Nonparametric analysis of simultaneously recorded spike trains considered as a realization of a multivariate point process

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Most neurons can be viewed as branching structures with a large branch length over branch diameter ratio–akin to cables (Hodgkin and Rushton, 1946; Rall, 1977)–. They transmit, along their branches, signals through propagated local membrane potential changes. Since the neuronal membrane is leaky from the electrical viewpoint, so called "passive" spread of electrical potential cannot reliably carry signals over distances larger than a few tens of micrometers and "active" mechanisms resulting in propagated action potentials (AP) are used for longer distances. These action potentials, first quantitatively described and modeled by Hodgkin and Huxley (1952), are brief deviations–in the millisecond range–of the membrane potential from its resting state; their short duration explains why they are referred to as spikes in the literature. They are, to a very good approximation, all-or-none phenomena (Adrian and Forbes, 1922); an observation that led, almost a century ago, neurophysiologists (Adrian and Zotterman, 1926) to postulate that the action potential time is the sole information carrier over "long distances". Experimental techniques whose main (processed) output are sequences of action potentials from many identified neurons are moreover commonly used in neurophysiological labs, making for a pressing need of spike trains analysis methods.

Spike trains are presently analyzed with a wide range of methods going from very descriptive to information theory based. Following D. Brillinger (1988) we are going to "analyze" spike trains by estimating their conditional intensity; since this quantity, if known exactly, leads to the sampling distribution–most of the time through simulation–of any alternative statistics used in the spike train analysis context. But we want a more generally applicable estimation than the "semi-parametric" method proposed by Brillinger and his followers (Truccolo et al, 2005; Paninski et al, 2008) and we are going to develop a fully nonparametric approach–that does not require the setting of a bin width or the size of a basis functions (Kass and Ventura, 2001) by the user–. Our approach is "built on top" of the smoothing splines methodology giving us the benefits of: fully worked out theoretical results (Wahba, 1990); years of applications in widely different settings (Gu, 2013); open source and well tested software implementations (Gu, 2013).

Independently of the inference method used, the goodness of fit of our models has to be assessed. This issue is not as straightforward in a counting process as in a regression framework as discussed by Ogata (1988) who introduced a "group of tests". Ogata's tests are all based on a mapping of the actual events' times onto a homogeneous Poisson process times. We propose a new test based on the convergence (in law) of the properly re-scaled difference between the observed counting process and the integrated conditional intensity towards a Brownian motion; an application of the invariance principle (Taylorand Karlin, 1998).

Our approach is motivated by the analysis of a data set recorded in the first olfactory relay, the antennal lobe, of an insect, the cockroach Periplaneta americana using multi-eletrodes arrays (Pouzat and Chaffiol, 2009).

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