# Statistical Models and Data Analysis

Summer term 2018 — Prof. Dr. Christian Leibold

## Problem Set 2 / Solutions 4.16.2018

**1.** (Filtering spike trains) Many neurons emit sequences of stereotypical pulse-like electrical discharges known as spike trains. A mathematical bare-bones description $S(t)$ of the spike train represents it as a sum of delta-functions,

$$S(t) = \sum_{i=1}^{N} \delta(t - t_i),$$

where the $t_i$ denote the times at which the neuron generated an action potential.

(a) Write down the formula for $S(t)$ for a spike train with four spikes at times $t_i = 2, 4, 5$ and 8 ms and sketch it.

(b) Assume that this signal is filtered either by a Gaussian filter with width $\sigma_f = 1$ ms or a filter that is zero for negative $\tau$ and decays exponentially for positive $\tau$ with a time-constant $\tau_f = 1$ ms. Write these two filters in mathematical terms, assuming that they are normalized such that the total area under each filter function is unity. For the precise shape of the Gaussian filter, you may use information you can find on the internet or suitable textbooks, for the exponential filter, you should calculate the normalization constant yourself.

(c) Sketch the filtered spike trains in both cases. The resulting curves are often interpreted as smoothed "firing rates" of a neuron. Discuss the qualitative differences between these two cases.

(d) Finally, plot the instantaneous firing rate, defined for every point in time $t$ as the inverse inter-spike interval between the last spike before $t$ and the next spike after $t$. What are the most important differences to the findings in (c)?

**Solution:**

(a)

$$S(t) = \delta(t - 2) + \delta(t - 4) + \delta(t - 5) + \delta(t - 8)$$

(b) Define

$$k_g(t) = \frac{1}{\sqrt{2\pi}} \exp\left(-\frac{t^2}{2}\right) \qquad \text{Gaussian Filter}$$

and

$$k_e(t) = \frac{1}{\tau} \exp\left(-\frac{t}{\tau}\right) \theta(t) \qquad \text{Exponential Filter}$$

The normalization is such that the kernel function integrates to unity. That is, if we integrate

$$\begin{aligned}
\int_{-\infty}^{\infty} \exp\left(-\frac{t}{\tau}\right) \theta(t)\, dt &= \int_{0}^{\infty} \exp\left(-\frac{t}{\tau}\right)\, dt \\
&= -\tau \exp\left(-\frac{t}{\tau}\right)\Bigg|_{t=0}^{t=\infty} \\
&= \tau,
\end{aligned}$$

so we normalize by a factor $1/\tau$.

In general, given a delta-function train, the convolution of this train with a kernel function is written as

$$\begin{aligned}(k * S)(t) &= \int_0^t k(\tau)S(t-\tau)\ d\tau \\ &= \int_0^t k(\tau)\sum_{i=1}^{N}\delta\left(t-\tau-t_i\right)\ d\tau \\ &= \sum_{i=1}^{N}\int_0^t k(\tau)\delta\left(t-\tau-t_i\right)\ d\tau \\ &= \sum_{i=1}^{t\geq t_i} k(t-t_i)\end{aligned}$$

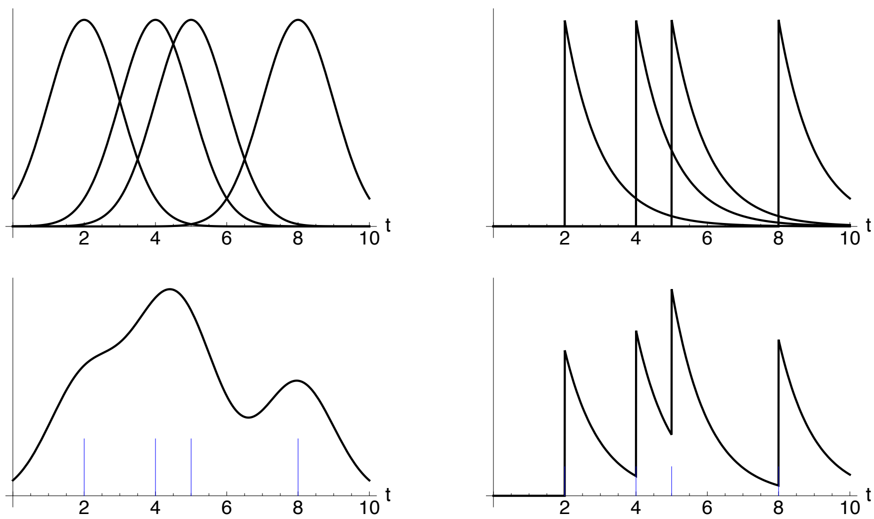



Figure 0.1: Filtering spike trains. Above, convolution replaces each spike time-point by a copy of the kernel function. Below, these convolved spikes are summed–note that this is the end result of convolution. The spike times are indicated by thin blue line segments in the lower panels.

(c) Examine Fig. 0.1 Note that the "smoothed" firing rate in the Gaussian filtering case takes into account both the past and the future, whereas the exponential filter (as defined here) only takes into account past spikes.

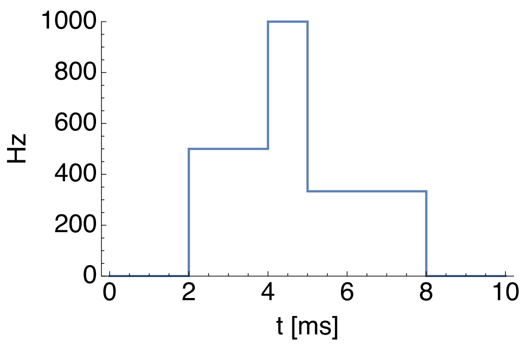
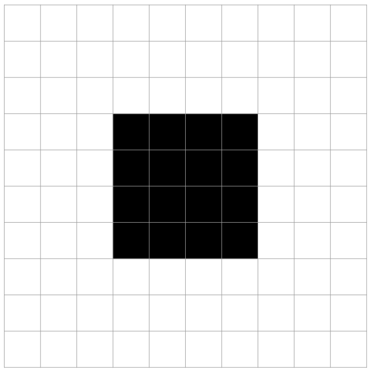



Figure 0.2: The instantaneous firing rate as the the inverse of the time interval between successive spikes.

(d) Note that the instantaneous firing rate (Fig. 0.2) cannot easily be represented by a convolution.

**2.** (Convolution) Consider the following $10 \times 10$ matrix:



where black represents the value $-1$ and white represents the value $+1$.

(a) Convolve the matrix with the following stencil: , where, once again, black represents the value $-1$ and white represents the value $+1$. Specifically, replace each element in the matrix by

$$x_{i,j} \to -x_{i,j} + x_{i,j+1}$$

and assume that any values outside of the bounds of the matrix can be replaced by the value of $+1$. In other words, replace each element in the matrix by the difference between the element just to the right and the element itself.

Sketch the result as a $10 \times 10$ matrix. (Recommendation: don't try to write down mathematical formulae to solve this problem).

A stencil is a discrete version of a convolution kernel.

(b) Propose a stencil that will pick out the edges of the square in the $10 \times 10$ matrix. You may allow for a shift of the edges by a pixel in either direction.

**Solution:**

(a) The key point to realize is that the stencil is defined such that the convolution result is zero whenever neighboring pixels are identical. Only when neighboring pixels are *different* does the filter yield a non-zero result.

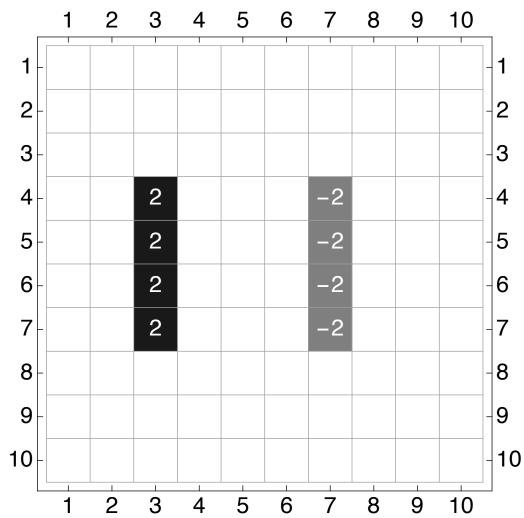
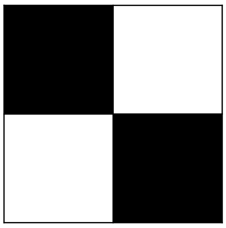



Figure 0.3: The result of convolving the stencil with the $10 \times 10$ matrix.

(b) One possible stencil is . Note that this is not a "perfect" stencil, particularly for the corners of the image. To do this properly, one might consider adding a nonlinearity after the convolution step.

**3.** (Integral transforms) Convolutions are integrals of the type

$$(x * y)(t) = \int_0^t x(\tau)y(t-\tau)\, d\tau$$

You will soon learn about Fourier transforms in the lectures, and how taking the Fourier transform makes convolutions very simple. An integral transform that is closely related to the Fourier transform is called the Laplace transform

$$\mathcal{L}f(s) = \int_0^\infty \exp(-st)f(t)\, dt.$$

(a) Compute the Laplace transform for

$$f(t) = 1 \qquad \text{and} \qquad f(t) = \exp(-at) \quad \text{for } a > 0$$

(b) For a convolution of two functions $g$ and $f$,

$$\mathcal{L}(g * f)(s) = \mathcal{L}g(s) \cdot \mathcal{L}f(s),$$

so that a convolution becomes a simple multiplication in the integral transform space. (Bonus points for showing why this is true!) Use this convolution property to show that

$$\mathcal{L}(\exp(-at) * \exp(-bt)) = \frac{1}{s+a} \cdot \frac{1}{s+b}$$

(c) Use the fact that

$$\frac{1}{s+a} \cdot \frac{1}{s+b} = \frac{1}{a-b}\left[\frac{1}{s+b} - \frac{1}{s+a}\right]$$

and the result from part (a) to compute the result of convolving $\exp(-at)$ with $\exp(-bt)$.

(d) Plot the result of convolving $\exp(-at)$ with $\exp(-bt)$ as a function of $t$ when you set $a = 1$ and $b = 5$.

In neurobiological terms, you might imagine that a synaptic current has an exponential time-course, but that this is convolved by the membrane time constant to yield an EPSP (excitatory postsynaptic potential). The EPSP time-course would then be given by an expression like the one you just calculated.

**Solution:**

(a) First, let's prove the convolution theorem for Laplace transforms

$$\mathcal{L}\left[\int_0^t k(\tau)f(t-\tau)\, d\tau\right] = \widetilde{k}(s)\widetilde{f}(s)$$

Apply the definition of the Laplace transform

$$\begin{aligned}\widetilde{k}(s)\widetilde{f}(s) &= \int_0^\infty e^{-su}k(u)\, du \int_0^\infty e^{-sv}f(v)\, dv \\ &= \int_0^\infty du \int_0^\infty dv\; e^{-s(u+v)}k(u)f(v).\end{aligned}$$

Now, substitute $\tau = u + v$.

$$\widetilde{k}(s)\widetilde{f}(s) = \int_0^\infty k(u)\, du \int_u^\infty e^{-s\tau}f(\tau-u)\, d\tau$$

In general, we need to be careful to ensure that the volume element $du\, dv = d\tau du$ remains the same. In this case, it is. We will want to interchange the order of integration. We remark that the integration occurs over a triangular region (which is unbounded from above). Initially, we integrate from $\tau$ from $u$ to $\infty$, as in Fig. 0.4 (left). But we could just as well integrate $u$ first from 0 to $\tau$, as in the right panel of Fig. 0.4.

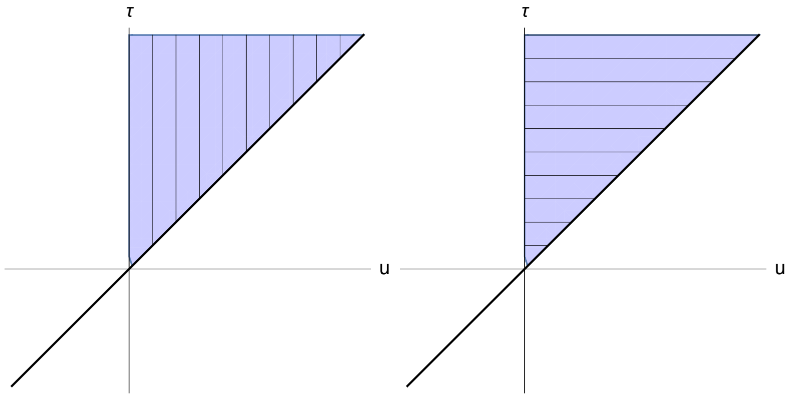



Figure 0.4: Equivalent integration schemes for the convolution integral

$$\widetilde{k}(s)\widetilde{f}(s) = \int_0^\infty d\tau\ e^{-s\tau} \int_0^\tau k(u) f(\tau - u)\ du$$

which, by definition, is

$$\widetilde{k}(s)\widetilde{f}(s) = \mathcal{L}\left[\int_0^\tau k(u) f(\tau - u)\ du\right]$$

(b)

$$\int_0^\infty e^{-st}\ dt = -\frac{1}{s} e^{-st}\Big|_0^\infty = 0 - \left(-\frac{1}{s}\right) = \frac{1}{s}$$

$$\int_0^\infty e^{-st} \exp(-at)\ dt = -\frac{1}{a+s} e^{-(s+a)t}\Big|_0^\infty = 0 - \left(-\frac{1}{s+a}\right) = \frac{1}{s+a}$$

Another set of standard Laplace transforms can be derived by integration by parts. Recall that the chain rule for the product of two functions is

$$(uv)' = u'v + uv',$$

where the prime superscript denotes differentiation. Rearranging, this is equivalent to

$$u'v = (uv)' - uv'.$$

Integrating, we obtain

$$\int_a^b u'v\ dx = (uv)|_b^a - \int_a^b uv'\ dx,$$

which is called "integration by parts". Now let's compute the Laplace transform of the trigonometric functions

$$\begin{aligned} I_s &= \int_0^\infty e^{-st} \sin(bt)\ dt = -\frac{1}{b} \cos(bt) \exp(-st)\Big|_0^\infty - \frac{1}{b} \int_0^\infty e^{-st} s \cos(bt)\ dt \\ I_c &= \int_0^\infty e^{-st} \cos(bt)\ dt = \frac{1}{b} \sin(bt) \exp(-st)\Big|_0^\infty + \frac{1}{b} \int_0^\infty e^{-st} s \sin(bt)\ dt \\ &= \frac{s}{b} \int_0^\infty e^{-st} \sin(bt)\ dt = \frac{s}{b} I_s \end{aligned}$$

| $f(t)$ | $\widetilde{f}(s)$ |
|---|---|
| $c$ | $\frac{c}{s}$ |
| $c\ t$ | $-\frac{c}{s^2}$ |
| $\exp(-at)$ | $-\frac{1}{s+a}$ |
| $\sin(bt)$ | $\frac{b}{s^2+b^2}$ |
| $\cos(bt)$ | $\frac{s}{s^2+b^2}$ |

Table 0.1: Functions and their Laplace transforms

Hence

$$\begin{aligned} I_s = \int_0^\infty e^{-st} \sin(bt)\ dt =& \frac{1}{b} - \frac{s}{b} \int_0^\infty e^{-st} \cos(bt)\ dt \\ =& \frac{1}{b} - \left(\frac{s}{b}\right)^2 I_s I_s \left(1 + \left(\frac{s}{b}\right)^2\right) = \qquad \frac{1}{b} \\ I_s \left(\frac{b^2+s^2}{b^2}\right) =& \frac{1}{b} \\ I_s = \frac{b}{s^2+b^2} \end{aligned}$$

if we use $I_c = \frac{s}{b} I_s$, we get

$$I_c = \frac{s}{s^2+b^2}$$

Another important property of the Laplace transform is

$$\begin{aligned} \mathcal{L}\left[\frac{df}{dt}\right] =& \int_0^\infty e^{-st} \frac{d}{dt} f(t)\ dt \\ =& f(t) \exp(-st) \Big|_0^\infty - \int_0^\infty \left(\frac{d}{dt} e^{-st}\right) f(t)\ dt \\ =& -f(0) + s \int_0^\infty e^{-st} f(t)\ dt \\ =& -f(0) + s\widetilde{f}(s) \end{aligned}$$

Also, by integration by parts,

$$\mathcal{L}\left[t^n f(t)\right] = (-1)^n \frac{d^n \widetilde{f}(s)}{ds^n}$$

In many cases, to get the inverse Laplace transform $\mathcal{L}^{-1}$, one uses a table of pairs of functions with their transforms, as seen in Table 0.1.

(c) Partial fractions

$$\frac{1}{s+a} \cdot \frac{1}{s+b} = \frac{1}{a-b}\left[\frac{1}{s+b} - \frac{1}{s+a}\right]$$

Therefore,

$$\mathcal{L}^{-1} = \frac{1}{a-b}\left(\exp(-bt) - \exp(-at)\right)$$

For the values of $a = 1$, $b = 5$, the result of the convolution is

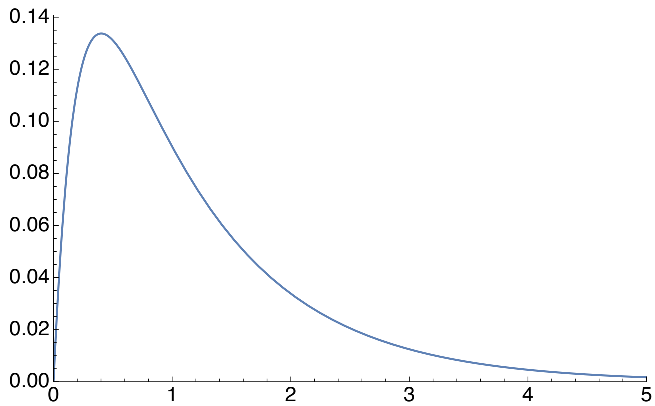



Figure 0.5: The result of convolving an exponential $\exp(-at)$ with another exponential $\exp(-bt)$. Parameter values are $a = 1, b = 5$.