

A direct, interval-based method for reconstructing stimuli from noise-robust tuning curves

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Abstract

We present a method for reconstructing stimuli from a tuning curve, completing a tuning curve estimation method published earlier. Stimuli are reconstructed by dividing the stimulus space into intervals and providing boundaries for the probabilities with which they contain a given stimulus. The endpoints of these intervals are calculated as zeros of polynomials of high degree using the efficient direct method of Dixon polynomial resultants. Repeated measurements refine the decomposition, allowing for more accurate statements about the associated probabilities. Our method employs no special assumptions about the noise distribution, removing tractability problems of Bayesian or Maximum Likelihood estimation.

Key words: tuning curves, reconstruction, computation in the presence of nonlinearities, stochastic neural responses, visual cortex

Introduction. The relationship between sensory stimuli presented to an animal and their representations in the nervous system may be expressed by a neural tuning curve. We assume that an abstract, *ideal tuning curve* $f(\varphi)$ exists, where φ is a stimulus parameter which is to be approximated by a constructed tuning curve given measured data. In earlier publications [1, 2], a noise-robust method achieving this was presented which uses data from all measured stimulus conditions *at once*. The method exploits the fact that for a number of different approximation criteria, approximation theory specifies sets of polynomials as optimally approximating functions to any continuous function. For instance, a linear combination of $1, \cos(k\varphi), \sin(k\varphi)$, (k is a positive

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integer) optimally approximates any continuous ideal tuning curve by minimizing the area enclosed by the two functions [5]. Evaluating the polynomials specified by the approximation criterion at measured stimulus conditions allows to determine rows of a matrix X_φ so that, given a vector of observations Y , a matrix equation $Y = X_\varphi \beta + \varepsilon$ may be solved for a coefficient vector β of the approximating tuning curve [1, 2]. In this contribution, we propose a method for reconstructing stimuli from such a tuning curve.

An interval-based method for reconstruction. The constructed tuning curve f is a polynomial. In each stimulus condition φ , there is a certain variability $\hat{\sigma}^2(\varphi)$ in the firing of the cell due to its stochasticity, for which we will give an exact definition later. Thus, all the stimuli which are mapped by the tuning curve to an interval of responses around the value of the tuning curve are stimuli which might have given the recorded response. Let a sample of $n \geq 2$ responses to a stimulus parameter φ of unknown value be given. The noise may be of *any distribution*. In this situation, it is possible to bound the probability that a newly measured response will deviate from the mean response in a given stimulus condition, i.e., from the tuning curve value. This deviation is expressed as some multiple of the sample variance introducing a number λ . The following variant of the *Chebyshev inequality* holds [4; 6, § 3.37]. Given $n \geq 2$ responses Y_1, \dots, Y_n to the same stimulus, then, for a further observation Y_{n+1} , we have

$$P(|Y_{n+1} - \bar{Y}| > \lambda Q) \leq \left(\frac{1}{n} + \frac{1}{\lambda^2} \right), \quad (1)$$

where $n\bar{Y} = \sum_{i=1}^n Y_i$, $\lambda \geq 1$, $Q = \sqrt{\frac{n+1}{n}} \sqrt{\sum_{i=1}^n (Y_i - \bar{Y})^2 / (n-1)}$. The inequality bounds the probability that a response deviates more than a certain distance from the mean response in that condition, where this distance depends on the parameter λ . By choosing a value between 0 and 1 for the right-hand side of the inequality, one obtains λ which measures the required certainty in the stimulus reconstruction (to be described in detail later): by choosing a value close to 0, a larger set of intervals of possible stimuli is identified than if a higher value was chosen. As the Chebyshev inequality (1) holds for all noise distributions, the uncertainty in the decoding of a stimulus as a result of the

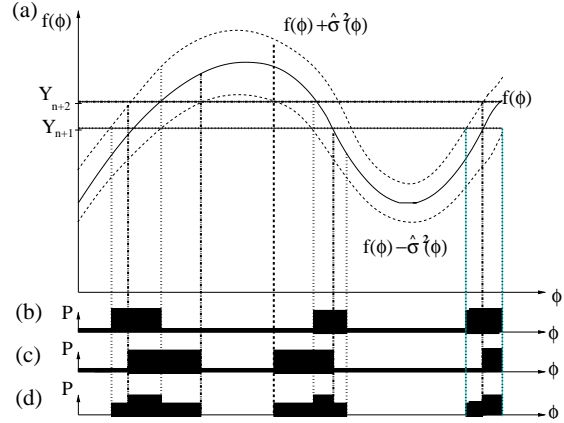


FIGURE 1: (a) Tuning curve $f(\varphi)$ (solid line) and firing variability $\hat{\sigma}^2(\varphi)$ (dotted lines). In the reconstruction, for responses Y_{n+1} (b) and Y_{n+2} (c), intervals and respective probabilities are assigned. (d) shows intervals and probabilities obtained from a combination of Y_{n+1} and Y_{n+2} .

stochasticity of the firing of a cell can be assessed without need to specify a particular model for the noise distribution. As the mean of the responses to the same stimulus converges to the value of the tuning curve as the number of trials grows, the sample quantity \bar{Y} , obtained for responses at a particular stimulus condition, may be replaced by the value of the tuning curve at that stimulus condition. In particular, since the values of the presented stimuli were known in the construction of the tuning curve, Q may be calculated from the residuals $(Y_i - \bar{Y})$, ($i = 1, \dots, n$) in each of the different stimulus conditions separately. We choose a function $\lambda = \lambda(\varphi)$ to reflect differences in the cell's firing variability: for each of the different stimulus conditions φ_m for which multiple responses were collected in the tuning curve construction phase, values Q_m can be calculated from the residuals in that particular stimulus condition. As Q_m for several m are available, they can be interpreted as realizations of a stochastic function linking the value of the tuning curve to the variability in the cell's firing. We assume that this function is smooth and can thus be expanded into a series in powers of $f(\varphi)$ which may be broken off after the first few terms. Define the function $\lambda(\varphi)$ as the result of this operation. Since the constructed tuning curve is a trigonometric polynomial, $\lambda(\varphi)$ is also a trigonometric polynomial. Now define the variability described above as $\hat{\sigma}^2(\varphi) = \lambda(\varphi)Q$. In virtue of (1), the probability that for any response $Y_{n+1} = f(\varphi) + \varepsilon_{n+1}$, the corresponding value of the tuning curve $f(\varphi)$ will fall outside an interval associated to stimuli ψ defined by

$$f(\varphi) + \varepsilon_{n+1} - \hat{\sigma}^2(\varphi) \leq f(\psi) \leq f(\varphi) + \varepsilon_{n+1} + \hat{\sigma}^2(\varphi)$$

is smaller than $\left(\frac{1}{n} + \frac{1}{\lambda^2}\right)$. Consider points s_i from each of the intervals of the stimulus space that are delimited by the real zeros of the polynomials $f(\varphi) + \varepsilon_{n+1} \pm \hat{\sigma}^2(\varphi)$. Either $f(s_i) \geq f(\varphi) + \varepsilon_{n+1}$ or $f(s_i) \leq f(\varphi) + \varepsilon_{n+1}$. The interval containing s_i will fall outside the interval

$$f(s_i) - f(\varphi) - \varepsilon_{n+1} \geq \hat{\sigma}^2(\varphi) \Leftrightarrow f(s_i) \leq f(\varphi) + \varepsilon_{n+1} + \hat{\sigma}^2(\varphi)$$

in the first case and to

$$f(\varphi) + \varepsilon_{n+1} - f(s_i) \geq \hat{\sigma}^2(\varphi) \Leftrightarrow f(s_i) \geq f(\varphi) + \varepsilon_{n+1} - \hat{\sigma}^2(\varphi)$$

in the second case. Thus, the parameter values φ of the stimulus that delimit the intervals which are mapped to the interval of uncertainty around a measured response, satisfy one of the conditions $f(\varphi) + \varepsilon_{n+1} \pm \hat{\sigma}^2(\varphi) = 0$. Both $f = f(\varphi)$ and $\hat{\sigma} = \hat{\sigma}(\varphi)$ are trigonometric polynomials. Transforming them, so that the new variable can have value on the real line, gives polynomials of the form $f(t) = t^n + a_1 t^{n-1} + \dots + a_{n-1} t + a_n$, with complex coefficients a_i , or equivalently, $f(t) = (t - x_1)(t - x_2) \dots (t - x_n)$. Multiplying out this product gives the following relation between the coefficients of the polynomial and its (complex) zeros: $a_1 = (-1)^1(x_1 + x_2 + \dots + x_n)$, $a_2 = (-1)^2 \sum_{i,j=1,\dots,n; i < j} x_i x_j$, $a_3 = (-1)^3 \sum_{i,j,k=1,\dots,n; i < j < k} x_i x_j x_k$, \dots , $a_n = (-1)^n x_1 x_2 \dots x_n$. The terms on the

right-hand side of these equations are, up to the factor $(-1)^k$, the *symmetric polynomials* $s_k(x_1, \dots, x_n)$, $k = 1 \dots n$, in the zeros of the polynomial. If the common zeros of the multivariate polynomials $(-1)^k s_k(x_1, \dots, x_n) \pm \hat{\sigma}^2(\varphi)$, $k = 1 \dots n$, in the zeros x_1, \dots, x_n can be determined, the zeros of a generic tuning curve polynomial can be found and the intervals of the stimulus space which can generate the observed response of the cell can be determined.

We propose to use the method of Dixon resultants to achieve this task. It consists of forming a determinant, in which each entry is a polynomial obtained from the set of multivariate polynomials whose common zeros are to be found, and identifying the polynomial values where the determinant vanishes using Gaussian elimination. These values are the endpoints of our stimulus intervals. A detailed description of the method can be found in [3]. There, constraints are identified which ensure that the method will work for all parameters except for a set of measure zero. Thus, whereas Galois theory states that for polynomials of high degree, no general formula for calculating their zeros exist, the Dixon resultant method provides those zeros in all cases except for a neglectable set of parameters of $f = f(\varphi)$ and $\hat{\sigma} = \hat{\sigma}(\varphi)$.

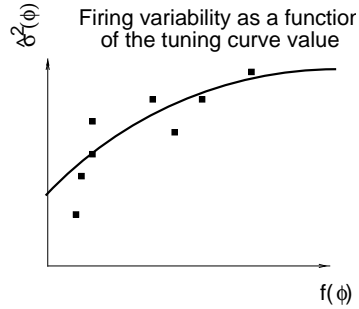


FIGURE 2: The firing variability $\hat{\sigma}^2(\varphi)$ is fitted from the measured variances Q_m (shown as dots) upon repeated measurements of the same respective stimuli φ_m .

When reconstructing from multiple measurements of a single cell, we assume that firing is statistically independent. Then, a set of intervals with associated probabilities is associated to the entire experiment by multiplying the obtained probability values of each of the intervals of the set of intersections of intervals obtained from the individual measurements (see Fig. 1d). Reconstruction from a population of cells is done in a similar way, keeping in mind that the Chebyshev inequality has to be applied to each cell's noise distribution individually.

Discussion. We briefly discuss the relationship between our method and traditional methods for reconstructing stimuli, such as Bayesian or maximum likelihood analysis. Our method uses a reconstruction based on the intervals which are mapped to an interval of uncertainty around the value of the tuning curve at a particular location φ . It may be sufficient to employ interval estimation rather than point estimation: if the reconstructed intervals are sufficiently small, there will be no behavioural difference between these cases. We use a very general inequality to determine the uncertainty in the firing around the value of the tuning curve. It holds for any distribution, and relies solely on data that are available from the experiment. To-

gether with our method for constructing a tuning curve from all responses of a cell using a criterion from approximation theory, we can use this reconstruction method to deal with sparsely firing cells, showing a considerable deal of noise. Traditional methods for assessing the acuity of neural populations often use maximum likelihood, Bayesian or Fisher information techniques. These techniques are used because they enjoy optimality properties, such as giving estimators of the smallest variance, and thus the narrowest confidence interval for large samples, or convergence to a normal distribution under particular conditions [6, §18]. All these methods require that the noise distributions used are known. The optimality properties may not apply for small samples. In the context of modelling neuronal data, where the sample sizes are often very limited, this is a serious drawback. Calculating likelihood equations or Fisher information for distributions is very cumbersome for most distributions, confining theoretical analysis mainly to Poissonian, Gamma or Gaussian noise distributions. It is however questionable whether real-world neurons fire according to any of these distributions and whether statements obtained from an analysis based on this assumption hold true.

In Fig. 3, we compare our method with the results of a Bayesian reconstruction of stimulus intervals for some standard distributions and mixtures thereof in order to illustrate the behaviour of reconstruction methods when the assumption that neuronal firing is Poissonian is not valid. For Bayesian reconstruction, intervals are chosen by selecting the most probable stimuli up to a total probability P (as chosen in the Chebyshev inequality), where the value of P can be chosen according to the desired confidence. For demonstration purposes, we assume that we know that the stimulus of the preferred direction of a cell showing cosine tuning is presented, and that neuronal noise arises as a mixture of Gaussian, Poisson or Gamma distributions. Ratios of interval lengths for $P = 0, 0.05, \dots, 1$ of the two methods are shown for various distributions of neuronal noise. The noise level was chosen so that the total length of the reconstructed intervals obtained by our method was $1/4$ of the total stimulus space. We show the total length of the reconstructed intervals obtained by Bayesian reconstruction for different noise distributions generated as mixtures of Poisson-Gaussian, Poisson-Gamma,

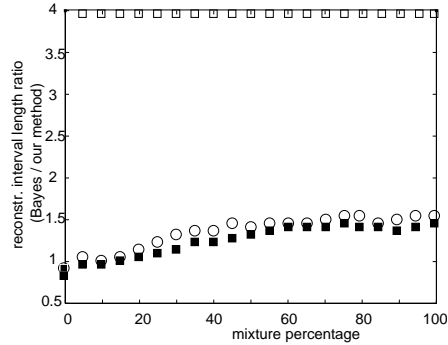


FIGURE 3: Example for ratios of reconstructed interval lengths in Bayesian and our reconstruction method for various noise distributions arising as mixtures of Poisson-Gaussian (filled squares), Poisson-Gamma (circles) and Poisson-Cauchy (open squares) distributions. On the abscissa, the non-Poisson part of the mixture is shown. Stimulus reconstruction with Poisson-Cauchy distributions yields intervals covering the whole stimulus space: Reconstruction becomes impossible for this case.

Poisson-Cauchy. Cauchy distributions are sometimes used to model contamination by outlying data.

The gravest objection to using any of the traditional methods is that they are not robust against small changes in the parameters, as differentiations or quotients arise in the fitting procedure, which are very sensitive to small changes in the distributions. The fact that the tuning curve is in general modelled in a nonlinear fashion aggravates this problem. In contrast to this, our method of tuning curve construction and reconstruction relies entirely on linear methods, exploiting the fact that polynomials are linear in their coefficients in the Dixon resultant method.

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