



Origin of the thalamic projection to dorsal auditory cortex in hearing and deafness



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ARTICLE INFO

Article history:

Received 1 April 2016

Received in revised form

18 May 2016

Accepted 26 May 2016

Available online 2 June 2016

Keywords:

Cat

Dorsal zone

Sensory loss

Hearing loss

Cross-modal

ABSTRACT

While it is now well accepted that the brain reorganizes following sensory loss, the neural mechanisms that give rise to this plasticity are not well understood. Anatomical tract tracing studies have begun to shed light on the structural underpinnings of cross-modal reorganization by comparing cerebral connectivity in sensory-deprived animals to that of their non-deprived counterparts. However, so far, full documentation of connectional patterns within hearing, congenitally deaf, as well as animals deafened early versus later in life exist only for primary auditory cortex, a region not known to undergo cross-modal reorganization in the deaf. The purpose of the present investigation was to examine thalamo-cortical patterns of connectivity in hearing, late- and early-deafened cats to the dorsal zone (DZ), a region of auditory cortex that cross-modally reorganizes to mediate enhanced visual motion perception following deafness. In hearing cats, the largest projections to DZ arose from the dorsal division of the medial geniculate body (MGB) with lesser projections originating in the medial and ventral MGB and from the supragenulate and the lateral posterior nuclei. In general, while some variations in the strength of specific thalamic projections were noted, the pattern of projections arising from the thalamus in early- and late-deafened animals remained consistent with that of hearing subjects. These results complement the existing thalamic connectivity data described for congenitally deaf animals, which together demonstrate that thalamo-cortical connectivity patterns to DZ are conserved following deafness, irrespective of the time of onset and etiology of deafness.

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1. Introduction

Over the past few decades, an increasing number of studies have convincingly demonstrated that the brain is capable of reorganization following the loss or impairment of a sensory system (reviewed in Bavelier and Neville, 2002; Merabet and Pascual-Leone, 2010). This cross-modal plasticity occurs in regions of the brain that would normally process the missing sense, which then become capable of processing sensory information in the remaining modalities following sensory deprivation. In some cases, this

reorganization manifests as superior behavioral performance in sensory-deprived individuals compared to control participants (reviewed in Frasnelli et al., 2011; Kupers and Ptito, 2014). Moreover, these neuroplastic changes are known to occur in multiple sensory systems, as well as in both humans and animals, and have been observed using a variety of techniques, including functional magnetic resonance imaging, electrophysiological recordings and psychophysical testing.

While it is now well-accepted that the brain is capable of reorganization following sensory loss, the neural mechanisms underlying this plasticity are not well understood. Several putative mechanisms have been advanced including making use of connections that would otherwise be pruned during development, making use of existing 'silent' connections from other sensory modalities (unmasking), and/or via the creation of new sensory pathways (Rauschecker, 1995). Likewise, this connectional re-

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wiring could occur at any or all levels of the sensory hierarchy from the receptors (e.g. the retina or cochlea) to midbrain and thalamic sensory nuclei, to sensory cortex.

Anatomical tract tracing studies have begun to shed light on the structural underpinnings of cross-modal reorganization by comparing cerebral connectivity in sensory-deprived animals to that of their non-deprived counterparts. Initial investigations into the structural basis of cross-modal reorganization occurred in animal models of blindness. Injections made into the lateral geniculate nucleus of the thalamus (LGN), the major visual nucleus of the thalamus, resulted in ectopic labeling in the inferior colliculus, the principal midbrain nucleus of the auditory pathway, in neonatally bilaterally enucleated hamsters (Izraeili et al., 2002) and in the blind mole rat (Doron and Wollberg, 1994). Additionally, several investigations have documented aberrant subcortical inputs from non-visual regions of the thalamus associated with the limbic system following tracer injections in V1 in mice lacking functional rods (*Gnat-1*^{-/-}; Larsen et al., 2009), congenitally anophthalmic mice (Charbonneau et al., 2012), and neonatally bilaterally enucleated opossums (Karlen et al., 2006). However, in neonatally bilaterally enucleated opossums, substantial labelling in the primary auditory and somatosensory cortices, multimodal cortex, as well as in regions of the thalamus associated with somatosensory, and motor systems was also found (Karlen et al., 2006). Together, these studies suggest that in animal models of blindness, cross-modal reorganization occurs at multiple stages of the visual system hierarchy. However, these studies also raise questions in terms of the generalizability of the findings: are the documented changes species-specific, or would phylogenetically higher-order mammals follow the same principles of reorganization (Meredith and Lomber, 2016)? Does the etiology and timing of sensory loss play a role in determining how the brain structurally reorganizes following the loss or impairment of a sense (Butler and Lomber, 2013)?

These same questions persist with respect to investigations of neuroplasticity following sensory loss in other modalities. As in the visual system, evidence of structural reorganization within the auditory system following deafness has begun to accumulate. Ectopic retinal projections to auditory thalamus have been demonstrated in congenitally deaf mice (Hunt et al., 2005). However, despite electrophysiological evidence of cross-modal reorganization in the same animals, tracer injections in primary auditory cortex of adult-deafened ferrets failed to show evidence of structural reorganization of cortico-cortical or thalamo-cortical afferents (Allman et al., 2009). A series of recent investigations within specific regions of cat auditory cortex has compared projection patterns in hearing animals to those of the congenitally deaf (Barone et al., 2013), as well as to early- and late-deafened animals (Kok et al., 2014; Chabot et al., 2015; Wong et al., 2015; Meredith et al., 2016; Butler et al., 2016). To date, these studies have indicated that the overall pattern of cortical and thalamic projections does not change as a consequence of hearing loss, even though the strength of some existing cortical projections from other senses may be stronger in deaf animals than in hearing, depending on the region investigated.

To the best of our knowledge, the series of studies mentioned above collectively represent the first systematic investigation of cortico-cortical and thalamo-cortical reorganization following sensory loss. These studies offer a unique opportunity to comprehensively examine the structural changes that occur as a consequence of deafness for multiple auditory cortical regions within a single species, for which numerous reports of behavioral and electrophysiological evidence of cross-modal reorganization already exist (Lomber et al., 2010, 2011; Meredith and Lomber, 2011; Meredith et al., 2011), and within which there exists

extensive cortico-cortical and thalamo-cortical connectivity data for multiple sensory systems in intact animals (Scannell et al., 1995, 1999).

With that in mind, cortical and thalamic connectivity in hearing and congenitally deaf animals has been compared for the dorsal zone (DZ; Barone et al., 2013), an auditory cortical region that is known to cross-modally reorganize to confer behaviorally superior visual motion detection in congenitally deaf animals (Lomber et al., 2010). Electrophysiological findings have demonstrated that this region also contains visually-driven cells (Yaka et al., 2002; Allman and Meredith, 2007). Changes in cortical projection strength have been documented for this same region in animals deafened during development or in maturity (Kok et al., 2014). The same study indicated that animals deafened earlier in life showed greater evidence of structural reorganization than did late-deafened animals. However, it remains unknown whether the projection strength of thalamic afferents to DZ become altered as a consequence of early- or late-deafness, and whether any changes in thalamo-cortical connectivity that occur are altered as a function of the timing of the onset of deafness within the lifespan of the animal. Therefore, the present study sought to examine this possibility by comparing thalamo-cortical projection strength to DZ in hearing, early- and late-deafened animals. In total, we found little evidence of altered projection patterns in thalamo-cortical afferents to DZ as a consequence of deafness. With the addition of the present study, there is now comprehensive cortical and thalamic connectivity data for area DZ in hearing, congenitally deaf, early-deafened and late-deafened animals of the same species. This will allow for unique conclusions to be drawn that would not otherwise be possible.

2. Materials and methods

Thalamo-cortical connectivity was examined in 15 adult domestic cats obtained from a licensed commercial breeding facility (Liberty Laboratories, Waverly, NY). The animals used in this study were divided into three groups: five adult cats with normal hearing,

Table 1
List of abbreviations.

Thalamic	
<i>Visual</i>	
LGN	Lateral geniculate nucleus
LP	Lateral posterior nucleus
Pv	Pulvinar nucleus
<i>Auditory</i>	
MGd	Dorsal division, medial geniculate nucleus
AD	Anterodorsal subdivision
D	Dorsal subdivision
DD	Deep dorsal subdivision
DS	Dorsal superficial subdivision
MGm	Medial division, medial geniculate nucleus
MGv	Ventral division, medial geniculate nucleus
RP	Rostral pole
<i>Multisensory</i>	
SGL	Lateral division, supragenulate nucleus
SGm	Medial division, supragenulate nucleus
<i>Other</i>	
ILC	Intralaminar complex
LD	Lateral dorsal nucleus
OT	Optic tract
VP	Ventral posterior nucleus
General	
A	Anterior
D	Dorsal
L	Lateral
M	Medial
P	Posterior
V	Ventral

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