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Research paper

Towards a unifying basis of auditory thresholds: Distributions of the first-spike latencies of auditory-nerve fibers

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Abstract

Detecting sounds in quiet is the simplest task performed by the auditory system, but the neural mechanisms underlying perceptual detection thresholds for sounds in quiet are still not understood. Heil and Neubauer [Heil, P., Neubauer, H., 2003. A unifying basis of auditory thresholds based on temporal summation. Proc. Natl. Acad. Sci. USA 100, 6151–6156] have provided evidence for a simple probabilistic model according to which the stimulus, at any point in time, has a certain probability of exceeding threshold and being detected. Consequently, as stimulus duration increases, the cumulative probability of detection events increases, performance improves, and threshold amplitude decreases. The origin of these processes was traced to the first synapse in the auditory system, between the inner hair cell and the afferent auditory-nerve fiber (ANF). Here we provide further support for this probabilistic "continuous-look" model. It is derived from analyses of the distributions of the latencies of the first spikes of cat ANFs with very low spontaneous discharge rates to tones of different amplitudes. The first spikes in these fibers can be considered detection events. We show that, as predicted, the distributions can be explained by the joint probability of the occurrence of three independent sub-events, where the probability of each of those occurring is proportional to the low-pass filtered stimulus amplitude. The "temporal integration" functions of individual ANFs, derived from their first-spike latencies, are remarkably similar in shape to "temporal integration" functions, which relate threshold sound pressure level at the perceptual level to stimulus duration. This further supports a close link between the mechanisms determining the timing of the first (and other) evoked spikes at the level of the auditory nerve and detection thresholds at the perceptual level. The possible origin and some functional consequences of the expansive power-law non-linearity are discussed.

Keywords: Auditory nerve; Spike timing; Ribbon synapse; Hair cell; Poisson process; Variability; Latency; Distribution; Absolute threshold; Rate-level function

1. Introduction

The detection of sounds in quiet is arguably the simplest task performed by the auditory system, but the physiological mechanisms underlying perceptual thresholds for detection of sounds in quiet (here termed "detection thresholds", although another common term is "absolute thresholds"; see e.g. Moore, 2003 [p. 55ff; p. 399]) are still not thoroughly understood. Because there is a trade-off at threshold between stimulus amplitude and duration, frequently referred to as the "temporal integration" function (for review see e.g. Fay, 1992; Gleich et al., 2007), a widely held view is that thresholds are mediated by a long-term integration process somewhere in the central auditory system (e.g. Zwislocki, 1960; Eddins and Green, 1995). However, the time constants needed to fit the data are often

Abbreviations: ANF, auditory-nerve fiber; CF, characteristic frequency; FSL, first-spike latency; L_{min}, minimum mean first-spike latency; SPL, sound pressure level; SR, spontaneous rate

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hundreds of milliseconds long (for review see Gerken et al., 1990; O'Connor et al., 1999), an outcome that is at variance with the finding that threshold amplitudes for pairs or trains of short sounds do not change once the temporal separation of the sounds exceeds a few milliseconds (e.g. Flanagan, 1961; Gerken et al., 1990; Viemeister and Wakefield, 1991; Krumbholz and Wiegrebe, 1998). The required long time-constants are also at variance with the high temporal resolution of the auditory system, creating the "resolution-integration" paradox (deBoer, 1985; Green, 1985).

As an alternative to long-term temporal integration, Viemeister and colleagues (Viemeister and Wakefield, 1991; Viemeister et al., 1992) have proposed a "multiple-looks" model, according to which the stimulus is sampled at a high rate. The samples or "looks" are assumed to be based upon short time-constant integration of stimulus intensity, to be stored in memory and to be independent, and the information from the looks is assumed to be combined in the central auditory system in a near-optimal fashion. As stimulus duration increases, the number of looks increases. Consequently, performance improves and, equivalently, threshold amplitude decreases. The model can account for the shapes of "temporal integration" functions, and for the fact that threshold amplitudes are independent of the temporal separation of pairs of short sounds above a few milliseconds. However, several questions remain: these include the nature of the look, the shape of the temporal window that defines a look, the problem that successive samples might not be independent, the nature and characteristics of the memory, and the issue of how the information from the looks is combined to arrive at the decision stage.

Another alternative to long time-constant temporal integration is that, following short time-constant temporal integration (and possibly additional processes such as an event-forming step, coincidence detection, etc.), the stimulus, at any point in time, has a certain probability of exceeding threshold and being detected. Consequently, as stimulus duration increases, the cumulative probability of exceeding threshold increases, performance improves, and threshold amplitude decreases. Such a probabilistic "continuous-look" model is much simpler than the multiple-looks model, because it does not require storage or optimal combination of information from multiple looks. Heil and Neubauer (2003, 2005) and Neubauer and Heil (2004) have provided strong support for this idea. They found, in all vertebrate species examined, that the detection threshold for tones of different temporal envelopes and durations can be understood as a constant product of stimulus duration and a mean rate, or probability per unit time, of detection events. The latter was proportional to the mean amplitude of the stimulus, raised to a power α, where α was between 3 and 5. Consequently, the higher (lower) the mean stimulus amplitude, the higher (lower) the mean rate, and the shorter (longer) the mean time needed to accumulate a criterion fraction of detection events. The probability of the occurrence of the individual detection events can be viewed as the joint probability of the occurrence of α independent sub-events, with the probability of each of those occurring being proportional to the mean stimulus amplitude. A more direct test of this probabilistic model ideally requires knowledge of the point in time at which a particular stimulus has exceeded threshold on a given trial, but psychophysical techniques determine only the minimum amplitude of a given stimulus necessary for its detection on a criterion fraction of trials, and thus can provide only limited information.

Fortunately, the situation is different at the level of single neurons, whose thresholds show striking similarities with detection thresholds (Kitzes et al., 1978; Fay and Coombs, 1983; Dunia and Narins, 1989; Viemeister et al., 1992; Clock Eddins et al., 1998; Heil and Neubauer, 2001, 2003). Heil and Neubauer have shown, for auditory-nerve fibers (ANFs) and cortical neurons, that a measure of threshold can be obtained from the stimulus-dependent timing of the first spike (Heil and Neubauer, 2001, 2003; Heil, 2004; Neubauer and Heil, 2007). They reasoned that the first-spike latency (FSL) contains components which collectively constitute a "transmission delay" and which can thus be regarded as the theoretically shortest latency (referred to as L_{min}) of sound-evoked first spikes. For clarity of the argument, the fact that most ANFs also generate spikes spontaneously will be set aside. The difference between the FSL on an individual trial, measured from tone onset, and L_{min} represents the FSL corrected for this transmission delay and hence the time since stimulus onset that was necessary for the first spike to be triggered. The corresponding initial portion of the stimulus thus yields an estimate of the stimulus quantity that occurred prior to the instant at which the first spike was triggered. In a sense, this quantity may be viewed as a measure of threshold for the individual spike. From the mean FSL across several repetitions of the same stimulus a mean threshold can be derived in this way. Remarkably, such estimates of threshold resulted in functions of time-to-threshold which were strikingly similar in shape to functions relating detection thresholds to stimulus duration (Heil and Neubauer, 2003), suggesting a close link between first-spike timing in the auditory nerve and detection thresholds at the perceptual level (Heil and Neubauer, 2001, 2003; see also Meddis, 2006).

Thus, the characteristics of the latencies of stimulus-evoked first spikes of ANFs may shed new light onto the mechanisms underlying detection thresholds and the phenomenon of"temporal integration". ANFs with high spontaneous rates are more sensitive than ANFs with low spontaneous rates (e.g. Sachs and Abbas, 1974; Yates, 1991) and, therefore, are more likely to mediate detection thresholds. However, the separation of stimulus-evoked and spontaneously generated (first) spikes is not straightforward for ANFs with high spontaneous rates. Therefore, ANFs with very low spontaneous activity are better suited for the present purpose, because essentially all of their spikes are stimulus-evoked, so that the first spike following