

Neural coding of carrier- and envelope periodicity in the auditory brainstem

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Introduction

Complex periodic sounds evoke a pitch sensation when their envelope- or carrier period is in the range between about 0.7 and 30 ms (fundamental frequency, f_0 , about 33 to 1400 Hz). Electrophysiological recordings in the auditory nerve of mammals have shown that an autocorrelation of the temporal discharge patterns of auditory-nerve fibres provides a good physiological correlate of the pitch perceived by humans. But how is a computation akin to autocorrelation performed in the central auditory system? Here I show that neurons with intrinsic oscillations (chopper neurons) in the cochlear nucleus provide a selectivity for the f_0 of periodic sounds. A chopper neuron with an intrinsic oscillation equal to f_0 synchronises to f_0 if it is stimulated by f_0 or an integer multiple (a harmonic) of f_0 . These neurons behave like a template-matching device, only this template is neurally implemented in the time domain, not in the frequency domain. Thus, this physiological model of pitch shows characteristics of both temporal and spectral functional models of pitch extraction.

Chopper neurons, together with the neurons they project to in the inferior colliculus, provide a neural place code for pitch as it has been described in the auditory cortex.

What is a chopper neuron?

Chopper neurons are one of several neuron types found in the cochlear nucleus, the first neural auditory processing stage in any mammal. Chopper neurons receive direct excitatory input from the auditory nerve. They are called choppers because they reveal a neural chopping, due to an elongated refractory time. This chopping is mirrored in a regularity of the PSTHs (Fig. 1) and in a low coefficient of variation, ($CV < 0.35$, [1]). In the following, we investigate, how a neuron's chopping rate (CR) interacts with the carrier- or envelope periodicity of acoustic stimuli. The investigations are performed with a computer model of the

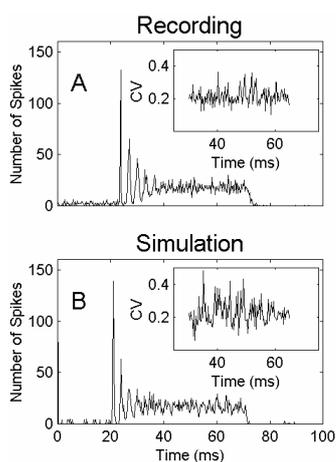


Figure 1: Peri-stimulus time histograms (PSTHs) of responses of a chopper neuron recorded from the cochlear nucleus of a guinea pig. The best frequency (BF) of the unit was 3 kHz. The lower panel shows the simulated responses in a computer model of the guinea pig's auditory system.

auditory system of the guinea pig which can be downloaded from

<http://www.essex.ac.uk/psychology/hearinglab/models>.

Analysis of neural temporal response characteristics

Temporal response characteristics are analyzed in terms of 1st-order inter-spike interval histograms (ISIHS). ISIHS were scaled according to Abeles [2] to make them independent of binwidth and overall firing rate. Periodic sounds produce a peak in the ISIH at an ISI equal to the stimulus period. Shofner [3] quantified changes in the height of this peak using the formula

$$\text{Normalized, CR-locked Rate} = \frac{R_{\tau} - R_{ave}}{R_{ave}}, \quad (1)$$

where R_{τ} equals the ISIH firing rate at an inter-spike interval corresponding to the CR of the unit and R_{ave} equals the ISIH firing rate averaged across all inter-spike intervals.

As the ISIH firing rates are independent of binwidth and overall firing rate [2], also the normalized, CR-locked firing rate is independent of these parameters. We use the same measure of peak height here. Binwidths of 250 μ s are used throughout this paper.

The coding of envelope periodicity (amplitude modulation)

Viemeister [4] and Burns and Viemeister [5] demonstrated that sinusoidally amplitude-modulated noise (SAM noise) could produce a weak musical pitch sensation. The pitch of SAM noise has been taken as evidence for the existence of a temporal pitch mechanism. Viemeister [6] showed that sensitivity to SAM decreases with increasing modulation frequency across the range of modulation frequencies that produce a pitch sensation (about 50 to 500 Hz). This effect is simulated here using populations of chopper neurons with a CR equal to the particular modulation frequency for that stimulus and 20 different BFs of the chopper neurons equally spaced between 200 and 6000 Hz on a logarithmic frequency axis. The normalized, CR-locked rate as a function of modulation frequency is shown in Fig. 2.

In general, the normalized, CR-locked rate in response to SAM noise is weak. This agrees with the weak SAM noise pitch reported in psychophysical experiments. Moreover, the normalized, CR-locked rate declines with increasing modulation frequency. This also agrees with the data of Viemeister [6]. While the difference values of the normalized, CR-locked rate are small, the error bars indicate that the SAM noise sensitivity is significant.

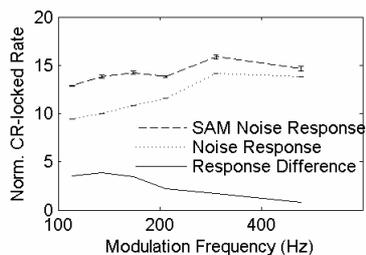


Figure 2: Normalized, CR-locked rate averaged over a population of chopper neurons as a function of the modulation frequency of SAM noise (dashed line). The

population CR always matched the modulation frequency. Error bars represent standard errors across three simulations. The dotted line shows the normalized, CR-locked rate in response to unmodulated-noise stimulation. The difference of the two functions (solid line) indicates the effect of sinusoidal amplitude modulation on the normalized, CR-locked rate. This curve reveals the low-pass shape typical for amplitude-modulation sensitivity.

The coding of carrier periodicity (harmonicity)

Iterated rippled noise stimuli were used to investigate the coding of carrier periodicity or harmonicity in simulated chopper neurons. The IRN stimuli were generated in an add-same configuration [7]. They are designated 'IRNS(d,g,n)' where 'd' is the delay in ms, 'g' is the linear gain in the delay loop, and 'n' is the number of iterations.

Yost [8] showed that the pitch strength of IRN can be predicted using the height of the first major peak in the autocorrelation function of the stimulus waveform (h_1). Specifically, the perceived pitch strength is proportional to ten raised to the power of h_1 . The chopper model is evaluated by measuring the normalized, CR-locked rate to IRN stimuli with different pitch strengths. The growth of the normalized, CR-locked rate (averaged over a population of chopper neurons) is plotted against the number of iterations for both Yost's function and the model (Fig. 3). As in the previous simulation, the chopper neurons are spread over a wide range of CFs (200 to 6000 Hz) but CRs were fixed at 200 Hz, equal to the IRN delay reciprocal. Thus, the stimuli were IRNS(5, 1, n) where n, the number of iterations was 1, 2, 4, 8, and 16.

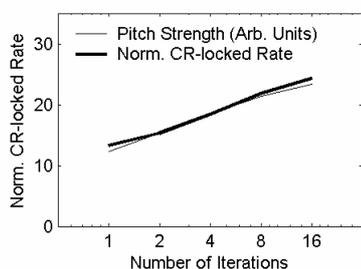


Figure 3: The change of pitch strength (fine line; after Yost [8]) and normalized, CR-locked rate (strong line) as a function of the number of iterations of IRNS (5,1,n). The normalized, CR-locked rate was averaged over an

array of 20 chopper neurons with BFs between 200 and 6000 Hz and a CR of 250 Hz. The data indicate the linear relationship between normalized, CR-locked rate and the perceived pitch strength.

The fine line in Fig. 3 represents Yost's estimate of pitch strength of the stimulus, based on h_1 , as a function of the number of iterations. The strong line show the normalized, CR-locked rate averaged across an array of simulated

chopper neurons. It can be seen that the normalized, CR-locked rate for a population of simulated Chop-S units grows in proportion with Yost's estimate of perceived pitch strength. This is an important feature of the normalized, CR-locked rate because it implies that the measure can be used additively when it is investigated how different units contribute to overall pitch strength.

Summary and Conclusions

The simulation results indicate that changes in the interspike interval statistics of populations of chopper neurons compare well with changes in the perception of carrier and envelope periodicity by humans. It is proposed that chopper neurons in the ventral cochlear nucleus may play an important role in the extraction of periodicity: They can convert a purely temporal code of periodicity as observed in the auditory nerve into a temporal *place* pitch code in populations of cochlear-nucleus, chopper neurons with different characteristic frequencies and chopping rates. Thus, populations of chopper neurons, together with their target units presumably located in the inferior colliculus, may serve to establish a stable rate-place code of periodicity at the level of the auditory cortex.

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