



A computational model of human pitch strength and height judgments

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ABSTRACT

A synchronization model of pitch processing was extended to include lateral inhibition mechanisms that have been observed in the mammalian mid brain, and information integration mechanisms consistent with observed changes to response fields of mammalian auditory cortex neurons. Model parameters for the inhibition mechanisms were adapted to fit model outputs to observed temporal dynamics of pitch height difference limens from the literature. Pitch strength was defined as the certainty of pitch height judgment, and was calculated by normalizing model responses by their mean. The model was adapted to fit experimental pitch strength data reported in the literature for pure tones and harmonic complexes. It was proposed that pitch height is first estimated in relation to patterns (or templates) of tonotopic activation on the auditory nerve for particular stimulus types. These patterns are stored in long term memory. This pitch height estimation primes cortical pitch neurons to integrate finely tuned pitch information from the inferior colliculus across the periodotopic and tonotopic dimensions. Predicted pitch strength for complexes of unresolved harmonics, iterated rippled noise and amplitude modulated tones using this model also conformed to behavioral data from the literature.

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1. Introduction

The neurophysiological mechanisms of pitch processing are not yet fully understood and there are a number of competing computational models in the current literature (Dicke et al., 2007; Meddis and O'Mard, 2006; Guérin et al., 2006; Nelson and Carney 2004; Shamma and Klein, 2000; Dau et al., 1997). These models focus on processing up to the level of the inferior colliculus, where electrophysiological data from microelectrode studies in animals have shown the presence of tightly tuned place-rate coding across both periodotopic and tonotopic dimensions in response to sinusoidal amplitude modulated tones (Langner and Schreiner, 1988). Electrophysiological data from the region near the anterolateral border of the primary auditory cortex of marmoset monkeys has revealed an array of tightly tuned pitch sensitive neurons that respond to pure tones and virtual pitches (Bendor and Wang, 2005). It is not known how the multidimensional response fields found in the inferior colliculus are processed to generate this pitch array at the level of the auditory cortex for varying stimulus types.

In this paper an algorithm based on the synchronization models of Meddis and O'Mard (2006) had been adapted to jnd data in the literature by the addition of models of the lateral inhibition mechanisms that have been observed in the cochlear nucleus (CN) and IC of animals. Data integration schemes were then applied to the model outputs to adapt the model to behavioral pitch strength data. These schemes were interpreted in terms of neurophysiological mechanisms that are likely to occur at the level of the thalamus and auditory cortex.

1.1. The neurophysiology

1.1.1. Synchronization and rate coding of pitch

The first neural processing site in the central auditory system is the CN. It may be further subdivided into dorsal, anteroventral and posteroventral CN subnuclei, with the latter often referred to together as simply the ventral cochlear nucleus. Each of these subnuclei are tonotopically arranged, receiving direct innervation from the auditory nerve (AN), and through frequency specific projections between the nuclei.

Stellate cells in the ventral CN have been shown to receive both excitatory and inhibitory dendritic and somatic input (Oertel, 1985). A large percentage of these cells, the sustained choppers (Cs), may be characterized by their highly regular firing pattern with a frequency of firing that was independent of the stimulus frequency at their characteristic frequency, CF (Blackburn and Sachs, 1991). Cs units are innervated from a narrow range of AN

Abbreviations: AN, auditory nerve; BMF, best modulation frequency; CF, characteristic frequency; CN, cochlear nucleus; Cs, sustained chopper neuron; Ct, transient chopper neuron; IC, inferior colliculus; ISR, integrated auditory nerve spike rate; jnd, just noticeable difference limen; MF, modulation function; PSTH, peri-stimulus time histogram

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fibers which define their characteristic frequency. Each unit is likely to have between 5 and 10 AN synapses. Under current clamp conditions ventral CN Cs units fire with near perfect regularity with a frequency defined by the rate at which input current was integrated to reach the cells' activation potential (Oertel, 1985). The cell's synchronization to the modulation frequency of the stimulus, as measured by the fraction of phase locked spikes, varies with frequency and exhibits a peak at the best modulation frequency, BMF (Frisina et al., 1990). The frequency of firing under current clamp conditions corresponds to the cell's BMF (Wiegube and Winter, 2001). An array of Cs units with varying BMF generate a periodotopic dimension in later stages of auditory processing.

Under auditory stimulation multiple repetitions of a cell's responses are summed to produce a peri-stimulus time histogram, PSTH (Blackburn and Sachs, 1991; Wiegube and Meddis, 2004). The PSTH for Cs units show the effects of jitter between responses to stimulus presentations, and the peak heights in the PSTH decay to a constant level of randomly distributed spikes after about 8 prominent peaks. This jitter was caused by the variations in the time at which the post synaptic potential reaches the action potential, due to small variations in the time of arrival of AN spikes.

The mechanism of the Meddis' synchronization model of pitch may be summarized as follows. Synaptic inputs arriving before the *best modulation period* (BMP), the inverse of the BMF, are summed until the post synaptic potential in the cell soma exceeds the action potential and the cell fires. The length of the BMP is determined by the Cs unit's maximum rate of integration. Therefore the unit is unlikely to fire again if the next peak in AN spike rate arrives before the BMP. The closer together the input spikes arrive, the greater the resulting increase in post synaptic potential, as chloride leakage currents have less time to cause its decay. Therefore a volley of well synchronized inputs, which occur at peaks in the firing rate of phase-locked ANs, will be more likely to cause an action potential than a volley of dispersed input spikes. The time at which the cell fires will be more variable if the next peak in AN spike rate arrives after the BMP, because the incoming spikes are more widely spread over time. Therefore jitter will increase and synchronization between similarly tuned Cs units will decrease.

It was proposed that the rate code for pitch in the IC is created by coincidence detection in neurons innervated by these Cs units (Wiegube and Meddis, 2004). High synchronization of Cs units will cause more coincidence detection events in these IC neurons and hence increased firing rates. The best frequencies of IC neurons are defined by the BMF of the Cs units that innervate them.

1.1.2. Lateral inhibition

Many researchers have observed that neural tuning sharpens higher in the auditory pathways (Yang et al., 1992; Bendor and Wang, 2005; Bitterman et al., 2008). Lateral inhibition mechanisms are the ideal candidate to account for this. They have been observed in the ventral CN (Paolini et al., 2004; Paolini et al., 2005), the IC of bats (Yang et al., 1992, and Caspary et al., 2002) and primary auditory cortex (A1) of ferrets (Shamma et al., 1993).

Dorsal CN stellate cells (Ct units) are directly innervated by the AN. They have been shown to project to ventral CN stellate cells, and so are believed to be the source of inhibitory inputs to these cells (Paolini et al., 2005). Ct units largely exhibit transient chopper responses to CF tones. That is, they fire with much less regularity than sustained choppers, resulting in just one or two prominent peaks in their PSTH. Inhibitive innervation from the dorsal CN arrives at Cs units just before off-CF excitatory innervation, despite the extra processing stage in the dorsal CN. This was because excitation of the inhibiting neurons at their CF occurs sooner (Paolini et al., 2004). Therefore off-CF stimulation leads to a delay in the Cs units first spike by about 2 ms. Continuing inhibition over the

length of the stimulus by random spikes from Ct units will greatly reduce the synchronization of the Cs units, thereby reducing the pitch strength responses to off-CF stimulation. Hyperpolarization was observed to occur for stimuli up to two octaves below, and one octave above the CF of Cs units at around 3 kHz (Paolini et al., 2004).

Blackburn and Sachs (1992) suggested that inhibition sharpened the tuning of Cs units in the ventral CN by reducing of the overall rate and the regularity of Cs firing in the presence of simultaneous off-CF stimulation. Furthermore Paolini et al. (2005) speculated that pitch processing of complex stimuli may be facilitated by the delay in onset spikes of Cs units that received less excitatory innervation than stellate cells in other iso-frequency lamina.

Blockade of γ -aminobutyric acid-ergic receptors in the IC of Mustache Bats resulted in widespread broadening of tuning curves by around 20%, independent of sound intensity. The blockade also caused an approximate doubling of firing rates in other neurons that didn't show this broadening of tuning. These results indicated the presence of strong inhibition (Yang et al., 1992). The diversity of the response changes to γ -aminobutyric acid-ergic blockade suggested that multiple circuits may be involved in the inhibitory mechanisms. Lateral inhibition, due to neurons with tuning curves that flank the excitatory response, occurred before or simultaneously with the excitation. However inhibition that only suppressed the magnitude of the excitatory response had a longer latency, suggesting the involvement of a more complex neural circuit.

Shamma et al. (1993) reported a range of response types from single and multi-cell recordings in primary auditory cortex of ferrets for two-tone stimuli. The variety of responses was due to variations in the balance of excitatory and inhibitory innervation around the best frequency. Close to the center of the iso-frequency planes in primary auditory cortex the neural response fields tended to exhibit a single excitatory region closely flanked by symmetrical inhibitory regions. Closer to the ends of the iso-frequency planes more complex and asymmetric response fields were observed. These could be grouped into types that were found to cluster along repeated bands parallel to the tonotopic axis. Many of these complex response fields exhibited multiple excitatory and inhibitory regions at higher stimulus amplitudes. The source of the inhibitory innervation recorded by Shamma et al. (1993) may be local interneurons in primary auditory cortex, or it may be due to the inhibitory mechanisms that occur in earlier auditory processing centers such as the IC.

2. Methods

A computational model of pitch was written in Matlab software (MathWorks). This enabled a range of pre-programmed subroutines to be used to execute the mathematical operations required in the model. A Matlab implementation of a linear Gammatone filterbank and Meddis haircell model written by Slaney (1994) was used to model the auditory periphery. Default parameters for this implementation were used throughout this study. Sounds were synthesized and normalized to full scale using Adobe Audition software in "wav" file formats that could be read by Matlab.

3. The model

3.1. Modeling Cs units

Synchronization models of pitch processing based on the behavior of CN stellate cells have been very successful in accounting for pitch perception of a range of tonal stimuli and iterated rippled noise. Iterated rippled noise is generated by iteratively adding

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