia which result in unreliable, unbalanced competing visual signals from the deprived eye. Monocular enucleation results in only one stream of normal visual input from the remaining eye to the visual system. Monocular enucleation also provides an excellent model for investigating the interaction between vision and other senses, since vision has not been completely eliminated (see Kelly et al., 2013; Steeves et al., 2008 for reviews).

It has been well documented that the visual system changes in response to the loss of one eye. People who have had one eye removed early in life when the visual system is not yet mature demonstrate altered processing in their remaining senses. For example, they show intact (Cattaneo, 2014) or enhanced visual spatial form ability (Nicholas et al., 1996; Reed et al., 1997; Steeves et al., 2004), but reduced visual motion processing (see Steeves et al., 2008; Kelly et al., 2013 for reviews). Some evidence of cross-modal adaptation in response to the compromised enucleated visual system has also been demonstrated. People who lost an eye early in life show enhanced auditory localization in the horizontal azimuth compared to binocular controls (Hoover et al., 2012). Further, they do not show the typical pattern of visual over auditory dominance (i.e., Colavita visual dominance effect; Colavita, 1974) that binocular controls exhibit, but rather show equivalent auditory and visual processing (Moro and Steeves, 2012). Lastly, although people with one eye do not integrate audiovisual stimuli any differently from controls during audiovisual spatial localization, they are slower to respond when localizing visual stimuli (Moro et al., 2014).

There have been few studies investigating the morphology of sensory systems of people who have lost an eye early in life (Kelly et al., 2014; Kelly et al., 2015). Subcortically, people with one eye have an overall decrease in LGN (the visual relay station of the thalamus) volume compared to binocular viewing controls (Kelly et al., 2014). This is not surprising given the 50% deafferentation of signal to the visual system with eye enucleation. What is surprising, however, is that the LGN contralateral to the remaining eye is less reduced in volume likely from recruitment of some of the deafferented LGN cells (Kelly et al., 2014). This finding provides evidence that the visual system, even at the level of the subcortex, is vulnerable to reorganization after losing one eye early in life during the period of normal maturation (Kelly et al., 2014).

Functional neuroimaging can be used to successfully localize the MGB in humans, however, this methodology is limited by sensory stimuli and in its sensitivity (Devlin, 2006). Devlin et al. (2006) have been able to structurally image the MGB to resolve the functional localization concerns. Their method is now considered the gold standard for anatomical localization of the MGB and other thalamic structures. Given the existing auditory and audiovisual behavioural differences and the morphological changes in the LGN in people with one eye, we investigated whether structural changes in the MGB also exist in this group.

2. Methods

2.1. Participants

2.1.1. People with one eye (monocular enucleation, ME)

Ten adult participants who had undergone monocular enucleation (ME) at The Hospital for Sick Children participated in this study (mean age = 26 years, SD = 10; 5 female). All ME participants had been unilaterally eye enucleated (5 right eye removed) due to retinoblastoma, a rare childhood cancer of the retina. Age at enucleation ranged from 4 to 60 months (mean age at enucleation = 21 months, SD = 16).

2.1.2. Binocular viewing control participants (BV)

Fifteen binocularly intact controls with a mean age of 30 years (SD = 11; 6 female; 11 right eye dominant) were tested and reported no history of abnormal visual experience.

All participants (ME, BV) reported normal hearing, normal or corrected-to-normal acuity as assessed by an EDTRS eye chart (Precision Vision™, La Salle, IL) and wore optical correction if needed. All participants gave informed consent prior to inclusion in the study, which adhered to the tenets of the Declaration of Helsinki and was approved by the York University Office of Research Ethics.

2.2. Data acquisition, processing and measurements

All scans were acquired on a Siemens MAGNETOM Trio 3 T MRI scanner with a 32-channel head coil in the Sherman Health Sciences Research Centre at York University. Proton density (PD) weighted images were processed using tools from the freely available FMRIB's Software Library (FSL; version 4.1.8) (<http://www.fmrib.ox.ac.uk/fsl>.) All data acquisition and processing were conducted according to methods used in Kelly et al. (2014) for assessing LGN volume. Thalamic nuclei have been successfully identified using PD weighted images previously (Devlin et al., 2006; Kelly et al., 2014). See Kelly et al. (2014) for more detailed data acquisition and processing procedures.

High-resolution T₁ weighted images were acquired with the following parameters: rapid gradient echo, 1 mm³ isotropic voxels, TR = 1900 ms, TE = 2.52 ms, 256x256 matrix, and flip angle = 9°. Either 30 or 40 PD weighted images per participant were acquired coronally with the following parameters: turbo spin echo, 800 x 800 μm in-plane resolution, slice thickness = 2 or 1 mm, TR = 3000 ms, TE = 22 or 26 ms, 256x256 matrix, and flip angle = 120°. Total scan time per participant was approximately 1.5 h. The smaller number (30) of PD weighted images for some participants was due to time constraints.

Using FSL toolbox applications, all PD weighted images for each participant were interpolated to twice the resolution and half the voxel size using FLIRT (Jenkinson and Smith, 2001; Jenkinson et al., 2002) to increase the signal-to-noise ratio. These images were then concatenated using fslmerge and motion-corrected using MCFLIRT (Jenkinson et al., 2002). From the series of interpolated PD weighted images, a mean high resolution PD image was created per participant using fslmaths.

Following image acquisition and processing, three independent raters manually traced the left and right MGB region of interest (ROI)

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