Reply to comment on "Auditory-nerve first-spike latency and auditory absolute threshold: A computer model" (L)

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Krisha [J. Acoust. Soc. Am., in press (2006)] has commented that an explanation based on presynaptic calcium accumulation at the inner hair cell is an incorrect explanation for the success of a model of the auditory periphery [Meddis, R., J. Acoustic. Soc. Am. **119**, 406–417 (2006)] in explaining data on first-spike auditory nerve latency. This reply accepts the criticism and accepts the strength of an alternative explanation based on expected latencies in random sequences of low-probability events. This reply also goes on briefly to explore the application of this argument to other phenomena, including the dependence of absolute auditory threshold on the duration of the stimulus. This has wide-ranging implications for the concept of "temporal integration" in psychophysics. © *2006 Acoustical Society of America.* [DOI: 10.1121/1.2221413]

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In his comment, Krishna (2006) questions my interpretation of how a model of the auditory periphery (Meddis, 2006) was able to simulate the auditory-nerve (AN) first-spike latency data of Heil and Neubauer (2001). The model in question simulated a speculation of Heil and Neubauer (2001), where delays between the onset of a tone stimulus and the first driven AN spike might be explained by the time taken to accumulate presynaptic calcium in inner hair cells (IHCs). A computer model of the auditory periphery, which included a specific account of presynaptic calcium, was able to simulate first-spike latency data. In particular, the model was able to simulate latencies, as long as 100 ms, to stimuli at threshold intensities despite having calcium integration time constants in the submillisecond range. The conclusion was drawn that presynaptic calcium dynamics were a sufficient explanation of the result.

Krishna (2006) claims that this explanation is unsatisfactory, and that a simpler statistical explanation of the same phenomenon is to be preferred. He demonstrates that the integration of calcium in the Meddis' model (2006) reaches its highest steady-state level within a few milliseconds of the onset of a stimulus, even though the latency of response is expected to be much longer. This is a convincing objection. It is a reasonable conclusion, therefore, that a alternative explanation for the success of the model is required.

Krishna then draws attention to an alternative, and much simpler, explanation based on the statistics of low probability events. Put simply, this argument says that low probability events, by virtue of their scarcity, are necessarily characterized by long delays between each event. The expected delay to the first event in a randomly distributed series of events is the inverse of its probability. At threshold, it is assumed that the release of transmitter into the IHC/AN cleft is a rare event, and that the delay between the onset of the stimulus on the first event will necessarily be longer for lower probabilities. This simple and elegant explanation was implicit in his earlier publication (Krishna, 2002), and was missed by the present author. The same idea was proposed much earlier to account for visual thresholds as a function of duration (Watson, 1969). It is also similar in some respects to the theory of "temporal integration and multiple looks" by Viemeister and Wakefield (1991). Heil and Neubauer (2003), in the discussion section of a more recent paper, also propose a similar idea.

If, as seems reasonable, the statistical account of first-spike latencies is accepted, it has ramifications well beyond those indicated in Krishna's comment. For example, Heil and Neubauer (2001) discussed their first-spike latency data in the context of the auditory receptor as an "energy integrator." This is based on the many observations that sentient biological systems are likely to detect longer, rather than shorter, stimuli when presented at the same intensity in the threshold region. The standard explanation for this phenomenon is that the organism integrates the energy of the stimulus, in some way, until some critical level is reached and the detection is made. Heil and Neubauer (2001) originally presented their results as a challenge to the idea that stimulus energy is being integrated over time. They argued that their data were more consistent with the idea that pressure was the integrated quantity.

The statistical account, however, suggests that nothing is being integrated. On the contrary, it affirms that longer stimuli are more likely to be detected simply because a longer stimulus provides a longer time window in which a rare stimulus-triggered event might occur. This is a fundamentally different interpretation from the "energy integration" notion, and deserves careful consideration because of its wide implications across the biological spectrum of sentient organisms.

Heil and Neubauer (2003) have, themselves, moved on to a more statistical approach and widened the scope of the discussion to include psychophysically measured thresholds by indicating parallels with both AN and cortical first-spike latencies. Their link between AN first-spike latency and absolute threshold was the motivation for the final evaluation

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of the peripheral model in Meddis (2006). Here, it was explained that the model showed the expected relationship between absolute threshold and the duration of a stimulus. At least for the shorter stimuli, there was a close parallel between the model and the psychophysical data. The (unspoken) implication was that calcium accumulation was also a candidate explanation for this phenomenon. However, Krishna's comments suggest that this might be another inappropriate conclusion. In the computer model (Meddis, 2006), some integration was taking place at the level of calcium accumulation at the AN synapse, but this is on a much shorter timescale than required by the psychophysical data. Krishna's comments point the way to a more radical theory of the dependence of auditory thresholds on stimulus duration.

Unfortunately, in auditory psychophysics, the term "temporal integration" has now become synonymous with the phenomenon of lower thresholds for longer stimuli. This is an unfortunate example of how the name of a putative mechanism is used to indicate a phenomenon that it might (or might not) explain. The name has become so entrenched in conventional thinking that it becomes difficult to consider the possibility that any alternative mechanism might be involved; i.e., "temporal integration does not require a temporal integrator!" However, that is exactly what needs to be considered.

This alternative view can be stated very simply as follows. A near-threshold stimulus of steady intensity establishes a (low) probability of a neural event whose occurrence will signal the presence of the stimulus. When the probability of occurrence is low, it is possible that the event will not occur before the end of the tone, and the stimulus will go undetected. The longer the stimulus, the greater the chance of detection. When the stimulus is more intense, the probability of the event will be greater and the duration of a detectable stimulus can be shorter. Stimulus thresholds are lower for longer stimuli and no integration is required.

It is not appropriate here to debate, at length, whether or not this theory is the correct one. However, the case is made that the relevance of the statistical inevitability of the association of longer delays with less probable events should be taken seriously, as indicated in Krishna's letter. At least for this author, this applies not only to discussions of first-spike latencies but also to the relationship between auditory threshold and stimulus duration. It also implies that we should abandon the habit of using the mechanism-implying descriptor of temporal integration to refer to the empirical phenomenon of lower thresholds for longer stimuli.

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