The Relationship Between the Temporal Structure of Motor Output Variability and Motor Learning Ability

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It is well-known that when subjects make reaching motions, they can learn to compensate for forces that are proportional to their reach velocities but perpendicular to their reach directions (Shadmehr and Mussa-Ivaldi 1994). We recently examined how subjects adapt to these velocity-dependent force-fields (FFs), compared to FFs based on position, and FFs based on linear combinations of position and velocity. We showed that learning a FF based on a positive combination of position and velocity (i.e. a FF where the contributions from position and velocity perturb the hand in the same direction) is faster than learning a purely velocity-dependent or purely position-dependent FF (Sing et al 2009). We also showed that learning a negative combination FF (i.e. a FF where the contributions from position and velocity perturb the hand in opposite directions) is significantly slower than the positive combination, or the purely velocity- or position-dependent FFs. The force patterns produced by these FFs during point-to-point reaching movements are displayed in Figure 1B. To account for the differences in learning rates, we proposed a model in which a population of learning elements exhibited joint dependence on position and velocity. The key idea is that in the population, position-dependence is positively correlated with velocity-dependence, so that most learning elements in the population produce motor output that reflects a positive combination of position- and velocity-dependence. If the motor output from each learning element displays signal-dependent noise, then the net motor output will display noise that reflects the distribution of position- and velocity-dependence in the population. In particular, motor output noise should display positively correlated dependence on position and velocity from one trial to the next.

We investigated the temporal structure of variability in the lateral force patterns that subjects produced during a baseline pre-learning period in order to understand the relationship between motor output variability and learning ability. In general, lateral force profiles were quite variable as shown in Figure 1A. To study the specific relationships between this variability and different types of visco-elastic dynamics, we projected each force profile on to time-varying traces for position, velocity, a positive combination, and a negative combination of the two. In this pre-learning period, we found that the amount of variability displayed by the projections of the lateral force profiles onto each type of dynamics (pos-combo, neg-combo, position, and velocity) was highly predictive (r=0.95) of the single-trial learning rate for each type of dynamics (Fig 1C-E), consistent with the idea that motor output noise reflects the population of learning elements and therefore the rate of motor adaptation.

To understand the temporal structure of motor output variability in greater detail, we performed principal component analysis on the force profiles from the pre-learning period. We found that the first principal component accounted for about 20% of the total variability, nearly twice as much as any other component (Fig 2A). Interestingly, the shape of this first principal component is well characterized by a positive combination of position and velocity (R2=0.80) (Fig 2B). Some of the next 10 components are partially explained by position and velocity while the remaining components are essentially orthogonal to this space (Fig 2C), indicating that position and velocity variability exist primarily in the first several principal components with the largest fraction of this variability residing in the first principal component.

The strength of the relationship that we observed between motor output variability and motor adaptation rates during the pre-learning period suggests that one might result from the other. We tested the hypothesis that changes in motor adaptation rates would lead to changes in motor output variability by comparing motor output variability before and after a training regimen designed to increase the learning rate for a particular type of dynamics. We accomplished this learning rate increase by repeatedly learning and washing out a particular pattern of dynamics (either a position-dependent or a velocity-dependent FF) with blocks of 7 consecutive training trials followed by 9-14 washout trials (Fig 3A) (Gonzalez-Castro et al. ACMC 2008). This manipulation led to increased learning rates and increased the specificity of single trial adaptation for both position-dependent and velocity-dependent FF training (Fig 3B: middle column, bottom panel), consistent with what we previously observed for velocity-dependent FF training. Interestingly, we found that after this training, both the first principal component of the variability (Fig 3B: left column) and the total variability showed an increase in specificity towards the trained dynamic (see the top two panels of the middle & right columns in Fig 3B). This indicates that motor output variability can be reshaped through extensive training. If motor output variability reflects the distribution of learning elements, these findings suggest that this distribution rotates with extensive training (Fig 3C) to reflect an increased specificity for the trained dynamics. This work provides the first link between the ability to learn and the temporal structure of motor output variability.
**Figure 1:** Comparison of Motor Output Variability and Learning Rates for Different Viscoelastic Dynamics

Fig 1A: In the (pre-learning) period, force profiles show substantial variability. Individual Pre-learning Lateral Force Profiles

Fig 1B: Different viscoelastic (position and velocity dependent) combinations. These shapes correspond to the ideal force profiles to be produced in force field learning:

- Purely velocity-dependent (Vel)
- Purely position-dependent (Pos)
- Positive combination (PC)
- Negative combination (NC)

**Figure 2:** Principal Component Analysis of Variability before Learning

Fig 2A: The first principal component (PC) of pre-learning force profiles accounts for nearly 20% of the total variability and nearly twice as much variability as any other component.

Fig 2B: The first PC has a shape that closely resembles a positive combination of position and velocity ($R^2 = 0.8$).

Fig 2C: The first PC is almost fully accounted for by position and velocity, and some of the next ten can also be fit by position and velocity, while the rest are essentially orthogonal to the state space.

**Figure 3:** Changes in the Specificity of Motor Variability and Motor Learning Ability

Fig 3A: The experiment consisted of a pre-learning variability measurement period, 48 cycles of learning and washout of a position- or velocity-dependent force field, and a post-learning variability measurement period.

Fig 3B: When comparing variability between the pre-learning and post-learning measurement periods, variability became more specific to the type of dynamic (either position or velocity) experienced. This specificity was also reflected in the first PC through changes in regression coefficient of the first PC onto position and velocity. Changes in fraction of variance accounted for, regression coefficients of the first PC onto position and velocity, and single-trial learning rate at the beginning and end of learning are shown in the middle column. The angle of specificity is shown in the right column (*: $p < 0.05$, **: $p < 0.01$).

Fig 3C: The changes in specificity and learning rate can be explained by a rotation in the distribution of learning elements.