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Do Synergies Improve Accuracy? A Study of Speed-Accuracy Trade-Offs During Finger Force Production

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We explored possible effects of negative covariation among finger forces in multifinger accurate force production tasks on the classical Fitts's speed-accuracy trade-off. Healthy subjects performed cyclic force changes between pairs of targets "as quickly and accurately as possible." Tasks with two force amplitudes and six ratios of force amplitude to target size were performed by each of the four fingers of the right hand and four finger combinations. There was a close to linear relation between movement time and the log-transformed ratio of target amplitude to target size across all finger combinations. There was a close to linear relation between standard deviation of force amplitude and movement time. There were no differences between the performance of either of the two "radial" fingers (index and middle) and the multifinger tasks. The "ulnar" fingers (little and ring) showed higher indices of variability and longer movement times as compared with both "radial" fingers and multifinger combinations. We conclude that potential effects of the negative covariation and also of the task-sharing across a set of fingers are counterbalanced by an increase in individual finger force variability in multifinger tasks as compared with single-finger tasks. The results speak in favor of a feed-forward model of multifinger synergies. They corroborate a hypothesis that multifinger synergies are created not to improve overall accuracy, but to allow the system larger flexibility, for example to deal with unexpected perturbations and concomitant tasks.

Keywords: variability, force, synergy, Fitts's law

Several recent studies have reported force-stabilizing synergies in finger force production tasks (Latash, Scholz, Danion, & Schöner, 2001, 2002; Scholz, Danion, Latash, & Schöner, 2002; Shim, Olafsdottir, Zatsiorsky, & Latash, 2005; reviewed in Latash, Scholz, & Schöner, 2002, 2007). In those studies, synergies have been defined as neural organizations that allow for covariation of elemental variables (those produced by elements of a system) that stabilize important performance variables (Gelfand & Latash, 1998; Latash, Scholz, & Schöner, 2002).

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In multifinger force production studies, elemental variables were associated with individual finger forces or commands to fingers (i.e., finger modes, Danion et al. 2003), while performance variables were associated with the total force produced or total moment of force produced. In particular, during slow, accurate force production tasks, individual finger forces (and finger modes) have been shown to covary negatively across trials, leading to a drop in the total force variability as compared with what could be expected in the absence of covariation.

However, do synergies actually improve accuracy? Surprisingly, there is no clear answer to this question. One reason is that variability of individual finger forces may increase in multifinger tasks as compared with single-finger tasks. As a result, even in the presence of negative covariation among finger forces, the total force may show higher, lower, or unchanged variability. Another complicating factor is that indices of force variability scale with force magnitude (Newell & Carlton, 1988; Carlton, Kim, Liu, & Newell, 1993), and finger groups are known to be stronger as compared with single fingers in isometric force production tasks (Li, Latash, & Zatsiorsky, 1998). This means that tasks should be set differently to allow comparisons between single-finger and multifinger tasks.

Previously, one study examined how finger force variability changed as the number of fingers in a cyclic force-production task changed (Latash et al., 2001). In that study, using two fingers decreased the coefficient of variation of the total force as compared with one-finger tasks. However, adding a third finger did not change the coefficient of variation. In all cases, the tasks were set as equal percentages of the maximal force-producing ability of the explicitly involved finger groups (cf. Christou, Grossman, & Carlton, 2002).

In this study, we address the issue of variability in force production between single- and multifinger tasks using two types of speed-accuracy trade-off. The first is the famous Fitts's law (Fitts, 1954; Fitts & Peterson, 1964; reviewed in Plamondon & Alimi, 1997), which states that, when humans are required to perform movements to a target "as fast and as accurately as possible," movement time (*MT*, the time between the initiation and the end of an action) is a logarithmic function of the ratio between movement amplitude (*A*) and target width (*W*): $MT = a + b \times \log_2 (2A / W)$. This relation is frequently expressed using the notion of index of difficulty (*ID*), $ID = \log_2 (2A/W)$. Fitts's law has been confirmed over a variety of populations, conditions, and tasks, including isometric force-production tasks (Kantowitz & Elvers, 1988; Billon, Bootsma, & Mottet, 2000). Although the location of mechanisms that produce Fitts's law is still under debate (Meyer, Smith, & Wright, 1982; Plamondon & Alimi, 1997), it is likely to reflect processes at the level of motor planning (Gutman & Latash, 1993; Duarte & Latash, 2007).

Hence, our first hypothesis is that the central neural controller will take advantage of the negative force covariation in multifinger tasks and show faster force production (smaller *MT*) for comparable *IDs* as compared with single-finger tasks. We expected the decrease in *MT* (as compared with what could be expected in the absence of multifinger force-stabilizing synergies) to be higher for tasks with higher *ID*, which require slower force rates, since such tasks are associated with stronger negative force covariation (Latash, Scholz, Danion, & Schöner, 2002). We expected the decrease in *MT* to be absent during very fast movements (low *ID* and low *MT*) since negative covariation is commonly absent in such tasks (Latash, Scholz, Danion, & Schöner, 2002; Olafsdottir, Yoshida, Zatsiorsky, & Latash, 2005).

Another well-established paradigm of the speed-accuracy trade-off links variability in final position (expressed as the effective target width, W_E) and actual movement amplitude to movement time: $W_E = a + b \times (A/MT)$, where a and b are constants (Schmidt, Zelaznik, Hawkins, Frank, & Quinn, 1979). To test whether negative covariation among finger forces helps improve finger force variability in multifinger tasks, we explored the relation between MT and W_E. Our second hypothesis is that multifinger tasks will be associated with smaller W_E expressed in percentage of maximal voluntary force for similar MT values.

Methods

Participants

Four male and four female students served as subjects in this study. Average data for the subjects were (mean ± *SD*): 27 ± 3 years of age, 1.71 ± 0.11 m in height, 70.9 ± 12.8 kg in mass, 18.8 ± 1.8 cm for right hand length, 8.5 ± 1.0 cm for right hand width, 18.9 ± 1.9 cm for left hand length, and 8.3 ± 1.0 cm for left hand width. Hand length was measured as the distance from the tip of the distal phalanx of digit three to the distal crease of the wrist with the hand in a neutral flexion/extension pose. Hand width was measured between the lateral aspects of the index and little finger metacarpophalangeal (MCP) joints. All subjects were strongly right-handed according to their preferential use of the hand during daily activities such as writing, drawing, and eating. The subjects had no previous history of neuropathies or traumas to the upper limbs. None of the subjects had a history of long-term involvement in hand or finger activities such as typing and playing musical instruments. All subjects gave informed consent according to the procedures approved by the Office of Regulatory Compliance of the Pennsylvania State University.

Experimental Setup

Eight unidirectional piezoelectric force sensors (model 208AO3; PCB Piezotronic Inc., Depew, NY, USA), were used to measure forces produced by the tips of individual fingers of both hands. Each sensor was covered with a cotton pad to increase friction and prevent the influence of finger skin temperature on the force measurements. Two groups of four force sensors were placed within aluminum frames (14 cm × 9 cm each) in a groove on a wooden board. The two frames were spaced 40 cm apart. The sensors were medio-laterally spaced 3 cm apart within the aluminum frames. The position of the sensors in the anterior-posterior direction could be adjusted within 6 cm to fit individual subject hand anatomy, see Figure 1. Subjects were instructed to rest their fingers on the sensor, but to apply no force prior to each trial. At the beginning of each trial, the signal from each of the sensors was set to zero with the subject's fingers resting on the sensors.

During the experiment, the subject sat in a chair facing the testing table with his or her upper arms at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, and the elbows at approximately 45° of flexion (Figure 1). The forearms were secured to the wooden board by two sets of Velcro straps. The midline of the board was aligned with the midline of the participant's body, and the positions of the hands were symmetrical with respect to the midline of

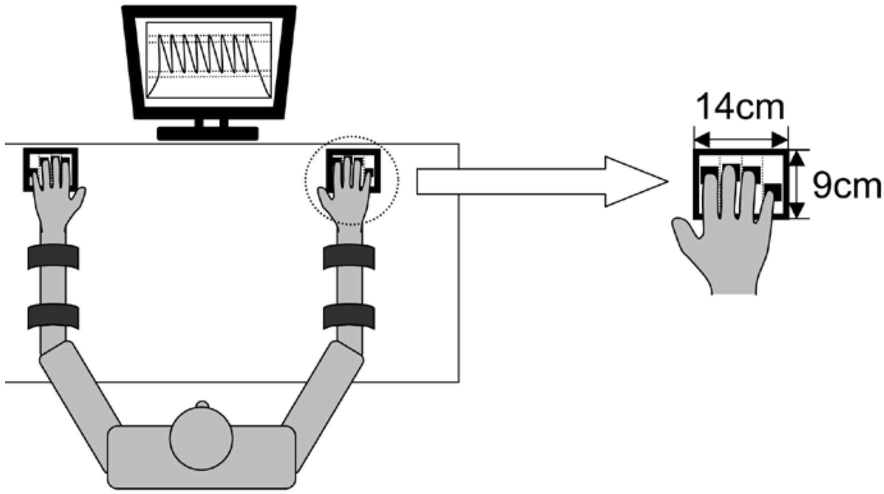


Figure 1 — An illustration of the sensor setup and the visual feedback display for this experiment.

the body. A custom-fitted support object was placed under each of the participant's palms to help maintain a constant configuration of the hand and fingers. The MCP joints were approximately 20° in flexion, and all interphalangeal joints were slightly flexed so that each hand formed a dome. Subjects were permitted to select comfortable positions for their thumbs during the experiment. A computer monitor was located 0.65 m away from the subject. The monitor displayed the task (described in the next section). Force data were sampled at 200 Hz with a National Instruments A/D board (NI PCI-6023E, National Instruments, Austin, TX, USA) and LabView-based program (LabView 6.1, National Instruments, Austin, TX, USA).

Procedure

The experiment consisted of a few control trials and a main set of tasks. In the control trials, the subjects were required to produce maximal voluntary contraction (MVC) force by finger sets used in the main task. The nine finger sets were: I_R, M_R, R_R, L_R, M_L, IM_R, IMR_R, $IMRL_R$, and I_RM_L; where I = index, M = middle, R = ring, L = little, and the subscripts denote the hand to which the fingers belong (R = right, L = left). These particular fingers and finger combinations were selected to explore possible differences across the four fingers, across finger combinations with different numbers of fingers, and across one-hand and two-hand finger combinations. The subjects were required to press with the designated set of fingers "as hard as possible." Each MVC trial started with the subject sitting quietly with the hands resting on the sensors. A sound signal was given, and then a cursor showing the total force produced by the designated fingers started to move over the screen. The subject was given a time interval of 3 s to reach maximal force by pressing down with the designated set of fingers. There were intervals of at least 30 s between successive MVC trials. Two MVC trials per finger combination were collected, and the trial with the highest total peak force produced by the instructed fingers (MVC_{IF}) was selected for setting subsequent tasks.

In the set of main tasks, subjects were instructed to press with the specified set of fingers so that the total force produced by the fingers oscillated between two target windows as quickly as possible. Subjects were instructed to complete a minimum of 12 accurate oscillations (out of 15 consecutive oscillations) between the two target windows in each trial. After the oscillations, subjects were instructed to stop producing finger forces to reduce the effects of fatigue. The distance (A) between the centers of the two targets was set at 10% and 20% of MVC_{IF}. The lowest of the two targets was centered at 10% MVC_{IF} to avoid the floor effect on the target window. For the A = 10% MVC_{IF} condition, the targets were centered at 10% and 20% MVC_{IF}; for the A = 20% MVC_{IF}, the targets were centered at 10% and 30% MVC_{IF}, respectively. The width of the target windows (W) displayed for the subjects was selected to correspond to six indices of difficulty (ID), $ID = \log_2(2A / W)$, such that *IDs* = 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0 were used. For the 10% *MVC* distance between targets, these *IDs* correspond to target widths of 7.07, 5.00, 3.54, 2.50, 1.77, and 1.25% *MVC*. For the 20% *MVC* distance between targets, these *IDs* correspond to target widths of 14.14, 10.00, 7.07, 5.00, 3.54, and 2.50% *MVC*. We purposely explored a broad range of *ID* values to compare very high rates of force production (that were not expected to show high negative force covariation—see the Introduction) and relatively slow force production. Thus, each of the nine finger combinations was tested at 12 different target conditions, resulting in 108 trials in the main set of tasks and total minimum of 1,296 force cycles. One trial per testing condition (108 testing conditions) was collected for each subject. Trial rejection criterion is presented in subsequent paragraphs.

Prior to each trial the subject sat relaxed with the digits of each hand resting on the sensors. The computer generated two beeps (a “get ready” signal), and a cursor showing the total force produced by the instructed finger(s) started to move along the screen. The screen also showed the two targets (see Figure 1), and the task was to oscillate between the two targets with the cursor as quickly as possible while keeping the number of errors (landing outside a target) under 20%.

In each condition, subjects performed 1 trial with 60-s intervals between consecutive trials. There were 3-min rest intervals after every 15 trials to reduce the effects of fatigue. If subjects claimed fatigue between such scheduled rest intervals, an additional rest period of 3–5 min was given to the subject immediately. Prior to each trial, subjects were permitted to practice the condition until they were comfortable with the tasks. Typically, subjects did not need a practice trial before most conditions. However, for conditions with high *ID* values (*ID* = 3.5 and 4.0) some subjects needed practice trials. On average, subjects performed one practice trial for *ID* conditions 3.5 and 4.0. Presentation of tasks was randomized across the subjects. Trials in which the subject failed to achieve 12 accurate oscillations out of 15 consecutive oscillations were rejected and repeated immediately. On average, less than three trials were rejected per subject.

Data Analysis

The data were processed off-line using customized MATLAB software (Mathworks Inc., Natick, MA, USA). The force data from the main task were low-pass filtered at 10 Hz using a 2nd order, zero-lag Butterworth filter. For the finger force data, the oscillations between targets were considered to consist of two components: increase (*UP*) and decrease (*DN*) of total force.

Movement time (*MT*) was determined as the time between the two consecutive occurrences of 5% of the absolute maximum force rate ($|VF_{max}|$) within a half-cycle of an oscillation. The value of VF_{max} was defined using the first-time derivative of the total force produced by the designated fingers. Thus, *MT* for the increase component (MT_{UP}) was determined as the time between the two 5% $|VF_{max}|$ occurrences of an increase in total force, although *MT* for the decrease component (MT_{DN}) was determined as the time between the two 5% $|VF_{max}|$ occurrences of a decrease in total force. The first-time derivative of the total force was used to determine *MT* since some subjects exhibited dwell time at the targets during the task; thus the intervals between total force maxima and minima would not accurately reflect actual *MT*. MT_{UP} and MT_{DN} were averaged separately across each trial. An example of *MT* definitions is shown in Figure 2. Force variability was estimated using the effective target width (W_E), computed as 4 times the standard deviation (*SD*) of force amplitude across oscillations within a condition. This interval for W_E corresponds to the range $\pm 2 \times SD$, which will contain 95.4% of the data of interest (here, final force level) given a normal data distribution (Duarte & Latash, 2007).

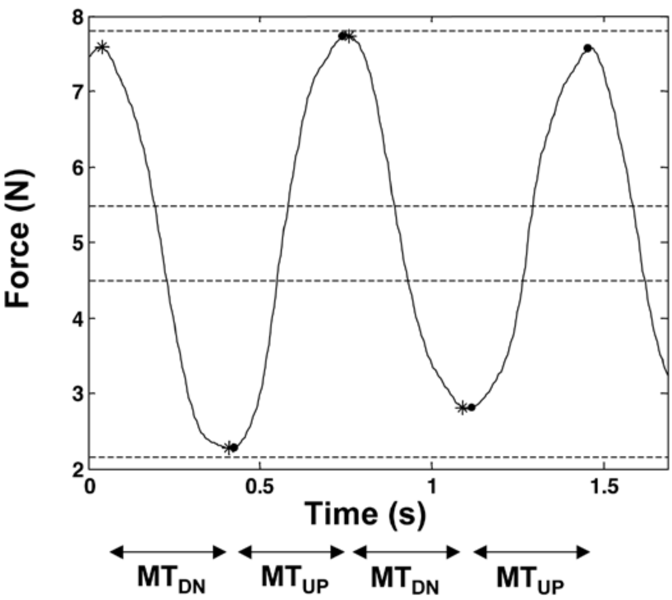


Figure 2 — An example of *MT* definitions for two MT_{UP} and two MT_{DN} time intervals for a task (actual data are shown). Force output by designated fingers is shown as a solid line; targets are denoted by bands between two sets of thin dashed lines. The beginning and end of MT_{UP} intervals are denoted by filled-in circles; the beginning and end of MT_{DN} intervals are denoted by asterisks. Both MT_{UP} and MT_{DN} intervals are also denoted by arrows for clarity. Note that both MT_{UP} and MT_{DN} intervals are defined by 5% of the absolute maximum velocity ($|VF_{max}|$) within a half-cycle of an oscillation.

Statistics

The data are presented in the text and figures as means and standard errors. Mixed model analyses of variance (ANOVAs) were performed on the *MT* and W_E data with these factors: *Subject* (random factor, 8 levels), *ID* (six levels, 1.5, 2.0, 2.5, 3.0, 3.5, and 4.0), *Amplitude* (two levels, 10% MVC_{IF} and 20% MVC_{IF}), *Fingers* (nine levels, one for each finger condition, levels were selected depending on particular comparisons), *#Fingers* (four levels, one for the number of fingers involved in both single- and multifinger tasks), and *Force Change* (two levels, one for MT_{UP} and the other for MT_{DN}). Both the *MT* and W_E data were $\log_{10}$-transformed to comply with normality assumptions during statistical testing. Pairwise comparisons were performed using Bonferroni statistics to analyze significant effects of ANOVAs. Linear and exponential regressions were also performed to determine overall correlations of movement time and effective target width to index of difficulty.

Results

All subjects were able to perform each of the main sets of tasks without obvious difficulty. Generally, all subjects showed a nearly linear dependence of movement time (*MT*) on index of difficulty (*ID*) as elucidated by Fitts's Law (see Introduction). Figure 3 shows the performance of a typical subject for several finger combinations across *ID* levels for both MT_{UP} and MT_{DN}. Across all subjects, *MT* (both MT_{UP} and MT_{DN}) could be described by a linear relationship with *ID*, which was verified with linear regressions. Such models explained, on average, 59.5% of the variance in the data across all finger combinations for MT_{UP} and 62.0% of the variance in the data across all finger combinations for MT_{DN}. A summary of the *MT* data for all subjects in all tested conditions can be found in Table 1.

MT Dependence on Amplitude, Index of Difficulty, and Force Changes

Overall, force production amplitude did not affect *MT* significantly. However, *ID* level and force change affected *MT* across all finger combinations. Namely, *MT* increased as *ID* level increased and $MT_{UP} < MT_{DN}$, when *MT* was analyzed across all finger combinations, as shown in panel A of Figure 4. This was confirmed by a four-way, mixed effects ANOVA with factors: *Subject, ID, Amplitude,* and *Force Change*. Main effects of *Subject* [$F(7, 1697) = 313.41, p < .001$], *ID* [$F(5, 1697) = 302.81, p < .001$], and *Force Change* [$F(1, 1697) = 29.02, p < .001$] were found without any significant interactions. Pairwise Tukey's comparisons revealed significant differences across all pairs of the *ID* levels except 1.5 versus 2.0. The significant effects reflected an increase in *MT* with *ID* and smaller MT_{UP} as compared with MT_{DN}. This pattern of significant differences among *ID* levels was consistent across all of the mixed-effect ANOVAs with *ID* as a factor performed on the *MT* data.

An *Amplitude* × *ID* interaction was found for *MT* in only the two two-finger combinations, IM_R and I_RM_L, so that, for *IDs* less than or equal to 2.5, *MT* was lower for the smaller force production amplitude (A_{10}) as compared with the larger force production amplitude (A_{20}). For *IDs* larger than or equal to 3.0, *MT* was lower for A_{20} as compared with A_{10}. This was confirmed using a four-way mixed effects

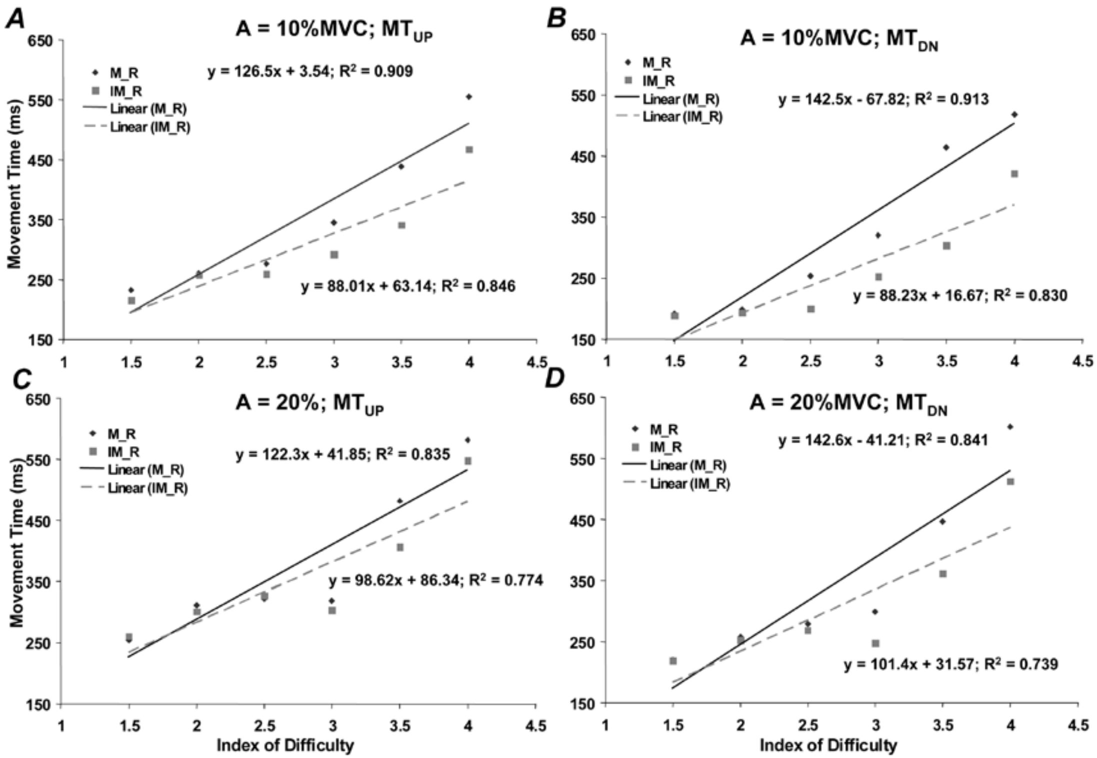


Figure 3 — An exemplary subject's movement time performance (MT_{UP} and MT_{DN}) across *ID* levels for both the M_R (solid diamonds) and IM_R (gray squares) finger combinations, as well as their linear regressions with respect to *ID*. ***A:*** MT_{UP} for force production amplitude = 10% *MVC*, ***B:*** MT_{DN} for force production amplitude = 10% *MVC*, ***C:*** MT_{UP} for force production amplitude = 20% *MVC*, ***D:*** MT_{DN} for force production amplitude = 20% *MVC*.

ANOVA with the factors: *Subject, ID, Amplitude,* and *Force Change*. Main effects of *Subject* [$F(7, 353) = 68.06$, $p < .001$], *ID* [$F(5, 353) = 56.76$, $p < .001$], and *ID* × *Amplitude* [$F(5, 353) = 4.3$, $p < .005$] were found. This interaction is illustrated in panel B of Figure 4. Pairwise Tukey's comparisons revealed significant differences across all pairs of the *ID* levels except 1.5 versus 2.0–2.5.

Table 1 Movement Time

				A = 10 % MVC			
	ID	*1.5*	*2*	*2.5*	*3*	*3.5*	*4*
UP	I	263 ± 22	248 ± 28	311 ± 34	367 ± 40	398 ± 42	464 ± 72
	M	278 ± 30	257 ± 30	305 ± 39	328 ± 48	344 ± 32	419 ± 57
	R	263 ± 21	255 ± 19	298 ± 37	336 ± 39	413 ± 525	451 ± 61
	L	265 ± 16	285 ± 20	294 ± 29	348 ± 48	392 ± 37	484 ± 46
	M_L	261 ± 25	287 ± 37	293 ± 32	312 ± 45	380 ± 47	492 ± 80

				A = 10 % MVC			
	ID	*1.5*	*2*	*2.5*	*3*	*3.5*	*4*
DOWN	I	257 ± 18	237 ± 24	309 ± 29	379 ± 41	403 ± 38	490 ± 90
	M	276 ± 27	260 ± 25	319 ± 33	341 ± 46	405 ±40	439 ± 69
	R	286 ± 23	264 ± 22	339 ± 36	380 ± 47	454 ± 43	562 ± 77
	L	279 ± 15	310 ± 20	338 ± 29	394 ± 47	459 ± 48	574 ± 58
	M_L	275 ± 18	321 ± 34	324 ± 32	324 ± 48	418 ± 51	508 ± 71

				A = 10 % MVC			
	ID	*1.5*	*2*	*2.5*	*3*	*3.5*	*4*
UP	M_R	278 ± 30	257 ± 30	305 ± 39	328 ± 48	344 ± 32	419 ± 57
	IM_R	269 ± 35	257 ± 33	260 ± 22	344 ± 55	416 ± 48	425 ± 51
	IM_RL	251 ± 23	259 ± 35	291 ± 32	329 ± 36	422 ± 58	448 ± 45
	IMR_R	237 ± 21	266 ± 28	294 ± 32	339 ± 37	378 ± 38	447 ± 37
	IMRL_R	235 ± 24	312 ± 56	310 ± 47	357 ± 60	421 ± 50	493 ± 68

				A = 10 % MVC			
	ID	*1.5*	*2*	*2.5*	*3*	*3.5*	*4*
DOWN	M_R	276 ± 27	260 ± 25	319 ± 33	341 ± 46	405 ± 40	439 ± 69
	IM_R	251 ± 28	248 ± 30	264 ± 23	353 ± 48	397 ± 54	475 ± 70
	IM_RL	241 ± 15	263 ± 29	275 ± 26	322 ± 23	421 ± 55	474 ± 38
	IMR_R	246 ± 18	260 ± 16	290 ± 23	333 ± 32	364 ± 30	466 ± 41
	IMRL_R	230 ± 16	293 ± 44	309 ± 43	349 ± 47	429 ± 40	528 ± 70

(continued)

Table 1 Movement Time *(continued)*

	ID	A = 20 % MVC 1.5	2	2.5	3	3.5	4
UP	I	235 ± 23	308 ± 35	338 ± 40	316 ± 46	368 ± 45	383 ± 40
	M	278 ± 38	300 ± 40	264 ± 28	278 ± 31	379 ± 50	429 ± 53
	R	274 ± 42	286 ± 31	292 ± 34	328 ± 44	405 ± 52	442 ± 63
	L	240 ± 19	275 ± 32	298 ± 43	353 ± 42	428 ± 49	500 ± 44
	M_L	303 ± 55	289 ± 37	310 ± 31	367 ± 58	394 ± 68	460 ± 66

	ID	A = 20 % MVC 1.5	2	2.5	3	3.5	4
DOWN	I	245 ± 20	289 ± 26	329 ± 33	323 ± 45	394 ± 35	415 ± 47
	M	267 ± 28	284 ± 29	260 ± 24	285 ± 21	398 ± 38	446 ± 46
	R	290 ± 37	299 ± 30	311 ± 29	381 ± 42	470 ± 47	516 ± 62
	L	276 ± 27	309 ± 32	336 ± 48	398 ± 44	466 ± 46	543 ± 50
	M_L	300 ± 46	287 ± 30	297 ± 24	378 ± 50	439 ± 58	505 ± 76

	ID	A = 20 % MVC 1.5	2	2.5	3	3.5	4
UP	M_R	278 ± 38	300 ± 40	264 ± 28	278 ± 31	379 ± 50	429 ± 53
	IM_R	293 ± 37	300 ± 35	312 ± 32	320 ± 41	377 ± 51	451 ± 55
	IM_RL	266 ± 27	291 ± 37	307 ± 34	317 ± 38	361 ± 46	400 ± 60
	IMR_R	251 ± 30	298 ± 38	270 ± 28	325 ± 29	393 ± 54	475 ± 52
	IMRL_R	250 ± 27	257 ± 26	297 ± 36	332 ± 29	411 ± 44	444 ± 50

	ID	A = 20 % MVC 1.5	2	2.5	3	3.5	4
DOWN	M_R	267 ± 28	284 ± 29	260 ± 24	285 ± 21	398 ± 38	446 ± 46
	IM_R	290 ± 29	302 ± 30	305 ± 28	315 ± 32	387 ± 39	490 ± 67
	IM_RL	278 ± 15	286 ± 27	314 ± 27	316 ± 30	364 ± 31	416 ± 58
	IMR_R	273 ± 30	306 ± 33	291 ± 22	321 ± 17	420 ± 46	548 ± 67
	IMRL_R	270 ± 23	259 ± 19	295 ± 25	384 ± 53	431 ± 45	474 ± 50

Group averages and standard deviations of movement time data are shown for all force production amplitudes (*A*) and indices of difficulty (*ID*). *UP* refers to force increase half-cycles and *DOWN* refers to force decrease half-cycles. *I* = index, *M* = middle, *R* = ring, *L* = little, and the subscripts denote the hand to which the fingers belong (*R* = right, *L* = left). Movement time values are presented in ms.

Effects of Finger Combination on Movement Time

To determine possible effects of finger combinations on *MT*, the following analyses were run. First, we investigated whether there were differences for both MT_{UP} and MT_{DN} across the single-finger tasks (I_R, M_R, R_R, L_R, and M_L) at each *ID* level. For MT_{UP}, there was no difference among the single-finger tasks across *ID* levels.

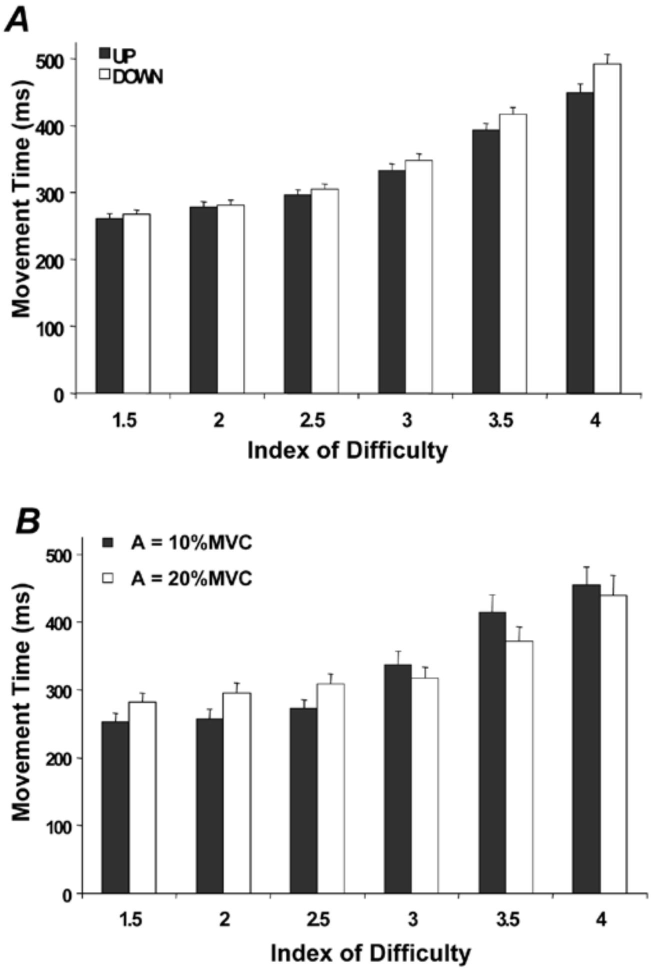


Figure 4 — Average movement time for different *ID* levels (across all subjects with standard error bars). ***A:*** MT_{UP} (solid bars) and MT_{DN} (white bars) both increase as *ID* level increases, ***B:*** The Amplitude × ID interaction for IM_R and I_RM_L tasks is shown. For *IDs* less than or equal to 2.5, *MT* (the average of MT_{UP} and MT_{DN}) was smaller for the smaller force production amplitude (A_{10}, solid bars). For *IDs* larger than or equal to 3.0, *MT* was smaller for the larger force production amplitude (A_{20}, white bars).

However, for MT_{DN} there was a difference among the single-finger tasks so that on average, MT_{DN} for the "radial" fingers (I_R and M_R) was about 50 ms shorter than MT_{DN} for the "ulnar" fingers (R_R and L_R). It was also found that, on average, MT_{DN} for the M_R task was 33 ms less than for the M_L task.

This was confirmed with three-way mixed effects ANOVAs, run separately for MT_{UP} and MT_{DN}, with the factors *Subject, ID,* and *Fingers*. Main effect of *Subject*

[F(7, 443) = 134.33, $p < .001$] and *ID* [F(5, 443) = 81.52, $p < .001$] were found for MT_{UP}, confirming an increase in MT_{UP} with *ID* with no significant interactions (see Figure 4A). MT_{DN} showed main effects of *Subject* [F(7, 443) = 79.75, $p < .001$], *ID* [F(5, 443) = 96.92, $p < .001$], and *Fingers* [F(4, 443) = 10.29, $p < .001$] with no significant interactions. Pairwise Tukey's comparisons revealed differences between the "radial" and "ulnar" fingers on the right hand (I_R and M_R were significantly different from R_R and L_R) as well as between M_R and M_L. Namely, I_R and M_R showed lower MT_{DN} as compared with R_R and L_R, while M_R showed lower MT_{DN} as compared with M_L.

Next, we investigated whether there was a difference for both MT_{UP} and MT_{DN} between the two two-finger tasks, one task involving the fingers from the right hand and the other task involving fingers from the two hands (IM_R and I_RM_L), at each *ID* level. For both MT_{UP} and MT_{DN}, there was no difference between the two-finger tasks across *ID* levels. This was confirmed with three-way mixed effects ANOVA with the factors: *Subject, ID,* and *Fingers*. Main effects of *Subject* [F(7, 173) = 28.02, $p < .001$; F(7, 173) = 43.34, $p < .001$] and *ID* [F(5, 173) = 31.56, $p < .001$; F(5, 173) = 25.14, $p < .001$] were found for MT_{UP} and MT_{DN}, respectively. However, no effect of *Fingers* and no significant interactions were found.

In the next step, we investigated whether there was a difference for both MT_{UP} and MT_{DN} across tasks involving different numbers of fingers (single-finger tasks versus two-finger tasks versus three-finger tasks versus four-finger tasks). Since there was no difference among single-finger tasks for MT_{UP}, the M_R task was chosen as the representative single-finger task. Similarly, IM_R was chosen as the representative two-finger combination.

MT_{UP} showed no dependence on the number of designated fingers at each of the *ID* levels. This was confirmed with a three-way mixed effects ANOVA with the factors: *Subject, ID,* and *#Fingers*. Main effects of *Subject* [F(7, 353) = 116.6, $p < .001$] and *ID* [F(5, 353) = 76.53, $p < .001$] were found, but there were no effects of *#Fingers* or any significant interactions.

Since there were differences in MT_{DN} between the "radial" and "ulnar" fingers in single-finger tasks, separate analyses were run to study the dependence of MT_{DN} on the number of designated fingers. An analysis comparing a "radial" finger (M_R) to multifinger combinations showed no differences among the tasks at each of the *ID* levels. This was confirmed with a three-way mixed effects ANOVA with the factors: *Subject, ID,* and *#Fingers*. Main effects of *Subject* [F(7, 353) = 68.38, $p < .001$] and *ID* [F(5, 353) = 87.92, $p < .001$] were found, but no effect of *#Fingers* and no significant interactions were found.

However, when data from an "ulnar" finger (L_R) were used, there were differences in MT_{DN} among the tasks at each of the *ID* levels. The multifinger tasks showed faster force production (lower MT_{DN}) as compared with the single-finger task (on average, by 44 ms). This was confirmed with a three-way mixed effects ANOVA with the factors: *Subject, ID,* and *#Fingers*. Main effects of *Subject* [F(7, 353) = 61.12, $p < .001$], *ID* [F(5, 353) = 95.14, $p < .001$], and *#Fingers* [F(3, 353) = 9.97, $p < .001$] were found with no significant interactions. Pairwise Tukey's comparisons revealed significant differences between L_R and each of the multifinger combinations (IM_R, IMR_R, and $IMRL_R$), so that MT_{DN} for L_R was larger as compared with the multifinger combinations without significant differences across the multifinger combinations.

Speed-Accuracy Trade-Off and Effective Target Width

In general, there was a close to linear relationship between presented target width (W) and effective target width (W_E, estimated as 4 times SD of the final position, see Methods) across all finger combinations, force production amplitudes, and force changes, as shown in Figure 5. This was verified with a linear regression between presented target width and effective target width. This model explained 49.6% of the variance in the data across all finger combinations, force production amplitudes, and force changes.

After logarithmic transformation of both variables, W_E and MT showed a linear relationship so that an increase in MT was associated with a drop in W_E. Figure 6 presents a typical subject's performance across all finger combinations for both force increase and force decrease half-cycles. Across all subjects, $\log_{10}(W_E)$ could be described as a linear function of $\log_{10}(A / MT)$, which was verified with linear regressions: $\log_{10}(W_E) = c + b \times \log_{10}(A / MT)$. This model explained 49.9% of the variance in the data across all finger combinations and force changes. A summary of the W_E data for all subjects in all tested conditions can be found in Table 2.

Effects of Finger Combination on Effective Target Width

To determine possible effects of finger combinations on W_E, the following analyses were run. First, we investigated whether W_E differed among the single-finger tasks (I_R, M_R, R_R, L_R, and M_L). W_E showed a difference between the "radial" single-finger

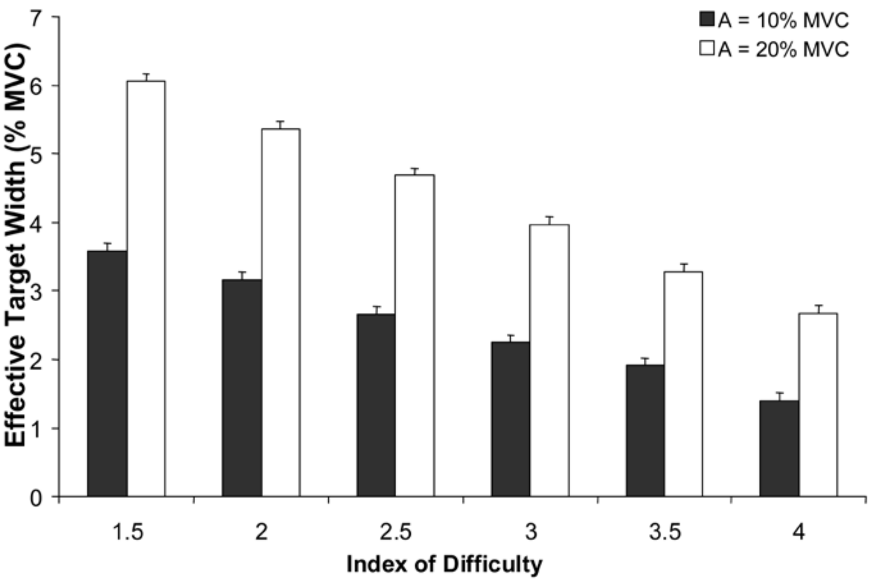
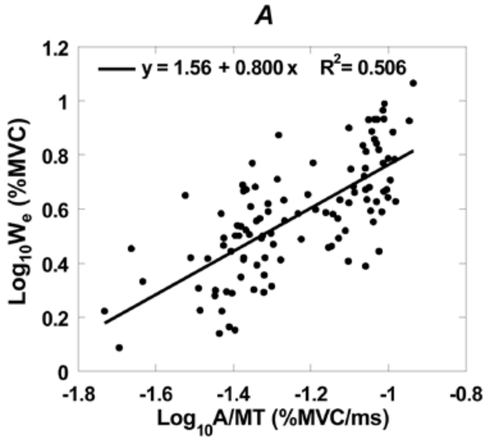


Figure 5 — Average effective target width for different *ID* levels (across all finger combinations, subjects, and force production directions). Standard error bars are shown. Effective target width with respect to force production amplitude of 10% (solid bars) and 20% (white bars) decreases as *ID* level increases.



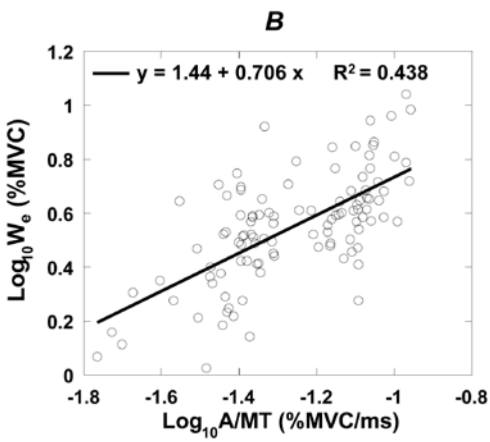


Figure 6 — Dependences of the log-transformed $W_{E,UP}$ (filled circles, ***A***) and $W_{E,DN}$ (open circles, ***B***) on the log-transformed ratio *Amplitude* / *MT* across all finger combinations with linear regression lines and equations. Data for a typical subject are shown.

tasks (I_R and M_R) as compared with the "ulnar" single-finger tasks (R_R and L_R) as well as the left middle finger task (M_L) at each of the *ID* levels and force production amplitudes. On average, W_E for the "radial" fingers was smaller than W_E of the other fingers by 9.6%. This was confirmed with a four-way mixed effects ANOVA with the factors: *Subject, ID, Amplitude,* and *Fingers*. Main effects of *Subject* [$F(7, 893) = 15.19$, $p < .001$], *ID* [$F(5, 893) = 235.28$, $p < .001$], *Amplitude* [$F(1, 893) = 979.38$, $p < .001$], and *Fingers* [$F(4 ,893) = 6.76$, $p < .001$] were found with no significant interactions. Pairwise Tukey's comparisons revealed significant differences between I_R and R_R, L_R, M_L; M_R and R_R, L_R, M_L; corresponding to smaller W_E in the I_R and M_R tasks as compared with the other three tasks. W_E also showed a difference across force production amplitudes and *IDs*, so that W_E was higher for the larger force production amplitude and smaller *ID* values.

There was no difference for W_E between the two two-finger tasks (IM_R and I_RM_L) at each *ID* level and force production amplitudes. This was confirmed with four-way mixed effects ANOVAs with the factors: *Subject, ID, Amplitude*, and *Fingers*. Main effects of *Subject* [$F(7, 353) = 7.9$, $p < .001$], *ID* [$F(5, 353) > 68.29$, $p < .001$], and *Amplitude* [$F(1, 353) = 376.4$, $p < .001$] were found. However, there was no effect of *Fingers* and no significant interactions. The W_E values were higher for the larger force production amplitude and smaller *ID* values.

We then investigated whether there was a difference in W_E with regard to the number of fingers involved in a task (single-finger tasks versus two-finger tasks versus three-finger tasks versus four-finger tasks). When the "radial" finger (I_R data were used) was evaluated against the multifinger combinations, W_E did not depend on the number of explicitly involved fingers at each *ID* level and force production amplitudes. This was confirmed with a four-way mixed effects ANOVA with the factors: *Subject, ID, Amplitude*, and *#Fingers*. Main effects of *Subject* [$F(7, 713) = 15.57$, $p < .001$], *ID* [$F(5, 713) = 158.93$, $p < .001$], and *Amplitude* [$F(1, 713) = 742.44$, $p < .001$] were found without any significant interactions or effects of *#Fingers*. When the "ulnar" finger (L_R data were used) was evaluated against the

Table 2 Effective Target Width

				A = 10 % MVC			
	ID	1.5	2	2.5	3	3.5	4
UP	I	0.033 ± 0.003	0.030 ± 0.002	0.023 ± 0.002	0.018 ± 0.002	0.018 ± 0.002	0.013 ± 0.001
	M	0.034 ± 0.004	0.030 ± 0.004	0.028 ± 0.002	0.026 ± 0.002	0.019 ± 0.002	0.013 ± 0.001
	R	0.041 ± 0.005	0.035 ± 0.002	0.026 ± 0.002	0.023 ± 0.001	0.030 ± 0.012	0.015 ± 0.001
	L	0.046 ± 0.003	0.038 ± 0.002	0.032 ± 0.003	0.021 ± 0.001	0.020 ± 0.002	0.015 ± 0.001
	M_L	0.039 ± 0.005	0.032 ± 0.003	0.029 ± 0.002	0.023 ± 0.002	0.018 ± 0.001	0.014 ± 0.002

				A = 10 % MVC			
	ID	1.5	2	2.5	3	3.5	4
DOWN	I	0.032 ± 0.003	0.033 ± 0.003	0.024 ± 0.003	0.023 ± 0.002	0.019 ± 0.001	0.013 ± 0.001
	M	0.032 ± 0.002	0.032 ± 0.002	0.027 ± 0.004	0.026 ± 0.003	0.018 ± 0.001	0.014 ± 0.001
	R	0.037 ± 0.004	0.044 ± 0.003	0.029 ± 0.002	0.022 ± 0.001	0.017 ± 0.001	0.014 ± 0.001
	L	0.041 ± 0.002	0.031 ± 0.004	0.026 ± 0.004	0.022 ± 0.002	0.020 ± 0.002	0.014 ± 0.001
	M_L	0.040 ± 0.003	0.029 ± 0.002	0.029 ± 0.002	0.025 ± 0.001	0.017 ± 0.002	0.013 ± 0.001

				A = 10 % MVC			
	ID	1.5	2	2.5	3	3.5	4
UP	I_R	0.033 ± 0.003	0.030 ± 0.002	0.023 ± 0.002	0.018 ± 0.002	0.018 ± 0.002	0.013 ± 0.001
	IM_R	0.030 ± 0.002	0.033 ± 0.005	0.027 ± 0.002	0.021 ± 0.002	0.017 ± 0.001	0.017 ± 0.004
	IM_RL	0.034 ± 0.004	0.028 ± 0.003	0.027 ± 0.003	0.017 ± 0.003	0.017 ± 0.002	0.015 ± 0.001
	IMR_R	0.039 ± 0.004	0.030 ± 0.002	0.024 ± 0.001	0.024 ± 0.002	0.017 ± 0.002	0.013 ± 0.001
	IMRL_R	0.033 ± 0.002	0.027 ± 0.003	0.027 ± 0.002	0.024 ± 0.002	0.021 ± 0.002	0.014 ± 0.001

				A = 10 % MVC			
	ID	1.5	2	2.5	3	3.5	4
DOWN	I_R	0.032 ± 0.003	0.033 ± 0.003	0.024 ± 0.003	0.023 ± 0.002	0.019 ± 0.001	0.013 ± 0.001
	IM_R	0.034 ± 0.005	0.030 ± 0.003	0.028 ± 0.002	0.023 ± 0.002	0.022 ± 0.003	0.014 ± 0.003
	IM_RL	0.030 ± 0.003	0.025 ± 0.002	0.023 ± 0.003	0.022 ± 0.001	0.020 ± 0.002	0.012 ± 0.001
	IMR_R	0.037 ± 0.003	0.033 ± 0.003	0.025 ± 0.002	0.020 ± 0.002	0.016 ± 0.001	0.016 ± 0.003
	IMRL_R	0.033 ± 0.003	0.028 ± 0.0003	0.026 ± 0.003	0.024 ± 0.004	0.019 ± 0.001	0.013 ± 0.001

(continued)

Table 2 Effective Target Width *(continued)*

	ID	1.5	2	2.5	3	3.5	4
				A = 20 % MVC			
UP	I	0.067 ± 0.007	0.055 ± 0.007	0.050 ± 0.005	0.040 ± 0.003	0.033 ± 0.003	0.026 ± 0.001
	M	0.062 ± 0.008	0.060 ± 0.008	0.054 ± 0.008	0.040 ± 0.003	0.032 ± 0.003	0.035 ± 0.010
	R	0.073 ± 0.007	0.060 ± 0.003	0.054 ± 0.004	0.041 ± 0.003	0.046 ± 0.008	0.027 ± 0.002
	L	0.111 ± 0.021	0.066 ± 0.007	0.055 ± 0.006	0.051 ± 0.013	0.039 ± 0.001	0.045 ± 0.020
	M_L	0.064 ± 0.007	0.060 ± 0.006	0.048 ± 0.004	0.045 ± 0.005	0.034 ± 0.004	0.027 ± 0.001
				A = 20 % MVC			
	ID	1.5	2	2.5	3	3.5	4
DOWN	I	0.059 ± 0.008	0.045 ± 0.006	0.045 ± 0.009	0.034 ± 0.004	0.029 ± 0.004	0.024 ± 0.001
	M	0.051 ± 0.007	0.061 ± 0.008	0.044 ± 0.004	0.040 ± 0.004	0.030 ± 0.003	0.026 ± 0.003
	R	0.056 ± 0.005	0.048 ± 0.004	0.041 ± 0.005	0.041 ± 0.005	0.031 ± 0.002	0.025 ± 0.002
	L	0.064 ± 0.006	0.049 ± 0.007	0.049 ± 0.005	0.032 ± 0.003	0.030 ± 0.006	0.023 ± 0.001
	M_L	0.059 ± 0.004	0.062 ± 0.006	0.060 ± 0.006	0.043 ± 0.005	0.036 ± 0.003	0.028 ± 0.001

	ID	1.5	2	2.5	3	3.5	4
				A = 20 % MVC			
UP	I_R	0.067 ± 0.007	0.055 ± 0.007	0.050 ± 0.005	0.040 ± 0.003	0.033 ± 0.003	0.026 ± 0.001
	IM_R	0.056 ± 0.005	0.054 ± 0.005	0.048 ± 0.004	0.037 ± 0.004	0.034 ± 0.003	0.026 ± 0.003
	IM_RL	0.058 ± 0.003	0.067 ± 0.008	0.040 ± 0.007	0.039 ± 0.004	0.033 ± 0.004	0.025 ± 0.001
	IMR_R	0.066 ± 0.007	0.051 ± 0.005	0.043 ± 0.004	0.040 ± 0.005	0.033 ± 0.002	0.026 ± 0.002
	IMRL_R	0.067 ± 0.010	0.050 ± 0.005	0.047 ± 0.007	0.043 ± 0.003	0.032 ± 0.003	0.023 ± 0.001
				A = 20 % MVC			
	ID	1.5	2	2.5	3	3.5	4
DOWN	I_R	0.059 ± 0.008	0.045 ± 0.006	0.045 ± 0.009	0.034 ± 0.004	0.029 ± 0.004	0.024 ± 0.001
	IM_R	0.054 ± 0.007	0.049 ± 0.004	0.047 ± 0.004	0.036 ± 0.004	0.029 ± 0.002	0.025 ± 0.002
	IM_RL	0.043 ± 0.004	0.048 ± 0.005	0.043 ± 0.006	0.036 ± 0.004	0.031 ± 0.002	0.028 ± 0.002
	IMR_R	0.039 ± 0.003	0.042 ± 0.004	0.037 ± 0.004	0.038 ± 0.002	0.029 ± 0.003	0.021 ± 0.002
	IMRL_R	0.041 ± 0.003	0.036 ± 0.004	0.037 ± 0.003	0.039 ± 0.003	0.029 ± 0.003	0.023 ± 0.003

Group averages and standard deviations of effective target width data are shown for all force production amplitudes (*A*) and indices of difficulty (*ID*). *UP* refers to force increase half-cycles and *DOWN* refers to force decrease half-cycles. Abbreviations are the same as in Table 1. Effective target width values are presented in percentage of MVC.

multifinger combinations, on average, W_E of the multifinger combinations was less than W_E of L_R by 17.9%. This was confirmed with a four-way mixed effects ANOVA with the factors: *Subject, ID, Amplitude,* and *#Fingers.* Main effects of *Subject* [$F(7, 713) = 13.26, p < .001$], *ID* [$F(5, 713) = 159.05, p < .001$], *Amplitude* [$F(1, 713) = 661.84, p < .001$], and *#Fingers* [$F(3, 713) = 11.07, p < .001$] were found with no significant interactions. Pairwise Tukey's comparisons revealed smaller variability in the performance (smaller W_E) by the multifinger combinations as compared with L_R.

Discussion

Overall, the findings have not been supportive of the hypotheses formulated in the Introduction. There were minimal differences across the fingers and finger combinations in both speed-accuracy relations linking movement time *(MT)* to task difficulty *(ID)* and linking motor variability (assessed with W_E) to *MT*. This is an unexpected finding given the well-documented negative covariation among finger forces (reviewed in Latash, Scholz, & Schöner, 2002) and the earlier report on lower coefficients of variation in the total force in two-finger tasks as compared with single-finger tasks (Latash et al., 2001). The remainder of the Discussion is going to be focused on these questions: What do patterns of covariation among finger force do, if they do not provide for higher accuracy in the total force? Or do they?

Accuracy in Multielement Tasks

There are at least two good reasons to expect multifinger tasks to be more accurate than single-finger tasks. First, the close to linear scaling of force, standard deviation with force level (reviewed in Carlton & Newell 1993) allows one to expect lower across-trials variance of force in multifinger tasks because of the force-sharing and the fact that total variance is the sum of standard deviations squared. For example, imagine that a person performs a series of force production trials with one finger to a target at 20 N and shows a standard deviation of force across trials of 2 N (and variance of 4 N^2). Now imagine that two fingers share the same task and produce 10 N each. Then, assuming standard deviation scales in a linear manner with the force level, standard deviation of their total force is expected to be 1.4 N, and variance is expected to be 2 N^2. So, simply sharing total force between two fingers is expected to lead to a substantial drop in total force variability because the absolute force produced by each finger is less. If more fingers are involved, the drop is expected to be higher. In the example presented, a three-finger task is expected to show variance of about 1.5 N^2, and a four-finger task, about 1 N^2 (assuming equal sharing of the total force across the involved fingers).

This example can easily be generalized to forces expressed in percentage of *MVC*, as it was done in the reported experiments. When fingers act in a group, their total *MVC* is smaller than the sum of *MVC* values in single-finger tasks. This phenomenon, called force deficit (Ohtsuki, 1981; Li et al., 1998) leads to force attenuation by a scaling factor of about $1 / N^{0.71}$ (Danion et al., 2003), where N is the number of explicitly involved fingers. However, the scaling factor applies to both force amplitude and standard deviation; hence expressing both in percentage of *MVC* does not lead to a qualitative change in the overall effect.

In addition, a series of earlier studies has shown predominance of negative covariation among finger forces in multifinger tasks (reviewed in Latash, Scholz, & Schöner, 2002, 2007). This negative covariation is expected to lower variance even more as compared with what could be expected in the absence of the covariation. So, why did our study show no major difference in W_E across tasks performed with different numbers of fingers? Why did the subjects not speed up when they used multifinger combinations as compared with single-finger tasks? What is the purpose of the negative force covariation if it fails to improve accuracy?

The first point to make is that negative covariation is expected to improve accuracy as compared with the same data set without negative covariation, not as compared with a set of single-finger tasks. The total amount of variance in the space of individual finger forces per unit of force production is considerably higher when fingers act in a group as compared with their single-finger tasks (Goodman, Shim, Zatsiorsky, & Latash, 2005). Our results suggest that this increase in each finger's force variability is so high that it obliterates completely the expected gain from the two mentioned factors. The surprising bottom line is that the expected effects of the two favorable factors are exactly balanced by the increase in single finger force variability in multifinger tasks. This result speaks in favor of one of the competing hypotheses on motor variability, to be discussed in the next subsection.

The second point is that an increase in variance of individual fingers in combination with negative covariation that keeps total force variability basically unchanged may be revealing of a particular neural strategy. A recent study has shown that variability of elements (e.g., fingers) along directions in the finger force (or finger mode, see Danion et al., 2003) space that do not affect total force may play an important role in allowing the controller to handle several tasks at the same time, while avoiding detrimental interactions among the tasks that share the same elements (Zhang, Scholz, Zatsiorsky, & Latash, in press). Taken together, this idea, in combination with the current results, suggests the following hypothesis: In multielement tasks of producing an accurate level of a performance variable, the central nervous system facilitates variability of individual elements and organizes covariation among the elemental variables that preserve an unchanged (acceptable) level of variability of the performance variable, while simultaneously allowing for accurate production of other performance variables by the same set of elements.

Origins of Finger Force Covariation

There have been several attempts at modeling the experimentally observed phenomenon of covariation among elemental variables that is organized so that it keeps the variability of an important performance variable low (reviewed in Latash et al., 2007). Two of the models are based on feedback schemes. In particular, a model by Todorov and Jordan (2002) uses principles of optimal feedback control, while a model by Latash and colleagues (Latash, Shim, Smilga, & Zatsiorsky, 2005) is based on action of central back-coupling loops. Two other models assume that the controller is aware of the current Jacobian of the system (a matrix describing the mapping of small changes in the elemental variables on changes in the selected performance variable) but is not using an explicit feedback control scheme. One of these models (Martin, Scholz, and Schöner, 2004) uses a Jacobian augmentation technique developed in robotics (Baillieul, 1985) to augment the Jacobian matrix with additional constraints making the matrix invertible. The other model (Goodman & Latash, 2006) assumes that the controller uses two separate input signals into the system of elements, one related to changes in a particular performance variable ("relevant"), and the other one that keeps this variable unchanged ("irrelevant").

Our finding of basically unchanged relations MT (ID) and W_E (MT) seems to be more directly compatible with the two latter models. These results suggest that accuracy of performance is defined by the controller independently of the number of involved effectors corresponding to the "relevant control signal" in the model of Goodman and Latash (2006). This signal is set depending on task constraints as elucidated by the Fitts's law. In multielement tasks, elemental variables are allowed to vary more than in single-finger tasks, but only as long as this added variability is not affecting performance compared with a single-finger task. In other words, an "irrelevant control signal" is added in multifinger tasks that increases variability in the space of elements but does not affect the total force variability, in line with the hypothesis offered at the end of the previous subsection.

The ideas of feed-forward control of multidigit action have been invoked recently in many studies of grip force adjustments associated with manipulation of hand-held objects (reviewed in Flanagan, Bowman, & Johansson, 2006). We would like to emphasize an important distinction between feed-forward grip force adjustments and the feed-forward scheme of multifinger synergies (as in Goodman & Latash, 2006). The former produces changes in the overall hand action to satisfy constraints imposed by the mechanics of the task including, in particular, friction between the object and the fingertips. The latter generates patterns of covariation of individual finger actions compatible with the task. For example, when lifting an object, the former mechanism is expected to produce an increase in the grip force prior to the lifting action, while the latter is expected to make sure that individual finger forces covary such that the grip force changes show minimal variations from a required time profile.

Origins of the Speed-Accuracy Trade-Off

Overall, our subjects scaled *MT* with *ID* as expected from the Fitts's law and scaled effective target width (Force variability) with *MT* in support of earlier reports (reviewed in Schmidt et al., 1979; Keele, 1986; Meyer, Smith, Kornblum, Abrams, & Wright, 1990) Why do people slow down when they are asked to move to a small and distant target? We believe that the model linking Fitts's law to accuracy in specification of two parameters at the level of motor planning (a timing parameter and an amplitude parameter related to the planned movement time and amplitude, respectively; Gutman, Gottlieb, & Corcos, 1992; Gutman & Latash, 1993) offers the most natural and noncontroversial explanation for the current findings. In particular, this model is compatible with similar *MT*(*ID*) relations for single- and multifinger tasks. This model has also received support in a recent study (Duarte & Latash, 2007) that showed reflections of Fitts's law in anticipatory postural adjustments that, by definition, cannot reflect the action of feedback signals (reviewed in Massion, 1992).

Why do people show higher force variability at higher force levels? Studies by Slifkin and Newell (1999, 2000) attribute this increase in force variability to recruitment of larger motor neurons during tasks that require higher levels of force output, thus, reducing the precision of the total force output. Note, however, that the relative increase in net force caused by the recruitment of larger motor units has been shown to decrease as a function of muscle force (Fuglevand, Winter, & Patla, 1993).

Along somewhat different lines, Harris and Wolpert (1998) and Jones, Hamilton, and Wolpert, (2002) attribute an increase in force variability to signal dependent noise in the synaptic input to motor neurons leading to variable signals to the muscles. Both of these models assume that the source of variability is inherent in the processing of a control signal (that is, assumed to be perfectly matching the task) by hierarchically lower structures. In addition, there is also variability in muscle force because of the contractile properties of the muscle fibers. However, given all these factors, when several fingers share a force production task, a substantial drop in the total force variability is expected as illustrated by the example in the opening subsection of the Discussion. The lack of such an improvement in force variability in multifinger tasks is a sign that force variability is defined at a higher hierarchical level, possibly at a level that defines the control signal in each particular trial somewhat differently (as in Goodman & Latash, 2006).

Although we did not find consistent, major differences between the performance of single fingers and finger groups, some significant effects were, indeed, present. These, however, were mostly reflective of differences in the accuracy of individual fingers, not between single- versus multifinger tasks. Our results suggest that the two "radial" fingers (index and middle) are significantly more accurate than the two "ulnar" ones (ring and little). This is not a surprising finding. For example, R and L fingers show higher indices of unintended force production in tasks in which they are not supposed to produce force (enslaving, Li et al., 1998; Zatsiorsky, Li, & Latash, 2000). These fingers also tend to show higher indices of variability in prehensile tasks (Zatsiorsky, Gregory, & Latash, 2002; Zatsiorsky, Gao, & Latash, 2003). When fingers from both groups act together, indices of accuracy are closer to those of the I and M fingers and are better than those of the R and L fingers. This finding may be interpreted as corroborating the hypothesis that accuracy in multifinger tasks is defined at a high hierarchical level, before the signals to neural structures controlling individual fingers are generated.

The conclusions drawn from our study may be task-specific. In particular, several recent studies have suggested qualitative differences in the control of discrete and cyclic actions (Schaal, Sternad, Osu, & Kawato, 2004; Hogan & Sternad, 2007). So, we cannot generalize our conclusions to discrete force production tasks. On the other hand, however, a number of recent studies have compared indices of multifinger synergies during discrete and cyclic force and moment of force production tasks (reviewed in Latash, Scholz, & Schöner, 2002; Latash et al., 2007). These studies have not revealed qualitative differences between discrete and cyclic force production. So, while we cannot be confident that our conclusions are valid over a broader range of tasks, this seems likely.

Acknowledgments

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