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Research Report

Auditory signal detection appears to depend on temporal integration of subthreshold activity in auditory cortex

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ABSTRACT

The threshold of hearing decreases with increasing sound duration up to a limit of a few hundred milliseconds, whereas other auditory time constants are orders of magnitude shorter. A possible solution to this resolution–integration paradox is that temporal integration occurs more centrally than computations depending on high temporal resolution. But this would require information about subthreshold events in the periphery to reach higher centers. Here we show that this prerequisite is fulfilled. The auditory evoked response to a just perceptible pulse series does basically not depend on whether single pulses are below or above behavioral threshold. The failure to find evidence of temporal integration up to response latencies of 30 ms suggests that the integrator is located more centrally than primary auditory cortex. By using noise to its advantage, the auditory system apparently has established a central integration mechanism that is about as efficient as the peripheral one in the visual system.

1. Introduction

In various sensory channels, a percept can be formed by the aggregation of subthreshold activations over time, which is often denoted as temporal integration. Within limits, this process yields a roughly reciprocal relationship between stimulus duration and threshold intensity. A particularly well-studied case is the human auditory system, where a tenfold increase in stimulus duration reduces the threshold by 8–10 dB (perfect energy integration would lead to an improvement by 10 dB) and thresholds continue to improve up to stimulus durations of 500 ms (Florentine et al., 1988). Auditory temporal integration at threshold has puzzled researchers for decades (for a review, see, e.g., Algom and Babkoff, 1984; Eddins and Green, 1995), and the subject is still a matter of controversy (see, e.g., the discussion triggered by Heil and Neubauer, 2004). While the idea of temporal integration at a *peripheral* site, in the synapse between hair cell and afferent auditory nerve fiber, is still being discussed (Heil and Neubauer, 2003; Heil et al., 2008; Neubauer and Heil, 2008), psychoacoustic experiments suggest a *central* origin of auditory temporal integration (e.g., Viemeister and Wakefield, 1991). The latter hypothesis naturally raises the question as to where and how the integration takes place. Since unequivocal electrophysiological correlates of auditory temporal integration are missing, the nature of the underlying processes can only be speculated about. It is noteworthy in this context that the auditory system has the most extensive subcortical

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Abbreviations: ABR, auditory brainstem response; AEF, auditory evoked field; AEP, auditory evoked potential; SEM, standard error of the mean; SL, sensation level

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component of all sensory systems. Thus, any response property described in the auditory cortex could be generated subcortically (Nelken et al., 2004).

Single-unit studies devoted to temporal integration in the auditory pathways are scarce, and only limited conclusions can be drawn from them (see the recent review by Recanzone and Sutter, 2008). While providing a less detailed view than single-unit data, auditory evoked potentials (AEP) recorded from the scalp have the advantage of being representative for populations of neurons. Moreover, different levels of the auditory pathways can be studied simultaneously. In the present study, wave V of the auditory brainstem response (ABR) and the early cortical response P_a are considered. A series of eight tone pulses with interpulse-intervals of 16 ms was presented at a rate of 4/s. At the lowest sound level tested, a single pulse was *just below* behavioral threshold, whereas the pulse series *just exceeded* threshold. A previous study (Lütkenhöner and Seither-Preisler, 2008) had shown that ABR measurements at such low levels are extremely time-consuming, but feasible. The idea underlying the present study was as follows. If there is no temporal integration occurring more peripheral to the generator of a specific AEP component, the response to the first pulse should not differ from the responses to the subsequent pulses in the series. Such an outcome would consequently suggest a more central origin of temporal integration.

2. Results

2.1. *Visual inspection of the response waveforms*

Fig. 1 shows, for four different stimulus levels, the time course of the AEP elicited by the tone pulse series. The upper curve represents the highest level tested (60 dB SL_1). Most conspicuous is a positive wave that occurs about 26 ms (gray vertical lines) after each of the eight pulses. Regarding its latency, the wave can be identified as the middle-latency response component P_a (see e.g., Pratt, 2007). Clearly visible is also an early positive wave, which occurs about 6 ms after each pulse (dotted vertical lines; response peaks additionally marked by filled triangles). This is wave V of the ABR (see e.g., Burkard and Don, 2007). With the exception of the response to the first pulse, wave V interferes with the rising slope of the P_a response to the preceding pulse. The other three curves represent the three lowest sound levels. The response amplitudes are much smaller now (note the different amplitude scale), and the response latencies are significantly prolonged (indicated by the asynchrony of dotted lines and filled triangles). Wave P_a has a prolonged latency as well so that the peaks are found a few milliseconds later than the gray vertical lines. Apart from these differences in amplitude and latency, the four curves closely resemble each other.

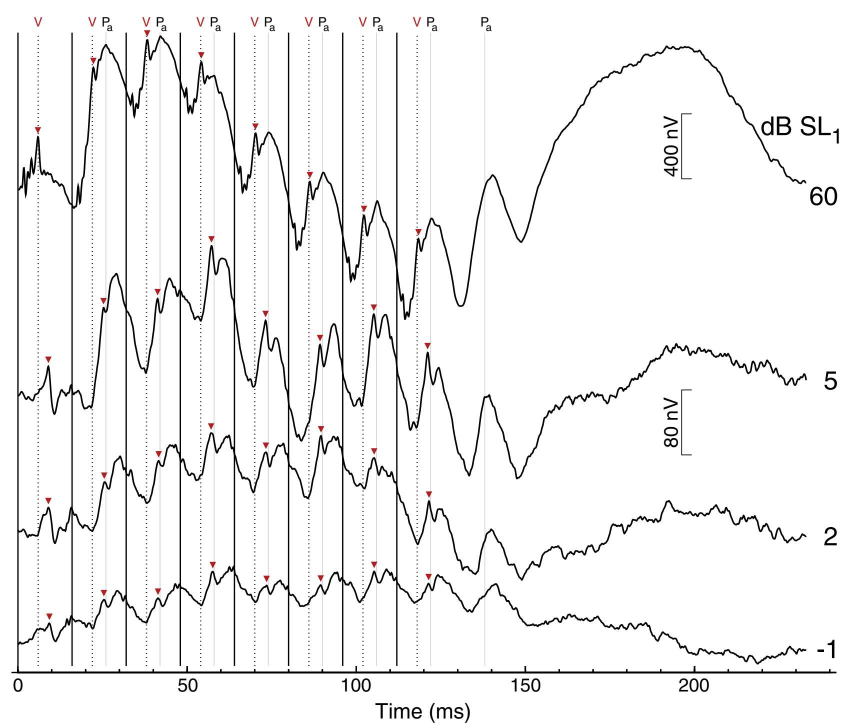

Fig. 1 – Auditory evoked potential elicited by a series of eight tone pulses presented at 16-ms intervals (pulse occurrence times indicated by black vertical lines). Response waveforms (ipsilateral channel) are shown for −1, 2, 5, and 60 dB SL_1 (dB values relative to the behavioral threshold for a single pulse). Each pulse elicited a clear wave V (peaks marked by filled triangles); at the highest level, this response had a latency of 6 ms (dotted vertical lines). The dominant response component was the middle-latency wave P_a, with a latency of about 26 ms (gray vertical lines) at the highest level. Sound level has a tremendous effect on the response *amplitudes* (note that the upper curve has a different scale), and there is also a clear effect on the response *latencies*. However, the basic pattern of the response appears to be largely independent of level.