Constructing the Rate Function

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1 Philosophy

The continuous rate function $\lambda(t)$ for the renewal process is obtained from discrete spike train responses to repeated stimuli. This construction is done in two stages with adaptive filters. In the first stage, which we refer to as a transformation from lab time t to a "time A" time $t^A(t)$, we define a new clock that speeds up and slows down with the local response rate. A continuous cosine bell function (see equation 1) replaces each spike time t_{kl} (the k^{th} spike in trial l), where the width of the bell is determined by the largest of the interspike intervals preceding and following the spike. The idea is to smooth out the slower response modulations within a trial. The cosine bells are summed together within a trial, and then an average across trials gives a "time A" rate function $\lambda^A(t)$. With this time A rate function we can associate a time A, t_{kl}^A , to each recorded spike (see below). If at this point we are lucky and the set of event times t_{kl}^A are distributed as a homogeneous Poisson process with unit rate parameter, then our work is done, because our ultimate goal is to find a transformation that respects the *time-rescaling theorem*. In general, however, this first stage of the transformation is too crude to achieve this purpose. Notice also that no free parameters in the method have been introduced yet.

The second stage of the transformation to a "time B" is designed to smooth out some of the sharper response features missed in the time A transformation. To achieve this, we collapse onto a single axis each time A spike time. After this, we again replace each time t_{kl}^A with a cosine bell function, whose width in this case is given by the average of the distances b spikes in advance and b spikes prior to t_{kl}^A . In regions of the time A axis where the response modulation is large and there are many nearby spikes on the collapsed axis, this bell width will be small and the associated cosine bell function very sharp, reflecting the large firing rate there. Similarly, if one has to move a large distance in time to see b spikes to the left and right of the target spike, then the cosine bell will be short and wide, indicating a slower response rate.

The parameter b of the time B transformation is free for us to choose. We fix it by constraining the new set of time B spikes $\{t_{kl}^B\}$ to be distributed as nearly as possible to a unit-rate homogeneous Poisson process. A set of time B interspike intervals are defined on the collapsed time B axis, and b is varied to minimize a mean-squared residual between the time B intervals and the order statistics of the unit-rate exponential distribution.

1.1 Time A

For purposes of exposition we ignore the fact that each spike time is associated with a particular trial, and simply call the k^{th} spike in a trial t_k (original lab time). Each spike, in both the time A and time B transformation, is replaced by a cosine bell function $C(t;t_k,\omega_k)$ of the form

$$C(t;t_k,\omega_k) = \frac{1}{2\omega_k} \left(1 + \cos\left(\frac{\pi(t-t_k)}{\omega_k}\right)\right) , |t-t_k| < \omega_k$$

$$0 , |t-t_k| \ge \omega_k$$
(1)

Notice that the cosine bell is symmetric about the target spike, t_k , and vanishes outside the interval $t \in (t_k - \omega_k, t_k + \omega_k)$. It is also a smooth function, which is important since we will also be interested in the first derivative of the rate function. The cosine bell width ω_k , denoted by ω_k^A for the time A transformation, is defined by

$$\omega_k^A = \max(t_k - t_{k-1}, t_{k+1} - t_k) \equiv \max(I_k, I_{k+1})$$

where the interspike interval $I_k \equiv t_k - t_{k-1}$. Notice also that $C(t_k; t_k, \omega_k) = \omega_k^{-1}$ and $\int_{t_k - \omega_k}^{t_k + \omega_k} C(t; t_k, \omega_k) dt = 1$, so the cosine bells define a family of functions that converge to a delta distribution $\delta(t - t_k)$ as $\omega_k \to 0$. Figure 1 graphically illustrates the time A cosine bell construction and summation within a single trial. For spikes at the beginning and end of a trial, for which there is only a single adjacent spike interval, the width ω_k^A is set to the interval associated with the only adjacent spike. Spikes near the beginning or end of a trial might also have their associated cosine bells clipped and not integrating to unity.

With each spike represented as a continuous function C, we define a rate function $\lambda_l^A(t)$ by summing the bells within the trial l:

$$\lambda_l^A(t) = \sum_k C\left(t; t_{kl}, \pmb{\omega}_k^A\right).$$

If there are N trials, then there are N rate functions constructed in this way, one for each trial. The "time A" rate function, finally, is given by a trial average of the set of rate functions $\left\{\lambda_l^A(t)\right\}_{l=1}^N$:

$$\lambda^A(t) \equiv rac{1}{N} \sum_{l=1}^N \lambda_l^A(t) \, .$$

We use the rate function $\lambda^A(t)$ to transform each original spike time t_{kl} into a time A spike time t_{kl}^A . For notational clarity we suppress the indices denoting spike and trial numbers:

$$t^A \equiv \int_0^t \lambda^A(\tau) d\tau$$

 $\frac{dt^A}{dt} = \lambda^A(t).$

Note that no free parameters have been introduced up to this point. The time A rate function is determined completely by the data.

Since each of the cosine bells comprising the continuous rate function $\lambda^A(t)$ has unit area, in principle the integral of λ^A over a trial duration T, by definition $t^A(T)$, should correspond to the average number of spikes per trial. In practice, $t^A(T)$ is slightly less than the mean spike count because some of the cosine bells at the edges of a trial interval are clipped. If it is important to correct for this, the cosine bells whose support extends beyond the range [0,T] can be multiplied by a scale factor so that they too integrate to unity. At present this correction is not made in the Matlab code.

Construction of time A transformation

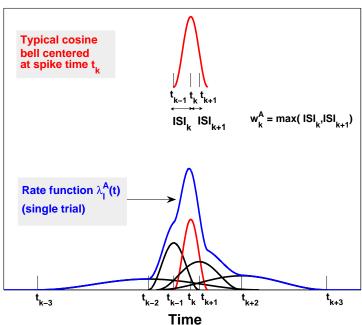


Figure 1: Demonstration of the construction of time A cosine bells within a single trial. Cosine bells associated with the endpoint spike times are not shown. The cosine bells within trial l are summed to form the continuous rate function $\lambda_l^A(t)$.

1.2 Time B

The second time transformation from time A to time B is similar to the time A transformation, in that each we replace each event time with a cosine bell, except now we introduce a free parameter b. The time-rescaling theorem (Brown et. al, 2000)

states that any point process described by a rate function $\lambda(t)$ can be transformed into a homogeneous unit-rate Poisson process. Thus, if $U(t) \equiv \int_0^t \lambda(\tau) d\tau$, then $U \sim \text{Poiss}(1)$. In our notation, the set of event times $\{U\}$ will be the "time B" times $\{t^B\}$, and we choose the free parameter b such that $t^B \sim \text{Poiss}(1)$ is satisfied as best as possible according to an order statistic criterion.

The time A transformation has the shortcoming of not being able to "speed up the new clock" sufficiently when the neuron is firing rapidly. This second transformation to a time B attempts to correct this by first collapsing all of the time A spikes $\{t^A\}$ onto a single axis, and then replacing each t_k^A with an appropriately chosen cosine bell (note that with all the time A events on a single axis we no longer need to reference individual trials). With retinal and LGN data, we have found it sufficient to choose the cosine bell width ω_k^B to span the mean of the distances b spikes to the left and b spikes to the right of t_k^A on the collapsed time A axis. For rapid firing regimes, many events will be clustered near t_k^A , so ω_k^B will be relatively small and the associated cosine bell relatively tall, consistent with a higher firing probability. In low firing regimes the opposite will be true. We thus define the time B cosine bell widths

$$\omega_{k}^{B} = \frac{1}{2} \left(\left[t_{k}^{A} - t_{k-b}^{A} \right] + \left[t_{k+b}^{A} - t_{k}^{A} \right] \right) = \frac{1}{2} \left(t_{k+b}^{A} - t_{k-b}^{A} \right).$$

With these widths, replace each time A event with the associated cosine bell and sum them (and divide by the number of trials *N*) to get the time B rate function:

$$\lambda^{B}(t^{A}(t)) = \frac{1}{N} \sum_{k} C\left(t^{A}(t); t^{A}(t_{k}), \omega_{k}^{B}\right).$$

This somewhat complicated notation serves to remind us that the time B rate function is ultimately a function of the original lab time t. The cosine bell construction of the rate function $\lambda^B(t^A(t))$ is illustrated in figure 2.

The rate function $\lambda^B(t)$ is then used to map time A events into time B events:

$$t_k^B = \int_0^{t^A(t_k)} \lambda^B(\tau) \, d\tau$$

As mentioned above, the free parameter b is optimized so that the set of spike times $\{t_k^B\}$ are distributed as closely as possible to a unit rate homogeneous Poisson process.

The final step is to obtain a rate function $\lambda(t)$ that is expressed explicitly as a function of the original lab time t, just as one would have with a conventional PSTH. Since the aim is to achieve a time B point process with $t^B \sim \text{Poiss}(1)$, we have by definition

$$t^B = \int_0^t \lambda(\tau) d\tau,$$

where $\lambda(t)$ is our best estimate of the rate function for the assumed time-dependent point process that describes our data. The rate function $\lambda(t)$ can be determined from the subsidiary rate functions $\lambda^A(t)$ and $\lambda^B(t^A(t))$ via the chain rule:

$$\lambda(t) \equiv \frac{dt_B}{dt} = \frac{dt_B}{dt_A} \frac{dt_A}{dt} = \lambda^B(t) \lambda^A(t).$$

This completes the specification of our rate function $\lambda(t)$ with the two-stage cosine bell procedure.

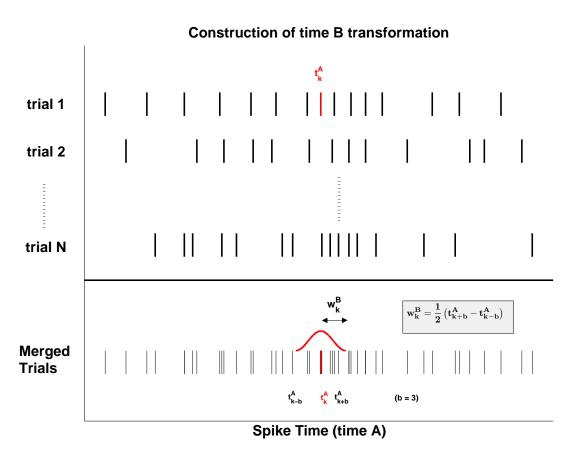


Figure 2: Illustration of the time B cosine bell construction.