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A balanced motor primitive framework can simultaneously explain motor learning in unimanual and bimanual movements

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ABSTRACT

Certain theoretical frameworks have successfully explained motor learning in either unimanual or bimanual movements. However, no single theoretical framework can comprehensively explain motor learning in both types of movement because the relationship between these two types of movement remains unclear. Although our recent model of a balanced motor primitive framework attempted to simultaneously explain motor learning in unimanual and bimanual movements, this model focused only on a limited subset of bimanual movements and therefore did not elucidate the relationships between unimanual movements and various bimanual movements. Here, we extend the balanced motor primitive framework to simultaneously explain motor learning in unimanual and various bimanual movements as well as the transfer of learning effects between unimanual and various bimanual movements; these phenomena can be simultaneously explained if the mean activity of each primitive for various unimanual movements is balanced with the corresponding mean activity for various bimanual movements. Using this balanced condition, we can reproduce the results of prior behavioral and neurophysiological experiments. Furthermore, we demonstrate that the balanced condition can be implemented in a simple neural network model.

1. Introduction

In our daily lives, we flexibly switch from unimanual to bimanual movements and vice versa (e.g., we unimanually manipulate a smartphone and bimanually manipulate a tablet). Although motor learning in unimanual and bimanual movements has been intensively investigated, distinct theoretical frameworks have been proposed for each type of movement. In the motor primitive framework (Donchin, Francis, & Shadmehr, 2003; Takiyama, 2015; Takiyama, Hirashima, & Nozaki, 2015; Thoroughman & Shadmehr, 2000; Yokoi, Hirashima, & Nozaki, 2011), a theoretical framework for motor learning, neural activities $A_i(\theta)$ are nonlinearly determined by the desired movement direction θ, and a linear combination of these activities determines motor command: $x(\theta) = \sum_{i=1}^{N} W_i A_i(\theta)$ (where N is the number of neurons). In this framework, the compatibility of nonlinear motor commands appropriate for nonlinear upper limb dynamics and linear learning curves in motor learning experiments, a characteristic of motor learning, can be explained (Donchin et al., 2003; Takiyama, 2015; Thoroughman & Shadmehr, 2000). An original motor primitive framework successfully reproduced the basic pattern of trial-dependent changes in the movement error and how motor learning can be generalized under changing kinematics (e.g., alterations in movement direction) (Donchin et al., 2003; Thoroughman & Shadmehr, 2000). The transfer of learning effects from a trained movement to other untrained movements is referred to as generalization. In the framework, the activities of motor primitives determine motor commands and a recruitment pattern of motor primitives is determined by the desired movement direction. An extended framework of motor primitives was proposed to reproduce the generalization pattern in bimanual movements (Yokoi et al., 2011); after training left arm movements with bimanual movements, generalization to other bimanual movements is restricted to similar kinematics of the left (trained) arm but also spread among wide-range kinematics of the right (untrained) arm.

However, the distinct modeling of unimanual and bimanual movements cannot explain the generalization between the two types of movements. Learning effects in bimanual movements

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toward a fixed target direction are "partially" generalized to unimanual movements (Nozaki, Kurtzer, & Scott, 2006; Wang, Lei, Xiong, & Marek, 2013). A state space model (a model for trial-dependent changes of motor commands) can explain this partial generalization (Nozaki & Scott, 2009). This model abstractly assumed that there are three different neural populations: one for unimanual, one for bimanual, and one for both unimanual and bimanual movements (i.e., a neural population for unimanual movements overlaps with that for bimanual movements). Although the overlap model predicts that the generalization between the two types of movements is always partial, learning effects in bimanual reaching movements toward eight directions are "perfectly" generalized to unimanual movements (Wang et al., 2013). The difference exists in the number of target directions during the bimanual training phase, but it is not clear why the number of training target directions affects the generalization between bimanual and unimanual movements. Our recent model (Takiyama & Sakai, 2016), a balanced motor primitive framework, suggested a novel relationship between unimanual and bimanual movements. In the model, each motor primitive shows a different activity pattern for unimanual and bimanual movements, but the averaged activity across various unimanual movements equals the averaged activity across bimanual movements, which was termed unimanual–bimanual balance. Our proposal is that unimanual–bimanual balance determines the relationship between the two types of movements. However, the balanced motor primitive model assumed only parallel bimanual reaching movements in which the target directions are the same for the left and right arms, which leaves the relationship between unimanual and bimanual reaching movements toward various patterns of target directions unresolved. Generalizations of bimanual movements from one pattern to another pattern of target directions have been investigated in detail (Yokoi et al., 2011), but our conventional balanced motor primitive model failed to explain those generalization patterns. When considered together, we have not yet identified a single framework that can concurrently explain motor learning effects in unimanual movements, those in bimanual movements, and the generalization between the two types of movements.

Here, we extended the balanced motor primitive model to simultaneously explain motor learning in unimanual and in various bimanual movements as well as the generalization between those movements in a unified manner (within a single framework with an identical set of parameters). Our model is proposed based on the experimental results of the perfect generalization from bimanual to unimanual movements when bimanual movements for training trials are parallel or symmetrical (the sign of the target direction is different for the left and right arms ($\theta^{\mathrm{L}} = -\theta^{\mathrm{R}}$)) (Wang et al., 2013), which yields an extended version of the unimanual–bimanual balanced condition. The extended version of the balanced motor primitive model can successfully explain not only the results of behavioral experiments, motor learning in unimanual and in various bimanual movements, as well as the generalization between those movements, but also the results of neurophysiological experiments (Donchin et al., 2002; Rokni, Steinberg, Vaadia, & Sompolinsky, 2003). Furthermore, we demonstrate that the extended version of unimanual–bimanual balance can be implemented in a simple biologically inspired neural network model.

2. Results

2.1. General framework

The present study focused on reaching movements toward radially distributed target directions: $\theta_1, \ldots, \theta_K$. The target direction was randomly sampled from the K target directions in each trial. During each reaching movement, an unpredictable perturbation was given, such as a force field (Shadmehr & Mussa-Ivaldi, 1994), which yielded a movement error e perpendicular to the movement direction (Fig. 1(a), (c)). The aim of the task was to accurately reach toward a given target by generating additional motor command x perpendicular to the movement direction to compensate for the movement error.

Following the original motor primitive model (Donchin et al., 2003; Thoroughman & Shadmehr, 2000), we assumed that the motor command x was a linear summation of motor primitive activities $A_1(\theta), \ldots, A_N(\theta)$ that were determined by a target direction θ (Fig. 1(a), (c)) (i.e. $x = \sum_{i=1}^{N} W_i A_i(\theta)$, where W_i determined how the ith primitive contributed to generate the motor command). Each weight W_i was modified by $-\frac{\eta}{2}\frac{\partial e^2}{\partial W_i}$ (gradient descent rule) in each trial to reduce the squared movement error e^2 (see Methods), where the positive constant η denoted the learning rate. This framework could explain trial-dependent changes of the movement error and the generalization effects on untrained movements (Donchin et al., 2003; Thoroughman & Shadmehr, 2000).

The framework of motor primitives could be applied for bimanually reaching movements (Takiyama & Sakai, 2016; Yokoi et al., 2011). Throughout this study, we supposed a perturbation imposed only on the left arm (the left arm was trained, and the right arm was untrained). Therefore, the additional motor command x should be considered only for left arm movements. We considered various types of bimanual movements in which target directions for the left and right arms were defined as θ^{L} and θ^{R}, respectively. The present study assumed that the activity pattern of each motor primitive for bimanual movements was determined by $\theta^{\mathrm{L}} \in \{\theta_1, \ldots, \theta_K\}$ and $\theta^{\mathrm{R}} \in \{\theta_1, \ldots, \theta_K\}$, and for unimanual movement, it was determined by θ^{L}, $A_i^{\mathrm{uni}}(\theta^{\mathrm{L}})$. The weight value W_i was assumed to be common for unimanual and bimanual movements. This assumption did not mean common contributions of a weight W_i to unimanual and bimanual movements. The contribution of W_i depended on the primitive activities $A_i^{\mathrm{uni}}(\theta^{\mathrm{L}})$ in unimanual movements and $A_i^{\mathrm{bi}}(\theta^{\mathrm{L}}, \theta^{\mathrm{R}})$ in bimanual movements (i.e., each motor primitive contributed $W_i A_i^{\mathrm{uni}}(\theta^{\mathrm{L}})$ or $W_i A_i^{\mathrm{bi}}(\theta^{\mathrm{L}}, \theta^{\mathrm{R}})$ to the generation of motor command).

2.2. Unimanual–bimanual balance

The learning effect trained with a parallel bimanual movements ($\theta^{\mathrm{L}} = \theta^{\mathrm{R}} = \theta_1$) toward a fixed target direction, $K = 1$, was partially generalized to unimanual movements with $\theta^{\mathrm{L}} = \theta_1$ (Nozaki et al., 2006; Wang et al., 2013), whereas the learning effect for $K = 8$ with $\theta^{\mathrm{L}} = \theta^{\mathrm{R}}$ (parallel bimanual movements) or $\theta^{\mathrm{L}} = -\theta^{\mathrm{R}}$ (symmetric bimanual movements) was perfectly generalized to unimanual movements (Wang et al., 2013). When the generalization from bimanual to unimanual movements was partial, movement error increased at the trial when bimanual movements were switched to unimanual movements. In contrast, when the generalization from bimanual to unimanual movements was perfect, movement error did not change at the trial when bimanual movements were switched to unimanual movements. The goal in this section was to analytically derive the condition to reconcile the partial generalization when $K = 1$ and the perfect generalization when $K = 8$. The learning speed for unimanual movements was not significantly different from that for bimanual movements (Tcheang, Bays, Ingram, & Wolpert, 2007). Under the assumption of equivalent learning speeds, we analytically proved that the generalization was perfect if and only if $\sum_{k=1}^{K} A_i^{\mathrm{uni}}(\theta_k) = \sum_{k=1}^{K} A_i^{\mathrm{bi}}(\theta_k, \theta_k) = \sum_{k=1}^{K} A_i^{\mathrm{bi}}(\theta_k, -\theta_k)$ for all primitives and was partial otherwise (see Methods).

The partial generalization for $K = 1$ was observed in the case of a certain target direction θ (Nozaki et al., 2006; Wang et al., 2013);