Spike-Train Statistics and Firing-rate model
Testing the Poisson Model

Figure 1.17: Intracellular recordings from cat V1 neurons. The left panel is the response of a neuron in an in vitro slice preparation to constant current injection. The center and right panels show recordings from neurons in vivo responding to either injected current (center), or a moving visual image (right). (Adapted from Holt et al., 1996.)

Although some of the basic statistical properties of firing variability may be captured by the Poisson model of spike generation, the spike generating mechanism itself in real neurons is clearly not responsible for the variability. We explore ideas about possible sources of spike-train variability in chapter 5.

Some neurons fire action potentials in clusters or bursts of spikes that cannot be described by a Poisson process with a fixed rate. Bursting can be included in a Poisson model by allowing the firing rate to fluctuate to describe the high rate of firing during a burst. Sometimes the distribution of bursts themselves can be described by a Poisson process (such a doubly stochastic process is called a Cox process).

The nature of the neural code is a topic of intense debate within the neuroscience community. Much of the discussion has focused on whether neurons use rate coding or temporal coding, often without a clear definition of what these terms mean. We feel that the central issue in neural coding is whether individual action potentials and individual neurons encode independently of each other, or whether correlations between different spikes and different neurons carry significant amounts of information. We therefore contrast independent-spike and independent-neuron codes with correlation codes before addressing the issue of temporal coding.
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Models that allow for a dependence of firing rate on stimulus history are discussed in chapter 2. In figure 1.13, the orientation angle increases in a sequence of steps. The firing rate follows these changes, and the Poisson process generates an irregular firing pattern that reflects the underlying rate but varies from trial to trial.

Certain features of neuronal firing violate the independence assumption that forms the basis of the Poisson model, at least if a constant firing rate is used. We have already noted that there are periods of time, the absolute and relative refractory periods, following the generation of an action potential when the probability of a spike occurring is greatly or somewhat reduced. Refractory effects can be incorporated into a Poisson model of spike generation by setting the firing rate to zero immediately after a spike is fired, and then letting it return to its predicted value according to some dynamic rule such as an exponential recovery.

Comparison with Data

The Poisson process is simple and useful, but does it match data on neural response variability? To address this question we examine Fano factors, interspike interval distributions, and coefficients of variation.

Figure 1.14: Variability of MT neurons in alert macaque monkeys responding to moving visual images. A) Variance of the spike counts for a 256 ms counting period plotted against the mean spike count. The straight line is the prediction of the Poisson model. Data are from 94 cells recorded under a variety of stimulus conditions. B) The multiplier $A$ in the relationship between spike-count variance and mean as a function of the duration of the counting interval. C) The exponent $B$ in this relation as a function of the duration of the counting interval. (Adapted from O'Keefe et al., 1997.)

The Fano factor describes the relationship between the mean spike count over a given interval and the spike-count variance. Mean spike counts $\langle n \rangle$ and variances $\sigma_n^2$ from a wide variety of neuronal recordings have been...
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Figure 1.15: (A) Interspike interval distribution from an MT neuron responding to a moving random dot image. The probability of interspike intervals falling into the different bins, expressed as a percentage, is plotted against interspike interval. B) Interspike interval histogram generated from a Poisson model with a stochastic refractory period. (Adapted from Bair et al., 1994.)
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Val, equivalent to $1/\langle r \rangle$. Except for short mean interspike intervals, the values are near one, although they tend to cluster slightly lower than one, the Poisson value. The small $C_V$ values for short interspike intervals are due to the refractory period. The solid curve is the prediction of a Poisson model with refractoriness.

Figure 1.16: Coefficients of variation for a large number of V1 and MT neurons plotted as a function of mean interspike interval. The solid curve is the result of a Poisson model with a refractory period. (Adapted from Softky and Koch, 1992.)

The Poisson model with refractoriness provides a reasonably good description of a significant amount of data, especially considering its simplicity. However, there are cases when the accuracy in the timing and numbers of spikes fired by a neuron is considerably higher than would be implied by Poisson statistics. Furthermore, even when it successfully describes data, the Poisson model does not provide a mechanistic explanation of neuronal response variability. Spike generation, by itself, is highly reliable in real neurons. Figure 1.17 compares the response of V1 cells to constant current injection in vivo and in vitro. The in vitro response is a reg...

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Where does the stochasticity come from?

- Channel noise
- Presynaptic sources are noisy
Impact of channel noise on spike generation threshold
Neurons *in vitro* respond reliably to fluctuating stimulus

**Fig. 1.** Reliability of firing patterns of cortical neurons evoked by constant and fluctuating current. (A) In this example, a superthreshold dc current pulse (150 pA, 900 ms; middle) evoked trains of action potentials (approximately 14 Hz) in a regular-firing layer-5 neuron. Responses are shown superimposed (first 10 trials, top) and as a raster plot of spike times over spike times (25 consecutive trials, bottom). (B) The same cell as in (A) was again stimulated repeatedly, but this time with a fluctuating stimulus [Gaussian white noise, \( \mu_s = 150 \) pA, \( \sigma_s = 100 \) pA, \( \tau_s = 3 \) ms; see (14)].
Where does the stochasticity come from?

- Channel noise
- Presynaptic sources are noisy
Integrate and Fire Neuron with $K=1000$ uncorrelated Poisson synaptic inputs
Simulating synaptic inputs in-vitro

CV = 0.28
Fano factor = 0.06

Stevens and Zador,
Two possible solutions

• Correlated Inputs

• Balanced Excitation and Inhibition to push the membrane potential near threshold
Large Fluctuations due to Correlated Inputs

Integrate and Fire Neuron with $K=1000$

Poisson inputs with $c=0.1$ correlations
Membrane potential near threshold

A

B

\( V \) (mV)

-50
-52
-54
-56
-58

250 500 750 1000

\( t \) (ms)

-70
-50
-30
-10

250 500 750 1000

\( t \) (ms)
Balanced excitation and inhibition as an autoencoder

\[ E(r) = r^T \Gamma r^2 + c \] (6)

and \( c \) is a constant.

Now, we can use this expression to derive the conditions that connectivity must satisfy so that the network operates in an optimal balanced state. In balanced networks, excitation and inhibition cancel to produce an input that is the same order of magnitude as the spiking threshold. This is very small, relative to the magnitude of excitation or inhibition alone [12, 13]. In tightly balanced networks, which we consider, this cancellation is so precise that \( V_i \to 0 \) in the large network limit (for all active neurons) [15, 17, 18]. Now, using equation 5, we can see that this tight balance condition is equivalent to saying that our loss function (Eqn. 6) is minimised.

This has two implications for our choice of network connectivity and spiking thresholds. First, the loss function must have a minimum. To guarantee this, we require \( \Gamma \) to be positive definite.

Secondly, the spiking threshold of each neuron must be chosen so that each spike acts to minimise the cost function. This spiking condition can be written as:

\[ E(\text{no spike}) > E(\text{with spike}) \]

Using equation 6, this can be rewritten as:

\[ E(\text{no spike}) > E(\text{no spike}) + 2\Gamma r^k + 2F x^k \Gamma k \].

Finally, (A) (C) (B)

Figure 1: Optimal balanced network example. (A) Schematic of a balanced neural network providing an optimal spike-based representation \( \hat{x} \) of a signal \( x \). (B) A tightly balanced network can produce an output \( \hat{x}_1 \) (blue, top panel) that closely matches the signal \( x_1 \) (black, top panel). Population spiking activity is represented here using a raster plot (middle panel), where each spike is represented with a dot. For a randomly chosen neuron (red, middle panel), we plot the total excitatory input (green, bottom panel) and the total inhibitory input (red, bottom panel). The sum of excitation and inhibition (black, bottom panel) fluctuates about the spiking threshold (thin black line, bottom panel) indicating that this network is tightly balanced. A spike is produced whenever this sum exceeds the spiking threshold. (C) Firing rate tuning curves are measured during simulations of our balanced network. Each line represents the tuning curve of a single neuron. The representation error at each value of \( x_1 \) is given by equation 7.