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Adaptations to fatigue of a single digit violate the *principle of superposition* in a multi-finger static prehension task

Tarkeshwar Singh^{1,2}, Vladimir M. Zatsiorsky¹, and Mark L. Latash¹

¹Department of Biomedical Engineering, Cleveland Clinic, Cleveland, OH 44195

²Department of Kinesiology, The Pennsylvania State University, University Park, PA 16802

Abstract

We investigated the effects of exercise-induced fatigue of a digit on the biomechanics of a static prehension task. The participants were divided into two groups. One group performed the fatiguing exercise using the thumb (*group-thumb*) and the second group performed the exercise using the index finger (*group-index*). We analyzed the prehensile action as being based on a two-level hierarchy. Our first hypothesis was that fatigue of the thumb would have stronger effects at the upper level (action shared between the thumb and all four fingers combined – virtual finger) and fatigue of the index finger would have stronger effects at the lower level of the hierarchy (action of the virtual finger shared among actual fingers). We also hypothesized that fatigue would cause a decrease in the normal force applied by the exercised digit and correspondingly lead to a decrease in the normal force applied by the opposing digit(s). Our third hypothesis was that fatigue would leave the tangential forces unaffected. Fatigue led to a significant drop in the normal force of both exercised and non-exercised (opposing) digits. The tangential forces of the exercised digits increased after fatigue. This led to a drop in the safety margin in the *group-thumb*, but not *group-index*. As such, the results supported the first two hypotheses but not the third hypothesis. Overall, the results suggested that fatigue triggered a chain reaction that involved both forces and moments of force produced by individual digits leading to a violation of the principle of superposition. The findings are interpreted within the framework of the referent configuration hypothesis.

Keywords

hand; fatigue; grasping; prehension; hierarchical control; superposition

Introduction

The human hand is versatile and dexterous in its interaction with the environment in that it allows for both powerful and stable grasps (Cutkosky 1989; Vilaplana and Coronado 2006; Prattichizzo and Trinkle 2008) and fine dexterous manipulation by the digits (Zatsiorsky and Latash 2009). When a person holds an object steadily with all five digits using a prismatic grasp (the thumb opposing the four fingers), the action has been discussed as organized in a hierarchical way (Arbib et al. 1985; Baud-Bovy and Soechting 2001; Shim et al. 2005; Gorniak et al. 2009). At the upper level (TH–VF level), the action is shared between the thumb (TH) and a virtual finger (VF). VF is a hypothetical digit producing the same

mechanical effect as the four fingers combined (Iberall 1997). At the lower level (IF level), the VF action is shared among the fingers.

In this study, we were interested in investigating the effects of exercise-induced fatigue of the thumb and index finger on the kinetics of a static grasping action at both levels of the hierarchy. On one hand, fatiguing the thumb could be obviously expected to have a stronger effect at the TH-VF level, to which it directly contributes. On the other hand, we have also shown that fatigue of the index (I) finger increases the variability of the force output of other individual fingers but has a minimal effect on the variability of the combined force output of the VF in an accurate force production task (Singh et al. 2010b). Therefore, our first hypothesis was that fatigue of TH would have stronger effects at the TH-VF level and fatigue of the index finger (I) would have stronger effects on the IF level.

For the present study, we assumed that all the digits and the VF make soft contacts (Mason and Salisbury 1985; Mason 2001) that apply a four-dimensional wrench on a planar surface. At the TH-VF level of the hierarchy, the following two vector equations of statics have to be satisfied for a hand-held handle:

$$\{\mathbf{F}_{\text{TH}}\} + \{\mathbf{F}_{\text{VF}}\} + \Sigma\{\mathbf{F}_{\text{ext}}\} = 0; \quad (1)$$

$$\{\mathbf{M}_{\text{TH}}\} + \{\mathbf{M}_{\text{VF}}\} + [0, 0, \{T_{\text{TH}}^z\}] + [0, 0, \{T_{\text{VF}}^z\}] + \Sigma\{\mathbf{M}_{\text{ext}}\} = 0; \quad (2)$$

where $\mathbf{F}$ are the vectors of applied forces, $\mathbf{M}$ are the moments of force applied by $\mathbf{F}$, and T^z denotes the free moments applied by the soft digit contacts about the local Z axis of the sensor (the axes are shown in Figure 1A). During fatigue, concomitant changes were expected in $\mathbf{F}_{\text{TH}}$ and $\mathbf{F}_{\text{VF}}$ to ensure that the mechanics of static prehension were satisfied. The selected fatiguing exercises (described in detail in Methods) primarily involved normal force production; hence, our second hypothesis was that fatigue would cause a decrease in the normal force of the exercised digit and a corresponding decrease in the normal force applied by the opposing digit(s). Previously, we have shown that fatigue of the index finger also affects the performance of the middle and ring fingers (Singh et al. 2010b); therefore, we expected that for *group-index*, fatigue would cause a reduction in the normal force applied by the VF and a corresponding decrease in the normal force of the TH. It should be noted that the first two hypotheses are not trivial because fatigue of the TH and index(I) finger would result in a drop in MVC of the fatigued digit (as we have previously shown in (Singh et al. 2010b; Singh et al. 2010a). However, there is no obvious reason for the normal grip forces to decrease during fatigue because the grip forces are small compared to the maximal forces (~15–20% of the MVC values). It should also be noted that the reduced normal grip force during fatigue should still be above the threshold of slippage to prevent the grasped object from slipping (Westling and Johansson 1984).

One possibility is that the changes in the grip (normal) forces of the exercised digit and the opposing digits would have minimal effects on the tangential forces and moments of force (cf. principle of superposition in Zatsiorsky et al. 2004). According to the principle of superposition, the control of multi-finger prehension can be viewed as a superposition of two independent processes controlling the grasping force (“slip prevention synergy”) and the orientation of the object (“tilt prevention synergy”) (Zatsiorsky et al. 2004). For example, a decrease in the normal force applied by TH during fatigue of the TH could be directly compensated by a decrease in the normal forces applied by the middle (M) and ring (R) fingers to ensure that the moment about the Y-axis of the *handle* (see Figure 1A) is not compromised. Other strategies that do not compromise the orientation could also be adopted (for example, $\Delta(2 \times F_{\text{I}}^z + F_{\text{M}}^z) = \Delta(F_{\text{R}}^z + 2 \times F_{\text{L}}^z)$, Δ represents change during fatigue). Similarly a

decrease in the normal force of the index finger during fatigue could be balanced by a similar decrease in the normal force of the little (L) finger and a corresponding decrease in the normal force applied by TH. Alternatively, to stabilize the grasp, the changes in the grip forces during fatigue could trigger chain effects in the tangential forces as well as moments of force applied by the digits (Zatsiorsky et al. 2004). In the absence of any prior evidence, we hypothesized (third hypothesis) that the vertical tangential forces applied by the exercised digit would not change during fatigue.

Methods

Participants

Sixteen participants (eight males) were assigned to two experimental groups. The first group performed thumb-fatiguing exercises (*group-thumb*) and the second group performed index finger fatiguing exercises (*group-index*). Both groups had four male and four female participants. Average data of the participants of the two groups were (mean $\pm$ SD): 28.3 ± 4.9 & 25.7 ± 4.7 years of age, 1.73 ± 0.10 m & 1.79 ± 0.10 m in height, 67.9 ± 9.02 & 78.4 ± 14.6 kg in mass, 18.1 ± 1.1 & 18.6 ± 0.9 cm for hand length, 7.8 ± 0.6 cm & 7.9 ± 0.6 cm for hand width respectively. Hand length was measured as the distance from the tip of the distal phalanx of the middle finger to the distal wrist crease with the wrist in a neutral pose. Hand width was defined as the distance between the lateral aspects of the metacarpophalangeal joints of the index and little fingers. All the participants were free of known neurological or muscular disorders. All participants were right hand dominant. They gave informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University, University Park, PA.

Apparatus

The Handle—Five six-component force/torque sensors (model Nano 17-R; ATI Industrial Automation, Apex, NC, USA) were used to measure the forces and moments of force produced by the tips of the individual digits. Sandpaper (100 grit) was placed on the contact surface of each sensor to provide friction. These sensors were attached to an aluminum frame (see Figure 1A). The total weight of the frame with 5 sensors was 0.2 kg and we call it the *handle*. An aluminum beam (0.21 kg, 5.0 $\times$ 60.0 $\times$ 0.8 cm) was attached to the handle. A 6-component (3 position and 3 orientation components) electromagnetic tracking device (Polhemus Liberty, Colchester, VT, USA) was affixed to the top of the handle. A bull's eye level was also attached on top of the Polhemus sensor (Figure 1A) to provide feedback on the orientation of the handle. During trials, a load of 0.475 kg was attached to the beam with an eyehook that could be moved horizontally along a slot in the beam to change the torque about the coronal axis. The total weight of the setup (handle + external load + Polhemus sensor) was 8.96 N. The external load could be suspended from the beam at three different locations: at $(-0.1, 0, \pm 0.1)$ m and at $(-0.1, 0, 0)$ m, providing a *pronation-torque*, *supination-torque* and *zero-torque* about the geometrical center of the handle. It should be noted that because the *handle* was asymmetric about the Z-axis (one sensor on one side and four on the other), the load suspended at $(-0.1, 0, 0)$ m exerted a small external moment about the geometrical center of the handle $(0, -0.032, 0)$ Nm). When the load was suspended at $(-0.1, 0, \pm 0.1)$ m, it applied a moment (M_{Ext}^Y) of +0.43 Nm (pronation) and -0.43 Nm (supination) respectively.

Fatigue Setup—Two fatiguing exercise setups were used for the two experimental groups. *Group-thumb* performed fatiguing exercises with the thumb on the apparatus shown in Figure 1B. A one-dimensional LCKD-50 strain gauge sensor (Omega Engineering Inc., Stamford, CT) recorded the force output of the thumb. Feedback on the force exerted by the thumb was provided to the participants on a Dell laptop that was placed 0.8 m in front of the

participant. This setup was expected to induce fatigue in the thumb flexors, opponens pollicis (OP), flexor pollicis brevis (FPB), flexor pollicis longus (FPL), as well as the first dorsal interosseous (FDI). This setup was similar to the setup used by Luu and colleagues (Luu et al. 2011).

Group-index performed a fatiguing exercise on the setup shown in Figure 1C. This setup was the same as the one used in our previous studies (Singh et al. 2010b; Singh et al. 2010a; Park et al. 2012). Feedback was provided to the participant for the normal force produced by the exercised digit. This setup was expected to primarily induce fatigue in the extrinsic flexors of the fingers, the flexor digitorum profundus (FDP) and flexor digitorum superficialis (FDS).

Procedures

Before the experiment, the participants washed their hands with soap and warm water. The participants were first familiarized with the experimental setup and given practice trials. The experiment was conducted in a single session that lasted about 1.5 hours. Before the participants performed the actual trials, we measured the maximal voluntary contraction (MVC) force of all the digits in a pressing task. The MVC of the thumb was measured on the setup shown in Figure 1B and the MVC of the fingers was measured on the setup shown in Figure 1C. Each MVC trial was 5-s long.

During the experiment, the participants sat on a chair facing a computer screen that gave them feedback on the position of the handle in the XZ plane of the laboratory (see inset, Figure 1). The upper arm was abducted about 45° in the frontal plane and flexed 45° in the sagittal plane. The forearm was in the sagittal plane of the participant and at an angle of approximately 30–40° about the horizontal. At the beginning of each trial, the participants grasped the setup (handle + external load + Polhemus sensor) by grasping the handle on all the five sensors and lifted it to a natural and comfortable holding position (see inset, Figure 1). The participants kept the setup in that position for 5 s and then relaxed for 6 s. This procedure was repeated four times and the trial was terminated at the end of the 4th *sub-trial* (each trial was 38-s long). We collected four *sub-trials* within a trial to keep the number of during-fatigue trials and the total experiment time within reasonable limits.

Participants were not allowed to hyperextend the wrist joint during the trials. The instructions to all the participants were the same: grasp the handle in the same way by placing the fingertips at the centers of the sensors and apply a minimal effort. Participants were instructed to keep the orientation of the handle vertical by looking at the bull's eye level and to reproduce the location of the handle during all trials by looking at the feedback of the XZ coordinates of the handle on a computer screen (see inset, Figure 1). A circle of 3.0 cm diameter was shown at the center of the screen. At the beginning of each trial (when the participants were holding the handle steadily), the six channels from the Polhemus sensor were zeroed by collecting data for 1 s. The center of the circle was defined as the mean of the XZ coordinates of the Polhemus sensor during that time.

The data recording started when the participants reported that they were holding the handle comfortably. For the before-fatigue conditions, a total of five trials were collected for each torque condition, for a total of 15 trials and 60 *sub-trials*. The data were collected at a sampling frequency of 50 Hz. A minimum 45-s rest interval was given to the participants between trials, and a rest interval of 3–4 min was given between torque conditions to avoid fatigue. The order of torque conditions was randomized across participants. After the completion of the before fatigue trials, a 5–10 min rest was given to the participants. Then both groups performed a one-minute long fatiguing exercise at 100% MVC. After the fatiguing exercise, participants performed the MVC trials for all the digits. After the MVC

trials, the participants performed prehension trials with the handle in the same order as the before fatigue trials. After each trial, the participants performed a 20-s fatiguing (also at 100% MVC) exercise to minimize recovery from fatigue and dried their hands with a paper towel to ensure that the friction coefficient between the skin and the sandpaper on the ATI sensors did not change due to perspiration. The average of the 20 *sub-trials* (for each torque condition) was used for statistical analysis.

Model

The apparatus (along with the frames of references) is shown in Figure 1A. There were three frames of references used in the study: laboratory frame of reference $[XYZ]_{lab}$; the frame of reference attached to the geometrical center of mass of the handle $[XYZ]_{handle}$; and the local frames of reference attached to the geometrical centers of the surfaces of the force sensors $[x'y'z']_{sensor}^i$. Here 'i' stands for the individual digits (i=TH, I, M, R, L). For the current study, we assumed that the handle was always held horizontally (in static equilibrium) and therefore all analysis were performed in the handle frame of reference.

Kinetics—We measured the changes in the grip (normal) force, load-resisting (tangential) force, moments of force applied by the normal and tangential forces, and point of resultant force application of the VF, and safety margin. The safety margin has been defined as the proportion of normal force above the threshold for slippage (Johansson and Westling 1984; Pataky et al. 2004) as:

$$SM = \left[|F^n| - \frac{|F^t|}{\mu_s} \right] / |F^n| \quad (3)$$

$$\mu_s = 1.44(F^n)^{-0.293} \quad (4)$$

where μ_s is the coefficient of static friction between the finger pad and the contact interface of the object. The maximum value for SM is one when no tangential force (F^t) is exerted on the object and the minimum value for SM is zero when just sufficient normal force (F^n) is exerted on the object to prevent slippage. It has been shown that μ_z between the skin and the object changes with the magnitude of the normal force. We used the equation from Seo et al. (Seo et al. 2009) and fit a log-log regression to the data obtained from (Savescu et al. 2008). Fisher transformation was applied to the SM values before using parametric statistics. We measured the SM only for the exercised digit.

Statistics

The descriptive statistics are presented in the text and figures as means $\pm$ SE. The study had a 4-factor nested design with *Fatigue* (before-fatigue and during-fatigue as two levels) and *Torque* (PR, 0, SU) as the repeated fixed-factors; *Group* as the nested fixed-factor; and *Participants* as a random factor. Repeated-measures ANOVAs were used to test hypotheses on the effects of *Fatigue* and *Group*. An interaction between the factors, *Fatigue* and *Group* would show that the effects of exercise of the thumb and index finger were statistically different. A linear-mixed model for repeated measures (RM) was fit to the data. We chose the appropriate covariance structure for our analyses based on maximizing the Akaike's Information Criterion (AIC) (Vallejo et al. 2008). For multiple comparisons, Bonferroni's correction was used. The level of significance was chosen as $\alpha = 0.05$. The effects of the factor *Torque* were significant for almost all the reported kinetic variables ($\sim p < 0.001$). Thus, the statistical effects of *Torque* are not enumerated unless we found a *Fatigue* $\times$ *Torque* interaction or if we were reporting the effects of the fatiguing exercises on moments about the Y_{handle} axis.

Results

Fatigue induced a significant drop in the maximal voluntary contraction (MVC) forces of the digits. For *group-thumb*, during fatigue, MVC of TH dropped by 31.6% ($p<0.001$), of I by 11.6% ($p<0.05$), of M by 10.9% ($p<0.05$), and of R by 11.1% ($p<0.001$) (see Figure 2A). For *group-index*, fatigue of the index finger induced a significant drop in the MVC of the I (32%, $p<0.001$), M (16%, $p<0.05$), and R (20%, $p<0.001$) fingers (see Figure 2B).

Spread of fatigue to non-exercised digits

The two fatiguing exercises induced significant fatigue in the exercised as well as non-exercised digits. The magnitudes of drop in MVC of the I, M, and R fingers for *group-index* were similar to the results reported in our previous studies (Singh et al. 2010b; Singh et al. 2010a) whereas the drop in MVC of the thumb was small (~6%) and not significant. For *group-thumb*, the fatiguing exercise would have fatigued the intrinsic as well as extrinsic muscles spanning the thumb metacarpophalangeal, interphalangeal and carpometacarpal joints since all these joints were involved in the fatiguing exercise. There was also a ~10% drop in MVC of the I, M and R fingers. During the study, we observed that by the end of the 60-s fatiguing exercise (and during the subsequent re-fatiguing exercises), all the participants were not just pressing on the force sensor with the thumb but were also clenching their fists tightly around the cylindrical rod (see Figure 1B) to maintain the target force of the thumb. This might have inadvertently led to higher motor unit (MU) synchronization between the FPL and the extrinsic flexors like FDP and FDS (Winges and Santello 2004; Hockensmith et al. 2005; Danna-dos-Santos et al. 2010) causing partial fatigue of the finger flexors and a drop in their MVC. An increase in MU synchronization during the fatiguing exercise could decrease the 'gain' of the motoneuron pool of the digits making them less responsive to the supraspinal input during an MVC contraction (Taylor and Gandevia 2008). Even though the effects of the fatiguing exercise spilled over to the non-exercised digits for the MVC tasks, they were localized for the prehension tasks (which are performed at ~15–20% of MVC). The changes in the normal and tangential forces (see Figure 3) were localized only to the affected digit and there was a concomitant change in the opposing digit(s) to satisfy task mechanics.

Kinetics of Prehension

Effects of Fatigue on Normal Forces—At the TH-VF level, due to the mechanical constraints of maintaining static equilibrium, the normal forces exerted by the thumb, F_{TH}^Z and virtual finger, F_{VF}^Z had to be equal and opposite in direction. Overall, fatigue caused a drop of ~9% (on average, over both groups) in the normal force of TH ($F_{(1, 64.41)}=4.2$, $p<0.05$). A three-way RM ANOVA on F_{TH}^Z with *Fatigue*, *Torque*, and *Group* as factors showed a main effect of *Fatigue* ($F_{(1, 26.28)}=11.7$, $p<0.01$), *Torque*, and the *Fatigue* $\times$ *Group* interaction approached significance ($p=0.07$). There was a decrease in the normal forces of the index (I) finger, F_I^Z (11.3%, $p<0.01$), R finger, F_R^Z (8.6%, $p<0.05$), and L finger, F_L^Z (13.0%, $p<0.001$) as well. Post-hoc analysis revealed that the fatiguing exercise significantly decreased F_{TH}^Z for *group-thumb* (by ~12%, $p<0.01$, see Figure 3A) but not for *group-index* (Figure 3B). There was a *Fatigue* $\times$ *Group* interaction for R and L. Post-hoc analysis showed that for *group-thumb*, there were no significant changes in F_I^Z and F_M^Z while F_R^Z (17.6%, $p<0.01$) and F_L^Z (21%, $p<0.001$) decreased significantly (Figure 3A). For *group-index*, F_I^Z decreased significantly during fatigue (16.0%, $p<0.01$) while there were no other significant changes (Figure 3B). Overall, for *group-thumb*, F_{TH}^Z , F_R^Z and F_L^Z and for *group-index*, only F_I^Z decreased significantly.

Effects of Fatigue on Tangential Forces—At the TH-VF level, the sum of the tangential (vertical) forces applied by the TH and VF had to be equal to the total weight of the handle. *Fatigue* significantly affected the distribution of the tangential forces in the vertical (X) direction between TH and VF. For *group-thumb*, fatigue led to an increase in the magnitude of the tangential force of the thumb, F_{TH}^X , by ~29% (from -4.53 ± 0.51 to -5.79 ± 0.49 N, Figure 3C). To satisfy the constraints of statics, F_{VF}^X decreased for *group-thumb*. For *group-index*, fatigue led to an increase in F_I^X that was accompanied by a decrease in F_{TH}^X by ~11.8% (from -5.12 ± 0.46 to -4.54 ± 0.49 N, Figure 3D). A three-way RM ANOVA on F_{TH}^X with *Fatigue*, *Torque*, and *Group* as factors showed a main effect of *Fatigue* ($F_{(1,26.69)}=6.3$, $p<0.05$), *Torque*, and an effect of *Fatigue* $\times$ *Group* ($F_{(1,26.69)}=46.2$, $p<0.001$).

At the IF level, fatigue had different effects on the tangential forces exerted by I(F_I^X), R(F_R^X), and L(F_L^X) fingers for the two groups. This was confirmed by a *Fatigue* $\times$ *Group* interaction. F_I^X decreased in magnitude by ~90% (from -0.50 to -0.05 N, $p<0.05$) for *group-thumb* (Figure 3C) and increased by ~71% (from -0.46 to -0.79 N, $p<0.05$) for *group-index* (Figure 3D). F_R^X showed a tendency to decrease ($p=0.06$), while F_L^X decreased by ~27% (from -2.52 to -1.84 N, $p<0.01$) for *group-thumb*. There were no significant changes for *group-index* for these two variables. There were no changes in F_M^X for either of the groups.

Effects of fatigue on moments of force by the normal and tangential forces

Before fatigue, the ratio of the moments applied by the normal and tangential forces, M^N/M^T (see equation 5 and equation 6, superscript N denotes normal and T denotes vertical tangential), across all *Torque* conditions was 1.84 ± 0.57 for *group-thumb* and 1.76 ± 0.65 for *group-index*. Fatigue had no significant effect on M^N/M^T in either of the two groups. However, fatigue led to significant effects on the M^N and M^T components produced by individual digits. For obvious mechanical reasons, these effects were opposite on M^N and M^T because the sum of the two had to equal the external torque, F_{Ext}^Y (Equation 5).

$$M_{DIGITS}^Y = M_{Ext}^Y = M_{TH}^N + M_{TH}^T + M_{VF}^N + M_{VF}^T = M_{TH}^Z + M_{TH}^X + M_{VF}^Z + M_{VF}^X \quad (5)$$

$$M^N/M^T = [M_{TH}^N + M_{VF}^N] / [M_{TH}^T + M_{VF}^T] \quad (6)$$

For $M^N (M_{TH}^N + M_{VF}^N)$, there was a main effect of *Torque*, no main effect of *Fatigue* but *Fatigue* $\times$ *Group* interaction was significant ($p<0.001$) and, therefore, we analyzed the results for each group separately. For *group-thumb*, M^N became more counterclockwise during fatigue (change of ~40%, $p<0.05$, see Figure 4A, top panel). Post-hoc comparisons (after Bonferroni corrections) showed significant differences for the PR and SU torque conditions. For *group-index*, fatigue of the index finger resulted in a more clockwise M^N (change of ~20%, $p<0.05$, see Figure 4B top panel). We also computed changes in M_{VF}^N separately. For *group-thumb*, the normal force of the VF applied a larger counterclockwise moment (M_{VF}^N) during fatigue (change of ~100%, $p<0.05$, Figure 4C top panel). For *group-index*, the VF applied a larger clockwise moment (M_{VF}^N) during fatigue (change of ~38%, $p<0.05$, Figure 4D top panel).

A similar *Fatigue* $\times$ *Group* effect was significant ($p < 0.001$) for $M^T (M_{TH}^T + M_{VF}^T)$, and there was no main effect of *Fatigue* (there was a main effect of *Torque*). For *group-thumb*, fatigue caused a clockwise increase in M^T (change of $\sim 38\%$, $p < 0.001$, Figure 4A bottom panel). There was also a *Fatigue* $\times$ *Torque* interaction ($F_{(2,31.66)} = 4.46$, $p < 0.05$) that showed that the changes were larger for the PR and SU torque compared to the zero-torque condition. Post-hoc comparisons (after Bonferroni corrections) showed significant differences for all the torque conditions. For *group-index*, fatigue caused a counterclockwise increase in M^T (change of $\sim 30\%$, $p < 0.05$, Figure 4B bottom panel). For *group-thumb*, the VF applied a smaller counterclockwise moment (M_{VF}^T) during fatigue (decrease of $\sim 26\%$, $p < 0.05$, Figure 4C bottom panel). For *group-index*, the VF applied a larger counterclockwise moment (M_{VF}^T) during fatigue (increase of $\sim 12\%$, $p < 0.05$, Figure 4D bottom panel).

In summary, fatigue of the TH and I finger caused changes in opposite direction for M_{TH+VF}^N , M_{TH+VF}^T , M_{VF}^N and M_{VF}^T . The effects were significant for both *group-thumb* and *group-index*, but TH fatigue showed stronger effects. As necessitated by the task, the changes in M^N , M^T , M_{VF}^N and M_{VF}^T during fatigue were in opposite directions for both groups (see Equation 5).

Effects of fatigue on point of wrench application

The point of wrench application of the VF, $\mathbf{r}_{VF} (r_{VF}^X, r_{VF}^Y, -0.025\text{m})$ was computed by balancing the moments applied by the digit forces and the free moments in 3D space. $\mathbf{r}_{VF}$ was then projected onto the XZ plane. Fatigue induced significant changes in r_{VF}^X . A three-way RM ANOVA on r_{VF}^X showed a main effect of *Torque*, and a *Fatigue* $\times$ *Group* effect ($F_{(1,70.00)} = 12.92$, $p < 0.01$). For *group-thumb*, r_{VF}^X moved rostrally from -2.96 ± 2.29 mm to -5.58 ± 2.63 mm during fatigue ($p < 0.05$, Figure 5A). For *group-index*, r_{VF}^X moved caudally from -4.44 ± 2.55 mm to -2.41 ± 2.64 mm during fatigue ($p < 0.05$, Figure 5B). Fatigue also had an effect on r_{TH}^X . For *group-thumb*, r_{TH}^X moved caudally by $\sim 45\%$ (from -1.99 ± 0.34 mm to -1.11 ± 0.41 mm, $p < 0.05$, Figure 5C) during fatigue. There was no effect of fatigue on r_{TH}^X for *group-index*. A three-way RM ANOVA on r_{TH}^X showed a main effect of *Fatigue* ($F_{(1,24.29)} = 4.54$, $p < 0.05$), *Torque*, and a *Fatigue* $\times$ *Group* ($F_{(1,24.29)} = 8.28$, $p < 0.01$) interaction. Fatigue also increased r_{TH}^Y significantly for *group-thumb* by $\sim 85\%$ ($p < 0.001$, Figure 5D) confirmed by a main effect of *Fatigue* ($F_{(1,26.30)} = 47.68$, $p < 0.001$) and a *Fatigue* $\times$ *Group* interaction ($F_{(1,26.30)} = 22.28$, $p < 0.001$).

Safety Margin

Before fatigue, the safety margin (SM) for the index finger was larger than the thumb by $\sim 34\%$ ($p < 0.001$, unpaired t-test on Fisher transformed SM, see Figure 6). SM computed for the thumb decreased under fatigue for *group-thumb* by $\sim 29\%$ ($p < 0.001$). A two-way RM ANOVA on Fisher Z-transformed SM showed a main effect of *Fatigue* ($F_{(1, 31.42)} = 31.42$, $p < 0.001$) and *Torque* for *group-thumb*. For *group-index*, SM for the index (I) finger decreased by $\sim 9\%$ during fatigue but this effect did not reach significance ($p = 0.12$). There was a main effect of *Torque* for *group-index*.

Discussion

Our first hypothesis was that fatigue of TH would have stronger effects at the TH-VF level and fatigue of the index (I) finger would have stronger effects at the IF level. This

hypothesis was supported. Indeed, fatigue of the TH caused a reduction in the normal force of the TH and a simultaneous decline in the normal forces applied by the R and L fingers. On the other hand, fatigue of the index (I) finger decreased its normal force but had no overall effect on the total normal force applied by the VF. Similarly, TH fatigue caused a change in the point of wrench application for the TH as well as VF whereas fatigue of the index finger caused a change only for the VF. Our second hypothesis was also supported. Fatigue caused a drop in the MVC and the normal force applied by the exercised digit in the prehension task. Lastly, during fatigue, there was an increase in the vertical tangential force of the exercised digit. This was the most unexpected result. Therefore, our third hypothesis was not supported. The results on safety margin (SM) showed that the changes in the normal and tangential forces during fatigue significantly decreased the SM for *group-thumb* but had no effect on *group-index*.

Implications of fatigue for hierarchical control

Our results supported our second hypothesis. Fatigue of the I (index) finger did not induce large enough changes in the normal forces and point of wrench application of the VF that would have necessitated a simultaneous change in the output of the thumb. On the other hand, fatigue of the TH caused changes in the mechanical output of both the TH as well as the VF.

These results are not surprising. The normal forces applied by TH and VF have to be equal in magnitude and opposite in direction. Therefore, a change in the mechanical output of TH entails changes in the mechanical output of VF to satisfy the mechanics of the task. During fatigue of TH, changes in the normal and tangential force of TH were compensated by opposite changes in the output of VF. On the other hand, fatigue of the index (I) finger causes small changes in the normal force of the VF output and correspondingly requires small or no changes in the TH output. For *group-thumb* there was no effect of fatigue on the SM of the index(I) finger and there was no effect of fatigue on the SM of thumb for *group-index*. We also measured the SM for the M, R, and L (results not presented) digits for *group-index* and found no changes in their SM. These results indicate that the changes in the SM for the two groups were largely determined by the changes in the normal force of the TH and VF respectively.

Furthermore, a reduced safety margin (SM) for *group-thumb* indicates that the stability of the grasp was significantly compromised when TH was fatigued but not when the index (I) finger was fatigued. Taken together, the changes in the mechanical output during fatigue at the TH-VF level are critical to the stability of the grasp and that stability is significantly compromised during TH fatigue.

Fatigue of a digit triggers chain effects to maintain stable grasp

The total moment due to the forces applied by the digits to the handle (about Y_{handle}) can be represented as the sum of four components (two normal and two tangential) produced by the thumb and the VF (see Equation 5). In order to maintain a stable grasp without tilting the handle, a change in M_{TH}^N or M_{VF}^N could be directly compensated by a concomitant change in M_{VF}^T or M_{TH}^T respectively (see Equation 5) without initiating a change in M_{TH}^T and M_{VF}^T . However, our results showed changes in all four moment components.

Previous studies have shown a positive correlation between normal and tangential forces in grasping as well as pressing tasks (Flanagan et al. 1993; Burstedt et al. 1997; Zatsiorsky et al. 2005). Opposite changes of the normal and tangential forces produced by a digit have also been reported previously. For example, when the friction at the area of contact decreased, the normal force increased and the tangential force decreased (Niu et al. 2007). In

our study, the two forces also changed in opposite directions, the tangential forces increased during fatigue and the normal forces decreased. For *group-thumb*, during fatigue, the contribution of M_{TH}^N decreased because both $\|F_{TH}^Z\|$ and $\|r_{TH}^X\|$ decreased (see Figure 3A and Figure 5C). $\|M_{TH}^T\|$ increased because of the increased $\|F_{TH}^X\|$ (see *tangential forces*, Figure 3C). $\|F_{VF}^X\|$ decreased to counter the increase in $\|F_{TH}^X\|$, and therefore, the magnitude of the opposing counterclockwise moment M_{VF}^T decreased leading to an increase in the net clockwise moment. To counter this net increase in clockwise moment, the counterclockwise contribution of M_{VF}^N had to increase (M_{VF}^N was computed assuming that F_{TH}^Z was acting at r_{VF}). The controller accomplished this by decreasing F_R^Z and F_L^Z (a net decrease in F_{VF}^Z). Note that the R and L fingers exert a clockwise moment about Y_{handle} and when the magnitudes of these forces decreased, there was a net increase in counterclockwise moment. This chain strategy is illustrated in Figure 7A.

For *group-index*, during fatigue, $\|M_{TH}^N\|$ did not change significantly. The counterclockwise moment, $\|M_{VF}^T\|$ (lower panel, Figure 4D), increased because of the increase in $\|F_{VF}^X\|$ during fatigue. The clockwise moment M_{TH}^X decreased because of the decreased F_{TH}^X . Therefore, F_{VF}^Z had to produce a clockwise moment (M_{VF}^N) to oppose the net increase in the counterclockwise moment. Because there was no significant change in $\|F_{VF}^Z\|$ during fatigue, this was accomplished by a change in the moment arm, r_{VF}^X of F_{VF}^Z . For the zero-torque and SU conditions, $\|r_{VF}^X\|$ decreased while it increased for the PR torque condition (r_{VF}^X becomes more positive, $p < 0.05$). This chain strategy for *group-index* is illustrated in Figure 7B.

Modifying the lever arm of the normal component of the force (at the TH-VF level) to adjust for smaller normal forces and larger tangential forces during fatigue reflects a particular strategy by the controller to solve the problem of moment balance. When the controller was forced to adjust to the new levels of force during fatigue, it adapted by changing the moment arm of the VF normal force.

In the previous analysis we considered changes in the vertical tangential force of the exercised digit during fatigue as a direct, obligatory effect of fatigue. We started with an assumption that the fatiguing exercise for TH would only decrease the normal force applied by the exercised digit, then a decrease in $\|F_{TH}^Z\|$ should be balanced by a decrease in $\|F_{VF}^Z\|$ (at the TH-VF level) and $\Delta\|F_{VF}^Z\| \approx (\Delta\|F_I^Z\| + \Delta\|F_M^Z\|)/2 \approx (\Delta\|F_R^Z\| + \Delta\|F_L^Z\|)/2$ (at the IF level) to ensure that the force handle does not tilt. Similarly, for *group-index*, $\Delta\|F_I^Z\| \approx \Delta\|F_L^Z\| \approx 0.5 \times \Delta\|F_{TH}^Z\|$. However, the controller does not employ the above-mentioned strategy. We therefore conclude that a change in the vertical tangential force is a direct effect of fatigue rather than an adaptation to changes in other mechanical variables. This strategy would reduce the safety-margin (SM) but still ensure that a decrease in normal force does not compromise the orientation of the force handle.

Why do exercised digits produce higher shear force components?

One of the least trivial results was the concomitant increase in the tangential force of the exercised digits along with a decrease in the normal force during the static prehension trials. The changes in tangential forces of the exercised digit were not necessarily required to compensate for the decrease in the normal force of the exercised digit (see the Introduction and previous section). Note that in the present experiment, the normal force decreased even though its values during the prehensile task were far below the MVC forces produced by the

digits. A decrease in normal force during fatigue could be due to a combination of multiple factors: a) minimizing further fatigue (Johansson 1996) ; b) strain energy minimization (Pataky 2005; Williams et al. 2010); and c) mismatch in sense of effort and applied normal force during fatigue (Cain and Stevens 1971; Jones and Hunter 1983). Jones and Hunter showed that for the same sense of effort, the applied force decreases with time during a sustained contraction (our instruction to the participants was to apply a minimal effort to grasp the handle). However, the increase in tangential force exerted by the exercised digit cannot be explained by any of these three ideas.

We tested a hypothesis that the increase in the vertical tangential force was to maintain the moment-of-force contribution of the exercised digit opposing the external torque. The change in the moment-arms of $\mathbf{F}_{TH}^{X,Z}$ from the COM of the *handle* (O'A before-fatigue and O'A' during-fatigue in Figure 8) and $\mathbf{F}_{VF}^{X,Z}$ (O'B before-fatigue and O'B' during-fatigue) was computed. The average increase in the moment arm was ~26% ($p < 0.001$) for $\mathbf{F}_{TH}^{X,Z}$ and ~20% ($p < 0.05$) for $\mathbf{F}_{VF}^{X,Z}$. The increase in the moment arm about the COM of the *handle* was more than twice as large as the decrease in $\|\mathbf{F}_{TH}^{X,Z}\|$ and $\|\mathbf{F}_{VF}^{X,Z}\|$ (for the sake of brevity these data are not presented in the paper). A strategy to increase the moment arm during fatigue, could be a mechanically efficient compensatory strategy for the decrease in $\|\mathbf{F}_{TH}^{X,Z}\|$ and $\|\mathbf{F}_{VF}^{X,Z}\|$ and would assist in countering M_{Ext}^Y about Y_{handle} . However, this strategy would be effective only when $M_{Ext}^Y \geq 0$, but would be counterproductive when $M_{Ext}^Y < 0$, as the torque produced by $\mathbf{F}_{TH}^X$ is also negative. Our results showed that the $\|\mathbf{F}_{TH}^X\|$ increased even when $M_{Ext}^Y < 0$. Therefore, a biomechanical advantage in the form of an increase in moment-arm for $\mathbf{F}_{TH}^{X,Z}$ or $\mathbf{F}_{VF}^{X,Z}$ is perhaps not a potential control mechanism responsible for the increase in the tangential forces during fatigue. The increase in the tangential forces could be due to motor control and neurophysiological mechanisms that require further investigation.

Implications of fatigue for the principle of superposition

The principle of superposition (see the Introduction and Zatsiorsky et al. 2004) can be restated as- the commands for $\mathbf{F}_{VF}^Z$ and M_{VF}^N are uncorrelated and the effects of the two commands on individual digit forces are summed-up to maintain a stable grasp. Consistent with previous results (Shim et al. 2005), before fatigue, we found no significant Pearson correlation between $\mathbf{F}_{VF}^Z$ and M_{VF}^N ($R=0.04$, $p=0.37$, averaged over the three torque conditions) for both groups. A decrease in $\mathbf{F}_{VF}^Z$ during fatigue could be expected to have a 'proportional' effect on M_{VF}^N . For example, during TH fatigue, a decrease in $\|\mathbf{F}_{TH}^Z\|$ could be balanced by a decrease in $\|\mathbf{F}_{VF}^Z\|$ (at the TH-VF level). According to the *principle of superposition*, if $\mathbf{F}_{VF}^Z$ and M_{VF}^N remain independent, then across participants, $\|M_{VF}^N\|$ could increase, decrease or remain unchanged. However, fatigue of TH and I resulted in a consistent change in $\|M_{VF}^N\|$ as well as $\|M_{VF}^T\|$.

Furthermore, during fatigue, there was a decrease in the normal force, an increase in the tangential force component, changes in the point of wrench application of the digits, and changes in moments due to both normal and tangential forces. Fatigue triggered a chain reaction that required adjustments in both the slip prevention strategy as well as the tilt prevention strategy.

When participants are given enough resting time between trials to avoid fatigue, the *principle of superposition* has been shown to hold for a wide range of normal forces (Zatsiorsky et al. 2004). During fatigue, complex physiological changes interact with each other (Fuglevand 1996; Gandevia 2001; Gibson and Noakes 2004). Changes, such as a decrease in the gain of short and medium latency reflexes (Balestra et al. 1992); a decrease in muscle stiffness (Edman and Lou 1990; Zhang and Rymer 2001); changes in the activity of group III and IV afferents and the corresponding changes in the motor cortex activity (Martin et al. 2008); and an increase in motor unit synchronization (Bigland and Lippold 1954; Yao et al. 2000; Dartnall et al. 2008; Contessa et al. 2009) could interfere with the independence of the two commands posited by the principle of superposition and trigger a chain reaction to ensure that the handle maintains translational and rotational equilibrium.

The findings can be interpreted within the referent configuration hypothesis (Feldman 2009), which is a relatively recent development of the equilibrium-point hypothesis (Feldman 1966; Feldman 1986). According to the referent configuration hypothesis, the neural controller uses neural variables to set referent values for a relatively small group of task-specific, salient variables. The difference between those referent values and actual values of those variables leads to a chain of few-to-many mappings resulting in shifts of the tonic stretch reflex thresholds for all muscles that contribute to shifts of the actual to referent values of the salient variables. The hierarchical sequence of the few-to-many redundant mappings is organized in a synergic way (Latash 2010). This means that the relatively higher-dimensional sets of variables at the lower level co-vary from trial to trial to ensure relatively low variability of the few variables at the higher level.

Within this scheme, a change in physiological properties of some of the elements, for example as a result of fatigue, is expected to lead to adjustments in many elements that keep variability of salient performance variables relatively unchanged. Such changes may involve elements that contribute to different aspects of performance resulting in chain reactions. In other words, if one muscle (effector, digit) is fatigued and produces low force levels, other muscles will automatically re-distribute their forces to ensure that total force stays at an adequate level. Some of those muscles may contribute to other aspects of the performance, for example if they cross two joints or produce torques about two axes of rotation. This will lead to a chain effect: An adjustment of muscle forces to ensure that all salient performance variables associated with the task are kept at desired values.

In summary, we have shown that adaptations in the mechanical outputs of the exercised digit do not follow the principle of superposition. A chain reaction is triggered that apparently starts with increased tangential forces applied by the exercised digit. The increase in the tangential force and the decrease in the normal force resulted in the grasp being maintained closer to the threshold of slippage for *group-thumb*. It is possible that the grasp is maintained close to the slippage threshold during fatigue to increase the tactile feedback. The amplified tactile feedback could provide accurate information on the propensity of the handle to slip during fatigue (Westling and Johansson 1987; Haugland and Hoffer 1994), direction of the force vector (Edin et al. 1992) and free moments applied by the digits (Birznieks et al. 2010). Further investigation is required to understand the mechanisms responsible for the increase in the tangential components of the forces during fatigue.

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Figure 1.

A) A schematic representation of the force handle. The coordinate frames associated with the lab, $[XYZ]_{lab}$; handle, $[XYZ]_{handle}$; and individual sensors $[x'y'z']_i$ are shown. B) The fatiguing setup for the right thumb for *group-thumb*. C) The fatiguing setup for the right index finger for *group-index*. (Inset) The experimental setup along with the computer feedback of the coordinates of the handle in the XZ plane.

Maximum voluntary contraction (MVC) force produced by digits before and during fatigue for *group-thumb* and *group-index*.

Figure 2.

A) Maximal voluntary contraction force before and during fatigue for *group-thumb*. B) Maximal voluntary contraction force before and during fatigue for *group-index*. *, significant differences after Bonferroni correction ($p < 0.05$) between the before fatigue and during fatigue conditions. Mean data across the participants are shown with SE bars. TH, thumb; I, index; M, middle; R, ring; L, little finger.

Figure 3.

A) Normal force, F^Z , for the digits before and during fatigue for *group-thumb*. B) Normal force, F^Z , for the digits before and during fatigue for *group-index*. C) Vertical tangential force, F^X , for thumb before and during fatigue for *group-thumb*. D) Vertical tangential force, F^X , for thumb before and during fatigue for *group-index*. *, significant differences after Bonferroni correction ($p < 0.05$) between the before fatigue and during fatigue conditions. Mean data across the participants are shown with SE bars. The normal force values are averaged over the three torque conditions (pronation, 0 torque and supination). TH, thumb; I, index; M, middle; R, ring; L, little finger.

Figure 4.

A) Moment about Y_{handle} due to the normal forces ($\{M^N_{\text{TH+VF}}\}$, upper panel) and tangential forces ($\{M^T_{\text{TH+VF}}\}$, lower panel) applied by all the digits (TH, I, M, R, and L), before and during fatigue for *group-thumb*. B) Moment about Y_{handle} due to the normal forces ($\{M^N_{\text{TH+VF}}\}$, upper panel) and tangential forces ($\{M^T_{\text{TH+VF}}\}$, lower panel) applied by all the digits (TH, I, M, R, and L) M^N , before and during fatigue for *group-index*. C) Moment about Y_{handle} due to the normal forces ($\{M^N_{\text{VF}}\}$, upper panel) and tangential forces ($\{M^T_{\text{VF}}\}$, lower panel) applied by all the fingers (I, M, R, and L), M^T , before and during fatigue for *group-thumb*. D) Moment about Y_{handle} due to the normal forces ($\{M^N_{\text{VF}}\}$, upper panel) and tangential forces ($\{M^T_{\text{VF}}\}$, lower panel) applied by all the fingers (I, M, R, and L), M^T , before and during fatigue for *group-index*. *, significant differences after Bonferroni corrections ($p < 0.05$) between the before fatigue and during fatigue conditions. Mean data across the participants are shown with SE bars. The data are shown for the three torque conditions: pronation (PR); 0 torque (0); and supination (SU). Note the opposite changes in the two groups for both M^N and M^T .

Figure 5.

A) The X coordinate of the point of application of the resultant wrench for VF, r_{VF}^X , before and during fatigue for *group-thumb*. B) The X coordinate of the point of application of resultant wrench VF, r_{VF}^X , before and during fatigue for *group-index*. C) The X coordinate of the point of application of the resultant wrench for TH, r_{TH}^X , before and during fatigue for *group-thumb*. D) The Y coordinates of the point of application of the resultant wrench for TH, r_{TH}^Y , before and during fatigue for *group-thumb*. *, significant differences after Bonferroni correction ($p < 0.05$) between the before fatigue and during fatigue conditions. Mean data across the participants are shown with SE bars. The data are shown for the three torque conditions: pronation (PR); 0 torque (O); and supination (SU). Note the opposite changes in the two groups for r_{VF}^X (panels A and B).

Figure 6.

A) The Z-transformed Safety Margin (SM) for thumb, before and during fatigue for *group-thumb*. B) The Z-transformed Safety Margin (SM) for index, before and during fatigue for *group-index*. *, significant differences ($P < 0.05$) between the before fatigue and during fatigue conditions. Mean data across the participants are shown with SE bars. The data are shown for the three torque conditions: pronation (PR); 0 torque (O); and supination (SU). Note the significant decrease in SM for *group-thumb*.

Schematic representation of changes to the applied force vector during fatigue for *group-thumb* and *group-index*.

Figure 7.

Shows the chain mechanisms employed by the controller to ensure static equilibrium of the handle during fatigue. The light grey arrows show a decrease in the magnitude of the output variable during fatigue. The dark grey arrows imply an increase in the magnitude of the output variable during fatigue. A) For *group-thumb*, first there is a decrease in F_{TH}^Z but this decrease does not have a large effect on the moment about Y_{handle} ; then an increase in F_{TH}^X increases the clockwise moment about Y_{handle} ; a compensatory decrease in F_I^X , F_R^X and F_L^X to prevent the handle from translating in the X direction also contributes to an increase in the clockwise moment about Y_{handle} ; to prevent the handle from translating in the Z direction and to counter the clockwise moment, F_R^Z and F_L^Z decrease simultaneously to decrease the clockwise moment provided by them. B) For *group-index*, F_I^Z decreases significantly but there is no overall change in F_{VF}^Z and consequently in F_{TH}^Z , F_I^X increases and also increases the counter clockwise moment about Y_{handle} ; to compensate for the increase in F_I^X and to prevent the handle from translating in the X direction, F_{TH}^X decreases and this decrease also contributes to an increase in the counterclockwise moment about Y_{handle} ; to prevent the handle from rotating in the counterclockwise direction, the only strategy the controller can adopt is to change the moment arm of the application of F_{VF}^Z (bold black arrow).

Projection of the force vectors in the XZ plane

Figure 8.

Schematic projection of F_{TH} and F_{VF} in the XZ plane before (black arrows) and during fatigue (grey arrows). O is the geometrical center of the prehension handle and O' is the COM of the handle. $O'A$ is the moment arm of $F_{TH}^{X,Z}$ about the COM before fatigue and $O'A'$ is the moment arm during fatigue. The point of application of $F_{TH}^{X,Z}$, $r_{TH}^{X,Z}$, and $F_{VF}^{X,Z}$, $r_{VF}^{X,Z}$, has been shown in the figure based on the average values across participants.