Applying Information-theoretic Measures To Computation and Communication in Neural Ensembles

Jose M. Carmena[1,2,3], Ryan T. Canolty[1,2], Kelvin So[1], and Michael C. Gastpar[1]

[1]Department of EECS, [2]Helen Wills Neuroscience Institute and [3]Program in Cognitive Science
University of California, Berkeley
Berkeley, CA 94720
{carmena,canolty,sokelvin,gastpar}@eecs.berkeley.edu

I. Extended Abstract

The novel methods used to develop brain machine interfaces (BMIs) present systems neuroscientists with the opportunity to now ask fundamentally new types of questions. This paradigm shift has been driven by three key developments. First, it is now possible to perform simultaneous, massively parallel recording of brain signals from microelectrode arrays chronically implanted in multiple brain areas over several months. Second, advances in computing power enables sophisticated, real-time signal processing to be performed on these large data sets. Third, recent theoretical advances clarify how the mutual information between individual neurons or between distinct neuronal populations could play a key role in neural coding. We contend these advances present a high-leverage opportunity to accelerate understanding of neuronal computation and communication.

Neuronal oscillations have been suggested to play a role in cortical computation and communication. Oscillations which can be recorded using multi-site, multi-electrode methods are rhythmic fluctuations in neuronal excitability which modulate both output spike timing and sensitivity to synaptic input. Therefore, effective communication between neuronal populations requires precise matching of the relative phase of distinct rhythms to axonal conduction delays. In addition, neuronal oscillations facilitate synaptic plasticity, influence reaction time, and correlate with both attention and perceptual binding. Oscillatory synchronization appears to be a function of both frequency and distance, such that high frequency activity binds local areas while low frequency activity binds distinct cortical areas. Thus, an oscillatory hierarchy operating across multiple spatial and temporal scales could regulate communication both within and between brain areas. Clarifying the nature of dependence and redundancy in multi-site brain signals is critical for determining the way cortical networks communicate and engage in effective computation.

Information theory has been used as an organizing principle in neuroscience for several decades. The most popular approaches are various flavors of information maximization problems. However, these approaches fail to unlock the full potential hidden in the new multi-variate, multi-neuron recordings experimental data. Here we propose using new information theoretic measures concerning the interplay between communication and computation. Both tasks are clearly of crucial importance to brain functionality. The specific question we propose to address is to understand whether communication and computation are dealt with as separate tasks, or jointly. This is motivated by recent work [1] showing that separate communication and computation can come at a very large performance penalty. By separate tasks, we mean that data is first communicated to a dedicated brain region, and then used inside this region for computation; the results are then communicated back to other brain regions. By jointly, we mean that if communication links interfere, then it can be much more efficient to simultaneously execute communication and computation: that is, one communicates just enough such that a particular operation can be computed, rather than communicating the full data.

II. Emerging Experimental Paradigms in Neuroscience

In contrast to classic receptive field experiments which employed single microelectrodes recording spikes from one neuron in one area acutely for a handful of hours for simple offline analysis, BMI protocols simultaneously record spikes and local field potentials from multiple neurons in distinct brain areas chronically over weeks or months and employ advanced real-time signal processing algorithms. It is the integrated combination of several of these new elements which gives this approach its power.

First, moving from single microelectrodes to simultaneous, massively parallel recordings present the opportunity to exploit the dependence between neurons in the investigation of brain function, rather than just looking at the connection between stimulus properties and the activity of single neurons. Extracting the correlated activity of populations of cells improves both the signal-to-noise ratio of the features of interest but can be used to make inferences about the nature of computation and communication in large-scales systems. Furthermore, recent studies have shown evidence for recurring patterns of spike
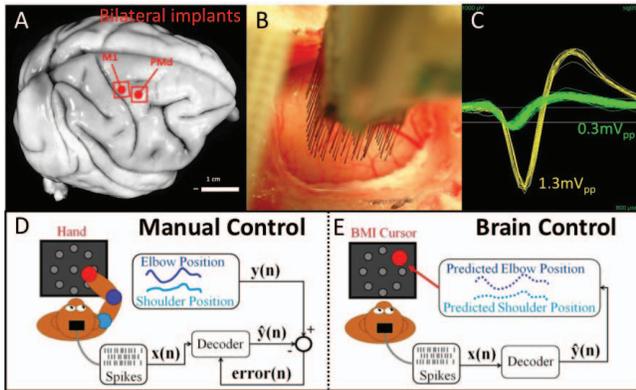
Fig. 1. Chronic, massively parallel, simultaneous multi-site microelectrode recordings present new opportunities for offline data mining of spontaneous and task-related neuronal activity, real-time online decoding and operant conditioning, as well as studies of the effects of long-term training, learning, and development. A) Example placement of multiple microelectrode arrays. Here four 64-electrode arrays were implanted bilaterally in the primary motor strip (M1) and the dorsal premotor area (PMd), for a total of 256 electrodes in 4 distinct cortical regions. B) Photo of one 8x8 microelectrode array prior to implantation. Each tungsten electrode is 0.035 mm in diameter, with 0.5 mm inter-electrode spacing. Impedance is 0.2-1 MOhm at 1 kHz, 5 nA. C) Spikes from multiple cells can be identified on each electrode. Example spike waveforms from two distinct neurons recorded on one electrode. D-E) Brain-machine interface (BMI) paradigm involves subject performing different movements while neuronal activity is recorded in order to train both decoding algorithm and active cell population (manual control), after which intended movement is predicted using neuronal activity alone (brain control). Related paradigms include real-time operant conditioning of arbitrary activity patterns and electrical microstimulation. See [12].

timing in neuronal populations, both in vivo [2] as well as in biophysically realistic simulations [3].

Second, recording the same neuronal population chronically over months versus acutely over hours greatly increases the amount of data available to constrain competing models and opens up entirely new questions related to long-term learning and development. Rather than 30 minutes of data to work with, investigators now have access to thousands of trials over many thousands of hours for use in constraining competing models of cortical function. Importantly, rather than speaking about the response of an average neuron in a given cortical area, neuroscientists can now observe or condition the responses of a particular neuron over days, weeks, and perhaps months

Third, recording spikes as well as local field potentials (LFPs) allows researchers to investigate how information is passed between different spatial and temporal scales and exploit this dependence for improved decoding performance. LFPs are generated by the summed synaptic action of the neuronal population within a given local cortical area, and can thus be considered a measure of the organization occurring at a larger spatial and temporal scale than the spiking of an individual neuron. By accounting for this statistical dependence between multiple levels, investigators can improve the performance of decoders, as has been shown for place cells in the hippocampus [4]. Given that distinct brain rhythms appear to modulate each other in characteristic ways [5], [6], the simultaneous recording of neuronal signals generated on

multiple scales can reveal more about neuronal computation than simply recording any single level alone

Fourth, simultaneous recording from multiple areas helps researchers clarify the nature of long-range communication and computation, which cannot be done using recordings (even multi-electrode recordings) from a single cortical area. The neuronal oscillations which can be recorded using multi-site, multi-electrode methods are rhythmic fluctuations in neuronal excitability which modulate both output spike timing and sensitivity to synaptic input [7]. Therefore, effective communication between neuronal populations requires precise matching of the relative phase of distinct rhythms to axonal conduction delays. An oscillatory hierarchy operating across multiple spatial and temporal scales could therefore regulate long-range communication between brain areas and across multiple scales [5]. In addition, neuronal oscillations facilitate synaptic plasticity [8], influence reaction time [9], and correlate with both attention [10] and perceptual binding [11]. Clearly, oscillations are well positioned to coordinate activity in many different brain networks, especially the network involved in motor control. Clarifying the nature of dependence and redundancy in multi-site signals is critical for determining the way brain networks communicate and engage in effective computation.

Fifth, modern computers now enable researchers to analyze data using real-time algorithms in addition to more traditional, offline approaches. Real-time techniques open the possibility of employing optimized, adaptive experimental designs to generate high-leverage data in as short a time as possible. Furthermore, these real-time analysis methods open the door to new experimental designs centered around response-contingent electrical cortical microstimulation, where the location, timing, and pattern of electrical stimulation delivered to subjects depends on the ongoing pattern of motor or cognitive activity.

III. EMERGING INFORMATION-THEORETIC MEASURES AND METHODS FOR NEUROSCIENCE

Classically, *direct* stimulus-response information measures have been studied as a model-independent assessment of neural coding performance. In the new experimental paradigms, it will be interesting to revisit these measures in an attempt to understand the behavior of large populations of neurons.

A. Preliminary Study: Pairwise Information Measures

We examined the contribution of single neurons to an ensemble by applying information-theoretic measures such as mutual information to quantify the predictive power of ensembles and individual neurons. We analyzed neural activity recorded from the motor cortex of a macaque monkey performing a delayed center-out reaching task to eight different targets, as in [12]. Prior to classification, low-pass filtering and decimation were performed, as in [13], followed by Principal Component Analysis (PCA) to reduce the dimensionality to facilitate the statistical classifying step. Learning vector quantization (LVQ) was used for classification. From the
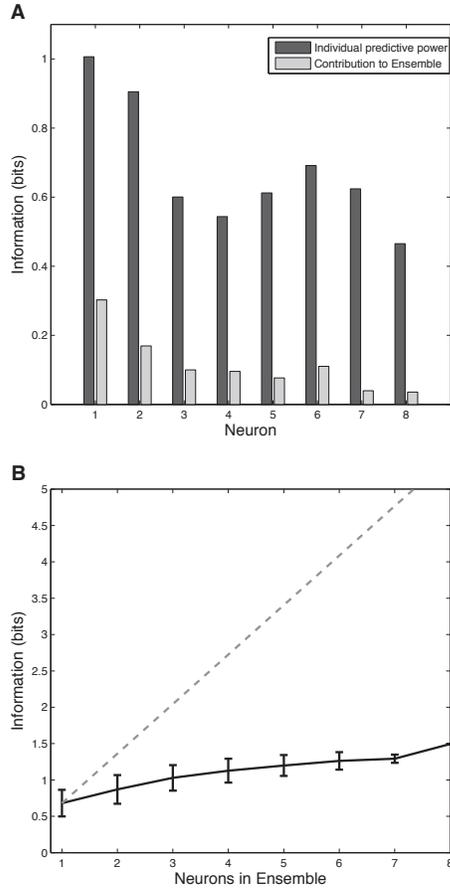
Fig. 2. A) Individual predictive power and contribution to ensemble for each neuron. B) Average predictive power of ensemble as function of ensemble size. Dotted line represents expected predictive power if information contribution by each neuron is independent.

classification we computed the mutual information according to the following formula to assess the predictive power of each individual neuron:

$$I(S; R) = \sum_{s \in S} \sum_{r \in R} p(s, r) \log_2 \frac{p(s, r)}{p(s)p(r)}$$

where S is the distribution of the actual reach target and R is the predicted target.

To determine the ensemble information, we selected the top eight neurons with the highest predictive power as part of the ensemble. We define the contribution of an individual neuron to an ensemble as the difference between the predictive power (as measured in bits by the mutual information) of all ensembles containing the given neuron and the predictive power of the remaining ensemble without the neuron, as in [13]. By comparing this measure of contribution to the individual predictive power of each neuron, we can evaluate whether a particular neuron adds redundant information. We found that the individual predictive power of all neurons were higher than the contribution to the ensemble. This result

indicates that the information contributed by each neuron is very much redundant, since the increase in predictive power of the ensemble when adding the neuron is much less than its individual predictive power. To determine the redundancy of information at each ensemble size, we computed the average predictive power at each ensemble size, see Figure 2. Hence, if the information contributed by each additional neuron is independent of the information in the ensemble, we expect the predictive power to increase proportionally with ensemble size (dotted line). However, the predictive power scales much slower, which supports the notion of redundant information amongst neurons. These results are consistent with past studies that have investigated the idea of redundancy in neural encoding, such as [13], [14]. Hence, by drawing from information-theoretic measures, we can now quantify aspects of computation in neural ensembles.

REFERENCES

[1] B. Nazer and M. Gastpar, "Computation over multiple-access channels," *IEEE Transactions on Information Theory*, vol. 53, pp. 3498–3516, October 2007.

[2] A. E. P. Villa, I. V. Tetko, B. Hyland, and A. Najem, "Spatiotemporal activity patterns of rat cortical neurons predict responses in a conditioning task," *Proceedings of the National Academy of Sciences of the USA*, vol. 96, pp. 1106–1111, 1999.

[3] E. M. Izhikevich, "Polychronization: computation with spikes," *Neural Computation*, vol. 18, no. 2, pp. 245–282, 2006.

[4] K. D. Harris, J. Csicsvari, H. Hirase, G. Dragoi, and G. Buzsaki, "Organization of cell assemblies in the hippocampus," *Nature*, vol. 424, pp. 552–556, 2003.

[5] P. Lakatos, A. S. Shah, K. H. Knuth, I. Ulbert, and G. Karmos, "An oscillatory hierarchy controlling neuronal excitability and stimulus processing in the auditory cortex," *Journal of Neurophysiology*, vol. 94, no. 3, pp. 1904–11, 2005.

[6] R. T. Canolty, E. Edwards, S. S. Dalal, M. Soltani, H. E. Kirsch, M. S. Berger, N. M. Barbaro, and R. T. Knight, "High gamma power is phase-locked to theta oscillations in human neocortex," *Science*, vol. 313, pp. 1626–1628, 2006.

[7] P. Fries, "A mechanism for cognitive dynamics: neuronal communication through neuronal coherence," *Trends in Cognitive Science*, vol. 9, no. 10, pp. 474–480, 2005.

[8] G. Buzsaki and A. Draguhn, "Neuronal oscillations in cortical networks," *Science*, vol. 304, pp. 1926–1929, 2004.

[9] K. Linkenkaer-Hansen, V. V. Nikulin, S. Palva, R. J. Ilmoniemi, and J. M. Palva, "Prestimulus oscillations enhance psychophysical performance in humans," *Journal of Neuroscience*, vol. 24, no. 45, pp. 10186–10190, 2004.

[10] T. Womelsdorf, P. Fries, P. P. Mitra, and R. Desimone, "Gamma-band synchronization in visual cortex predicts speed of change detection," *Nature*, vol. 439, pp. 733–736, 2006.

[11] J. P. Lachaux, N. George, C. Tallon-Baudry, J. Martinerie, L. Hugueville, L. Minotti, P. Kahane, and B. Renault, "The many faces of gamma band response to complex visual stimuli," *Neuroimage*, vol. 25, pp. 491–501, 2005.

[12] K. Ganguly and J. M. Carmena, "Emergence of a stable cortical map for neuroprosthetic control," *PLoS Biol*, vol. 7, no. 7, 2009.

[13] N. S. Narayanan, E. Y. Kimchi, and M. Laubach, "Redundancy and synergy of neuronal ensembles in motor cortex," *Journal of Neuroscience*, vol. 25, no. 17, pp. 4207–4216, 2005.

[14] J. M. Carmena, M. A. Lebedev, C. S. Henriquez, and M. A. L. Nicolelis, "Stable ensemble performance with single neuron variability during reaching movements in primates," *Journal of Neuroscience*, vol. 25, no. 46, pp. 10712–10716, 2005.