Role of local field potentials in encoding hand movement kinematics

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trates the musculoskeletal system to produce complex three-dimen-

sional movements is still poorly understood. Despite first promising

results in brain-machine interfaces that translate cortical activity to

control output, there is an ongoing debate about which brain signals

provide richest information related to movement planning and execu-

tion. Novel results by Bansal and colleagues (2011) now suggest that

neuronal spiking and local field potentials jointly encode kinematics

during skilled reach and grasp movements.

Since pioneering work in the last century (Cheney and Fetz

1980; Georgopoulos et al. 1982), it has been known that

discharge of cells in primary motor cortex is related to various

parameters of movement execution. In the following 50 years,

a large number of studies extended our knowledge of this

relationship, but up to date, it remains unclear what the de-

cending motor signal originating from cortex is primarily

encoding. One view is that of a signal dominated by limb

dynamics, i.e., muscle force and torque, while there is also

evidence for a kinematic nature directly reflecting movement

features like position or speed. With the advent of brain-

machine interfaces (BMIs) in the late 1990s, this basic issue

has progressed to a new, more practical level. In a so-called

motor BMI, one tries to read out movement-related informa-

tion from cortex without considering the numerous hierarchical

parts of the motor system from brain stem to spinal cord to

motoneurons. Using sophisticated algorithms, this neural ac-

tivity is then mapped to control output of an external effector,

e.g., moving a cursor on a computer screen or even driving

robotic devices. Thus, to achieve a reasonable performance,

one has to record a neural signal that is sufficiently specific to

the respective task but at the same time robust enough to ensure

reliable application in BMIs. Due to the former constraint, one

part of the neuroscientific community has focused on local

spiking activity. On the other hand, cortical areas engaged in

movement-related processing are distributed over the brain

providing an argument for more global recordings like field

potentials.

This Neuro Forum article reviews a contribution by Bansal

et al. (2011), recently published in this Journal, that compared

decoding of kinematic variables from single neuron spiking

and field potentials. An outstanding strength of the study was

a naturalistic experimental design where two monkeys contin-

uously reached and grasped up to nine different objects swing-

ing in front of them (Fig. 1). Optical recordings of reflective

markers placed on arm and hand allowed for reconstruction of

kinematic movement data in 3-D space (hand position, speed,

and aperture). Simultaneously neural signals were recorded

from two microelectrode arrays placed in primary motor and

ventral premotor cortices of the hemisphere contralateral to the

moving hand. From these recordings, low-frequency local field

potentials (lf-LFPs) in a range 0.3–2 Hz as well as single unit

spiking activity were extracted.

Most notably, Bansal and colleagues successfully decoded

kinematics of monkeys’ freely moving hand from lf-LFP. The

mean cross-correlation between original and reconstructed

movement parameter ranged between 0.4 and 0.8, depending

on the respective kinematic variable. These results demonstrate

remarkably high decoding accuracies given the almost infinite

ways a monkey could reach and grip each object. In contrast,

the majority of past studies has focused on discrete 2-D

movements, e.g., center-out movement tasks or assessed single

joint kinematics. Hence, to infer overall hand trajectory as well

as more specific details like grip aperture from one and the

same, recordings may represent the next milestone in BMI

research.

A crucial part of the high decoding accuracy observed may

be attributable to the Kalman filter applied to neural data. This

computational algorithm is a linear state-space model that

recursively estimates the properties of a system. Specifically,

any future state is predicted based on the current measures,

and, once progressed in time, this past guess can be updated by

considering the actually measured, noisy data. Refining the

prediction model with each time step in this way seems an

appropriate strategy to decode the continuous, repetitive move-

ments of high complexity used in the task at hand. One concern

discussed by the authors directly relates to the rhythmic be-

havior as it could potentially result in false positive correlations

using the “feedback loop” design of Kalman filters. That is,

knowledge from prior movements could give decoding informa-

tion even when the present brain activity would be non-

informative. The elegant control analysis for this issue was that

randomizing phase of lf-LFPs post hoc dramatically reduced

cross-correlation values, i.e., prediction was less accurate.

Therefore, one can assume a true dependence between brain

oscillations and movement parameters.

Having revealed that lf-LFPs generally provide sufficient

information about the executed movement, the authors next

examined the relation between these field potentials and spiking

activity. It is generally believed that LFPs reflect mem-

brane potentials at dendritic synapses equivalent to incoming

information. In contrast, spiking clearly denotes the output of

a neuron. Thus, a widely accepted concept is that LFPs lead to

spiking output. This is, of course, an oversimplified view
because nonlinear transformation of multiple synaptic inputs to outgoing action potentials takes place. As a consequence, we cannot expect a fixed relation between LFP and spiking for different tasks and brain areas. One remarkable outcome of the present study was that individual IF-LFP channels on average revealed higher decoding across the neuron population in motor cortex than single spiking units. This may seem surprising at first glance as the output of cells in motor areas should provide the most accurate estimation of movement. When considering the overall best unit or channel, however, the reverse was true: the “optimal” single spiking cell mostly provided higher fidelity. These findings confirm that spiking activity of single neurons reflects more specific local activity, whereas field potentials are broadly tuned to movement-related processing over neuronal populations.

Yet, a standard procedure is to combine information of several sites within an electrode grid so that the question arises how well such pooled neural activity can be decoded. Here, Bansal et al. (2011) used two approaches: 1) the “best case” procedure repeatedly added a single LFP channel or unit that provided the highest independent information gain while 2) in the “average case” procedure, a certain number of channels/units was randomly picked for 100 iterations. As a first result, pooled units outperformed IF-LFPs in the best case analysis. Interestingly, the average case revealed ambiguous trends for the two monkeys but decoding performance was generally lower compared with best case. The authors concluded that the pooled population of spiking units would give richer kinematic information. Moreover, they speculated that differences to previous findings that showed equal or higher decoding from LFPs (Mehring et al. 2003) were mainly due to increased number of electrodes in their current study. The crux of this interpretation, in my view, is the method they used to pool units. First, consider that the nature of LFPs is that of a coarser signal, implying a lesser degree of independence between single recording sites. In fact, the authors themselves presented increased pair-wise correlation for LFP channels compared with units’ correlation. This is well in line with another study that could decode movement target direction from spatial correlation patterns of LFP signals (Ince et al. 2010). Second, there were generally more single units available in the current experiments than LFP channels (up to 200%, see their Fig. 6A). Both of these constraints will significantly boost the chance of adding a highly informative spiking cell to the pool of already selected cells, while this is not necessarily true for LFP channels. Although one can agree on the finding that single units may substantially benefit from the suggested best case evaluation, the authors could have compared equal numbers (i.e., the least common denominator of 48 channels/units in their experiment) to further clarify their somewhat conflicting evidences. Additionally, future studies will have to assess how stable extracted information is over longer time periods, e.g., over months. Exciting new insights demonstrated that 10–15 selected single units can actually reach a state of consolidation so that stable neuroprosthetic control is, in principle, possible (Ganguly and Carmena 2009).

The aforementioned decoding from brain activity also raises a more fundamental issue, that is, whether the underlying neurophysiological signals are reflecting sensory or motor processing. This is extremely relevant to BMI research, as most studies have sought for a predictive neuronal signal that could be used as a driver to control external devices. While this approach seems logical per se, it neglects the fact that movements always produce interaction with our environment and thus result in rich sensory information closely associated with motor output. Bansal et al. (2011) contributed to this open question in two ways. First, LFPs could not only predict spiking output in the future but were even more useful in reconstructing past spike events. This likely indicates that besides dendritic input, local output processing also contributes to generation of LFPs. Second, and somewhat conflicting, decoding of movements was always more efficient when kinematics preceded neuronal signals around 150 ms. In other words, both LFPs and single unit spiking were dominated by sensory feedback from the moving limb. In conclusion, a strict dissociation between sensory input and motor output seems, therefore, not reasonable.

One appealing solution to the issue of sensory vs. motor processing, in my view, is a model of dynamic sensorimotor interaction. The main idea is that a descending motor signal might concurrently act as a periodic “test pulse” that produces a sensory volley (McKay 1997). During movement preparation without overt movements, such self-induced afferent feedback would inform sensorimotor brain areas about the current musculoskeletal state, a necessary step for preparing accurate movements. Support for this notion comes from a human study where increased premovement activity in somatosensory and motor cortices was accompanied by slightly higher muscle tone (Favorov et. al 1988). Beyond this early function, the same mechanism could also account for ongoing sensorimotor ad-
justments during movement execution. An example for this mode was observed in thalamo-cortical oscillations that temporarily aligned to exploratory whisker movements in rats (Nicolelis et al. 1995). The report at hand (Bansal et al. 2011) showed a similar phenomenon as LFP, summed spiking and kinematics revealed tight rhythmic coupling in the low-frequency range (see their Fig. 1). Despite preliminary evidence for significant phase-locking between single units and LFPs, the authors did not test whether this coupling is crucial for decoding of motor behavior. Therefore, instead of using spikes binned in fixed intervals with respect to movement onset, a valuable procedure would have been to align to the peak of lf-LFP oscillations (for details, see Reimer and Hatsopoulos 2010). In this way, slow oscillations set the framework and precise phase-locking of single unit spiking to this rhythm would ensure that sensory information from the limb arrives in a common state of depolarized cortical neurons. This in turn would promote efficient sensorimotor processing and integration over distributed motor areas.

In summary, Bansal et al. demonstrated highly efficient decoding of reach and grasp kinematics in 3-D space from local field potentials. Their results suggest that lf-LFPs mainly reflect sensory information from the moving limb but also can be used to predict kinematics. This finding potentially could soften the boundaries that commonly exist between sensory and motor research lines. Future decoding approaches may thus benefit from recording lf-LFPs along with local spiking activity. Given that the precise temporal relation between both signals can be further clarified, such combined signal analysis may ultimately lead to improved applications in BMI research.

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