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

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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

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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.

42 somatosensory stimulation on cell activities in first- and
43 higher order auditory thalamic nuclei, focusing on possi-
44 ble distinctions in cross-modal modulation of cell activities
45 in the two types of thalamic nuclei.

46 Cross-modal modulation of cortical cell activities in the
47 primary auditory area by somatosensory stimulation that
48 includes cutaneous electrical stimulation (Kayser et al.,
49 2005; Murray et al., 2005; Lakatos et al., 2007; Basura
50 et al., 2012) represents the cross-modal sensitivity of pri-
51 mary sensory areas in the cortex. Since somatosensory
52 influence on the primary auditory area in the cortex
53 includes feedforward effects emerging with short laten-
54 cies (Lakatos et al., 2007; Basura et al., 2012), a part of
55 the influence is assumed to originate in thalamocortical
56 projections of higher order thalamic nuclei (Hackett
57 et al., 1998, 2007; Kimura et al., 2003; Smiley and
58 Falchier, 2009) that receive somatosensory as well as
59 auditory inputs from brain stem nuclei (LeDoux et al.,
60 1987; Bordi and LeDoux, 1994). Besides, our previous
61 study has revealed robust alterations of auditory response
62 magnitude by cutaneous electrical stimulation in the ven-
63 tral division (MGV) of the medial geniculate nucleus (MG)
64 of the rat, the first-order thalamic nucleus (Donishi et al.,
65 2011), which is considered devoted to unisensory infor-
66 mation processing of auditory modality (Komura et al.,
67 2001). This suggests that first- as well as higher order
68 auditory thalamic nuclei mediate somatosensory influ-
69 ence on cortical cell activity in the primary auditory area.
70 It is conceivable that somatosensory influence incorpo-
71 rated into auditory cell activity in the cochlear nuclei (Wu
72 et al., 2015) is merely reflected on cell activities of the
73 MGV that does not receive somatosensory inputs
74 (LeDoux et al., 1987; Bordi and LeDoux, 1994). Alterna-
75 tively, it could be possible to assume that MGV as well
76 as higher order thalamic nucleus cells incorporate sub-
77 threshold somatosensory influence into cell activities,
78 most likely by receiving inhibition driven or modulated by
79 cutaneous electrical stimulation, as suppression predom-
80 inates in the alterations of auditory response in both the
81 MGV and higher order thalamic nuclei (Donishi et al.,
82 2011). A noteworthy finding likely relevant to this assump-
83 tion is that cutaneous electrical stimulation robustly mod-
84 ulates auditory responses of thalamic reticular nucleus
85 (TRN) cells that send inhibitory projections to either the
86 MGV or higher order auditory thalamic nuclei (Kimura,
87 2017). The somatosensory influence, along with distinc-
88 tions in cell activity (Hu, 2003; Yu et al., 2004a,b; Smith
89 et al., 2006) and efferent connectivity (LeDoux et al.,
90 1985; Shammah-Lagnado et al., 1996; Jones, 1998;
91 Campeau and Watson, 2000; Kimura et al., 2003; Smith
92 et al., 2012) between the MGV and higher order auditory
93 thalamic nuclei, could then lead to distinct alterations of
94 thalamic auditory response that subsequently impose dif-
95 ferential impacts on cortical and subcortical sensory pro-
96 cessing. In the present study we examined the
97 subthreshold effects of cutaneous electrical stimulation
98 on auditory responses in first- and higher order thalamic
99 nuclei in detail, using juxta-cellular recording and labeling
100 techniques that allow us to precisely determine single cell
101 activity, location and morphology. In an attempt to delin-
102 eate 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 somatosen-
sory 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 influ-
ence 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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