Auditory Modeling Gets an Edge

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Since the seminal work by Hubel and Wiesel (Hubel and Wiesel 1962), visual neurophysiologists have had a powerful model for understanding responses of neurons in the primary visual cortex. According to this model, simple cells in the visual cortex respond optimally to edges of the appropriate orientation and spatial location; responses of complex and hypercomplex cells can be constructed from these simpler responses. While, of course, neural responses in primary visual cortex are more complicated, this simple model has provided a solid foundation upon which to build. Now in a paper by Fishbach et al 2003 (this issue, pgs. 3663–3678), a similar framework is being proposed for auditory research.

The success of the Hubel-Wiesel model left cortical auditory physiologists with a serious case of stimulus-envy. After decades of research, there is no consensus about what auditory stimulus constitutes the equivalent of an edge or whether it is even reasonable to expect an equivalent. It has, of course, long been recognized that the primary auditory cortex is organized in a tonotopic fashion, with nearby neurons typically responding best to tones of similar frequencies (Goldstein et al. 1970; Merzenich et al. 1976). However, this organization is merely the manifestation in the auditory cortex of the tonotopic organization in the cochlea, in the same way that the visual cortex retains a map of spatial (retinal) location as a central organizing principle. In the absence of a clear candidate optimal stimulus, researchers have probed neurons in auditory cortex with a bewildering, almost Tourettean, array of clicks, pips, sweeps, noise bursts, modulated tones, and animal vocalizations.

In a first attempt to unify these diverse findings, Fishbach and colleagues (2001) proposed that auditory neurons, like their visual counterparts, implement a form of edge detection. However, while visual edges are defined in terms of the spatial derivative of light intensity, the comparable quantity for audition was posited to be the temporal derivative of sound intensity; auditory neurons were hypothesized to act as "temporal edge detectors." For such auditory edge detectors, the optimal stimulus is a sound transient. Such transients may be particularly important in audition, where stimulus amplitude can change over many orders of magnitude—i.e., over tens of decibels—in a fraction of a second; comparably wide and rapid swings in light intensity are only rarely encountered under natural viewing conditions (except in environments illuminated by a disco ball or a strobe light).

In this issue, Fishbach, Nelken, and Yeshurun (FNY) have gone the next step, adding a spectral dimension to their original model. The extended FNY model consists of a three-layer network, with two subcortical stages and a cortical output neuron. The first layer implements a filter bank similar to the one found in the cochlea. The next layer is two-dimensional and adds a delay axis (along which neurons vary in their response latency) to the frequency axis. The third layer represents a cortical neuron that receives both inhibitory and excitatory inputs from the frequency-delay layer. The synaptic weights of the inputs are then set to form an on-off spectro-temporal receptive field (STRF). Hence the cortical neurons act as spectro-temporal edge detectors.

The power of the extended FNY model lies in its simplicity. The model has only four free parameters. The first two, carried over from the original tone-deaf FNY model, determine the behavior of the first two layers. The spectro-temporal receptive fields are determined by the two remaining parameters; the first specifies a rotation angle in the spectro-temporal domain, and the second specifies the bandwidth along the spectral axis. It is this parameterization that is key to the model, for it constrains the STRFs to one particular shape—a rotatable on-off receptive field. By contrast, previous accounts of responses properties in the auditory cortex have usually allowed all the spectro-temporal parameters to vary (deCharms et al. 1998; Depireux et al. 2001).

A further intriguing finding is that the parameters of the FNY model are organized topographically in the auditory cortex. It will be of interest to understand how this organization interacts with other forms of topographic organization, such as the recently described directional selectivity index (Zhang et al. 2003).

The extension of the original FNY model to the spectral domain allows it to reach beyond its initial domain of amplitude transients, and provide an account of cortical responses to various frequency sweeps and two-tone interactions. The ability of the model to explain two-tone suppression is particularly surprising, since the model does not include any explicit nonlinearities designed to reproduce this effect. Of course, the ultimate test of any model is of its ability to predict responses to arbitrary natural stimuli; but for now, the FNY model is surely the current benchmark against which future models of auditory cortex will be compared.

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