Chapter 1

Neural Encoding I: Firing Rates and Spike Statistics

1.1 1.1

Principle 1.1 (Conservation of angular momentum)**.** The rate of change of angular momentum of a system is equal to the net torque acting on the system, i.e.,

$$\frac{\mathrm{d}\mathbf{L}}{\mathrm{d}t} = \boldsymbol{\tau}, \tag{1.1}$$

where $\boldsymbol{\tau}$ is the torque of all external forces on the system about any chosen axis, and $\mathrm{d}\mathbf{L}/\mathrm{d}t$ is the rate of change of angular momentum of the system about the same axis.

1.2 1.2

Remark 1.1. Many physical laws are cumbersome when written in coordinate form but become more compact and attractive looking when written in tensorial form. For example, the incompressible Navier-Stokes equations in cylindrical coordinates are

$$\rho\left(\frac{Dv_r}{Dt} - \frac{v_\theta^2}{r}\right) = \rho f_r - \frac{\partial p}{\partial r} + \mu\left(\Delta v_r - \frac{v_r}{r^2} - \frac{2}{r^2}\frac{\partial v_\theta}{\partial \theta}\right),$$
$$\rho\left(\frac{Dv_\theta}{Dt} + \frac{v_r v_\theta}{r}\right) = \rho f_\theta - \frac{1}{r}\frac{\partial p}{\partial \theta} + \mu\left(\Delta v_\theta + \frac{2}{r^2}\frac{\partial v_r}{\partial \theta} - \frac{v_\theta}{r^2}\right),$$
$$\rho\frac{Dv_z}{Dt} = \rho f_z - \frac{\partial p}{\partial z} + \mu\Delta v_z,$$

where

$$\Delta = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial}{\partial r}\right) + \frac{1}{r^2}\frac{\partial^2}{\partial \theta^2} + \frac{\partial^2}{\partial z^2},$$

and

$$\frac{D}{Dt} = \frac{\partial}{\partial t} + v_r\frac{\partial}{\partial r} + \frac{v_\theta}{r}\frac{\partial}{\partial \theta} + v_z\frac{\partial}{\partial z}.$$

1.3 1.3

Proposition 1.2. The mass of fluid in a region W at time t is

$$m(W,t) = \int_W \rho(\mathbf{x},t)\mathrm{d}V, \tag{1.2}$$

where $\mathrm{d}V$ is the area element in the plane or the volume element in space.

Assumption 1.3. From now on, assume that

$$\text{force on } S \text{ per unit area} = -p(\mathbf{x},t)\mathbf{n} + \mathbf{n}\cdot\boldsymbol{\sigma}(\mathbf{x},t), \tag{1.3}$$

where $\boldsymbol{\sigma}$ is the *(deviatoric) stress tensor* and $\mathbf{n}$ is the unit outward normal of S.

1.4 Spike-Train Statistics

Definition 1.4. A complete description of the stochastic relationship between a stimulus and a response would require us to know the probabilities corresponding to every sequence of spikes that can be evoked by the stimulus.

Definition 1.5. Throughout this book,we use the notation P[] to denote probabilities and p[] to denote probability densities.

Theorem 1.6. The probability of a spike sequence appearing is proportional to the probability density of spike times,$p[t_1, t_2, ..., t_n]$.In other words,the probability $P[t_1, t_2, ..., t_n]$that a sequence of n spikes occurs with spikes ocurs with spike i falling between times $t_i$and $t_i+ \triangle\ t$ for i = 1,2,...,n is given in terms of this density by the relation

$$P[t_1, t_2, ..., t_n] = p[t_1, t, ..., t_n](\triangle\ t)^n. \tag{1.4}$$

Proof. □

Definition 1.7. A stochastic process that generates a sequence of events ,such as action potentials ,is called a pont process.

Definition 1.8. In general, the probability of an event occurring at any given time could depend on the entire history of preceding events.

Definition 1.9. If this dependence extends only to the immediately preceding event,so that the intervals between successive events are independent,the point process is called a renewal process.

Definition 1.10. To make the presentation easier to follow,we separate two cases,the homogeneous Poisson process,for which the firing rate is constant over time, and the inhomogeneous Poisson process,which involves a time-dependent firing rate.

1.4.1 The Homogeneous Poisson Process

Definition 1.11. We denote the firing rate for a homogeneous Poisson process by $r(t) = r$,because it is independent of time.

Definition 1.12. $P_T[n]$,which is the probality that an arbitrary sequence of exactly n spikes occurs within a trial of duration T.

Theorem 1.13.

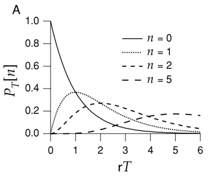
$$P_T[n] = \frac{(rn)^n}{n} exp(-rT). \tag{1.5}$$

This is called the Poisson distribution.

Proof. □

Example 1.14. The probabilities $P_T[n]$,for a few n values, are plotted as a function of rT in firgue 1.4.1 .Note that as n increase, the probability reaches its maximum at larger T values and that large n values are more likely than small ones for large T.

Example 1.15. Figure B shows the probabilities of various numbers of spikes occurring when the average number of spikes is 10.



Theorem 1.16. The probability $P[t_1, t_2, ..., t_n]$can be expressed in terms of another probability function $P_T[n]$,which is the probality that an arbitrary sequence of exactly n spikes occurs within a trial of duration T.Assuming that the spike times are ordered so that $0 \le t_1 \le t_2 \le ... \le t_n \le T$,the relationship is

$$P[t_1, t_2, ..., t_n] = n!_T[n](\frac{\triangle t}{T})^n \tag{1.6}$$

Proof. □

1.5 1.5

Assumption 1.17. From now on, assume that

$$\text{force on } S \text{ per unit area} = -p(\mathbf{x}, t)\mathbf{n} + \mathbf{n} \cdot \boldsymbol{\sigma}(\mathbf{x}, t), \tag{1.7}$$

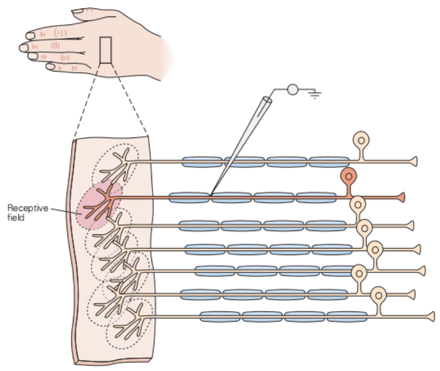
where $\boldsymbol{\sigma}$ is the *(deviatoric) stress tensor* and $\mathbf{n}$ is the unit outward normal of S.

Chapter 2

Neural Encoding II: Reverse Correlation and Visual Receptive Fields

Notation 1. The skin area, location in the body, retinal area, or tonal domain in which stimuli can activate a sensory neuron is called its *receptive field*.

Remark 2.1. The following figure is the receptive field of a touch-sensitive neuron, which denotes the region of skin where gentle tactile stimuli evoke action potentials in that neuron. Sometimes receptive fields would change over time.



Notation 2. *Reverse-correlation* is a technique for studying how sensory neurons add up signals from different locations in their receptive fields, and also how they sum up stimuli that they receive at different times, to generate a response.

Remark 2.2. The goal of the reverse-correlation technique is to find a function $r = f(s)$ that maps from the stimulus s to the neuronal response r, where the stimulus is a function dependent on spatial location and time $s = s(x, y, z, t)$.

Remark 2.3. The reason that this technique is called "reverse" is that we align the time origin with the neuron's response and then reverse the timeline to find what stimulus ($t < 0$) triggered the neuron's response at the current moment ($t = 0$).

Notation 3. *Descriptive Models* approximate descriptions of neural responses, and do not explain how visual responses arise from the synaptic, cellular, and network properties of neoral circuits. Nevertheless, they provide an important framework for characterizing response selectivities, a reference point for identifying and characterizing novel effects, and a basis for building mechanistic models, some of which are discussed at the end of this chapter.

Assumption 2.1. As discussed in chapter 1, sensory systems tend to adapt to the absolute intensity of a stimulus. We therefore assume throughout this chapter that the stimulus parameter $s(t)$ has been defined with its mean value subtracted out, that is,

$$\frac{1}{T}\int_0^T s(t)dt = 0. \tag{2.1}$$

2.1 Estimating Firing Rates

Remark 2.4. The response tuning curve discussed in Chapter 1 is a simple model in which firing rates were estimated as instantaneous functions of the stimulus. Nevertheless, the activity of a neuron at time t typically depends on the behavior of the stimulus over a period of time starting a few hundred milliseconds prior to t and ending perhaps tens of milliseconds before t. Reverse-correlation methods can be used to construct a more accurate model that includes the effects of the stimulus over such an extended period of time.

Remark 2.5. The **basic problem** is to construct an estimate $r_{est}(t)$ of the firing rate $r(t)$ evoked by a stimulus $s(t)$.

2.1.1 The Linear Rate Estimate

Definition 2.2. The *linear rate estimate* at any given time t is the weighted sum of the values taken by the stimulus at earlier times. With the continuous change in time, this sum actually takes the form of an integral, that is,

$$r_{est}(t) = r_0 + \int_0^\infty D(\tau)s(t-\tau)d\tau, \tag{2.2}$$

where r_0 accounts for any background firing that may occur when $s = 0$, $D(\tau)$ is a weighting factor that determines how strongly, and with what sign, the value of the stimulus at time $t - \tau$ affects the firing rate at time t.

Remark 2.6. The integral in equation 2.2 is a linear filter.

Definition 2.3. The *error* of an estimate $r_{est}(t)$ to an actual neural response $r(t)$ is defined as

$$E = \frac{1}{T}\int_0^T (r_{est}(t) - r(t))^2 dt. \tag{2.3}$$

Definition 2.4. The kernel D that minimizes the linear rate estimate error E defined in equation 2.3 is called *optimal linear kernel* or simply called *optimal kernel.*

Proposition 2.5. The optimal kernel D satisfies

$$\int_0^\infty Q_{ss}(\tau-\tau')D(\tau')d\tau' = Q_{rs}(-\tau), \tag{2.4}$$

where $Q_{ss}(\tau) = \int s(t)s(t+\tau)/T$ is the stimulus autocorrelation function, and $Q_{rs}(\tau) = \int r(t)s(t+\tau)/T$ is the firing rate-stimulus correlation function, both of which were defined in chapter 1.

Solution. Using equation 2.2 for the estimated firing rate, the expression in eqution 2.3 to be minimized is

$$E = \frac{1}{T}\int_0^T \left(r_0 + \int_0^\infty D(\tau)s(t-\tau)d\tau - r(t)\right)^2. \tag{2.5}$$

The minimum is obtained by setting the derivative of E with respect to functional derivative the function D to 0. E that depends on a function D is a functional. Finding the extrema of functionals is the subject of a branch of mathematics called the calculus of variations. A simple way to define a functional derivative is to introduce a small time interval Δt and evaluate all functions at integer multiples of Δt. We define $r_i = r(i\Delta t)$, $D_k = D(k\Delta t)$ and $s_{i-k} = s((i-k)\Delta t)$. If Δt is small enough, the integrals in equation 2.5 can be approximated by sums,

$$E = \frac{\Delta t}{T}\sum_{i=0}^{T/\Delta t}\left(r_0 + \Delta t\sum_{k=0}^{\infty} D_k s_{i-k} - r_i\right)^2. \tag{2.6}$$

E is minimized by setting its derivative with respect to D_j for all values of j to 0,

$$\frac{\partial E}{\partial D_j} = 0 = \frac{2\Delta t}{T}\sum_{i=0}^{T/\Delta t}\left(r_0 + \Delta t\sum_{k=0}^{\infty} D_k s_{i-k} - r_i\right) s_{i-j}\Delta t. \tag{2.7}$$

Rearranging and simplifying this expression gives the condition,

$$\Delta t\sum_{k=0}^{\infty} D_k\left(\frac{\Delta t}{T}\sum_{i=0}^{T/\Delta t} s_{i-k}s_{i-j}\right) = \frac{\Delta t}{T}\sum_{i=0}^{T/\Delta t}(r_i - r_0)s_{i-j}. \tag{2.8}$$

If we take the limit $\Delta t \to 0$ and make the replacements $i\Delta t \to t$, $j\Delta t \to \tau$, and $k\Delta t \to \tau'$, the sums in equation 2.8 turn back into integrals, the indexed variables become functions, and we find

$$\begin{aligned}&\int_0^\infty D(\tau')\left(\frac{1}{T}\int_0^T s(t-\tau')s(t-\tau)dt\right)d\tau' \\ &= \frac{1}{T}\int_0^T (r(t)-r_0)s(t-\tau)dt.\end{aligned} \tag{2.9}$$

And,

$$\begin{aligned}&\frac{1}{T}\int_0^T s(t-\tau')s(t-\tau)dt \\ &= \frac{1}{T}\int_0^T s(t-\tau+\tau-\tau')s(t-\tau)d(t-\tau) \\ &= \frac{1}{T}\int_{-\tau}^{T-\tau} s(t+\tau-\tau')s(t)dt \\ &= \frac{1}{T}\int_0^T s(t+\tau-\tau')s(t)dt = Q_{ss}(\tau-\tau'),\end{aligned}$$

where the third step follows from the translation invariance of $s(t)$. Also,

$$\begin{aligned}&\frac{1}{T}\int_0^T (r(t)-r_0)s(t-\tau)dt \\ &= \frac{1}{T}\int_0^T r(t)s(t-\tau)dt + r_0\frac{1}{T}\int_0^T s(t-\tau)dt \\ &= \frac{1}{T}\int_0^T r(t)s(t-\tau)dt = Q_{ss}(-\tau),\end{aligned}$$

where the second step follows from Assumption 2.1. Thus, equation 2.9 can be re-expressed in the form of equation 2.4.

Remark 2.7. The method we are describing is a kind of reverse-correlation technique because the firing rate-stimulus correlation function is evaluated at $-\tau$ in equation2.4.

Definition 2.6. The *white-noise kernel* is the optimal kernel with a white-noise stimulus that satisfies $Q_{ss}(\tau) = \sigma_s^2\delta(\tau)$.

Proposition 2.7. The *white-noise kernel* satisfies

$$D(\tau) = \frac{\langle r\rangle C(\tau)}{\sigma_s^2}, \tag{2.10}$$

where $C(\tau)$ is the spike-triggered average stimulus and $\langle r\rangle$ is the average firing rate of the neuron.

Solution. The left side of equation 2.4 is

$$\sigma_s^2\int_0^\infty \delta(\tau-\tau')D(\tau')d\tau' = \sigma_s^2 D(\tau). \tag{2.11}$$

Thus, we have

$$D(\tau) = \frac{Q_{rs}(-\tau)}{\sigma_s^2} = \frac{\langle r\rangle C(\tau)}{\sigma_s^2}, \tag{2.12}$$

where the second step follows from the relation $Q_{rs}(-\tau) = \langle r\rangle C(\tau)$ from chapter1.

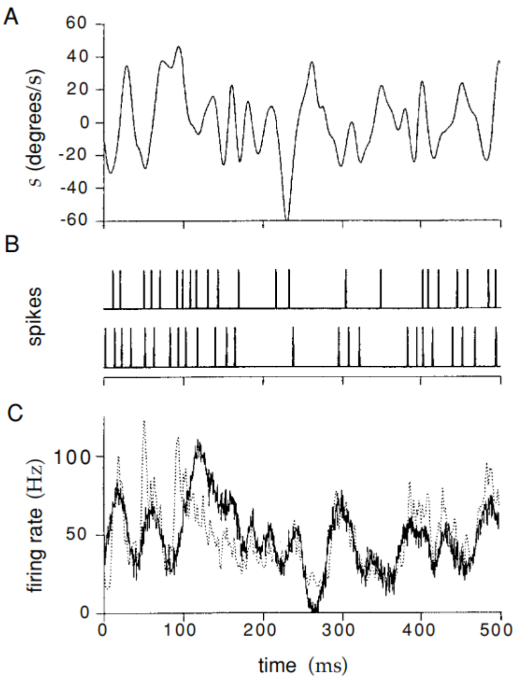
Proposition 2.8. The general solution of 2.4 for an arbitrary stimulus is

$$D(\tau) = \frac{1}{2\pi}\int_{-\infty}^{\infty}\frac{\tilde{Q}_{rs}(-\omega)}{\tilde{Q}_{ss}(\omega)}e^{-i\omega\tau}d\omega, \tag{2.13}$$

where $\tilde{Q}_{rs}(\omega)$ and $\tilde{Q}_{ss}(\omega)$ are the Fourier transforms of $Q_{rs}(\omega)$ and $Q_{ss}(\omega)$, respectively.

Solution. The result could be obtained by the method of Fourier transforms.

Example 2.9. The H1 neuron of the fly visual system responds to moving images. The following figure shows a prediction of the firing rate of this neuron obtained from a linear filter. The velocity of the moving image is plotted in A, and two typical responses are shown in B. The linear rate estimate with optimal kernel (the solid line) and the firing rate computed from the data by binning and counting spikes (the dashed line) are compared in figure C.



Definition 2.10. Neuronal selectivity is often characterized by describing stimuli that evoke maximal responses, subject to a constraint. This stimulus is called the *most effective stimulus.*

Remark 2.8. A constraint is essential because the linear estimate in equation 2.2 is unbounded.

Definition 2.11. The *fixed energy constraint* is

$$\int_0^T \left(s(t')\right)^2 dt' = constant, \tag{2.14}$$

where the integral $\int_0^T \left(s(t')\right)^2 dt'$ is called *stimulus energy.*

Proposition 2.12. With the optimal kernel $D(\tau)$ and the fixed energy constraint 2.14, the most effective stimulus $s(t)$ is proportional to the optimal kernel $D(\tau)$ with

$$D(\tau) = -2\lambda s(t-\tau), \tag{2.15}$$

where $\lambda < 0$.

Solution. We impose this constraint by the method of Lagrange multipliers, which means that we must find the unconstrained maximum value with respect to s of

$$\begin{aligned} r_{est}(t) + \lambda \int_0^T s^2(t')dt' = r_0 + \int_0^\infty D(\tau)s(t-\tau)d\tau \\ + \lambda \int_0^T \left(s(t')\right)^2 dt', \end{aligned} \tag{2.16}$$

where λ is the Lagrange multiplier. Setting the derivative of this expression with respect to the function s to 0 (similar with the derivative of E in the solution to the proposition 2.5) gives 2.15.

Remark 2.9. The value of λ (which is less than 0) in equation 2.15 is determined by requiring that condition 2.14 is satisfied, but the precise value is not important for our purposes. The essential result is the proportionality between the optimal stimulus and $D(\tau)$.

Remark 2.10. The most effective stimulus analysis provides an intuitive interpretation of the linear rate estimate 2.2. At fixed stimulus energy, the integral in 2.2 measures the overlap between the actual stimulus and the most effective stimulus. In other words, it indicates how well the actual stimulus matches the most effective stimulus. Mismatches between these two reduce the value of the integral and result in lower predictions for the firing rate.

Remark 2.11. As the example 2.9 shows, the linear rate estimate is a good agreement in regions where the measured rate varies slowly, but the estimate fails to capture high-frequency fluctuations of the firing rate, presumably because of nonlinear effects not captured by the linear kernel. Some such effects can be described by a static nonlinear function or including higher-order terms in a Volterra or Wiener expansion, as discussed below.

2.1.2 Volterra and Wiener Expansion

Definition 2.13. The *Volterra expansion* is the functional equivalent of the Taylor series expansion used to generate power series approximations of functions. For the case we are considering, it takes the form

$$\begin{aligned} r_{est}(t) =& r_0 + \int D(\tau)s(t-\tau)d\tau \\ &+ \int D_2(\tau_1,\tau_2)s(t-\tau_1)s(t-\tau_2)d\tau_1 d\tau_2 \\ &+ \int D_3(\tau_1,\tau_2,\tau_3)s(t-\tau_1)s(t-\tau_2)s(t-\tau 3)d\tau_1 d\tau_2 d\tau_3 \\ &+ \ldots. \end{aligned} \tag{2.17}$$

Definition 2.14. The series rearranged by Wiener from 2.17 to make the terms easier to compute has the same first two terms of the Volterra expansion, and it is called *Wiener expansion.* And the linear kernel D is called the *first Wiener kernel.*

2.1.3 Static Nonlinearities

Remark 2.12. The linear prediction has two obvious problems:

1. there is nothing to prevent the predicted firing rate from becoming negative,

2. the predicted rate does not saturate, but instead increases without bound as the magnitude of the stimulus increases.

One way to deal with these and some of the other deficiencies of a linear prediction is to write the firing rate as a background rate plus a nonlinear function of the linearly filtered stimulus.

Definition 2.15. The *estimate with static nonlinearity* is

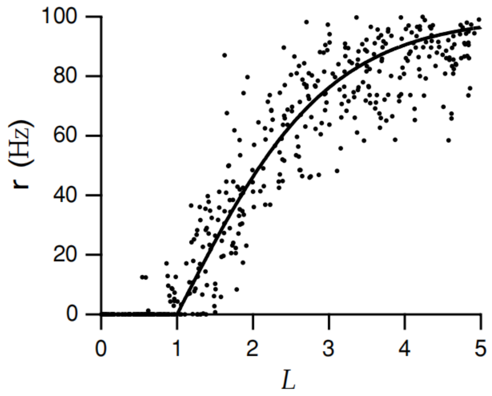
$$r_{est}(t) = r_0 + F(L(t)), \tag{2.18}$$

where F is an arbitrary function and

$$L(t) = \int_0^\infty D(\tau)s(t-\tau)d\tau. \tag{2.19}$$

F is called a *static nonlinearity* to stress that it is a function of the linear filter value evaluated instantaneously at the time of the rate estimation.

Example 2.16. F can be extracted from data by means of the graphical procedure illustrated in the following figure. First, a linear estimate of the firing rate is computed using the optimal kernel defined by equation 2.4. Next, a plot is made of the pairs of points $(L(t), r(t))$ at various times and for various stimuli, where $r(t)$ the actual rate extracted from the data. There will be a certain amount of scatter in this plot due to the inaccuracy of the estimation. F can be extracted by fitting a function to the points on the scatter plot.



Remark 2.13. The function F typically contains constants used to set the firing rate to realistic values. These give us the freedom to normalize $D(\tau)$ in some convenient way, correcting for the arbitrary normalization by adjusting the parameters within F.

Example 2.17. The *threshold function*

$$F(L) = G[L - L_0]_+, \tag{2.20}$$

is a static nonlinearity used to introduce firing thresholds into estimates of neural responses. Here L_0 is the threshold value that L must attain before firing begins.

Remark 2.14. Above the threshold, the firing rate is a linear function of L, with G acting as the constant of proportionality. Half-wave rectification is a special case of this with $L_0 = 0$. That this function does not saturate is not a problem if large stimulus values are avoided.

Example 2.18. The *sigmoidal function*

$$F(L) = \frac{r_{max}}{1 + e^{g_1(L_{1/2} - L)}}, \tag{2.21}$$

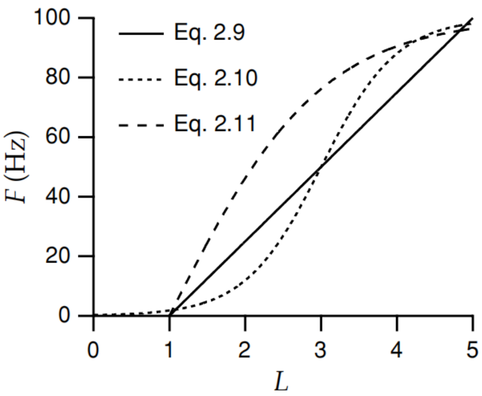
is a static nonlinearity used to introduce saturation into estimates of neural responses. Here r_{max} is the maximum possible firing rate, $L_{1/2}$ is the value of L for which F achieves half of this maximal value, and g_1 determines how rapidly the firing rate increases as a function of L.

Example 2.19.

$$F(L) = r_{max}[\tanh(g_2(L - L_0))]_+ \tag{2.22}$$

is a static nonlinearity that combines a hard threshold with saturation uses a rectified hyperbolic tangent function. Here r_{max} and g_2 play similar roles as in equation 2.21, and L_0 is the threshold.

Example 2.20. The following figure shows the different nonlinear functions that we have discussed.



Remark 2.15. Although the static nonlinearity can be any function, the estimate of equation 2.18 is still restrictive because it allows for no dependence on weighted autocorrelations of the stimulus or other higher-order terms in the Volterra series.

Remark 2.16. Once the static nonlinearity is introduced, the linear kernel derived from equation 2.4 is no longer optimal because it was chosen to minimize the squared error of the linear estimate $r_{est}(t) = r_0 + L(t)$, not the estimate with the static nonlinearity $r_{est}(t) = r_0 + F(L(t))$.

Definition 2.21. The *self-consistency condition* is that when the nonlinear estimate $r_{est}(t) = r_0 + F(L(t))$ is substituted into equation 2.12, the relationship between the linear kernel and the firing rate-stimulus correlation function should still hold. In other words, we require that

$$D(\tau) = \frac{1}{\sigma_s^2 T}\int_0^T r_{est}(t)s(\tau-t)dt = \frac{1}{\sigma_s^2 T}\int_0^T F(L(t))s(\tau-t)dt, \tag{2.23}$$

where the second step follows from Assumption 2.1.

Theorem 2.22 (Bussgang Theorem)**.** An estimate based on the optimal kernel for linear estimation can still be self-consistent (although not necessarily optimal) when nonlinearities are present, if the stimulus used to extract the optimal kernel is Gaussian white noise.

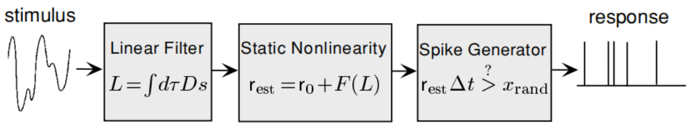
Solution. If stimulus used to extract D is Gaussian white noise, we have

$$\frac{1}{\sigma_s^2 T}\int_0^T F(L(t))s(\tau - t)dt = \frac{D(\tau)}{T}\int_0^T \frac{dF(L(t))}{dL}dt. \quad (2.24)$$

For the right side of this equation to be $D(\tau)$, the remaining expression must be equal to 1 by appropriate scaling of F. The critical identity 2.24 is based on integration by parts for a Gaussian weighted integral.

Remark 2.17. The Bussgang Theorem suggests that equation 2.12 will provide a reasonable kernel, even in the presence of a static nonlinearity, if the white noise stimulus used is Gaussian.

Example 2.23. A model of the spike trains evoked by a stimulus can be constructed by using the firing-rate estimate of equation 2.18 to drive a Poisson spike generator (see chapter 1). The following figure shows the structure of such a model with a linear filter, a static nonlinearity, and a stochastic spike generator.



Remark 2.18. In some cases, the linear term fails to predict even when static nonlinearities are included and in practice including more terms in the Volterra series is quite difficult to go beyond the first few terms. We can replace the parameter s in equation 2.19 with an appropriately chosen function of s to improve the accuracy, that is,

$$L(t) = \int_0^\infty D(\tau)f(s(t-\tau))d\tau. \quad (2.25)$$

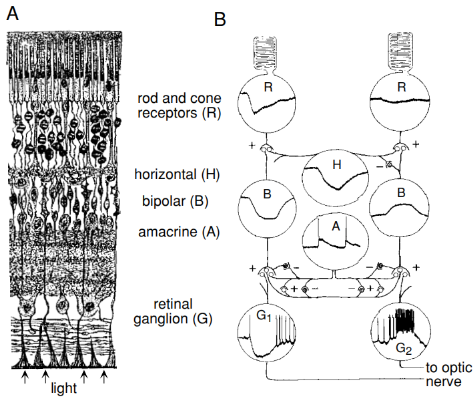
A reasonable choice for this function is the response tuning curve. For time-dependent stimuli, we can think of equation 2.25 as a dynamic extension of the response tuning curve.

2.2 The Early Visual System

Principle 2.24 (Retinal Signal Conversion)**.** The conversion of a light stimulus into an electrical signal and ultimately an action potential sequence occurs in the retina. The retina is roughly composed of 3 layers of cells, *photoreceptor cells*, *bipolar cells* and *ganglion cells*. First, photoreceptor cells convert light signals into electrical signals. And then, bipolar cells are responsible for sorting and processing these electrical signals. Finally, ganglion cells will convert electrical signals into action potential sequences. In the intact eye, counterintuitively, light enters through the side opposite from the photoreceptors because Vertebrate retinal cell layers are arranged in reverse order of signaling.

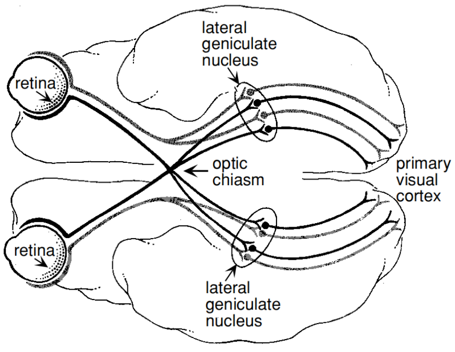
Remark 2.19. Changing membrane potentials is adequate for signaling within the retina, where distances are small. However, it is inadequate for the task of conveying information from the retina to the brain. Thus, the ganglion cells are needed.

Example 2.25. The following figure A is an anatomical diagram showing the five principal cell types of the retina and figure B is a rough circuit diagram and intracellular recordings made in neurons of the retina of a mud puppy (an amphibian). The rod cells, especially the one on the left side of figure B, are hyperpolarized by the light flash. This electrical signal is passed along to bipolar and horizontal cells through synaptic connections. Note that in one of the bipolar cells, the signal has been inverted, leading to depolarization. Pluses and minuses represent excitatory and inhibitory synapses, respectively. The two retinal ganglion cells shown in the figure have different responses and transmit different sequences of action potentials. G_2 fires while the light is on, and G_1 fires when it turns off. These are called *ON* and *OFF responses*, respectively



Notation 4. The output neurons of the retina are the retinal ganglion cells, whose axons form the *optic nerve*.

Principle 2.26 (Visual Pathway)**.** As the following figure shows, the optic nerve carry information from each visual hemifield up to the *optic chiasm*, where some retinal ganglion cell axons cross the midline at the optic chiasm, and then to the LGN. Cells in this nucleus send their axons along the optic radiation to the primary visual cortex.



Definition 2.27. The restricted regions of the visual field where light stimuli could active Neurons in the retina, LGN, and primary visual cortex is called *receptive fields* of the corresponding visual neuron.

Assumption 2.28. Patterns of illumination outside the receptive field of a given neuron cannot generate a response directly, although they can significantly affect responses to stimuli within the receptive field. We do not consider such effects, although they are of considerable experimental and theoretical interest.

Remark 2.20. Within the receptive fields, there are regions where illumination higher than the background light intensity enhances firing, and other regions where lower illumination enhances firing. The spatial arrangement of these regions determines the selectivity of the neuron to different inputs. The term *receptive field* is often generalized to refer not only to the overall region where light affects neuronal firing, but also to the spatial and temporal structure within this region.

Notation 5. Visually responsive neurons in the retina, LGN, and primary visual cortex are divided into two classes, depending on whether or not the contributions from different locations within the visual field sum linearly. *Simple cells* in primary visual cortex appear to satisfy this assumption. *Complex cells* in primary visual cortex do not show linear summation across the spatial receptive field, and nonlinearities must be included in descriptions of their responses.

Assumption 2.29. To streamline the discussion in this chapter, we consider only gray-scale images, although the methods presented can be extended to include color. We also restrict the discussion to two-dimensional visual images, ignoring how visual responses depend on viewing distance and encode depth.

Remark 2.21. In discussing the response properties of retinal, LGN, and V1 neurons, we do not follow the path of the visual signal, nor the historical order of experimentation, but instead begin with primary visual cortex and then move back to the LGN and retina. And the emphasis of this chapter is on properties of individual neurons.

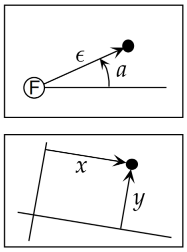
2.2.1 The Retinotopic Map

Definition 2.30. The *retinotopic map* is a map from the visual world to the cortical surface that make sure neighboring points in a visual image evoke activity in neighboring regions of visual cortex.

Remark 2.22. The retinotopic map refers to the transformation from the coordinates of the visual world to the corresponding locations on the cortical surface.

Notation 6. The image point that focuses onto the fovea or center of the retina is called the *fixation point.*

Notation 7. Polar and Cartesian coordinate systems used to parameterize image location is shown in the following figure. Each rectangle represents a tangent screen, and the filled circle is the location of a particular image point on the screen.



The origin of the polar coordinate system is the fixation point F, the *eccentricity* ϵ is proportional to the radial distance from the fixation point to the image point, and *azimuth* a is the angle between the radial line from F to the image point and the horizontal axis. The origin and the orientation of the axes are usual chosen to center and align the coordinate system with respect to a particular receptive field being studied.

2.3 2.4

Assumption 2.31. From now on, assume that

$$\text{force on } S \text{ per unit area} = -p(\mathbf{x}, t)\mathbf{n} + \mathbf{n} \cdot \boldsymbol{\sigma}(\mathbf{x}, t), \quad (2.26)$$

where $\boldsymbol{\sigma}$ is the *(deviatoric) stress tensor* and $\mathbf{n}$ is the unit outward normal of S.

Chapter 3

Neural Decoding

3.1 3.1

Principle 3.1 (Conservation of angular momentum)**.** The rate of change of angular momentum of a system is equal to the net torque acting on the system, i.e.,

$$\frac{\mathrm{d}\mathbf{L}}{\mathrm{d}t} = \boldsymbol{\tau}, \tag{3.1}$$

where $\boldsymbol{\tau}$ is the torque of all external forces on the system about any chosen axis, and $\mathrm{d}\mathbf{L}/\mathrm{d}t$ is the rate of change of angular momentum of the system about the same axis.

3.2 3.2

Remark 3.1. Many physical laws are cumbersome when written in coordinate form but become more compact and attractive looking when written in tensorial form. For example, the incompressible Navier-Stokes equations in cylindrical coordinates are

$$\begin{aligned}
\rho\left(\frac{Dv_r}{Dt} - \frac{v_\theta^2}{r}\right) &= \rho f_r - \frac{\partial p}{\partial r} + \mu\left(\Delta v_r - \frac{v_r}{r^2} - \frac{2}{r^2}\frac{\partial v_\theta}{\partial \theta}\right), \\
\rho\left(\frac{Dv_\theta}{Dt} + \frac{v_r v_\theta}{r}\right) &= \rho f_\theta - \frac{1}{r}\frac{\partial p}{\partial \theta} + \mu\left(\Delta v_\theta + \frac{2}{r^2}\frac{\partial v_r}{\partial \theta} - \frac{v_\theta}{r^2}\right), \\
\rho\frac{Dv_z}{Dt} &= \rho f_z - \frac{\partial p}{\partial z} + \mu\Delta v_z,
\end{aligned}$$

where

$$\Delta = \frac{1}{r}\frac{\partial}{\partial r}\left(r\frac{\partial}{\partial r}\right) + \frac{1}{r^2}\frac{\partial^2}{\partial \theta^2} + \frac{\partial^2}{\partial z^2},$$

and

$$\frac{D}{Dt} = \frac{\partial}{\partial t} + v_r\frac{\partial}{\partial r} + \frac{v_\theta}{r}\frac{\partial}{\partial \theta} + v_z\frac{\partial}{\partial z}.$$

3.3 3.3

Proposition 3.2. The mass of fluid in a region W at time t is

$$m(W,t) = \int_W \rho(\mathbf{x},t)\mathrm{d}V, \tag{3.2}$$

where $\mathrm{d}V$ is the area element in the plane or the volume element in space.

3.4 3.4

Assumption 3.3. From now on, assume that

$$\text{force on } S \text{ per unit area} = -p(\mathbf{x},t)\mathbf{n} + \mathbf{n}\cdot\boldsymbol{\sigma}(\mathbf{x},t), \tag{3.3}$$

where $\boldsymbol{\sigma}$ is the *(deviatoric) stress tensor* and $\mathbf{n}$ is the unit outward normal of S.