

The Importance of Planning in Motor Learning

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<http://dx.doi.org/10.1016/j.neuron.2016.11.003>

The addition of differentiating follow-through motions can facilitate simultaneous learning of multiple motor skills that would otherwise interfere with each other. In this issue of *Neuron*, Sheahan and colleagues (2016) demonstrate that it is the preparation, not execution, of different follow-through movements that separates motor memories and reduces interference.

Suppose you are a daring mountain biker practicing to jump off a ramp. You've spent months perfecting your technique, learning to build up speed, to navigate the ramp, and to gracefully negotiate the landing. Now, you feel confident enough to attempt a new trick, a backflip performed mid-air. To give yourself sufficient time aloft for the maneuver, you'll need a steeper ramp to launch you higher into the air (Figure 1A). You could modify your existing ramp for the new trick. Alternatively, you might construct a second, steeper ramp elsewhere and follow a distinct downhill path to this new ramp from a different starting point. Building a second ramp has the advantage that any adjustments made to the second ramp won't interfere with your performance of the basic jump off the original ramp, sans mid-air acrobatics. In this issue of *Neuron*, Sheahan and colleagues demonstrate that the motor system may employ an analogous strategy, wherein distinct motor plans engaged during movement preparation (starting points) can be independently modified by motor learning (adjustments to the ramps), permitting multiple motor skills to be learned without interference.

The ability to learn new motor skills without interfering with old ones is essential to our ability to acquire and maintain a broad motor repertoire. During learning, the motor system makes a series of adjustments to the motor plans and control processes engaged during movements. The knowledge acquired during this process—the dynamics of the body and the environment, along with effective control strategies for dealing with them—is re-

tained as a motor memory. This learning can be precisely operationalized in the laboratory setting by asking human participants to make reaching movements while holding the handle of a manipulandum that generates a force field (Shadmehr and Mussa-Ivaldi, 1994). Through time, the participant becomes familiar with the structure of this force field and learns to generate predictive compensatory forces that lead to the desired movements straight to the target. These predictive forces can be directly observed by constructing a force channel that constrains the hand to the direct path toward the target. If the force field is later removed, the learned structure of the environment can be measured as aftereffects, where the predictive forces curve the hand trajectories in the opposite direction of the now-absent force field.

The representation of the force field dynamics is believed to be learned through small adjustments to a motor memory after each trial. However, if the adjustments made to the memory during learning cancel out, the learning process is ineffective. For example, if participants are asked to move through a curl force field whose direction alternates or switches randomly from trial to trial, the opposing learning directions interfere and neither environment is learned. This interference can be substantially reduced by associating each field with a unique contextual cue, including some classes of sensory cues and differences in the physical or visual state of the limb during movement (Howard et al., 2013). Recently, it was demonstrated that associating each field with a unique preceding lead-in move-

ment (Howard et al., 2012) or subsequent follow-through movement (Howard et al., 2015) substantially reduces interference. These experiments collectively suggest that appropriate contextual cues can segregate learning of the opposing force field into distinct motor memories, enabling context-appropriate compensatory forces to be generated in each context.

In this issue of *Neuron*, Sheahan and colleagues perform a set of experiments that provide fundamental new insight into the mechanism by which separate motor memories are independently learned and recalled. Through clever experimental design, the authors dissociate the role of motor planning from that of execution in separating motor memories associated with distinct environmental dynamics. In their task, participants move a manipulandum toward a primary target through a velocity-dependent curl force field whose direction randomly switches across trials. The direction of the force field was perfectly associated with the location of a secondary reach target, located northeast or northwest of the first target. One group of participants ("full follow-through") was shown both the primary and secondary target and asked to move to both targets in succession (Howard et al., 2015). As expected, the follow-through movements to the different secondary targets successfully separates the motor memories for the two fields, reducing interference and facilitating learning for this group. In contrast, a second group ("no follow-through") did not perform any follow-through movements and was unable to

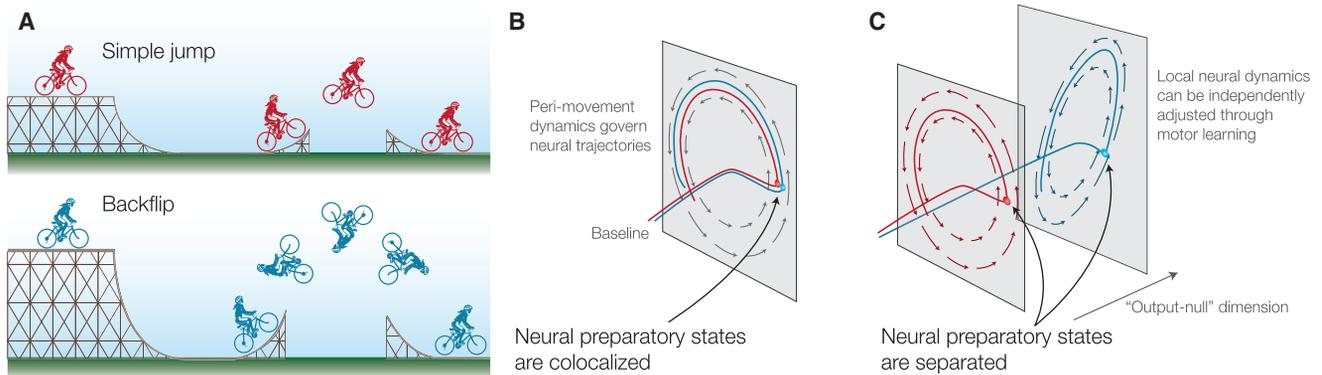


Figure 1. Separated Preparatory States Enable Independent Motor Learning

(A) Illustration of two bicycle jumps with different midair maneuvers, analogous to reaches with different follow-through movements. Here, the construction of a second, higher starting platform and steeper ramp facilitates the more sophisticated backflip. The physical dynamics of the bicycle are loosely analogous to those of neural activity, initiated from two different preparatory initial conditions.

(B) Schematized neural trajectories in which planning brings the neural population activity state (red and blue dots) to the same location in neural state space. The neural dynamics (gray vector field) that govern the peri-movement trajectories are shared, such that adjustments to these dynamics through motor learning interfere.

(C) Schematized neural trajectories in which planning brings the neural population activity state to separate locations in state space. The local dynamics around each neural trajectory (red and blue vector fields) can be independently adjusted, facilitating independent motor learning.

learn either environment due to interference, even though the secondary target location was visible before each trial and cued the direction of the field.

To dissociate the contributions of movement planning and execution, two additional groups were included. For a third group ("execution only"), the secondary target appears only mid-movement to the primary target, such that the direction of the follow-through movement and the force field is not available during the preparation period before the initial movement. In this setup, a participant could potentially associate the two fields with the distinct follow-through movements, even if this information would not be immediately available during learning trials. In probe trials with a force channel, however, the secondary target was presented at the same time as the initial target, such that the participant could theoretically recall the motor memory associated with the cued follow-through movement and generate the appropriate compensatory forces. However, this was not the case: this group showed no significant reduction in interference relative to the "no follow-through" group. Evidently, merely executing the different follow-through movements associated with each field is insufficient to separate the motor memories.

Instead, using a fourth group of participants ("planning only"), Sheahan and

colleagues demonstrate that information about the follow-through movement must be available before the initial movement is executed in order to dissociate the motor memories and facilitate learning of both fields. In this group, both targets are presented simultaneously, but the secondary targets were extinguished during the initial movement, and participants were instructed not to perform the subsequent movement when this occurred. To encourage planning of the follow-through movement, in force channel trials (four of twelve in each block), the secondary targets were not extinguished and follow-through movements were performed. In this group, even though the follow-through movements were never actually performed when the force field was present (non-channel trials), interference between the memories was substantially reduced and learning was similar to the "full follow-through" group. Collectively, these results demonstrate that it is motor planning, and not execution, that is responsible for the establishment of multiple separate memories. This suggests that a distinct motor memory is engaged during the preparation stage and that the subsequently experienced force field will modify only that particular motor memory.

One intriguing aspect of these findings is that they square nicely with recent work on motor cortical neurophysiology in non-human primates. This line of work

takes a dynamical systems perspective of motor cortex, refocusing on its role as a temporal pattern generation circuit to support movement production through spinal cord circuitry (Shenoy et al., 2013). These time-varying patterns are generated by the dynamics of motor cortical circuits and are seen in the activity of neuronal populations. To produce the correct patterns for a given movement, the dynamical system in motor cortex must be seeded with an appropriate initial condition, which appears to occur during the preparation phase. As we learn to compensate for a force field, synaptic plasticity adjusts the dynamical trajectory followed by the neuronal population activity during motor execution, leading to the production of new forces at each point in time.

Within this framework, if the modifications due to both fields are made around a single dynamical trajectory, initiated from the same preparatory neural activity state, interference will occur (Figure 1B). In Sheahan and colleagues' experiments, the distinct, planned follow-through movements likely bring the motor cortical population activity to two separate preparatory states, which lead into two separate dynamical trajectories during movement (Figure 1C). Learning-induced changes could then modify the distinct, local dynamics around each trajectory independently, which can then be

recalled during subsequent movements that invoke the appropriate preparatory state. Returning to our bike ramp analogy, by constructing a second ramp and digging out a new approach to the ramp designed for the new trick you wish to learn, you can independently modify this second ramp as needed to adjust your speed approaching the ramp. It appears the motor system employs a similar strategy, exchanging the initial position and trajectory of the bike for those of the neural population activity state and leveraging synaptic plasticity in lieu of a shovel.

Several experiments have characterized some of the neurophysiological consequences of motor learning in similar force field reaching tasks in non-human primates. Changes to neural responses during motor learning have been observed in primary motor cortex (M1), dorsal and ventral premotor cortex (PMd and PMv), and supplementary motor area (SMA) (e.g., Xiao et al., 2006). These reports have primarily analyzed neural responses through the lens of tuning curves (response as a function of reach direction) and preferred directions. Through this lens, there is an overall average trend for neurons to rotate their directional tuning curve in a direction concordant with compensating for the curl field being learned.

Nevertheless, the changes appear confusing and heterogeneous at the level of individual neurons. Some of the changes observed in individual, so-called memory neurons persist through a subsequent washout period when the force field is removed. One could hypothesize that although the instantaneous relationship between neural tuning and movement direction is unreliable, learning-induced changes will become clearer when viewed as systematic modifications to the neural population activity trajectory. The time would appear ripe to revisit these neurophysiological findings from a dynamical systems perspective of motor cortex.

When multiple motor memories are learned or recalled independently, an intriguing possibility is that learning exploits “output-null” dimensions in motor cortex to separate memories. These extra dimensions exist because there are many more neurons in motor cortex (and linearly independent patterns of neural activity)

than there are skeletal muscles to control. Recently, it was demonstrated that motor cortex uses some of these output-null dimensions for motor preparation and local computation, allowing firing rates to change without affecting downstream circuitry or causing movement of the body (Kaufman et al., 2014). This extra neural flexibility also enables the motor cortex to produce the same movement even as its neural population activity state traverses distinct neural trajectories, as is the case for identical reaches performed with and without a preceding delay period (Ames et al., 2014). We anticipate that similar neural mechanisms enable our ability to recall distinct motor memories even when producing the same kinematic movement (Hirashima and Nozaki, 2012). One could speculate that neuronal variability, thought to enable motor learning through exploration (Tumer and Brainard, 2007), would produce a spread of preparatory states that could be subject to partially independent motor learning as well.

Another promising connection between motor behavior and physiology lies in the connection with sequences of motor movements and the separation of motor memories associated with these sequences. SMA, PMd, PMv, and M1 all show sequence-related neural activity, in which individual neurons can encode the entire sequence, specific movements within a sequence, or transitions between specific successive movements. Recently, Lu and Ashe (2015) demonstrated that when a single movement within an over-learned sequence is changed, sequence-specific M1 activity is completely disrupted. This suggests that sequential memories are encoded as a cohesive entity, rather than as a series of individual sub-movements. Future experiments in non-human primates could further elucidate this close link between the neurophysiological encoding of motor sequences with sequence-specific motor memories. Moreover, sequence learning could be an especially interesting substrate with which to probe the interactions between cortical motor areas and the cerebellum and basal ganglia, which are critically important for skill acquisition and motor control.

Bridging the gap between computational theories of motor control and their

neural substrate is a challenging but important goal for the field of motor neuroscience. This gap has arisen, in part, because the mapping between the implementation level and the algorithmic and computational levels of description is not one to one; there are often many potential neural implementations of any particular computation. Nevertheless, insightful experiments like those conducted by Sheahan, Franklin, and Wolpert can make direct predictions linking the neural dynamics of motor cortical implementation with the computations of motor learning. One can envision many future experiments that leverage this rich body of theoretical and computational work alongside novel tools for observing, perturbing, and modeling neural populations. This approach is likely to yield key insights into the mechanisms of motor learning and control.

ACKNOWLEDGMENTS

This work was funded by DARPA NEUROFAST (W911NF-14-2-0013; D.J.O. and K.V.S.) and the NIH PIONEER award (8DPIHD075623; K.V.S.).

REFERENCES

- Ames, K.C., Ryu, S.I., and Shenoy, K.V. (2014). *Neuron* 81, 438–451.
- Hirashima, M., and Nozaki, D. (2012). *Curr. Biol.* 22, 432–436.
- Howard, I.S., Ingram, J.N., Franklin, D.W., and Wolpert, D.M. (2012). *J. Neurosci.* 32, 12756–12768.
- Howard, I.S., Wolpert, D.M., and Franklin, D.W. (2013). *J. Neurophysiol.* 109, 2632–2644.
- Howard, I.S., Wolpert, D.M., and Franklin, D.W. (2015). *Curr. Biol.* 25, 397–401.
- Kaufman, M.T., Churchland, M.M., Ryu, S.I., and Shenoy, K.V. (2014). *Nat. Neurosci.* 17, 440–448.
- Lu, X., and Ashe, J. (2015). *Eur. J. Neurosci.* 42, 2172–2178.
- Shadmehr, R., and Mussa-Ivaldi, F.A. (1994). *J. Neurosci.* 14, 3208–3224.
- Sheahan, H.R., Franklin, D.W., and Wolpert, D.M. (2016). *Neuron* 92, this issue, 773–779.
- Shenoy, K.V., Sahani, M., and Churchland, M.M. (2013). *Annu. Rev. Neurosci.* 36, 337–359.
- Tumer, E.C., and Brainard, M.S. (2007). *Nature* 450, 1240–1244.
- Xiao, J., Padoa-Schioppa, C., and Bizzi, E. (2006). *Exp. Brain Res.* 168, 106–119.