

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

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Abstract

We present a new 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 [7], [8], 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

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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 integer) optimally approximates any continuous ideal tuning curve by minimizing the area enclosed by the two functions [1, p. 206-208]. Several other criteria leading to other trigonometric polynomials exist. 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 [7], [8]. In this contribution, we consider the possibility of reconstructing stimuli from such a tuning curve and propose a new method to do this. It considers both the variability of neural responses and uncertainties in the tuning curve due to the limited amount of data available for its estimation.

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. 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 an (unknown) stimulus φ be given. The noise may be of *any distribution* for which the mean and variance are known to exist, but are assumed unknown. Then, for a further observation Y_{n+1} ,

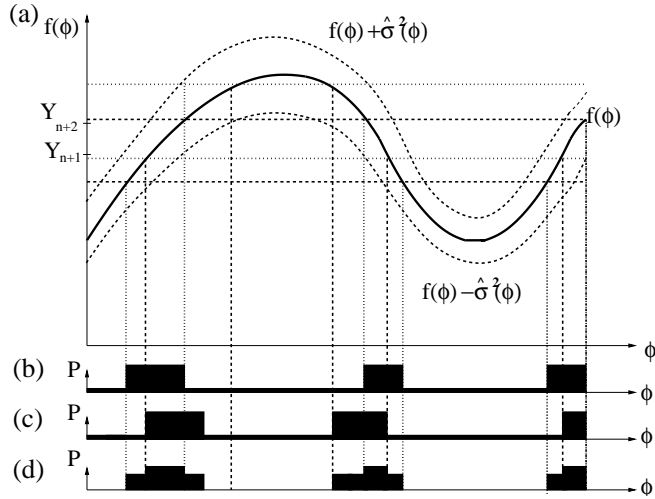


FIGURE 1: (a) Tuning curve $f(\varphi)$ and firing variability $\hat{\sigma}^2(\varphi)$. In the reconstruction, for responses Y_{n+1} (b) and Y_{n+2} (c), intervals and respective probabilities are assigned. (d) shows intervals and probabilities obtained from a combination of Y_{n+1} and Y_{n+2} .

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

holds [10], [2, § 3.37], where $n\bar{Y} = \sum_{i=1}^n Y_i$, $\lambda \geq 1$, $Q = (n+1) \sum_{i=1}^n (Y_i - \bar{Y})^2 / (n(n-1))$. This inequality allows to assess the uncertainty in the decoding of a stimulus as a result of the stochasticity of the firing of a cell for *all* noise distributions without need to specify a particular model as follows. Since the values of the presented stimuli were known in the construction of the tuning curve, Q may be calculated from *all* residuals $(Y_i - \bar{Y})$, ($i = 1, \dots, n$). We choose

a function $\lambda(\varphi)$ to reflect differences in the cell's firing variability in the following way: 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. Set $\hat{\sigma}^2(\varphi) = \lambda(\varphi)Q$. In virtue of (1),

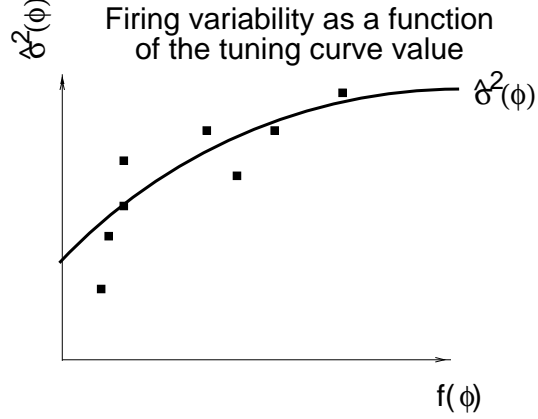


FIGURE 2: The firing variability $\hat{\sigma}^2(\varphi)$ is fitted from the measured variances Q_m (shown as dots) upon repeated measurements of the same respective stimuli φ_m .

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 (1) $f(s_i) \geq f(\varphi) + \varepsilon_{n+1}$ or (2) $f(s_i) \leq f(\varphi) + \varepsilon_{n+1}$. The interval containing s_i will be mapped to $[f(\varphi) + \varepsilon_{n+1} - \hat{\sigma}^2(\varphi), f(\varphi) + \varepsilon_{n+1} + \hat{\sigma}^2(\varphi)]$ if $f(s_i) - f(\varphi) - \varepsilon_{n+1} \geq \hat{\sigma}^2(\varphi) \Leftrightarrow f(s_i) \leq f(\varphi) + \varepsilon_{n+1} + \hat{\sigma}^2(\varphi)$ in case (1) and $f(\varphi) + \varepsilon_{n+1} - f(s_i) \geq \hat{\sigma}^2(\varphi) \Leftrightarrow f(s_i) \geq f(\varphi) + \varepsilon_{n+1} - \hat{\sigma}^2(\varphi)$ in case (2). Upon a repeated measurement, a new response and a new set of intervals is obtained, yielding a finer decomposition of the stimulus space. In particular, the probability that the stimulus lies outside the union of the intervals obtained from them individual measurements is the product of the individual probabilities and is thus reduced. Alternatively, it is possible to decrease the size of the intervals from multiple measurements. The probability that the stimulus falls into the intersection of the respective sets of intervals from k measurements is bounded from below by $\prod_{m=1}^k \left(1 - \left(\frac{1}{n} + \frac{1}{\lambda^2}\right)\right)$. This, however, reduces the probabilities of the respective intervals. When different cells are used for reconstruction, the method can be applied in the same fashion as for repeated measurements from a single cell. The only difference is that the individual tuning curves and firing variabilities have to be calculated separately. Our method yields decoding properties of a cell without any assumptions on the firing statistics of the cell. If more information on the cell's noise distribution is available, sharper versions of (1) may be used, giving tighter bounds for the

probability and reconstruction.

A direct method for determining stimuli intervals using Dixon polynomial resultants The constructed tuning curve f and $f(\varphi) + \varepsilon_{n+1} \pm \hat{\sigma}^2(\varphi)$ 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 directly, which will work in all practically relevant cases. The Dixon resultant method consists of forming a determinant, in whose first line, each entry is a polynomial from the set of polynomials whose common zeros are to be found. The remaining lines of the determinant are generated by repeating the first line, but successively replacing all original indeterminates by new ones. In the one-variable case, this gives: $\Delta(x, \alpha) = \begin{vmatrix} p_1(x) & p_2(x) \\ p_1(\alpha) & p_2(\alpha) \end{vmatrix}$. Setting $x = \alpha$ would make the determinant vanish, thus $x - \alpha$ is a factor of the determinant. Let $\delta(x, \alpha) = \frac{\Delta(x, \alpha)}{x - \alpha}$. Every common zero of p_1 and p_2 is also a zero of the *Dixon polynomial* $\delta(x, \alpha)$, no matter what value α has. Thus, at a common zero of p_1 and p_2 , every power product of α in $\delta(x, \alpha)$ must be zero. This gives a set of equations for the coefficients of the power products of α , each of which is a polynomial in x . Introducing a coefficient matrix D , one can write these equations as a *linear system*

$$D \begin{pmatrix} 1 & x & x^2 & \dots & x^{\max(\text{degree}(p_1), \text{degree}(p_2)) - 1} \end{pmatrix}^t = \begin{pmatrix} 0 & \dots & 0 \end{pmatrix}^t. \quad (2)$$

If each power product of x is viewed as a new variable, we have to solve a set of homogeneous linear equations to find common zeros of the polynomials p_1 and p_2 . In the multi-variable case, the approach is similar. A determinant is set up by replacing successively $0, 1, 2, \dots, n$ variables in each polynomial in successive lines of the matrix and a Dixon polynomial is formed by dividing that determinant by all factors $x_k - \alpha_k$. Cayley proved in [5] that vanishing of the Dixon resultant is a necessary and sufficient condition for the set of two polynomials with generic coefficients in one variable to have a nontrivial common zero. The generalization of this theorem to generic multivariable polynomials (i.e., polynomials of the form $\sum_{i_1=1}^{k_1} \dots \sum_{i_n=1}^{k_n} a_{j, i_1, \dots, i_n} x_1^{i_1} \dots x_n^{i_n}$, where each a is a

distinct indeterminate), was given by Dixon [6]. Again, a linear matrix equation can be formed, where the power polynomials now include all products in all variables, with exponents up to the highest exponent obtained in each variable when multiplying all polynomials. However, the coefficient matrix in the linear system might become *singular*, causing this solution approach to fail. Even then, it is still possible to obtain the common zeros of the respective polynomials, provided that the polynomials considered satisfy an additional constraint [9], i.e., there is a subset of variables I_k so that $x_{i_k} \neq 0$ for each $i_k \in I_k$ at the common zeros. In this case, it is possible to eliminate some columns from the matrix equation in D while maintaining the rank of the matrix positive. The additional constraint corresponds to having a subset of zeros of the polynomials $f(t) + \varepsilon_{n+1} \pm \hat{\sigma}^2(\varphi)$ not being zero. The subspace of polynomials defined by those polynomials which violate the additional constraint is of measure zero. Therefore, the polynomials $f(\varphi) \pm \hat{\sigma}^2(\varphi)$ arising from the approximation of a generic ideal tuning curve will satisfy this constraint with probability 1 and it will be possible to obtain the zeros of this polynomial by using the approach given in [9].

Discussion. We briefly discuss the relationship between the new 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 of use to reconstruct intervals rather than points in animal behaviour tasks. 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. Together 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 particular 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 [3, §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 of this method. 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. The gravest objection to using any of the traditional methods is that they are not robust against small changes in the parameters. Differential

equations or quotients 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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