

# Spike Train

## Definition

A spike train is a sequence of recorded times at which a neuron fires an *action potential*. When the voltage drop across a neural soma or axon membrane is recorded, intermittent pulses of roughly 100 millivolts over 1-2 milliseconds are observed—these are action potentials or “spikes.” On a behavioral time scale of several hundred milliseconds, each spike may be considered to occur at a single point in time. Sequences of such spike times form spike trains. The total duration of a recorded spike train can range from less than a second to many minutes or even, in chronic recordings, to many days. Spike trains are considered to be the primary mode of information transmission in the nervous system.

## Detailed Description

When action potentials are recorded repeatedly from a neuron in response to changing stimuli (or while an organism produces changing behaviors), they maintain a relatively consistent shape. However, the pattern of spike times varies as the stimulus changes. Most prominently, the rate at which spikes occur, the firing rate (FR), varies with conditions. When firing rate is defined in terms of the number of spikes that occur over a time interval of length  $\Delta t$  (such as  $\Delta t = 500$  milliseconds), using

$$FR = \frac{\text{number of spikes}}{\Delta t}, \quad (1)$$

this phenomenon of firing rate varying with stimulus is called *rate coding*. While analysis of neural activity in terms of varying firing rates, as defined in Equation (1), is useful in many contexts, more subtle alterations of the pattern of spike times also occur and these, too, may convey information. For example, the lengths of gaps between spikes, known as inter-spike intervals (ISIs), often vary substantially across an observed spike train. In principle, a neural communication “code” could carry enormous amounts of information in the specific patterns of spike times, but even in highly-controlled in vitro preparations repeated injection of the same time-varying current can lead to varying spike times, due to the stochastic behavior of ion channels and related sources of noise. Furthermore, synaptic noise is introduced at multiple connections across a neural network. Thus, a good deal of the irregularity of ISIs observed in many parts of the nervous system (especially, in cortex) may be unrelated to any stimulus or behavior. The problem of *neural coding* is to determine the ways that patterns of spike times convey information in particular contexts, possibly extending beyond rate coding. For this purpose, spike trains are subjected to statistical methods of data analysis.

In probability and statistics, irregular sequences of event times are modeled as *point processes*. If we start at time  $t = 0$  and let  $X_1, X_2, \dots$  be a sequence of random variables representing the ISIs, then the time of the  $j$ th spike is given by  $S_j = \sum_{i=1}^j X_i$  and the sequence  $S_1, S_2, \dots$  forms a point process. In practice, point processes representing spike trains are considered only over some finite interval of time  $[0, T]$ .

The oldest and most basic model for spike trains is the *integrate-and-fire model*, according to which a neuron is equivalent to an electrical circuit involving a resistor and a capacitor in parallel, together with an input current; the neuron fires whenever the voltage reaches a threshold, then it resets to a fixed resting potential. A component of the input current may be used to represent stochastic synaptic activity. This idea, and many variations on it, is commonly used to generate artificial spike trains in computational studies (Gerstner and Kistler, 2002). The resulting spike trains follow point processes and, under simplifying assumptions, can be subjected to theoretical analysis. For example, when excitatory and inhibitory inputs are conceptualized (in the theoretical limit) as Brownian motion, the ISI distribution may be derived analytically (Tuckwell,

1988), and it turns out that certain features of this ISI distribution bear a striking qualitative resemblance to corresponding features of observed spike trains.

Point process representations of spike trains are governed by a theoretical instantaneous firing rate. If we replace the spike count in the numerator of (1) by its theoretical counterpart, the expected spike count, and then pass to the limit as  $\Delta t \rightarrow 0$ , we obtain

$$FR(t) = \lim_{\Delta t \rightarrow 0} \frac{P(\text{spike in } (t, t + \Delta t))}{\Delta t}. \quad (2)$$

(For small intervals  $\Delta t$  there is at most 1 spike and the expected count is equal to the probability of spiking.) However, the definition in (2) omits any mention of both the spiking behavior prior to time  $t$ , and the experimental context. For instance, immediately after a neuron fires a spike, the probability of the neuron firing again is greatly reduced—this is known as the refractory period. If we write all relevant variables that affect the probability of a neuron firing (including the time of the most recent previous spike) as a vector  $x_t$  we instead obtain the more explicit definition of neural firing rate:

$$FR(t|x_t) = \lim_{\Delta t \rightarrow 0} \frac{P(\text{spike in } (t, t + \Delta t)|x_t)}{\Delta t}. \quad (3)$$

Acknowledging that the numerator of (3) may involve complicated functions of stimuli, prior spiking patterns, and other variables, a statistical model for spike trains involves two things: (i) a simple, universal formula for the probability density of the spike train in terms of the instantaneous firing rate function defined in (3), and (ii) a specification of the way the firing rate function depends on the variables  $x_t$  (the numerator of (3)). This representation provides a framework that may be called *point process regression* because it relates the specific pattern of spike times, i.e., the spike train, to variables collected as  $x_t$ . The full battery of modern statistical machine learning methods may then be applied to the problem of neural coding.

The simplest point process regression models take a special form known in the statistics literature as *generalized linear models* (GLMs). In computational neuroscience the term GLM may refer to any type of point process regression model.

## Cross-References

Estimation of Neuronal Firing Rate

Generalized Linear Model as Application to Point Processes

Integrate-and-fire models

Neural coding

Spike Train Analysis: Overview

## References

Gerstner, W. and Kistler, W. (2002) *Spiking Neuron Models: Single Neurons, Populations, Plasticity*, Cambridge.

Tuckwell, H. (1988). *Introduction to Theoretical Neurobiology, vol. 2: Non Linear and Stochastic Theories*. Cambridge.

### **Further Reading**

Kass, R.E., Eden, U.T., and Brown, E.N. (2014) *Analysis of Neural Data*, Springer.