Published in final edited form as:

Exp Brain Res. 2001 June ; 138(3): 322–329.

The effect of a fatiguing exercise by the index finger on single- and multi-finger force production tasks

F. Danion,

Department of Kinesiology and Biomechanics Laboratory, The Pennsylvania State University, University Park, PA 16802, USA

M.L. Latash,

Department of Kinesiology and Biomechanics Laboratory, The Pennsylvania State University, University Park, PA 16802, USA, mll11@psu.edu, Fax: +1-814-8634424

Z.-M. Li, and

Department of Physical Therapy, Walsh University, OH 44720, USA

V.M. Zatsiorsky

Department of Kinesiology and Biomechanics Laboratory, The Pennsylvania State University, University Park, PA 16802, USA

Abstract

We studied the effects of fatigue, induced by a 60-s maximal isometric force production with the index finger, on multi-finger coordination and force production by the other fingers of the hand. Finger forces were measured during single- and multi-finger maximal voluntary force production (MVC) at two sites, the middle of the distal or the middle of the proximal phalanges. Two fatiguing exercises involving force production by the index finger were used, one at the distal phalanx and the other at the proximal phalanx. The MVC of the index finger dropped by about 33% when it was produced at the site involved in the fatiguing exercise. In addition, large transfer effects of fatigue were observed across sites of force application and across fingers. Force deficit increased under fatigue, especially due to a drop in the recruitment of the index finger. Under fatigue, the index finger was less enslaved during force production by other fingers. During multi-finger tasks, the percentage of total force produced by the index finger was significantly reduced after the fatiguing exercise. The principle of minimization of secondary moments was violated under fatigue. We suggest that the most impaired (fatigued) finger shows less interaction with other fingers or, in other words, is being progressively removed from the multi-finger synergy. Some of the observed changes in finger coordination suggest effects of fatigue at a central (neural) level.

Keywords

Finger; Fatigue; Coordination; Synergy; Human

Introduction

When an attempt is made to maintain a strong contraction of a human muscle for a long time, the muscle force ultimately falls. Failure to maintain the required force is referred to as “fatigue” (Stephens and Taylor 1972). Fatigue has been shown to involve changes at different

levels of the system for muscle force production (for a review, see Enoka and Stuart 1992). Most earlier studies of fatigue focused on changes in the properties of a fatigued muscle (Bigland-Ritchie and Woods 1984) and its reflex circuitry (Woods et al. 1987; Hagbarth et al. 1995).

In most everyday movements, large groups of muscles, joints, or limbs are used in a coordinated manner. There have been reports suggesting that the central organization of such multi-element systems may change under fatigue (Bonnard et al. 1994; Sparto et al. 1997; Forestier and Nougier 1998; Danion et al. 2000). In most studies, fatigue within a multi-element system was induced in a natural way. That is, the subject was asked to maintain performance of a motor task involving all the elements of a multi-element system, and the experimenter tracked the changes in the performance over time (Bonnard et al. 1994; Sparto et al. 1997; Forestier and Nougier 1998). Hence, all the elements were fatigued in parallel to an extent that was likely to be proportional to their participation in the task. We do not know how coordination among elements is affected if only one element is the target of a fatiguing exercise. This issue will constitute the core of this paper.

In a recent series of papers (Li et al. 1998a, 1998b; Latash et al. 1998a, 1998b; Zatsiorsky et al. 1998), our group has studied the organization of multi-element systems through maximal isometric flexion of a set of fingers acting in parallel (each finger being considered as an element). In particular, total force has been shown to be shared among the fingers in a certain manner independently of the total force level (force sharing). Peak forces of individual fingers in multi-finger tasks were smaller than their peak forces in single-finger maximal voluntary contraction (MVC) tasks (force deficit; for similar findings see also Ohtsuki 1981; Kinoshita et al. 1996). Force production by a finger in a single-finger MVC task was accompanied by an involuntary force production by other fingers of the hand (“enslaving”; Zatsiorsky et al. 1998; for similar findings, see Kilbreath and Gandevia 1994). A principle of minimization of secondary moments about the longitudinal functional axis of the hand (Li et al. 1998a, 1998b) was suggested as an organizational principle defining sharing patterns among the fingers.

In an earlier experiment, we studied the effects of fatigue, induced by a 60-s maximal isometric flexion force production by the four fingers of a hand (Danion et al. 2000). Some of the results indicated that the effects of fatigue were not limited to changes in the force-generating capabilities of the muscles, but had a significant central neural component. The present experiment investigated changes in finger coordination when only one finger was directly fatigued. Two main issues were addressed.

The first issue concerns the spread of fatigue across fingers and phalanges. Several studies have reported that effects of fatigue can spread to muscles that are not directly involved by the exercise or electrical stimulation used to induce fatigue (Wolf et al. 1984; Aymard et al. 1995; Sacco et al. 1997; Zijdwind et al. 1998). Though many studies have investigated the endurance properties of individual digits, especially of the thumb (Bemben et al. 1996; Sheean et al. 1997) and the index finger (Stephens and Taylor 1972; Milner-Brown et al. 1986; Fuglevand et al. 1993; Zijdwind et al. 1995; Radwin and Buffalo 1999), none of them, to our knowledge, investigated the possibility that fatigue effects could transfer to other digits. The present experiment studied the possibility of a spread of fatigue across fingers after prolonged exercise by one finger. The muscular apparatus of the hand, in particular the different anatomical points of attachment of extrinsic and intrinsic muscles (Kendall et al. 1971; Close and Ralston 1973; Basmajian and De Luca 1985), presents an opportunity to vary the relative involvement of these muscle groups by changing the point of force application along the finger axis. By alternating force application at the proximal and distal phalanges, the present

experiment tested the possibility of a spread of fatigue across phalanges, with implications for its spread across extrinsic and intrinsic muscles.

The second issue concerns potential changes in the force-sharing pattern after prolonged exercise by a single finger. Patterns of force sharing among the fingers during four-finger tasks have been shown to persist within a wide range of forces (Li et al. 1998a), under informational perturbations (Latash et al. 1998b), and under fatigue of all four fingers (Danion et al. 2000). These patterns were assumed to reflect the principle of minimization of secondary moments. Two hypotheses can be formulated with respect to possible effects of fatigue on the central commands defining the force-sharing pattern among the fingers. First, the pattern of force sharing among the fingers may stay unchanged so that the principle of minimization of secondary moments holds under fatigue. If one finger is selectively fatigued and its force-generating capabilities are decreased, the only way to maintain the same sharing pattern is to reduce the relative intensity of the central commands sent to the nonfatigued fingers.

According to the second hypothesis, the pattern of central commands is unaffected by fatigue, and all the changes in finger forces are due to peripheral effects of fatigue. In this case, the sharing pattern is expected to change so that the fatigued finger has a reduced share of the total force. The principle of minimization of secondary moments is expected to be violated. Another prediction can be made with respect to force-deficit changes under fatigue. One can view force deficit prior to fatigue as being defined by muscle fibers that contribute to finger force production in the single-finger but not in the multi-finger tasks (Li et al. 1998a). If fatigue does not affect these muscle fibers, force deficit of the fatigued finger is expected to stay unchanged (when measured in absolute units); if these fibers are affected by fatigue, force deficit is expected to drop.

We selected the index finger as the target of our fatiguing exercise for the following reasons. First, the effects of a prolonged exercise by the index finger have been better documented than for other fingers (Stephens and Taylor 1972; Zijdwind and Kernell 1994; Radwin and Buffalo 1999). Second, the index finger shows the largest or second largest MVC, its share during multi-finger force production is also large, and it has a lateral position relative to the longitudinal axis of the hand, making this finger an excellent candidate with which to challenge the principle of minimization of secondary moments. Third, the index finger is generally envisaged as the finger that human beings are better capable to control individually (Fahrer 1981; Valero-Cuevas et al. 1998; Zatsiorsky et al. 1998), so that it represents the best option for a selective fatiguing exercise.

Materials and methods

Besides the nature of the fatiguing exercise, the methods used in the present experiment and in those of Danion et al. (2000) were identical. Therefore, only essential details will be reported, additional information being available in the previous paper.

Subjects

Fourteen right-handed subjects without any history of neurological or motor problems participated in this experiment (nine men, five women), 29.9 ± 8.4 years old. Half of the subjects were also participants in the experiment of Danion et al. (2000) where all four fingers of the right hand were fatigued simultaneously. All subjects gave informed consent according to the procedures approved by the Office for the Regulatory Compliance of the Pennsylvania State University.

Apparatus

Four unidirectional piezoelectric force sensors (208A03; PCB Piezotronics, Depew, NY) were used for force measurement. The sensors were each connected in series with wire cables that were suspended by swivel attachments from slots in the top plate of the inverted U-shaped frame of the experimental device (see Fig. 1A for a schematic illustration of the experimental set-up). The fingers applied force downward to rubber-coated loops located at the bottom of each wire. These loops could be placed either in the middle of the distal phalanges or in the middle of the proximal phalanges. Owing to the employed experimental procedure, all four finger forces were parallel to each other. As shown in Fig. 1B, a hand-fixation device was located at the bottom of the frame and used to stabilize the palm of the hand and to ensure a constant hand configuration throughout the experiment (the wrist was fixed at 20° of extension and the fingers were positioned so that there was 20° of flexion at the metacarpophalangeal joints). All the precautions were taken to avoid motion of the wrist during the tests without compromising the subjects' comfort.

Procedure

In each trial the subjects were asked to press as hard as possible (MVC) with a certain finger or with all four fingers of the right hand during a period of about 2 s. The rate of force was not explicitly prescribed, but the subjects had to reach it within 2 s. All the individual finger forces and their sum were displayed on-line on the screen in front of the subject. Two vertical lines were drawn on the screen to indicate to the subject when he or she had to generate a MVC. During single-finger tests, the subject was asked to pay no attention to forces produced by the others fingers. The explicitly involved fingers will be addressed as “master fingers,” while other force-producing fingers will be called “slave fingers.” The subjects were given several practice trials before testing.

Three experimental factors were manipulated: (1) Measurements before and after fatiguing exercise were used to evaluate the effects of fatigue (Fatigue factor). The fatiguing exercise consisted of 60 s at 100% of the MVC with the index finger; (2) the protocol was repeated on different days for two sites of force application during the fatiguing exercise, the middle of the proximal phalanx and the middle of the distal phalanx (Exercise site factor); (3) during tests prior to and after the fatiguing exercise, MVCs were recorded during force application at the distal and at the proximal phalanges (Test site factor).

Each session (preexercise, PRE; and postexercise, POST) consisted of ten trials organized in two mini-sessions (see Fig. 1B in Danion et al. 2000). Within a mini-session, MVCs were performed in single-finger tasks: index (I), middle (M), ring (R), and little (L); and in the four-finger task (IMRL). The order of tests within a mini-session was randomized. Each session included one minisession with the loops positioned at the proximal phalanges and one with the loops at the distal phalanges. To avoid fatigue in the PRE session (before the fatiguing exercise), individual trials were separated by 20 s of rest (cf. Valero-Cuevas et al. 1998). In order to maintain the level of fatigue during the POST session (after the fatiguing exercise), at the end of each trial, the subjects had to repeat the same fatiguing exercise for an additional period of 20 s. This kept MVC recovery during the POST session to under 10%. There was at least 1 day of rest between two tests that involved fatiguing exercises at the proximal site and at the distal site of force application. Half of the subjects started the experiment with the fatiguing exercise at the proximal site of force production, and the other half started with the fatiguing exercise at the distal site of force production.

Data acquisition and processing

Within each trial, the force value of each finger was extracted at the moment when the maximal force value was reached for the explicit task. A typical set of data recorded during a mini-

session is presented in Fig. 1C. Within each mini-session, several dependent variables were calculated:

1. Force deficit. The maximal force produced by four fingers acting in parallel was smaller than the sum of the maximal forces of each finger during single-finger force production. Force deficit was defined as the difference between the sum of MVCs during the single-finger tasks and the maximal total force in the four-finger task. Force deficit was further expressed as a percentage of the former value. The contribution of one finger, L, to force deficit is emphasized in Fig. 1 C.
2. Force sharing. Force share of a finger in a four-finger task was defined as the percentage of total force generated by this finger in the task (see Fig. 1C). Note that the sum of four individual shares is equal to 100%.
3. Enslaving. Twelve enslaving forces were produced within a mini-session (see the nonbold numbers in Fig. 1C). Each of these forces was further expressed as a percentage of the corresponding MVC of the finger that produced it. All these percentages were then averaged. As a result, our index of enslaving represents the mean percentage of MVC developed by a slave finger.

Statistical analysis

Repeated-measures, three-factor ANOVAs were used; the factors (Test site, Fatigue, and Exercise site) are described in the section Procedure. Sharing patterns were compared using MANOVAs including the same three factors. Rao's R was used to assess the significance of these tests. Because the four individual shares did not constitute a set of independent variables (since their sum is always 100%), sharing patterns were compared using three shares only (for M, R, and L).

Several ANOVAs with a Finger factor were also performed to assess possible differences across the digits. Whenever a significant effect of Finger was found, a post-hoc analysis (Newman-Keuls) was run.

Results

Some of the findings of the present study are similar to those reported previously (Danion et al. 2000). In particular, as compared to force production at the distal site, force production at the proximal site led to higher forces, higher enslaving, and higher force deficit, but resulted in similar force-sharing patterns. We are not going to present these data in detail.

Changes in MVC

There were no significant differences in most of the studied indices between the male and female subgroups (with the obvious exception of higher MVCs demonstrated by the men). Therefore, we present analyses of pooled data across all the subjects.

After the fatiguing exercise, the MVC of the I finger (MVC-I) dropped in all subjects ($F_{1, 13}=52.02$; $P<0.001$) from 51.7 N to 35.2 N (data averaged across all conditions; Table 1 shows data for all tests and conditions separately). When measured at the site of the fatiguing exercise, the drop in the MVC-I was similar after the proximal and distal exercises ($F_{1, 13}=0.51$; $P>0.1$). However, when measured at the other site, the magnitude of the drop in MVC-I was different for the two sites of the fatiguing exercise. After the fatiguing exercise at the proximal site, the mean force drop across individuals was larger during force production at the proximal site than at the distal site (34.8% and 16.5%, respectively; $F_{1, 13}=26.12$; $P<0.001$; Fig. 2A). By contrast, after the fatiguing exercise at the distal site, the drop was similar at both distal and proximal sites (33.4% and 33.3%, respectively; $F_{1, 13}=0.05$; $P>0.1$). We will address the drop

in force measured at a site other than the one involved in the fatiguing exercise as a “transfer effect.”

The M, R, and L fingers showed lower MVCs in the POST session ($F_{1,13} > 18.20$; $P < 0.001$). Asymmetrical transfer effects were observed. When measured at the site other than the exercise site, the mean drop in MVC across the M, R, and L finger was 19.1% and 12.6%, respectively, after the distal and proximal exercise. A three-way ANOVA (Finger, Exercise site, Test site) revealed a main effect of Finger ($F_{3,39} = 34.55$; $P < 0.001$) demonstrating different drops in MVC across the I, M, R, and L fingers.

Fatigue of the I finger induced by force production at the proximal site showed preferential weakening of digits closer to it, whereas fatigue at the distal site showed similar weakening in all other fingers (Fig. 2A). A two-way MANOVA (Exercise site, Test site) showed a significant effect of Test site ($R_{3,11} = 4.32$; $P < 0.05$). In particular, after an exercise at the proximal site, the mean magnitude of the transfer effect was 0.89, 0.71, and 0.30 for the M, R, and L finger, respectively. These differences were confirmed by a post-hoc analysis (Neuman-Keuls) among all possible pairs of these three fingers ($P < 0.05$).

During four-finger tests, forces developed in the POST session were smaller than in the PRE session (100.1 N versus 148.6 N, respectively; $F_{1,13} = 35.52$, $P < 0.001$). After the exercise at the proximal site, the MVC dropped more at the proximal site (by 38.5%) than at the distal site (by 25.1%). In contrast, after the exercise at the distal site, the MVC drops were comparable when measured at the distal (28.6%) and proximal (28.8%) sites of force production.

Additional analysis was run to compare relative force losses of individual fingers in single- and multi-finger tasks. Figure 2B shows that the relative force loss of the I finger during the multi-finger task was larger ($F_{1,13} = 23.79$; $P < 0.001$). By contrast, the M, R, and L fingers showed similar relative force losses in the single- and multi-finger tasks ($F_{1,13} < 1.04$; $P > 0.1$). Note that the force loss of the I finger was larger during the multi-finger tasks when measured in absolute units also (24.9 N versus 19.1 N; $F_{1,13} = 6.41$; $P < 0.05$).

Force deficit

As shown in Fig. 3, force deficit increased in the POST session ($F_{1,13} = 9.97$; $P < 0.01$). After the fatiguing exercise at the proximal phalanges, force deficit increased considerably more during force production at the proximal site than at the distal site (13.9% versus 7.5%). By contrast, after the fatiguing exercise at the distal phalanges, force deficit increased similarly for both distal and proximal sites of force production (7.3% versus 6.4%).

The I finger played a dominating role in the increase in force deficit. Across all conditions, prior to fatigue, the I finger in the four-finger tests showed the force deficit of 15.7%, while after fatigue the force deficit reached 38.2% ($F_{1,13} = 22.59$; $P < 0.001$). No comparable significant changes were observed for the M, R, and L fingers (on average, 7.7% versus 12.1%; $F_{1,13} < 2.99$; $P > 0.1$). The force deficit for the I finger increased with fatigue even when expressed in absolute units (12.9 N versus 8.4 N, respectively; $F_{1,13} > 6.4$; $P < 0.05$).

Enslaving

During MVC production by the I finger, prior to a fatiguing exercise, fingers were enslaved differently ($F_{2,26} = 11.5$; $P < 0.01$). Post-hoc comparisons (Neuman-Keuls) revealed that the M finger was enslaved more than the R and L fingers ($P < 0.01$), while the levels of enslaving of the R and L fingers were similar ($P > 0.1$). This was true for both distal (M finger 13%, R finger 4%, L finger 5%) and proximal sites of force production (M finger 23%, R finger 9%, L finger 11%). The same patterns of enslaving were seen under fatigue.

A tendency for lower enslaving was found under fatigue (22.1% versus 20.7%; $F_{1,13}=3.86$; $P=0.07$). After the exercise at the distal site, drops in enslaving were significant for both proximal and distal sites of force production ($F_{1,13}=5.54$; $P<0.05$).

By analyzing the enslaving effects for each finger separately, we found a significantly reduced ability of the I finger to be enslaved by other fingers (12.5% versus 9.7% in the PRE and POST session, respectively, ($F_{1,13}=5.60$; $P<0.05$). This drop in I-finger enslaving accounted for about 50% of the overall change in enslaving across all four fingers. By contrast, the ability of the I finger to enslave other fingers remained unaffected by fatigue (10.9% versus 10.8% in the PRE and POST session, respectively).

Sharing patterns

Sharing patterns are shown in Fig. 4. MANOVA revealed main effects of Fatigue ($R_{3,11}=22.76$; $P<0.001$) and Test site ($R_{3,11}=3.6$; $P<0.05$), but not of Exercise site ($R_{3,11}=0.58$; $P>0.1$). The effect of fatigue consisted mainly in a reduction in the share of the I finger ($F_{1,13}=78.50$; $P<0.001$). This effect was consistent across all conditions. When the sites of the fatiguing exercise and of the test were identical, the redistribution of the share lost by the I finger (on average, 9.3% of the total force) among the others fingers (M, R, L) was different for the two sites of force production. During tests at the proximal site, each finger received a different percentage of the share lost by the I-finger ($F_{2,26}=3.2$; $P<0.05$): The L finger got 60%, followed by the R finger with 30%, and then by the M finger with 10% (the share lost by the I finger is considered as 100%). By contrast, during tests at the distal site, the M, R, and L finger received approximately one-third each.

Discussion

Effects of fatigue transfer

After the 60 s of flexion MVC by the I finger, we observed a 33% drop in the MVC at the site of exercise. This observation is within the range of the values reported in the literature. For instance, Sheean et al. (1997) observed a 20% drop after 45-s MVC with the adductor pollicis muscle (adductor of the thumb), while Stephens and Taylor (1972) reported a 50% drop after 60 s of MVC with the FDI muscle (abductor of the I finger).

Effects of fatigue were also seen when the subjects were asked to produce MVC with the I finger at the other site (i.e., at the distal phalanx after the fatiguing exercise at the proximal phalanx or vice versa) or with other fingers (M, R, or L fingers) at both sites of force application, thus demonstrating transfer of fatigue across both phalanges and fingers.

The magnitude of the transfer effects of fatigue across phalanges depended on the site of force production. After the exercise at the proximal site, the drop in the I-finger MVC at this site was twice as large as at the distal site (i.e., the magnitude of the transfer effect was about 0.5). By contrast, after the exercise at the distal site, the drop in the I-finger MVC was similar at both sites (i.e., the magnitude of the transfer effect was close to one). Changes in other indices such as the four-finger MVC, sharing pattern, and force deficit, confirmed the existence of larger transfer effects of fatigue induced by exercise at the distal site (see Table 2). In our previous experiments (Danion et al. 2000), when all four fingers were explicitly involved by the fatiguing exercise, transfer effects between the two sites were also found, but these effects were symmetrical (i.e., equal in magnitude, about 0.5) after exercises at both sites. Due to force deficit, the I finger produced less force during the four-finger fatiguing exercise than in the single-finger one. This could lead to different patterns of motor-unit recruitment, and hence possibly to different transfer effects of fatigue across the phalanges.

Transfer of fatigue was also observed across fingers. Anatomically, the extrinsic muscle equipment of the I finger is relatively independent, the flexor digitorum profundus typically has a separate muscular head for the I finger (Wood-Jones 1942), while flexor digitorum superficialis has independent muscular masses and digital tendons for all fingers (Fahrer 1981). Concerning, the intrinsic muscles, the first dorsal interosseous is essentially a muscle of the I finger (Fahrer 1981), as well as the first palmar interosseous. Nevertheless, all digits exhibited a drop in the MVC after the fatiguing exercise by the I finger, as revealed by the single-finger tests. The patterns of these effects depended on the site of force production. For the proximal site, the closer a finger was to the I finger the greater was its loss of force. During force production at the distal site, the loss of force was evenly distributed across the M, R, and L fingers.

During the fatiguing exercise by the I finger, other fingers produced force due to enslaving effects (Li et al. 1998b). These effects may be viewed as potential contributors to the transfer effects of fatigue across fingers. However, there are findings suggesting that enslaving alone was insufficient to account for the results. During I-finger MVC tasks, peak forces of the M, R, and L fingers were rather small (less than 20% of their MVCs in single-finger tasks). One minute of force generation at such a low force level is not expected to lead to any visible effects of fatigue (cf. data in Kahn et al. 1997). Furthermore, the pattern of the enslaving effects during I-finger MVC tests did not match the pattern of the transfer effects of fatigue: For instance, during force production at the distal site, the M finger was enslaved stronger than the R or L fingers; however, the drop in its MVC was similar to those of the R and L fingers. In addition, the distribution of the enslaving effects across the M, R, and L fingers was similar at both sites of force generation (no significant differences), while the transfer effects were significantly different.

Relations among forces produced by different fingers get contributions from both peripheral and central factors ranging from the presence of intertendinous connections to shared muscle fibers, and to the divergence of the corticomotoneuronal projections (Fetz and Cheney 1980; Cheney and Fetz 1985). The complexity of the interplay of these factors does not allow one to exclude a contribution of peripheral factors to fatigue transfer not reflected proportionally in enslaving effects.

Changes in force deficit and force-sharing patterns

Force deficit increased under both single- and four-finger fatigue. However, the contribution of each finger to this raise depended on the nature of the fatiguing exercise. After a multi-finger exercise (Danion et al. 2000), all the fingers showed similar drops in their MVCs (by about 25%), and each finger was similarly less recruited during four-finger tasks. By contrast, after a single-finger fatiguing exercise, the contributions of individual fingers became much more heterogeneous: The I finger, exhibiting the higher level of fatigue, was the main contributor to the increase in force deficit. Force deficit exhibited by the I finger increased in its absolute value (in newtons). This finding contradicts one of the predictions of a hypothesis assuming unchanged central commands under fatigue (see the Introduction).

Patterns of force sharing among the fingers during four-finger tasks have been shown to persist within a wide variety of tasks (Li et al 1998a; Latash et al. 1998b; Danion et al. 2000). In earlier studies, we hypothesized that these patterns reflected a minimization of moments generated by all the fingers with respect to the longitudinal axis of the arm (Li et al. 1998a, 1998b). Until now, these patterns have been shown to change only during grip tasks when the position of the thumb changed following changes in the mechanical constraints of the task (Li et al. 1998a). The present study demonstrated the possibility of changes in the sharing pattern without changes in the explicit mechanical constraints of the task. After each fatiguing exercise, the sharing pattern during the multi-finger tests was always modified, with a considerable drop in

the I-finger share. This finding violates the principle of minimization of secondary moments, meaning that this principle should no longer be considered universal. This result may be specific for pressing tasks, which do not involve additional task constraints such as maintaining an orientation of an object, typical of grasping. This result is in line with the hypothesis assuming unchanged central commands, but it contradicts the main prediction of the other hypothesis formulated in the Introduction.

So, both hypotheses formulated in the Introduction have been found incompatible with at least one finding. Therefore, we would like to suggest another hypothesis, which assumes that the most impaired (fatigued) finger shows less interaction with other fingers or, in other words, is being progressively excluded from the multi-finger synergy. This hypothesis emphasizes central effects of fatigue and it is compatible with effects due to changes in the muscle force-generating properties. We think that it provides a unifying, parsimonious explanation for many of the results.

According to this hypothesis, during multi-finger tasks, the central command to the fatigued finger is reduced as compared to commands to other fingers (unlike the two alternative hypotheses that assume either unchanged commands or relatively reduced commands to other fingers). In this case, the fatigued finger is expected to contribute more to force deficit as observed in the experiments. Note that when all four fingers are fatigued to a similar degree, all fingers contribute similarly to the increase in force deficit (Danion et al. 2000). Besides, this hypothesis naturally incorporates the finding that the fatigued finger (I) showed a drop in the level of its enslaving by other fingers.

Fatigue can be viewed as a factor leading to different changes in the force-generating properties of individual fingers. Within a multi-element synergy, the overall performance is likely to be limited by the weakest link. There appears to be a trade-off: On the one hand, having more elements within a synergy increases its flexibility and adaptability; on the other hand, if one element is considerably weaker, using it to the same extent as other elements may limit the overall performance. Besides, by recruiting a fatigued finger less, this finger is given better chances for a faster recovery, leading to its faster reintegration into the synergy. The phenomenon of element exclusion under fatigue should be viewed as an adaptive mechanism within a multi-finger synergy, rather than a dysfunction of the synergy.

Acknowledgments

Frederic Danion was supported by the Fyssen foundation. The study was in part supported by NIH grant NS-35032. The authors would like to acknowledge the anonymous reviewers for helpful suggestions.

References

- Aymard C, Katz R, Laffite C, Le Bozec S, Penicaud A. Changes in reciprocal and transjoint inhibition induced by muscle fatigue in man. *Exp Brain Res* 1995;106:418–424. [PubMed: 8983985]
- Basmajian, JV.; De Luca, CJ. *Muscles alive*. 5th edn.. Baltimore, MD: Williams and Wilkins; 1985.
- Bemben MG, Massey BH, Bemben DA, Misner JE, Boileau RA. Isometric intermittent endurance of four muscle groups in men aged 20–74 yr. *Med Sci Sport Exer* 1996;28:145–154.
- Bigland-Ritchie B, Woods JJ. Changes in muscle contractile properties and neural control during human muscle fatigue. *Muscle Nerve* 1984;7:691–699. [PubMed: 6100456]
- Bonnard M, Sirin AV, Oddson L, Thorstensson A. Different strategies to compensate for the effects of fatigue revealed by neuromuscular adaptation processes in humans. *Neurosci Lett* 1994;166:101–105. [PubMed: 8190349]
- Cheney PD, Fetz EE. Comparable patterns of muscle facilitation evoked by individual corticomotoneuronal (CM) cells and by single intracortical microstimuli in primates: evidence for functional groups of CM cells. *J Neurophysiol* 1985;53:805–820. [PubMed: 2984355]

- Close, JR.; Ralston, HJ. Functional anatomy of the extremities: some electronic and kinematic methods of study. Springfield, IL: Thomas; 1973.
- Danion F, Latash ML, Li Z-M, Zatsiorsky VM. The effect of fatigue on multi-finger coordination in force production tasks. *J Physiol (Lond)* 2000;523:523–532. [PubMed: 10699094]
- Enoka RM, Stuart DG. Neurobiology of muscle fatigue. *J Appl Physiol* 1992;72:1631–1648. [PubMed: 1601767]
- Fahrer, M. Interdependent and independent actions of the fingers. In: Tubiana, R., editor. *The Hand*. Philadelphia, PA: Saunders; 1981. p. 399–403.
- Fetz EE, Cheney PD. Post-spike facilitation of forelimb muscle activity by primate corticomotoneuron cells. *J Neurophysiol* 1980;44:751–772. [PubMed: 6253604]
- Forestier N, Nougier V. The effects of muscular fatigue on the coordination of a multijoint movement in human. *Neurosci Lett* 1998;252:187–190. [PubMed: 9739992]
- Fuglevand AJ, Zackowski KM, Huey KA, Enoka RM. Impairment of neuromuscular propagation during human fatiguing contractions at submaximal forces. *J Physiol (Lond)* 1993;460:549–572. [PubMed: 8387589]
- Hagbarth KE, Bongiovanni LG, Nordin M. Reduced servo-control of fatigued human finger extensor and flexor muscles. *J Physiol (Lond)* 1995;485:865–872. [PubMed: 7562624]
- Kahn JF, Favriou F, Jouanin JC, Monod H. Influence of posture and training on the endurance time of a low-level isometric contraction. *Ergonomics* 1997;40:1231–1239. [PubMed: 9375537]
- Kendall, HO.; Kendall, FP.; Wadsworth, GE. *Muscles: testing and function*. Baltimore, MD: Williams and Wilkins; 1971.
- Kilbreath SL, Gandevia SC. Limited independent flexion of the thumb and fingers in human subjects. *J Physiol (Lond)* 1994;479:487–497. [PubMed: 7837104]
- Kinoshita H, Murase T, Bandou T. Grip posture and forces during holding cylindrical objects with circular grips. *Ergonomics* 1996;39:1163–1176. [PubMed: 8681936]
- Latash ML, Li Z-M, Zatsiorsky VM. A principle of error compensation studied within a task of force production by a redundant set of fingers. *Exp Brain Res* 1998a;122:131–138. [PubMed: 9776511]
- Latash ML, Gelfand IM, Li Z-M, Zatsiorsky VM. Changes in the force-sharing pattern induced by modifications of visual feedback during force production by a set of fingers. *Exp Brain Res* 1998b;123:255–262. [PubMed: 9860263]
- Li Z-M, Latash ML, Newell KM, Zatsiorsky VM. Motor redundancy during maximal voluntary contraction in four-finger tasks. *Exp Brain Res* 1998a;122:71–78. [PubMed: 9772113]
- Li Z-M, Latash ML, Zatsiorsky VM. Force sharing among fingers as a model of the redundancy problem. *Exp Brain Res* 1998b;119:276–286. [PubMed: 9551828]
- Li Z-M, Zatsiorsky VM, Latash ML. The effect of finger extensor mechanism on the flexor force during isometric tasks. *Clin Biomech* 2000;15:203–211.
- Milner-Brown HS, Mellenthin M, Miller RG. Quantifying human muscle strength, endurance and fatigue. *Arch Phys Med Rehabil* 1986;67:530–535. [PubMed: 3741078]
- Ohtsuki T. Inhibition of individual fingers during grip strength exertion. *Ergonomics* 1981;24:21–36. [PubMed: 7227358]
- Radwin RG, Buffalo BA. Computer key switch force-displacement characteristics and short-term effects on localized fatigue. *Ergonomics* 1999;42:160–170. [PubMed: 9973878]
- Sacco P, Newberry R, Mc Fadden L, Brown T, Mc Comas AJ. Depression of human electromyographic activity by fatigue of a synergistic muscle. *Muscle Nerve* 1997;20:710–717. [PubMed: 9149078]
- Sheean GL, Murray NMF, Rothwell JC, Miller DH, Thompson AJ. An electrophysiological study of the mechanism of fatigue in multiple sclerosis. *Brain* 1997;120:299–315. [PubMed: 9117377]
- Sparto PJ, Parnianpour M, Reinsel TE, Simon S. The effect of fatigue on multijoint kinematics and load sharing during a repetitive lifting test. *Spine* 1997;22:2647–2654. [PubMed: 9399451]
- Stephens JA, Taylor A. Fatigue of maintained voluntary muscle contraction in man. *J Physiol (Lond)* 1972;220:1–18. [PubMed: 5059236]
- Valero-Cuevas FJ, Zajac FE, Burgar CG. Large index-fingertip forces are produced by subject-independent patterns of muscle excitation. *J Biomech* 1998;31:693–703. [PubMed: 9796669]

- Wolf E, Blank A, Shochina M, Gonen B. Effect of the lower limbs on the nonexercised biceps brachii-muscle. *Am J Phys Med* 1984;63:113–121. [PubMed: 6731599]
- Wood-Jones, F. The principles of anatomy as seen in the hand. 2nd edn.. London: Tindall; 1942. p. 248-249.
- Woods JJ, Furbush F, Bigland-Ritchie B. Evidence for a fatigue-induced reflex inhibition of motoneuron firing rates. *J Neurophysiol* 1987;58:125–137. [PubMed: 3039078]
- Zatsiorsky VM, Li Z-M, Latash ML. Coordinated force production in multi-finger tasks: finger interaction and neural network modeling. *Biol Cybern* 1998;79:139–150. [PubMed: 9791934]
- Zijdwind I, Kernell D. Index finger position and force of the human first dorsal interosseous and its ulnar nerve antagonist. *J Appl Physiol* 1994;77:987–997. [PubMed: 8002556]
- Zijdwind I, Kernell D, Kukulka CG. Spatial differences in fatigue-associated electromyographic behaviour of the human first dorsal interosseous muscle. *J Physiol (Lond)* 1995;483:499–509. [PubMed: 7650617]
- Zijdwind I, Zwarts MJ, Kernell D. Influence of a voluntary fatigue test on the contralateral homologous muscle in humans? *Neurosci Lett* 1998;253:41–44. [PubMed: 9754800]

Fig. 1.

A The experimental setup (adapted with permission from Li et al. 2000). **B** Side view of the hand fixation and finger configuration. The hand is clamped and the forearm is strapped to a solid board (adapted with permission from Li et al. 2000). **C** A typical set of data recorded during a mini-session (adapted with permission from Danion et al. 2000). For each test, the force of each finger is reported at the time of maximal voluntary contraction (MVC; in newtons). *Numbers in bold* represent the forces produced by the master fingers, and the others are the forces produced by the slave fingers. See text for more details of enslaving, force deficit, and sharing (*I* index finger, *M* middle finger, *R* ring finger, *L* little finger, *IMRL* all four fingers acting together)

Fig. 2.

Drop in MVC induced by the fatiguing exercise. **A** Averaged across subjects, values are presented for each task, exercise site, and test site of force production. *Error bars* show the standard errors. **B** Averaged across subjects, values are presented for each finger depending on the nature of the task (single- or multi-finger exercise). Data for tests performed at the site of the fatiguing exercise. *Stars* indicate significant differences in force loss between multi- and single-finger tests. (*Prox.* Proximal, *Dist.* distal, *I* index finger, *M* middle finger, *R* ring finger, *L* little finger, *IMRL* all four fingers acting together)

Fig. 3.

Force deficit in the four-finger tests. Averaged across subjects, values are presented for each exercise site and test site of force production. *Error bars* show the standard errors of the means. For abbreviations, see Fig. 2

Fig. 4.

Force-sharing patterns in the four-finger tests. Averaged values across subjects are presented for each exercise site and test site of force production. Note the reduced share of the index finger across all experimental conditions. For abbreviations, see Fig. 2

Table 1

MVCs (in newtons) across all experimental conditions and tests. Means and SE across subjects are presented (*PROX* proximal, *DIST* distal, *I* index finger, *M* middle finger, *R* ring finger, *L* little finger, *IMRL* all four finger acting together, *I+M+R+L* the sum of the forces generated by individual finger in single-digit MVC tests, *E* Exercise site factor, *F* Fatigue factor, *T* Test site factor)

The last column shows statistically significant main effects and interactions ($P<0.05$) in corresponding ANOVAs

Exercise (E)	PROX				DIST				P<0.05
	Pre		Post		Pre		Post		
Fatigue (F)	Pre		Post		Pre		Post		
Test (T)	Prox	Dist	Prox	Dist	Prox	Dist	Prox	Dist	
IMRL	Mean	195.8	109.8	82.7	176.6	112.1	120.3	78.5	F,T,ET,FT,EFT
	SE	21.9	9.3	8.1	20.5	8.9	14.3	5.2	
I	Mean	66.2	38.5	32.5	60.5	41.6	38.6	27.9	F,T,FT,EFT
	SE	6.7	2.9	2.4	5.3	2.6	3.2	1.9	
M	Mean	66.8	34.4	29.7	56.7	35.9	41.5	29.3	F,T,ET,FT,EFT
	SE	7.9	2.5	2.3	6.4	2.3	4.3	2.0	
R	Mean	39.8	23.0	20.7	37.1	25.3	28.3	20.9	F,T,ET,FT
	SE	3.9	1.9	1.9	5.2	2.1	3.2	1.8	
L	Mean	39.8	23.4	20.2	40.4	25.3	33.1	21.0	F,T
	SE	4.6	2.2	2.1	4.5	2.0	3.2	1.5	
I+M+R+L	Mean	212.6	119.3	103.0	194.7	128.0	141.6	99.0	F,T,ET,FT,EFT
	SE	22.0	9.0	7.9	20.1	8.2	12.2	6.3	

Table 2

Effects of fatigue across experimental conditions. Various parameters are presented: drop in MVC in single-finger tests (*MVC-I*, *MVC-M*, *-R*, *-L*) and in the four-finger test (*MVC-4F*), force deficit, enslaving, and changes in sharing patterns. The symbols + and – indicate the magnitude of the effect of fatigue on each parameter. For other abbreviations, see Fig. 2

Exercise	Proximal		Distal	
	Prox	Dist	Prox	Dist
MVC-I drop	++	+	++	++
MVC-M, -R, -L drop	M>R>L	M=L=R	M>R>L	M=L=R
MVC-4F drop	++	+	++	++
Deficit	++	+	++	++
Enslaving	–	0	–	–
Share-I drop	++	+	++	++