

## Neural Population Dynamics Underlying Motor Learning Transfer

### Highlights

- Covert learning via a brain-machine interface transfers to overt reaching behavior
- Covert learning systematically changes motor cortical preparatory activity
- Covert and overt movements share preparatory neural states and facilitate transfer
- Covert and overt movements engage a similar neural dynamical system

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### In Brief

Vyas et al. ask whether learning “covertly,” without physical movements, can transfer to overt behavior. By using visuomotor perturbations, they show that covert and overt movements derive from a common neural substrate consisting of motor cortical preparatory activity that facilitates transfer of learning.

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## SUMMARY

Covert motor learning can sometimes transfer to overt behavior. We investigated the neural mechanism underlying transfer by constructing a two-context paradigm. Subjects performed cursor movements either overtly using arm movements, or covertly via a brain-machine interface that moves the cursor based on motor cortical activity (in lieu of arm movement). These tasks helped evaluate whether and how cortical changes resulting from “covert rehearsal” affect overt performance. We found that covert learning indeed transfers to overt performance and is accompanied by systematic population-level changes in motor preparatory activity. Current models of motor cortical function ascribe motor preparation to achieving initial conditions favorable for subsequent movement-period neural dynamics. We found that covert and overt contexts share these initial conditions, and covert rehearsal manipulates them in a manner that persists across context changes, thus facilitating overt motor learning. This transfer learning mechanism might provide new insights into other covert processes like mental rehearsal.

## INTRODUCTION

Understanding motor-related covert mental processes, such as imagined or intended movements, and mental rehearsal is tantalizing as these internal behaviors have been shown to exhibit varying degrees of motor learning transfer (Denis, 1985; Papaxanthis et al., 2002). Decades of human behavioral studies have shown that mental rehearsal can improve motor skills such as throwing darts or making free throws (Feltz and Landers, 1983), and mental rehearsal has also been shown to sometimes

aid in rehabilitation (Warner and McNeill, 1988; Buch et al., 2008; Saposnik et al., 2010; Silvoni et al., 2011). Working theories posit that motor learning transfer is a result of covert learning engaging neural population activity similar to that employed during overt practice. In support of this, “mirror neurons” in ventral premotor cortex have been shown to discharge both when actions are overtly performed and when they are observed (Rizzolatti et al., 2001). These results, however, are still debated (Hickok, 2009) and do not propose mechanistic hypotheses about why neural similarity is helpful for learning transfer.

This debate stems primarily from the fact that mental rehearsal, and covert processes in general, are difficult to define and even more challenging to experimentally study. They are open-loop hidden processes, where experimenters cannot directly observe the internal process or the trial-by-trial progression of learning. In this study, we present a covert process that enables a direct and real-time probe into this evolution, by “closing the loop.” We use a brain-machine interface (BMI), which takes as input neural activity from dorsal premotor and primary motor cortex. This neural activity is mapped through a fixed mathematical function, i.e., “decoder,” to produce a two-dimensional cursor movement. This defines a closed-loop system by which subjects receive visual feedback of the on-screen cursor, and the experimenters observe both the behavior and the evolving neural activity on a trial-by-trial basis. The BMI context elicits internal motor processes that share an end-goal with overt processes because subjects use the decoder (i.e., neural activity without overt movements) to make the same cursor movements as they will perform subsequently using arm movements. We constructed the decoder by associating the kinematics of automated cursor movements with neural activity recorded while subjects observed these movements (Gilja et al., 2012). This was done in contrast to using neural activity measured during overt movements. Previous findings have shown that neural signals involved in watching cursor movements are engaged in mental rehearsal and involve many of the same cells as when generating movement (Cisek and Kalaska, 2004).

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