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Learning new gait patterns: Exploratory muscle activity during motor learning is not predicted by motor modules ☆

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ABSTRACT

The motor module hypothesis in motor control proposes that the nervous system can simplify the problem of controlling a large number of muscles in human movement by grouping muscles into a smaller number of modules. Here, we tested one prediction of the modular organization hypothesis by examining whether there is preferential exploration along these motor modules during the learning of a new gait pattern. Healthy college-aged participants learned a new gait pattern which required increased hip and knee flexion during the swing phase while walking in a lower-extremity robot (Lokomat). The new gait pattern was displayed as a foot trajectory in the sagittal plane and participants attempted to match their foot trajectory to this template. We recorded EMG from 8 lower-extremity muscles and we extracted motor modules during both baseline walking and target-tracking using non-negative matrix factorization (NMF). Results showed increased trajectory variability in the first block of learning, indicating that participants were engaged in exploratory behavior. Critically, when we examined the muscle activity during this exploratory phase, we found that the composition of motor modules changed significantly within the first few strides of attempting the new gait pattern. The lack of persistence of the motor modules under even short time scales suggests that motor modules extracted during locomotion may be more indicative of correlated muscle activity induced by the task constraints of walking, rather than reflecting a modular control strategy.

1. Introduction

The degrees-of-freedom problem (Bernstein, 1967) is one of the long-standing problems in motor control – i.e., how does the motor system coordinate and control the numerous degrees of freedom in the body to produce goal-directed movement? One hypothesis is that the motor system groups muscles into functional units or motor modules and then controls each of these modules independently – cf. coordinative structures – (Easton, 1972; Kugler et al., 1980). In principle, this hierarchical organization could simplify the control problem since there is a reduction of the available degrees of freedom – i.e., instead of controlling the activity of each muscle independently, the nervous system only needs to control the activity of a smaller number of modules, each of which in turn regulates the activity of muscles within that module.

There have been several lines of evidence for the existence of motor modules in motor behavior. Initial approaches used simple pairwise correlation methods to infer that muscle activity of multiple muscles were correlated during tasks (Maier and Hepp-Reymond, 1995). More recent methods have used dimensionality reduction methods like PCA (Krishnamoorthy et al., 2003), factor analysis (Ivanenko et al., 2004) or non-negative matrix factorization (NMF) (d'Avella et al., 2003; Tresch et al., 1999), in which a single muscle may be part of more than one module. Evidence of motor modules has been provided in a wide repertoire of behaviors including balance (Ting and Macpherson, 2005; Torres-Oviedo and Ting, 2010), reaching (Cheung et al., 2009), isometric force production (Roh et al., 2012), and locomotion (Clark et al., 2010), with some of these papers providing evidence that that the

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composition of these motor modules is affected by neurological conditions such as stroke.

However, there has also been some debate about the evidence for such motor modules (Kutch and Valero-Cuevas, 2012). A central argument against inferring motor modules solely from statistical dimensionality reduction methods comes from examining the source of the correlations in the muscle activity – i.e. do the high correlations in activity seen in muscles within a module represent a neural control strategy or are they simply a by-product of simultaneous muscle activity due to task and biomechanical (i.e. "non-neural") constraints (Buchanan et al., 1986; Kutch and Valero-Cuevas, 2011)? Several modeling studies have shown that despite the large number of muscles present, the musculoskeletal system is not redundant for many tasks and therefore biomechanical constraints may lead to correlated muscle activity in certain portions of the workspace (Kutch and Valero-Cuevas, 2011). Furthermore, studies that have examined correlations in the variability of the muscle activation (which is less influenced by these task constraints when compared to the average muscle activation) have shown little support for the motor modules hypothesis (Ranganathan and Krishnan, 2012; Valero-Cuevas et al., 2009). One methodological caveat however is that variability in EMG is affected by low signal-to-noise ratios and therefore, it still remains unclear whether motor modules extracted by dimensionality reduction methods truly reflect a neural control strategy (see Fig. 1).

Given that there are several versions of the motor module hypothesis that either keep muscle activation patterns (Ivanenko et al., 2004) or muscle weightings invariant (Ting and Macpherson, 2005), our focus was restricted to the version where the muscle weightings in each motor module were invariant. Here, we tested one prediction of this particular hypothesis – i.e., if motor modules truly reflect a neural control strategy during a task, then there should be preferential exploration along these modules when attempting to learn a new variation of the task – i.e., the muscle activity during the initial phases of learning should be explained largely with the same motor modules as that observed during the original task. Previous studies have shown that the initial strategies that participants use to adapt to new tasks are heavily influenced by both habitual (de Rugy et al., 2012) as well as previously learned coordination strategies (Kobak and Mehring, 2012; Ranganathan et al., 2014). To test this prediction, we used a locomotion task where the novel task was to modify the kinematics during swing phase of locomotion. We specifically focused the manipulation on the swing phase and the associated hamstring activity because it is less constrained mechanically (since the foot is not in contact with the ground and has minimal interaction with the environment) and so there are different ways to change the hamstring muscle activation during the swing phase while still being able to walk. The hypothesis was that if motor modules are a neural control strategy, then the motor modules during initial phases of learning the novel gait pattern should resemble the motor modules during normal walking.

2. Methods

2.1. Participants

Participants ($n=7$) were healthy young males (age range 18–35 years) who were free of neurological or musculoskeletal injury. All participants were right-leg dominant as determined by their preferred leg for kicking a ball (Krishnan and Williams, 2009). Written informed consent was obtained from each participant and all procedures were approved by the Institutional Review Board at Northwestern University.

2.2. Equipment

Participants walked in a lower-extremity robotic exoskeleton (Lokomat, Hocoma, Switzerland). The Lokomat was configured to be in a "co-operative control mode", which essentially means that the participant had to actively walk in order to produce a walking pattern (i.e., the robot did not move the participant's legs passively) (Duschau-Wicke et al., 2010; Krishnan et al., 2013a). In addition, the stiffness of the robot was minimal in this mode so that participant could exert force against the robot and change the locomotion pattern if required. There was also a computer monitor in front of the participant which displayed the x–y position of the lateral malleolus in the sagittal plane (hereafter referred to as the "foot trajectory"). The foot trajectory was computed using a forward-kinematic model that uses the hip and knee joint angles recorded from the Lokomat (sampling rate$=$1000 Hz) and also the segment lengths of the thigh and shank (Krishnan et al., 2012).

Surface EMG signals (Motion Labs, Baton Rouge, LA) from 8 muscles on the right leg were recorded simultaneously. The muscles recorded were vastus medialis (VM), rectus femoris (RF), medial hamstring (MH), lateral hamstring (LH), tibialis

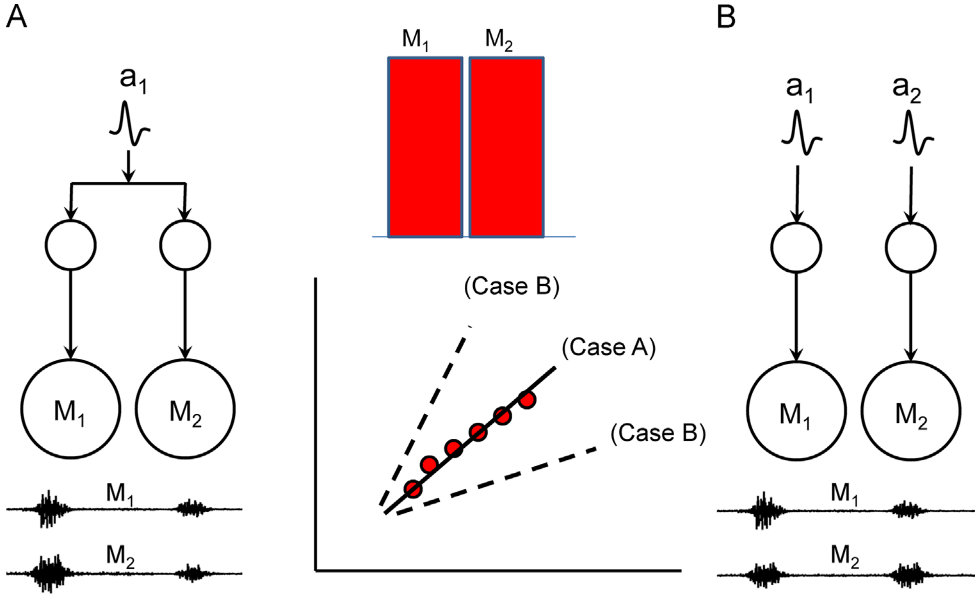

Fig. 1. Schematic of alternative models of correlated muscle activity. On the left panel (A), there is a common input to both muscles M1 and M2. On the right panel (B), the two muscles share independent inputs that are correlated. Dimensionality reduction methods in these two cases will yield identical muscle modes shown (central panel, top). However, these two conditions can be differentiated when learning a novel task-the EMG activity of the two muscles will still share the same relation in (case A), but may alter their relation in (case B) (central panel, top).