Comments

Comment by Delgutte and Anna. A. Dreyer (Eaton-Peabody Laboratory, Massachusetts Eye and Ear Infirmary, Boston, MA)

Is phase locking to “transposed stimuli” as good as phase locking to low-frequency pure tones? The rationale for using “transposed stimuli” (van de Par and Kohlrausch 1997) is to produce the same temporal discharge patterns in high-frequency neurons as observed in low-frequency neurons for pure tone stimuli in the hope of improving sensitivity to interaural time differences at high frequencies (Bernstein and Trahiotis 2002, 2003, this paper). Here, we report findings from physiological experiments that directly test the extent to which the responses of auditory-nerve fibers (ANF) to transposed stimuli resemble responses to pure tones and how they differ from responses to sinusoidally amplitude-modulated (SAM) tones.

Standard techniques were used to record from ANFs in anesthetized cats using glass micropipettes (Kiang et al. 1965). Two types of stimuli were presented via closed acoustic systems: SAM tones and transposed stimuli. The modulation frequencies of both stimuli were 60 Hz, 125 Hz, 250 Hz, 500 Hz or 1000 Hz. The carrier frequency was always above 3000 Hz, and usually at the fiber’s characteristic frequency (CF). Responses were measured as a function of stimulus level from 0 to about 60 dB above threshold. The synchronization index (SI) computed from period histograms was used to characterize the strength of phase locking to the modulation frequency (Johnson 1980).

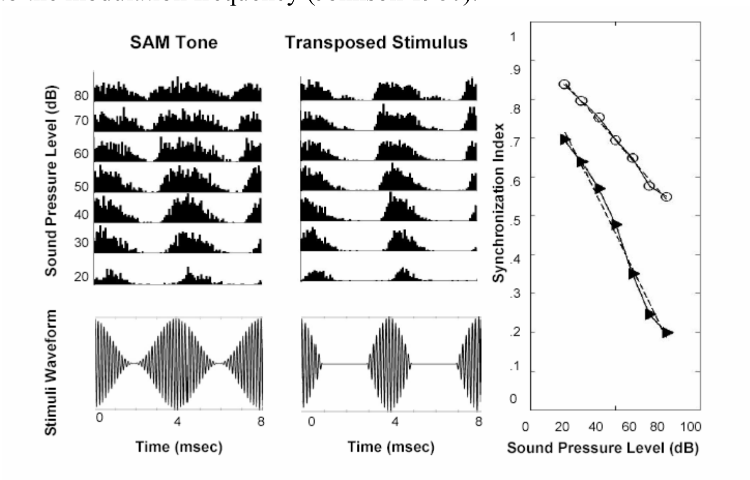

Fig. A1. Response patterns of an ANF to two cycles of a SAM tone (left) and transposed stimulus (middle) as a function of stimulus level. The carrier frequency was at the fiber CF (7000 Hz), and the modulation frequency was 250 Hz. Right: SI to the modulation frequency as a function of stimulus level for the transposed stimulus (open circle) and SAM tone (filled triangle). Dashed lines are least-squares fits to the data.

Figure A1 shows the response patterns of an auditory-nerve fiber as a function of stimulus level for two cycles of a SAM tone and transposed stimulus. Spike discharges to the transposed stimulus are restricted to a smaller fraction of modulation cycle than those for the SAM tone. This observation is reflected in the higher SI for the transposed stimulus (right). However, for both stimuli, spikes occur over an increasingly wide fraction of the modulation cycle as stimulus level is raised; correspondingly, SI falls almost linearly with increasing level, although not as fast for the transposed stimulus as for the SAM tone.

For each fiber and stimulus, we determined both the maximum SI over stimulus level, and the rate of decrease in SI above this maximum. For the medium-spontaneous fiber in Fig. A1, the maximum SI occurred at the lowest level studied; in other units it occurred as high as 15 dB above threshold. Figure A2 (top) shows the median maximum SI across our ANF sample as a function of modulation frequency for SAM tones and transposed stimuli. The range of SI in the Johnson (1980) pure tone data is also shown for comparison. The maximum SI for transposed stimuli is higher than that for SAM tones for all modulation frequencies, and is comparable to the pure-tone SI for frequencies below 500 Hz. However, the maximum SI for transposed stimuli at 1000 Hz is lower than that for pure tones, suggesting that phase locking falls faster with frequency for transposed stimuli than for pure tones.

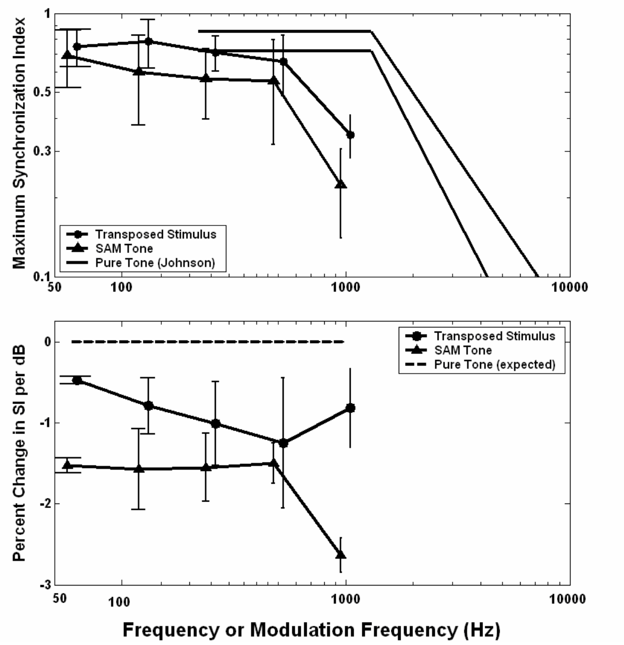

Fig. A2. Maximum SI (top) and percent change in SI per dB (bottom) as a function of modulation frequency for SAM tones and transposed stimuli. Symbols show the median values across the ANF sample, error bars show the interquartile ranges. Black lines on top show upper and lower bounds to the Johnson (1980) SI data for pure tones. Dashed line in the bottom shows the expected rate of change in SI for pure tones.

The bottom panel of Fig. A2 shows the rate of change in SI with increasing sound level as a function of modulation frequency for both SAM tones and transposed stimuli. The rate of change is expressed as a percentage of the level-maximum SI. For both stimuli, the rate of change is always negative, indicating that SI drops with increasing sound level. For example, for a 250-Hz transposed stimulus, the rate of change is -1%/dB, indicating that, over a 50 dB range of levels, SI drops from a maximum of 0.8 to only 0.4. In this respect, responses to these modulated stimuli clearly differ from those to pure tones, which show little or no decrease in SI with level (Johnson 1980). Nevertheless, the rate of change is only about twice smaller in magnitude for transposed stimuli than for SAM tones.

In summary, temporal discharge patterns of ANFs to transposed stimuli better resemble responses to pure tones than do responses to SAM tones, consistent with the rationale for using transposed stimuli in studies of binaural hearing. However, responses to transposed stimuli clearly differ from responses to pure tones in their level dependence, suggesting that the level dependence of psychophysical performance with transposed stimuli should be systematically examined in further studies.

Bernstein, L. R.. and Trahiotis, C. (2002) Enhancing sensitivity to interaural delays at high frequencies by using “transposed stimuli”. J. Acoust. Soc. Am. 112, 1026-1036.

Bernstein, L. R.,. and Trahiotis, C. (2003) Enhancing interaural-delay-based extents of laterality at high frequencies by using “transposed stimuli.” J. Acoust. Soc. Am. 113, 3335-3347.

Johnson, D. H. (1980). The relationship between spike rate and synchrony in responses of auditory-nerve fibers to single tones. J. Acoust. Soc. Am. 68, 1115-1122.

Kiang N. Y. S., Watanabe T., Thomas E. C., and Clark L. F. (1965) *Discharge Patterns of Single Fibers in the Cat's Auditory Nerve*. (Cambridge, MA: The MIT Press).

Van de par, S. and Kohlrausch, A. (1997) A new approach to comparing binaural masking level differences at low and high frequencies. J. Acoust. Soc. Am. 101, 1671-1680.

Reply:

Thank you for this little paper within a paper. You found that phase locking declines more rapidly with frequency for envelopes of transposed stimuli than for their pure tone counterparts. We do not believe that your findings reflect the operation of the 150-Hz low-pass-envelope-processing filter that explains the psychophysical data. Rather, we believe your findings at the level of the auditory nerve can be explained simply and directly by considering that frequencies of modulation greater than 500 Hz produce sidebands that are attenuated by the auditory filter at the CF. Such attenuation reduces the depth of modulation of the envelope.

We have discussed how such reductions of depth of modulation lead to increased threshold-ITDs (Bernstein and Trahiotis, 1996). In that paper (pg. 1761) we argued: *It is clearly the case that as depth of modulation decreases, nerve fibers can exhibit poorer synchrony to the modulation frequency while, simultaneously, exhibiting responses that are well synchronized to the envelope of the stimulus. Such an outcome can be understood by noting that 1) reducing the depth of modulation reduces the power at the modulating frequency in relation to the total power of the* *envelope and 2) the neural responses may reflect synchrony to the envelope of the stimulus rather than to the modulating frequency per se. An excellent illustration of these effects is provided by Joris and Yin (1992) in Figs. 1 and 2 of their physiological study of eighth-nerve responses to amplitude modulated tones.* This explains why, in our view, the synchronization index, which is commonly used by auditory neurophysiologists, is an inappropriate metric of how well neural responses "follow" the half-wave rectified waveforms that stem either from low-frequency pure tones or their high-frequency transposed counterparts.

Your findings as a function of overall level may be explained by the envelope compression that is included in our modeling, and which appears to be crucial for its success. In the case of a high-frequency transposed stimulus, the envelope compression alters the shape of the effective waveform at the input to the putative binaural processor. In the case of a pure tone, envelope compression only serves to scale its constant (i.e., flat) envelope. One would expect to observe level-related differential effects for these two types of stimuli to the extent that compression varies with overall level. All of this serves to reinforce the notion that high-frequency transposed stimuli cannot, in the limit, be expected to produce patterns of neural discharges that are the *identical* to those produced by their low-frequency counterparts. In our publications and in our oral presentations, we have been quite careful to point out that high-frequency transposed stimuli can be only expected to produce inputs to the binaural processor that are *similar* to those produced by their low-frequency counterparts. It has been part of our plan all along to conduct psychophysical experiments with transposed stimuli so that we can determine whether and to what degree the manipulation of overall level affects threshold-ITDs and extents of laterality.

Bernstein, L. R. and Trahiotis, C. (1996). "On the use of the normalized correlation as an index of interaural envelope correlation," Journal of the Acoustical Society of America, 100, 1754-1763.

Joris, P. X. and Yin, T. C. T. (1992). "Responses to amplitude-modulated tones in the auditory nerve of the cat," J. Acoust. Soc Am. 91, 215-232.

Delgutte:

We agree that peripheral auditory filtering may be partly responsible for the degradation in phase locking to the modulator for higher modulation frequencies. Indeed, the results of Joris and Yin (1992) suggest that peripheral filtering determines the cutoff frequency of ANF modulation transfer functions for characteristic frequencies (CF) up to at least 10 kHz. Since all our fibers had CF below 10 kHz, peripheral filtering is likely to play a role in our data for both SAM tones and transposed stimuli. However, to get a complete picture of the coding of the envelope in the auditory nerve, it would be important to record responses to stimuli whose carrier frequency differ from the neuron CF, for which sideband attenuation by peripheral filtering would operate differently.

Our goal in using the synchronization index (SI) was not to characterize how well neural responses follow the stimulus envelope, but rather to have a quantitative measure of the precision of phase locking (i.e. the fraction of a stimulus cycle to which spikes are restricted) for SAM and transposed stimuli that could be directly compared with existing data for pure tones. Our results (e.g. Fig. 1) show that the SI does this job very well, clearly paralleling the changes in the strength of phase locking observed in the temporal discharge patterns. The "envelope compression" seen in the neural data is much more severe than the power-law compression used in your model, in some cases leading to almost complete obliteration of phase locking to the envelope at moderate stimulus levels. Although there are several stages of compression in the cochlea, the most severe most likely occur at the synapses between inner hair cells and ANFs, not in basilar-membrane mechanics (Ruggero, 1992).

Joris, P.X., Yin, T.C.T. (1992). Responses to amplitude-modulated tones in the auditory nerve of the cat. J. Acoust. Soc. Am. 91, 215-232.

Ruggero, M. (1992). Physiology and coding of sound in the auditory nerve. In: AN Popper, R.R. Fay, (Eds), *The Mammalian Auditory Pathway: Neurophysiology.* Springer-Verlag, New-York. pp. 34-93.

Bernstein and Trahiotis:

Our point is that the synchronization index (SI) can, with multi-component stimuli, be misleading and be a poor measure of how well the temporal characteristics of the neural data reflect the temporal characteristics of the effective stimulus, be it a tone, two-tones, noise, SAM, or a transposed stimulus. This issue notwithstanding, your goal of measuring and comparing neural activity with conventional high-frequency SAM stimuli and their transposed counterparts has clearly provided important new data.

Comment by Yost

Another way to view the "transposed" process is that this process has "sharpened" the envelope relative to that provided by SAM. So, one might predict that even better performance would occur if a pulse train, for instance, were used as a modulator in that the envelope would be even "sharper." Have you investigated other modulators in addition to SAM and the transposed multiplier to see if there is anything "unique" about the transposed multiplier?

Reply:

Not yet. Our goal has been to evaluate binaural performance with comparable low- and high-frequency inputs to the binaural comparator. Transposed stimuli may be unique in that they are designed to fulfill that requirement. Setting such issues aside, we do not believe that transposed stimuli are the only class of stimuli that can be expected to enhance binaural performance at high frequencies. We agree that the "sharpness" of the envelope function is an important attribute, especially amount of "off-time" between envelope-peaks. One difficulty with pulse-train modulators is that their spectra are not restricted sufficiently to yield a desired and known envelope within a single auditory filter. One advantage of the transposition technique as we have employed it is that it allows direct comparison between performance obtained with “natural” low-frequency stimuli and their transposed counterparts when the majority of the energy in each is restricted to the width of relevant auditory filters.