Exploring modular strategies for coordinating muscles during multidirectional human locomotion

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Abstract

Introduction: It has been hypothesized that the nervous system simplifies muscle coordination through modularity, using neural patterns to activate muscles in groups called synergies (Tresch et al., 1999; d' Avella et al., 2003; Ting and Macpherson, 2005; Ivanenko et al., 2006). Here we investigated how simple modular controllers based on invariant motor primitives (synergies or patterns) might generate muscle activity for multidirectional locomotion. Methods: We extracted motor primitives from unilateral electromyographic recordings of 25 lower-limb muscles during five multidirectional locomotor tasks, walking forwards, backwards, leftwards, rightwards and stepping in place. A subset of subjects also performed five variations of forward (unidirectional) walking: self-selected cadence, fast cadence, slow cadence, tiptoe and uphill (20% incline). Motor primitives were extracted from individual tasks using standard non-negative matrix factorization techniques, and also extracted collectively from all five multi- and uni-directional tasks in order to investigate shared primitives. We then assessed the ability of these primitives to reduce the dimensionality of control. To evaluate dimensionality we introduced the modular control ratio, defined as the minimum number of neural outputs needed to generate task-specific muscle activity divided by the number of muscles controlled. Results: When considering each task individually we found that modularity had the potential to reduce dimensionality compared to independent muscle control, by as much as two-thirds. However, these benefits were degraded when motor primitives were shared amongst locomotor tasks. For instance, the total number of shared synergies required to generate muscle activity for five multidirectional gaits was nearly as high as the number of muscles activated during each task. Shared patterns also exhibited limitations in reducing dimensionality, specifically related to their ability to accommodate tasks involving more rapid muscle contractions or longer cycle durations. Discussion: These results suggest that the utility of shared motor primitives may depend on if they can be flexibly adapted for specific task demands, for instance, by multisensory feedback or by inclusion in a more complex sensorimotor control architecture. However, specific neural mechanisms that explain or overcome the limitations of shared primitives remain to be posited and tested. Alternatively, the principal benefit of modularity may be related to other aspects of control (e.g., motor learning), rather than to dimensionality reduction during performance of a task. Regardless, our findings motivate the need for more sophisticated and testable formulations of modular control or alternative motor control hypotheses that help elucidate the neurophysiological basis for muscle coordination during locomotion.