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Buried in the Noise. Focus on “Temporal Properties of Responses to Broadband Noise in the Auditory Nerve”

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The auditory system is faced with two tasks when a sound is heard. One is to identify the sound and the other is to localize it in space. Both tasks depend on the remarkable ability of auditory nerve fibers (ANFs) to synchronize their responses to the temporal envelope or to the fine structure of the sound. For example, to understand speech, we must track the envelopes of speech sounds (Shannon et al. 1995), whereas to determine where a growling bear hidden in the bushes is located, we depend primarily on detecting the small (10–800 μ s) interaural time disparities between the signals' fine structure at the two ears (Wightman and Kistler 1992). ANFs are also tuned in frequency, each with a particular characteristic frequency (CF) that depends on the location along the cochlea of the inner hair cell that innervates it. The coding of the temporal information in the sound depends on the directional polarization of the hair cells in the cochlea. The alternating inward and outward movements of the eardrum in response to the pressure waves of a sound are first encoded by depolarizing and hyperpolarizing currents in the inner hair cells, which are then reflected in the discharge of ANFs as synchronized responses to the temporal fluctuations.

In most studies of “phase-locking” of ANFs and more central auditory neurons to the fine structure or to the envelope of sounds, pure tones or amplitude-modulated tones have been used. These studies show that phase-locking to the fine structure is restricted to low-frequency stimuli, in mammals <4–5 kHz (Johnson 1980). At higher frequencies, phase locking to the fine structure is lost due to the membrane capacitance of the hair cell, but if the sound has a time-varying envelope then ANFs will phase lock to the low-frequency envelope, though only up to \sim 1.5 kHz (Joris and Yin 1992). ANFs can also synchronize to more complex signals, such as Gaussian noise. The reverse correlation (or revcor) technique, which has become popular to use in studies of the visual system (Freeman and Ohzawa 1990; Jones and Palmer 1987; Smyth et al. 2003), was first developed (de Boer and Kuyper 1968) to analyze the ability of ANFs to encode the low-frequency components of a broadband noise stimulus. However, this technique is limited by phase locking and cannot reveal the synchronization to the envelope of the noise for ANFs at higher CFs.

In this issue, Louage et al. (p. 2051–2065) describe a novel application of a classic analytic tool, autocorrelation, that enabled them to determine not only synchrony to low-frequency fine structure but also the locking to the envelope at high frequencies. Autocorrelograms have been used for some time to study the temporal properties of ANFs (Ruggero 1973). However, traditional autocorrelation techniques are limited to frequencies less than \sim 1.5 kHz by the refractory period of

fibers. The new insight in the present paper was to cross-correlate spike trains of the same nerve fiber to repeated repetitions of the same “frozen” noise stimulus, which they refer to as shuffled auto-correlograms (SAC) (Joris 2003). By cross-correlating across repetitions, the hole due to refractoriness in autocorrelograms is filled in thereby extending the usefulness to high frequencies as well. SACs also have the advantage over traditional autocorrelograms of an almost squared increase in the number of intervals computed, resulting in much smoother functions.

Another clever manipulation was to use the response to the same broadband noise but with the phase inverted and to then cross-correlate the responses to the original and inverted noises to get cross-stimulus autocorrelograms (XAC). They then computed the difference (*difcors*) between SAC and XAC. Because the envelope of a waveform is not affected by polarity inversion but the fine structure is inverted, the temporal locking to the envelope is removed in the *difcors*, allowing discrimination between phase locking to the fine structure and to the envelope. Fibers the CFs of which fall in the mid-frequency range of 2–4 kHz show phase locking in the SACs to both fine structure and envelope, whereas the *difcor* of these fibers reveals the synchronization to the fine structure by itself.

Difcors were also computed for responses to pure tones so comparisons could be made for the same response between *difcor* peak height and vector strength, the standard metric for measuring the strength of phase locking (Goldberg and Brown 1969). In general, the *difcor* analysis yielded results that were consonant with traditional measures but provided more insightful information. For example, differences between fibers of different spontaneous rates were more marked in the new analysis using SACs and *difcors* than with traditional vector strength.

In summary, the novel analysis allows studies of temporal coding using more complex, nonperiodic stimuli. The results described by Louage et al. (2004) demonstrate the feasibility of the technique and only hint at further treasures to be uncovered. In future studies, we can look forward to further insights into cochlear filtering, modulation transfer functions and spontaneous rate using this new analysis.

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