TEMPORAL PROCESSING IN THE AUDITORY SYSTEM.

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ABSTRACT

In spite of the fact that the auditory system is the best available acoustic signal processor, so far computational modelling in neuroacoustics has concentrated on the auditory periphery. The first auditory stage, the cochlea, may be considered as filter bank performing a kind of frequency analysis. However, this is only the first step of complex hierarchical processing which finally, at the level of the cortex, leads to perception and recognition of sound signals. On the basis of our neurophysiological investigations, a spiking neural network has been simulated which implements temporal processing in the central auditory system. Essential elements of the first level of this network are coding of amplitude modulations by oscillatory neurons in the ventral cochlear nucleus (VCN) and by integrating neurons in the dorsal nucleus cochlearis (DCN). At the second level undelayed responses from the VCN and delayed responses from the integrated response in the DCN coincide on neurons in the inferior colliculus (IC). Finally, synchronized inhibition originating in the nucleus of the lateral lemniscus (VNLL) provides additional timing and low pass filtering. In the auditory system the result of temporal analysis is represented along a neuronal axis orthogonal to the well-known tonotopic axis. Corresponding evidence comes from different methods of mapping auditory midbrain and cortex in various animal, including man.

INTRODUCTION

The amplitude of many complex acoustic signals is periodically modulated. Normally, the periodicity of such sounds is due to the periodic vibration of sound sources, for example of vocal chords in speech. The harmonic components of such a sound remain largely unresolved by the cochlea. Their interference produces amplitude modulations (AM) along the basilar membrane with modulation frequencies corresponding to the fundamental frequency. Accordingly, the pitch of such modulated signals is equal to that of the fundamental frequency – although their centre or carrier frequencies have also an influence (Schouten, 1970). It was suggested that this so-called periodicity or 'virtual' pitch or pitch of the 'missing fundamental' results from a temporal analysis of these modulations in the central auditory system (for a summary, see Langner, 1992). This percept is also a major clue for detection and understanding of a human voice, especially under noisy conditions

(Bregman, 1990; Cooke and Brown, 1994). In order to explain why periodicity pitch of AM signals as well as the preference of neurons in the midbrain for certain modulation frequencies (Figure 3) both depend on the carrier and the modulation frequency (Langner 1983; Langner and Schreiner, 1988), a correlation model was suggested which performs a correlation between signal fine-structure and the modulated envelope (Langner 1988, 1992). The constituents of this model, the underlying experimental evidence, and exemplary results from computer simulations will be discussed in this paper.

NOMENCLATURE

AM = amplitude modulation
CF = center frequency
BMF = best modulation frequency
DCN = dorsal cochlear nucleus
IC = inferior colliculus
VCN = ventral cochlear nucleus
VNLL = ventral nucleus of lateral lemniscus

COMPUTER SIMULATION AND EXPERIMENTAL EVIDENCE

Based on electrophysiological recordings in different animals a neuronal model has been developed for a correlation analysis of signal periodicity in the IC (Langner, 1997). The model was also simulated on computer (Borst et al., 2004; Voutsas et al, 2004). Neuronal elements of this model are a trigger, an oscillator, a reducer unit, and a coincidence detector (Figure 1). These elements are assumed to have their counterparts in on-type, chopper neurons in VCN, pauser neurons in DCN, and disc cells in IC.

Spike trains in the auditory nerve and of neurons in the nucleus cochlearis show phase coupling to amplitude modulations and therefore also to the (often missing) fundamental frequency of harmonic sounds. Neurons in the cochlear nucleus encode modulated signals temporally (Frisina, 1990). The model makes use of neuronal response patterns in the cochlear nucleus (VCN and DCN) which are termed ‘trigger’ (onset response) ‘oscillator’ (chopper response), and reducer (pauser response). The trigger unit is activated by each cycle of the modulation and provides synchronization of the oscillator and the reducer. The oscillator responds with regular interspike intervals in response to each

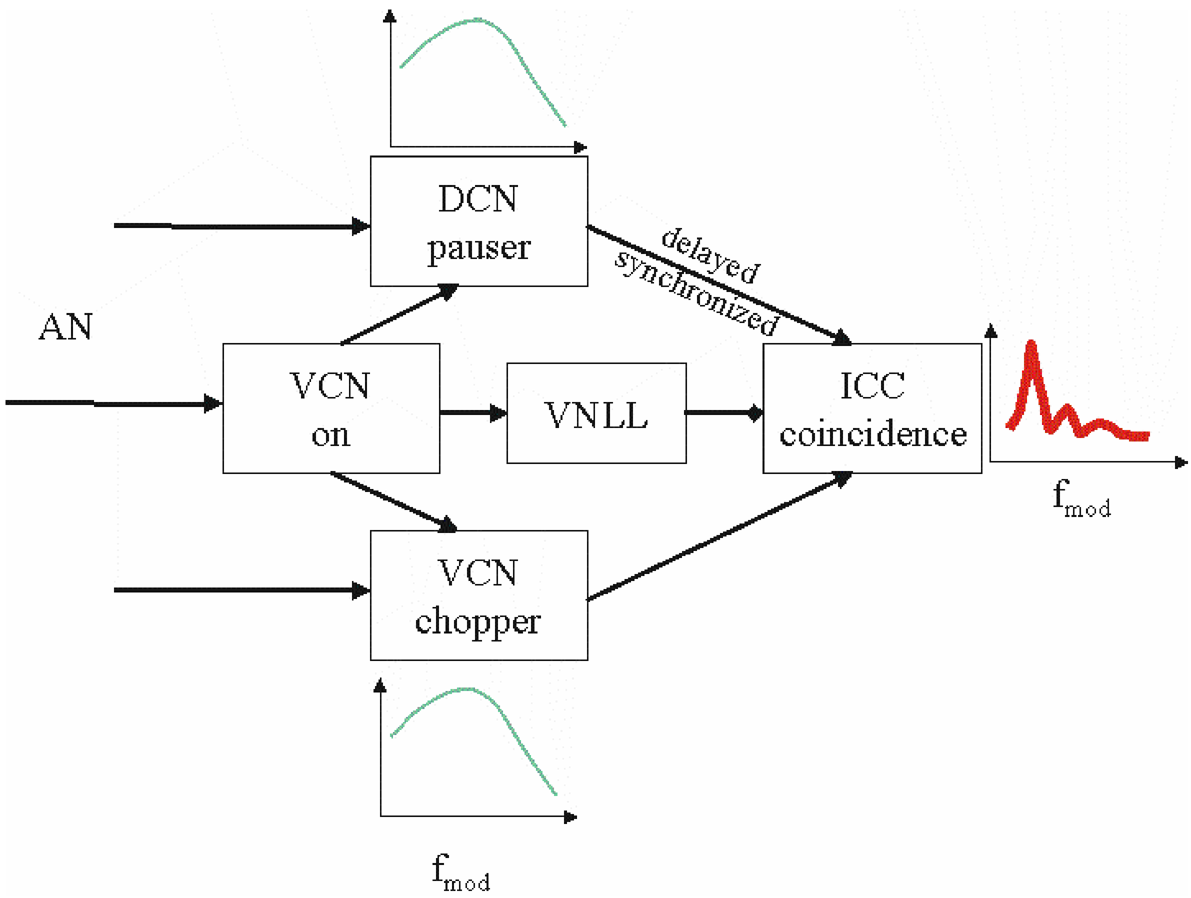

Figure 1 A neuronal model of periodicity processing

After the frequency analysis of the cochlea, periodicity information converges with different delays on coincidence neurons in the IC. Oscillator (chopper) in the VCN and reducer (pauser) responses in the DCN are synchronized to signal envelopes by means of a trigger (on) neuron. The delay, resulting from the integration time of the reducer circuit (DCN), has to be compensated by the period of the signal and the period of the oscillation for the coincidence unit to be activated. While the coincidence of inputs from DCN and VCN provide a correlation between the fine-structure (or carrier) of the signal and its envelope modulation, an additional synchronized inhibition, provided by neurons in the VNLL, shapes the resulting comb-filter into a band-pass MTF.

modulation cycle. The reducer unit provides regular intervals related to the signal fine structure with phase delays equal to an integer multiple of the carrier period. By integrating synchronized activity of many nerve fibers, it makes use of the volley principle (Wever, 1949) and is therefore able to code frequencies up to the upper limit of phase coupling at 5 kHz. The output of the model is provided by coincidence units which receive its inputs from the oscillator and the reducer circuit. Corresponding units in the IC are tuned to a certain modulation frequency (BMF) in rate (Langner, 1981, 1983; Langner and Schreiner, 1988; Langner et al., 2002; Biebel and Langner, 2002). They respond when carrier frequency and envelope frequency are correlated and the envelope period (=1/BMF) matches the reducer delay.

Finally, in order to avoid that multiples of BMF also elicit a response, the coincidence unit needs an additional inhibitory input synchronized to the envelope period. As demonstrated in bat (Vater et al., 1997; Covey and Casseday, 1999) and rat (Riquelme et al., 2001) an appropriate inhibitory input to the IC seems to be provided by neurons in the ventral part of the nuclei of the lateral lemniscus (VNLL). In accordance with model expectations, the neurons in the VNLL obtain their input via giant synapses mainly from on-type neurons (octopus and multipolar cells) in the CN (Adams, 1997; Vater et al., 1997).

As a result of periodicity analysis, the IC may be considered as a decoder for temporal information, transforming periodicity into rate/space information (Figure 2). But the IC is also an obligatory relay station in the ascending auditory pathway which contains about 30 laminae. Each lamina represents a small band of the cochlear frequency analysis. This layered network provides a framework for the representation of different signal parameters. It has been demonstrated that periodicity analysis creates a second frequency axis which represents periodicity information orthogonal to the tonotopic axis (Langner, 1992, 1997, 2002; Schreiner and Langner, 1988, 1997). This orthogonal representation of frequency and periodicity in the IC of different animals is supported by electrophysiological recording from neurons in the IC, by the 2-deoxyglucose method, and by c-fos mapping studies. Similar results were obtained also in the auditory cortex of different animals and man (Langner et al., 1997).

The periodicity model has the advantage that all response properties and anatomical connections of its neuronal elements remind closely of actual neurons in the auditory system and, at the same time, it offers explanations for certain pitch effects (Langner, 1997).

The model was simulated on a computer and reproduced transient and steady-state responses of coincidence units faithfully (Langner, 1997; Borst et al., 2004; Voutsas et al., 2004). According to the model the postulated periodicity analysis is on the one hand performed on a cycle-by-cycle basis: each modulation cycle is estimated by the neuronal response rather independently from the previous ones.

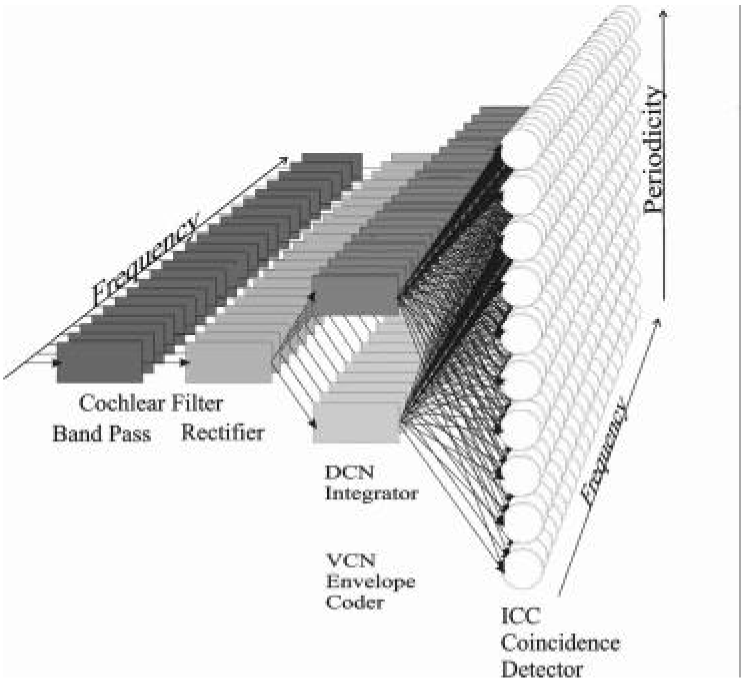

Figure 2: The model, depicted in Figure 1, is only the basic circuit of a neuronal cross-correlator. Each elementary circuit codes a certain frequency and a certain periodicity of acoustic signals. After the frequency analysis in the cochlea (cochlear filter) and a temporal correlation analysis in the brainstem, both parameters are mapped along orthogonal axes on stacked neuronal laminae in the inferior colliculus (only 1 is shown).

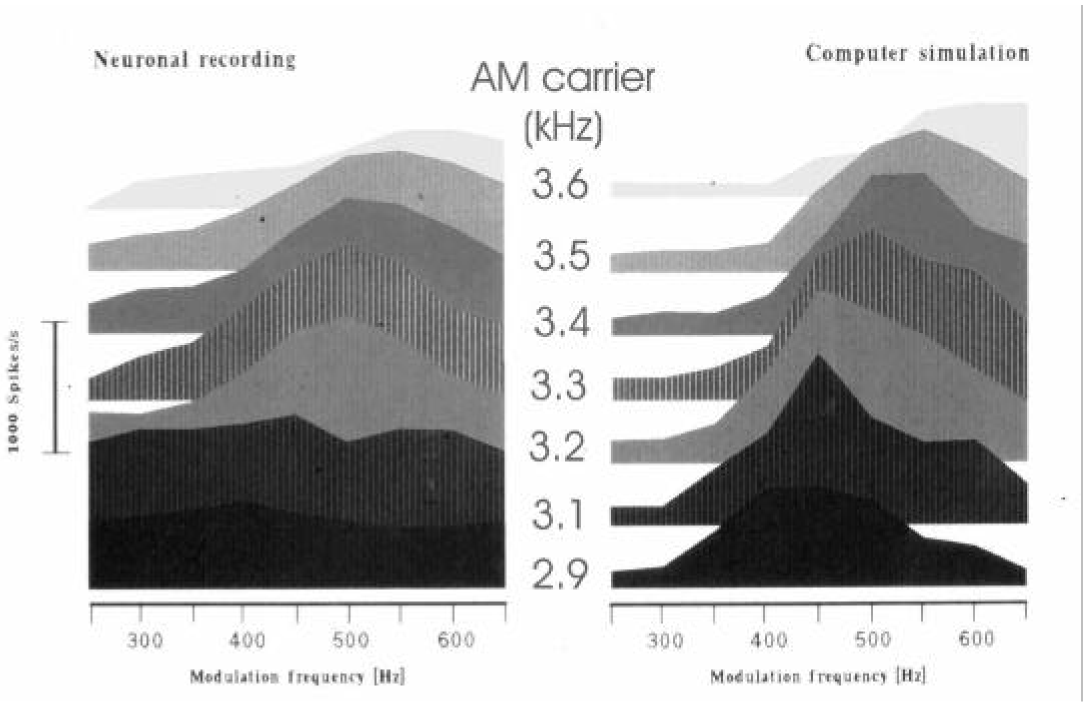

Figure 3:

Left: Modulation transfer functions of neuron in the IC depend on the carrier of AM signals.

Right: Similar carrier dependence of modulation transfer functions of a simulated neuronal circuit.

As a result of this analysis amplitude modulations are analyzed in the time domain, but it are also correlated to the fine structure of the signal (Figure 3). Therefore, the unit in the IC which responds best to a periodic sound is at the same time signaling a certain frequency at its best frequency (CF) and a certain pitch at its best modulation frequency and probably also a certain level at its best intensity. It is evident that such coding is not done by one neuron alone, but by the frequency and periodicity tuning of a large assembly of neurons in the IC. The response of this assembly is reflecting amplitude, carrier, and modulation frequency or formant and fundamental frequencies of broad band signals. This explanation of a combined frequency and periodicity analysis is in line with modern experiments and discussions of this topic (Hartmann and Doty, 1996).

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