

NEURAL DECODING OF MOVEMENT TARGETS BY UNSORTED SPIKE TRAINS

Zhiming Xu, Kai Keng Ang, and Cuntai Guan

Institute for Infocomm Research, ASTAR, Singapore, 138632
{xuz, kkang, ctguan}@i2r.a-star.edu.sg

ABSTRACT

Decoding movement targets from neural activity in motor cortex using invasive brain-computer interface (BCI) has potential application to help disabled patients. Most works employed spike sorting to obtain the single units (SUs) for decoding from the extracellular electrode recordings. However, spike sorting is difficult, computational demanding, and is often limited by the spike waveform variability especially in low SNR and high neuronal density conditions. To address these issues, we proposed a decoding method using unsorted spike trains from recording electrodes based on the maximal likelihood (ML) estimation approach. An experiment was performed to test neuronal data recorded from a rhesus monkey performing the center-out movement task of eight targets. The results showed that the proposed method yielded average correct decoding rate of 98.5% compared to the SU based method that yielded correct decoding rate of 96.3%. The results also showed that the proposed method yielded improved computational efficiency. Thus the proposed method showed potential for real time BCI applications with large scale of neuronal recordings.

Index Terms— Brain computer interface, maximal likelihood, motor cortex, neural decoding, Poisson distribution.

1. INTRODUCTION

Signal processing has recently emerged to study brain signals communicated by neurons, i.e., so called action potentials or spikes [1, 2]. One popular application for such study is to help disabled patients with disease in the motor system such as spinal cord injury, pontine stroke and amyotrophic lateral sclerosis, to restore movements by BCI which could translate the neural activity into control signals to operate on efferent prosthetic devices [3, 4, 5]. One of the core part in such system is of course the neural signal processing which provides such translation from brain activity to device. During the last decade, several groups have demonstrated the capability of extracting cortical neural activity from the motor areas of brain for guiding cursor movement on computer screen through experiments on both non-human primates [6, 7, 8, 9, 10] and humans [11, 12, 13]. These experiments showed great promise for the restoration of functional limb mobility for the patients with broken neural pathway in between brain and limbs. However, it is still far from practically usable and commercially available.

The current invasive BCI employed the intracortical electrode array implanted in the cerebral cortex to record extracellular neuronal activity. Through threshold detection, the neuronal spikes can in principle be obtained and the spike waveforms can be extracted out. Usually, these spikes may not come from only one SU but also several individual neurons. The conventional systems have to further identify and attribute the spike waveforms to each SU by spike

sorting. Although lots of works on spike sorting through recognizing the spike waveforms of different neurons, it has been reported that there is some limitation on sorting [14, 15] due to the inherent neuronal noise and waveform variability. The current BCI operation needs experienced human operator intervention to adjust parameters and this becomes an obstacle for clinically practical uses of BCI.

Recently, the aggregated neuronal activity attracted BCI community after the promising results by local field potential in neural decoding. Multiunit activity, other than spike trains, was shown to be able to provide the comparable performance of predicting hand movement in monkeys [16]. In addition, Ventura presented a computational paradigm of spike train decoding without explicit sorting [17], but through statistical estimation the SU tuning parameters. In [18], a BCI without spike sorting was further built by using particle filtering and parametric modeling of tuning curves. These works suggested that unsorted spike trains detected from recording channels of the implanted electrode array also contain some stimulus-specific information and indicated the possibility of neural decoding without sorting for movement. Different from these works, we investigated neural decoding using unsorted spike trains without statistical estimation or parametric modeling of SU tuning. Instead, we employed ML approach and adapted nonparametric tuning curves to unsorted spike trains for estimating movement targets.

2. MAXIMAL LIKELIHOOD MODEL

2.1. Population of single unit spike trains

Probabilistic inference based methods for neural decoding such as ML or more general Bayesian methods, have been widely used in neuroscience. These approaches are efficient when only the identification from a finite set of objects is desired, such as the target locations of center-out reaching movements. Although it is possible to decode single neuron to reconstruct the sensory stimulus in simple biological systems [1], evidence from nonhuman primates showed that single neuron is only broadly tuned with movements and not enough for the purpose movement decoding. However, a population of motor cortical neurons could provide a good estimate of movement parameters [19, 20]. Moreover, a neural network model has been presented in [21] which can implicitly perform the probabilistic computation by a population of spiking neurons. Same as the existing works [21, 22, 23], we modeled the probability distribution of spiking neuronal activity conditioned on movement direction. It usually assumes the probability of a spike within a time interval is uniform and independent, which yields the Poisson distribution model for conditional probability given target direction d ,

$$P(r|d) = [\sigma(d)\Delta t]^r \exp[-\sigma(d)\Delta t]/r! \quad (1)$$

where r is the number of spikes within the observation interval Δt second, and $\sigma(d)$ is the tuning curve of the sorted SU which repre-

sents the average firing rate to each direction [21, 24]. By assuming conditional independence of spike counts r_i of each SU indexed by i extracted from the same channel, a joint conditional distribution for the ensemble neuronal activities $\{r_i\}$ can be obtained.

$$P(\{r_i\}|d) = \prod_i P(r_i|d) = \prod_i \frac{[\sigma_i(d)\Delta t]^{r_i}}{r_i!} \exp[-\sigma_i(d)\Delta t] \quad (2)$$

In fact, the spike count correlation coefficients are generally very small among cortical neurons within short time interval as documented in [25, 26] and thus such conditional independence is a reasonable approximation. Moreover, we defined log likelihood (LLH) function $L_c^{su}(d)$ for the c -th recording channel of an electrode array as taking log of $P(\{r_i\}|d)$ and further removing the terms irrelevant of d as,

$$L_c^{su}(d) = \sum_i L_i(d) = \sum_i r_i \log[\sigma_i(d)] - \sum_i \sigma_i(d)\Delta t. \quad (3)$$

Due to the physical configuration of the electrode array and large distance of neighboring channels, the neuronal activities of different channels are uncorrelated. Given the available sorted spike trains from all channels, the estimated movement direction \hat{d}^{su} could be inferred through maximal likelihood estimation (MLE), so that the sum of LLH functions of all SUs from all channels is maximum.

$$\hat{d}^{su} = \arg \max_d \sum_c L_c^{su}(d) \quad (4)$$

2.2. Unsorted spike trains

The signal recorded from each channel of the implanted electrode array describes the extracellular neuronal activity only. The single unit spike trains are not immediately available due to the mixing activities of different nearby neurons, and thus can only be extracted by spike sorting. However, the SNR of recording, waveform variability and local neuronal density greatly limit the reliability of spike sorting [14] and thus possibly yield the biased rate code estimate [15].

Recently, [16] has demonstrated that the multiunit activity could predict the hand movement very well possibly due to the movement specific information embedded in multiunit activity. In addition, [17] presented a statistical computation framework to estimate the tuning parameters of the underlying SUs from the unsorted spike train. These works indicated that the stimulus specific information is possibly contained in the unsorted spike train. This could be due to the possible columnar structure related to movement in motor cortex which was reported to exhibit local spatial organization by the kinematics [27, 28, 29, 30]. The nearby neurons recorded from the same channel usually tend to prefer similar values of kinematic parameters and thus have similar tuning characteristics.

Considering these new evidences, we investigated neural decoding using unsorted spike trains in this paper. In contrast to [17], we did not try to estimate the individual tuning parameters of each SU underlying the unsorted spike trains, but instead focused on the overall tuning characteristics of the unsorted spike trains. Similar to previous works [17], we modeled the unsorted spike trains as the superimposed SU spike trains by pooling them together. It is known that the superposition of Poisson processes is also a Poisson process [31]. Since we employed the Poisson model for the spike counts of SU spike trains, the similar Poisson model was used for that of the unsorted spike train. Hence, the LLH function can be similarly derived as in (3) for the unsorted spike train of the c -th channel as following,

$$L_c(d) = r_c \log[\sigma_c(d)] - \sigma_c(d)\Delta t \quad (5)$$

where r_c is the spike count within the time bin Δt second, and $\sigma_c(d)$ is the tuning curve for the c -th recording channel. The MLE \hat{d} using the unsorted spike trains can be similarly defined as

$$\hat{d} = \arg \max_d \sum_c L_c(d). \quad (6)$$

From (3), we can see that LLH function is *linear* on the spike counts r_i given the neuronal tuning curves, i.e., a weighted average over spike counts. Based on the evidences of cortical columnar structure presented in [27, 28, 29, 30], if the tuning characteristics of SUs from the same recording channel are similar such as cosine tuning with similar preferred directions [28], the summed LLH from SUs shown in (3) can in fact be approximated well by (5) using the unsorted spike train. Such approximation will be shown in Sec. 4.1 on neuronal data recorded *in vivo* from a monkey experiment.

3. MOVEMENT TASK AND RECORDINGS

The experiment on reaching movements was conducted in Kording Lab at Northwestern University. A rhesus monkey was trained to perform the center-out reaches to eight peripheral targets evenly spaced in a circle presented on a computer screen in front of it. The monkey operated on a two-link planar manipulandum and feedback about the movement was shown on the screen. The handle position was displayed as circular cursor while the peripheral targets were displayed as a square of larger size than the circular cursor. Every trial started with acquisition of the origin displayed as a square target and holding it for 0.3-0.5s set randomly by computer. After this hold period, the monkey controlled the manipulandum to move the circular cursor to reach a pseudo-randomly chosen peripheral target. After reaching the chosen target and holding it at least 0.2-0.5s, the monkey received a liquid reward.

One 100-channel intracortical electrode array was implanted in the arm area of primary motor (MI) cortex. Spike sorting was carefully performed offline by manual clustering. Totally 172 single units were sorted from 90 channels recorded with data, and 175 successful trials for all eight targets (about 20 trials for each direction) were obtained in one session. Table 1 showed the distribution of sorted SUs over the recording channels, i.e., how many sorted SUs on one channel (and its percentage over all 90 channels). More details of neuronal recording can be found in [32].¹

Table 1. Distribution of SUs over recording channels.

# SUs	1	2	3	4
# Channels	39 (43%)	23 (26%)	25 (28%)	3 (3%)

4. RESULTS AND DISCUSSION

The proposed decoding method was tested on the neuronal data recorded *in vivo* from a rhesus monkey performing center-out reaching movement task [32]. Since the available neuronal data has already been carefully sorted, we simulated the unsorted spike trains by superimposing the SU spike trains from the same recording channel. Although there are 39 channels with only one SU recorded as shown in Table 1, we still treated them as unsorted spike trains since in practical neuronal recording there is no prior information about whether the recorded spike train is composed of only SU or mixture

¹In this paper, only the data from monkey C was analyzed and it is available at <http://crcns.org/data-sets/movements/dream>.

of multiple units. Although the superposition of SU spike trains is slightly different from the unsorted spike train in practical neuronal recording, [18] has shown that the superimposed spike trains have very similar tuning parameters to the unsorted spike trains. Thus, it is appropriate to use the superimposed spike trains for testing and comparing with SU spike trains for neural decoding.

4.1. Directional tuning and LLH for unsorted spike trains

At the training phase of ML model, 5 training trials for each direction $d \in \{0^\circ, 45^\circ, 90^\circ, 135^\circ, 180^\circ, 225^\circ, 270^\circ, 315^\circ\}$ were selected randomly for estimating the tuning curves of both sorted SUs and unsorted spike trains. Instead of using the statistical estimation or parametric modeling of tuning parameters as in [17, 18], we used the nonparametric tuning curves, i.e., averaged responses conditioned on direction. The whole training process thus used 40 trials of total 175 trials available, and the other 135 trials not used in training were employed for test. One single observation interval was fixed at $\Delta t = 500\text{ms}$ for all trials for counting spikes.

We showed our results on a single trial first and then followed by the whole data set. First, the comparison of LLH for SUs and the unsorted spike trains was shown in Fig. 1(a) and 1(b) for two different channels 39 and 84, respectively. The results were based on a single test trial (trial 134) with actual movement direction of 180° . The dashed lines showed the LLH of three SUs while the black solid line showed the sum of them, corresponding to (3). It can be seen that the SUs can only provide limited or even none discriminative LLH information over the eight possible directions. However, the summed LLH by SUs could yield better distinction over different directions, although it is still not informative enough to give correct estimate. Moreover, the LLH for unsorted spike train of the same channel denoted by the red solid line can approximate the summed LLH of SUs very well within a constant level, which shows the good approximation of (5) to (3). Although the SU or the single recording channel is not capable to provide enough discriminative LLH, the population of all SUs or recording channels can yield a good discriminant which is a bell shaped function over the directions as shown in Fig. 1(c). Although the SU-based method usually could yield a correct estimate of actual direction, Fig. 1(c) showed an example of failure case for it, while the proposed method still can give the correct estimation of direction. This is partly due to the noisy LLH of SUs as shown in Fig. 1(a) where the summed LLH of SUs has a significant drop at the actual direction compared to the strong competitors 225° and 135° . This is particular evident for the SU 1 of channel 39 which dominates the summed LLH of SUs at the directions 135° , 180° and 225° shown in 1(a). On the contrary, the proposed method can yield stable and reliable LLH which is more smooth and less fluctuating.

The LLH function by the proposed method is narrower and sharper compared to that by the SU-based approach as shown in a single trial in Fig. 1(c). This phenomenon is not by chance and actually consistent in the whole data set and we showed it in Fig. 1(d) and Fig. 1(e), respectively, in the form of the probability confusion matrix. Such matrix showed the mean posterior probability distribution of movement direction given the whole data set. The color code denotes the mean probability of a possible direction estimate (in the x -axis) given the true movement direction d (in the y -axis) for the whole data set. The diagonal elements indicate the correct estimates, while any off-diagonal element indicates an incorrect estimate. It can be seen that the proposed method can yield shaper probability distribution and thus could provide more accurate estimate. In addition, the most probable candidates for direction estimate clustered (circularly) along the diagonal. Hence, it is more important for LLH

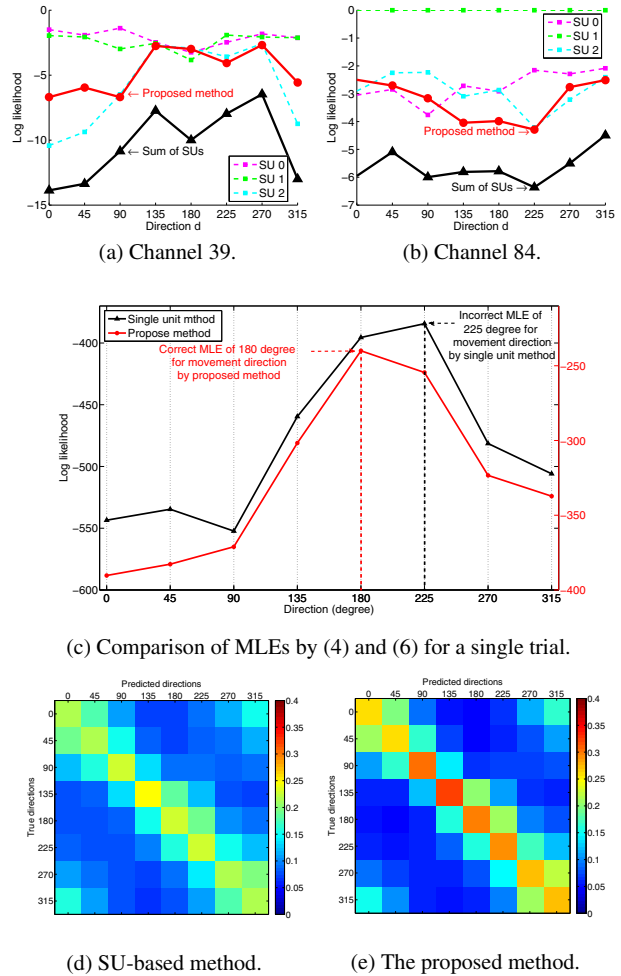


Fig. 1. Comparison of the SU-based and the proposed methods by LLH and probability confusion matrix.

to discriminate the MLE over the nearby directions (usually the second most probable candidate) in order to provide more robust and reliable estimate. This can be seen in 1(c) for the proposed method which showed the MLE has a larger margin over the direction of 225° , compared to the SU-based approach.

4.2. ML decoding with different parameters

We further conducted experiments over two different periods of 500ms for both SU-based and the proposed methods. One is before movement ($-500\text{ms} - 0\text{ms}$, where 0ms is the movement onset) and the other is peri-movement ($0\text{ms} - 500\text{ms}$). The decoding performance was measured by the correct estimation of directions. We further assessed one critical parameter in population coding, i.e., the number of units used for decoding. To develop statistically meaningful results, such procedure was repeated 100 times for estimating the standard error (SE) of the mean correct estimation rate by the bootstrap method, which reflected the cross validated results.

Fig. 2 showed the results of decoding where the filled dots de-

noted the mean correct estimation rate overlaid with SE bars. First, it can be seen clearly the significantly better decoding performance by both SU-based and the proposed methods over the peri-movement period than those over the period of before movement, and all exceed the chance level (12.5%) significantly. This can be explained by the much stronger response of MI cortex at the period of peri-movement than that before movement, which is consistent with [23] that the MI cortex is largely related to the movement execution rather than the decision making of the target. Second, we can see that in both periods, the decoding performance using unsorted spike trains is comparable to or even slightly better than that of SUs. When using 90 units, the SU-based method only yielded 91.3% correct accuracy while the proposed method attained 98.5%. Such direct comparison is not totally meaningful since the same number of unsorted spike trains usually contain more neurons than SU spike trains. However, the decoding by all SU spike trains only yielded correct accuracy of 96.3%, even still slightly lower than that by unsorted spike trains. Furthermore, the region of small number of units showed superiority of neural decoding using unsorted spike trains, since it can obtain better performance without demanding computation imposed by spike sorting and thus can achieve more efficient power consumption which is very critical for chronically implantable neural device.

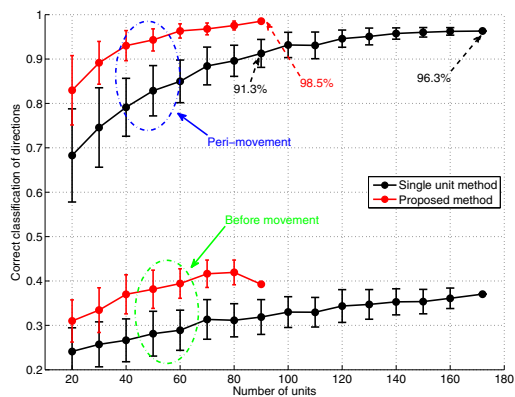


Fig. 2. ML decoding performance using the single unit based approach and the proposed method.

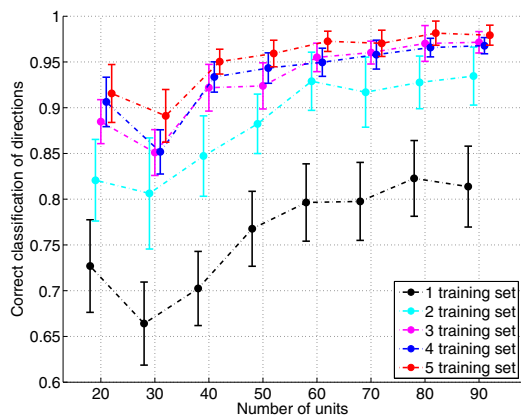


Fig. 3. Decoding performance of the proposed method with respect to the number N_{tr} of training sets.

It is well known that the training process for BCI is tedious. Here, we tested how fast training our proposed method can achieve and showed the decoding performance upon different number N_{tr} of training sets (the number N_{tr} of training trials for each direction d) as shown in Fig. 3. It can be seen clearly the better performance with larger training sets. Notice that only three training sets can yield a reasonable performance, almost comparable to that attained by five training sets. In particular, the performance increases very fast from single training set to three training sets, showing the fast adaptation capability of ML decoding using unsorted spike trains. Similar evidence for Skellam distribution based ML decoding with SUs has also been reported in [33] for decoding finger movements. Our work has shown it also happens in neural decoding using unsorted spike trains. This is very desirable for BCI applications whose calibration for new user is usually slow. We hope our work can speed up the training process for invasive BCI, especially without tedious and time-consuming spike sorting.

4.3. Discussion

This work has adapted ML decoding to the unsorted spike trains, which avoids the difficult and tedious spike sorting that could yield biased firing rate estimate. Different from [17] which capitalized on statistical estimation of individual tuning parameters of SUs from the unsorted spike train, we focused on the unsorted spike trains and their tuning characteristic and LLH function. Our results showed the unimodal characteristic of LLH function of the unsorted spike train. Although [18] has reported that the unimodal tuning curves by parametric modeling were often found for the unsorted spike trains, we employed nonparametric tuning in contrast to [18] and instead studied the LLH discriminant function for decoding. In addition, results in Sec. 4.1 showed the possible probabilistic computations implicitly done by the population of neurons, which is consistent with findings of [21, 22, 34, 35, 36], and hence further promoted the probabilistic inference method for neural decoding.

5. CONCLUSION

This paper proposed a neural decoding method using unsorted spike trains based on the maximal likelihood approach. We tested the proposed method on neuronal data recorded from a monkey during an experiment of eight-target movement task. The results showed that the movement direction can be classified with 98.5% accuracy using the proposed method, compared to 96.3% using sorted SU-based method. In addition, the proposed method can be trained very fast with only 3-5 training sets, and thus has an immediate relevance for BCI application. Note that unsorted spike trains are less computationally demanding and hence more efficient on power consumption compared to sorted spike trains. It provides a balance between performance and computational efficiency that appears to be critical for future large scale neural recordings on the order of one thousand electrodes [37].

Our results showed that the performance fluctuation with random selection of subset of units. Hence the optimal selection of subset of units needs to be further investigated to achieve more computational efficiency for practical BCI applications. In addition, since we explicitly used the movement onset timing as a cue, the performance of the proposed method for asynchronous (i.e., self-paced) neural decoding has to be further studied for online neural prosthetic applications such as self-feeding reported in [38].

6. REFERENCES

- [1] P. Dayan and L. F. Abbot, *Theoretical Neuroscience: Computational and Mathematical Modeling of Neural Systems*, Cambridge, MA: The MIT Press, 2001.
- [2] E. N. Brown, "Signal processing and statistical challenges in neuroscience data analysis," *SIAM News*, vol. 40, pp. 1 – 2, 2007.
- [3] F. A. Mussa-Ivaldi and L. E. Miller, "Brain-machine interfaces: computational demands and clinical needs meet basic neuroscience," *Trends in Neurosci.*, vol. 26, pp. 329 – 334, 2003.
- [4] A. B. Schwartz, X. T. Cui, D. J. Weber and D. W. Moran, "Brain controlled interfaces: movement restoration with neural prosthetics," *Neuron*, vol. 52, pp. 205 – 220, 2006.
- [5] N. G. Hatsopoulos and J. P. Donoghue, "The science of neural interface systems," *Annu. Rev. Neurosci.*, vol. 32, pp. 249 – 266, 2009.
- [6] D. M. Taylor, S. I. Tillery, and A. B. Schwartz, "Direct cortical control of 3D neuroprosthetic devices," *Science*, vol. 296, pp. 1829 – 832, 2002.
- [7] M. D. Serruya, N. G. Hatsopoulos, L. Paninski, M. R. Fellows, and J. P. Donoghue, "Instant neural control of a movement signal," *Nature*, vol. 416, pp. 141 – 142, 2002.
- [8] J. M. Carmena *et al.*, "Learning to control a brain-machine interface for reaching and grasping by primates," *PLoS Biol.*, vol. 1, pp. 193 – 208, 2003.
- [9] S. Musallam, B. D. Corneil, B. Greger, H. Scherberger, and R. A. Andersen, "Cognitive control signals for neural prosthetics," *Science*, vol. 305, pp. 258 – 262, 2004.
- [10] G. Santhanam *et al.*, "A high-performance brain-computer interface," *Nature*, vol. 442, pp. 195 – 198, 2006.
- [11] L. R. Hochberg *et al.*, "Neuronal ensemble control of prosthetic devices by a human with tetraplegia," *Nature*, vol. 442, pp. 164 – 171, 2006.
- [12] C. L. Ojakangas *et al.*, "Decoding movement intent from human premotor cortex neurons for neural prosthetic applications," *J. Clinical Neurophysiol.*, vol. 23, pp. 577 – 584, 2006.
- [13] L. R. Hochberg *et al.*, "Reach and grasp by people with tetraplegia using a neurally controlled robotic arm," *Nature*, vol. 485, pp. 372 – 377, 2012.
- [14] P. Stratton *et al.*, "Action potential waveform variability limits multi-unit separation in freely behaving rats," *PLoS One*, vol. 7, pp. 1 – 16, 2012.
- [15] V. Ventura, "Traditional waveform based spike sorting yields biased rate code estimates," *Proc. Natl. Acad. Sci. USA*, vol. 106, pp. 6921 – 6926, 2009.
- [16] E. Stark and M. Abeles, "Predicting movement from multiunit activity," *J. Neurosci.*, vol. 27, pp. 8387 – 8394, 2007.
- [17] V. Ventura, "Spike train decoding without spike sorting," *Neural Computation*, vol. 20, pp. 923 – 963, 2008.
- [18] G. W. Fraser, S. M. Chase, A. Whitford, and A. B. Schwartz, "Control of a brain-computer interface without spike sorting," *J. Neural Eng.*, vol. 6, pp. 1 – 8, 2009.
- [19] A. P. Georgopoulos, A. B. Schwartz, and R. Kettner, "Neuronal population coding of movement direction," *Science*, vol. 233, pp. 1416 – 1419, 1986.
- [20] R. Q. Quiroga and S. Panzeri, "Extracting information from neuronal populations: information theory and decoding approaches," *Nature Rev. Neurosci.*, vol. 10, pp. 173 – 185, 2009.
- [21] T. D. Sanger, "Probability density methods for smooth function approximation and learning in population of tuned spiking neurons," *Neural Computation*, vol. 10, pp. 1567 – 1586, 1998.
- [22] R. S. Zemel, P. Dayan, and A. Pouget, "Probabilistic interpretation of population codes," *Neural Computation*, vol. 10, pp. 403 – 430, 1998.
- [23] N. Hatsopoulos, J. Joshi, and J. G. O'Leary, "Decoding continuous and discrete motor behaviors using motor and premotor cortical ensembles," *J. Neurophysiol.*, vol. 92, pp. 1165 – 1174, 2004.
- [24] T. D. Sanger, "Neural population codes," *Curr. Opin. Neurobiol.*, vol. 13, pp. 238 – 249, 2003.
- [25] K. Padmanabhan and N. N. Urban, "Intrinsic biophysical diversity decorrelates neuronal firing while increasing information content," *Nature Neurosci.*, vol. 13, pp. 1276 – 1282, 2010.
- [26] A. S. Ecker *et al.*, "Decorrelated neuronal firing in cortical microcircuits," *Science*, vol. 327, pp. 584 – 587, 2010.
- [27] T. Naselaris, H. Merchant, B. Amirkian, and A. P. Georgopoulos, "Large-scale organization of preferred directions in the motor cortex. II. Analysis of local distributions," *J. Neurophysiol.*, vol. 96, pp. 3237 – 3247, 2006.
- [28] A. P. Georgopoulos, H. Merchant, T. Naselaris, and B. Amirkian, "Mapping of the preferred direction in the motor cortex," *Proc. Natl. Acad. Sci. USA*, vol. 104, pp. 11068 – 11072, 2007.
- [29] E. Stark, R. Drori, and M. Abeles, "Motor cortical activity related to movement kinematics exhibits local spatial organization," *Cortex*, vol. 45, pp. 418 – 431, 2009.
- [30] N. G. Hatsopoulos, "Columnar organization in the motor cortex," *Cortex*, vol. 46, pp. 270 – 271, 2010.
- [31] A. Papoulis and S. U. Pillai, *Probability, Random Variables and Stochastic Processes*, New York: McGraw-Hill, 4th edition, 2002.
- [32] I. H. Stevenson *et al.*, "Statistical assessment of the stability of neural movement representations," *J. Neurophysiol.*, vol. 106, pp. 764 – 774, 2011.
- [33] H.-C. Shin *et al.*, "Neural decoding of finger movements using Skellam-based maximal-likelihood decoding," *IEEE Trans. Biomed. Eng.*, vol. 57, pp. 754 – 760, 2010.
- [34] A. Pouget, P. Dayan, and R. S. Zemel, "Inference computation with population codes," *Annu. Rev. Neurosci.*, vol. 26, pp. 381 – 410, 2003.
- [35] W. J. Ma *et al.*, "Bayesian inference with probabilistic population codes," *Nature Neurosci.*, vol. 9, pp. 1432 – 1438, 2006.
- [36] M. Jazayeri and J. A. Movshon, "Optimal representation of sensory information by neural populations," *Nature Neurosci.*, vol. 9, pp. 690 – 696, 2006.
- [37] I. H. Stevenson and K. P. Kording, "How advances in neural recording affect data analysis," *Nature Neurosci.*, vol. 14, pp. 139 – 142, 2011.
- [38] M. Velliste *et al.*, "Cortical control of a prosthetic arm for self-feeding," *Nature*, vol. 453, pp. 1098 – 1101, 2008.