

Predictive Modulation of Muscle Coordination Pattern Magnitude Scales Fingertip Force Magnitude Over the Voluntary Range

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Valero-Cuevas, Francisco J. Predictive modulation of muscle coordination pattern magnitude scales fingertip force magnitude over the voluntary range. *J. Neurophysiol.* 83: 1469–1479, 2000. Human fingers have sufficiently more muscles than joints such that every fingertip force of submaximal magnitude can be produced by an infinite number of muscle coordination patterns. Nevertheless, the nervous system seems to effortlessly select muscle coordination patterns when sequentially producing fingertip forces of low, moderate, and maximal magnitude. The hypothesis of this study is that the selection of coordination patterns to produce submaximal forces is simplified by the appropriate modulation of the magnitude of a muscle coordination pattern capable of producing the largest expected fingertip force. In each of three directions, eight subjects were asked to sequentially produce fingertip forces of low, moderate, and maximal magnitude with their dominant forefinger. Muscle activity was described by fine-wire electromyograms (EMGs) simultaneously collected from all muscles of the forefinger. A muscle coordination pattern was defined as the vector list of the EMG activity of each muscle. For all force directions, statistically significant muscle coordination patterns similar to those previously reported for 100% of maximal fingertip forces were found for 50% of maximal voluntary force. Furthermore the coordination pattern and fingertip force vector magnitudes were highly correlated ($r > 0.88$). Average coordination pattern vectors at 50 and 100% of maximal force were highly correlated with each other, as well as with individual coordination pattern vectors in the ramp transitions preceding them. In contrast to this consistency of EMG coordination patterns, predictions using a musculoskeletal computer model of the forefinger show that force magnitudes $\leq 50\%$ of maximal fingertip force can be produced by coordination patterns drastically different from those needed for maximal force. Thus when modulating fingertip force magnitude across the voluntary range, the number of contributing muscles and the relative activity among them was not changed. Rather, the production of low and moderate forces seems to be simplified by appropriately scaling the magnitude of a coordination pattern capable of producing the highest force expected.

INTRODUCTION

Task-specific motor strategies have been hypothesized to simplify the coordination of redundant musculature to reduce delays and improve performance in the nervous system (Bernstein 1967). However, in the case of the redundant musculature of the fingers, little attention has been paid to the basic question of how a muscle coordination pattern is selected from a large pool of valid alternatives to achieve a specific submaximal

fingertip force magnitude. The coordination of finger musculature is redundant because fingers have sufficiently more muscles than joints. As a result, every fingertip force of submaximal magnitude can in theory be produced by an infinite number of different, yet functionally equivalent, muscle coordination patterns (Chao and An 1978; Valero-Cuevas et al. 1998). Even the common task of grasping, lifting, and placing objects requires selecting an appropriate sequence of muscle coordination patterns to modulate fingertip force magnitudes between zero (when the fingertips first come in contact with or releases the object) and the magnitude necessary to lift the object. Thus the control of finger musculature during grasping could be simplified by a motor strategy that did not require adopting a different muscle coordination pattern for each level of submaximal fingertip force magnitude. One such simplifying motor strategy would be to implement a muscle coordination pattern capable of producing the largest expected fingertip force and scale down this pattern to produce fingertip forces of lower magnitudes. Unfortunately the lack of direct methods for recording descending motor commands has made it difficult both to describe complete muscle coordination patterns for finger musculature and to identify motor strategies during fingertip force production. Luckily there are practical tools that can describe these patterns *indirectly*, as intramuscular electromyograms (EMGs) can characterize descending motor commands to multiple finger muscles (Basmajian and De Luca 1985).

To date, no EMG study has reported subject-independent muscle coordination patterns for the modulation of fingertip force magnitude over the voluntary range, which has been interpreted as evidence that the control of redundant finger musculature may be idiosyncratic and variable. EMG has been used to study the activity of different muscles during the production of low fingertip forces (Close and Kidd 1969; Long et al. 1970; Maier and Hepp-Reymond 1995a,b) and of moderate and maximal voluntary fingertip forces (MVF) of the thumb (Chao et al. 1989; Cooney et al. 1985). The lack of consistent coordination patterns in these studies is not necessarily evidence of idiosyncratic motor strategies during ramp-and-hold force tasks. Various experimental limitations may have rendered the experimental task ambiguous or introduced variability into the EMG recordings. Because the digits have three flexion mechanical degrees-of-freedom, the distal phalanx can impart a torque to an object in contact with it (i.e., fingertip torque) independently of the force it produces. Thus previous force measurement techniques may confound the

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interpretation of EMGs because the compliant and high-friction interface between the bare finger pad and dynamometer allow production of fingertip torque, which is not measured, and latitude in the direction of force application. In addition, finger (Mathiowetz et al. 1985; Weightman and Amis 1982) and wrist (O'Driscoll et al. 1992) posture affect finger mechanics and muscle fiber length, which influence muscle force and EMG output (Zajac 1992). Similarly, the high EMG scatter reported for fingertip forces of low magnitude (Maier and Hepp-Reymond 1995a) underscores that factors particular to low force production may obscure the detection of motor strategies. These include the nonlinearities at the low end of the force-EMG curve (Basmajian and De Luca 1985; Lawrence and De Luca 1983) and the stronger variability in the relationship between EMG and force caused by other modulating factors such as the influence of peripheral receptors (Garnett and Stephens 1981). Such factors may explain the inconsistency in reported maximal tip and key pinch forces [19 to 106 N (Mathiowetz et al. 1985; Weightman and Amis 1982)] and EMG patterns (Close and Kidd 1969; Long et al. 1970; Maier and Hepp-Reymond 1995a). Furthermore these studies did not simultaneously record from all muscles of the digit in question and therefore do not describe complete muscle coordination patterns. In a previous study designed to isolate fingertip force magnitude from direction and fingertip torque while standardizing forefinger posture (Valero-Cuevas et al. 1998), we reported subject-independent muscle coordination patterns for maximal voluntary fingertip forces. This consistency of coordination patterns is evidence of intersubject consistency of motor strategies for static ramp-and-hold force production. The analysis of these coordination patterns, using a three-dimensional musculoskeletal computer model of the forefinger, indicated that these coordination patterns were mechanically advantageous. This suggests that mechanical principles may govern the selection of muscle coordination patterns. However, we did not study muscle coordination patterns for low and moderate forces.

Another indirect method to elucidate motor strategies in redundant systems such as the fingers is musculoskeletal computer modeling (Chao and An 1978). Musculoskeletal computer models can numerically predict coordination patterns that fulfill specific functional requirements during the simulated performance of a task. Similarly, musculoskeletal models of redundant systems can explicitly predict a variety of valid muscle coordination patterns for a specific task. The predicted variability among these functionally equivalent muscle coordination patterns then can provide valuable insight into the nature and extent of the redundancy of control of finger musculature. To date, no three-dimensional musculoskeletal model that includes all finger muscles has been used to explore the redundancy of finger motor control.

This study examines the hypothesis that the selection of muscle coordination patterns to span a broad range of fingertip force magnitudes is simplified by appropriately modulating the coordination pattern capable of producing the largest expected force. Simultaneous EMG recordings from all seven muscles of the forefinger are used to estimate muscle coordination patterns during the sequential production of fingertip force from 0 to 50% MVF, from 50 to 100% MVF, and from 100 to 50% MVF. A three-dimensional, seven-muscle musculoskeletal computer model is used to predict the variability among

muscle coordination patterns that can produce forces $\leq 50\%$ of maximal magnitude. The hypothesis was tested for three fingertip force directions by comparing the variability among EMG coordination patterns that subjects used to span the voluntary range of fingertip force magnitude with the variability among different coordination patterns predicted by the model to produce fingertip forces $\leq 50\%$ of maximal magnitude. The hypothesis would be supported if similar EMG coordination patterns were used by the subjects to span the voluntary range of fingertip force magnitude, yet the model showed that substantially different coordination patterns could have been used to produce fingertip forces of $\leq 50\%$ MVF magnitude. If confirmed, this hypothesis would be an example of a task-specific motor program for the coordination of redundant muscles.

METHODS

Subjects

Eight right handed individuals (6 female, 2 male; age 27 ± 6 yr; mean \pm SD) with no history of hand injury or dysfunction participated. Before participation, each subject read and signed a consent form approved by the Medical Committee for Protection of Human Subjects in Research at Stanford University.

Experimental production of fingertip forces

In a manner similar to that previously reported (Valero-Cuevas et al. 1998), subjects produced fingertip forces by ramping from 0 to 50% MVF, to 100% MVF and back to 50% MVF while maintaining their forefingers in a standardized posture, Fig. 1. Subjects placed their forearm in a trough, wrapped their dominant right hand around a fixed dowel to isolate forefinger function. Subjects generated three maximal forefinger forces in the dorsal, palmar, and distal, directions in randomized order while maintaining the standard posture. The standardized finger posture was defined as neutral ad-abduction, 45° flexion at metacarpophalangeal and proximal interphalangeal joints, and 10° flexion at distal interphalangeal joint. The forefinger did not rest

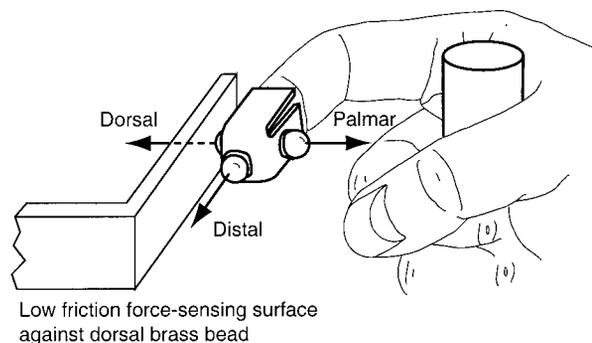


FIG. 1. Experimental paradigm allowing subjects to modulate fingertip force magnitude while maintaining fingertip force direction constant. In a manner previously described (Valero-Cuevas et al. 1998), subjects placed their right forearm in a trough and wrapped their dominant right hand around a fixed dowel to isolate forefinger function. Each subject placed their forefinger in neutral ad-abduction with 45° flexion at the metacarpophalangeal and proximal interphalangeal joints, and 10° flexion at the distal interphalangeal joint with the forefinger not resting against the middle finger. The wrist of each subject was in full extension and neutral radial deviation. In each 10-s trial, subjects were asked to produce force in 1 of 3 force directions labeled dorsal, palmar, and distal. The low friction between the brass beads embedded in the custom molded thimble and the force-sensing surface guaranteed that as long as the finger maintained its posture, fingertip forces were directed in the desired directions.

against the middle finger. The wrist was held in full extension and neutral radial deviation by the trough and dowel without requiring straps. Subjects wore custom thimbles made of thermoplastic splinting material (MaxD, North Coast Medical, Morgan Hill, CA) with 5-mm brass balls that defined the directions of force production. A 6-axis dynamometer (Gamma F/T Transducer, ATI Industrial Automation, Garner, North Carolina; 0.1 N resolution in force axes) was positioned and rigidly held by a 6-DOF robot arm (Puma 260, Stäubli-Unimate, Faverges, France; 0.5-mm position accuracy) such that one ball at a time came in contact with the low-friction surface of the dynamometer. The friction characteristics of the contact required finger force to be directed within 16° of the surface normal for the ball in contact not to slip. Fingertip torque had to be zero for the thimble not to rotate about the contact point. In each 10-s trial, subjects were asked to sequentially achieve and hold three fingertip force plateaus (50, 100, and 50% of MVF, in that order) for 2 s under concurrent visual and auditory feedback of the 50% MVF and 100% MVF targets (see diagram in Table 1). Two sessions were run on separate days. In the first session, the experimental set-up was adjusted to the dimensions of the subject's hand, and a test trial was done for each direction to estimate the starting 100% MVF target. The programmable robot arm quickly positioned and rigidly held the force-sensing surface against the appropriate aspect of the fingertip, and subjects performed a battery of three trials in each of the three directions in randomized order. Subjects were encouraged verbally to exceed the 100% MVF target in every trial to maximize their force production. If exceeded, the 100% MVF targets were increased automatically for that direction and the new maximal value used in all subsequent trials. The maximal force values recorded in the first session were used as the starting targets for the second session and also were adjusted upward if exceeded during the second session. In the second session on the following day, fine-wire EMG was recorded simultaneously from all muscles of the forefinger while subjects repeated the battery of trials in a new randomized sequence.

Electromyography

Fine-wire intramuscular electrodes were placed in all muscles and muscle slips acting on the forefinger using previously reported techniques (Burgar et al. 1997). The muscles of the forefinger are *flexor digitorum profundus* (FDP), *flexor digitorum superficialis* (FDS), *extensor indicis proprius* (EI), *extensor digitorum communis* (EC), *first lumbrical* (LUM), *first dorsal interosseous* (DI), and *first palmar interosseous* (PI). EMGs were 100 Hz to 20 kHz band-pass filtered, amplified, full-wave rectified and smoothed ($t = 20$ ms), and digitized at 200 s/s. The EMG signals from each muscle were normalized by dividing by the largest EMG level found during maximal voluntary contractions of that muscle. Maximal voluntary contractions of individual muscles were done immediately before and after fingertip force production with the forefinger braced in the same posture used for fingertip force production (Burgar et al. 1997; Valero-Cuevas et al. 1998). This normalization allowed the description of the level of EMG activity of each muscle as a value between 0 and 1. The presence of multiple fine-wire electrodes does not significantly affect fingertip force production (Burgar et al. 1997).

Definition of fingertip force vectors and EMG coordination pattern vectors

For every sample of every trial (200 S/s over 10 s make 2,000 sample points per trial), the three force components recorded by the force-sensing surface were assembled into a three-dimensional fingertip force vector $\{\mathbf{f}_x, \mathbf{f}_y, \mathbf{f}_z\}^T$. Similarly, the seven EMG signals from individual muscles were assembled into a "coordination pattern vector" $\{\mathbf{FP}, \mathbf{FS}, \mathbf{EI}, \mathbf{EC}, \mathbf{LUM}, \mathbf{DI}, \mathbf{PI}\}^T$.

Correlation between force and coordination pattern vector magnitudes

The Euclidean magnitude (defined as the square root of the sum of squares of the elements of the vector) of every fingertip force and muscle coordination pattern vector was calculated at every sample of every trial. In this way, as shown in Fig. 4B, the time histories of the vector magnitudes of fingertip force and muscle coordination pattern were obtained for each trial. The Pearson product-moment correlation coefficient between these two time histories was calculated and averaged across trials. Similarly, the correlation coefficient between the time histories of fingertip force vector magnitude and EMG level for each muscle was calculated and averaged across trials.

Definition of force plateaus and transition regions

Force plateaus were defined at the first 50% MVF level, at the 100% MVF level, and at the second 50% MVF level of each trial (Fig. 2). Each plateau was defined as a 750-ms window centered on each of the three periods in which force was held level. For each trial, transition regions a, b and c were defined, respectively, from time 0 to the beginning of the first 50% plateau; from the end of the first 50% to the beginning of the 100% plateau; and from the end of the 100% to the beginning of the second 50% plateau (see the legend in Table 1).

The average fingertip force vector within each plateau was defined by averaging each of the three fingertip force components: $\{\mathbf{f}_{x_{avg}}, \mathbf{f}_{y_{avg}}, \mathbf{f}_{z_{avg}}\}^T$. Similarly, the average muscle coordination pattern vector within each plateau was defined as the average normalized EMG signals from each muscle, $\{\mathbf{FP}_{avg}, \mathbf{FS}_{avg}, \mathbf{EI}_{avg}, \mathbf{EC}_{avg}, \mathbf{LUM}_{avg}, \mathbf{DI}_{avg}, \mathbf{PI}_{avg}\}^T$ (Valero-Cuevas et al. 1998).

Correlation between fingertip force vectors at different levels of fingertip force magnitude

To determine the consistency of force direction during modulation of force magnitude, the degree of alignment between average fingertip force vectors at different force plateaus was quantified by the square

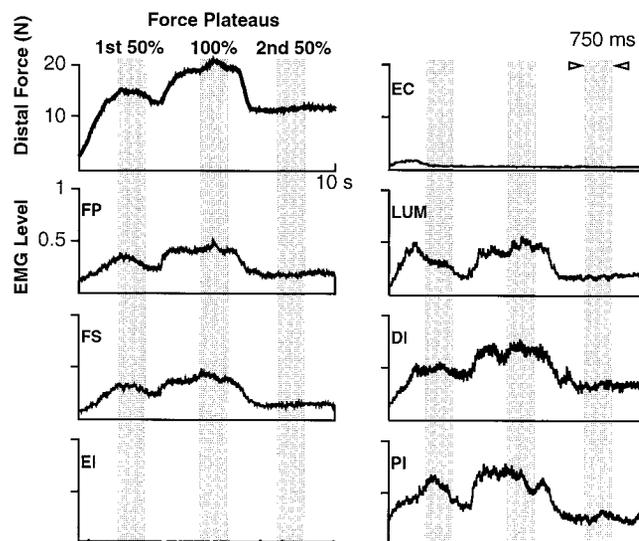
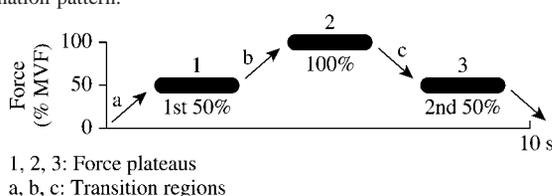


FIG. 2. Representative sample trial of distal force and fine-wire electromyographic (EMG) recordings from the 7 muscles of the forefinger. In each 10-s trial, subjects were asked to sequentially achieve and hold 3 fingertip force plateaus (50, 100, and 50% of maximal voluntary fingertip force, in that order) under concurrent visual and auditory feedback. Force and normalized EMG signals were each averaged over 750 ms of each force plateau. Three trials in each of 3 force directions (dorsal, palmar, and distal) were collected in randomized order.

TABLE 1. Degree of alignment among 3-dimensional fingertip force and among 7-dimensional coordination pattern vectors

Comparison	Force Direction		
	Dorsal	Palmar	Distal
Force vectors			
1:2	0.9976 ± 0.0032	0.9983 ± 0.0020	0.9988 ± 0.0014
1:3	0.9948 ± 0.0163	0.9985 ± 0.0019	0.9983 ± 0.0026
2:3	0.9930 ± 0.0236	0.9983 ± 0.0019	0.9982 ± 0.0039
a:1	0.9908 ± 0.0174	0.9909 ± 0.0314	0.9831 ± 0.0653
b:2	0.9811 ± 0.0456	0.9972 ± 0.0025	0.9976 ± 0.0033
c:3	0.9786 ± 0.0506	0.9968 ± 0.0063	0.9919 ± 0.0400
CP vectors			
1:2	0.9747 ± 0.0194	0.9854 ± 0.0140	0.9835 ± 0.0154
1:3	0.9682 ± 0.0349	0.9816 ± 0.0208	0.9825 ± 0.0206
2:3	0.9739 ± 0.0207	0.9823 ± 0.0164	0.9814 ± 0.0196
a:1	0.9751 ± 0.0198	0.9692 ± 0.0336	0.9781 ± 0.0267
b:2	0.9589 ± 0.0360	0.9729 ± 0.0210	0.9717 ± 0.0229
c:3	0.9640 ± 0.0262	0.9780 ± 0.0190	0.9758 ± 0.0191

Values are means ± SD. Comparisons are made between force plateaus (number:number), and between transition regions and subsequent force plateau (letter:number). See legend below. CP, coordination pattern.



root of the dot product of their unit vectors. This measure of alignment is provided by the correlation coefficient between two unit vectors (Klecka 1989; Strang 1980), denoted by a value between 0 (perpendicular) and 1 (parallel). These correlation coefficients are labeled 1:2, 1:3, and 2:3 in the top half of Table 1.

The consistency of fingertip force vector direction between transition regions and subsequent force plateaus was calculated similarly. First, the unit vector of the fingertip force vector at each digitized sample in the transition region was calculated. Second, the square root of the dot product of each of these unit vectors with the unit vector of the average fingertip force vector at the subsequent force plateau was calculated and averaged for each transition region of every trial. And third, these average correlation coefficients were averaged across subjects and force directions. These correlation coefficients are labeled a:1, b:2 and c:3 in the top half of Table 1.

Correlation between muscle coordination pattern vectors at different levels of fingertip force magnitude

When the excitation of a muscle is represented as a value between 0 and 1 along an axis, a muscle coordination pattern vector can be thought of as a point in seven-dimensional "muscle space." Then, every muscle coordination pattern vector can be thought of as having a magnitude and direction in seven-dimensional muscle space. Therefore the correlation coefficient (i.e., degree of alignment) between average muscle coordination pattern vectors at different force plateaus also was calculated by the square root of the dot product of their unit vectors. As was done for fingertip force vectors in the preceding text, the correlation coefficients between muscle coordination pattern vectors at different force plateaus were calculated and labeled 1:2, 1:3, and 2:3 in the bottom half of Table 1. Similarly, the correlation coefficients of muscle coordination pattern vectors in a transition region with the average muscle coordination pattern vector in the subsequent plateau were calculated, averaged, and labeled a:1, b:2 and c:3 in the bottom half of Table 1.

Statistical analysis of muscle coordination patterns at each force plateau

For each force plateau in each force direction, average muscle coordination pattern vectors from all subjects were pooled, and repeated-measures ANOVA was used to test for differences among EMG signals from individual muscles (Valero-Cuevas et al. 1998). When a significant difference was found, Turkey-Kramer post hoc pairwise comparisons were used to test for significant groupings of EMG signals within the average coordination patterns vectors. In this way, a muscle coordination pattern for each force direction was described statistically in absolute terms as the ranking of muscles by EMG level (Valero-Cuevas et al. 1998). This ranking succinctly conveys the coordination pattern by indicating the statistical differences in excitation levels among muscles.

Prediction of muscle coordination patterns capable of producing 50% of maximal fingertip force magnitude

A previously validated three-dimensional, seven-muscle, four-joint musculoskeletal computer model of the forefinger was used to predict different muscle coordination patterns that can produce 50% of maximal biomechanically possible fingertip force (Valero-Cuevas et al. 1998). The model is a matrix equation that relates coordination pattern vectors to fingertip force vectors. The model was used to predict different muscle coordination patterns that can produce 50% of maximal fingertip force, consistent with the 50% MVF force plateaus and finger posture of the experimental part of this study.

The model uses computational geometry to identify coordination patterns that can produce maximal and submaximal fingertip forces in a specific direction as previously described by Valero-Cuevas et al. (1998). Briefly, the excitation of a muscle is modeled as a value between 0 and 1 along an axis. By assembling as many orthogonal axes as there are muscles, a modeled muscle coordination pattern vector also can be thought of as a point in seven-dimensional muscle space. Furthermore every possible muscle coordination pattern vector is contained in the positive seven-dimensional hyper-cube of sides of

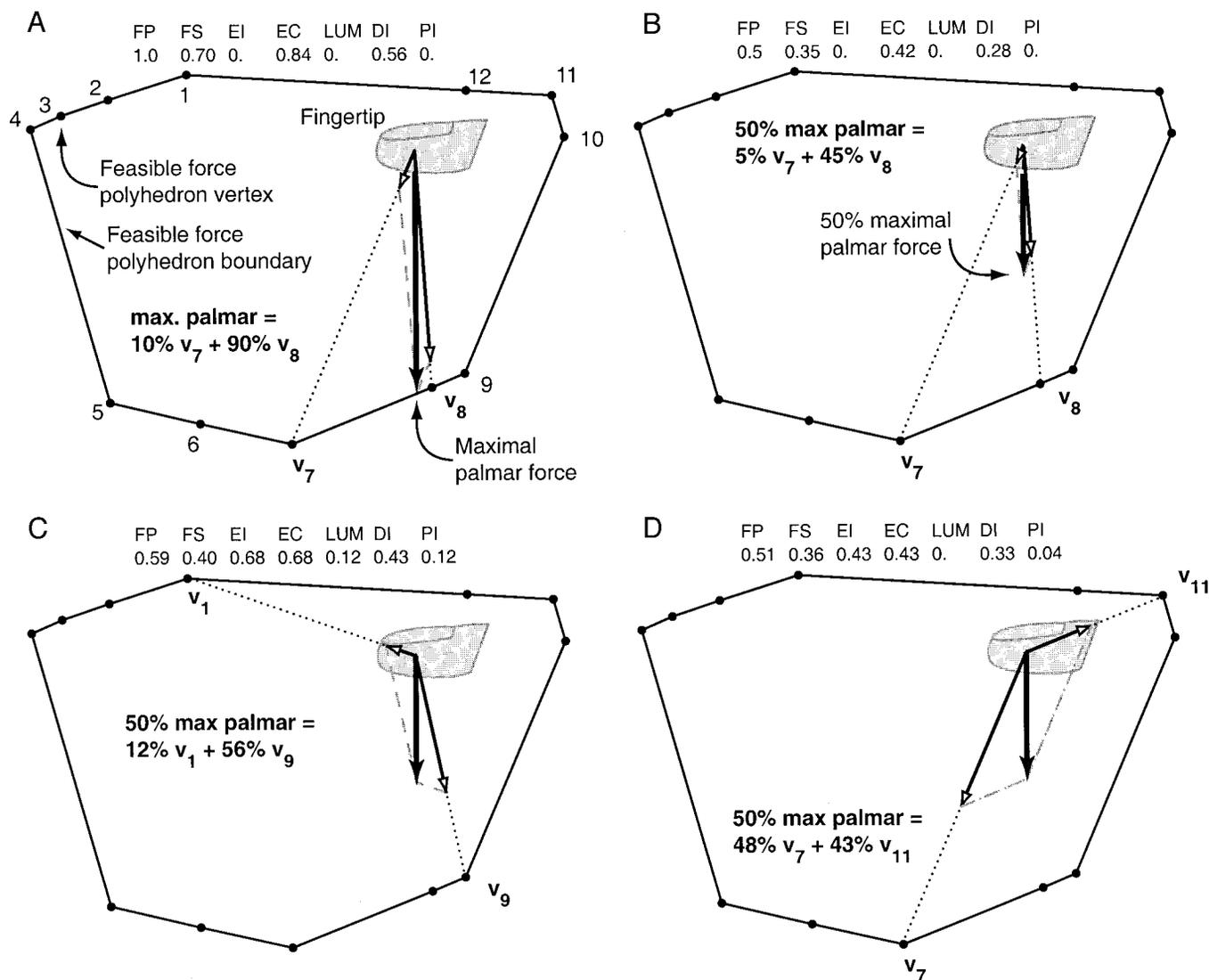


FIG. 3. Graphic interpretation of muscle redundancy for submaximal forces. A previously validated model describes the “feasible force polyhedron,” which predicts the maximal fingertip forces that are biomechanically possible in the plane that includes the dorsal, palmar, and distal fingertip forces studied (Kuo and Zajac 1993; Valero-Cuevas et al. 1998). Every fingertip force of maximal magnitude (point along boundary) is produced by a unique muscle coordination pattern. A: maximal palmar force. In contrast, every point inside boundary, i.e., a submaximal force, can be achieved by an infinite number of different muscle coordination patterns. Three sample of coordination patterns capable of producing 50% of maximal palmar force are calculated as linear combinations (i.e., vector sum) of some of its 12 vertices. B: using vertices 7 and 8, which is simply produced by setting coordination pattern that produces the maximal palmar force at half magnitude. C: using vertices 1 and 9. D: using vertices 7 and 11. Excitation pattern for each valid solution then was found by applying the same vector sum to the 2 coordination patterns of the force vertices used and are shown next to each case. All 99 coordination patterns predicted for 50% of maximal force (see METHODS) are summarized as excitation level histograms for each muscle in Fig. 6.

length one. Its 128 vertices define the boundary of the hyper-cube. A functional specification of fingertip force direction and fingertip torque magnitude is interpreted geometrically as a constraint plane that contains all possible coordination patterns that satisfy the functional constraint. Thus, the region of the hyper-cube that satisfies all constraints is the intersection of all such hyper-planes with the hyper-cube. Computational geometry algorithms (Avis and Fukuda 1992) identify 46 vertices that describe the region of the hyper-cube containing all possible muscle coordination patterns that produce fingertip forces with zero medial-lateral force and zero fingertip torque components. These functional constraints on fingertip force direction and torque are equivalent to those imposed on subjects when producing palmar, dorsal, and distal fingertip forces. Multiplying all 46 coordination pattern vertices through the musculoskeletal model matrix equations resulted in 46 fingertip force vectors (Chvátal 1983).

Twelve of the 46 fingertip force vectors define the boundary of the feasible force polyhedron that specifies the biomechanical limit on fingertip force magnitudes (Fig. 3A) (Chvátal 1983; Valero-Cuevas et al. 1998). The distance from the origin to a point on the boundary of the feasible force polyhedron in a given three-dimensional direction is proportional to the maximal fingertip force that can be produced in that direction (Fig. 3A). Because every point along a face of the boundary is uniquely defined by the weighted sum of the vertices that define that edge, every maximal fingertip force (i.e., point on the boundary) also is produced by a unique muscle coordination pattern (Chao and An 1978; Kuo and Zajac 1993; Spoor 1983; Valero-Cuevas et al. 1998). In contrast, points internal to the boundary can be produced by different vector sums of vertices. Thus a geometric interpretation of redundancy of control of finger musculature is that every submaximal force, i.e., point internal to the boundary, can be

achieved by more than one vector sum of force vertices. Figure 3, *B–D*, shows three such solutions for palmar force using force vertices from the boundary. The coordination pattern that achieves each of the vector sums of force vertices then is found by applying the same vector sum to the unique coordination patterns associated with the force vertices used (see Fig. 3, *B–D*). A combination of two force vertices is considered biomechanically valid if the coefficients of their vector sum and the resulting muscle excitations are positive values between 0 and 1 (i.e., fingertip forces and tendon tensions act only in their positive sense).

This geometric interpretation of redundancy of finger musculature control was used to predict different muscle coordination patterns that can produce fingertip force magnitudes of $\leq 50\%$ of maximal in the dorsal, palmar, and distal directions. For each force direction, an ordered lexicographic search tested all possible combinations of 2 of the 46 force vertices to find valid coordination patterns that can produce 50% of maximal force.

RESULTS

Correlation between fingertip force vectors at different levels of fingertip force magnitude

The direction of fingertip force vectors remained consistent while subjects varied the magnitude of fingertip force vectors over the voluntary range. The correlation coefficient between average fingertip force vectors at different plateaus was in excess of 0.99 (comparisons labeled 1:2, 1:3, and 2:3 in the top half of Table 1) and in excess of 0.97 (comparisons labeled a:1, b:2, and c:3 in the top half of Table 1) between force vectors in the transition regions and the average fingertip force vector in the subsequent force plateau. Figure 4A shows a three-dimensional view of the time history of fingertip force vector for one representative fingertip force in the distal direction.

Correlation between muscle coordination pattern vectors at different levels of fingertip force magnitude

Similarly, the coordination pattern vectors maintained a consistent seven-dimensional direction in muscle space while pro-

ducing fingertip forces of different magnitudes. Average coordination pattern vectors were correlated highly between plateaus (in excess of 0.96; see comparisons labeled 1:2, 1:3, and 2:3 in the bottom half of Table 1) as were coordination pattern vectors in the transition regions with the average coordination pattern vector in the subsequent force plateau (in excess of 0.95; see comparisons labeled a:1, b:2, and c:3 in the bottom half of Table 1). The high correlation between measured coordination pattern vectors at different force magnitudes suggests subjects altered the vector magnitude of the motor command, whereas the vector direction of the motor command remained consistent.

Correlation between force and coordination pattern vector magnitudes

The vector magnitudes of coordination patterns and fingertip forces were highly correlated (0.89 ± 0.06 , 0.88 ± 0.05 , and 0.91 ± 0.07 for dorsal, palmar, and distal forces, respectively; column labeled CP in Fig. 5). Figure 4, *B* and *C*, shows the time histories of fingertip force and coordination pattern magnitudes for the trial shown in Fig. 4A. The correlation of some muscles with fingertip force magnitude was statistically similar to that of the coordination pattern with force (gray box plots in Fig. 5, $P < 0.05$). Other muscles had a statistically lower correlation with fingertip force magnitude (white box plots in Fig. 5, $P < 0.05$).

Doubling or halving fingertip force magnitude between force plateaus was associated with a similar change in average coordination pattern vector magnitudes. For all force directions, the ratio of average fingertip force vector magnitudes between the 100 and 50% force plateaus was 2.07 ± 0.51 . The corresponding ratio for coordination pattern vector magnitudes was 1.86 ± 0.62 . Comparing across force directions, the average fingertip force ratios were lowest for palmar force (1.93 ± 0.32) and highest for distal force (2.18 ± 0.78 ; $P < 0.05$). This difference also was found in coordination pattern vector ratios, which were significantly higher for distal force (2.06 ± 0.64)

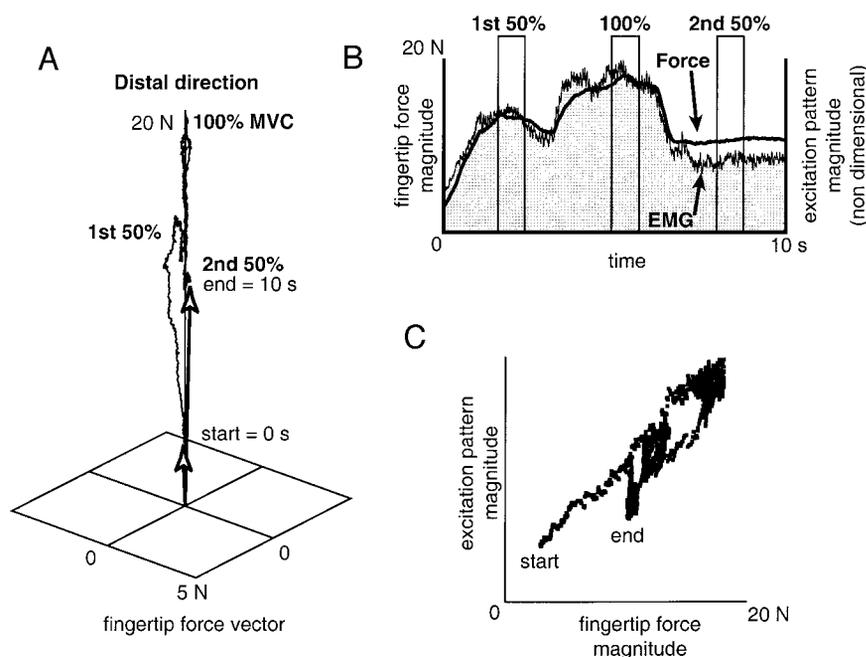


FIG. 4. Example of fingertip force production in the distal direction. *A*: 3-dimensional (3-D) plot of the fingertip force time history. *B*: time histories of the magnitudes (Euclidean norms) of the 3-D fingertip force magnitude vector (*left scale*) and 7-D excitation pattern vector (*right scale*). *C*: plot of excitation pattern vector magnitude vs. fingertip force vector magnitude ($r = 0.91$ for this trial). Note that data collection began when the subject was already producing 5 N of force.

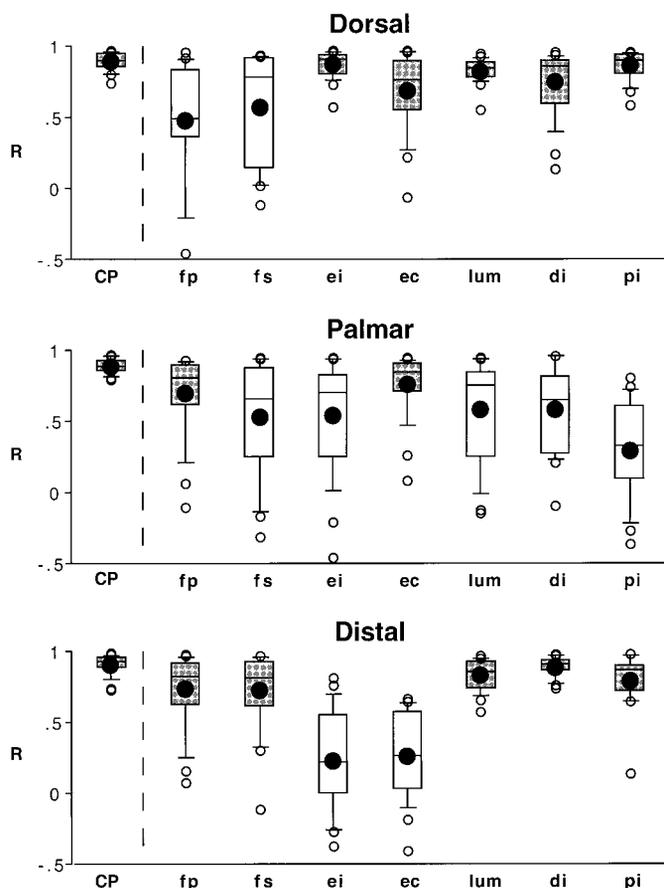


FIG. 5. Correlation coefficients of coordination pattern (CP) magnitudes and EMG from individual muscles with fingertip force magnitude. Magnitude of CP vectors was correlated highly with the magnitude of the fingertip force vectors (0.89 ± 0.06 , 0.88 ± 0.05 , and 0.91 ± 0.07 for dorsal, palmar, and distal forces, respectively). Correlation of EMG signals from some individual muscles with fingertip force magnitude was also statistically similar to that of the coordination pattern (gray box plots), and higher than that of other muscles (white box plots) (ANOVA post hoc tests, $P < 0.05$).

than for palmar and dorsal forces (1.64 ± 0.56 and 1.80 ± 0.58 , respectively; $P < 0.05$).

EMG signals from individual muscles also reflected the changes in fingertip force magnitude. For dorsal force, the ratio of average EMG signal between the 100 and 50% force plateaus ranged between 1.61 ± 0.41 for *dorsal interosseous* to 2.31 ± 1.13 for *lumbrical*, which were significantly different ($P < 0.05$). For palmar force, *palmar interosseous* had the lowest ratio (1.16 ± 0.30) and extensor muscles the highest ratios (2.30 ± 1.8 and 2.25 ± 1.76 , respectively, $P < 0.05$). Last, for distal force, extensor muscles had the lowest ratios (1.53 ± 0.79 and 1.50 ± 1.33 , respectively) and dorsal interosseous with the highest (2.43 ± 1.3 ; $P < 0.05$). Note that the muscles with the lowest ratios for palmar and distal forces are also among the muscles that are excited the least in these force directions (see Table 2).

Statistical analysis of muscle coordination patterns at each force plateau

Subject-independent muscle coordination patterns were found for fingertip force production in all three directions at the 50% MVF plateaus. For all force directions (Table 2), the

statistical rankings of average EMG levels among muscles seen at both 50% force plateaus were similar to each other and consistent with coordination patterns reported in an earlier study for 100% MVF (Valero-Cuevas et al. 1998). Although there were instances of individual muscles changing rank order among force plateaus, only in four cases did a muscle become part of a statistically different grouping (see solid lines between columns in Table 3). The remaining six instances of rank changes did not affect the statistical ranking of muscle groups.

Prediction of muscle coordination patterns capable of producing 50% of maximal fingertip force magnitude

The musculoskeletal model of the forefinger predicted that dramatically different muscle coordination patterns can produce fingertip force magnitudes of $\leq 50\%$ of maximal in the three force directions studied. In all, 72 valid coordination patterns were identified for dorsal force, 99 for palmar force, and 73 for distal force. All valid coordination patterns for 50% of maximal force for each force direction were summarized as excitation level histograms for each muscle in each force direction (see Fig. 6). The excitation level histograms show that some muscles can have more variability than others when producing fingertip force magnitudes of $\leq 50\%$ of maximal in all three force directions. In particular, extensor, and *lumbrical* muscles can be excited between 63 and 100% of their excitation range; and *dorsal* and *palmar interosseous* muscles between 27 and 63% of their excitation range. In contrast, flexor muscles can only be excited over 25% of their excitation range for dorsal and palmar forces and over a broader range for distal force.

DISCUSSION

There is much kinematic and kinetic evidence suggesting that the control of manipulation is simplified by memory and sensory-modulated scaling of stereotypical profiles of hand displacement and grasp force (Cole and Johansson 1993; Forssberg et al. 1991, 1992, 1995; Gordon et al. 1992; Johansson 1996). This study provides evidence that the control of the redundant musculature of the forefinger also is simplified when sequentially producing fingertip forces of different magnitudes by scaling a coordination pattern capable of producing the largest expected force. Because modulating fingertip force magnitudes is essential to dexterous manipulation (Murray et al. 1994), this scaling strategy also may simplify the control of the manipulation skills common to daily living. However, to truly investigate everyday manipulation strategies, additional studies are needed that extend the methodology presented here to multiple fingers.

This study is unique in examining complete muscle coordination patterns for a finger while fingertip force magnitude is modulated independently of other functional factors. An experimental paradigm was used in which subjects modulated fingertip force magnitude over the entire voluntary range while force direction, finger posture, and amount of fingertip torque were held constant. This justified interpreting changes in EMG muscle coordination pattern vectors as the encoding of descending motor commands that modulated force magnitude.

The limitations of EMG data should be taken into account when interpreting the results. EMG is an indirect, yet practical,

TABLE 2. Average muscle coordination patterns for each force plateau for all directions

	First 50% MVF			100% MVF			Second 50% MVF		
	Muscle	Mean	Statistical grouping	Muscle	Mean	Statistical grouping	Muscle	Mean	Statistical grouping
Dorsal force	FP	0.1713	a	FP	0.2857	a	FP	0.1710	a
	DI	0.1991	a	DI	0.3136	a b	DI	0.1809	a
	LUM	0.2209	a	FS	0.3754	a b	LUM	0.1812	a
	FS	0.2285	a	LUM	0.4212	a b	FS	0.1944	a
	PI	0.2449	a	PI	0.4560	b	PI	0.2382	a b
	EC	0.3697	b	EC	0.5889	c	EI	0.2997	b c
	EI	0.4294	b	EI	0.7126	d	EC	0.3300	c
Palmar force	PI	0.0905	a	PI	0.0998	a	PI	0.0777	a
	EI	0.1469	a b	EI	0.2651	b	EI	0.1189	a b
	DI	0.1631	a b	DI	0.2929	b	DI	0.1618	a b
	LUM	0.1953	b	LUM	0.3342	b	LUM	0.2074	b c
	EC	0.2198	b	FS	0.3610	b	EC	0.2078	b c
	FS	0.2423	b	EC	0.3699	b	FS	0.2698	c
	FP	0.2565	b	FP	0.4260	b	FP	0.3069	c
Distal force	EI	0.0395	a	EI	0.0649	a	EI	0.0562	a
	EC	0.0644	a	EC	0.0956	a	EC	0.0712	a
	LUM	0.2377	b	FP	0.4377	b	LUM	0.2208	b
	FP	0.2426	b	FS	0.4466	b	DI	0.2700	b c
	FS	0.2678	b	LUM	0.4625	b	FS	0.2837	b c
	DI	0.2961	b c	DI	0.5785	c	FP	0.2871	b c
	PI	0.3527	c	PI	0.6188	c	PI	0.3032	c

Muscle coordination patterns can be described in absolute terms as the ranking of muscles by normalized electromyographic (EMG) level (Valero-Cuevas et al. 1998). The statistical rankings of coordination patterns for maximal voluntary force (100% MVF) are those reported in an earlier study (Valero-Cuevas et al. 1998). Group letters indicate grouping of muscles by mean EMG level, with the letter a representing the lowest level in the pattern. $P < 0.05$. FP and FS, *flexor digitorum profundus* and *superficialis* muscle slips; EI and EC, *extensor indicis proprius* and *digitorum communis* muscle slips; LUM, *first lumbrical* muscle; DI and PI, *first dorsal* and *palmar interosseous* muscles.

estimate of the neural drive to a muscle that has a strong stochastic component (Basmajian and De Luca 1985). Moreover, the relationship between EMG and force is known to change with force magnitude and muscle type (Basmajian and De Luca 1985; Lawrence and De Luca 1983) and excitation history (Bigland-Ritchie et al. 1983; Burke et al. 1976; Zajac and Young 1980). Also, muscle fiber shortening due to stretching of passive musculo-tendon elements in isometric contractions further affect relationship between force and EMG (Zajac 1989). Thus the relationship between EMG and muscle force cannot be considered linear over the entire range of activation. The cumulative effect of these EMG-related artifacts is to add to the variability in the direction and magnitude of the excitation pattern vectors assembled. Therefore the consistency among EMG coordination patterns for 50 and 100% force plateaus may only be interpreted as an indication of motor command similarity not equality (Tables 2 and 3). These changes in the relationship between EMG and force at different levels of activation also may explain in part the discrepancy between curves in Fig. 4B as well as the hysteresis for the ramp-up and ramp-down phases in Fig. 4C. Also, muscles that are excited at lower levels (i.e., EI and EC for distal force, Tables 2 and 3) will naturally have lower correlation coefficients with force because the influence of the stochastic component of EMG will be greater. Last, these EMG-related artifacts also may explain why the correlation between coordination pattern vectors is lower than the correlation between fingertip force vectors (Table 1).

The vector magnitude and vector direction of a coordination pattern can change in one of three ways when adjusting fingertip force magnitude. First, both the vector magnitude and

direction of the coordination pattern can change. Second, the vector direction, but not magnitude, of the coordination pattern can change. These two cases can be achieved by altering the number of active muscles and the relative excitation among them as fingertip force magnitude is adjusted. And third, the hypothesis of this study, the vector magnitude, but not direction, of the coordination pattern can change. A single joint musculoskeletal model with two agonist and one antagonist muscles can be used to show examples of all three cases.

Some studies have proposed that different coordination patterns are used to produce different magnitudes of a given fingertip force vector (Chao et al. 1989; Cooney et al. 1985; Maier and Hepp-Reymond 1995a). These EMG studies proposed that the number of active muscles varies with fingertip force magnitude with primary muscles active throughout the force range, secondary muscles contributing to the intermediate range, and tertiary muscles contributing only at the highest range of force magnitude. However, their results were not conclusive because they did not find statistically significant muscle coordination patterns at each force level, probably because the experimental paradigms of these studies did not isolate force magnitude from force direction or control the posture of the digit studied. Thus the reported differences in number of active muscles for low, moderate, and high force magnitudes reported by Cooney et al. (1985) and Chao et al. (1989) may be due to changes in force direction or digit posture, which would require different muscle-coordination patterns. The ramp-and-hold study of fingertip forces of low magnitude by Maier and Hepp-Reymond (1995a) qualitatively reported a constant set of muscles active in each subject that were thought to be the primary muscles for that subject. How-

TABLE 3. Instances of average EMG level of individual muscles changing rank order between force plateaus

	First 50% MVF	100% MVF	Second 50% MVF		
Dorsal force	FP	a	a	a	Lower rank by EMG level ↓ Higher rank by EMG level
	DI	a	ab	a	
	LUM	a	ab	a	
	FS	a	ab	a	
	PI	a	b	ab	
	EC	b	c	bc	
	EI	b	d	c	
Palmar force	PI	a	a	a	Lower rank by EMG level ↓ Higher rank by EMG level
	EI	ab	b	ab	
	DI	ab	b	ab	
	LUM	b	b	bc	
	EC	b	b	bc	
	FS	b	b	c	
	FP	b	d	c	
Distal force	EI	a	a	a	Lower rank by EMG level ↓ Higher rank by EMG level
	EC	a	a	a	
	LUM	b	b	b	
	FP	b	b	bc	
	FS	b	b	bc	
	DI	bc	c	bc	
	PI	c	c	c	

The arrows in this table track the rank of each muscle, as shown in Table 2, across all three force plateaus. Solid lines highlight those muscles that changed rank into a different statistically significant group ($P < 0.05$).

ever, moderate- and high-force magnitudes were not collected. Moreover, the high EMG scatter reported for all subjects underscores that artifacts particular to low force production may obscure the detection of motor strategies. These include the nonlinearities at the low end of the force-EMG curve (Basmajian and De Luca 1985; Lawrence and De Luca 1983), and the stronger variability in the relationship between EMG and force caused by other modulating factors such as the influence of peripheral receptors (Garnett and Stephens 1981).

This study presents several lines of evidence that scaled versions of a given muscle coordination patterns are used to produce different magnitudes of a given fingertip force vector. First, the high correlation between vector magnitude of fingertip forces and coordination patterns (Fig. 5) suggests that the magnitude of the descending motor command is correlated tightly with fingertip force magnitude. In this study, the correlation of fingertip force with coordination pattern vector magnitude is as high, and often higher, than correlations with individual muscles (Fig. 5). In fact, the correlation coefficients of EMG from individual muscle with fingertip force in this study are generally higher than those reported in previous

studies of finger musculature (Chao et al. 1989; Cooney et al. 1985; Maier and Hepp-Reymond 1995a). It is likely that the strict mechanical definition of the experimental task (see METHODS) played a major role in obtaining a strong correlation of EMG and force. Furthermore the consistency of EMG signals in this study was probably enhanced by studying force magnitudes spanning the voluntary range (reducing EMG artifacts particular to low force production) and using fine-wire electrodes (less susceptible than needle electrodes to muscle fiber migration artifacts during muscle contraction).

Second, the consistent vector direction of coordination pattern shows that the relative level of excitation among muscles remained uniform during the modulation of fingertip force magnitude over the voluntary range. Whether or not the vector directions of coordination patterns at each force magnitude are identical is beyond the resolution of the intramuscular EMG data (Basmajian and De Luca 1985) and may not be a realistic expectation for biological signals. Nevertheless the results show both in relative and absolute terms, a high consistency of descending motor command during the modulation of fingertip force magnitude. In relative terms, the lower half of Table 1

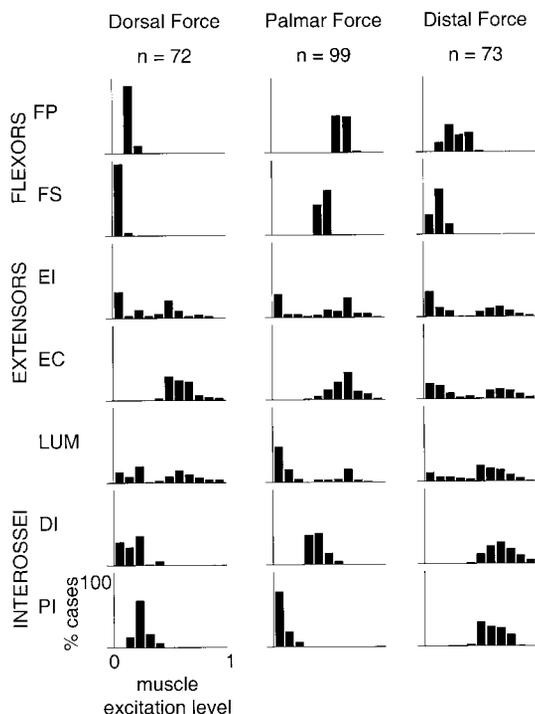


FIG. 6. Range of excitation level for each muscle in CPs predicted to produce 50% of maximal fingertip force in each direction. Muscle excitation is modeled as a value between 0 and 1 (abscissa in histograms), the frequency of occurrence at each excitation level among all valid CPs found is a value between 0 and 100% (ordinate). Because there is an infinite number of coordination patterns capable of producing 50% of maximal fingertip force (Chao and An 1978; Spoor 1983; Valero-Cuevas et al. 1998), these excitation ranges are conservative estimates.

shows a high correlation between seven-dimensional coordination pattern vectors in muscle space both in the low-force range (0–50% MVF, comparison a:1) and the high-force range (50–100% MVF, comparisons b:2 and c:3). Furthermore doubling fingertip force magnitude between 50 and 100% MVF plateaus produced a ratio for coordination pattern vector magnitudes close to two. In absolute terms, Tables 2 and 3 show statistically significant muscle coordination patterns for 50% MVF levels that are similar to each other and consistent with coordination patterns reported by us for 100% MVF (Valero-Cuevas et al. 1998). Previous studies of submaximal forces have not found subject-independent, statistically significant muscle coordination patterns (Close and Kidd 1969; Maier and Hepp-Reymond 1995a). Although there are instances in these results of individual muscles changing rank order (see horizontal lines between columns in Table 3), these changes do not affect the statistical ranking of muscle groups. A detailed description of the biomechanical interpretation of these coordination patterns has been published (Valero-Cuevas et al. 1998).

And third, in contrast to the observed consistency of coordination patterns, the previously validated musculoskeletal model here predicts that 50% of maximal fingertip force can be produced by coordination patterns that are drastically different from those needed for 100% MVF. The model predicts extensor, *interosseous*, and *lumbrical* muscles can be excited at very different levels and still produce a well-directed fingertip force of $\leq 50\%$ MVF. Because the tendons of the extensor, *lumbrical*,

cal, and *palmar interosseous* muscles insert into a common network (Zancolli and Cozzi 1992), the particularly broad latitude in their excitation may be due to different individual muscle forces producing the same net torque at the joints spanned by this network. Because there is conceivably an infinite number of coordination patterns capable of producing 50% MVF, the excitation ranges shown here are necessarily an underestimate. Finding additional valid coordination patterns can only increase the excitation ranges shown and strengthen the conclusions of this study.

The fact that this study focused on the performance of learned finger tasks that are strictly defined does not make these conclusions inapplicable to the control of grasping in general. Recent and distant learning and memory are instrumental in the predictive control of the kinematics and kinetics of reaching and grasping (Forsberg et al. 1992; Johansson 1996). Thus the expectation of producing large fingertip force magnitudes, and the recent memory of previous trials, may have contributed to the consistency of muscle coordination patterns at submaximal force magnitudes. This study suggests that the control of muscle coordination during learned grasping may also be predictive. Additional studies of muscle coordination patterns used for unknown and unexpected force magnitude targets in naïve subjects need to be done to reveal the extent to which distant learning and memory affect motor control strategies in finger musculature.

The rapid and consistent adjustment of fingertip forces is essential for dexterous manipulation. Individual digits are the building blocks of manipulation function (Murray et al. 1994), and thus simplifying the control of individual digits naturally simplifies the control of dexterous manipulation in general. Also, well-directed fingertip forces with no associated fingertip torque are necessary to grasp small and/or slippery objects (Murray et al. 1994), and fingertip forces that can grasp slippery objects also can grasp a high-friction objects but not vice versa. It is, of course, possible that humans change the control strategy as the mechanical constraints of the task become relaxed (e.g., by the presence of friction or a broader contact surface that allows the production of fingertip torque). Nevertheless using a stringent mechanical definition of the task in this study was useful to test the hypothesis that scaling of muscle coordination patterns is a simplifying strategy to control the redundant musculature of the digits. It is likely that the forefinger and other digits also can use this control strategy to scale the magnitude of fingertip forces under more relaxed mechanical conditions and other force directions. This study is the first to provide evidence of motor strategies at the level of the coordination of redundant finger muscles and reveals a neural process that may be instrumental to dexterous manipulation.

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