Estimating Erlang-k Stage Index from Motor Unit Event Timings

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1 Derivation

Consider the following k-stage Erlang renewal process, where inter-event intervals are determined by the sum of this random variable and some characteristic fixed absolutely refractory period such that the i-th event source has its own $t_{0,i} \in [t_{0,min}, t_{0,max}]$ with bounded domain peculiar to the physiology of motor units in this case.

$$\begin{aligned} T \;&=\; t_0 + G, \qquad G \sim \mathrm{Erlang}\big(k,\ \text{rate} = k\lambda\big), \\ \mathbb{E}[G] &= \frac{1}{\lambda}, \qquad \mathrm{Var}(G) = \frac{1}{k\lambda^2}. \end{aligned} \tag{1}$$

Thus the interspike interval (ISI) has mean and variance

$$\begin{aligned} \mathbb{E}[T] = t_0 + \mathbb{E}[G] \;&=\; t_0 + \frac{1}{\lambda}, \\ \mathrm{Var}(T) = \mathrm{Var}(G) \;&=\; \frac{1}{k\lambda^2}. \end{aligned} \tag{2}$$

Expanding the moments of the random process along with properties of expectations shows that the coefficient of variation of the ISI is

$$\mathrm{CV}_{\mathrm{ISI}} \;=\; \frac{\sqrt{\mathrm{Var}(T)}}{\mathbb{E}[T]} \;=\; \frac{\frac{1}{\sqrt{k}\,\lambda}}{t_0 + \frac{1}{\lambda}} \;=\; \frac{1}{\sqrt{k}} \cdot \frac{1}{1 + \lambda t_0}. \tag{3}$$

Equation (3) provides the *exact* relationship between $\mathrm{CV}_{\mathrm{ISI}}$, the absolute refractory time t_0, the mean rate λ, and the Erlang shape k. For small λt_0 one can use the first-order expansion $(1+\lambda t_0)^{-1} = 1-\lambda t_0+\mathcal{O}((\lambda t_0)^2)$, giving

$$\mathrm{CV}_{\mathrm{ISI}} \approx \frac{1}{\sqrt{k}}\Big(1-\lambda t_0\Big) = \underbrace{\frac{1}{\sqrt{k}}}_{\text{intercept}} - \underbrace{\frac{1}{\sqrt{k}}}_{\text{slope}}\big(\lambda t_0\big). \tag{4}$$

Hence, plotting $\mathrm{CV}_{\mathrm{ISI}}$ versus $x = \lambda t_0$ yields a straight line to first order with both intercept and (negative) slope equal to $1/\sqrt{k}$. The nonlinear form (3) is preferred when data include larger values of λt_0. Often, this is the case; refer to **Table 1** for heuristic values; therefore, in all subsequent work presented here, we shall consider estimates obtained using the nonlinear form (3).

Fortunately, despite the nonlinearity, the exact solution (3) is readily estimated using modern curve-fitting techniques, it can be seen that k is recovered readily from any record of motor unit inter-spike intervals (ISI), provided there is a *reasonable* assumption that λ is constant *within tolerance* over the record. Therefore, these two assumptions are a critical consideration for the work of the investigator designing the experiment, and it is hereafter assumed that the experimenter is able to determine what is *reasonable* and what is *within tolerance* based on his or her own experiment requirements.

Table 1: Accuracy of the linear approximation $(1+\lambda t_0)^{-1} \approx 1-\lambda t_0$ for representative values of λt_0.

λt_0	$(1+\lambda t_0)^{-1}$	Linear approx. $(1-\lambda t_0)$	Relative error (%)
0.05	0.9524	0.9500	0.25
0.20	0.8333	0.8000	4.0
0.50	0.6667	0.5000	25.0
1.00	0.5000	0.0000	100.0

2 Practical Recipes

Within an epoch of interest:

$$\widehat{t}_0 \;=\; \min\{\text{observed ISI in epoch}\}, \tag{5}$$

$$\widehat{\lambda} \;=\; \frac{1}{M}\sum_{m=1}^{M}\widehat{r}(t_m), \tag{6}$$

where $\widehat{r}(t)$ is the smoothed firing-rate estimate obtained by first applying a sliding boxcar count with window $W = 1$ s to form raw rate samples, followed by the One-Euro smoother with $f_{c,\min} = 1$ Hz and $\beta = 0.05$. Let $\widehat{\mathrm{CV}}_{\mathrm{ISI}}$ denote the empirical coefficient of variation of ISIs measured within the same epoch.

2.1 Regression target

Define the composite predictor

$$x_i \;=\; \widehat{\lambda}_i\,\widehat{t}_{0,i}, \tag{7}$$

representing the product of the mean estimated discharge rate and the minimum interspike interval observed for unit i. From the exact relationship in (3), the expected coefficient of variation is

$$\widehat{\mathrm{CV}}_{\mathrm{ISI},i} \;=\; \frac{1}{\sqrt{k}}\cdot\frac{1}{1+x_i} \;+\; \varepsilon_i, \tag{8}$$

where ε_i captures measurement noise and finite-sample error. It is convenient to re-parameterize

$$a \;=\; \frac{1}{\sqrt{k}}, \qquad k \;=\; \frac{1}{a^2}, \qquad a > 0, \tag{9}$$

so that the regression becomes a single-parameter nonlinear model

$$\widehat{\mathrm{CV}}_{\mathrm{ISI},i} \;=\; \frac{a}{1+x_i} \;+\; \varepsilon_i. \tag{10}$$

2.2 Estimator

The optimal amplitude $\widehat{a}$ is obtained by minimizing the sum of squared residuals

$$\widehat{a} \;=\; \arg\min_{a>0} \sum_i \Bigl(\widehat{\mathrm{CV}}_{\mathrm{ISI},i} - \tfrac{a}{1+x_i}\Bigr)^2, \tag{11}$$

and the corresponding Erlang index is $\widehat{k} = \frac{1}{\widehat{a}^2}$. This is fit directly in MATLAB as `fittype(‘‘a./(1 + x)’’)`, with bounds on a (e.g., $0.5 \le a \le 1$) to ensure positive, physiologically reasonable values. Because the dependence on x is nonlinear, this exact form is preferred over the small-x linearization of (4), particularly when λt_0 spans a broad range across motor units.

2.3 Group-specific extension.

When data are collected from two or more groups that may differ in their effective discharge regularity (e.g., injury levels A/B versus C/D), a simple extension of (10) introduces a linear dependence of the amplitude parameter on a group code $G_i \in \{0, 1\}$:

$$\widehat{\mathrm{CV}}_{\mathrm{ISI},i} \;=\; \frac{a + b\,G_i}{1 + x_i} \;+\; \varepsilon_i, \qquad x_i = \widehat{\lambda}_i\,\widehat{t}_{0,i}. \tag{12}$$

Here $a > 0$ represents the baseline amplitude for the reference group ($G = 0$), and b encodes a shift in that amplitude for the comparison group ($G = 1$). The implied group-specific Erlang indices are therefore

$$k_{G=0} \;=\; \frac{1}{a^2}, \qquad k_{G=1} \;=\; \frac{1}{(a+b)^2}. \tag{13}$$

Equation (12) is fit by nonlinear least squares using

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fittype(‘‘(a + b*G)./(1 + x)’’)
```

in MATLAB, with bounds chosen to enforce $a > 0$ and $a + b > 0$

(e.g., `[0.5, −0.25]` $\le$ `[a b]` $\le$ `[1, 0.25]`)

From the fitted coefficients, the effective shape parameters $k_{G=0}$ and $k_{G=1}$ are obtained via (13), and confidence intervals are computed by transforming the confidence limits of a and $a + b$.

3 Applications to Motor Unit Physiology

One practical application of the k-stage ISI estimator is in evaluating changes in the effective renewal statistics of motor unit discharges across experimental conditions or epochs. Because the model captures how the coefficient of variation of interspike intervals ($\mathrm{CV}_{\mathrm{ISI}}$) depends on the fundamental shape parameter k, it can be used to test whether a manipulation alters the number or regularity of underlying summation stages that precede spike generation. In such analyses, the baseline epoch ($G = 0$) represents the control or pre-manipulation period, and the comparison epoch ($G = 1$) represents a later state expected to differ in its synaptic or intrinsic driving conditions.

3.1 Example: trapezoidal ramp–and–hold contractions.

A common paradigm for assessing intrinsic motoneuron properties is the *trapezoidal ramp–and–hold* contraction, in which voluntary or electrically evoked force is gradually increased, maintained at a plateau, and then decreased [e.g., 1, 2, 3, 4, 5]. During the first (ascending) hold phase, motor units typically discharge at steady rates governed primarily by synaptic drive and recruitment threshold, whereas during a second hold phase—after prior activation or neuromodulatory conditioning—firing often becomes more regular or sustained due to the engagement of persistent inward currents (PICs) [6, 7]. Applying the present framework to interspike intervals extracted from the first and second hold phases therefore provides a quantitative means of testing whether the apparent number of effective "wait stages" increased or decreased.

3.2 Interpreting changes in k

Let the k subthreshold "wait" stages be independent exponentials

$$S_i \sim \mathrm{Exp}(\mu_i), \qquad G = \sum_{i=1}^{k} S_i \tag{14}$$

Then

$$\mathbb{E}[G] = \sum_{i=1}^{k} \frac{1}{\mu_i} \equiv m, \qquad \mathrm{Var}(G) = \sum_{i=1}^{k} \frac{1}{\mu_i^2} \equiv v. \tag{15}$$

By Cauchy–Schwarz,

$$\Big(\sum_{i=1}^{k} \tfrac{1}{\mu_i}\Big)^2 \;\le\; \Big(\sum_{i=1}^{k} 1^2\Big)\Big(\sum_{i=1}^{k} \tfrac{1}{\mu_i^2}\Big) \;=\; k \sum_{i=1}^{k} \tfrac{1}{\mu_i^2}, \tag{16}$$

with equality iff all μ_i are equal. Equivalently,

$$v \;\ge\; \frac{m^2}{k}.$$

Define an *effective shape* from the squared coefficient of variation of G:

$$k_{\text{eff}} \;\stackrel{\text{def}}{=}\; \frac{m^2}{v} \;=\; \frac{1}{\mathrm{CV}(G)^2} \;\le\; k,$$

with equality only for the i.i.d. Erlang case. Thus, for fixed total mean m, *any* perturbation that introduces inequality among stage durations (μ_i not all equal) necessarily *decreases* k_{eff} and increases variability.

Including an absolute refractory t_0 (so $T = t_0 + G$) gives

$$\mathrm{CV}(T) \;=\; \frac{\sqrt{v}}{t_0 + m} \;\ge\; \frac{m/\sqrt{k}}{t_0 + m} \;=\; \frac{1}{\sqrt{k}} \cdot \frac{1}{1 + t_0/m},$$

with equality only when stages are equal. Therefore, when comparing epochs with the same m (or after normalizing for changes in m), any stage-specific alteration in duration that breaks equality will manifest as a ***decrease*** in the estimated k_{eff}.

3.3 Experimental considerations

Because the estimator depends on the accurate determination of both the mean discharge rate $\widehat{\lambda}$ and the minimal refractory interval $\widehat{t_0}$, it is most robust when applied to well-isolated, tonic firing segments. For ramp–and–hold tasks, these are typically extracted from the steady-state plateau periods rather than from the transient rise or fall, ensuring that λ remains approximately constant within each epoch. When the same motor unit can be tracked across epochs, the pairwise comparison of estimated shape indices $(\widehat{k}_{G=0}, \widehat{k}_{G=1})$ provides a sensitive test for post-activation changes in intrinsic motoneuron properties or modulation of PIC strength.

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