

Journal Club

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Baseline Motor Cortex Activity Contains an Internal Model Representation

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Review of Stavisky et al.

As we age, our bodies change, for better or for worse. In response, our nervous system must adapt to its new physical relationship with the world. One way to handle the ever-changing interaction between our bodies and our environment is to create and update internal models that relate neural activity to movement (Shadmehr et al., 2010). In other words, these models represent how the body is expected to respond when a specific motor command is issued. By keeping track of this relationship, the nervous system can counter environmental change by altering motor commands on subsequent trials to produce the desired movement. This process is termed adaptation.

While brain structures, such as the cerebellum, have been implicated in the learning and storage of adapted motor responses (Wolpert and Miall, 1996), motor command structures, such as motor cortex, are thought to be responsible for implementation of the updated motor plan (Guo et al., 2015). Thus, conventional wisdom suggests that internal model information should be present in motor cortex during movement preparation and execution (Mandelblat-Cerf et al., 2011). In a recent paper, Stavisky

et al. (2017) examined neural activity before a motor plan was selected (“baseline activity”) and asked whether representations of a recently adapted internal model existed in motor cortex.

The authors trained 2 monkeys to perform a visuomotor forelimb adaptation task while they recorded neural activity in motor cortex (primary motor and premotor cortex). The animals performed arm movements that were tracked in real time and translated into cursor movement on a screen. Animals were rewarded after successful movement to a central starting location, and again after they moved the cursor to one of eight radial target locations that appeared on the screen. This two-part instruction allowed the researchers to analyze neural activity before the radial target appeared, which they refer to as “baseline” or “pretarget” activity. To induce adaptation, the gain scaling between arm velocity and cursor velocity was modified: 0.5 gain, in which cursor velocity was relatively slow, resulted in faster arm movements to obtain reward more quickly, whereas 2.0 gain, in which cursor velocity was relatively fast, resulted in slower adapted movements to avoid target overshoot. Finally, the researchers chronically implanted multielectrode arrays into motor cortex to measure neural activity.

Stavisky et al. (2017) first sought to determine whether motor cortex activity contains a representation of the visuomotor adaptation. To do this, they measured differences in the population firing patterns measured under different adaptation gain

conditions. Unsurprisingly, the differences between behavioral conditions were large during movement, consistent with the known contribution of motor cortex to kinematic control. However, when analyzing baseline activity (before the target appeared), there were significant differences in neural activity patterns between the two gain conditions. Population firing rate distances initially decreased during the center-hold epoch, and then increased before presentation of the radial target. The significant differences observed during baseline neural activity implies that motor cortex contains unique information related to the current visuomotor gain, separate from the specific motor plan about to be executed. However, further experiments and analyses were needed to confirm that these neural activity differences meaningfully represented properties of adaptation.

The authors followed up on these results by asking how the neural correlates of adaptation changed trial-by-trial. Instead of presenting a single, consistent level of adaptation (e.g., 0.5 gain) during a block, they randomly varied the gain on each trial, analyzing the data on the subsequent trials for effects on movement or neural activity. Random gain blocks resulted in intermediate effects: after 0.5 gain trials, the limb moved faster than normal, but not as fast as in the fully adapted constant gain 0.5 block. Thus, the authors created a range of “adaptation levels,” with random gain trials resulting in intermediate levels of adaptation compared with constant gain trials. Stavisky

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et al. (2017) reasoned that, if the differences in motor cortex activity identified above represent visuomotor gain, then intermediate adaptation levels (observed in random gain trials) should correlate with firing rate patterns that are “intermediate” to the two constant gain conditions. To test this idea directly, they calculated a “cursor gain axis” in neural state space, defined by the vector connecting the neural population activity centroids of the constant gain 0.5 and constant gain 2.0 conditions. They then projected single-trial neural activity onto the cursor gain axis and found an ordered, collinear arrangement of the average projection magnitude for each condition. In other words, movement in neural state space along the cursor gain axis was correlated with the current state of visuomotor gain; if the animal recently experienced 0.5 gain, it was more likely to move fast on the next trial, and also more likely to display neural activity similar to a constant gain 0.5 trial. The ordered arrangement of motor cortex activity patterns during different levels of visuomotor adaptation strongly implies that baseline activity contains some representation of an internal model of visuomotor gain.

Finally, the authors sought to determine whether the identified neural activity patterns were important for movement, and whether their analysis method could be applied to improve brain-machine interfaces (BMI). First, they tested whether baseline activity during a specific trial could predict the arm’s upcoming velocity. They found that projection of baseline neural activity onto the cursor gain axis explained ~25% of the variance in reach velocity, supporting the hypothesis that the cursor gain axis is a meaningful measure of the current level of visuomotor adaptation. Next, they furthered this result by testing the relevance of their discovery to BMI. By collecting neural data and projecting onto a defined cursor gain axis, BMI devices could detect an incorrect estimate of movement gain and correct it in real time. The authors conducted an offline proof-of-concept experiment in which they modified cursor gain based on baseline neural activity. This procedure reduced positional overshoot of the target that occurred on random gain 2.0 trials, when the monkey underestimated the speed of the cursor. In the future, this algorithm could be used for individuals with BMI to detect an underestimation of artificial limb gain and correct it in real time.

These results raise two questions: where is the internal model learned, and where is it stored? Because electrical recording experi-

ments are correlational by nature, this study cannot offer any mechanistic insight into the generation, maintenance, or alteration of the internal model itself. One possibility mentioned by the authors is that the cerebellum learns the internal model and sends it to motor cortex (via thalamus) during baseline activity to “ready” the system for generation of the specific motor plan (Stavisky et al., 2017). An alternative possibility is that the cerebellum continuously updates motor cortex with an internal model of body movement; that way, the information relating motor commands to body position is always available for movement generation. Future experiments using rodent models could directly test via circuit manipulations whether cerebellar input to motor cortex is necessary for motor adaptation. Furthermore, electrophysiological recordings in motor cortex could reveal how manipulation of cerebellar input to motor cortex affects the generation of adaptation-relevant neural activity patterns (e.g., projection onto the cursor gain axis in this study).

The results and insightful interpretations garnered by this work are tempered by several inherent limitations in revealing the nature of the internal model under study. Internal models, defined by the authors as “the information. . . that movement-related areas use to generate motor commands appropriate to the current physical relationship between the nervous system and the effector,” can take on unique functional roles (Stavisky et al., 2017). For example, forward models calculate a prediction of future movement from a motor command, whereas inverse models calculate the necessary motor commands to create a desired kinematic effect (Wolpert et al., 1998). Because the results from Stavisky et al. (2017) are consistent with both forward and inverse models, future work could attempt to determine the functional relationship between internal model activity and ongoing movement, which is expected to depend directly on the internal model implementation.

In addition, it remains unknown whether internal models, including the one identified by Stavisky et al. (2017), operate on a specific movement-related parameter. In the current study, adaptation-related changes in baseline motor cortex activity predicted upcoming reach velocity, suggesting that arm velocity was an important neural control parameter during the task and may be important for arm movements in general (Yttri and Dudman, 2016). Interestingly, population encoding of a forward model of movement velocity was recently demonstrated in the cerebellum (Herzfeld et al.,

2015). An alternative to parameter control is presented by the authors in the present study, who argue for a dynamical systems perspective of motor cortex activity, in which encoding of movement parameters is deemphasized for analysis of how neural activity patterns produce temporal sequences required for movement (Shenoy et al., 2013). Finally, as the current study was limited to examining the effects of motor adaptation, it remains unknown what other aspects of the internal model may be encoded by baseline motor cortex activity.

Overall, Stavisky et al. (2017) demonstrate that baseline motor cortex activity patterns (i.e., before a specific motor plan is generated) represent some aspect of an internal model relating motor commands to movement. Moreover, adaptation of the internal model occurs on a trial-by-trial basis, demonstrating the incredible responsiveness of the nervous system to environmental change. As we continue to learn about the basic neural strategies underlying motor control, we can begin to ascribe functional relevance to the circuits under study, paving the way for technological cures of neurological disease.

References

- Guo JZ, Graves AR, Guo WW, Zheng J, Lee A, Rodríguez-González J, Li N, Macklin JJ, Phillips JW, Mensh BD, Branson K, Hantman AW (2015) Cortex commands the performance of skilled movement. *Elife* 4:e10774. [CrossRef Medline](#)
- Herzfeld DJ, Kojima Y, Soetedjo R, Shadmehr R (2015) Encoding of action by the Purkinje cells of the cerebellum. *Nature* 526:439–442. [CrossRef Medline](#)
- Mandelblat-Cerf Y, Novick I, Paz R, Link Y, Freeman S, Vaadia E (2011) The neuronal basis of long-term sensorimotor learning. *J Neurosci* 31:300–313. [CrossRef Medline](#)
- Shadmehr R, Smith MA, Krakauer JW (2010) Error correction, sensory prediction, and adaptation in motor control. *Annu Rev Neurosci* 33:89–108. [CrossRef Medline](#)
- Shenoy KV, Sahani M, Churchland MM (2013) Cortical control of arm movements: a dynamical systems perspective. *Annu Rev Neurosci* 36:337–359. [CrossRef Medline](#)
- Stavisky SD, Kao JC, Ryu SI, Shenoy KV (2017) Trial-by-trial motor cortical correlates of a rapidly adapting visuomotor internal model. *J Neurosci* 37:1721–1732. [CrossRef Medline](#)
- Wolpert DM, Miall RC (1996) Forward models for physiological motor control. *Neural Netw* 9:1265–1279. [CrossRef Medline](#)
- Wolpert DM, Miall RC, Kawato M (1998) Internal models in the cerebellum. *Trends Cogn Sci* 2:338–347. [CrossRef Medline](#)
- Yttri EA, Dudman JT (2016) Opponent and bidirectional control of movement velocity in the basal ganglia. *Nature* 533:1–16. [CrossRef Medline](#)