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Research paper

A possible role for a paralemniscal auditory pathway in the coding of slow temporal information

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ABSTRACT

Low-frequency temporal information present in speech is critical for normal perception, however the neural mechanism underlying the differentiation of slow rates in acoustic signals is not known. Data from the rat trigeminal system suggest that the paralemniscal pathway may be specifically tuned to code low-frequency temporal information. We tested whether this phenomenon occurs in the auditory system by measuring the representation of temporal rate in lemniscal and paralemniscal auditory thalamus and cortex in guinea pig. Similar to the trigeminal system, responses measured in auditory thalamus indicate that slow rates are differentially represented in a paralemniscal pathway. In cortex, both lemniscal and paralemniscal neurons indicated sensitivity to slow rates. We speculate that a paralemniscal pathway in the auditory system may be specifically tuned to code low-frequency temporal information present in acoustic signals. These data suggest that somatosensory and auditory modalities have parallel sub-cortical pathways that separately process slow rates and the spatial representation of the sensory periphery.

1. Introduction

A prominent acoustical characteristic of animal communication calls, as well as human speech (Rosen, 1992), is low-frequency temporal information. For example, acoustical analysis of the guinea pig chutter and purr calls shows peaks in their temporal envelopes at approximately 5 and 10 Hz (Huetz et al., 2009; Suta et al., 2003).

In the auditory system, it has been suggested that temporal rate information is represented with a two-stage mechanism in auditory thalamus (Bartlett and Wang, 2007) and cortex (Lu et al., 2001). This model proposes that two populations of neurons in auditory thalamus and cortex facilitate the representation of a wide range of temporal features in acoustical signals in a complementary fashion. One population of neurons, referred to as the "synchronized" population, produces stimulus-synchronized discharges at long inter-stimulus intervals (i.e., low-frequency stimuli < 40 Hz) and little activity at shorter intervals. Another population of neurons, referred to as the "non-synchronized" population, does not exhibit stimulus-synchronized activity; rather, they represent acoustical stimuli with brief inter-stimulus intervals (higher-frequency stimuli > 50 Hz) with monotonically changing discharge rates (Wang et al., 2008). Results from the rat trigeminal system demonstrate that slow rates (between 2 and 8 Hz) are differentially coded by lemniscal and paralemniscal pathways (Ahissar et al., 2000). Lemniscal neurons in both thalamus and cortex code stimulation frequency with constant latencies while paralemniscal neurons code stimulation frequency as systematic changes in latency. Based on its unique sensitivity for slow rates, it is suggested that the paralemniscal pathway is "optimally tuned for temporal processing of vibrissal information around the whisking frequency range (8 Hz)" (Ahissar et al., 2000).

A hypothesis based on the somatosensory results is that a paralemniscal pathway in the auditory system may be tuned to code slow rates in acoustic signals. A parallel pathway system has been proposed by Rauschecker et al. (1997) and additionally it has been suggested that parallel pathways originate in sub-cortical structures (He and Hashikawa, 1998; Kosaki et al., 1997). The results of temporal integration in the dorsal cortex of the cat further suggest that the paralemniscal pathway might be involved in temporal information

Abbreviations: MGv, medial geniculate body of thalamus; MGs, shell nucleus of the medial geniculate body; MGcm, caudomedial nucleus of the medial geniculate body; A1, primary auditory cortex; DC, dorsocaudal field of cortex; VCB, ventral caudal belt of auditory cortex; NMDA, N-Methyl-D-aspartic acid; AMPA, α-amino-3-hydroxyl-5-methyl-4-isoxazole-propionate; EPSP, excitatory post-synaptic potential.

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processing (He et al., 1997). Surprisingly, there has been no systematic investigation of paralemniscal representation of acoustic rate in auditory thalamus and whether it differs from the lemniscal representation. To investigate temporal response properties of lemniscal and paralemniscal regions of the thalamocortical auditory system, we measured local field potentials (LFPs) from lemniscal and paralemniscal neurons in guinea pig thalamus and cortex in response to click trains with rates between 2 and 8 Hz.

2. Materials and methods

The research protocol was approved by the Animal Care and Use Committee of Northwestern University.

2.1. Animal preparation

The experimental materials and procedures were similar to those reported previously (Cunningham et al., 2002; McGee et al., 1996). Eighteen pigmented guinea pigs of either sex, weighing between 400 and 600 g, were used as subjects. Animals were initially anesthetized with ketamine hydrochloride (100 mg/kg) and xylazine (8 mg/kg). Smaller supplemental doses (25 mg/kg ketamine; 4 mg/kg xylazine) were administered hourly or as needed throughout the rest of the experiment. Following the induction of anesthesia, the animal was mounted in a stereotaxic device, located in a sound-treated booth (IAC), for the duration of the experiment. Body temperature was maintained at 37.5 °C by using a thermistor-controlled heating pad on the guinea pig's abdomen (Harvard). Normal hearing sensitivity was confirmed by auditory brainstem response. The auditory brainstem response was elicited by a click stimulus at 70 and 40 dB HL (referenced to normal guinea pig click (ABR) thresholds) from a recording site located at the posterior vertex/midline of the scalp using an EMG needle electrode. A rostro-caudal incision was made along the scalp surface and the tissue was retracted to expose the skull. Holes were drilled in the skull under an operating microscope. The dura was removed with a cautery to prevent damage to the recording electrode, and the cortical surface was coated with mineral oil.

2.2. Anatomical structures

The lemniscal and paralemniscal auditory nuclei investigated in the present study were selected because they have the same reciprocal and parallel connectivity patterns as the lemniscal and paralemniscal pathways in the rat trigeminal system (somatosensory: (Diamond and Armstrong-James, 1992; Woolsey, 1997); auditory: (Redies et al., 1989b)). The lemniscal pathway described here consists of the ventral nucleus of the medial geniculate body of thalamus (MGv) and primary auditory cortex. MGv is tonotopically organized, shows a preference for tonal stimuli and exhibits short-latency responses (He, 2002; Redies and Brandner, 1991). Primary auditory cortex in guinea pig consists of two areas, A1 and the dorsocaudal field (DC), which are characterized by tonotopic organization, sharp frequency tuning, a preference for tonal stimuli and short response latencies (Redies et al., 1989a; Wallace et al., 2000). Lemniscal cortex receives its afferent thalamic input from MGv (Redies et al., 1989b).

The paralemniscal nucleus of thalamus described here is the shell nucleus of the medial geniculate body (MGs) (He, 2002; Redies et al., 1989b). The shell nucleus is a band of neurons that surround the MGv dorsally, laterally and ventrally. Neurons of the MGs are generally characterized by broad frequency tuning and long-latency responses (He, 2002; Redies and Brandner, 1991). This nucleus projects to the ventral caudal belt of auditory cortex (VCB), the paralemniscal cortical area described in the present work. Neurons of VCB show broad frequency tuning, are more responsive to noise compared to pure tones, and have long-latency responses (Wallace et al., 2000). Based on these particular anatomical connections, it is postulated that these auditory thalamocortical connections represent parallel pathways in the ascending auditory system.

We performed histology on MGv and MGs using hematoxylin and eosin staining and only subtle differences were evident between MGv and MGs with respect to the density of cell bodies. This corroborates previous anatomical investigations of guinea pig MG using Nissl-staining indicating an indistinct cytoarchitectonic division between these nuclei; it was proposed that the cell population of these nuclei is intermingled (Redies et al., 1989b). During data collection, we relied on the relative anatomical locations of these nuclei, as well as the substantial differences between their response properties to various probe stimuli, as means to distinguish these two nuclei.

2.3. Acoustic stimuli

Acoustic stimuli were generated digitally and presented in Matlab (Mathworks). Acoustic stimuli were delivered to the contralateral ear using Etymotic insert earphones (ER2) through the hollow earbars of the stereotaxic device. The sound pressure level (SPL, expressed in dB re 20 mPa) was calibrated over a frequency range of 0.02–20 kHz using a condenser microphone (Brüel and Kjaer). Three-second-long click train stimuli were delivered at a level of 75 dB SPL (peak intensity). Click trains of 2, 5 and 8 Hz were randomly presented with an inter-stimulus interval of 1 s. At all electrode penetrations, each of the three click rates was presented 100 times. Clicks consisted of 100 μs rectangular pulses. Clicks with alternating polarities were presented to remove any possibility of a stimulus artifact within the response. The delivery system outputted the signal through a 16-bit converter at a sampling rate of 16 kHz. That system triggered the PC-based collection computer. Third-octave tone-pips were used to map auditory cortex. Mapping of auditory cortex was essential to properly locating the paralemniscal cortical nucleus. Tones were 100 ms in duration with a rise-fall time of 10 ms.

2.4. Neurophysiological recording

Both thalamus and cortex were accessed with a vertical approach using tungsten microelectrodes (Micro Probe) with impedance between 1 and 2 MΩ at 1 kHz. An electrode was advanced perpendicular to the surface of cortex using a remote-controlled micromanipulator (Märzhäuser-Wetzlar). For both MG and cortical recordings, the dorsal/ventral reference of the electrode was determined at a point slightly above cortex at the first penetration, and this coordinate was kept for the remainder of the experiment.

Typically, recordings of MG and cortex were performed on different animals and recording sessions. For recording MGv, rostral/caudal and medial/lateral references were set at the interaural line and bregma, respectively. Locations were approximately 4.8 mm rostral to the interaural line, 4.0 mm left or right of bregma, and 7.2 mm ventral to the surface of the brain. During penetration, auditory stimuli were delivered (clicks at 3.5 Hz), and visual inspection, using a monitoring oscilloscope, of the response size and waveform morphology was considered. If the response was small in amplitude and broad in shape, electrode penetration was continued. This process was repeated until the morphology of the waveform conformed to the large amplitude, sharp onset response commonly observed in recordings obtained from the ventral division of the MG. Previous use of this technique has shown a 100% hit rate for the ventral division of the medial geniculate using the