Research paper

Equivalent-rectangular bandwidth of single units in the anaesthetized guinea-pig ventral cochlear nucleus

Mark Sayles *, Ian M. Winter

Centre for the Neural Basis of Hearing, The Physiological Laboratory, University of Cambridge, CB2 3EG, UK

ARTICLE INFO

ABSTRACT

Frequency-tuning is a fundamental property of auditory neurons. The filter bandwidth of peripheral auditory neurons determines the frequency resolution of an animal's auditory system. Behavioural studies in animals and humans have defined frequency-tuning in terms of the "equivalent-rectangular bandwidth" (ERB) of peripheral filters. In contrast, most physiological studies report the Q[best frequency/bandwidth] of frequency-tuning curves. This study aims to accurately describe the ERB of primary-like and chopper units in the ventral cochlear nucleus, the first brainstem processing station of the central auditory system. Recordings were made from 1020 isolated single units in the ventral cochlear nucleus of anesthetized guinea pigs in response to pure-tone stimuli which varied in frequency and in sound level. Frequency-threshold tuning curves were constructed for each unit and estimates of the ERB determined using methods previously described for auditory-nerve-fibre data in the same species. Primary-like, primary-notch, and sustained- and transient-chopper units showed frequency selectivity almost identical to that recorded in the auditory nerve. Their tuning at pure-tone threshold can be described as a function of best frequency (BF) by $ERB = 0.31 * BF^{0.5}$.

© 2010 Elsevier B.V. All rights reserved.

1. Introduction

Frequency selectivity is the single most dominant concept in auditory neuroscience, and is a defining feature of auditory-system neurons. Sharp tuning arises along the basilar membrane as an active process relying on outer hair-cell motility (Ashmore, 2008; Brownell et al., 1985; Dallos, 2008; Robles and Ruggero, 2001; Sellick et al., 1982), and is reflected in the responses of neurons at each subsequent processing station. Fletcher's band-widening experiments (Fletcher, 1938, 1940) established the concept of the "critical band," such that different acoustic frequencies are processed in separate "channels" within the auditory system. Human psychoacoustic and animal physiological studies of auditory-filter bandwidths, each with subtly different methodology, abound (e.g., Evans, 2001; Glasberg and Moore, 1986, 1990; Patterson, 1976; Ruggero and Temchin, 2005; Shera et al., 2002). The "equivalent-rectangular bandwidth" (ERB) is a useful measurement of auditory-filter bandwidth, allowing comparisons to be made across species and methodologies. Auditory filters are asymmetrical, and are not rectangular in shape (e.g., Hartmann, 1997; Moore, 2003); however, the ERB of an auditory filter is the bandwidth of a rectangular filter having the same peak transmission as that filter and which passes the same total power for a white-noise input.

Although "critical-band filters" arise peripherally from the mechanical tuning of the basilar membrane, tonotopically-arranged frequency-tuned arrays of neurons are present at all central auditory loci from the auditory nerve, through the brainstem nuclei to cortex. Like other sensory systems, such as vision, the response properties of auditory neurons become more complex as the system is ascended from the periphery to higher cortical processing areas. The simple band-pass receptive fields of auditory nerve fibres (ANFs) give way to complex receptive fields in auditory cortex with high-level properties such as context dependency (Atiani et al., 2009; Elhilali et al., 2007; Evans, 1972, 2001; Fritz et al., 2007; Kiang et al., 1967). Basic neuronal response properties commonly underlie complex perception. Frequency selectivity forms the basis of many aspects of audition such as signal detection against background noise, stream segregation and pitch perception. The detection of signals against a background noise is dependent on both within-channel cues (Delgutte and Kiang, 1984; Geisler and Silkes, 1991; Kim and Parham, 1991; May et al., 1998; Sachs et al., 1983; Winslow and Sachs, 1987, 1988),

---

and between-channel cues (Neuert et al., 2004; Pressnitzer et al., 2001; Verhey et al., 2003). Frequency selectivity and temporal adaption effects have been shown to account for the build-up of perceptual stream segregation both in the auditory cortex (Micheyl et al., 2005, 2007), and peripherally in the cochlear nucleus (Pressnitzer et al., 2008). Information about the harmonic structure of a complex sound is present in the differential activation of cochlear filters, at least for low-numbered, "resolved," harmonics (Bernstein and Oxenham, 2003; Plomp, 1964). This allows us to hear out the partials of a complex tone, and may form the basis of pitch perception through harmonic template matching (Cedolin and Delgutte, 2007; de Cheveigné, 2008; Goldstein, 1973; Shamma and Klein, 2000; Terhardt, 1974; Wightman, 1973).

The cochlear nucleus (CN) is the central termination site of all ANFs and constitutes the initial processing station of the central auditory system, where parallel streams of information regarding parameters of the acoustic environment are processed in different neuronal sub-populations. The response properties of most CN units differ significantly from their ANF inputs and have been correlated with the diverse morphology of CN neurons. The diversity of CN neural response types is often taken as evidence of significant processing at this level. Indeed, many studies have examined the representations and transformations of simple and complex sounds in the CN. Simple properties such as frequency selectivity, temporal adaptation, and side-band inhibition in CN units have been shown to account for complex psychophysical phenomena such as co-modulation masking release and auditory stream segregation (Pressnitzer et al., 2001, 2008; Verhey et al., 2003).

Building on previous models of the auditory periphery (Holmes et al., 2004; Meddis and O'Mard, 2005, 2006; Sumner et al., 2003; Zilany and Bruce, 2006) and CN units (Bahmer and Langner, 2009; Meddis and O'Mard, 2006; Wiegrebe and Meddis, 2004), sophisticated models of neuronal circuits in the CN and other auditory nuclei are now being used to examine the contribution of brainstem circuits to complex perceptual abilities of whole animal observers (e.g., O'Mard and Winter, 2009; Pecka et al., 2007). For models to provide accurate physiological predictions the basic properties, such as adaptation time constants (Bleeck et al., 2006; Meddis and O'Mard, 2005), and frequency-tuning, of physiologically-characterised individual units in the circuit must be known. Despite the large number of studies reporting responses to simple and complex sounds in the guinea-pig ventral cochlear nucleus (VCN), and the development of computational models of CN processing, quantitative descriptions of frequency-tuning here are lacking. This study aims to fill this gap by providing quantitative estimates of the frequency selectivity of the major VCN unit types in terms of the equivalent-rectangular bandwidth of their frequency response areas. In contrast to other unit types, and as shown previously in the cat (Rhode and Smith, 1986), onset units in this study are significantly more broadly tuned than previous behavioural and ANF measurements. Importantly, we show that the ERB of primary-like, primary-notch, and transient- and sustained-chopper units does not differ significantly from that measured behaviourally, or from that of guinea-pig ANFs. The sharp tuning, which arises along the basilar membrane, and is reflected in the behavioural frequency selectivity of the awake guinea-pig is also present in the responses of the majority of ventral cochlear nucleus units in the anaesthetized animal.

2. Materials and methods

2.1. The preparation

Experiments were performed on 92 pigmented guinea pigs (*Cavia porcellus*), weighing between 320 and 610 g. Animals were anaesthetized with urethane (1.0 g/kg, *ip*). Hypnorm (*fentanyl citrate*, 0.315 mg/ml; *fluanisone*, 10 mg/ml; Janssen, High Wycombe,

UK) was administered as supplementary analgesia (1 ml/kg, *im*). Anesthesia and analgesia were maintained at a depth sufficient to abolish the pedal withdrawal reflex (front paw). Additional doses of hypnorm (1 ml/kg, *im*) or urethane (0.5 g/kg, *ip*) were administered on indication. Core temperature was monitored with a rectal probe and maintained at 38 °C using a thermostatically-controlled heating blanket (Harvard Apparatus, MA). The trachea was cannulated and on signs of suppressed respiration, the animal was ventilated with a pump (Bioscience, UK). Surgical preparation and recordings took place in a sound-attenuated chamber (IAC). The animal was placed in a stereotaxic frame, which had ear bars coupled to hollow speculae designed for the guinea-pig ear. A mid-saggital scalp incision was made and the periosteum and the muscles attached to the temporal and occipital bones were removed. The bone overlying the left bulla was fenestrated and a silver-coated wire was inserted into the bulla to contact the round window of the cochlea for monitoring compound action potentials (CAP). The hole was resealed with Vaseline. The CAP threshold was determined at selected frequencies at the start of the experiment and thereafter upon indication. If thresholds deteriorated by more than 10 dB and were non-recoverable (e.g., by removing fluid from the bulla or by artificially ventilating the animal) the experiment was terminated. A craniotomy was performed exposing the left cerebellum. The overlying dura was removed and the exposed cerebellum was partially aspirated to reveal the underlying cochlear nucleus. The hole left from the aspiration was then filled with 1.5% agar in saline to prevent desiccation. The experiments performed in this study were carried out under the terms and conditions of the project license issued by the United Kingdom Home Office to the second author.

2.2. Neural recordings

Single units were recorded extracellularly with glass-coated tungsten micro-electrodes (Merrill and Ainsworth, 1972). Electrodes were advanced in the saggital plane by a hydraulic microdrive (650 W; David Kopf Instruments, Tujunga, CA) at an angle of 45°. Single units were isolated using broadband noise as a search stimulus. All stimuli were digitally synthesized in real-time with a PC equipped with a DIGI 9636 PCI card that was connected optically to an AD/DA converter (ADI-8 DS, RME audio products, Germany). The AD/DA converter was used for digital-to-analog conversion of the stimuli as well as for analog-to-digital conversion of the amplified (1000×) neural activity. The sample rate was 96 kHz. The AD/DA converter was driven using ASIO (Audio Streaming Input Output) and SDK (Software Developer Kit) from Steinberg (Lloyd, 2002).

After digital-to-analog conversion, the stimuli were equalized (phonic graphic equalizer, model EQ 3600; Apple Sound) to compensate for the speaker and coupler frequency response and fed into a power amplifier (Rotel RB971) and a programmable end attenuator (0–75 dB in 5 dB steps, custom build) before being presented over a speaker (Radio Shack 40–1377 tweeter assembled by Mike Ravicz, MIT, Cambridge, MA) mounted in the coupler designed for the ear of a guinea pig. The stimuli were monitored acoustically using a condenser microphone (Brüel & Kjær 4134, Denmark) attached to a calibrated 1-mm diameter probe tube that was inserted into the speculum close to the eardrum. Neural spikes were discriminated in software, stored as spike times on a PC and analyzed off-line using custom-written MATLAB programs (The MathWorks, Inc., Natick, MA).

2.3. Unit classification

Upon isolation of a unit, its BF and excitatory threshold were determined using audio-visual criteria. Spontaneous activity was