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### Dynamic force-sharing in multi-digit task

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#### Abstract

*Background.* Dynamic hand grasping implies sophisticated motor coordination. Most knowledge on motor synergies used in grasping is deduced from experiments based on static precision grip. This experiment was aimed at better understanding the mechanisms of finger force-sharing in an active, dynamic hand task under repetitive strain conditions.

*Methods.* A multi-digit task consisting of holding a cylinder with the digit tips, in which the thumb and the finger opposed each other, was investigated during repetitive unidirectional wrist flexion and extension cyclic motion. Finger and thumb forces and wrist angular position were simultaneously recorded during repetitive wrist motion against 0.3–0.6 N m load in 10 healthy adults.

*Findings.* Load torques acting during wrist movements produced in-phase increases of the thumb and the finger forces with the wrist extension and the wrist flexion, respectively. Digit forces increased proportionally to the applied load. The alternating rise of thumb and finger forces changed instantaneously at the end of the flexion and extension phases of the movement, respectively. Six subjects predominantly used the index finger, two the middle finger, one the ring finger, and the remaining one used the small finger during wrist flexion against 0.6 N m to perform the task. Variations among individual finger forces were negatively correlated during the phase of constant rotational velocity of the wrist flexion. Repeated measures ANOVA revealed that the percentage of individual finger contribution to the total fingers' force significantly varied during the wrist flexion (P < 0.0001) and among wrist flexion cycles (P < 0.0001) in each subject.

*Interpretation.* Variations in finger force-sharing among cycles were not necessitated by task dependent activities, as the task was identical. These findings indicated that motor coordination of repeated multi-finger task allowed redundant solutions in finger force-sharing. The force-sharing variation may reflect a minimal intervention principle of the central nervous system controlling only the goal-directed parameters and might help to prevent muscle fatigue in repetitive tasks through modulation of activity in multi-digit muscles.

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Keywords: Wrist; Motion; Finger; Force; Motor coordination; Feedback

#### 1. Introduction

Although hand grasp is more often used in activity of daily living than precision grip, this second task is usual in manual works to grip and handle polyhedral (like books) or cylindrical objects. Repetitive tasks are often responsible for overuse syndromes and repetitive trauma disorders, which result in considerable burden to patients and society (Levenstein, 1999).

Motor synergies required for combined multi-digit grip and wrist movements have not been previously systematically investigated (Shim et al., 2005). Two

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groups of muscles are used to achieve multi-digit tasks (Yu et al., 2004): (1) single-digit muscles, mainly intrinsic muscles of the hand, and (2) multi-digit muscles, mainly extrinsic muscles in the forearm. Both groups of muscles contribute to movement, force production and joint stability. Wrist movements are dependent on the activation of specific extrinsic muscles. Co-contraction of agonist and antagonist muscles of the forearm are necessary to better stabilize the wrist and the digit joints, and that way increase the strength of the grasp (Chabran et al., 2001). Therefore, grasping during wrist movements implies sophisticated motor coordination to complete the task. To accomplish reaching and grasping tasks the central nervous system (CNS) involves appropriate neuronal connections required to generate reaching and object manipulation synergies. Descending inputs from supraspinal centers in the CNS select appropriate motor synergies to execute the task, which are then reinforced by proprioceptive feedback from the moving limb and cutaneous feedback from the hand obtained once the contact is established with the object (Stein and Smith, 1999; Witney et al., 2004). At the fingers and thumb levels, tactile afferents of the skin in contact with the object are providing essential information to adapt force generation to loads through continuous cutaneous input (Macefield and Johansson, 1996). Anticipatory postural adjustment is a mechanism allowing the central motor controller to select postural muscle synergy in advance, based on visual estimation of the object mass and inertia, and taking benefit from the experience gained when similar tasks were performed in the past (Chabran et al., 2001; Diedrichsen et al., 2005; Nowak et al., 2002; Ohki et al., 2002).

The study of motor synergies used in hand task is matter of intense investigations (for review see Zatsiorsky and Latash, 2004), but most knowledge on finger force-sharing is deduced from experiments based on static precision grip, which does not integrate the complexity of synergies involved at the wrist and digit muscles' levels during repetitive, dynamic hand tasks.

We have investigated a multi-joint task consisting of a prismatic precision grip with the digit tips in firm contact with the object, in which the thumb and the fingers opposed each other. During the grasp repetitive cyclic wrist flexion and extension motions were performed. The present study was designed to observe individual digit forces in healthy individuals generated during the above task and how they changed during active wrist movements against variable loads. The experimental design allowed an indirect assessment of digit muscle activities, through individual digit force recordings in an identically repeated task. The experiments were aimed at better understanding the mechanisms of finger force-sharing in an active dynamic task under repetitive strain conditions.

#### 2. Methods

#### 2.1. Subjects

Eight male (mean age 30.9 (SD 4.3) years, mean weight 73.0 (SD 7.5) kg) and 2 female (mean age 30.0 (SD 3.5) years, mean weight 62.0 (SD 4.2) kg) subjects volunteered to participate in the study. There were eight right-handed (mean wrist range of motion 134.4° (SD 11.8°), mean grip strength 450.0 (SD 157.0) N) and two left-handed volunteers (mean wrist range of motion 132.5° (SD 3.5°), mean grip strength 529.5 (SD 41.7) N). The subjects had no known injury or neuropathy in the hand or upper extremity. Consent, approved by the Institutional Review Board, was obtained from each subject prior to the experiments.

#### 2.2. Apparatus

The experimental device allowed simultaneous realtime measurements of the individual fingers and thumb forces and the wrist angular position during rhythmically repeated voluntary wrist flexion and extension movements against load. Five force sensors (ELFM-B1, Entran Devices, Fairfield, NJ, USA) were housed in customized aluminum housings and fixed to a hollow cylinder (Fig. 1). The thumb sensor was inclined in 20° pronation with respect to the cylinder axle in order to respect the spontaneous orientation of the thumb in circumduction and capture the force in its main exertion



Fig. 1. Experimental setup: Force sensors' placement could be adapted to virtually any hand size. Wrist position, and thumb and finger forces were simultaneously recorded. Various constant torque loads could be generated against which wrist had to move both in flexion and extension. These torque loads were generated with a work simulator. The arrow is pointing to the J-arm holding the sensors.

direction (Yu et al., 2004). The remaining four force sensors could be adjusted with respect to the thumb sensor to fit any hand size using adjustable rings, as previously reported (Keller et al., 2000). Spacing rings were placed among the force sensor housings to fit individual web spaces. Each force sensor had a force range of 125 N, and a resolution of 0.1 N. The wrist angular position was recorded with an absolute encoder (Novotechnik, Ostfildern, Germany) of which the range of motion was 360° and the resolution was 0.25°. The hollow cylinder with force sensors, further termed handle, was fixed to an adjustable J-arm and was equilibrated with a tare. A work simulator (Baltimore Therapeutic Equipment, Hanover, MD, USA) was connected to the J-arm to generate torques against which the wrist had to move. The resistive torques (0–0.6 N m) that had properties of kinetic friction were used to load equally the wrist motion in both flexion and extension directions. Data measured during the experiments was recorded using a 12-bit analog-digital converter (DAQCard-AI-16E-4, National Instruments, Austin, TX, USA) and a Laptop. The data sampling frequency was 500 Hz. A custom made LabVIEW-based program (National Instruments) was used to collect and process the data.

#### 2.3. Experimental procedures

The prehension task consisted in a prismatic precision grip that was a grip by the tips of the digits in which the thumb and the fingers opposed each other. Prior to adjusting the measurement system to individual participants, they were asked to hold with the digit tips a plastic cylinder of the same diameter as the handle. The placement of the fingers and thumb was unconstrained, meaning that each participant used the most comfortable digit placement to keep a stable finger tip position. The positions of all digit tips were marked on the plastic cylinder. Later the plastic cylinder, the digit tip markings, and the plastic cylinder grid were used to adjust the positions of the force sensors of the measurement system such that the sensors were placed at the locations where the digit tips were expected to be when the handle was grasped by the same subject. The diameter of the plastic cylinder corresponding to the prismatic grip was the same for all subjects. The aluminum sensor housings were marked at 5° intervals so that the angles of the force sensors in respect to a reference axis on the handle could be calculated. These angles were further used to calculate the orthogonal components of the digit forces perpendicular to the axis of the J-arm  $(F_{xo})$ . This was done by correcting angles' values using the difference between the reference axis on the handle and the  $F_{xo}$  axis to the wrist in neutral position. Double sided Scotch tape was applied between the digit tips and the force sensors to decrease sliding of the digit tips during the experiments. The handle axis could coaxially rotate with the J-arm center of rotation, so that no additional rotational constrains appeared at the finger tip/sensor interfaces during the entire wrist range of motion. Each participant was seated in a comfortable position such that the shoulder and elbow were relaxed while the participant was holding the measurement system. The forearm was positioned on a splint and fixed with a velcro strap after the wrist flexion/extension center of rotation was aligned with the rotational axle of the J-arm. Additional adjustments of the straps were used to further ensure that the participant felt comfortable during the motion of the wrist along its entire range of motion as the subject was holding the handle. Participants were instructed to maintain the same forearm position during the entire duration of the experiment. The absolute encoder used to record the wrist angle and the force sensors were zeroed and calibrated, respectively, when the wrist was in 0° flexion/extension position. The participants were asked to slowly and rhythmically flex and extend the wrist covering the entire range of the wrist motion. A pilot study showed that five times repeated wrist flexion/extension cycles with an angular velocity of 240°/s against 0.6 N m load produced decrease in the angular velocity < 8%, in both male and female subjects. The resistive wrist-load was kept at 0 N m during the learning phase of the task. The participants were instructed to alternate wrist flexion and extension with a constant frequency corresponding to an angular velocity of  $240^{\circ}/\text{s} \pm 20^{\circ}/\text{s}$ . They were told to hold the measurement system with the minimal force allowing a stable digit placement to further insure repeatability of the measurement without rapid onset of fatigue. All participants required a learning period of less than five cycles to learn how to execute this task successfully. Once the participants felt confident that they could execute the desired task, they were instructed to perform the experiment. The experiment consisted of four series of five trials in which the subject was moving the wrist against a load with an angular velocity of  $240^{\circ}/s \pm 20^{\circ}/s$  while holding the handle in stable manner. During each trial in a single series the wrist load was randomly adjusted to one of the following values 0.3, 0.4, 0.5 or 0.6 N m. Maximum load was set at 0.6 N m to prevent excessive fatigue during repeated exercises. The loads were applied against both wrist flexion and extension. An individual trial consisted of five continuous cycles of wrist flexion/extension against constant wrist load, starting from the 0° wrist position. A 5 min break was given between each series of cycles.

#### 2.4. Data processing and statistical analysis

Finger and thumb forces produced during both wrist flexion and extension, against a given wrist load, were recorded. The total finger force corresponding to the sum of the index, middle, ring and small fingers was calculated. Individual finger, total finger and thumb forces were normalized with respect to the maximal force and averaged across subjects. Correlation coefficients were determined by the least squares method using linear regression (Zou et al., 2003). Finger forces during wrist flexion against 0.6 N m were separately processed to determine force-sharing among fingers. Force-sharing of a finger at a given wrist position was defined as the percentage of the total finger force produced at this position during wrist flexion. Sixth order polynomial curves and the least-squares approach were used to describe the measured individual finger forces during each cycle of wrist flexion and extension. This technique was used to keep the essence of the measured signal while removing higher order noise. Interpolation was performed using Matlab 5.3 (MathWorks, Natick, MA, USA) to estimate instantaneous forces of individual fingers corresponding to the  $0^{\circ}$ ,  $10^{\circ}$ ,  $20^{\circ}$ ,  $30^{\circ}$ ,  $40^{\circ}$ wrist positions in both flexion and extension, as previously described (Li, 2002). Repeated measures ANOVA with Greehouse-Geisser corrections was used to compare variations of finger force sharing during wrist motion and among cycles and trials, using SPSS 11.5. Relative variance was defined by computing the trial-totrial variance separately for each subject, fingers and wrist position, as previously described (Todorov and Jordan, 2002). The results were averaged over subjects. Post hoc comparisons were tested with a Tukey's Honestly Significant Difference Test to determine the rank of individual finger contribution to the total finger force. Differences were considered statistically significant if *P* < 0.05.

#### 3. Results

### 3.1. Generation of rhythmic changes of finger and thumb forces

The subjects used a five-digit grip to hold the handle during rhythmical active wrist flexion/extension. The prismatic grip resulted in the placement of the thumb in opposition to the fingers, with respect to the handle axis. Thumb force increased during the wrist extension and total finger force during the wrist flexion (Fig. 2). The wrist angular velocity was constant in the  $-40^{\circ}$  to  $40^{\circ}$  and  $40^{\circ}$  to  $-40^{\circ}$  range-of-motion in all subjects, defining an isokinematic (constant rotation velocity) phase of wrist motion. The force vectors acting during the isokinematic phase of the wrist motion against load are schematically represented in Fig. 3. They produced the  $F_{xo}$  orthogonal forces indicated in Table 1. The prismatic grip resulted in a slight reorientation of the handle axis during wrist flexion and extension with respect to the orthogonal  $F_{xo}$  and  $F_{yo}$ , that represented force coordinates in a Cartesian coordinate space. Here, the  $F_{yo}$  Fig. 3. Schematic representation of the force vector equilibrium during the isokinematic phase of active wrist motion against load with  $\sum_{i=1}^{4} F_i + F_t + F_1 + F_r = 0$ .  $(\sum_{i=1}^{4} F_i)$ : sum of the individual finger forces,  $F_t$ : thumb force,  $F_t$ : applied load,  $F_r$ : reaction force to equilibrate the shift perpendicular to the wrist rotation axis.)

axe carried the shear forces present at the digit/sensors interfaces, as well as the reaction force of the handle to equilibrate the shift perpendicular to the wrist rotation axis during motion. The instantaneous angular variations of the handle were not recorded during wrist motion, but they were below 10° between the maximal wrist extension and the maximum wrist flexion positions, as assessed with a manual goniometer. The handle axial rotation was even less than 4° in the 40° to  $-40^{\circ}$  range-of-motion, and therefore this deviation was not taken into account to calculate orthogonal forces for the analyzed range-of-motion. The total finger force

Fig. 2. Thumb (—) force, and the sum of the individual finger forces (—) are shown during five consecutive cycles of wrist flexion and extension ( $\Box$ ) against 0.6 N m load. Subject #4.





Load (N m)	Wrist extension				Wrist flexion					
	Thumb	Index	Middle	Ring	Small	Thumb	Index	Middle	Ring	Small
0.3	11.8 (2.6)	2.0 (1.6)	1.6 (0.8)	1.8 (1.3)	1.7 (0.7)	8.1 (3.3)	3.9 (1.7)	2.6 (1.0)	2.6 (1.3)	2.2 (0.7)
0.4	15.8 (3.3)	2.1 (1.4)	1.5 (0.7)	1.9 (1.0)	1.7 (0.8)	8.4 (3.7)	5.3 (1.9)	4.0 (1.1)	4.1 (1.3)	3.8 (0.9)
0.5	19.5 (3.3)	2.1 (1.3)	1.7 (0.8)	2.0 (1.2)	1.8 (0.9)	8.6 (4.7)	6.0 (2.2)	4.7 (1.2)	4.8 (1.8)	4.4 (1.3)
0.6	21.2 (3.7)	2.3 (1.4)	1.6 (0.9)	1.9 (1.1)	1.7 (0.7)	9.1 (3.8)	7.2 (2.7)	5.2 (1.4)	5.4 (1.9)	5.1 (1.5)

Table 1 Thumb and individual finger forces (N) during rhythmical wrist motion

Instantaneous force values, when the wrist reached the neutral position, where used to calculate  $F_{xo}$  orthogonal force components. Values are means (SD) for all trials averaged across subjects.

increased proportionally to the applied load during wrist flexion (r = 0.98, P < 0.02), and the thumb force increased proportionally to the applied load during wrist extension (r = 0.98, P < 0.02). Conversely, the sum of the finger forces during wrist extension as well as the thumb force during wrist flexion was independent of the applied load and in a range of 8 N. This represented the holding force acting against tangential forces generated by the external torque to keep stable finger positions on the sensors during wrist motion (Shim et al., 2005). The inversion of the finger and thumb force vectors were <0.1 second at wrist flexion/extension and extension/flexion phase-transition resulting in a rectangular configuration of the graph mapping the wrist position and the finger force, as shown in Fig. 4.

#### 3.2. Force sharing among fingers during wrist flexion

The sum of the finger forces decreased linearly with mean difference 3.6 (SD 6.9) N between the 40° wrist extension and the 40° wrist flexion positions. The  $F_{xo}$ 

orthogonal forces produced by the index, middle, ring and small fingers were expected to be about the same during the isokinematic phase of wrist flexion, because the fingers were equally loaded. Tangential forces at the finger tip/sensor interfaces were kept low by carefully aligning the wrist axis with the rotational axis of the J-arm. We observed that six subjects predominantly used the index, two of them predominantly used the middle finger, and two predominantly used the ring or the small finger, respectively (Table 2). Repeated-measures ANOVA revealed that the percentage of individual fingers contribution to the total fingers' force significantly varied during wrist flexion (P < 0.0001), and among flexion cycles of the same (P < 0.0001) or different trials (P < 0.0001) in all tested subjects. No pattern of individual finger contribution was reproduced among flexion cycles of a given trial in any subject. However, variation of the relative variance was much more pronounced among cycles as compared to within cycles (Table 3). Variation of the relative variance among cycles was independent of the trial rank, meaning that



Fig. 4. Thumb and fingers forces generated during rhythmical wrist motion against 0.3, 0.5 and 0.6 N m. Rectangles on the top right panel (valid for the thumb) and on the middle panel (valid for all fingers) are indicating parts of the graph mapping motion during wrist flexion (dotted line) and extension (plain line). Subject #5.

Table 2 Rank of contribution among fingers

Subject no.	Finger rank
1	I > R = S > M
2	$\mathbf{M} > \mathbf{R} > \mathbf{I} > \mathbf{S}$
3	S > I > M = R
4	I > M = R > S
5	$\mathbf{I} > \mathbf{R} > \mathbf{M} > \mathbf{S}$
6	$\mathbf{I} > \mathbf{M} > \mathbf{R} > \mathbf{S}$
7	I > M = S > R
8	M > R = S > I
9	$\mathbf{I} > \mathbf{M} > \mathbf{S} > \mathbf{R}$
10	$\mathbf{R} > \mathbf{I} = \mathbf{M} = \mathbf{S}$

I: index, M: middle, R: ring, S: small.

Table 3

Averaged relative variance among wrist positions for a given cycle and among cycles

Finger	Variance among wrist position (%)	Variance among cycles (%)
Index	9	30
Middle	19	55
Ring	7	12
Small	19	39

the variance did not change as more experience was gained with the task. The middle and small fingers contributions to the total finger force had the higher variability within and among flexion cycles. Conversely, the ring finger had less variation within and among flexion cycles. Graphical representation of individual finger contributions showed progressive variations within a cycle, contrasting with tremendous variations in the percentage of individual finger force contribution among cycles of a given trial (Fig. 5). Taken together, individual finger forces varied slowly and moderately during wrist flexion. However, force-sharing varied considerably among cycles indicating that force-sharing was mostly cycle-dependent.

#### 4. Discussion

The present study used dynamic measurements to assess digit forces applied in a prismatic precision grip during active wrist flexion/extension against resistance. During this complex task the selected motor synergies were able to: (1) grasp the handle to prevent slipping, and (2) contribute to postural adjustment required for active voluntary motion of the wrist against resistance. This study was designed to characterize the degrees of freedom implicated in muscle synergies to generate individual digit strength during this complex task.

### 4.1. Biomechanical implications of the experimental design

Measurements were standardized among volunteers by both allowing a digit configuration adapted to indi-



Fig. 5. Force-sharing among fingers (%) in four consecutive wrist flexion cycles loaded with 0.6 N m. Index:  $\blacksquare$ , middle:  $\Box$ , ring:  $\aleph$ , and small:  $\mathscr{M}$ , Subject #2.

vidual hand size and the preferred digit configuration for the prismatic grip, while maintaining the resulting diameter of the grip constant. Special attention was paid to ensure that both the centers of rotation of the wrist and of the J-arm are coaxial and that way minimize the shear forces at the finger tips–sensor interface, which may have otherwise occurred due to relative changes in the hand/digit length during wrist motion. Although, most activity of daily living are performed in midprone position, the experimental design using a connection between a J-arm and a work simulator required the measurement to be assessed in full pronation of the forearm in order to correctly stabilize the measuring device. The grip strength in pronation is lower as compared to both neutral and supinated positions, but we postulated that identical repeats of flexion/extension wrist movements prevented from systematic error in data analysis, even if this forearm position was relatively non-physiologic (De Smet et al., 1998). The angular velocity of 240°/s was chosen because it is intensive and creates condition of fatigue during the test, according to the instruction of the work simulator manufacturer (BTE Prismus Documentation, Hanover, MD, USA) and as previously reported (Kennedy and Bhambhani, 1991). It was thought that as our main focus was to assess finger force-sharing during the isokinematic phase of movement, the combination of rapid movements and low exercise duration may improve the reproducibility of the measurements within and among cycles. Altogether, we favored the reproducibility of the experiments and therefore accepted an experimental design which did not mimic activities of daily living or manual works. Hence, this experimental design allowed data analysis in a Cartesian coordinate system to investigate if force-sharing variability was mechanically necessitated or not. The repeated wrist movements in flexion and extension, without any additional wrist deviation in both the coronal plane (radial or ulnar deviations) and the axial plane (pronation or supination), resulted in identically repeated digit loading among cycles during the isokinematic phase of the movement. The experimental design used repeated voluntary active motion to compare patterns of finger force-sharing under identical conditions. Combined wrist movements and digit manipulations require constant adaptation of the extrinsic finger muscles to the tension of the finger tendons, which depend on the wrist position. In this experiment it seems very unlikely that any difference of finger force-sharing may have reflected a mechanical necessity due to modifications of the digit placements among cycles. We did not test the equipment to assess inertial and weight effects. The inertia of the apparatus may have consistently contributed to modify finger forcesharing during the acceleration/deceleration phases of the wrist motion at the end of the flexion and extension cycles. For that reason the finger force-sharing analysis was restricted to the isokinematic phase of the wrist flexion, during which time the sum of the finger forces decreased linearly. Although inertial forces present at the wrist motion inter-phases might have slightly influence the force sharing during the isokinematic phase of the wrist flexion, we assume that this effect was identical within and among cycles so that it may not have influenced the observed changes in force-sharing.

#### 4.2. Thumb and finger synergies during wrist motion

The particular digits' placements in a prismatic precision grip resulted in muscle activities of the thumb and fingers acting out-of-phase. The subjects adapted spontaneously to the task and generated the required finger and thumb forces to actively contribute to the wrist movement against the load, as previously reported (Werremeyer and Cole, 1997). The alternatively generated rise of thumb and finger forces changed instantaneously at the end of the flexion and extension phases, suggesting an anticipatory adjustment of the muscle synergies used in this repeated task (Diedrichsen et al., 2005). The experimental design allowed simultaneous measurements of individual finger forces during their global reinforcement phase in wrist flexion. We focused our assessment of the force-sharing in the condition of maximal loading, to decrease the risk of misinterpretation of force variability at low force levels (Slifkin and Newell, 1999). We observed that the total finger force decreased during wrist flexion. This can be explained through the inherent lengthening of the extrinsic finger muscles during wrist flexion reducing muscle contractility and therefore reducing the finger strength (Delp et al., 1996). Apart from that the total force produced during the isokinematic phase of flexion was linear, indicating that variations among individual finger forces were negatively correlated. This means that when the force of a particular finger was larger, the force of at least another finger was smaller, indicating mutual dependence in the force distribution among fingers resulting in new set of force-sharing for the task (Zatsiorsky et al., 2003).

#### 4.3. Finger force-sharing during wrist flexion

Significance of finger force-sharing variations within and among wrist flexion cycles are analyzed in this paragraph. The direct assessment of individual finger forces and the position of the sensors allowed a simple calculation of orthogonal force-sharing variations. It allowed also intra- and inter-cyclic comparisons of the force generated by individual fingers for each subject. The observed intra- and inter-cyclic variability in force-sharing might be interpreted differently. The modification of the handle orientation with respect to the orthogonal  $F_{xo}$ and  $F_{vo}$  axis and the adaptation of the extrinsic finger muscle to maintain isotonicity implicated individual finger force adjustments during wrist flexion. The observed intra-cyclic finger force-sharing changes may have reflected a chain effect as mechanically necessitated by individual finger force adjustment during wrist flexion. This may account for variability in finger-sharing depending on the wrist position during wrist flexion.

The prismatic grip gave a mechanical advantage to the index and little fingers because of their longer moment arms, as previously reported (Shim et al., 2005). Therefore, both the observed differences in individual finger rank contribution among volunteers and the lesser variability in ring finger contribution to the total finger force cannot be explained as a mechanical necessity. The experimental design prevented from significant variation of mechanical configuration between flexion cycles, so that the observed inter-cyclic variability may reflect a particular non-conscious motor coordination behavior selected by the motor controller but not necessitated by the task mechanics. How much a large number of muscles or parts of a muscle, like multi-digit muscles, contribute to a common output is controversial (Schieber, 1995). Theoretically, an infinite number of combinations of muscle forces, termed "motor redundancy", can give rise to the same total force output (Bernstein, 1967).

The observed inter-cyclic variability of force-sharing had no influence on the produced total finger force. The force-sharing variability was therefore restricted into a sub-space or manifold in which the element variability had no effect on the task goal (Scholz and Schöner, 1999; Shim et al., 2003). Interestingly, the variation in force-sharing were the same among trials indicating that there were no particular optimization in force-sharing to find the best adapted configuration for this particular task. The observed variability in this task-irrelevant subspace can therefore have directly reflected a non-conscious motor coordination strategy of minimal intervention principle correcting only those deviations that interfere with task goals and allowing variability in the task-irrelevant dimension (Todorov and Jordan, 2002).

## 4.4. Assumptions about underlying motor control and muscle physiology

Repeated cycles of wrist flexion/extension against resistance would produce muscle fatigue. High intermittent motor unit discharge variations are observed with electrophysiology in response to fatigue (Miller et al., 1996). It is assumed that peripheral feedback can modulate individual motor-unit discharge levels through signals to the motoneuron pool, according to the contractile speed of active muscle fibers. This hypothesis, termed muscular wisdom (for review see Garland and Gossen, 2002) was observed in both extrinsic and intrinsic hand muscles (Fuglevand et al., 1999). We speculate that the motor firing rate should be regulated by the motor controller inside a multi-digit muscle submitted to loading to reduce fatigue of a particular muscle/ tendon unit during repeated contractions.

In conclusion, the present study described a method to reproducibly assess force-sharing in multi-finger task under dynamic strain, using a newly developed device. The observed variability in force-sharing can be explained with a minimal intervention principle correcting deviations interfering only with the task goal but allowing variability in a task-irrelevant subspace. It may also reflect a non-conscious strategy of the motor controller to decrease muscle fatigue resulting from repeated tasks. These observations have potential relevance in ergonomics, provide new insight in multi-digit muscles physiology, and are worth further investigations using muscle electrophysiology.

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