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Precision of neural timing: The small ε limit

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Abstract

We explore the precision of neural timing in a model neural system with n identical input neurons whose firing time in response to stimulation is chosen from a density f. These input neurons stimulate a target cell which fires when it receives m hits within ε msec. We prove that the density of the firing time of the target cell converges as $\varepsilon \to 0$ to the input density f raised to the mth and normalized. We give conditions for convergence of the density in L^1, pointwise, and uniformly as well as conditions for the convergence of the standard deviations.

Keywords: Coincidence detection; Order statistics; Neural timing

1. Introduction

Coincidence detection, in which a neuron (or group of neurons) fires only when it receives two or more inputs almost simultaneously, has long been thought to play an important role in the central nervous system [1,4,7–10] And, recently, coincidence detection has been proposed as the mechanism that creates "precise timers" in the auditory brainstem [1,2,5,12,13]. These cells fire a single action potential, if they fire at all, at a precise time delay after the onset of a sound. Under repeated trials with the same sound, the standard deviation of the time delay in these precise timers is typically 0.1 msec and can be as low as 0.03 msec. This is very surprising since all the information processed by these neurons

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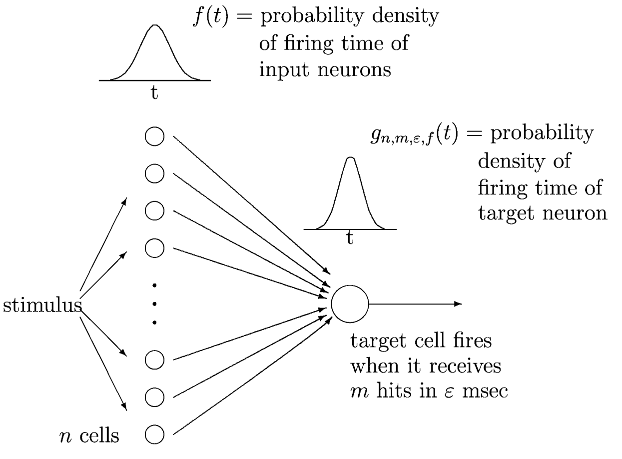

Fig. 1. Schematic of the model.

comes from the auditory nerve in which the time delays of individual fibers show standard deviations of approximately 1 msec under repeated trials. For further references and discussion of the biological background, see [14].

We formulate the question of the improvement of standard deviation by coincidence detection as follows. Imagine n identical input neurons each of which sends a projection of equal length to a target cell (see Fig. 1). In response to a stimulus each of the input neurons sends a signal after a time delay selected independently from a density f. The target cell fires, if it fires at all, at the first time that it received m inputs in the previous ε msec. We denote the random variable for the time of firing (conditioned on success) by $T_{m,n,\varepsilon,f}$, its density by $g_{m,n,\varepsilon,f}$ and its standard deviation by $\sigma_{m,n,\varepsilon,f}$. The mathematical question is to determine the behavior of $\sigma_{m,n,\varepsilon,f}$ (and $g_{m,n,\varepsilon,f}$) as a function of n, m, ε, and f.

In [14] it was shown using Monte Carlo simulations that the dependence of $\sigma_{n,m,\varepsilon,f}$ on ε and m is complex and often counter-intuitive. For example, one might expect that as ε increases, the timing would become less accurate, i.e., $\sigma_{n,m,\varepsilon,f}$ would be an increasing function of ε. In some cases, this is what was observed (for example, $n = 10$, $m = 2$, f is exponential). On the other hand, for the same f and n but with $m = 8$, $\sigma_{m,n,\varepsilon,f}$ is a decreasing function of ε and with $m = 5$, $\sigma_{n,m,\varepsilon,f}$ is non-monotone and has a peak at an intermediate value of ε. Similarly, one might expect that as m increases, $\sigma_{n,m,\varepsilon,f}$ would decrease. In fact, for most choices of parameters, $\sigma_{n,m,\varepsilon,f}$ is a non-monotone function of m. A scaling argument showed that it is sufficient to consider f with standard deviation equal to 1 msec.

This paper is devoted entirely to the mathematical issues involved in the small ε limit. Specifically, the purpose of this paper is to prove that the density $g_{m,n,\varepsilon,f}$ of $T_{m,n,\varepsilon,f}$ converges to the input density f raised to the mth power and normalized as $\varepsilon \to 0$. L^1 is the most natural type of convergence since the normalization requires division by a constant multiple of the L^1 norm of $g_{m,n,\varepsilon,f}$. We begin with the lemmas used in the L^1 proof in Section 2, then prove L^1 convergence in Section 3. Lastly, in Section 4, we address other