Modeling constraints to redundancy in bimanual force coordination

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Hu X, Newell KM. Modeling constraints to redundancy in bimanual force coordination. J Neurophysiol 105: 2169–2180, 2011. First published February 23, 2011; doi:10.1152/jn.01086.2010.—This study investigated the interactive influence of organismic, environmental, and task constraints on the organization of redundant force coordination patterns and the hypothesis that each of the three categories of constraints is weighted based on their relative influence on coordination patterns and the realization of the task goal. In the bimanual isometric force experiment, the task constraint was manipulated via different coefficients imposed on the finger forces such that the weighted sum of the finger forces matched the target force. We examined three models of task constraints based on the criteria of task variance (minimum variance model) and efficiency of muscle force output (coefficient-independent and coefficient-dependent efficiency models). The environmental constraint was quantified by the perceived performance error, and the organismic constraint was quantified by the bilateral coupling effect (i.e., symmetric force production) between hands. The satisficing approach was used in the models to quantify the constraint weightings that reflect the interactive influence of different categories of constraints on force coordination. The findings showed that the coefficient-dependent efficiency model best predicted the redundant force coordination patterns across trials. However, the within-trial variability structure revealed that there was not a consistent coordination strategy in the online control of the individual trial. The experimental findings and model tests show that the force coordination patterns are adapted based on the principle of minimizing muscle force output that is coefficient dependent rather than on the principle of minimizing signal-dependent variance. Overall, the results support the proposition that redundant force coordination patterns are organized by the interactive influence of different categories of constraints.

satisficing model; variability; redundancy; bilateral coupling; isometric force

WHEN MOTOR ACTIONS ARE PERFORMED, there is redundancy in that the task goal can be fulfilled by an infinite number of motor solutions (Bernstein 1967). However, instead of fully exploiting this redundancy, we tend to use a limited set of solutions based on some minimization criteria or configuration of constraints. Different criteria or constraints have been proposed to account for the redundancy in movement patterns from a range of theoretical perspectives (Flash and Hogan 1985; Harris and Wolpert 1998; Nelson 1983; Uno et al. 1989).

While the task goal is achieved, the redundancy in the sensorimotor system also allows variability at the cortical (Churchland et al. 2006) and motor-unit pool (Jones et al. 2002) levels. This variability leads to moment-to-moment and trial-to-trial variations at the stages of execution and outcome of the action. At the execution stage, the variability is regarded as beneficial in that it offers flexibility and can facilitate compensation to perturbations from within the organism and the external environment (Bernstein 1967). Through the modeling of optimal feedback control (Todorov and Jordan 2002) and analysis on the structure of variability (Scholz and Schoner 1999), it has been proposed that the variability in movement execution is reduced only when it deteriorates task performance and that the variability irrelevant to the task performance is not controlled to allow adaptive behavior. As a result, the relative variability in movement outcome that leads to enhanced performance error is typically smaller than that of the individual degrees of freedom in movement execution (Aruyunyan et al. 1969; Vereijken et al. 1992). However, through practice and learning, the variability along the redundant uncontrollable dimension has been shown to decrease with learning (Kang et al. 2004). In some cases, it decreases even more than the task relevant variability (Domkin et al. 2002). These results lead to the proposition that a certain subspace within the uncontrollable subspace may be preferred over others due to the configuration of constraints. Moreover, in bimanual isometric force production, when the variability was calculated within a trial, the individual finger forces were positively correlated and destabilized the total force output within trials (Ranganathan and Newell 2008). Namely, more variability is observed in the task level than the execution level. This deteriorated task performance is due to the intrinsic bilateral positive coupling constraint (a tendency of producing bilateral symmetric actions, see Kelso et al. 1979) that originates from multiple levels of the sensorimotor system (Diedrichsen et al. 2003; Hortobagyi et al. 2003; Swinnen et al. 2001). It has been shown that a rather broadly distributed neural network is involved in shaping the bilateral coordination patterns (Debaere et al. 2001; Swinnen and Wenderoth 2004) and that the peripheral musculoskeletal system (e.g., the effectors and muscle groups used in the task) also influences the coordination to some degree (Hu et al. 2011; Levin et al. 2004).

It has been proposed that three categories of constraints (intrinsic to the organism, external in environment, and task) determine the optimal coordination patterns (Newell 1986). Organismic constraints arise from the intrinsic characteristics of the sensorimotor system. For example, the bimanual coupling effect mentioned above is regarded as an organic constraint of the individual. Other neuromuscular constraints including limited muscle strength and body segment length are also examples of organismic constraints. Environmental constraints include the ambient conditions, such as the availability and reliability of the performance relevant information that can be perceived by the exteroceptive sensory systems. Without visual feedback information, for example, enhanced constant and variable performance error is often observed in isometric force control (Tracy 2007; Vaillancourt and Russell 2002). Task constraints are the specific constraints imposed by the

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task about the goal and rules or ways to achieve the task goal. For example, a required movement distance within a required time interval reflects a task constraint.

In an earlier study, the interactive influence between the organismic and task constraints on force coordination was investigated (Hu and Newell 2011a); however, the relative influence of each category of constraints and the degree of interaction between constraints were not quantified in relation to models of motor redundancy. In the current study, we tested the hypothesis that each constraint is weighted based on the relative influence of the constraint in organizing the coordination patterns and that the coordination patterns emerge from the combined influence of the weighted constraints. Under this hypothesis, each constraint is associated with a cost; namely, violation of the constraints leads to increment of a certain cost. For example, high performance error with sufficient error feedback information leads to high error cost due to the violation of the environmental constraint. Similarly, bilateral asymmetric force production leads to a high cost due to the violation of the organismic coupling constraint. With the weighted combination of constraints, the goal of the system is to “minimize” the combined costs associated with the constraints. From this perspective, when one constraint is changed, the relative influence of the three categories of constraints on the patterns of coordination is also changed, and the weightings on the three constraints are reorganized accordingly, from which new coordination pattern may emerge.

To test this weighting hypothesis, a bimanual isometric force production task was used in the experiment. The task constraint was manipulated via imposing different coefficients on the finger forces such that the weighted sum of individual finger force output matched the force target. The unequal coefficient settings distinguished the influence of each category of constraint and allowed the reorganization of the force coordination patterns. The models of constraints were proposed to quantify the influence of the three categories of constraints with a cost function for each constraint. In the models, the environmental constraint was quantified by the perceived performance error that was displayed as the visual feedback. The organismic constraint was quantified by the bilateral positive coupling (i.e., symmetric force production) between hands (Hu and Newell 2011b). In both discrete (Schmidt et al. 1979) and continuous (Slifkin and Newell 1999) isometric force production, the variability in the force is scaled with force amplitude, and it has been suggested that the task variability is minimized during motor planning (Harris and Wolpert 1998). Alternatively, an efficient coordination strategy (i.e., minimum muscle force output) has been proposed (Goble et al. 2007; Nelson 1983). The unequal coefficients imposed on the finger forces essentially changed the finger “strength” or the relative efficiency of the individual finger force that contributes to the total force output. These two theoretical perspectives predict contrasting force combinations between fingers in the unequal coefficient settings (see Methods for details).

To investigate the influence of task constraints on force coordination, three models of motor redundancy were examined based on the criteria of minimum task variance (minimum variance model) and minimum muscle force output (coefficient-independent vs. coefficient-dependent efficiency models). The objective function was the combined costs of the three categories of constraints (1 environmental, 1 organismic, and 1 of the 3 in the task constraint). The weightings assigned to the constraints were estimated from the observed data. Instead of minimizing the objective function using the standard optimization approach (Aster et al. 2004), a “satisficing” method was used to estimate the weightings in that only small enough rather than the minimum value of the objective function was searched. The concept of satisficing has been proposed as the rational choice during decision making in economics (Simon 1955, 1989). In motor coordination, the observed variability in the sensorimotor system and in the task outcome may be due to the satisficing of constraints. In optimization, the best solution is chosen such that the objective function is minimized while certain constraints are satisfied. In contrast, the satisficing approach emphasizes that the constraints have to be satisfied, and as long as the objective function value is acceptably low enough, the solution can be used. This approach is less expensive computationally than optimization when limited time and resources are available.

In summary, the purpose of this study was to investigate the interactive influence of the three categories of constraints on the organization of coordination patterns under redundancy. The models of constraints were compared with estimate the constraint weightings that reflect the interactive process between the constraints (Newell 1986). Depending on the level of analysis (within a trial or between trials), a different structure in the variability has been found, which reveals contrasting interpretations of control strategies (Gottlieb et al. 1996; Ranganathan and Newell 2008; Scholz et al. 2003). In this study, we performed both within- and between-trial variability analysis and the relation between them was examined as a function of the manipulated task constraint. The predictions of the models of constraints on the between-trial coordination were assessed based on the within- and between-trial variability analyses.

METHODS

Participants

Ten right hand dominant healthy individuals (age = 27 ± 3 yr, 5 female and 5 male) volunteered to participate in this study. The participants gave informed consent to the experimental procedures that had been approved by the Pennsylvania State University Institutional Review Board.

Apparatus

Participants were seated facing a 14-in. LCD monitor with both hands pronated on the table. All the fingers extended out and the index fingers extended comfortably away from other digits. The participants were instructed to rest their forearms and palms on the table during the trials (Fig. 1A). Through isometric abduction, the distal phalange of the index finger contacted a load cell (ATI Industrial) that was fixed to the table 30 cm apart. Analog output from the load cell was amplified through an ISA F/T controller board with a 16-bit DSP card. The force output was sampled at 100 Hz. A red horizontal target line was centered at the screen and spanned the width of the screen. A yellow trajectory representing the total force output that moved from left to right of the screen was displayed to the participants (Fig. 1B). The visual gain was 80 pixels/N.

Procedures

Estimation of maximum voluntary contraction. The participants were instructed to produce maximal force by abducting their two
index fingers. Three trials of 6 s were recorded with 30-s rest between each trial. The average of the peak forces in the three trials was determined as the maximum voluntary contraction (MVC) of each finger and was used as the normalization terms (\(F_{1\text{max}}\) and \(F_{2\text{max}}\)) in the modeling. The summed MVC of both fingers was used to determine the force target (i.e., 20% MVC force level).

**Experimental design.** The participants were instructed to produce simultaneous constant forces with both index fingers, so that the weighted sum of finger forces matched the force target line of 20% MVC. The experiment consisted of five blocks of trials with one coefficient setting in each block. The five coefficient settings \(c_1, c_2\) imposed on the left and right finger forces were: 0.2:1.8, 0.5:1.5, 1:1, 1.5:0.5, and 1.8:0.2. Two unequal coefficients were chosen to examine the degree of influence of the task constraint and the weightings assigned to the constraints. The 1:1 ratio served as a control condition, and the possible hand-dominance effect was balanced out on the reversed coefficient ratios.

Before the main testing of each block, the specific coefficients imposed on each finger force were informed to the participants. Two practice trials were provided, where the participants were asked to produce force pulses using one finger at a time and to learn the coefficients imposed on each finger. There followed five more practice trials of simultaneous constant force production for task familiarization and selection of the preferred finger force combination. The participants then completed 10 consecutive 15-s trials in each block. The order of the blocks was randomized over the participants. A 5-s line and the possible hand-dominance effect was balanced out on the reversed coefficient ratios.

**Data Analysis**

To eliminate the transient effects, the initial 5 s and last 1 s of each trial were removed for data analysis. The task performance was quantified by the root mean squared error (RMSE) of the total force output. The ratio of individual force pairs and Pearson’s linear correlation coefficient between individual forces were calculated to evaluate the coordination strategy.

**Statistical analysis.** The dependent variables described above were analyzed using a repeated-measure ANOVA with the force error ratio (left:right) as repeated measures. A significant level of \(P < 0.05\) was used for all analyses. When necessary, post hoc pairwise multiple comparisons with Bonferroni correction was used. The dependent values are reported as means ± SE unless otherwise noted.

**Model of Constraints**

The models of constraints (Fig. 2A) that quantified the weighting on the influence of the three constraints during force coordination were implemented (Bryson and Ho 1975). The environmental constraint was quantified by the visually perceived performance error. The organismic constraint was quantified by the bilateral coupling effect (i.e., symmetric force production) between hands. In the task constraint, three models were examined based on the criteria of task variance (minimum variance model) and task efficiency (coefficient-independent vs. coefficient-dependent efficiency model). These two task efficiency models were proposed to examine whether the optimal force output ratio scales with the specific coefficient ratio on the finger forces. Although the optimization method was used during the weighting estimation, the property of the suboptimal solutions was also examined. The models are described below in detail.

**Environmental constraint as perceived performance error.** The perceived performance error is quantified by the squared normalized force error in Eq. 1.

\[
J_1[F_1(t), F_2(t)] = \left(\frac{c_1 \cdot F_1(t) + c_2 \cdot F_2(t) - F_T}{F_T}\right)^2
\]

\(F_1(t)\) and \(F_2(t)\) are the individual finger forces at an instant of time \(t\); \(c_1\) and \(c_2\) are the coefficients imposed on each finger force; and \(F_T\) represents the force target. The normalization by the target force reduces the dependency of the performance error on the target force levels that the participants have to produce. Any finger force combinations in the zero-error line (broken line) in Fig. 2B minimize the function \(J_1\) in the example of coefficient ratio of 0.5:1.5 condition.
Fig. 2. Model structure and estimated objective function (Eq. 4). A: structure of the models of constraints. Three models are included in the task constraint: minimum task variance model and task efficient force output model (coefficient-independent and coefficient-dependent models). B: predictions of finger force combinations from each category of constraint in the example of coefficient ratio of 0.5:1.5 with force target of 5.01 N. Point A: (0, 3.333 N) predicted by the coefficient-independent efficiency model. Point B: (0.122, 3.300 N) predicted by the coefficient-dependent efficiency model. Point C: (2.505, 2.505 N) predicted by the organismic coupling model, and Point D: (5.01, 1.67 N) predicted by the minimum variance model. C: estimated objective function with coefficient ratio of 0.5:1.5 and force target of 5.01 N. Each contour represents a specific objective function value and the difference between the contour values is 2.55. *Minimum value 0 of the objective function. The 95% confidence ellipse of each trial of the actual force output is presented in thin line and the ellipse of all the 10 trials is plotted in thick line. Dash line represents zero force error. Solid line with positive slope represents equal force line. $F_1$ and $F_2$: force for each finger.

Organismic constraint as bilateral coupling. The bilateral positive coupling is quantified by the squared difference between the normalized individual finger forces in Eq. 2.

$$J_2[F_1(t), F_2(t)] = \left(\frac{F_1(t)}{F_{1\text{max}}} - \frac{F_2(t)}{F_{2\text{max}}}ight)^2$$

(2)

$F_{1\text{max}}$ and $F_{2\text{max}}$ represent the maximum force of each finger. The normalization by the maximum force reduces the bilateral asymmetry in finger strength. The function $J_2$ increases as the two normalized force levels become asymmetrical. Function $J_2$ predicts that the optimal finger force combination is at point C (intersection between zero-error line and equal-force line) in Fig. 2B.

Task constraint as task variance. The variability (SD) of the individual finger force scaled with the force amplitude: $SD(F) = kF$, where $k$ is the coefficient of variation (CV) (Harris and Wolpert 1998; Schmidt et al. 1979). We assumed the same CV on the two fingers when they are normalized by their respective maximum forces. Given the bilateral cross talk is quantified in the organismic coupling constraint, here we assumed independent variability sources for the two fingers, so the total force output variance is associated with $(c_1·k·F_1/F_{1\text{max}})^2 + (c_2·k·F_2/F_{2\text{max}})^2$ in the current task settings. The coefficient $k$ is eliminated during the minimization process given it does not influence the optimal solution. The minimum variance model (Eq. 3) predicts that the optimal force combination is at point D in the 0.5:1.5 coefficient ratio example, because the optimal individual force output ratio scales inversely with the coefficient ratio imposed on the finger force (see Supplemental Material for the scaling relation; Supplemental Material for this article is available online at the J Neurophysiol website).

$$J_3[F_1(t), F_2(t)] = \left(\frac{c_1·F_1(t)}{F_{1\text{max}}} - \frac{c_2·F_2(t)}{F_{2\text{max}}}ight)^2$$

(3)

It should be noted that the linear scaling relation between force and force variability holds only in the intermediate force range. When a large range of force amplitude was examined, quadratic (Slifkin and Newell 1999), square-root (Carlton and Newell 1993; Yao et al. 2000), and s-shaped (Christou et al. 2002) scaling relations have been found. In the current study, the force output only covered a small range across different conditions, and the linear scaling function was used here as a close approximation.

Task constraint as task efficiency. We had no a priori information of what form of function was appropriate to quantify the task efficiency. Two forms of task efficiency function were proposed.

One model associated with the task constraint is the coefficient-independent efficiency model, where the task efficiency is quantified by the square of weighted sum of the normalized finger forces in Eq. 4. In this equation, the optimal force output ratio is independent of the specific coefficient ratio imposed on the finger force. Namely, maximal force production is expected in the finger with the larger coefficient and zero force production is expected in the finger with the smaller coefficient, and the coefficient ratio does not influence the optimal force output ratio strictly (see Supplemental Material). This model predicts that the optimal solution of $J_3$ is at point A in Fig. 2B.

$$J_3[F_1(t), F_2(t)] = \left(\frac{\beta_1·F_1(t)}{F_{1\text{max}}} + \frac{\beta_2·F_2(t)}{F_{2\text{max}}}ight)^2$$

(4)

where $\beta_1 = \frac{c_2}{c_1 + c_2}$, $\beta_2 = \frac{c_1}{c_1 + c_2}$. 

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A second model associated with the task constraint is the coefficient-dependent efficiency model in which the task efficiency is quantified by the weighted sum of the squared normalized finger forces in Eq. 5. In this equation, the optimal force output ratio scales with the coefficient ratio imposed on the finger force (see Supplemental Material). This model predicts that the optimal solution of \( J_3 \) is at point \( B \) in Fig. 2B in the 0.5:1.5 coefficient ratio condition.

\[
J_3[F_1(t), F_2(t)] = \left( \frac{\beta_1}{F_{1 \text{max}}} \right)^2 + \left( \frac{\beta_2}{F_{2 \text{max}}} \right)^2
\]

where \( \beta_1 = \frac{c_2}{c_1 + c_2} \), \( \beta_2 = \frac{c_1}{c_1 + c_2} \).

The task variance and efficiency models are task specific; namely, the minimum variance model predicts that the force output ratio is determined by the task coefficient ratio (i.e., lower force production on the finger that has larger coefficient and vice versa). In contrast, the coefficients \( \beta_1 \) and \( \beta_2 \), the task efficiency models penalize high force production with the smaller coefficient while allowing high force production with the larger coefficient. Even though the force output ratio in the coefficient-independent model does not scale strictly with the coefficient ratio, the coefficient ratio determines the exact force output (0 or maximum).

The three categories of constraints that predict different force coordination patterns were combined in Eq. 6, where \( \omega_i \) represents the weighting assigned to each constraint that organizes the motor coordination patterns. Three models were examined with the environmental (Eq. 1) and organismic constraint (Eq. 2) combined with one of the task constraints (the minimum variance model of Eq. 3, the coefficient-independent efficiency model of Eq. 4, and the coefficient-dependent efficiency model of Eq. 5). To reduce the number of free parameters in the weighting estimation and keep the generality between conditions, we assumed that the sum of the weightings \( \omega_i \) is constant and \( N = 3 \) which represents the number of constraints.

\[
J[F_1(t), F_2(t)] = \sum_{i=1}^{N} \omega_i J[F_i(t), F_2(t)]
\]

where \( \sum_{i=1}^{N} \omega_i = 1 \), \( \omega_i \geq 0 \).

In the model (Eq. 6), the coordination pattern is determined by the combined influence of the three categories of constraints (i.e., the weighted sum of the 3 constraints). The desired individual force outputs \( (F_1, F_2) \) emerge that minimize the objective function over time interval \( T \) as shown in Eq. 7. \( T \) is the trial duration.

\[
J(F_1, F_2) = \sum_{t=1}^{T} \sum_{i=1}^{N} \omega_i J(F_i(t), F_2(t))
\]

where \( \sum_{i=1}^{N} \omega_i = 1 \), \( \omega_i \geq 0 \).

Studies have shown that isotropic force variability has time-dependent properties (Newell et al. 2006; Sifkin and Newell 1999), and the assumption of the variability of force output as a random Gaussian noise does not hold. Therefore, the standard statistical parameter estimation approach (Aster et al. 2004) cannot be applied here. In the weighting estimation process, we made no assumption on the specific distribution and the independency of the force output. The weighting \( \omega_i \) imposed on the constraint was estimated directly from the observed force output. First, the objective function (Eq. 7) in force space was transformed to weighting space (Eq. 8) (see Supplemental Material for the interpretation of the transformation). The weighting \( \omega_i \) was estimated from minimization of \( J_w \) with the observed force output \( F_1(t), F_2(t) \) of each trial substituted into Eqs. 8.

\[
J_w(\omega_1, \omega_2, \omega_3) = \sum_{t=1}^{T} \left[ \left( \frac{\partial J}{\partial F_1(t)} \right)^2 + \left( \frac{\partial J}{\partial F_2(t)} \right)^2 \right]
\]

Given there is variability in the force output, it was assumed that at a time instance \( t \), the objective function (Eq. 6) is close to minimum rather than being minimum, that is \( \partial J/F_1(t) = 0 \), \( \partial J/F_2(t) = 0 \). The optimization of \( J_w \) (Eq. 8) minimizes \( \partial J/F_1(t), \partial J/F_2(t) \) over the trial duration \( T \) based on the observed forces but does not guarantee \( \partial J/F_1(t) = 0, \partial J/F_2(t) = 0 \) at any specific time \( t \), which allows nonzero incidence at certain time \( t \). One important property of the model is that it is similar in concept with the satisficing model (Simon 1955) in that the system does not try to find out solutions that minimize the objective function at any time instant but accept good enough solutions that lead to the objective function acceptably low. Furthermore, the suboptimal solutions of \( J_w \) were also examined in line with the satisficing idea.

Through minimizing \( J_w \), the estimated weightings \( \omega_i \) were substituted into Eq. 6, and one example of the objective function contour plot in force space is shown in Fig. 2B. The estimated weightings on the three constraints [environmental, organismic, and task (coefficient-dependent efficiency)] were 0.434, 0.205, and 0.361, respectively. The 95% confidence ellipses [2.45 times of SD (square root of the eigenvalues of the variance matrix)] for the individual trials and the 10 trials (see below for detail) are also shown around the center of the contours.

It is noteworthy that even though the elliptic contour of the model follows the ellipse of the 10 trials as a group, this property should not be taken for granted. The individual forces can have arbitrary distributions in the force space without substantial influence on the model parameters. The direction and shape of the elliptic contour of the model are determined by the performance error and the degree of force symmetry (or asymmetry), and these data properties are directly associated with the objective functions of the three categories of constraints (see Supplemental Material for simulations). However, the elliptic contour of the model provides a set of acceptable solutions from the satisficing concept, such that different coordination patterns that satisfy the combination of constraints (i.e., within an elliptic contour) can be used over time or trials.

**Model validation.** To validate the model parameter estimation, the covariance matrix of all the 10 trials of each subject in each coefficient condition was determined, and it was visualized by the 95% confidence ellipse (Fig. 2C). Three parameters of the data ellipse were compared with the elliptic contour of the model. First, the center of ellipse is a measure of the location of the ellipse in the force space, which was calculated as the ratio of the individual force outputs and the ratio of the estimated optimal force outputs. Second, the orientation of the ellipse was calculated as the directional angle of the eigenvector corresponding to the larger eigenvalue. Third, the shape of the ellipse was computed as the ratio of square root of the eigenvalues (the larger SD over the smaller one). A more circle-like ellipse has a smaller SD ratio and more elongated ellipse has a larger SD ratio. The prediction residuals (the difference between the predicted and the observed value described above) were calculated. The statistics of the residuals including the means ± SD, the norm of residuals, and the randomness of residuals were then calculated to evaluate the model.

**RESULTS**

**Task Performance and Coordination Patterns**

Figure 3A depicts the RMSE of the total force output. Because the force output ratio is lower bounded at 0, and the data at the 0.2:1.8 and 0.5:1.5 condition are clustered together in the regular scale, the log_{10} force output ratios were calculated for better illustration. The one-way repeated-measures ANOVA on RMSE revealed a significant effect on the coefficient ratio \( F(4, 36) = 3.95; P = 0.009 \). Post hoc analysis showed that the RMSE was significantly higher on the coeffi-
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Model Parameter Estimation

The estimated weightings from the objective function involving the minimum variance model are shown in Fig. 4, A–C. The results of the objective function with the coefficient-independent efficiency model are shown in Fig. 4, D–F. The results of the objective function with the coefficient-dependent efficiency model are shown in Fig. 4, G–I.

For the minimum variance model, the environmental weighting $w_1$ increased at the asymmetric compared with the symmetric coefficient conditions $[F(4, 36) = 38.03; P = 0.001]$ and no significant difference was found between the asymmetric coefficient conditions ($P > 0.05$). The force ratio was significantly different between conditions $[F(4, 36) = 68.35; P = 0.001]$. The force output ratio in the symmetric coefficient (1:1) condition was significantly different from the asymmetric coefficient conditions ($P < 0.05$). However, no difference was found between the two asymmetric 0.2:1.8 vs. 0.5:1.5 ($P = 0.297$) and 1.8:0.2 vs. 1.5:0.5 ($P = 0.312$) conditions. Figure 3 displays the correlation between the individual finger forces. A significant difference was found on the correlation between finger forces between conditions $[F(4, 36) = 13.82; P = 0.001]$. The correlation was significantly reduced on the coefficient ratio of 0.2:1.8, 1.5:0.5, and 1.8:0.2 compared with the 1:1 condition ($P < 0.05$).

Model Validation

In the minimum variance model, the predicted optimal force output ratio from the model (Eq. 6) did not correlate with the observed force ratio (Fig. 5A). As shown in Table 1, the prediction residuals were large and not randomly distributed, which are signs of a poor fit. The model was not able to predict the desired force ratios at different coefficient conditions. The predicted orientation (Fig. 5B) of the 95% confidence ellipse fitted reasonably well with the data, and the residuals were randomly distributed even though they are relatively large. The model was also able to predict the shape (SD ratio in Fig. 5C) of the ellipse. Although the residuals were relatively large compared with the other two models, they were randomly distributed.

In the coefficient-independent efficiency model, the predicted force output ratio (Fig. 5D) showed a reasonably good fit. However, a systematic bias was evident in that the model under estimated the force ratio (i.e., predicted closer to 1 than the data) when asymmetric coefficients were imposed on the finger forces. This bias was also evident in the nonrandom prediction residuals shown in Table 1. The predicted orientation (Fig. 5E) of the ellipse fitted well with the data, and the residuals were small and randomly distributed. In contrast, the coefficient-independent model was not able to predict the shape of the ellipse.
the ellipse (Fig. 5F) and the prediction residuals were not random.

In the coefficient-dependent efficiency model, the predicted force ratio correlated with the observed force ratio (Fig. 5G). The prediction residuals were small in the norm and randomly distributed around zero, which are signs of a good fit. The model was able to predict the desired force ratios at different coefficient conditions. The predicted orientation (Fig. 5H) of the ellipse also fitted well with the data, and the residuals were small and randomly distributed. The model was also able to predict the shape (Fig. 5I) of the ellipse. The prediction residuals were relatively small and were randomly distributed, which suggested a reasonable fit to the data.

**Single Trial Behavior Under Constraints**

The single trial behavior was compared with the between trial behavior (10 trials) of each subject at each condition using...
As shown in Fig. 6A, even though the individual force output ratio exhibited substantial variability, it correlated with the force ratio calculated across all the 10 trials ($r^2 = 0.86; P = 0.001$, based on log-transformed fit due to unequal variance). The orientation of the individual trial ellipse also showed large variability between trials and ranged from 45 to 225° (Fig. 6B). No correlation was found between the individual trial orientation and the orientation of the 10-trial ellipse ($r^2 = 0.006; P = 0.19$). The shape (SD ratio) of the individual trial ellipses tended to be more circle-like than the 10-trial ellipse of each condition (Fig. 6C). Namely, the SD ratio of the individual ellipse ranged from 1 to 1.83 and is smaller than the SD ratio of the 10-trial ellipse ranging from 1 to 3.46. No correlation was found between the shape of the individual ellipse and the shape of all the 10 trials ($r^2 = 0.001; P = 0.76$).

**DISCUSSION**

This study examined the interactive influence of multiple categories of constraints (organismic, environmental, and task)
Therefore, variation in the force coordination within the elliptical region satisfies the three categories of constraints. From the satisficing perspective (Simon 1955), the individual finger force combinations within the task constraint scales with the coefficient ratios imposed on the force fingers. The models of constraints were implemented to quantify the weightings imposed on the three categories of constraints during force coordination (Davids et al. 2007).

Experimental Results and Model Predictions

Consistent with the earlier study (Hu and Newell 2011a), the experimental results revealed that the performance error (RMSE) increased with asymmetric coefficients between finger forces, which indicated that the weighting on the environmental constraint was reduced at asymmetric coefficient conditions. The coefficients also influenced the force sharing patterns between fingers in that the force output ratio correlated with the coefficient ratio and higher forces were produced by the finger that had the larger coefficients. When the force between fingers became uneven, the weighting on the organismic constraint decreased and the weighting on the task constraint increased (Fig. 4, H and I), respectively. As the coefficients became asymmetric, the negative correlation between fingers was also reduced, which indicated a reduction of error compensation and possibly contributed to the enhanced performance error. Overall, the results revealed that when the task constraint was manipulated, the influence of all the three categories of constraints was reorganized and new coordination patterns were formed.

The interactive influence of the constraints on the force coordination patterns was quantified by investigating models of constraints. Each model predicted different force sharing patterns, the same orientation of the force ellipse, and similar shapes of the ellipse across trials (Fig. 5). For the task constraints, the results revealed that the system adopted the task efficiency strategy (minimum muscle force output) rather than the strategy of minimizing task variance. The results are consistent with previous findings showing preference on task efficiency over other minimization criteria, such as movement time (Lee et al. 2007; Nelson 1983) and task variability (O’Sullivan et al. 2009). On the task efficiency constraint, the results revealed that coefficient-dependent model was the best fitted model in that the optimal force sharing pattern predicted by the task constraint scales with the coefficient ratios imposed on the force fingers. The results reveal that the detailed characteristics of the task constraint significantly influence the coordination dynamics.

Satisficing of Constraints

The satisficing feature of the model is consistent with previous studies of satisficing the constraint hierarchy (a set of prioritized task requirement) during motor planning (Rosenbaum et al. 2001) and satisficing of suboptimal performance even with the experience of optimal solution (Ganesh et al. 2010). With the weightings estimated from the data, the model predicts an elliptical region with small enough values of the objective function that reflects the combined influence of the three categories of constraints. From the satisficing perspective (Simon 1955), the individual finger force combinations within the elliptical region satisfy the three categories of constraints. Therefore, variation in the force coordination within the elliptical region is predictable.

### Table 1. Prediction residuals between the model and the observed data

<table>
<thead>
<tr>
<th>Measures</th>
<th>Means ± SD</th>
<th>Norm</th>
<th>Randomness z-Score (P Value)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Force ratio</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variance model</td>
<td>-0.28 ± 0.84</td>
<td>6.18</td>
<td>-6.70 (0.001)</td>
</tr>
<tr>
<td>Efficiency model 1</td>
<td>-0.12 ± 0.42</td>
<td>3.10</td>
<td>-4.95 (0.001)</td>
</tr>
<tr>
<td>Efficiency model 2</td>
<td>0.03* ± 0.21*</td>
<td>1.46*</td>
<td>-0.25 (0.799*)</td>
</tr>
<tr>
<td>Orientation, degree</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variance model</td>
<td>-0.49 ± 1.33*</td>
<td>9.94</td>
<td>1.63 (0.103*)</td>
</tr>
<tr>
<td>Efficiency model 1</td>
<td>-0.23 ± 1.57</td>
<td>11.14</td>
<td>1.88 (0.060*)</td>
</tr>
<tr>
<td>Efficiency model 2</td>
<td>-0.19* ± 1.39</td>
<td>8.13*</td>
<td>-0.42 (0.678*)</td>
</tr>
<tr>
<td>SD ratio</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Variance model</td>
<td>0.45 ± 0.57</td>
<td>5.08</td>
<td>0.04 (0.939*)</td>
</tr>
<tr>
<td>Efficiency model 1</td>
<td>-0.20 ± 0.45*</td>
<td>3.47*</td>
<td>-5.00 (0.001)</td>
</tr>
<tr>
<td>Efficiency model 2</td>
<td>-0.12* ± 0.54</td>
<td>3.86</td>
<td>0.14 (0.884*)</td>
</tr>
</tbody>
</table>

Efficiency model 1, coefficient-independent model; efficiency model 2, coefficient-dependent model; Norm, square root of the sum of squared residuals. Null hypothesis of the randomness test: the residuals are random (P < 0.05 as significant). *Best measure in each variable.

### Fig. 6. Individual trial variability. A: force ratio of individual trial of all the subjects as a function of force ratio of 10 trials with different symbols denoting different coefficient ratio conditions. B: orientation of individual trial ellipse as a function of the orientation of 10-trial ellipse in each condition. C: shape of individual trial ellipse as a function of the shape of 10-trial ellipse in each condition.
tirical region is allowed because the variation leads to minimal change on the objective function value. However, the within-trial analysis reveals that the variability structure varies across trials, yet the variation is constrained within the elliptical region predicted by the model (Figs. 2C and 5). The results indicate that the variation does not have to cover the entire satisficing region. In fact, the variability structure in a single trial shows that only a small local area of the elliptical region is occupied (Fig. 2B and 6).

The elliptic region predicted by the model is consistent with the uncontrolled manifold approach, which has shown that the elemental variables (individual finger forces in our case) form elliptic shapes with smaller variability in the task-relevant dimension and larger variability in the task-irrelevant dimension (Scholz and Schoner 1999; Scholz et al. 2000; Schoner 1995). The current model prediction is also compatible with the predicted behavior of the optimal control model where a combined performance error cost and control effort cost has been used (Todorov and Jordan 2002). The feedback control rule in the model penalizes variability in the task-relevant dimension and allows variability in the task-irrelevant dimension. However, the current model is conceptually different from the above two approaches. The uncontrolled manifold approach decomposes the variability into two components: one deteriorates the task performance (bad variability) and the other one does not (good variability); typically the bad variability is smaller than the good one. The optimal feedback control rule also leads to different properties of variability in different dimensions (Todorov 2004). In contrast, there is no such distinction of variability property in different dimensions in our model. Namely, as long as the individual force outputs satisfy the combined influence of the three categories of constraints (i.e., the objective function value is acceptably low enough), the property of the variability is the same in any dimensions within the satisfied elliptic region.

Implications for Redundancy

In motor activities, redundancy can arise from different categories of constraints. At the task level, the same task requirement can be fulfilled by different task defined variables (Bernstein 1967). For example, in the current study different finger force combinations can lead to the same total force. At the organismic level, the neuromuscular redundancy (e.g., different neurons, motor units, and muscle groups) can result in the same motor output (Saltzman 1979; Tresch and Jarc 2009). At the environmental level, the redundant information from different modalities (e.g., visual and auditory information) is integrated based on input reliability (Ernst and Banks 2002; van Beers et al. 2002). However, the redundancy from multiple levels can lead to different or even conflicting coordination patterns; as a consequence, a compromise of the required patterns from different constraints may be necessary. The results of the current modeling have the redundancy defined through the interactive processes of multiple constraints rather than at any level of a single constraint. Specifically, the redundant solutions are the ones that lead to a low enough value of the objective function associated with the three categories of constraints, even if the solution is not the perfect task solution. In our exemplar task, the redundant solutions form an elliptical shape rather than a straight line that leads to zero performance error. Although the task performance error may vary within the ellipse, the different solutions are equivalent due to the satisficing of constraints.

Studies have shown that the variability in the task-irrelevant dimension reduces substantially through practice and learning (Domkin et al. 2002; Kang et al. 2004). Similarly, exploring the task redundancy via variable practice does not facilitate learning and generalization (Ranganathan and Newell 2010). The results of the current study may provide further interpretation for the above findings. In the previous studies, redundancy is defined at the task level, and the task solutions that lead to zero performance error are regarded as task equivalent solutions. However, these redundant solutions may not be equivalent when other configurations of constraints are taken into account. For example, certain task solutions may not satisfy the neuromuscular constraints (Kutch et al. 2008; Loeb 2000); as a result, some solutions that are equivalent at the task level are eliminated due to the influence of other categories of constraints. The relative influence of different constraints may change during the learning process, and the sets of solutions that satisfy these different constraints also change accordingly. However, the question of how the relative influence of different categories of constraints changes during learning requires further investigation.

It has been proposed that the redundancy is utilized during the control processes (Scholz et al. 2000; Todorov and Jordan 2002). The contrasting relation between the two-level (within- and between-trial) variability structure questions the generality of this proposition. The structure of the between-trial variability supports the notion of utilizing redundancy during the control process in that more variability is observed in the task-irrelevant dimension than in the task-relevant dimension. Furthermore, the orientation and the shape of the ellipse of the experimental data follow the expected orientation and shape of the elliptic contour of the model. However, consistent with an earlier study (Ranganathan and Newell 2008), the structure of the within-trial variability in the force outputs exhibits rather random characteristics that have little correlation with the between-trial variability and does not support the notion of a synergetic control strategy (Gelfand and Tsetlin 1971) in a single trial.

Interpretation of Contrasting Variability Structure

The variability structure of the within-trial analysis indicates that there was no consistent strategy during the control of a single trial. The results contrast the findings of consistent coordination pattern between joints within a trial during a reaching movement (Gottlieb et al. 1996). One interpretation of the within-trial variability is that the redundancy arises from the variation of the initial conditions rather than from the control process (Newell et al. 2008). From this perspective, the initial condition is regarded as an independent dimension, and the movement outcome is influenced by the initial bias. Namely, a specific solution is used depending on the initial condition of the organism, and random-like variations around the specific solution are allowed in a small region. Therefore, the observed between-trial variability may arise from the different initial conditions of the organism rather than reflecting a control strategy of fulfilling the task requirement.
The different within- and between-trial variability structure can also be influenced by the relatively short trial duration. In our study, only 9 s were analyzed; however, more variation is expected on the task-irrelevant dimension with longer trial duration. In a quiet standing task, it has been shown that the variability in the center of pressure (COP) is composed of different amplitudes at multiple time scales. Specifically, the COP oscillates around a specific region within the basis of support at the short time scales, and the COP drifts to different regions at the long time scales (Duarte and Zatsiorsky 2000). It has been shown that the multiple time scale process also holds in isometric force variability (Slifkin and Newell 2000). Therefore, longer trial duration may introduce larger amplitude of long time scale variability that is similar to the different initial conditions between different trials. In this view, with long enough trial duration, one would expect that the within-trial variability may become more similar to the between-trial variability.

Limitation of the Models and Future Investigations

The models of constraints were constructed based on the specific bimanual force production task, and the weighting relations between the constraints are also likely to be task specific. In the current experiment, the task was designed in a way such that the influence of organismic constraints other than the bilateral coupling was minimized. For example, the fatigue effect was minimized with the relative low force level and short trial duration. Nevertheless, with different task settings it is likely that multiple constraints within each category mediate the motor coordination patterns. For example, other organismic constraints such as different muscle groups used to control the movement (Levin et al. 2004) and different skill levels of the participants (Puttemans et al. 2005) also influence the coordination patterns. Therefore, further investigation that includes multiple constraints in each category (a constraint hierarchy) is required to examine more real life like tasks. In this study, only the task constraint was manipulated to examine the interactive influence of the constraints. Exploring the interactions among the constraints by manipulating multiple categories of constraints together (e.g., change the task and environmental constraints simultaneously) remains a research direction for future investigation.

In summary, this study investigated the interactive influence of the three categories of constraints on the organization of coordination patterns under redundancy. Three models of constraints were investigated to test the effect of weightings on the categories of constraints. When the task constraint was manipulated, the coefficient-dependent model was able to best predict the reorganized force coordination patterns across trials. The results support the notion of the interactive influence of the categories of constraints on coordination patterns. Namely, when the task constraint is changed, the weightings on the three categories of constraints are reorganized, and the reweighting process is sensitive to the specific coefficients imposed on the finger forces. The experimental and modeling results are consistent with the proposition that the redundancy arises from the satisfying of the combined influence of multiple categories of constraints rather than from a single constraint.

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DISCLOSURES

No conflicts of interest, financial or otherwise, are declared by the author(s).

REFERENCES


