

Journal Club

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Temporal Encoding of Movement in Motor Cortical Neurons

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Review of Hatsopoulos et al. (<http://www.jneurosci.org/cgi/content/full/27/19/5105>)

Although it is broadly accepted that primary motor cortex (M1) plays a critical role in controlling volitional arm movement, considerable debate remains about the details of the implementation. Most studies assume that individual M1 neurons encode time-invariant movement features within a direction, velocity, or force coordinate frame (Scott, 2003). For example, a neuron that encodes hand movements away from the body does not change this relationship over the duration of a reach.

A recent article in *The Journal of Neuroscience* by Hatsopoulos et al. (2007) questions this notion of static encoding. The authors contend that M1 neurons encode time-dependent trajectories, termed "pathlets," that can be temporally extensive and spatially complex. Within their model, a neuron that encodes hand movements away from the body early in a reach may encode movements toward the body at some later time. Although the concept of pathlets, or motor fragments, has a long history in motor control (Leyton and Sherrington, 1917), Hatsopoulos et al. (2007) are the first to provide a sophisticated model that calculates pathlet shape and duration. Furthermore, they show that pathlets better capture the tuning

properties of M1 neurons than previous models using time-invariant movement features.

Hatsopoulos et al. (2007) trained three macaque monkeys to perform various reaching tasks while neural activity was recorded from the arm area of motor cortex with a microelectrode array. In the first task, monkeys made hand movements from a central location to one of eight peripheral targets (5–7 cm distance). The results confirmed previous observations that preferred hand directions of M1 neurons change over the course of a center-out reach (Sergio and Kalaska, 1998). This confirmation is important because it provides empirical evidence that preferred directions (PDs) change over time. In fact, Hatsopoulos et al. (2007) report that many neurons exhibited dramatic rotations in PD over a 400 ms time window [Hatsopoulos et al. (2007), their Fig. 1A (<http://www.jneurosci.org/cgi/content/full/27/19/5105/F1>)], a result inconsistent with a static movement-encoding model. PDs were also calculated in a second reaching task called random target pursuit (RTP). In RTP, movements are made to sequentially appearing targets located randomly in the workspace, thus requiring a richer set of movements than during center-out reaching [Hatsopoulos et al. (2007), their Fig. 1B (<http://www.jneurosci.org/cgi/content/full/27/19/5105/F1>)]. Impressively, when the authors calculated the PD of the same neuron during both tasks, the changes in PD were qualitatively similar [Hatsopoulos et al. (2007), their Fig. 1D ([\[jneurosci.org/cgi/content/full/27/19/5105/F1\]\(http://www.jneurosci.org/cgi/content/full/27/19/5105/F1\)\)\].](http://www.</p>
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However, the novelty of this study is not merely confirming that PDs change with time; rather, it is the proposal of an encoding model in which the probability of a neuron spiking is related to the shape and duration of a particular time-dependent trajectory. The authors formalized this proposal with a general linear model that relates a neuron's conditional spiking probability to the scalar product of the current trajectory and the neuron's preferred trajectory, both of which develop over some predefined time window [Hatsopoulos et al. (2007), their Eq. 7 (<http://www.jneurosci.org/cgi/content/full/27/19/5105/#FD7>)]. Simply put, a neuron will fire most robustly when the arm moves through its preferred spatio-temporal trajectory. To find this ideal trajectory, the authors sampled RTP movements at 50 ms intervals and related them to the spikes of individual neurons. At each sample point, the procedure noted whether or not the neuron spiked and then extracted the surrounding trajectory within a window around the spike. By looking through thousands of available trajectories, the authors determined the shape and duration of the trajectory that was most likely associated with a spike.

The proposed encoding model performed well on several levels. First, pathlets were relatively stable over time and space because preferred trajectories calculated at different times or in different parts of the workspace yielded correlation coefficients of 0.75 and 0.56, respectively [Hatsopoulos et al. (2007), their Fig. 3

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(<http://www.jneurosci.org/cgi/content/full/27/19/5105/F3>). Second, temporally extensive pathlets were more accurate in predicting the occurrence of a spike than shorter pathlets that approach a time-invariant representation [Hatsopoulos et al. (2007), their Fig. 4 (<http://www.jneurosci.org/cgi/content/full/27/19/5105/F4>)]. Last, when decoding neural activity (predicting movement from the population of M1 neurons), the pathlet approach improved estimates of instantaneous hand direction by $\sim 10^\circ$ on average compared with population vector methods.

Although these results are intriguing, Hatsopoulos et al. (2007) leave several issues unresolved. First, pathlets generated in hand-based coordinates are strikingly circuitous, often radically changing repeatedly and rapidly over their 400 ms duration [Hatsopoulos et al. (2007), their Fig. 2C (<http://www.jneurosci.org/cgi/content/full/27/19/5105/F2>)]. This is in contrast to the qualitatively simpler pathlets generated in joint coordinates [Hatsopoulos et al., their Fig. 2E (<http://www.jneurosci.org/cgi/content/full/27/19/5105/F2>)]. Given that both models result in a statistically indistinguishable quality of fit and that simpler models are less prone to overfitting, it is not clear why the authors conclude that hand- and joint-based models are equally appropriate.

A second issue stems from the possibility that pathlets may reflect the complex dynamics of the musculoskeletal system

such as the force-length and -velocity dependence of muscles. In fact, modeling studies have revealed that these features can lead to correlations between M1 activity and hand movement, although no such relationships are explicitly specified (Todorov, 2000). It would be interesting to apply the proposed encoding model to generate pathlets relating muscle activity and movement trajectories. If muscle activity, which contains no higher-order representations, also results in spatially complex and time-varying preferred trajectories, how could one discern whether M1 neurons explicitly encode pathlets or whether they encode low-level time-invariant representations that are subsequently filtered by musculoskeletal dynamics?

Finally, the authors conclude that trajectory encoding represents a unified framework for understanding M1 function. Although we do not exclude the possibility that M1 neurons actually generate particular pathlets, it is unclear that any correlational technique, no matter how sophisticated, can establish such a link (Fetz, 1992; Robinson, 1992; Churchland and Shenoy, 2007). Rather, what is needed is a mechanistic model that specifies the causal relationship between M1 activity and motor behavior (Todorov, 2000).

In summary, Hatsopoulos et al. (2007) provide a timely examination of the temporally complex nature of M1 neurons (Churchland and Shenoy, 2007). The authors provide a sophisticated encoding

model and experimental paradigm to extract the time-dependent movement trajectories that best correlate with M1 activity. Furthermore, they demonstrate that incorporating temporal complexity improves both spike prediction and movement decoding when compared with currently used methods that will likely improve the functionality of various brain-machine interfaces.

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