Neuronal spiking - a threshold phenomena - is (largely) deterministic

Yet brain activity is noisy on every scale!

Fox et al., Nature Neuroscience, 2005

Kerr et al., J. Neuroscience, 2007

Carandini, PLoS Biology, 2004

Arieli et al., Science, 1996

Liu et al., Neuron, 1999

Notes of Brent Dorian
Cortical spiking in particular is irregular

Figure 1. Response variability of a neuron recorded from area MT of an alert monkey. A. Raster and peristimulus time histogram (PSTH) depicting response for 210 presentations of an identical random dot motion stimulus. The motion stimulus was shown for 2 sec. Raster points represent the occurrence of action potentials. The PSTH plots the spike rate, averaged in 2 msec bins, as a function of time from the onset of the visual stimulus. The response modulates between 15 and 220 impulses/sec. Vertical lines delineate a period in which spike rate was fairly constant. The gray region shows 50 trials from this epoch, which were used to construct B and C. B, Magnified view of the shaded region of the raster in A. The spike rate, computed in 5 msec bins, is fairly constant. Notice that the magnified raster reveals substantial variability in the timing of individual spikes. C, Frequency histogram depicting the spike intervals in B. The solid line is the best fitting exponential probability density function. D, Variance of the spike count is plotted against the mean number of spikes obtained from randomly chosen rectangular regions of the raster in A. Each point represents the mean and variance of the spikes counted from 50 to 200 adjacent trials in an epoch from 100 to 500 msec long. The shaded region of A would be one such example. The best fitting power law is shown by the solid curve. The dashed line is the expected relationship for a Poisson point process.

Shadlen & Newsome (J Neurosci 1998)
Balanced excitatory and inhibitory currents can lead to noisy input currents

Denuve & Machens (Nat Neuro 2016)
Balanced currents are observed in vivo under numerous conditions

Spatially Opponent Excitation and Inhibition in Simple Cells of the Cat Visual Cortex

David Ferster
Department of Neurobiology and Physiology, Northwestern University, Evanston, Illinois 60208

Figure 1. Immediately recorded responses of a single cell evoked by a bright light swept across its receptive field. The bar indicates the direction and duration of motion of the stimulus. The bar measured 0.13 × 0.66 and moved 10° in the 2 sec recorded in each trace. Whether EPSPs or IPSPs were visible in the records was controlled by the amount of current injected into the cell through the recording electrode. In this and all subsequent figures, the amount of current injected into the cell through the recording electrode while recording each set of traces is indicated in the lower right. EPSPs are shown to the left (4 nA), IPSPs to the right (6.7 nA). The bottom trace in each column (A) represents an average of 10 individual records.

Figure 5. Responses to a moving bright bar recorded simultaneously from a second single cell. The receptive field of this cell consisted of 2 ON regions flanking a central OFF region. The bar moved at a rate of 2/sec.

Ferster (J Neurosci 1988)
Balanced currents are observed in vivo under numerous conditions

Instantaneous Modulation of Gamma Oscillation Frequency by Balancing Excitation with Inhibition

Dong Xiao, Xiao-Wei Atallah and Massimo Scanziani

Figure 2. Excitation Instantaneously Balanced by Proportional Inhibition during Each Gamma Oscillation Cycle

(C) Dual patch-clamp recording from two neighboring CA3 pyramidal cells. Oscillations are monitored with an LFP electrode (black, positivity is up). EPSCs (red) and IPSCs (cyan) simultaneously recorded by holding two cells at the reversal potential for inhibition (−3 mV) and excitation (−87 mV), respectively. Note the correlated fluctuations in the amplitude of excitation and inhibition.

(D) (Left) Average time course of EPSC and IPSC (same cell as C) during an oscillation cycle recorded in the LFP, i.e., oscillation triggered average. EPSC is inverted for illustration purposes. LFPs recorded simultaneously with EPSCs and IPSCs are shown as black and gray traces, respectively. (Right) Summary of EPSC-IPSC lag during an oscillation cycle. Horizontal bar is the average.

(E) (Top) Cycle-by-cycle correlation between excitatory and inhibitory conductances recorded in the pair shown in (C). Summary of correlation between excitation and inhibition (bottom) and ratio of mean excitatory and inhibitory conductances (right) (n = 8 pairs). Vertical and horizontal bars illustrate respective averages.

Atallah & Scanziani (Neuron 2009)
Neocortical Network Activity *In Vivo* Is Generated through a Dynamic Balance of Excitation and Inhibition

Bilal Haider, Alvaro Duque, Andrea R. Hasenstaub, and David A. McCormick
Department of Neurobiology, Kavli Institute for Neuroscience, Yale University School of Medicine, New Haven, Connecticut 06510

Figure 7. Excitatory and inhibitory conductances are proportional and balanced during Up states. A. Plot of calculated excitatory and inhibitory conductances in a single neuron during the course of the Up state (0–500 ms, indicated by progressive movement through color bar) shows that excitation and inhibition remain proportional and nearly equal despite large changes in total conductance (slope of linear fit: $m = 0.98; r^2 = 0.78$). Note that the start of the Up state shows a deviation toward excitation, but rapidly swings toward inhibition and thereafter exhibits a balance between the two. C. Excitation and inhibition are proportional and balanced both within and across neurons during recurrent network activity. Scatterplot of excitatory versus inhibitory conductances for a population of neurons ($n = 8$), calculated for 500 ms from the start of the Up state. Note the linear relationship for each individual neuron, as well as the clustering around a ratio of equal excitatory and inhibitory conductances ($G_e = G_i$; dashed line; 4 of 8 cells biased toward excitation; 3 of 8 cells toward inhibition; 1 of 8 cells approximately equal; population reversal potential, $-37.2 \pm 6.5$ mV).
Synaptic scaling rule preserves excitatory–inhibitory balance and salient neuronal network dynamics

Jérémie Barral¹ & Alex D Reyes¹

Figure 1 Synaptic scaling in networks of different sizes. (a) Representative E (red) and I (blue) PSPs in low and high density networks (arrows in d). (c) Number of connections (K) vs. density for E-to-E (red), I-to-E (blue) and total (black); s.d. calculated by bootstrapping data in b. (d) Amplitudes (J) of unitary EPSPs (red, n = 261) and IPSPs (blue, n = 99) vs. K. Inset: data in log-log scales. Slope of linear fit is –0.59.
Network model

van Vresswijk & Sompolinsky (Science 1996; J Comp Neurosci 1998)
(A) Temporal structure of the inputs and activity of a single excitatory unit. The upper panel shows the total excitatory input (consisting of external input and excitatory feedback) (upper trace) and the total inhibitory input (lower trace), as well as the net input (middle trace). The currents are shown in units of the threshold (dashed line). They were calculated by sampling from the Gaussian statistics of the currents predicted by the theory.

Below, the times when the cell switched to the active state are indicated. The cell is set to the active state when a suprathreshold net input coincides with the update time of the cell.

(B) The mean activity of the excitatory neurons (solid line) and the inhibitory ones (dashed line) as functions of the activity of the external units. The activities shown here and in the following figures correspond to firing rates divided by their maximum value. Assuming a neuronal maximum rate of 1000 Hz, a mean activity of 0.1 corresponds to a firing rate of 100 Hz.
Neuronal spiking is best driven by noise with the mean input near threshold

Lognormal firing rate distribution reveals prominent fluctuation-driven regime in spinal motor networks

Peter C Petersen, Rune W Berg

![Graphs showing firing rate and irregularity](image)
Neuronal spiking can be driven by noise

Lundstrom, Higgs, Spain & Fairhall (Nat Neuro 2008)
Firing Rates of Single Neurons in the *Balanced* Regime

Average current is sub-threshold and spikes are triggered by fluctuations

spiking is temporally irregular

**concavity of the f-I curve makes the rates' distribution right-skewed**