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Mechanical properties of the human hand digits: Age-related differences

Jaebum Park [a,b], Nemanja Pažin [c], Jason Friedman [d], Vladimir M. Zatsiorsky [a], Mark L. Latash [a,*]

[a] Pennsylvania State University, University Park, PA, USA
[b] Montana State University, Bozeman, MT, USA
[c] University of Belgrade, Belgrade, Serbia
[d] Tel Aviv University, Tel Aviv, Israel

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ABSTRACT

Background: Mechanical properties of human digits may have significant implications for the hand function. We quantified several mechanical characteristics of individual digits in young and older adults.
Methods: Digit tip friction was measured at several normal force values using a method of induced relative motion between the digit tip and the object surface. A modified quick-release paradigm was used to estimate digit apparent stiffness, damping, and inertial parameters. The subjects grasped a vertical handle instrumented with force/moment sensors using a prismatic grasp with four digits; the handle was fixed to the table. Unexpectedly, one of the sensors yielded leading to a quick displacement of the corresponding digit. A second-order, linear model was used to fit the force/displacement data.
Findings: Friction of the digit pads was significantly lower in older adults. The apparent stiffness coefficient values were higher while the damping coefficients were lower in older adults leading to lower damping ratio. The damping ratio was above unity for most data in young adults and below unity for older adults. Quick release of a digit led to force changes in other digits of the hand, likely due to inertial hand properties. These phenomena of "mechanical enslaving" were smaller in older adults although no significant difference was found in the inertial parameter in the two groups.
Interpretations: The decreased friction and damping ratio present challenges for the control of everyday prehensile tasks. They may lead to excessive digit forces and low stability of the grasped object.

1. Introduction

Age-related changes within the neuromotor system (reviewed in Cole et al., 1999; Grabiner and Enoka, 1995) affect a variety of activities of daily living including prehensile tasks (Francis and Spirduso, 2000; Olafsdottir et al., 2008; Parikh and Cole, 2012; Rantanen et al., 1999; Shim et al., 2004). These behavioral changes may get contributions from changes both within the central nervous system and in mechanical characteristics of the digits. In particular, healthy aging is known to be associated with a significant decrease in the friction coefficient between the digit tips and surfaces of typical grasped objects; this factor has been discussed as a contributor to the higher grip forces typical of older adults (Cole, 1991; Cole et al., 1999; Gorniak et al., 2011).

Changes in mechanical properties of the digits may contribute to safety and stability of prehensile actions. In a first approximation, we consider each digit tip as a point object that can be characterized by such parameters as mass, apparent stiffness, and damping with a clear understanding that estimates of these parameters reflect properties of more proximal portions of the digits and the involved muscles.

We used two newly developed devices in the experiments. The earlier described device (Savescu et al., 2008) was used for estimation of the friction coefficient, which was expected to be lower in older subjects across all five hand digits (Hypothesis 1). The other device involved a handle equipped with spring-loaded force sensors that could be engaged and disengaged during steady-state normal force production leading to a quick, small-amplitude unloading of one of the digits. We used the recorded changes in the digit tip force and trajectory to compute its effective mass, apparent stiffness, and damping. Further, we computed the damping ratio. We expected the ratio to be smaller in older subjects (Hypothesis 2).

Despite the fact that only one digit was unloaded in each trial, we observed nearly instantaneous changes in the forces produced by the other digits involved in the task. These changes were not small and resembled the well-known phenomena of finger enslaving (lack of individuation; Kilbreath and Gandevia, 1994; Zatsiorsky et al., 2000). Older adults have been described as having lower enslaving expressed in percent to the maximal force-generation capability of the fingers (Kapur et al., 2010; Shinohara et al., 2003). Based on those studies, we expected the new phenomenon (we call it "mechanical enslaving",

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* Corresponding author at: Department of Kinesiology, Rec.Hall-268N, The Pennsylvania State University, University Park, PA 16802, USA.
E-mail address: mll11@psu.edu (M.L. Latash).

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ME) to follow the same pattern, that is, show proportionally smaller effects in the older group (Hypothesis 3).

2. Methods

2.1. Subjects

Ten healthy elderly subjects and ten healthy young subjects (age: mean = 76.1, SD = 5.6 years for the elderly; mean = 26.9, SD = 4.9 years for the young; 5 females in each group) were recruited. All subjects were right-handed determined by the Edinburgh Handedness Inventory (Oldfield 1971). None of the subjects had a previous history of neuropathies or traumas to their upper extremities. The elderly participants were screened with a cognition test (mini-mental status exam ≥ 24 points), a depression test (Beck depression inventory ≤ 20 points), a quantitative sensory test (monofilaments ≤ 3.22), and a general neurological examination. Prior to the experiment, the subjects signed a consent form approved by the Office for Research Protection of the University.

2.2. Equipment

2.2.1. The handle with yielding sensors

A handle was designed to provide a quick, low-amplitude release of a digit producing a pressing force on one of the four force/moment sensors. The subjects grasped the handle with three fingers in opposition to the thumb (Fig. 1B). The digit combinations were '*Thumb–Index–Middle–Ring*' (*TIMR*) or '*Thumb–Middle–Ring–Little*' (*TMRL*). The handle was fixed to the immovable table, and four miniature force sensors (Nano-17, ATI Industrial Automation, Garner, NC, USA) were used to measure forces exerted by the digits. The force signals were digitized using a 16-bit A/D converter (PCI-6225, National Instruments, Austin, TX, USA) and a customized LabVIEW program at 500 Hz. The force sensors were connected to a rod (Fig. 1C), which was screwed into an electromagnet. The rod passed through a circular hole in a circular disc, made of a ferromagnetic material. A compression linear spring was placed between the force sensor and the ferromagnetic disc. The force sensor and the rod were effectively rigid when the electromagnet was turned on. Turning the electromagnet off caused the force sensor to yield resulting in a quick (<40 ms), low-amplitude (<10 mm) translational motion of the sensor and the corresponding digit. The spring between the sensor and the disc was compressed providing resistive force. As a result, the digit stopped in a new equilibrium position. The electromagnet was turned-off unexpectedly for the subject at a time defined by the experimenter. After each trial, the electromagnet was reloaded.

A three-dimensional (3D) motion capture system with three cameras (ProReflex MCU 240, Qualisys AB, Sweden) was used to capture the 3D coordinates of the fingertips at 240 Hz. Reflective markers (5 mm in diameter) were placed on the centers of the fingertips (Fig. 1A). Before each trial, the force transducer signals were set at zero and the force and motion capture recordings were synchronized using the LabVIEW program.

2.2.2. The setup for friction coefficient estimation

The device was designed to measure digit downward force (normal force) and shear force (tangential force) simultaneously while the force sensor was moved horizontally by a linear motor with respect to the digit (Fig. 2; see Savescu et al., 2008). A multi-axis force sensor (Nano-25, ATI Industrial Automation, Garner, NC, USA) was attached to the frame to measure the normal and tangential forces. The top of the sensor (25 mm in diameter) was covered with 320-grit sandpaper. Forearm and wrist movement was prevented by Velcro straps, while a wooden piece placed underneath the subject's palm ensured a constant hand and finger configuration. The sampling frequency of the force sensor was 500 Hz, and the motor speed was 6 mm/s. Before each trial, all sensor signals were set to zero with the task-digit on the sensor and the hand relaxed; the sensor recorded only active downward force during the data acquisition.

2.3. Experimental procedures

Subjects washed their hands with soap and wiped the fingertips with alcohol to normalize the skin condition. After the 10–20 min orientation session, the subjects sat in a chair facing the 19 LCD screen, which provided force feedback. The entire experiment including orientation and main sessions for each subject lasted approximately 1 h.

2.3.1. Maximal voluntary contraction (MVC) tasks

The MVC forces of the right-hand digits were measured using the handle. Subjects were instructed to grasp the handle (Fig. 1B) with the four digits together and produce maximal total gripping force in a self-paced manner within 8 s. The subjects were instructed to relax immediately after reaching a maximal level of force. Two trials were given to subjects for each of the two digit combinations (*TIMR* and *TMRL*). Further, the trial with higher MVC_{TOT} was selected, and the forces of individual digits (MVC_i; $i = T,I,M,R,L$) at the time of reaching MVC_{TOT} were used to set the next tasks.

2.3.2. Trials with the handle with yielding sensors

There were fifteen conditions: 5 target digits (*Thumb*, *Index*, *Middle*, *Ring*, and *Little*) × 3 steady-state force levels (15, 30, and 45% of MVC_i). For each condition, the subjects were required to grasp the handle naturally and then to produce a prescribed steady-state force level for about 5 s. The feedback was provided on the target digit force only, but the subjects did not know this. The normal force (along z-axis in Fig. 1A) of the target digit was displayed in %MVC on the computer screen. At a random time, which was uniformly distributed between 5 and 8 s, the electromagnet holding the target digit was turned off, causing the digit to move into flexion. The displacement of the digit tip along z-axis was approximately 5–10 mm. The perturbation caused the target digit normal force to drop. The subjects performed three attempts for each perturbation condition, and the order of target digit (5 levels) and %MVC (3 levels) combinations was randomized.

2.3.3. Trials for friction coefficient estimation

There were fifteen experimental conditions: Five digits (*Thumb*, *Index*, *Middle*, *Ring*, and *Little*) × three normal force levels (15, 30, 45% of MVC_i). Each trial was 10-s long. The subjects were instructed to press on the sensor with one of the digits and match the given %MVC level as accurately as possible within the first 5 s. Then, the experimenter turned the linear motor on. The subjects were required to keep the steady level of normal force against the horizontal motion of the sensor ($-y$ direction in Fig. 2) without moving the hand/digits within the next 5 s. If the deviation of the normal force from the target level exceeded 10% for more than 1.5 s, the subject repeated the trial. The tip of instructed digit and the sensor surface were wiped with alcohol at the end of each trial to regulate the moisture level at the fingertip and contact surface. Each subject performed three consecutive trials for each digit and force level in a randomized order.

2.4. Data analysis

Data processing was performed using customized software written in Matlab (The MathWorks, Natick, MA, USA). The digit tip force and displacement data were digitally low-pass filtered with a zero-lag, 4th-order Butterworth filter at 200 Hz. The force data were down-sampled to 240 Hz to match the frequency of the motion capture system.

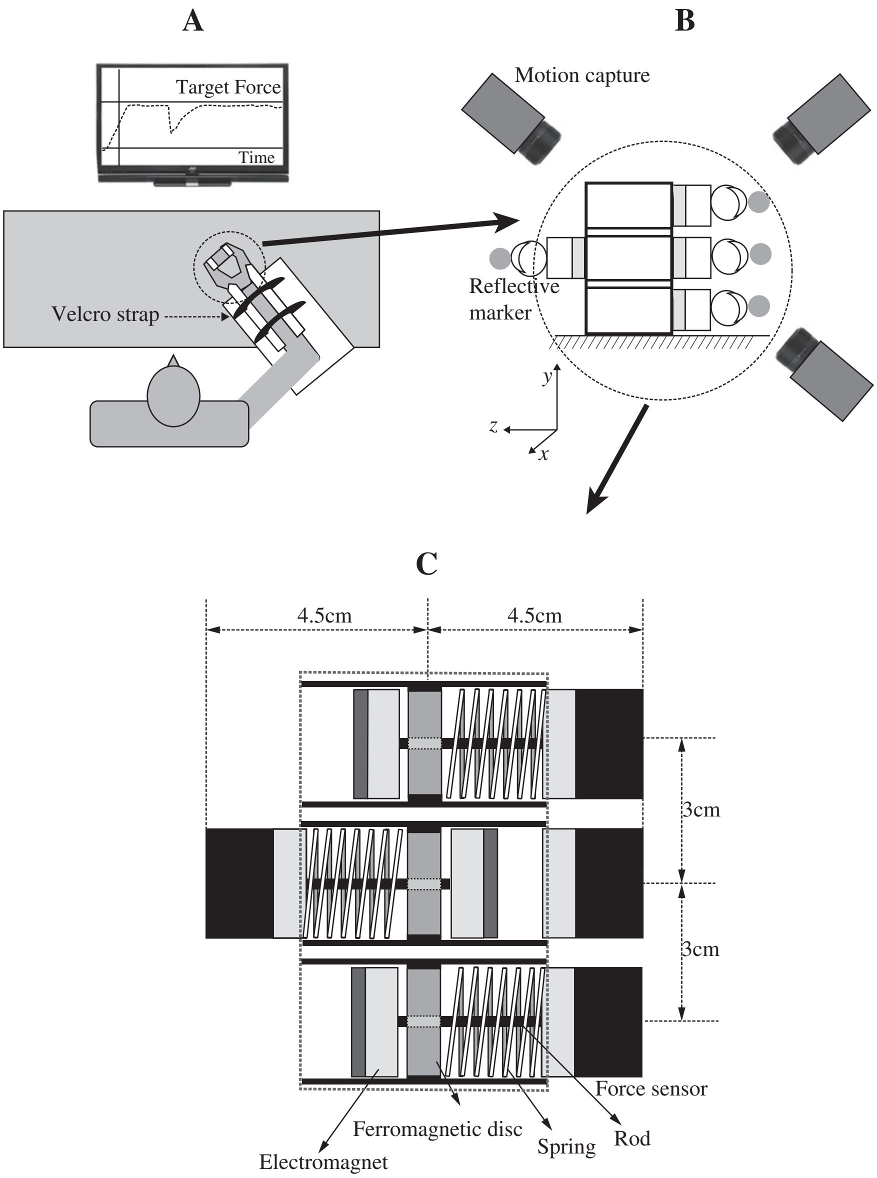

Fig. 1. The handle with yielding sensors. A: The subject held the handle, which was fixed to the immovable table. The computer screen displayed the force time series. B: The three-dimensional (3D) motion capture device with three cameras was used to capture the 3D position of the reflective markers on the digit tips. C: The force sensor was connected to a rod, which was screwed into an electromagnet. The rod passed through a low-frictional circular hole in a ferromagnetic disc, and a compression linear spring was placed between the force sensor and the ferromagnetic disc.

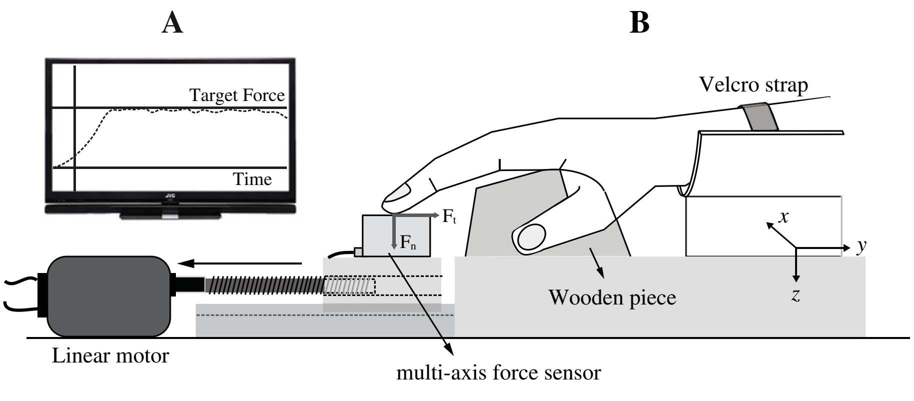

Fig. 2. The experimental setup for friction coefficient estimation. A: The computer screen displayed a task-digit normal force (F_n) in time-series. B: Force sensor measured digit downward force (normal force, F_n) and shear force (tangential force, F_t) simultaneously while the force sensor was moved horizontally by a linear motor with respect to the digit.

2.4.1. Apparent stiffness (k), damping (b), mass (m), and damping ratio (ζ) estimation

We considered digit motion along only one direction and assumed a linear damped second-order model (one degree-of-freedom) with lumped parameters for each hand digit:

$$m\mathrm{d}^2x(t)/\mathrm{d}t^2 + b\mathrm{d}x(t)/\mathrm{d}t + kx(t) = \Delta F(t) \tag{1}$$

where x, $\mathrm{d}x/\mathrm{d}t$, and $\mathrm{d}^2x/\mathrm{d}t^2$ are the digit tip position and its time derivatives along z-axis (Fig. 1A); ΔF—change in the task digit normal force; m—inertia; b—damping; and k—apparent stiffness. Multiple linear regression with a least-square fit was used to estimate m, b, and k for each target digit in each trial. To avoid the influence of reflexes and voluntary reactions, the parameters were estimated using the time window of 40 ms after the initiation of the perturbation (t_0, in Fig. 3). Thus, eleven data points (shown as dots on lines in Fig. 3) of force and position data of the task-digit after the initiation of the perturbation in a trial were used. Further, the damping ratio (ζ) was computed:

$$\zeta = b/2\sqrt{k \cdot m} \tag{2}$$

The subjects performed three attempts for each combination of digit and force level, and the average values of m, b, k, and ζ across three attempts were computed.

2.4.2. Mechanical enslaving (ME) and its time delay (ΔT_{ME})

The average steady-state normal force values (F_{SS}) within the time interval {−800 ms; −400 ms} before t_0 were computed. Maximal absolute magnitudes of the digit normal force changes ($|\Delta F|_{\max}$) with respect to F_{SS} were computed for each of the digits within the 40 ms time window after t_0. The digit mechanical enslaving (ME) was defined as the average non-target digit $|\Delta F|_{\max}$ expressed in percent of $|\Delta F|_{\max}$ of the task digit:

$$ME^i = \left[\left(\sum_{j=1}^{n} |\Delta F|^{ij}_{\max}/|\Delta F|^{i}_{\max}\right)/n-1\right] \times 100\% \tag{3}$$

where $i \neq j$, $n = 4$ (only four digits were involved in a single trial). $|\Delta F|^{ij}_{\max}$ is $|\Delta F|_{\max}$ by a non-target finger (j) during the i-digit task. $|\Delta F|^{i}_{\max}$ is $|\Delta F|_{\max}$ by a task-digit (i).

Fig. 3 shows typical examples of $\Delta F(t)$ of individual digits. Note the time delay of reaching $|\Delta F|_{\max}$ between the target (t_i) and non-target digits (t_{ij}). Time delay of enslaving effect (ΔT_{ME}) was defined as the average time delay across non-target digits with respect to the target digit.

2.4.3. Friction coefficient estimation (μ_D)

The dynamic friction coefficient (μ_D) was quantified as the ratio between the tangential and normal forces during the sensor motion. Average μ_D values were defined over the middle 2 s of the time period with steady-state values of the normal and tangential forces (Fig. 4). The average value across the three attempts was computed for each condition and subject.

2.5. Statistics

The data are presented as means and standard errors. Mixed-design ANOVAs with repeated measure were used. We explored how the main outcome variables (k, b, m, μ_D, ME, and ΔT_{ME}) were affected by *Age* (2 levels: young and elderly), *Digit* (5 levels: *T*, thumb; *I*, index; *M*, middle; *R*, ring; and *L*, little), and *Force* (3 levels: 15%, 30%, and 45% of MVC$_i$, $i = \{T, I, M, R, L\}$). A Greenhouse–Geisser adjustment was used in case of violation of the Mauchly sphericity test. Significant effects were further explored with Mann–Whitney tests with Bonferroni corrections for multiple comparisons. Since ME variable had computational boundaries (0–100%), these values were transformed using Fisher's z-transformation for statistic comparisons. Statistical significance was set at $P < 0.05$.

3. Results

3.1. Mechanical enslaving (ME) and its time delay (T_{ME})

In the trials performed with the handle with yielding sensors, disengaging the rod opposing the sensor (perturbation, see Methods) led to a nearly instantaneous drop in the force of the target digit (Fig. 3). The digit moved into flexion and reached a new steady state after a few tens of ms. Maximal change in the digit force was observed within 30 ms after the beginning of the perturbation. Forces produced by non-target digits also changed after the perturbation with a time delay of about 10 ms. When the thumb was perturbed, all non-target finger forces decreased, on average by about 27% of the thumb force change (Fig. 3A). When a finger was perturbed, non-target finger forces increased while the thumb force decreased (Fig. 3B).

The index of non-target digit force changes, mechanical enslaving (ME), in the elderly group was smaller compared to the young group (Elderly: 22.7%; Young: 34.4%, effect of *Age*, $F_{[1,18]} = 9.62$, $P < 0.01$). There was no difference in the relative timing of non-target digit force changes T_{ME} between the two groups, and no effects of baseline force on ME and T_{ME}. For both groups, T_{ME} of the R (mean = 6, SEM = 1 ms) and L fingers (mean = 6, SEM = 1 ms) was smaller than of the T (mean = 12, SEM = 1 ms), I (mean = 11, SEM = 1 ms), and M digits (mean = 11, SEM = 1 ms). ME was larger for the I (32.5%) and M fingers (33.9%) compared to the T (26.8%), R (28.4%), and L digits (21.1%) in both groups. There was a main effect of *Digit* for both T_{ME} and ME ($F > 8.1$, $P < 0.01$). Pairwise comparisons confirmed that $T,I,M > R,L$ for T_{ME} and $T,R,L < I,M$ for ME ($P < 0.05$).

3.2. Estimation of parameters within the second-order model

The target digit showed time profiles of the digit displacement resembling behavior of a critically damped second-order system (Fig. 3). Hence, the data across all subjects and conditions were fitted with the second-order linear model, Eq. (1). Overall, median R^2 value was about 0.82.

3.2.1. Apparent stiffness (k)

The elderly group showed larger values of the apparent stiffness (k in Eq. 1) as compared to the young group (Young: mean = 425.9, SEM = 23.1 N/m; Elderly: mean = 548.6, SEM = 23.1 N/m, effects of *Age*, $F_{[1,18]} = 14.13$, $P < 0.01$). The value of k increased with baseline force (15% < 30% < 45% of MVC$_i$, effect of *Force*, $F_{[1.52,\ 27.3]} = 96.80$, $P < 0.001$) in both groups (Table 1). Both groups showed significant differences in k across digits, with stronger digits showing a tendency for larger k values (effect of *Digit*, $F_{[2.54,\ 45.7]} = 97.68$, $P < 0.001$). There was also a significant interaction *Digit* × *Force* ($F_{[3.25,\ 58.5]} = 5.31$, $P < 0.01$) reflecting the fact that the effect of *Force* on k (15% < 30% < 45% of MVC$_i$) was significant only for the T, I, and M fingers (pairwise comparisons, $P < 0.05$).

3.2.2. Damping (b)

In contrast to the larger k values in the elderly group, the damping coefficient (b in Eq. 1) in the elderly group was smaller than in the young group (Table 2). The value of b increased with the magnitude of baseline force (15% < 30% < 45% of MVC, effect of *Force*, $F_{[2,\ 36]} = 52.34$, $P < 0.001$). The damping coefficient for T and I was larger than for the other fingers (effect of *Digit*, $F_{[2.20,\ 39.6]} = 41.87$, $P < 0.001$). There was also a significant *Digit* × *Force* interaction ($F_{[3.81,\ 68.54]} = 3.39$, $P < 0.01$) reflecting that the effect of *Force* on b was significant for the T (15% = 30% < 45% of MVC, $P < 0.05$), I, and M digits (15% < 30% < 45% of MVC, $P < 0.05$) only.

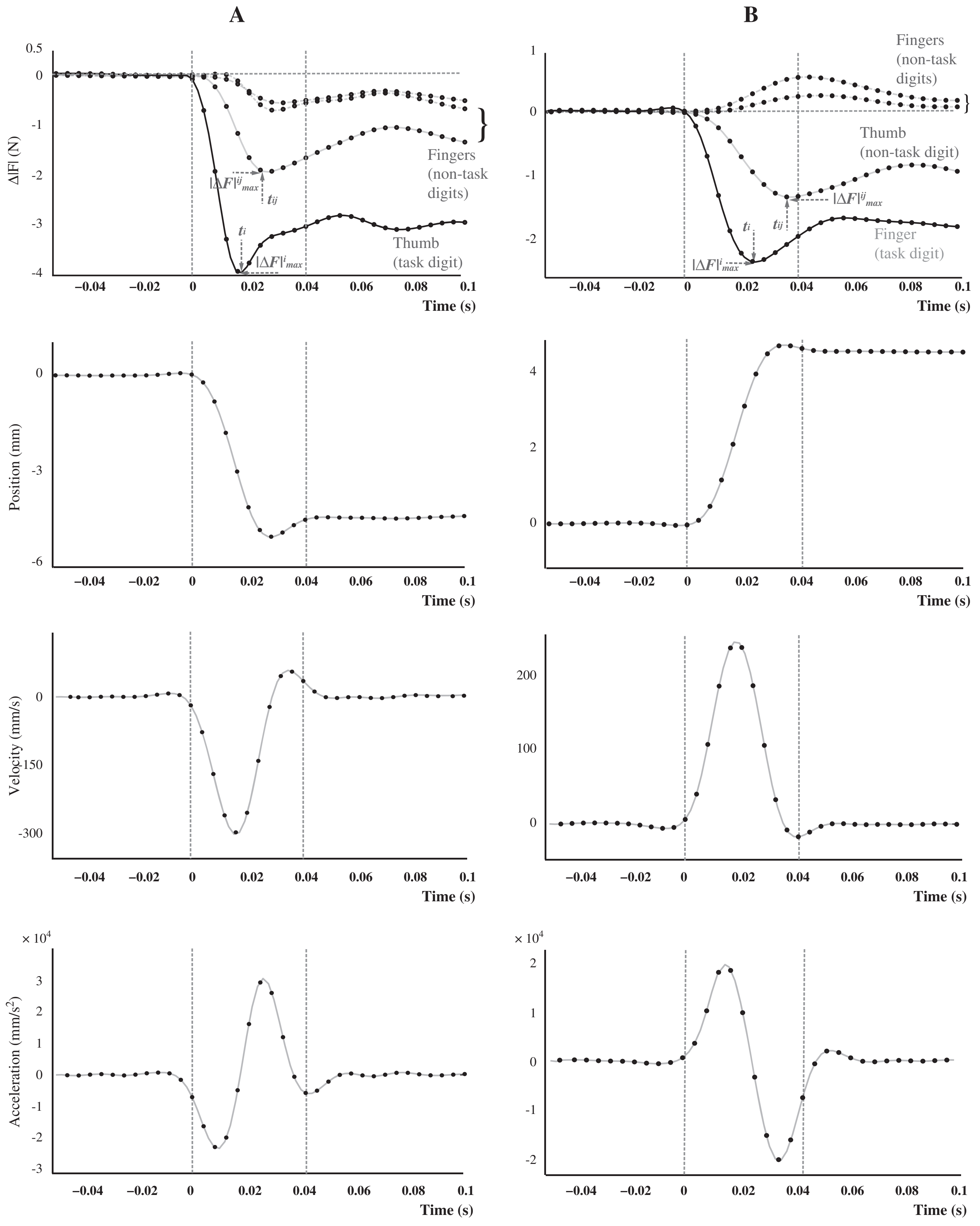

Fig. 3. Typical example of digit force and kinematic profiles for a young subject during A: The thumb perturbation and B: The finger perturbation. The top panels show the force changes in all four digits. The bottom six panels show the target digit position, velocity, and acceleration.

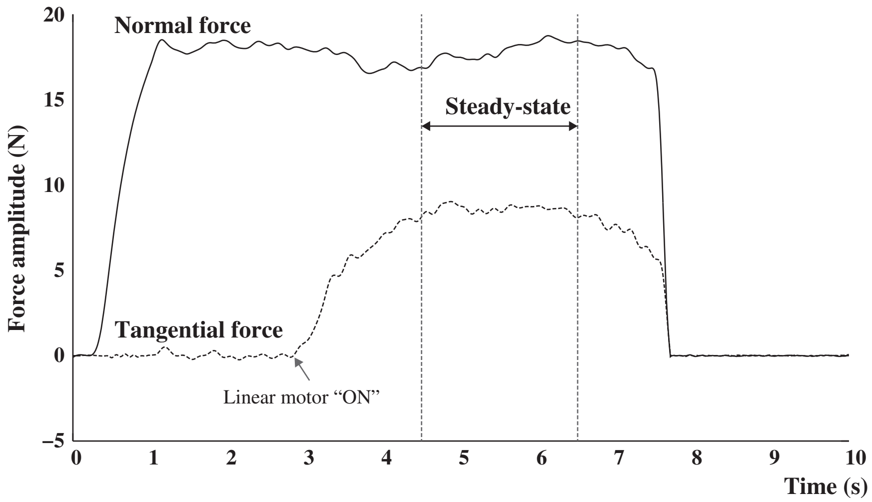

Fig. 4. The typical force profiles during the measurement of the friction coefficient.

Fig. 5 illustrates the findings for the two coefficients, *k* and *b*, across the two groups across all individual subjects and conditions. Note that *k* and *b* correlated positively within each group (Young: $R = 0.74$; Elderly: $R = 0.67$). However, the two points representing the overall average values of *k* and *b* across the subjects within each group (Young: large closed circle; Elderly: large open circle in Fig. 5) were located on a line with a negative slope reflecting the fact that $k_{\text{Young}} < k_{\text{Elderly}}$ while $b_{\text{Young}} > b_{\text{Elderly}}$.

3.2.3. Inertia (*m*)

There was no significant difference in the inertial parameter *m* in Eq. (1) between the young and elderly groups and no effects of baseline force. There was a difference across the digits: T—14.70 g > I—7.99 g; M—7.77 g; R—8.18 g; L—7.47 g (effect of *Digit*, $F_{[2.47,\ 44.47]} = 16.19$, $P < 0.001$) without other effects.

3.3. Damping ratio (ζ)

The elderly group showed smaller values of the damping ratio (Eq. 2) as compared to the young group (Young: mean = 1.22, SEM = 0.046; Elderly: mean = 0.75, SEM = 0.044, effect of *Age*, $F_{[1,\ 18]} = 53.48$, $P < 0.001$). The damping ratio was not affected by the magnitude of baseline force (Table 3). In addition, the damping ratios for the *T*, *I*, and *M* digits were larger than for the *R* and *L* fingers (effect of *Digit*, $F_{[2.40,\ 43.26]} = 19.50$, $P < 0.001$).

3.4. Friction coefficient

Overall, the elderly showed smaller friction coefficients (μ_D) as compared to the young group (Young: mean = 0.81, SEM = 0.03; Elderly: mean = 0.60, SEM = 0.03, effect of *Age*, $F_{[1,\ 21]} = 29.28$, $P < 0.001$). An increase in the normal force in the young group led to a drop in μ_D (15% > 30% > 45% of MVC; effect of *Force*, $F_{[2,\ 36]} = 32.95$, $P < 0.001$) while there was no such an effect in the elderly group (Table 4; *Age* × *Force*, $F_{[2,\ 36]} = 15.50$, $P < 0.001$). For both groups, there were no significant differences among μ_D of the digits.

4. Discussion

All three hypotheses formulated in the Introduction have been supported by the data. We observed smaller friction coefficients in the older group compared to the younger group in support of Hypothesis 1 (see also earlier reports, Cole, 1991; Cole et al., 1999). Within the second-order linear model, older subjects had larger apparent stiffness and smaller damping values with no significant differences in the inertial parameters resulting in smaller damping ratios as predicted by Hypothesis 2. Perturbations applied to one of the digits produced force changes in both perturbed and non-perturbed digits. The force changes in the non-perturbed digits (mechanical enslaving, ME) were smaller in the older subjects in support of Hypothesis 3 (cf. Kapur et al., 2010; Shinohara et al., 2003).

4.1. Mechanical properties of the hand digits and their changes with age

The values of friction coefficients observed in our study match well the previously reported values (Cole, 1991; Cole et al., 1999; Savescu et al., 2008). Our study is unique, however, in quantifying the friction of all five digits. Note that skin friction values have been recently associated with the role of different areas of the body in contact tasks (Uygur et al., 2010). The most commonly used digits, such as the thumb and the index finger, could be expected to show larger *k* values compared to digits that are used only in a subgroup of grasps, such as the ring and little fingers. We did not find such differences in either group.

Table 1
Apparent stiffness (*k*, N/m).

%MVC		15%					30%					45%				
Task-digit		*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*
Young	Mean	460.9	360.2	298.7	268.6	234.7	647.7	474.8	410.6	327.9	323.3	798.3	568.1	491.5	386.4	337.9
	SE	37.1	19.5	17.5	10.4	27.8	32.4	36.5	20.9	35.7	18.7	34.4	39.7	21.6	14.4	25.9
Elderly	Mean	632.6	500.5	413.2	360.3	313.3	777.8	637.2	536.0	402.9	392.0	952.4	717.4	628.4	495.6	469.1
	SE	58.0	34.0	31.9	34.4	26.9	74.5	42.3	37.7	27.5	23.5	74.7	46.8	54.0	26.3	32.1

T, *I*, *M*, *R*, and *L* represent thumb, index, middle, ring, and little finger, respectively.

Table 2
Damping coefficient (b, Ns/m).

%MVC		15%					30%					45%				
Task-digit		*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*
Young	Mean	6.07	4.15	3.21	2.03	2.04	7.84	5.06	3.52	2.10	2.05	7.99	6.08	4.61	2.86	2.45
	SE	0.69	0.29	0.29	0.28	0.17	0.68	0.36	0.31	0.36	0.33	1.18	0.34	0.47	0.34	0.24
Elderly	Mean	3.36	3.72	2.36	1.77	1.43	4.45	4.16	3.25	1.39	1.61	6.63	5.58	4.21	2.14	2.26
	SE	0.36	0.48	0.26	0.15	0.30	0.85	0.47	0.30	0.18	0.34	0.61	1.20	0.39	0.23	0.44

T, *I*, *M*, *R*, and *L* represent thumb, index, middle, ring, and little finger, respectively.

Our estimation of the mechanical parameters within the second-order linear model is an obvious simplification of the real object. Inadequacy of such linear models has been emphasized (reviewed in Zatsiorsky, 2002). Our main justifications for this method are in the results that show digit kinematics resembling trajectories of the second-order linear systems (Fig. 3). Besides, the only parameter, for which more or less reliable data are available in the literature (the inertial parameter, m), showed in our model values compatible with the published data (Hajian and Howe, 1997), ranging between 7.5 and 15 g.

The increased apparent stiffness in older persons could get contributions from peripheral changes in muscles (some muscle fibers turn into connective tissue) and maybe other tissues. Apparent stiffness tends to change in parallel with damping (Bennett et al., 1992; Cenciarini et al., 2010; Milner and Cloutier, 1998). Indeed, the two parameters, k and b, correlated positively across digits and across persons within each group, but between groups we observed opposite changes, an increase in k and a drop in b. This led to the drop in the damping ratio, which may have important implications for stability of prehensile actions (see later).

There were significant differences in a number of mechanical parameters between two groups of digits, R and L vs. T, I, and M. These can potentially be related to differences in digit strength, function, and independence (cf. Zatsiorsky et al., 2000). Unfortunately, our current data set is too limited to allow proper multi-factorial analysis to elucidate the origins of these differences.

4.2. Origins of mechanical enslaving

When a person moves a finger or presses with one finger, other fingers of the hand also move and generate force; these phenomena have been addressed as limited finger individuation or enslaving (Zatsiorsky et al., 2000). Several factors contribute to enslaving ranging from the connective tissue links between fingers to multi-tendon, multi-finger extrinsic hand muscles, to overlap in finger cortical projections (reviewed in Schieber and Santello, 2004; van Duinen and Gandevia, 2011).

Mechanical enslaving (ME) observed in our study is definitely of a non-neural origin: The non-target digits moved at time delays of under 10 ms, which is incompatible with action mediated by the central nervous system. The most straightforward explanation of ME is via inertial effects: When one digit accelerated after the release, the associated inertial forces induced forces in other digits due to the mechanical coupling. Indeed, this explanation is valid for the different ME patterns observed when the thumb was the target digit and when a finger was the target digit.

The group difference in ME resembles earlier reports on smaller enslaving effects in older persons (Kapur et al., 2010; Shinohara et al.,

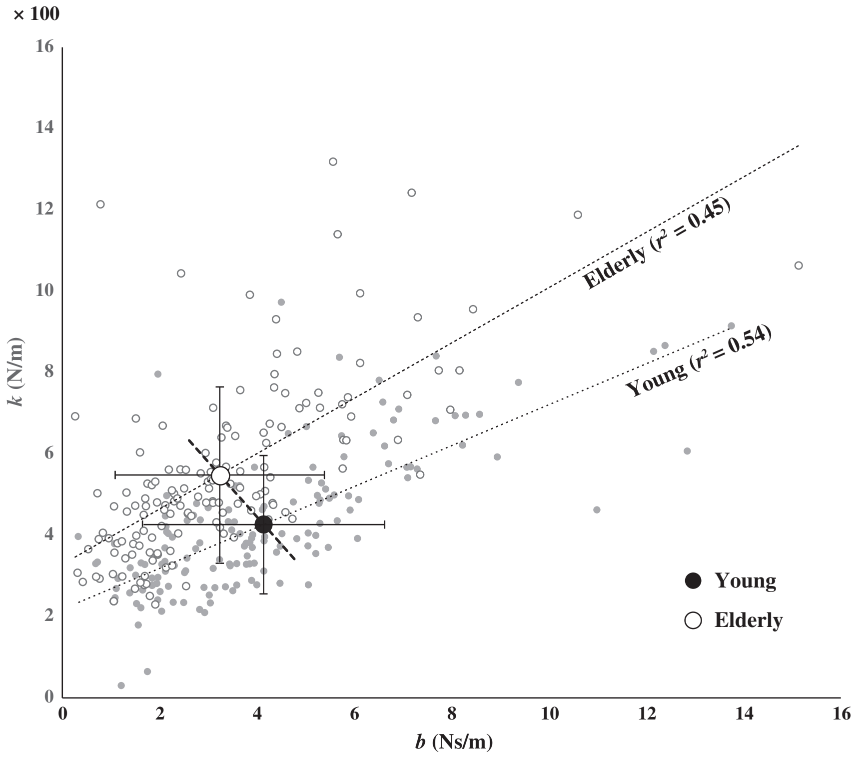

Fig. 5. All the data for all subjects are plotted on the apparent stiffness (k) vs. damping (b) plane. The data for the young group are shown with filled circles; the data for the elderly group are shown with open circles. The regression lines are shown with the coefficients of determination. The grand average data are shown with large symbols and standard deviation bars.

Table 3
Damping ratio (ζ).

%MVC		15%					30%					45%				
Task-digit		*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*
Young	Mean	1.56	1.45	1.23	0.69	0.87	1.70	1.89	1.20	0.73	0.66	1.27	1.81	1.19	1.09	0.99
	SE	0.24	0.13	0.08	0.07	0.08	0.27	0.20	0.14	0.14	0.08	0.16	0.19	0.13	0.28	0.07
Elderly	Mean	0.66	1.01	0.78	0.53	0.48	0.77	0.90	0.82	0.38	0.43	0.88	1.31	0.99	0.62	0.67
	SE	0.10	0.14	0.13	0.06	0.11	0.17	0.12	0.13	0.05	0.08	0.07	0.22	0.12	0.09	0.12

T, *I*, *M*, *R*, and *L* represent thumb, index, middle, ring, and little finger, respectively.

Table 4
Friction coefficient (μ_D).

%MVC		15%					30%					45%				
Task-digit		*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*	*T*	*I*	*M*	*R*	*L*
Young	Mean	0.94	0.97	0.96	0.98	0.96	0.75	0.83	0.81	0.77	0.77	0.67	0.72	0.69	0.69	0.68
	SE	0.03	0.05	0.05	0.05	0.06	0.02	0.03	0.03	0.04	0.04	0.03	0.03	0.03	0.03	0.03
Elderly	Mean	0.61	0.60	0.66	0.62	0.63	0.57	0.60	0.58	0.60	0.58	0.58	0.60	0.56	0.57	0.57
	SE	0.04	0.05	0.05	0.06	0.03	0.05	0.05	0.04	0.05	0.03	0.02	0.03	0.03	0.03	0.02

T, *I*, *M*, *R*, and *L* represent thumb, index, middle, ring, and little finger, respectively.

2003). A hypothesis on a shift of the neural control of the hand from more synergic to more element-based control has been offered to explain these findings (Kapur et al., 2010). The differences in ME obviously cannot be explained by reactions to the perturbations mediated by the central neural system; they could, however, be produced by different patterns of muscle activation prior to the perturbation. These observations suggest that the earlier findings of lower enslaving in older persons have to be taken cautiously until the reasons for lower ME become clear.

4.3. Implications for prehensile actions

The results of our study have implications for everyday prehensile actions. In particular, the low friction of the digits requires older people to exert larger grip forces (Cole, 1991; Cole et al., 1999; Gorniak et al., 2011; Zatsiorsky and Latash, 2008). This strategy has several drawbacks. First, manipulation of fragile objects becomes problematic (see Gorniak et al., 2011). Higher grip forces can also lead to quicker fatigue for long-lasting actions. Besides, higher forces are typically associated with higher force variability (Newell and Carlton, 1993).

The relatively low damping ratio (ζ) in older subjects is a novel and potentially important finding. While typically $\zeta > 1$ for the young group, for the elderly group $\zeta < 1$. So, a perturbation applied to a digit of a young person can be expected leading to a smooth digit motion with no lasting oscillation (over-damped system), while a similar perturbation applied to a digit of an older person can lead to an ongoing oscillation with an exponential decay (under-damped system). This difference may have direct implications for stability of everyday actions when unexpected changes in forces are quiet common.

4.4. Limitations of the study

We see the use of the second-order linear model as the biggest limitation of the study. While the finger kinematic profiles (illustrated in Fig. 3) justify using such a model and such models have been used in the field frequently (Hajian and Howe, 1997; Latash and Gottlieb, 1991; Tsuji et al., 1995), this remains a weakness. The importance of non-linearities in properties of muscles and joints has been emphasized (Karniel and Inbar, 1997; Lenzi et al., 2011; reviewed in Zatsiorsky and Prilutsky 2012), and more complex models could be needed to provide a more adequate description of digit mechanics. As of now, however, such models are not readily available and they involve more parameters, which presents another danger in fitting experimental results. Possible effects of moisture levels at the fingertip and contact surface during the experiments with the friction coefficient estimation remain unknown since we did not control for the moisture levels during the friction coefficient estimation procedure.

Conflict of interest

None.

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