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# A mode hypothesis for finger interaction during multi-finger force-production tasks

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**Abstract.** Finger forces are known to change involuntarily during multi-finger force-production tasks, even when a finger's involvement in a task is not consciously changed (the *enslaving effect*). Furthermore, during maximal force-production (MVC) tests, the force produced by a given finger in a multi-finger task is smaller than the force generated by this finger in its single-finger MVC test (the *force-deficit effect*). A set of hypothetical control variables – modes – is introduced. Modes can be estimated based on individual finger forces during single-finger MVC tests. We show that a simple formal model based on modes with only one free parameter accounts for finger forces during a variety of multi-finger MVC tests. The free parameter accounts for the force-deficit effect, and its value depends only on the number of explicitly involved fingers. This approach offers a simple framework for the analysis of finger interaction during multi-finger actions.

## 1 Theoretical framework

Studies of human voluntary movements commonly use performance variables – in particular kinematic, kinetic, and electromyographic ones – to formulate and test hypotheses on the control and coordination of movements (Hogan 1984; Atkeson 1989; Gottlieb et al. 1989; Uno et al. 1989; Rosenbaum et al. 1995). Indeed, it is very tempting to formulate control hypotheses using readily measurable variables rather than poorly accessible or even metaphorical ones (cf. the equilibrium-point hypothesis: Feldman 1986; Latash 1993; Feldman and Levin 1996). However, the theoretical impossibility of the central nervous system (CNS) issuing control signals expressed in performance variables has been emphasized in a number of now-classical works (Bernstein 1935; Gelfand and Tsetlin 1966). Within the current study, we propose an approach that allows switching the analysis of motor control problems from a set of performance variables to a set of hypothetical central control variables during tasks involving multi-finger force production.

When a person produces isometric force with a subset of fingers within a hand, the other fingers of the hand also produce certain forces (Zatsiorsky et al. 1998, 2000; for similar findings see also Kilbreath and Gandevia 1994). Such involuntary force production by nonintended fingers has been termed "enslaving." The explicitly involved fingers are termed *master-fingers*, and the other force-producing fingers are called *slave-fingers*. Due to the enslaving, there is no direct correspondence between neural commands to individual fingers and finger forces. It is unclear whether there exists a set of independent variables controlled by the CNS during multi-finger force production tasks. The purpose of this work is to introduce such a hypothetical set of central variables, that we call "modes."

We hypothesize that, for each single-finger task, the CNS controls a unique variable (a mode) leading to force production by the master-finger as well as by the enslaved fingers. For instance, when a subject produces force voluntarily with the index finger (I), mode I is recruited by the CNS. Due to the enslaving phenomenon, mode I also leads to force production by the middle (M), ring (R), and little (L) fingers. Similarly, voluntary force production by either of these latter fingers is assumed to involve corresponding modes (mode M, mode R, and mode L, respectively). Therefore, a mode can be viewed as a collective variable, which leads to activation of many hand muscles bringing about a specific relationship among finger forces. A following question emerges: can a superposition of modes account for finger interaction during two-, three-, and four-finger tasks? The objective of the present study is to show that the mode approach is able to account for force patterns during maximal voluntary contraction (MVC) tasks by several fingers, based on

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force patterns recorded during single-finger MVC tasks. We develop a formal model and test its ability to account for data published earlier by our group, for a broad variety of studies including those of the effects of fatigue, aging, and handedness on multi-finger force production.

## 2 Model

### 2.1 Notion of the mode

The outline of the model is presented in Fig. 1. The model assumes the existence of four modes that the CNS manipulates according to the task. During MVC tasks, each mode is assumed to be either maximally recruited (state = 1) or not recruited at all (state = 0), depending on the explicitly involved finger combination. Each mode contributes to force production by each finger. In Fig. 1, this is illustrated with symbols with two subscripts: the first refers to a finger while the second refers to a mode contributing to force production by this finger. For example, in a task IR (i.e., MVC by the index and ring fingers), the force of the index finger will reflect a superposition of $F_{I,I}$ and $F_{I,R}$. In the same task, the middle and little fingers will also produce force reflecting superpositions of ($F_{M,I}$ and $F_{M,R}$), and ($F_{L,I}$ and $F_{L,R}$), respectively.

Let us consider the simplest possibility when superposition of different modes results in a simple summation of forces. During MVC production by I and R fingers, one can expect:

$$F_i = \sum_j F_{i,j}$$

where $i$ refers to a finger ($i$ = I, M, R, L), and $j$ refers to a mode ($j$ = I,R). For instance, $F_I = F_{I,I} + F_{I,R}$.

The results obtained for each finger force are presented in Table 1. Actual forces measured during I, R, and IR tasks are presented in the upper part of Table 1. The model predicts much higher forces than those observed experimentally, which is due to the model failing to account for the phenomenon of *force deficit*. Indeed, many studies have reported that during MVC tasks, the force produced by a given finger in a multi-finger task is smaller than the force generated by this finger in its single-finger task (Li et al. 1998b; for similar findings see also Ohtsuki 1981; Kinoshita et al. 1996); typically, force deficit increases when the number of fingers explicitly involved in a task increases. In order to account for the force-deficit effect, we have introduced in the model a free parameter $G$ that attenuates the result of force summation. Figure 2 illustrates this modification of the model where, after summation of the effects of individual modes, the result is attenuated by a factor $G < 1$. The magnitude of $G$ is defined using published experimental data.

### 2.2 Identification of the G factor

To obtain the best estimate of $G$, we used the most complete data set (averages across subjects) on single-hand, multi-finger MVC production published by Zatsiorsky et al. (1998). For each finger combination, a value of the $G$ factor was defined as the ratio of the actual total force to the predicted force computed as the sum of forces expected from individual mode effects. For instance, in the previous example of the IR task (Table 1), $G$ equals 82.3/134.2, that is 0.61 (see row b).

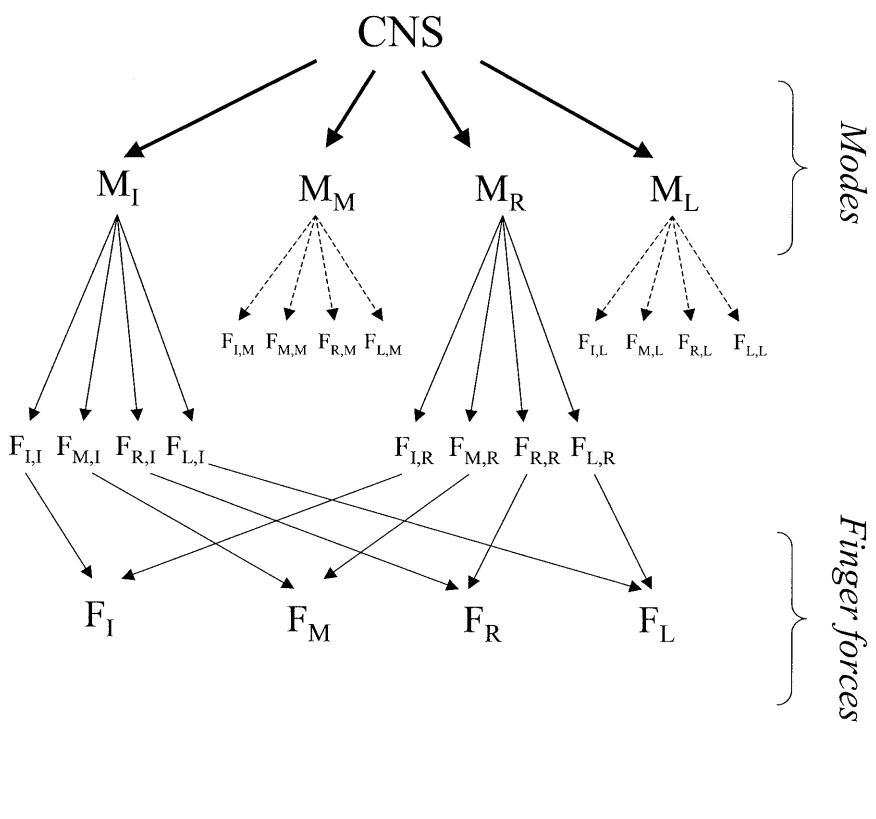


**Fig. 1.** The *mode* approach. This diagram illustrates the notion of modes during a maximal force-production (MVC) task by the index (*I*) and ring (*R*) finger (IR) task. During this two-finger task, two modes are activated ($M_I$ and $M_R$), while the two other ones ($M_M$ and $M_L$, involving the middle and little fingers, respectively) remains silent. Given that each mode influences the force produced by each finger, one needs to combine the effect of $M_I$ and $M_R$ to predict forces of individual finger during the IM task. See text for further details

**Table 1.** Computation of the gain factor $G$. This table shows how finger forces produced during MVC production by the index or the ring finger (*I* and *R* tasks) can be possibly used to predict individual finger forces during MVC production by the index and ring finger (*IR* task). In this task $G$ equals 0.61 (see *row b*), so that the predicted and experimental values of total force are identical (*circled numbers*). Other experimental values are provided for comparison. See text for further details

| | Task \ Fingers | $F_I$ | $F_M$ | $F_R$ | $F_L$ | $F_{Total}$ | |
|---|---|---|---|---|---|---|---|
| | I | 49.1 | 10.5 | 5.5 | 2.7 | 67.8 | Exp. Data |
| | R | 9.4 | 16.5 | 29.9 | 10.6 | 66.4 | |
| | IR | 37.0 | 14.5 | 21.6 | 9.2 | 82.3 | |
| a | I + R | 58.5 | 27.0 | 35.4 | 13.3 | 134.2 | Model |
| | ⇩ | | | | | | |
| b | 0.61 × (I + R) | 35.9 | 16.6 | 21.7 | 8.2 | 82.3 | |

**Table 2.** Values of the gain factor $G$ as a function of the task performed by different finger(s) to generate an MVC. The value of $G$ was computed using the method described in Table 1

| Task | G |
|---|---|
| I | 1 |
| M | 1 |
| R | 1 |
| L | 1 |
| IM | 0.61 |
| IR | 0.61 |
| IL | 0.61 |
| MR | 0.61 |
| ML | 0.6 |
| RL | 0.64 |
| IMR | 0.45 |
| IML | 0.43 |
| IRL | 0.44 |
| MRL | 0.45 |
| IMRL | 0.38 |

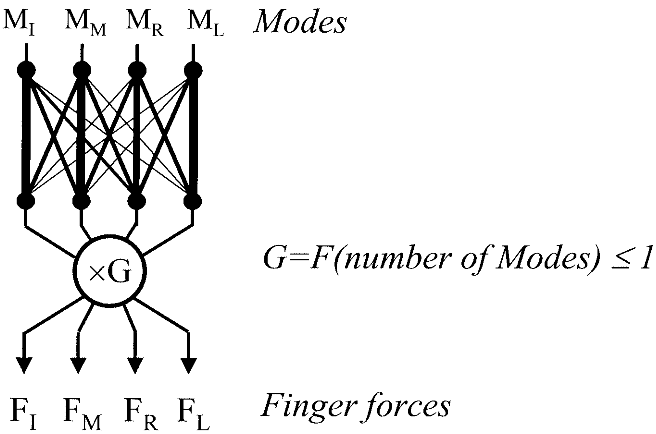


**Fig. 2.** The mode approach and force deficit. Modes do not sum up linearly. In order to account for the force-deficit effect, we propose that when several modes are simultaneously activated, their combined effect is altered by a gain factor $G < 1$

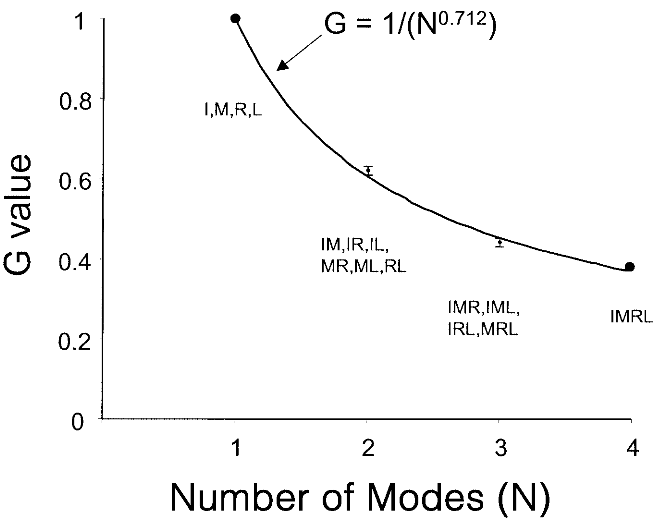


**Fig. 3.** Value of the gain factor ($G$) as a function of the number of modes simultaneously activated ($N$). For two- and three-finger tasks ($N = 2$ or 3), errors bars indicate the standard deviation of $G$ across the tasks; note the small size of the error bars. Curve-fitting techniques show that the equation $G = 1/N^{0.712}$ can account rather well for the drop in $G$ as $N$ increases

Table 2 shows that the $G$ values obtained for each task. When the number of fingers explicitly involved in a task increased, the value of $G$ decreased. By contrast, $G$ values were similar across tasks with the same numbers of explicitly involved fingers. For two-finger tasks $G$ ranged from 0.61 to 0.64, for three-finger tasks it ranged from 0.43 to 0.45, and for the four-finger task it was 0.38. Obviously, for one-finger tasks $G$ was equal to 1.

Figure 3 shows the relation between the value of $G$ (averaged across tasks with the same number of explicitly involved fingers, $N$) and $N$. To capture the dependence of $G$ on $N$, we fitted the data with a function $G = 1/N^y$ using the least-squares algorithm in MATLAB (MathWorks, MathWorks, Natick, Mass.). The best fit was obtained with the exponent $y = 0.712$, accounting for 99.9% of the variance. Based on this result we have decided to introduce a function $G = 1/N^y$ in the model, where $y$ is defined for each experimental condition and subject group to provide an optimal fit to the data.

It is fair to admit that other functions could account similarly well for the basic relation between $G$ and $N$. For instance, the following function could be used:

$$G = \frac{1}{\sqrt{N}} - a$$

where $N$ is the number of explicitly involved fingers. The square root of $N$ can be interpreted as the length of a mode vector, $M = (M_I, M_M, M_R, M_L)$, where $M_I, M_M, M_R$, and $M_L$ are either 1 or 0. The length of this vector is 1.41, 1.73, and 2 for $N = 2, 3$, and 4, respectively. Then, normalizing the length of the mode vector leads to $G$ factors of 0.71, 0.58, and 0.5. These values are higher than the experimental ones (0.61, 0.44, and 0.38) by a nearly constant value ($a \approx 0.12$). This formalization, similarly to $1/N^y$, also has one free parameter ($a$), which can be subject and task dependent.

## 3 Comparison to the published data

The model is tested with five data sets, all of them originating from our group. There are also studies by other groups reporting individual finger forces during multi-finger task (e.g., Ohtsuki 1981; Kinoshita et al. 1996; Santello and Soechting 2000). However, given that data relative to single-finger tasks are missing or incomplete, modes cannot be assessed. Note also that, in most of those studies, subjects performed a grasping task, and the mechanical constraints necessary to stabilize the handheld object are not taken into account by the present model. Among our own studies, data sets were selected bearing two intentions in mind: (i) we wanted to test the model in a wide spectrum of experimental conditions, and (ii) we gave priority to data sets that were explicitly reported in the original papers.

### *3.1 Zatsiorsky et al. (1998)*

In this study, young healthy subjects ($n = 10$) pressed with the fingertips of the dominant hand on sensors placed on a horizontal surface. All subjects were right-handed. All 15 finger combinations were tested (i.e., I, M, R, L, IM, IR, IL, MR, ML, RL, IMR, IML, IRL, MRL, and IMRL). Modes were defined based on data averaged across subjects in single-finger tasks. The function $G = 1/N^y$ was used to account for the force-deficit effect when several modes were simultaneously activated. As demonstrated earlier, $y = 0.712$ is the optimal value for this dataset.

Forty-four points are plotted in Fig. 4, with each point corresponding to the force of a particular finger in one of the eleven multifinger tasks. There is a significant strong correlation ($R = 0.978$, $p < 0.001$) between the predicted and actual data. The model is able to account for 95.3% of the variance. On average, individual finger forces are predicted with an absolute error of 2.2$N$.

A similar analysis was performed to quantify the performance of the model at the level of the force-sharing pattern. During each task, each finger produced a certain percentage of the total force produced by all involved fingers. The comparison between the predicted and experimental shares proved to be highly significant ($R = 0.978$, $p < 0.001$). On average, individual finger shares are predicted with an absolute error of 2.7%. Note that, because the gain factor $G$ affects all finger forces in a similar way, the force-sharing pattern (expressed as percentages of total force) predicted by the model is independent of $G$.

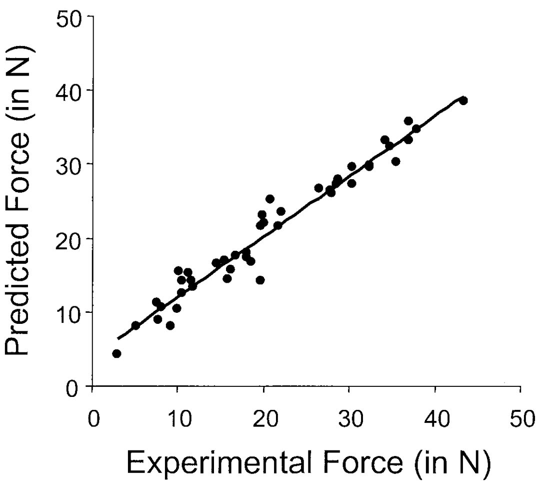


**Fig. 4.** Linear regression between the predicted and experimental forces. The individual finger forces predicted by the mode approach are plotted as a function of the experimentally recorded finger forces reported by Zatsiorsky et al. (1998). See text for further details

### *3.2 Danion et al. (2000a)*

This study investigated the effects of fatigue on multi-finger force production. Young healthy subjects ($n = 14$) generated force against loops positioned either at the middle of the distal phalanges (distal site), or at the middle of the proximal phalanges (proximal site). All subjects were right-handed and performed the tests with the dominant hand. Only single- and four-finger tasks were tested (i.e., I, M, R, L, and IMLR). These tasks were performed before and after a fatiguing exercise consisting of 60 s at 100% of MVC with all four fingers acting together. Modes were defined based on data averaged across subjects in the single-finger tasks. The quality of the fit was assessed by comparing the predicted finger forces during the four-finger tasks with the actual data. Optimal $G$ values were obtained separately for the two sites of force application, and also before and after the fatiguing exercise.

During force production at the distal site, the correlation between the predicted and experimental forces was significant both before ($R = 0.995$, $p < 0.01$), and after ($R = 0.999$, $p < 0.001$) the exercise. On average, the absolute errors were 1.5$N$ and 0.7$N$, respectively. The value of $G$ dropped during fatigue (0.60 vs 0.47).

During force production at the proximal site, the correlation between the predicted and experimental forces was just under the level of significance before the exercise ($R = 0.933$, $p = 0.07$), and not significant after the exercise ($R = 0.747$, $p > 0.1$). On average, the absolute errors were 3.3$N$ and 2.7$N$, respectively. The value of $G$ dropped during fatigue (0.51 vs 0.41).

### *3.3 Danion et al. (2000b)*

The goal of this study was to compare multi-finger force production in young ($n = 7$) and elderly ($n = 7$) subjects during MVC tasks at the distal and proximal sites. All subjects were right-handed and performed the tests with the dominant hand. Only single- and four-finger tasks were used. The setup was the same as that used in

Danion et al. (2000a), and the quality of the fit and the optimal $G$ values were assessed in the same way as for the earlier study.

During force production at the distal site, the correlation between the actual and predicted forces was significant for both young ($R = 0.987$, $p < 0.05$) and older adults ($R = 0.998$, $p < 0.01$). On average, the absolute errors were 1.4$N$ and 0.6$N$, respectively. The value of $G$ was very similar for both subject groups (0.592 vs 0.591).

During force production at the proximal site, the correlation between the predicted and actual forces was borderline significant for the young adults ($R = 0.938$, $p = 0.06$). However, this correlation was significant for the older adults ($R = 0.995$, $p < 0.01$). On average, the absolute errors were respectively 2.7$N$ and 0.9$N$, respectively. The value of $G$ was again very similar for both young and elderly subjects (0.518 vs 0.522).

### *3.4 Li et al. (2000a)*

This study compared multi-finger force production by the right and left hands in a group of right-handed subjects ($n = 13$). Forces were produced by the fingertips. Small wooden blocks shaped to fit comfortably under the subject's palms were placed underneath each palm. In this experiment, all single-, two- and four-finger tasks were tested. Data averaged across subjects were used to test the model. For each hand, the quality of the fit and the optimal $G$ values were defined using the same method as for the data of Zatsiorsky et al. (1998).

The value of $G$ was rather stable across the two-finger tasks. The average value of $G$ was $0.62 \pm 0.04$ (standard deviation across all six two-finger tasks) for the right hand, and $0.59 \pm 0.05$ for the left hand. For the four-finger tasks, the value of $G$ was 0.47 and 0.42 for the right and left hands, respectively. Based on the $G$ values, we have computed the 28 individual finger forces related to the seven multi-finger tasks. The correlation between the predicted and experimental forces was highly significant for both hands ($R > 0.986$, $p < 0.001$). On average, the absolute errors for the right and left hands were 1.0$N$ and 1.2$N$, respectively.

### *3.5 Li et al. (2000b)*

In this study, an objective was to investigate possible differences between the dominant and nondominant hands in a group composed of five right-handers and five left-handers. Force production was generated at the fingertips using the same setup as in Li et al. (2000a). In this experiment, subjects performed all single-finger tasks, two two-finger tasks (IM and RL), and the four-finger task. The method used to fit the data was the same as for Li et al. (2000a). The model was adjusted separately for the dominant and nondominant hands.

The value of $G$ was stable across the two-finger tasks, with small differences between the hands. For the dominant hand, the value of $G$ was 0.66 for the IM task and 0.65 for the RL task. For the nondominant hand, these values were 0.65 and 0.64, respectively. For the four-finger tasks, the value of $G$ was 0.44 and 0.43 for the dominant and nondominant hands, respectively. Based on the $G$ values, we computed the 12 individual finger forces related to the three multi-finger tasks. The correlation between the predicted and experimental forces was highly significant for both hands ($R > 0.985$, $p < 0.001$). The average absolute errors for the dominant and nondominant hands were 1.5$N$ and 1.4$N$, respectively.

## 4 Comparison with the neural network by Zatsiorsky et al. (1998)

A neural network (Zatsiorsky et al. 1998) has been proposed to account for finger interaction during maximal force production by one or several fingers. As illustrated in Fig. 5, the network consists of three layers: (i) the input layer that models a central neural drive, (ii) the hidden layer modeling the transformation of the central drive into signals to the muscles serving several fingers (multi-digit muscles), and (iii) the output layer representing force production by individual fingers. The output of the hidden layer is set inversely proportional to the number of fingers involved. In addition, direct connections between the input and output layers represent signals to the hand muscles serving individual fingers (unidigit muscles).

Zatsiorsky et al. (1998) used a complete data set for MVC tasks with all 15 finger combinations. They used the backpropagation-error algorithm to define an optimal set of weights within the three-layer network (Fig. 1). More formally, the model can be presented by the following equation:

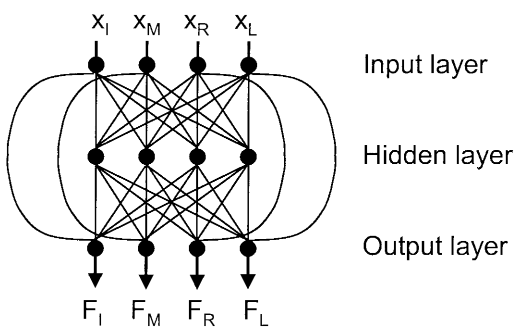


**Fig. 5.** The artificial neural network proposed by Zatsiorsky et al. (1998). The network consists of three layers: (i) the *input layer* that models a central neural drive, (ii) the *hidden layer* modeling the transformation of the central drive into signals to the muscles serving several fingers (multi-digit muscles), and (iii) the *output layer* representing force production by individual fingers. Figure adapted with permission from Zatsiorsky et al. (1998)

$$\begin{pmatrix} F_I \\ F_M \\ F_R \\ F_L \end{pmatrix} = \frac{1}{N}\begin{bmatrix} w_{I,I} & w_{I,M} & w_{I,R} & w_{I,L} \\ w_{M,I} & w_{M,M} & w_{M,R} & w_{M,L} \\ w_{R,I} & w_{R,M} & w_{R,R} & w_{R,L} \\ w_{L,I} & w_{L,M} & w_{L,R} & w_{L,L} \end{bmatrix} \bullet \begin{pmatrix} x_I \\ x_M \\ x_R \\ x_L \end{pmatrix} + \begin{pmatrix} v_I & 0 & 0 & 0 \\ 0 & v_M & 0 & 0 \\ 0 & 0 & v_R & 0 \\ 0 & 0 & 0 & v_L \end{pmatrix} \bullet \begin{pmatrix} x_I \\ x_M \\ x_R \\ x_L \end{pmatrix} \quad (1)$$

where $N$ is the number of fingers involved in the task, $F_i$ is the force of the $i$th finger ($i$ = I, M, R, L), $x_i$ are the inputs into the network, $w_{i,j}$ and $v_i$ are connection weights. The inputs to the network were set at $x_i = 1$ if the $i$th finger was explicitly recruited by the task, or $x_i = 0$ otherwise. The first term in the right-hand side of the equation represents the contribution to finger forces mediated by the hidden layer, while the second term represents the action of direct projections from the input layer.

Our mode approach can be formalized by the following equation:

$$\begin{pmatrix} F_I \\ F_M \\ F_R \\ F_L \end{pmatrix} = G\begin{bmatrix} w_{I,I} & w_{I,M} & w_{I,R} & w_{I,L} \\ w_{M,I} & w_{M,M} & w_{M,R} & w_{M,L} \\ w_{R,I} & w_{R,M} & w_{R,R} & w_{R,L} \\ w_{L,I} & w_{L,M} & w_{L,R} & w_{L,L} \end{bmatrix} \bullet \begin{pmatrix} M_I \\ M_M \\ M_R \\ M_L \end{pmatrix} \quad (2)$$

with the same abbreviations as for (1), plus $G$ as the scaling factor ($G = 1/N^y$) and $M_i$ as the input for each mode, with each mode being represented by a vector column of the $4 \times 4$ matrix. The inputs were set at $M_i = 1$ if the $i$th finger was explicitly recruited by the task, and $M_i = 0$ otherwise.

Coefficients in (1) were defined based on the data in all 15 finger tasks. In contrast, coefficients in (2) were defined based only on single-finger tasks. The optimal values for the data set of Zatsiorsky et al. (1998) are presented in (3) and (4):

$$\begin{pmatrix} F_I \\ F_M \\ F_R \\ F_L \end{pmatrix} = \frac{1}{N}\begin{bmatrix} 32.7 & 9.1 & 3.8 & 3.7 \\ 14.2 & 29.0 & 13.6 & 3.5 \\ 9.0 & 20.2 & 22.4 & 10.9 \\ 8.8 & 7.6 & 16.0 & 17.2 \end{bmatrix} \bullet \begin{pmatrix} x_I \\ x_M \\ x_R \\ x_L \end{pmatrix} + \begin{bmatrix} 16.9 & 0 & 0 & 0 \\ 0 & 10.1 & 0 & 0 \\ 0 & 0 & 8.3 & 0 \\ 0 & 0 & 0 & 7.2 \end{bmatrix} \bullet \begin{pmatrix} x_I \\ x_M \\ x_R \\ x_L \end{pmatrix} \quad (3)$$

$$\begin{pmatrix} F_I \\ F_M \\ F_R \\ F_L \end{pmatrix} = \frac{1}{N^{0.712}}\begin{bmatrix} 49.1 & 14.0 & 9.4 & 7.7 \\ 10.5 & 38.0 & 16.5 & 6.7 \\ 5.5 & 12.9 & 29.9 & 15.0 \\ 2.7 & 4.1 & 10.6 & 24.8 \end{bmatrix} \bullet \begin{pmatrix} M_I \\ M_M \\ M_R \\ M_L \end{pmatrix} \quad (4)$$

The performance of the neural network was tested by comparing the 60 individual forces predicted by this model to the actual forces. On average, the neural network provided a slightly better fit to the data than the mode approach, as indicated by the coefficient of correlation ($R = 0.989$ vs 0.976) and the average error (1.2$N$ vs 2.2$N$). There are, however, advantages to the mode approach. First, this approach uses only a few data sets (single-finger trials) to generate predictions for multi-finger tasks with only one free parameter ($y$), while the network uses data from both single- and multi-finger tasks to optimize connection weights. Second, even without this free parameter, the mode approach can still generate predictions for the force-sharing pattern (expressed as percentages of the total force).

## 5 Discussion

The mode approach has been tested in a wide variety of experimental conditions. The results show that in most of these conditions, the approach has been rather accurate. One notable exception is force production at the proximal phalanges. We would like to offer two mutually nonexclusive reasons for the relatively poor performance of the model in this task. First, subjects may feel clumsy during such tests, since everyday tasks rarely involve force production at proximal phalanges. Second, we could never completely secure the positions of the loops along the phalanges. Therefore the points of force application could differ across fingers and across trials. During force production at the distal site, such displacements have relatively small effects on the lever arms with respect to proximal phalanges. In contrast, during force production at the proximal site the relative change in the lever arms can become more significant, leading to more noise in the data.

### *5.1 A single framework for different phenomena*

The mode approach provides an attractive framework for the study of multi-finger interaction since it integrates in a simple way the phenomena of sharing, deficit, and enslaving. First, the mode approach suggests that the sharing pattern of the total force in multi-finger tasks results simply from a linear superposition of central variables (i.e., modes). The different shares of fingers during multi-finger MVC tasks (cf. Li et al. 1998a) result from the different enslaving patterns during single-finger tasks. Second, this approach proposes a simple relationship accounting for the force deficit observed during multi-finger tasks. Indeed, the gain factor $G$ depends only on the number of modes $N$ simultaneously activated (this $N$ dependence being captured by a decreasing function). More specifically, we found that, for a given value of $N$, the value of $G$ does not depend on the exact set of fingers involved in a task.

Third, the enslaving effect is captured in the settings of the modes themselves. The numbers accounting explicitly for the enslaving are the 12 off-diagonal terms in the $4 \times 4$ matrix in (4).

More specifically, the mode approach emphasizes that the enslaving and force-sharing phenomena are intimately related. For instance, a change in a single coefficient in the $4 \times 4$ matrix in (4) is accompanied by changes in both sharing and enslaving. In contrast, the model suggests that force deficit and enslaving are phenomena of different origins. Indeed, changing the value of the exponent $y$ has no effect on force sharing and enslaving, if both are expressed as percentages of the total force. This result is supported by published data. For instance, it has been shown that during fatigue, force deficit increases (leading to smaller values of $G$) while enslaving tends to decrease (see Danion et al. 2000a). Similarly, in elderly people there are relatively small changes in the force deficit (and in $G$), and relatively large and significant changes in the enslaving (Danion et al. 2000b).

### *5.2 Occlusion of enslaving*

Studies by Zatsiorsky et al. (1998, 2000) have shown that enslaving effects are nonadditive. Moreover, in certain cases, the enslaving effects induced by several explicitly activated fingers could be smaller than the enslaving when only one finger was explicitly recruited (this effect has been termed *occlusion of enslaving*). One can find such examples in Table 1 of Zatsiorsky et al. (1998), where data averaged across subjects are reported. For example, during a single-finger MVC task by the R finger, the enslaved force produced by the L finger is $10.6N$, whereas during a three-finger MVC task (IMR) the L finger force is only $5.1N$. Equation (4) also predicts a smaller enslaving force ($8N$) for the L finger during the IMR task based on the mode approach. Thus, this approach can account for relatively subtle effects such as the occlusion of enslaving, although quantitatively the prediction differs somewhat from the experimental results.

### *5.3 Force deficit in enslaved fingers*

In previous studies, the phenomenon of force deficit has been always emphasized for the master fingers (i.e., fingers explicitly required to produce force). The current approach views force deficit as being equally applicable to both master and slave fingers. The matrix in (4) implies that forces produced by slave fingers remain proportional to master-finger forces. This idea was partly introduced in Fig. 2 of Zatsiorsky et al. (2000), showing parallel changes in the slave- and master-finger forces during a force ramp. The gain factor in (4) applies to all components of the matrix and, as such, leads to proportional force-deficit effects in the forces produced by master- and slave-fingers.

### *5.4 Implications for the minimization of secondary moments*

It has previously been proposed that force sharing patterns emerge because the CNS tries to minimize the total moment produced by all fingers about the longitudinal functional axis of the hand (principle of minimization of secondary moments; Li et al. 1998a,b). It has also been shown that during one-, two-, or three-finger tasks, enslaving helps reduce the secondary moment (Zatsiorsky et al. 2000).

The mode approach suggests that minimization of secondary moments can follow from the force-sharing patterns during single-finger tasks. Are modes the cause or the consequence of secondary-moment minimization? We suggest that modes are developed based on everyday motor tasks involving the hand. Many everyday tasks involve stabilizing a gripped object, which requires balancing finger moments with respect to the thumb. If a person is asked to select a comfortable thumb position for a grip task, this position commonly coincides with the functional axis of the hand/forearm (Li et al. 1998b). Extensive practice of such tasks may be expected to lead ultimately to sharing patterns that comply with the principle of minimization of secondary moments.

### *5.5 Implications for the uncontrolled manifold hypothesis*

The notion of modes has been recently introduced in a series of studies investigating the structure of force variability during multi-finger tasks (Latash et al. 2001, 2002; Scholz et al. 2002). The analysis in these studies was based upon a hypothesis that the CNS controls the fingers using a set of central variables, or modes. The introduction of modes in those studies was done mostly for computational purposes. The present study suggests that the notion of modes is applicable across multi-finger force-production tasks and can be successfully applied to studies of different subject subpopulations and the effects of fatigue.

### *5.6 Generality of the mode approach*

In the present study we have shown that finger interaction can be captured by a matrix (representing the modes), a vector (defining which modes are recruited), and a gain factor (accounting for force deficit). A question emerges: how general are the matrix and the gain factor? First, there are obviously fluctuations in both across subjects. Besides differences in muscle strength, some subjects have a larger force deficit and/or enslaving. Second, the matrix and the gain factor depend on the experimental conditions. For instance, in young healthy subjects, the magnitude of force deficit depends on the setup used for force production, and on the site of force production (i.e., distal or proximal phalanges). Therefore, the main contribution of this work is not to propose a set of magic numbers that could account for finger interaction in all subjects and all tasks, but rather to introduce a specific framework that facilitates analysis of finger forces during both single- and multi-finger force-production tasks.

At a more general level, the main contribution of the force mode approach is to provide an example of how analysis of motor control problems can be performed using a set of hypothetical independent central control variables computed based on a set of performance variables (forces) measured in a few simple motor tasks. We hope that motor control studies that use kinematic and kinetic variables recorded during various motor tasks will follow this example and perform analyses of control processes using adequate sets of central control variables that are different from the performance ones. Such a generalization of the force mode approach is far from trivial and will probably require major effort.

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