

---

# Population decoding based on an unfaithful model

---

S. Wu, H. Nakahara, N. Murata and S. Amari

RIKEN Brain Science Institute

The Institute of Physical and Chemical Research  
Hirosawa 2-1, Wako-shi, Saitama, Japan

## Abstract

We study a population decoding paradigm in which the maximum likelihood inference is based on an unfaithful decoding model (UMLI). This is usually the case for neural population decoding because the encoding process of the brain is not exactly known, or because a simplified decoding model is preferred for saving computational cost. We calculate the decoding error of UMLI and show an example of an unfaithful model which neglects the neuronal correlation. The performance of UMLI is compared with that of the maximum likelihood inference based on a faithful model and that of the center of mass decoding method. It turns out that UMLI has advantage of decreasing the computational complexity remarkably and maintaining a high level decoding accuracy at the same time.

## 1 Introduction

It is certainly one of central issues in computational neuroscience to understand how the population of neural activities can encode, decode and/or infer the external world [4, 9, 12]. In population coding paradigm, various decoding methods have been investigated, particularly including the maximum likelihood inference (MLI), the center of mass (COM), the complex estimator (CE) and the optimal linear estimator (OLE) (see [10, 11] and reference therein). Among them, MLI has advantage such that it can *asymptotically* achieve the optimal decoding accuracy, that is, the Cramér-Rao bound. One caveat is, though, that it may suffer the expense of computational complexity, depending upon the choice of decoding model, for example, in comparison with COM.

Let us consider a population  $N$  neurons coding a variable  $x$ . The encoding process is specified by the conditional probability  $q(\mathbf{r}|x)$ , where the vector  $\mathbf{r} = \{r_i\}$  represents the population activities. Denote by  $p(\mathbf{r}|x)$  the decoding model on which MLI is based. So far, when people study MLI for population decoding, it normally (*implicitly*) assumes that  $p(\mathbf{r}|x) = q(\mathbf{r}|x)$  and the decoding error is calculated by the inverse of the Fisher information  $J = \int p(\mathbf{r}|x) [d \ln p(\mathbf{r}|x) / dx]^2 d\mathbf{r}$ . However, the encoding model  $q(\mathbf{r}|x)$  is usually not completely known in reality, since it stands for how the brain encodes the variable  $x$ . Thus, a decoding paradigm in which the assumed decoding model is different from the encoding one needs to be studied. In the context of statistical theory, this is called estimating based on an unfaithful model. Hereafter, we call the decoding paradigm of using MLI based on

an unfaithful model, UMLI, to distinguish the classical MLI based on the correct model.

UMLI turns out to have an attracting property. When a properly simplified unfaithful model is used, it can remarkably decrease computational cost and at the same time maintain a high-level decoding accuracy. This is confirmed in our calculation in Sec.3 and 4, where an uncorrelated neuron response model is used for decoding to replace the real correlated one.

The paper is organized as follows. The decoding error of UMLI is derived in Sec.2. An example of an unfaithful model is given in Sec.3, which neglects the correlation between the neurons' response. In Sec.4, the performances of UMLI, MLI and COM are compared when the tuning functions are triangular ones. Some overall discussion and conclusion are given in Sec.5.

## 2 The decoding error of UMLI

The decoding error of MLI based on an unfaithful model has been studied in the statistical theory [2, 8]. Here we generate it to the case of population coding. The result also holds for MLI.

For clearance, we introduce some notations.  $\nabla f(x)$  denotes  $df(x)/dx$ .  $E_q[f(x)]$  and  $V_q[f(x)]$  denote respectively the mean value and the variance of  $f(x)$  with respect to the distribution  $q(\mathbf{r}|x)$ .

Given an observation of population activity,  $\mathbf{r}^*$ , the ML estimate  $\hat{x}$  is the value of  $x$  that maximizes the likelihood  $L(\mathbf{r}^*, x) = \ln p(\mathbf{r}^*|x)$ . Denote by  $x_{\text{opt}}$  the optimal value of  $\hat{x}$  which satisfies  $E_q[\nabla L(\mathbf{r}^*, x_{\text{opt}})] = 0$ .

Let us consider the expansion of  $\nabla L(\mathbf{r}^*, \hat{x})$  at  $x_{\text{opt}}$ ,

$$\nabla L(\mathbf{r}^*, \hat{x}) \simeq \nabla L(\mathbf{r}^*, x_{\text{opt}}) + \nabla \nabla L(\mathbf{r}^*, x_{\text{opt}}) (\hat{x} - x_{\text{opt}}). \quad (1)$$

Since  $\nabla L(\mathbf{r}^*, \hat{x}) = 0$ , we have

$$\frac{1}{N} \nabla \nabla L(\mathbf{r}^*, x_{\text{opt}}) \sqrt{N} (\hat{x} - x_{\text{opt}}) \simeq -\frac{1}{\sqrt{N}} \nabla L(\mathbf{r}^*, x_{\text{opt}}), \quad (2)$$

where  $N$  is the number of neurons.

We consider that the neuronal correlation is negligible when their preferred stimuli is different enough. More precisely, we consider the case where the martingale convergence theorem holds. So, when  $N$  is large, by the weak law of large numbers,

$$\begin{aligned} \frac{1}{N} \nabla \nabla L(\mathbf{r}^*, x_{\text{opt}}) &\simeq \frac{1}{N} E_q[\nabla \nabla L(\mathbf{r}, x_{\text{opt}})] \\ &= \frac{1}{N} Q(x_{\text{opt}}). \end{aligned} \quad (3)$$

The random variable  $\nabla L(\mathbf{r}^*, x_{\text{opt}})/\sqrt{N}$  has zero mean, since  $E_q[\nabla L(\mathbf{r}, x_{\text{opt}})/\sqrt{N}] = 0$ , and variance proportional to  $G/N$ , where  $G$  is defined by

$$G \equiv V_q[\nabla L(\mathbf{r}, x_{\text{opt}})]. \quad (4)$$

Therefore, the total decoding error of UMLI is

$$(\hat{x} - x) \sim (x_{\text{opt}} - x) + Q^{-1} G^{1/2} \epsilon, \quad (5)$$

where  $\epsilon$  is a random variable with zero mean and variance 1.

Note that when a faithful model is used, i.e.,  $p(\mathbf{r}|x) = q(\mathbf{r}|x)$ , we have  $x_{\text{opt}} = x$  and  $G = Q = V_p[\nabla L(\mathbf{r}, x)]$  is the Fisher information. The decoding error is then the Cramér-Rao bound. When an unfaithful model is used,  $G$  and  $Q$  are usually different from the Fisher information, and the decoding error is larger than the Cramér-Rao bound.

We should point out that the above result is derived based on the condition that the neuronal correlation is negligible when their preferred stimuli is quite different. More generally, we need to use the martingale convergence theorem which guarantees the convergence for correlated signals. If this condition is not satisfied, the result may not hold. This is also true for MLI. We have found simple conditions which guarantee that both the central limit theorem and the law of large numbers hold.

### 3 An unfaithful model of neglecting the neuronal correlation

Cross-correlation in neuronal activity is observed in both primary sensory and motor areas, where population coding is believed to be used [3, 7, 13]. There have been a number of works analyzing the effect of correlation on the MLI decoding accuracy. [1, 14]. Their calculation is based on the assumption that the encoding and decoding models are the same. Taking into account the complexity of the neuronal correlation, it is of practical importance to consider a decoding paradigm without using the information of the correlation. The simplest way is to neglect the neuronal correlation.

Consider a pair-wise correlated neural response model in which the neuron activities are assumed to be multivariate Gaussian

$$q(\mathbf{r}|x) = \frac{1}{\sqrt{(2\pi)^N \det(\mathbf{A})}} \exp\left[-\frac{1}{2} \sum_{i,j} A^{-1}_{ij} (r_i - f_i(x))(r_j - f_j(x))/\sigma^2\right], \quad (6)$$

where  $f_i(x)$  is the mean value of the response of the  $i$ th neuron representing its tuning function,

$$\langle (r_i - f_i(x)) \rangle = 0. \quad (7)$$

$\mathbf{A}$  is the covariance matrix, which is defined by

$$\langle (r_i - f_i(x))(r_j - f_j(x)) \rangle = \sigma^2 A_{ij}. \quad (8)$$

For simplicity we assume it is stimulus-independent. The matrix  $\mathbf{A}^{-1}$  is its inverse.

The decoding error of MLI has been calculated in [1, 14], which is

$$\langle (\hat{x} - x)^2 \rangle_{\text{MLI}} \sim \frac{\sigma^2}{\sum_{ij} A^{-1}_{ij} f'_i(x) f'_j(x)}, \quad (9)$$

where  $f'_i(x) = df_i(x)/dx$ .

Consider a decoding model which neglects the correlation while keeps the tuning functions unchanged,

$$p(\mathbf{r}|x) = \frac{1}{\sqrt{(2\pi)^N \sigma^N}} \exp\left[-\sum_i (r_i - f_i(x))^2 / 2\sigma^2\right]. \quad (10)$$

The UMLI estimate is the solution of

$$\begin{aligned} \nabla \ln p(\mathbf{r}, \hat{x}) &= \sum_i [r_i - f_i(\hat{x})] f'_i(\hat{x}) \\ &= 0. \end{aligned} \quad (11)$$

From  $E_q[\nabla \ln p(\mathbf{r}, x_{\text{opt}})] = 0$ , we can get

$$\sum_i [f_i(x) - f_i(x_{\text{opt}})] f'_i(x_{\text{opt}}) = 0 \quad (12)$$

Hence  $x_{\text{opt}} = x$  and UMLI is an unbiased estimator in the present case.

From the eq.(3) and (4), we get

$$Q(x) = \frac{-\sum_i (f'_i(x))^2}{\sigma^2}, \quad (13)$$

$$G(x) = \frac{\sum_{ij} A_{ij} f'_i(x) f'_j(x)}{\sigma^2}. \quad (14)$$

Therefore, the decoding error of UMLI is

$$\langle (\hat{x} - x)^2 \rangle_{\text{UMLI}} \sim \frac{\sigma^2 \sum_{ij} A_{ij} f'_i(x) f'_j(x)}{[\sum_i (f'_i(x))^2]^2}. \quad (15)$$

Compared with MLI, UMLI has equivalent or larger decoding error according to the Cramér-Rao bound. Whereas, by omitting the operation of updating matrix inverse in MLI, UMLI largely decreases the computational cost.

To evaluate the performance of UMLI, we compare it with COM [5]. COM is a simple decoding scheme without using any information of the encoding process, whose estimate is

$$\hat{x} = \frac{\sum_i r_i c_i}{\sum_i r_i}, \quad (16)$$

where  $c_i$  is the preferred stimulus of the  $i$ th neuron. The shortcoming of COM is the large decoding error. Without loss of generality, we assume that the preferred stimuli is symmetrically distributed around the stimulus  $x$ , which leads to  $\sum_i f_i(x) c_i = 0$ . This assures that an unbiased COM estimate can be obtained.

It is not difficult to calculate the decoding error of COM, which is given by,

$$\langle (\hat{x} - x)^2 \rangle_{\text{COM}} \sim \frac{\sigma^2 \sum_{ij} A_{ij} c_i c_j}{[\sum_i f_i(x)]^2}. \quad (17)$$

#### 4 Performance comparison: the case of triangular tuning functions

To show the different performances of the above three methods, we consider the tuning functions to be triangular ones,

$$f_i(x) = \begin{cases} 1 - |x - c_i|/a & |x - c_i| < a \\ 0 & |x - c_i| \geq a \end{cases} \quad (18)$$

where the parameter  $a$  is the tuning width. A good point of the triangular function (due to its linearity) is that the decoding errors of MLI and UMLI can be exactly (*not asymptotically*) calculated by the eqs. (9) and (15) (see Appendix).

We assume that the preferred stimuli is uniformly distributed and locate at  $c_i = (i - 1/2)L$  for  $i = -\infty, \dots, \infty$  being integer, where  $L$  is the minimum distance between the preferred stimuli. The tuning width  $a$  takes value of  $nL$  with  $n$  an integer, and there are  $2n$  numbers of neurons involved in the decoding process (We set  $r_i = 0$  when  $f_i(x) = 0$  to make the Gaussian response model feasible.). The comparison is done at  $x = 0$ .

Two kinds of correlation structures are considered. One is of limited-range correlation, with the correlation matrix written as [1, 13]

$$A_{ij} = \sigma^2 \rho^{|i-j|}, \quad (19)$$

where the parameter  $\rho$  (with  $0 < \rho < 1$ ) determines the range of the correlation in the population. The inverse of the covariance matrix is

$$A^{-1}_{ij} = \frac{1 + \rho^2}{1 - \rho^2} [\delta_{ij} - \frac{\rho}{1 + \rho^2} (\delta_{i+1,j} + \delta_{i-1,j})] \quad (20)$$

This model captures a fact that the correlation strength between neurons decrease with the dissimilarity in the preferred stimuli, a property often observed in cortical areas.

Fig.1(a) shows the results of the three methods. We see that UMLI has lower decoding error than that of COM with a difference increasing with the tuning width. Compared with MLI, UMLI has larger decoding error with the relative difference, defined by  $[\langle (\hat{x} - x)^2 \rangle_{\text{UMLI}} - \langle (\hat{x} - x)^2 \rangle_{\text{MLI}}] / \langle (\hat{x} - x)^2 \rangle_{\text{MLI}}$ , decreases with the tuning width. This means UMLI becomes more comparable to MLI as the tuning width is larger.

In the above calculation we haven't considered neuronal spontaneous activity. If this factor is included, for example, set  $f_i(x) = \gamma$  when  $|x - c_i| > a$ , where  $\gamma$  is a small positive constant, the decoding error of COM will become larger (In this case, we need to restrict the range of stimuli to avoid the divergence of the decoding error). Its performance will have a property of decreasing with the tuning width when the tuning width is small, and increasing when the tuning width is large, a behavior observed in [12]. Whereas, the performance of MLI and UMLI won't be affected due to their nature of decoding using the derivative of the tuning functions. Thus, adding a spontaneous term will only enlarge the superiority of UMLI with respect to COM.

The other correlation structure we study is an uniform one [1, 6] with the correlation matrix written as

$$A_{ij} = \delta_{ij} + c(1 - \delta_{ij}), \quad (21)$$

where the parameter  $c$  (with  $-1 < c < 1$ ) determines the correlation strength. The inverse of the covariance matrix is

$$A^{-1}_{ij} = \frac{\delta_{ij}(2nc + 1 - c) - c}{(1 - c)(2nc + 1 - c)}. \quad (22)$$

The decoding errors of the three methods are calculated to be

$$\langle (\hat{x} - x)^2 \rangle_{\text{MLI}} = \frac{(1 - c)L^2\sigma^2n}{2} \quad (23)$$

$$\langle (\hat{x} - x)^2 \rangle_{\text{UMLI}} = \frac{(1 - c)L^2\sigma^2n}{2} \quad (24)$$

$$\langle (\hat{x} - x)^2 \rangle_{\text{COM}} = \frac{(1 - c)L^2\sigma^2(4n^2 - 1)}{6n} \quad (25)$$

Fig.1(b) shows the results of the three methods. We again observe that the decoding error of UMLI is lower than that of COM with the difference increase with the tuning width. And interestingly, UMLI has the same performance as MLI.

It is interesting to point out that, for general tuning functions and the uniform correlation model, we need to check if the law of large numbers and the central limit theorem hold. If not, we can't calculate the decoding errors of MLI and UMLI by using the formulas (9) and (15). We have proved that they hold in our cases from the facts that  $\sum_i f'_i(x) = \sum_i f''_i(x) = 0$ , although its proof is omitted.

## 5 Conclusion and discussion

In summary we studied the population decoding paradigm of using MLI and basing on an unfaithful decoding model. This is motivated by the fact that the encoding process of the brain is usually not exactly known to the estimator.

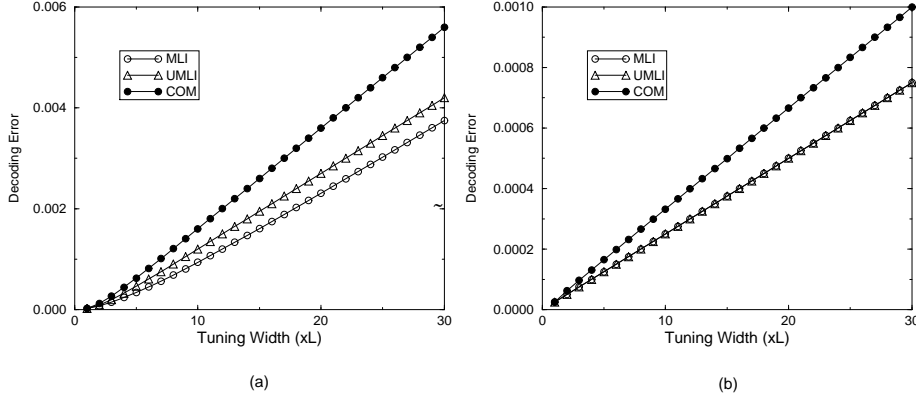


Figure 1: Comparing the decoding errors of UMLI, MLI and COM. The parameters  $L$  and  $\sigma$  are both set to be 0.1. (a) The correlation structure is of limited range with  $\rho = 0.5$ ; (b) The correlation structure is uniform with  $c = 0.5$ .

We derived the decoding error of UMLI. The performance of UMLI is compared with that of MLI and COM in an example of an unfaithful model where the neuronal correlation is neglected. It turns out that UMLI has lower decoding error than that of COM. Compared with MLI, UMLI decreases the computational cost remarkably by omitting the matrix inverse updating. Thus, UMLI is a good compromise between the decoding accuracy and the computational cost. Recently, the work of Pouget et al. has shown that a biological feasible recurrent network could implement MLI when no neuronal correlation is involved [10]. It is of the future work to understand the biological implication of UMLI.

## Appendix: The decoding errors of MLI and UMLI in the case of triangular tuning functions

For the triangular tuning function,

$$f'_i(x) = \begin{cases} \text{sign}(x - c_i)/a & |x - c_i| < a, \quad x \neq c_i \\ 0 & |x - c_i| > 0 \end{cases} \quad (26)$$

where  $\text{sign}(x - c_i)$  denoting the sign of  $(x - c_i)$ . The function  $f'_i(x)$  is singular at  $c_i = x$  and  $c_i = x \pm a$ . Without loss of generality, we assume no such preferred stimuli exist.

We denote  $\mathbf{f}'(x) = \{f'_i(x)\}$ ,  $\mathbf{f}(x) = \{f_i(x)\}$ , and  $\mathbf{r} = \mathbf{f}(x) + \boldsymbol{\xi}$  where  $\boldsymbol{\xi} = \{\xi_i\}$  and  $\{\xi_i\}$  are random numbers satisfying

$$\langle \xi_i \rangle = 0, \quad (27)$$

$$\langle \xi_i \xi_j \rangle = \sigma^2 A_{ij}. \quad (28)$$

The MLI estimate is the solution of

$$\nabla \ln q(\mathbf{r}|\hat{x}) = 0. \quad (29)$$

Substituting the eq. (6) into (29), we get

$$[\mathbf{r} - \mathbf{f}(\hat{x})]\mathbf{A}^{-1}\mathbf{f}'(x)^T = 0, \quad (30)$$

where  $T$  stands for the transposition operation.

Suppose  $\hat{x}$  is close enough to  $x$ , we have

$$\mathbf{r} - \mathbf{f}(\hat{x}) = \boldsymbol{\xi} + (\hat{x} - x)\mathbf{f}'(x). \quad (31)$$

Therefore,

$$\hat{x} = x + \frac{\boldsymbol{\xi} \mathbf{A}^{-1} \mathbf{f}'(x)^T}{\mathbf{f}'(x) \mathbf{A}^{-1} \mathbf{f}'(x)^T}. \quad (32)$$

and

$$\langle (\hat{x} - x)^2 \rangle_{\text{MLI}} = \frac{\sigma^2}{\mathbf{f}'(x) \mathbf{A}^{-1} \mathbf{f}'(x)^T}. \quad (33)$$

It is easy to see that the above result agrees with that of the eq. (9).

Similarly, the decoding error of UMLI is calculated to be

$$\langle (\hat{x} - x)^2 \rangle_{\text{UMLI}} = \frac{\sigma^2 a^4 \mathbf{f}'(x) \mathbf{A} \mathbf{f}'(x)^T}{4n^2}, \quad (34)$$

which agrees with the eq.(15).

## References

- [1] Abbott, L. F. & Dayan, P. (1999) The effect of correlated variability on the accuracy of a population code. *Neural Computation* **11**: 91-101.
- [2] Akahira, M. & Takeuchi, K. (1981) Asymptotic efficiency of statistical estimators: concepts and high order asymptotic efficiency. *Lecture Notes in Statistics* 7, Springer-Verlag.
- [3] Fetz, E., Yoyama, K. & Smith, W. (1991) Synaptic interactions between cortical neurons. In Alan Peters and Edward G. Jones, editors, *Cerebral Cortex* **9**. New York: Plenum Press.
- [4] Georgopoulos, A. P., Schwartz, A. B. & Kettner, R. E. (1986) Neuronal population coding of movement direction. *Science* **243**: 1416-1419.
- [5] Georgopoulos, A. P., Kalaska, J. F., Caminiti, R. & Massey, J. T. (1982) On the relations between the direction of two-dimensional arm movements and cell discharge in primate motor cortex. *J. Neurosci.* **2**(11): 1527-1537.
- [6] Johnson, K. O. (1980) Sensory discrimination: neural processes preceding discrimination decision. *J. Neurophys.* **43**: 1793-1815.
- [7] Lee, D., Port, N. L., Kruse, W. & Georgopoulos, A. P. (1998) Variability and correlated noise in the discharge of neurons in motor and parietal areas of the primate cortex. *J. Neurosci.* **18**(3): 1161-1170.
- [8] Murata, M., Yoshizawa, S. & Amari, S. (1994) Network information criterion-determining the number of hidden units for an artificial neural network model. *IEEE. Trans. Neural Networks* **5**(6): 865-872.
- [9] Paradiso, M. A. (1988) A theory for use of visual orientation information which exploits the columnar structure of striate cortex. *Biological Cybernetics* **58**: 35-49.
- [10] Pouget, A., Zhang, K., Deneve, S. & Latham, P. E. (1998) Statistically efficient estimation using population coding. *Neural Computation* **10**: 373-401.
- [11] Salinas, E. & Abbott, L. F. (1994) Vector reconstruction from firing rates. *Journal of Computational Neuroscience* **1**: 89-107.
- [12] Seung, H. S. & Sompolinsky, H. (1993) Simple models for reading neuronal population codes. *Proc. Natl. Acad. Sci. USA* **90**: 10749-10753.
- [13] Snippe, H. P. & Koenderink, J. J. (1992) Information in channel-coded systems: correlated receivers. *Biological Cybernetics* **67**: 183-190.
- [14] Yoon, H. & Sompolinsky, H. (1998) The effect of correlations on the Fisher information of population codes. *Advances in Neural Information Processing Systems* **11**.