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Robust Subthreshold Cross-modal Modulation of Auditory Response by Cutaneous Electrical Stimulation in First- and Higher order Auditory Thalamic Nuclei

Akihisa Kimura* and Hiroki Imbe

Department of Physiology, Wakayama Medical University, Wakayama Kimiidera 811-1, 641-8509, Japan

Abstract—Conventional extracellular recording has revealed cross-modal alterations of auditory cell activities by cutaneous electrical stimulation of the hindpaw in first- and higher order auditory thalamic nuclei (Donishi et al., 2011). Juxta-cellular recording and labeling techniques were used in the present study to examine the cross-modal alterations in detail, focusing on possible nucleus and/or cell type-related distinctions in modulation. Recordings were obtained from 80 cells of anesthetized rats. Cutaneous electrical stimulation, which did not elicit unit discharges, i.e., subthreshold effects, modulated early (onset) and/or late auditory responses of first- (64%) and higher order nucleus cells (77%) with regard to response magnitude, latency and/or burst spiking. Attenuation predominated in the modulation of response magnitude and burst spiking, and delay predominated in the modulation of response time. Striking alterations of burst spiking took place in higher order nucleus cells, which had the potential to exhibit higher propensities for burst spiking as compared to first-order nucleus cells. A subpopulation of first-order nucleus cells showing modulation in early response magnitude in the caudal domain of the nucleus had larger cell bodies and higher propensities for burst spiking as compared to cells showing no modulation. These findings suggest that somatosensory influence is incorporated into parallel channels in auditory thalamic nuclei to impose distinct impacts on cortical and subcortical sensory processing. Further, cutaneous electrical stimulation given after early auditory responses modulated late responses. Somatosensory influence is likely to affect ongoing auditory processing at any time without being coincident with sound onset in a narrow temporal window. © 2018 IBRO. Published by Elsevier Ltd. All rights reserved.

Key words: attention, auditory response, cross-modal, cutaneous electrical stimulation, juxta-cellular recording, Medial geniculate nucleus.

INTRODUCTION

Sensory thalamic nuclei play key roles in gain and/or gate control of sensory processing as anatomical nodes where cortical and subcortical connections intersect (Jones, 2007; Bartlett, 2013; Sherman, 2016). The conventional view considers that the control operates primarily for intra-modal sensory processing of a given sensory modality in first-order thalamic nuclei and for cross- as well as intra-modal sensory processing in higher order thalamic nuclei (Bordi and LeDoux, 1994; Komura et al., 2001; Hu, 2003). This distinction in contribution to cross-modal

sensory processing, however, becomes ambiguous, as recent studies have highlighted cross-modal sensory interactions in primary sensory areas in the cortex (Murray et al., 2005; Kayser et al., 2005, 2008; Lakatos et al., 2007; Driver and Noesselt, 2008; Brang et al., 2015). It is suggested that first-order thalamic nuclei, which subserve sensory processing in their tight loop connections with primary sensory areas in the cortex, could contribute to cross-modal sensory processing as well. In fact cross-modal modulation of thalamic cell activities has been revealed in first-order thalamic nuclei (Noesselt et al., 2010; Donishi et al., 2011; Allen et al., 2017). It thus seems necessary to reorganize our understanding of sensory processing with assumption of the hierarchy from early unisensory processing to late multi-sensory interplay (Ghazanfar and Schroeder, 2006; Tyll et al., 2011). This notion then raises the question of whether and how first- and higher order thalamic nuclei differentially contribute to cross-modal sensory processing. In the present study, to gain insights into this question, we examined cross-modal effects of

*Corresponding author. Fax: +81-73-441-0622.

E-mail address: akimura@wakayama-med.ac.jp (A. Kimura).

Abbreviations: AI, primary auditory field; CN, cochlear nucleus; CNIC, central nucleus of the inferior colliculus; DCN, dorsal cochlear nucleus; ECIC, external cortex of the inferior colliculus; IC, inferior colliculus; LTS, low-threshold calcium spike; MG, medial geniculate nucleus; MGD, dorsal division of the medial geniculate nucleus; MGN, medial division of the medial geniculate nucleus; MGv, ventral division of the medial geniculate nucleus; SG, supragenicular nucleus; PP, peripeduncular nucleus; TRN, thalamic reticular nucleus.

somatosensory stimulation on cell activities in first- and higher order auditory thalamic nuclei, focusing on possible distinctions in cross-modal modulation of cell activities in the two types of thalamic nuclei.

Cross-modal modulation of cortical cell activities in the primary auditory area by somatosensory stimulation that includes cutaneous electrical stimulation (Kayser et al., 2005; Murray et al., 2005; Lakatos et al., 2007; Basura et al., 2012) represents the cross-modal sensitivity of primary sensory areas in the cortex. Since somatosensory influence on the primary auditory area in the cortex includes feedforward effects emerging with short latencies (Lakatos et al., 2007; Basura et al., 2012), a part of the influence is assumed to originate in thalamocortical projections of higher order thalamic nuclei (Hackett et al., 1998, 2007; Kimura et al., 2003; Smiley and Falchier, 2009) that receive somatosensory as well as auditory inputs from brain stem nuclei (LeDoux et al., 1987; Bordi and LeDoux, 1994). Besides, our previous study has revealed robust alterations of auditory response magnitude by cutaneous electrical stimulation in the ventral division (MGV) of the medial geniculate nucleus (MG) of the rat, the first-order thalamic nucleus (Donishi et al., 2011), which is considered devoted to unisensory information processing of auditory modality (Komura et al., 2001). This suggests that first- as well as higher order auditory thalamic nuclei mediate somatosensory influence on cortical cell activity in the primary auditory area. It is conceivable that somatosensory influence incorporated into auditory cell activity in the cochlear nuclei (Wu et al., 2015) is merely reflected on cell activities of the MGV that does not receive somatosensory inputs (LeDoux et al., 1987; Bordi and LeDoux, 1994). Alternatively, it could be possible to assume that MGV as well as higher order thalamic nucleus cells incorporate sub-threshold somatosensory influence into cell activities, most likely by receiving inhibition driven or modulated by cutaneous electrical stimulation, as suppression predominates in the alterations of auditory response in both the MGV and higher order thalamic nuclei (Donishi et al., 2011). A noteworthy finding likely relevant to this assumption is that cutaneous electrical stimulation robustly modulates auditory responses of thalamic reticular nucleus (TRN) cells that send inhibitory projections to either the MGV or higher order auditory thalamic nuclei (Kimura, 2017). The somatosensory influence, along with distinctions in cell activity (Hu, 2003; Yu et al., 2004a,b; Smith et al., 2006) and efferent connectivity (LeDoux et al., 1985; Shammah-Lagnado et al., 1996; Jones, 1998; Campeau and Watson, 2000; Kimura et al., 2003; Smith et al., 2012) between the MGV and higher order auditory thalamic nuclei, could then lead to distinct alterations of thalamic auditory response that subsequently impose differential impacts on cortical and subcortical sensory processing. In the present study we examined the subthreshold effects of cutaneous electrical stimulation on auditory responses in first- and higher order thalamic nuclei in detail, using juxta-cellular recording and labeling techniques that allow us to precisely determine single cell activity, location and morphology. In an attempt to delineate subtle distinctions in auditory response modulation,

our interest was focused on alterations of burst spiking and latency besides response magnitude in early (onset) and late auditory responses. In the results auditory cells in higher order thalamic nuclei exhibited alterations of cell activity distinct from those in the MGV under somatosensory influence with regard to burst spiking. The results also suggest the existence of somatosensory influence on the MGV apart from already-processed multi-sensory effects. Further, there seems to be a subpopulation of auditory cells highly susceptible to somatosensory influence in the caudal MGV that have larger cell bodies and higher propensities for burst spiking.

EXPERIMENTAL PROCEDURES

Animals and surgical procedures

Experiments were carried out in 13 adult male Wistar rats (Kiwa Laboratory Animal, Wakayama, Japan) weighing 297–353 g (mean, 333 g). The ages of animals ranged from 8 to 10 weeks. All studies were performed according to the approved institutional animal care and use protocol of the Animal Research Committee of Wakayama Medical University, which conforms to the National Institutes of Health Guide for the Care and Use of Laboratory Animals.

After induction of an anesthetized state by an initial intraperitoneal (i.p.) bolus injection of pentobarbital (5–8 mg/100 g body weight), animals were maintained in an areflexic state throughout the experiment by continuous injections of chloral hydrate (4–6 mg/100 g body weight/h, i.p.) and pentobarbital (0.5–0.8 mg/100 g body weight/h, i.p.) through a cannula placed in the abdomen, using a microinjection pump (CFV-2100, Nihon Kohden, Tokyo, Japan). This eliminated supplemental bolus injections and minimized fluctuations of anesthetic levels. The animals were mounted on a stereotaxic apparatus, using hollow ear bars with blunted tips that do not damage the tympanic membrane. The cisterna magna was incised to drain cerebrospinal fluid so as to reduce edema and pulsations of the brain. A local anesthetic (2% xylocaine) was applied to all surgical wounds.

A burr hole was made in the skull and dura (anteroposterior, 2.5–5.0 mm posterior to bregma; mediolateral, 2.4–4.6 mm lateral to midline) to vertically insert a glass capillary into the brain and access auditory thalamic nuclei for juxtacellular recording and labeling.

Sensory stimulation and recording of unit discharges

Noise bursts (white noise; intensity, 35–97-dB SPL at the ear; duration, 100 ms including 5-ms rise and fall time), which were digitally generated (100 kHz) and converted to analog voltage signals through an A-D converter (PCI-MIO-16XE-10, National Instruments, TX, USA), were delivered from a free-field speaker (SRS-A41, Sony, Tokyo, Japan) placed lateral to the ear contralateral to the recording site. The intensity of noise burst (inter-intensity interval, 2 or 3 dB) was calibrated using a 1/4 inch condenser microphone (Type 4939;

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