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Prehension synergies during fatigue of a single digit: Adaptations in control with referent configurations

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Abstract

The purpose of the current study was to investigate the effects of exercise-induced fatigue of a digit on prehension synergies in a static precision grasp. One group of participants performed the fatiguing exercise using the thumb (*group-thumb*) and the second group performed the exercise using the index finger (*group-index*). Our first hypothesis was that fatigue would trigger changes in the co-variation of forces and moments of force that violate the principle of superposition. This hypothesis was not confirmed. The second hypothesis was that indices of force stabilizing synergies during fatigue would increase at both levels of the hierarchy. This hypothesis was partially confirmed only for *group-index*. The last hypothesis was that fatigue of TH would have stronger effects at the TH-VF level while fatigue of the index finger would have stronger effects at the IF level. This hypothesis was also partially confirmed.

Keywords

fatigue; hand; synergy; prehension; hierarchical control; principle of superposition; precision grasps

Introduction

Precision grasping (or prehension) tasks in humans are performed by the opposing action of the thumb (TH) and virtual finger (VF) (Iberall, Torras, & MacKenzie, 1991; MacKenzie & Iberall, 1994; Napier, 1956; Zatsiorsky & Latash, 2008). These tasks have been viewed as being controlled by a two-level hypothetical control hierarchy (Arbib, Iberall, & Lyons, 1985; Baud-Bovy & Soechting, 2001; Zatsiorsky & Latash, 2004). At the upper level (TH–VF level), the action is shared between the actions of the thumb and a virtual finger (VF), an imaginary digit with its mechanical action equal to the combined output of the four fingers combined. At the individual finger (IF) level (lower level), the VF action is shared among the fingers.

Previous studies on exercise induced muscle fatigue have shown an increase in motor variability (Enoka & Stuart, 1992; Singh, SKM, Zatsiorsky, & Latash, 2010b) and altered motor coordination (Côté, Mathieu, Levin, & Feldman, 2002; Forestier & Nougier, 1998; Missenard, Mottet, & Perrey, 2008). Some studies have shown that in motor tasks that involve a redundant set of elements, the goal-relevant features of performance are relatively preserved during fatigue (Gates & Dingwell, 2008; HufFenus, Amarantini, & Forestier, 2006). We have also shown this to be true in accurate force production tasks (Park, Singh, Zatsiorsky, & Latash, 2012; Singh et al., 2010b; Singh, Zatsiorsky, & Latash, 2012). In the current study, we investigated the effects of exercise-induced fatigue of a single digit on motor variability and digit coordination in a static prehension task.

Prehension tasks are redundant with respect to the resultant force and moments of force (wrenches) exerted on the grasped object. We analyze such tasks using the notion of *synergies*, defined as neural organizations that ensure high stability (low variability) of important performance variables (total force or moment) by co-variation of elemental variables, the digit forces and moments (reviewed in Latash, Scholz, & Schöner, 2007). Synergies have been quantified using the framework of the uncontrolled manifold (UCM) hypothesis (Scholz & Schöner, 1999). According to the UCM hypothesis, the neural controller acts in a space of elemental variables and organizes in that space a subspace (UCM) corresponding to a desired value of a performance variable. The controller limits the variance of the elemental variables orthogonal to the UCM (V_{ORT}) while allowing relatively large variance within the UCM (V_{UCM}).

Multi-finger prehension in humans obeys the principle of superposition according to which 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”), respectively (Zatsiorsky, Latash, Gao, & Shim, 2004). The principle has been shown to hold in a variety of experimental conditions (Ambike, Paclet, Latash, & Zatsiorsky, 2013; Niu, Latash, & Zatsiorsky, 2012; Robertson & Johnston, 2012; Shim, Latash, & Zatsiorsky, 2005b). In a recently published paper (Singh, Zatsiorsky, & Latash, 2013) we showed that adaptations to fatigue of a single digit violate the principle of superposition. The purpose of that paper was to investigate the changes in the average across trials values of the forces and moments of force. We showed that fatigue triggered a chain reaction that involved simultaneous changes in the average magnitudes of forces and moments of force produced by individual digits leading to a violation of the principle of superposition. For the current report (same data set as Singh et al., 2013), we were interested in examining the trial-by-trial variability of the forces and moments of force and we hypothesized that fatigue would also trigger concurrent changes in the co-variation of these mechanical variables such that the principle of superposition would be violated. In other words, synergies stabilizing forces and moments of force acting on the handle would show correlated changes during fatigue.

At the TH-VF level, it can be expected that if one of the elements (TH or VF) is weakened due to fatigue and produces lower force, then the other element has to provide mechanical compensation to ensure that the grasped object remains in static equilibrium (Gorniak, Zatsiorsky, & Latash, 2009; Shim, Latash, & Zatsiorsky, 2005a). In contrast, fatigue of only

one finger may have little effect on the variability of the total output of the VF (Singh et al., 2010b). In fact, our previous studies have shown a fatigue-induced increase in force stabilizing synergies during accurate force production tasks when the index finger was fatigued (Park et al., 2012; Singh et al., 2010b). Based on these results, we expected that synergies stabilizing task-related performance variables in prehension tasks would become stronger during fatigue and lead to a larger increase in V_{UCM} compared to V_{ORT} (the second hypothesis).

The third hypothesis was that fatigue of TH would have stronger effects at the TH-VF level while fatigue of the index finger would have stronger effects at the IF level. The rationale for the last hypothesis was that 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 shown that fatigue of the index finger increases the force stabilizing synergies in an accurate force production task with the four fingers (Singh et al., 2010b). Therefore, we expected that fatigue of the index finger would also increase force stabilizing synergies at the IF level in a prehension task.

Methods

The data collected for our publication (Singh et al., 2013) was reanalyzed for this study to quantify trial-by-trial variability and synergies. 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 (*group-index*) exercises. 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 signed informed consent based on the procedures approved by the Office for Research Protection of The Pennsylvania State University, University Park, PA.

Prehension Setup—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. These sensors were attached to an aluminum handle (see Figure 1A). The total mass of the handle and five Nano 17 sensors was 0.2 kg. An aluminum beam was attached to 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 apply an external torque about the coronal axis (see Figure 1A). The external load was suspended from the beam at three different locations providing a pronation-torque (PR), supination-torque (SU) and zero-torque (0) about the geometrical center of the handle +sensors setup. Our previous studies have shown that synergy indices for the grip force and

moment are affected by the applied external torque (Shim et al., 2005b; Sun, Park, Zatsiorsky, & Latash, 2011). Therefore, we were interested in finding if synergy indices for the grip force (F^Z) and moment (M^Y) would be sensitive to an interaction between the fatigued digit and pronation/supination torque though no specific hypothesis were formulated in this regard (see Figure 1D).

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. *Group-index* performed a fatiguing exercise on the setup shown in Figure 1C.

Procedures

Before the participants performed the precision grasp trials, we measured the maximum force (MVC) of all the digits. 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. The drop in MVC during fatigue was used as a measure of fatigue (Vøllestad, 1997).

During the experiment, the participants sat on a chair facing a computer screen that gave them feedback of the position of the force handle in the XZ plane of the laboratory (see inset of Figure 1). The details of the procedures are provided in Singh et al. (2013) and won't be repeated here. In summary, for the before fatigue condition, four *sub-trials* (5 s each) were performed within a trial (total 5 trials) for a total of 20 *sub-trials* for each torque condition (PR, 0 and SU). After the completion of the before fatigue trials, a 5–10 min rest was given to the participants. Then *group-thumb* performed a one-minute fatiguing exercise at MVC on the setup shown in Figure 1B and *group-index* performed a one-minute fatiguing exercise (also at MVC) on the setup shown in Figure 1C. After the fatiguing exercise, participants performed the MVC trials for all the digits. The participants performed the during fatigue trials in the same order as the before fatigue trials and a 20 s long fatiguing exercise was performed by the participant between every trial. Data were sampled at 50 Hz.

Kinetics—We performed kinetic analysis at two levels of the hierarchy. At the IF level, the wrenches and the points of applications of those wrenches were transformed from the local sensor based coordinates to handle based coordinates. At the TH-VF level, we vectorially summed the wrenches applied by the I, M, R, and L fingers to produce the net VF wrench (also in the handle based coordinates). We performed force and moment balance computations in the handle based frame of reference to obtain the point of application of the resultant VF wrench $\mathbf{r}_{VF}(\mathbf{r}_{VF}^X, \mathbf{r}_{VF}^Y, -0.025 \text{ m})$. The location of the surfaces of the ATI-sensors along the z-axis of the handle frame of reference was at -0.025 m (for the fingers) and 0.025 m (for the thumb). The magnitude of this distance is denoted as 'd' in Figure 1D.

For planar analysis, there are three equations of statics at the TH-VF level that need to be satisfied (also see Figure 1D):

$$\mathbf{F}_{TH}^X + \mathbf{F}_{VF}^X = \mathbf{F}(G) \quad (1)$$

$$F_{TH}^Z - F_{VF}^Z = 0 \quad (2)$$

$$\left\{ -d \times F_{TH}^X + r_{TH}^X \times F_{TH}^Z \right\} + \left\{ d \times F_{VF}^X + r_{VF}^Z \times F_{VF}^Z \right\} + M_{EXT}^Y = M_{TH}^Y + M_{VF}^Y + M_{EXT}^Y = 0 \quad (3)$$

Variance and synergy analyses—Variance analyses were performed at two levels of the assumed control hierarchy: the thumb- virtual finger level (TH-VF level); and the individual finger level (IF level). At the TH-VF level, the outputs of the TH and VF are viewed as elemental variables that produce mechanical action on the handle and keep the handle in static equilibrium. At the IF level, the outputs of each individual finger within the VF are elemental variables that produce the output of the VF (performance variable). At the TH-VF level, the trial-to-trial variability of the mechanical variables produced by the thumb and VF was analyzed using the uncontrolled manifold (UCM) hypothesis (Scholz & Schöner, 1999). The trial-to-trial variance in the elemental variables was divided into two components, within a subspace (V_{UCM} within the UCM) where the selected performance variable does not change and within the orthogonal complement to the UCM (V_{ORT}). Comparing the two components of the variance produces an index of variance (V , equation 4) that is compatible with stabilization of the performance variable. In equation 4, m represents F^X , F^Y , F^Z , and M^Y . UCM analysis was performed for each dependent variable (F^X , F^Y , F^Z , and M^Y) separately. $V > 1$ implies a presence of synergy, and $V \leq 1$ implies no synergy.

$$\Delta V(m) = \frac{V_{UCM}}{V_{ORT}} \quad (4)$$

Since $F_{TH}^X + F_{VF}^X = F(G)$ and $F_{TH}^Z = F_{VF}^Z$ (see equations 1 and 2), the Jacobians for the two equations would be $[1 \ 1]$ and $[1 \ -1]$ respectively. This implies that negative co-variation (on a trial-by-trial basis) between the vertical tangential forces would lead to $V(F^X) > 1$ and positive co-variation between normal forces would lead to $V(F^Z) > 1$. The Jacobians for the horizontal tangential force ($F_{TH}^Y + F_{VF}^Y = 0$, $J = [1 \ 1]$) and M^Y ($M_{TH}^Y + M_{VF}^Y = M^Y$, $J = [1 \ 1]$) are the same. The basis vectors of the null space of the Jacobian span the UCM.

At the IF level, V_{UCM} , V_{ORT} and V were computed in a similar way. For example, the Jacobian for the normal force was $J = [1 \ 1 \ 1 \ 1]$ since $F_I^Z + F_M^Z + F_R^Z + F_L^Z = F_{VF}^Z$. The other Jacobians were computed in a similar fashion. An index of synergy was computed (also using equation 4). Note that the limited independence of individual fingers in force

production (enslaving, (Danion et al., 2003; Zatsiorsky, Li, & Latash, 1998) was ignored in the analysis.

Data Processing and 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), *Torque* (PR, 0, SU) and *Group* (group-thumb and group-index as levels) as the fixed-factors; and *Participants* as a random factor; PR stands for pronation, 0 for zero-torque and SU for supination torque conditions. *Participants* were nested within the factor *Group*. 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 exercise of the thumb and index finger led to statistically different effects. A linear-mixed model for repeated measures (RM) was fit to the data. For multiple comparisons, Bonferroni's correction was used. The level of significance was chosen at $\alpha=0.05$. The effects of the factor *Torque* were significant for almost all the reported kinetic variables ($\sim p<0.001$). Since effects of the main effect of *Torque* are not crucial for testing the three hypotheses, the statistical effects of *Torque* are not enumerated in Results.

Results

Fatigue induced a significant drop in the MVC of the digits. The MVC results are described in detail in the previous paper (Singh et al., 2013). In summary, MVC of the exercised as well as non-exercised digits decreased during fatigue. For *group-thumb*, MVC of the thumb (TH), index (I), middle (M) and ring (R) fingers dropped during fatigue. Similarly, for *group-index*, MVC of the I, M and R fingers decreased during fatigue.

Further, this section has been structured in the following way. First we discuss the effects of fatigue on the variance of the forces and moments produced at the TH-VF and IF levels. Next, we discuss how fatigue affects projections of the variance onto the uncontrolled manifold (V_{UCM}) and the orthogonal space (V_{ORT}) computed for specific performance variables (resultant forces and moments). Following that, we present the relative changes in V_{UCM} and V_{ORT} ($V = V_{UCM}/V_{ORT}$) during fatigue. This sequence is repeated for the analyses performed at the TH-VF and IF levels.

Effects of fatigue on variance of forces and moments

At the TH-VF level, fatigue increased the variance of the tangential forces for the thumb and VF for both the groups. The variance of the load-resisting force, $\text{Var}(F_{TH}^X)$, increased by about 50% for *group-thumb* during fatigue and by $\sim 10\%$ for *group-index* (see Figure 2A). For the horizontal tangential force, fatigue increased $\text{Var}(F_{TH}^Y)$ for both the groups but a significant change was only seen in *group-thumb* (increase by $\sim 66\%$, see Figure 2C). These effects were confirmed by the three-way RM ANOVA *Fatigue* $\times$ *Group* $\times$ *Torque* (see Table A of the Appendix). The statistical results were very similar for $\text{Var}(F_{VF}^X) \sim \text{Var}(F_{TH}^X)$, and $\text{Var}(F_{TH}^Y) \sim \text{Var}(F_{VF}^Y)$, with the same main and interaction effects. In contrast, there were no

effects of fatigue on the variance of the grip (normal) forces, $\text{Var}(F_{\text{TH}}^Z)$ (see Figure 2B) and $\text{Var}(F_{\text{VF}}^Z)$.

Fatigue had no effect on the variance of the total moment applied by the thumb, $\text{Var}(M_{\text{TH}}^Y)$ but the total moment applied by the VF, $\text{Var}(M_{\text{VF}}^Y)$, increased by ~45% (see Figure 2D and Table A in the Appendix for statistical results). $\text{Var}(M_{\text{VF}}^Y)$ was further decomposed into variance due to grip (F^Z) and load-resisting (F^X) VF forces. The variance of the moment due to the VF grip force, $\text{Var}(M_{\text{VF},F^Z}^Y)$ increased during fatigue by ~35% (also see equations 5–7; $p < 0.05$). The variance of the moment due to the VF load force, $\text{Var}(M_{\text{VF},F^X}^Y)$ also increased during fatigue and the statistical results for $\text{Var}(M_{\text{VF},F^X}^Y)$ were similar to those for $\text{Var}(F_{\text{VF}}^X)$ (it is expected because the moment arm 'd' is constant).

$$M_{\text{VF}}^Y = M_{\text{VF},F^X}^Y + M_{\text{VF},F^Z}^Y \quad (5)$$

$$M_{\text{VF},F^X}^Y = d \sum_i^{I,M,R,L} F_i^X \quad (6)$$

$$M_{\text{VF},F^Z}^Y = \sum_i^{I,M,R,L} M_{i,F^Z}^Y = \sum_i^{I,M,R,L} r_i^{X,Y} - 0.025 F_i^Z \quad (7)$$

Only a few significant effects of fatigue on the variance indices for individual finger forces and moments were found. There was a main effects of fatigue on $\text{Var}(F^Y)$. In particular, $\text{Var}(F_M^Y)$ increased by ~59% ($p < 0.05$). There was no significant effect of fatigue on any of the other variables.

Effects of fatigue on variance components (V_{UCM} and V_{ORT}) and synergy indices (V) at the TH-VF level

At the TH-VF level, fatigue only affected one of the variance components (V_{ORT}) of the load-resisting force (F^X) and grip force (F^Z). For F^X , fatigue had no effect on V_{UCM} (see Figure 3A) but increased V_{ORT} by ~84% (see Figure 3B). The changes in V_{ORT} were in opposite directions for the two groups (confirmed by a *Fatigue* x *Group* interaction, see Table A in the Appendix). V_{ORT} increased for *group-thumb* by ~350% but decreased for *group-index* by ~45% during fatigue. Fatigue also had dissimilar effects on the variance components of F^Z at the TH-VF level for the two groups: Fatigue increased V_{ORT} for *group-thumb* by ~115% and had no significant effect on *group-index* (see Figure 3D and Table A in the Appendix). There were no effects of fatigue on $V_{\text{UCM}}(F^Z)$ (see Figure 3C).

We also computed changes in the variance components of the total moment in the grasp plane (M^Y). At the TH-VF level, before fatigue $V_{UCM}(M^Y)$ was greater than $V_{ORT}(M^Y)$ by ~375% ($p < 0.001$, see Figures 4A and 4B). *Fatigue* did not have a significant effect on $V_{UCM}(M^Y)$ but $V_{ORT}(M^Y)$ increased by ~70% (on average, across both groups). Specifically, for *group-thumb*, *Fatigue* increased $V_{ORT}(M^Y)$ by ~150% and for *group-index* by a miniscule ~4.5% (statistical results are shown in table A of the Appendix). Post-hoc tests following a *Fatigue* $\times$ *Group* interaction for M^Y revealed that the change in $V_{ORT}(M^Y)$ for *group-index* was not significant.

Before fatigue, synergies stabilized F^X (load-resisting), F^Y (horizontal tangential) and F^Z (grip) at the TH-VF level ($V > 1$). The increase in V_{ORT} for F^X and F^Z during fatigue affected the index of synergy, V . Synergy indices for F^X and F^Z at the TH-VF level are shown in Figure 5 (panels A and B respectively). *Fatigue* decreased $V(F^X)$ for *group-thumb* (~43%) and seemed to slightly increase it for *group-index* (~2.7%, $p = 0.1$). (Table A in the Appendix shows the *Fatigue* $\times$ *Group* and other interactions for $V(F^X)$). Post-hoc tests following a *Fatigue* $\times$ *Group* interaction showed that $V(F^Z)$ decreased by 30% for *group-thumb* and showed no significant change for *group-index* during fatigue (see Table A of the Appendix). Lastly, $V(M^Y)$ seemed to decrease during fatigue (Figure 4C) but *Fatigue* did not have a significant effect.

Effects of fatigue on variance components (V_{UCM} and V_{ORT}) and synergy indices (V) at the IF level

In contrast to the effects at the TH-VF level, where indices of synergies stabilizing the load force ($V(F^X)$) and the grip force ($V(F^Z)$) changed, at the IF level, fatigue affected the variance indices of the tangential forces, F^X and F^Y but not the normal force, F^Z .

For *group-thumb*, fatigue increased $V_{ORT}(F^X)$ by ~72% and for *group-index* by ~16%. These differences were confirmed by the three-way RM ANOVAs that showed a *Fatigue* $\times$ *Group* interaction (see Table A of the Appendix). *Fatigue* also increased $V_{UCM}(F^Y)$ (~35%, see Table A for statistical results) and the increase was similar for the two groups. These changes in $V_{ORT}(F^X)$ and $V_{UCM}(F^Y)$ were reflected in $V(F^X)$ and $V(F^Y)$ respectively (see Figures 5C and 5D). Post-hoc tests following a *Fatigue* $\times$ *Group* interaction showed that fatigue decreased $V(F^X)$ for *group-thumb* by ~39% and showed no significant effects for *group-index* (Table A of the Appendix). Post-hoc tests also showed that fatigue increased $V(F^Y)$ for *group-index* by ~70% and showed no significant change for *group-thumb* (see statistical results in Table A). Lastly, there were no effects of fatigue on the indices of synergy for F^Z and M_{VF}^Y at the IF level.

In summary, fatigue of the thumb caused a statistically significant decrease in the indices of force-stabilizing synergies $V(F^X)$ and $V(F^Z)$ at the TH-VF level, and $V(F^X)$ at the IF level. Fatigue of the index finger seemed to increase $V(F^X)$ ($p = 0.1$) at the TH-VF level, and caused a statistically significant increase in $V(F^Y)$ at the IF level. These results are summarized in Table 1.

Discussion

The main purpose of the current study was to investigate how the central nervous system (CNS) adapts to fatigue of one of the digits, the thumb or the index finger, to organize force and moment stabilizing synergies at the two levels of a hypothetical control hierarchy involved in static prehensile tasks. Within the proposed hierarchy, at the TH-VF (upper) level the task is distributed between the thumb and the hypothetical virtual finger (VF). At the IF (lower) level, the VF output is distributed among the individual digits that constitute the VF. The participants in our study performed the prehension trials at moderate forces, ~15–20% of MVC, so even though the effects of the fatiguing exercise spilled over to non-exercised digits during the MVC tasks, the effects were more local during the prehension trials. For example, the average normal and tangential forces during the prehension trials showed changes only for the exercised digit and an equivalent mechanical compensation by the non-exercised digits (see Figures 3 and 4 in Singh et al., 2013).

Our first hypothesis for the current paper was that that fatigue would trigger changes in the co-variation of forces and moments of force such that the principle of superposition would be violated. This hypothesis has been rejected (explained in the next subsection of the Discussion). Our second hypothesis was that the indices of force stabilizing synergies would increase at both levels of the hierarchy. This was partially confirmed for *group-index* but not for *group-thumb*. For *group-index*, $V(F^X)$ seemed to increase at the TH-VF level and $V(F^Y)$ increased significantly at the IF level.

Our third hypothesis was that fatigue of TH would have stronger effects at the TH-VF level while fatigue of the index finger would have stronger effects at the IF level. The effects of thumb fatigue were indeed stronger at the TH-VF level, and fatigue of the index finger produced larger changes in $V(F^Y)$ at the IF level. In addition, the *Fatigue x Group* interaction was significant for many of the variables of interest (see Table A of the Appendix) indicating that these two fatigue protocols had different effects on the force and moment stabilizing synergies. However, the *Fatigue x Group* interactions were not consistent for all the variables at the IF level (e.g. $V(F^X)$, Figure 5C). Therefore, the third hypothesis was partially confirmed.

The first three subsections of the Discussion address the effects of fatigue on the variances of the applied forces and moments by the digits. Within these subsections, we discuss the principle of superposition (first hypothesis) and the unexpected increase in the variance of the load-resisting forces and horizontal tangential forces. This is followed by a discussion on the effects of fatigue on the variance components (V_{UCM} and V_{ORT}) and the index of synergy (V) for the different mechanical variables (second hypothesis). We have not discussed the third hypothesis further because this hypothesis was confirmed (with the exception of $V(F^X)$). Lastly, we did not find *Fatigue x Torque* interaction effects for the normal force (F^Z) and the moment (M^Y) stabilizing synergies (see Table A of the Appendix). Therefore, we have not discussed the effects of *Torque* in the Discussion.

Implications of synergic adaptations to fatigue on the principle of superposition

In the previous paper (Singh et al., 2013) we have shown that the mechanical adaptations to changes in the force and moment output of the digits do not follow the principle of superposition (Arimoto, 2004; Zatsiorsky & Latash, 2008; Zatsiorsky et al., 2004) during fatigue. Fatigue interferes with the independence of the two commands posited by the principle of superposition and triggers a chain reaction to ensure that the handle is maintained in translational and rotational equilibrium. In other words, before fatigue $\|\mathbf{F}_{VF}^Z\|$ and $\|\mathbf{M}_{VF, FZ}^Y\|$ were uncorrelated but they showed correlated changes during fatigue (where $\|\|$ implies average value of the variable and $\mathbf{M}_{VF, FZ}^Y = \sum_i^{I, M, R, L} \mathbf{r}_i^{X, Y} \cdot -0.025 \mathbf{F}_i^Z$).

Another aspect of the principle of superposition is that the variances and synergies stabilizing the applied forces and moments by the digits are independent. An extension of the principle of superposition in this context can be explicitly stated as: Synergies stabilizing the resultant normal force ($\mathbf{F}_{VF}^Z$) and moments of normal force ($\mathbf{M}_{VF, FZ}^Y$) are relatively independent.

Our results in the current paper showed that fatigue increased $\text{Var}(\mathbf{M}_{VF}^Y)$ by ~45%, $\text{Var}(\mathbf{M}_{VF, FZ}^Y)$ by ~35%, and the area of the point of wrench application of the VF by ~36%.

The point of the net wrench application was computed for each sub-trial at the VF level. A 95% confidence ellipse was plotted around the 20 points obtained from the 20 *sub-trials* for each condition using principal component analysis (PCA). The parameters of the ellipse were obtained using direct least squares and then the area of the ellipse was computed from the parameters (see Figure 6). In contrast to the changes in $\text{Var}(\mathbf{M}_{VF}^Y)$, $\text{Var}(\mathbf{M}_{VF, FZ}^Y)$, and the area of the point of wrench application, $\text{Var}(\mathbf{F}_{VF}^Z)$ did not change during fatigue. Therefore, the increase in $\text{Var}(\mathbf{M}_{VF}^Y)$ could be mainly attributed to the participants exploring a larger solution space for the point of VF wrench application ($\mathbf{r}_{VF}^X, \mathbf{r}_{VF}^Y, -0.025 \text{ m}$) during fatigue.

Synergy indices for $\mathbf{F}^Z$ and the contribution of $\mathbf{F}^Z$ to the total VF moment, $\mathbf{M}_{VF, FZ}^Y$, were not affected by fatigue at the IF level and therefore do not provide enough evidence to claim that the synergies stabilizing the two variables are indeed independent. However, the uncorrelated changes between $\text{Var}(\mathbf{M}_{VF, FZ}^Y)$ and $\text{Var}(\mathbf{F}_{VF}^Z)$ indicate that the variances of these two variables are affected by independent mechanisms. Contrary to the results from the previous paper (Singh et al., 2013), the current results provide some support for the principle of superposition. Therefore, our first hypothesis was rejected and we conclude that the principle of superposition was preserved for synergies stabilizing the applied forces and moments by the digits.

These seemingly contradictory results from the two papers can be interpreted within a control scheme that has been proposed earlier with two groups of neural variables (Latash,

Shim, Smilga, & Zatsiorsky, 2005). The first group (NV_1) specifies the desired values (seen in average across trials values, vector μ) for elemental variables contributing to a performance variable. The second group (NV_2) specifies the synergies (via the matrix $[\sigma]$ of gains in the back-coupling loops) that may or may not stabilize that performance variable (see Figure 7A). NV_1 and NV_2 may or may not be adjusted independently. The results from our study suggest that these two neural variables for forces and moments of force may be affected by fatigue differently and perhaps independently. Fatigue has a coupled effect on the NV_1 s of performance variables $\|F_{VF}^Z\|$ and $\|M_{VF,F}^Y\|$ (Singh et al., 2013) but it affects NV_2 s of these performance variables independently (current paper).

Fatigue, physiological tremor and the referent configuration hypothesis

Our computations of the synergy indices rely on the assumption that the handle was maintained in static equilibrium. During fatigue, it was very difficult for the participants to maintain the handle in equilibrium. Indeed, kinematic deviations (measured using a Polhemus electromagnetic device at 50 Hz) of the handle from the mean position (within a trial and across trials) along the X (vertical) and Z (normal) increased during fatigue. The root mean square deviations of the handle position increased by $\sim 28\%$ (0.9 ± 0.04 to 1.16 ± 0.06 mm, $p < 0.001$) and by $\sim 26\%$ (1.05 ± 0.07 to 1.33 ± 0.07 mm, $p < 0.001$) along the two directions respectively during fatigue. It is likely that physiological tremor increased during fatigue (Halliday, Conway, Farmer, & Rosenburg, 1999) and significantly contributed to an increase in kinematic deviations. Physiological tremor is primarily due to central oscillations in the 8–12 Hz bandwidth but has a substantial contribution from peripheral reflex loops (Hallett, 1998; Lippold, 1970; McAuley & Marsden, 2000). Studies have shown an increase in the power of the EMG signals in the tremor band during fatigue (Allum, Dietz, & Freund, 1978; Kattla & Lowery, 2010) and this increase in power could be attributed to stronger peripheral afferent input to the α -motoneuronal pool (Creswell & Löscher, 2000). In fact, direct effects of fatigue are predominantly seen in peripheral structures such as muscles and reflex loops (Balestra, Duchateau, & Hainaut, 1992; Duchateau & Hainaut, 1993; Gerard & Forbes, 1928; Taylor, Butler, & Gandevia, 2000; Zhang & Rymer, 2001).

The effects of fatigue on physiological tremor and synergies can be interpreted within the framework of the referent configuration hypothesis (Feldman & Levin, 2009; Latash, 2010a, 2010b). Control with referent configurations leads to synergies at the TH-VF level of the hierarchy (Latash, 2010a). Consider grasping an object with two opposing digits (see Figure 7B). According to the referent configuration hypothesis, this action is associated with setting a referent aperture (AP_{REF}) between the digits (Pilon, De Serres, & Feldman, 2007) that is smaller than the actual aperture ($AP_{REF} < AP_{ACT}$). The rigid object does not allow the digits to move to AP_{REF} . As a result, the difference between AP_{ACT} and AP_{REF} leads to active grip force production.

If the object has to be maintained in static translational equilibrium, the forces produced by the opposing effectors (TH and VF) should be equal in magnitude (i.e. AP_{CTR} , the coordinates of the center of AP_{REF} should coincide with the geometrical center of the handle). Changes in AP_{CTR} about the center of the handle would produce changes in the

resultant force and cause the handle to translate. Therefore, setting AP_{REF} and AP_{CTR} together is expected to satisfy equation 2, while the forces produced by each of the digits may differ across trials (positive co-variation of normal forces).

The increase in physiological tremor during fatigue could cause unintended fluctuations in AP_{CTR} that could result in an increase in kinematic deviations of the handle. The relatively small changes in $Var(F_{TH}^Z)$ and $Var(F_{VF}^Z)$ indicate that the controller perhaps minimized the variance in AP_{REF} to compensate for the kinematic instability (fluctuations in AP_{CTR}) when it was faced an increase in physiological tremor during fatigue. Therefore, this is expected to lead to no major changes in variance of the grip forces and indices of grip-force stabilizing synergies during fatigue. Our results show that this was indeed the case.

Increase in variance of tangential forces during fatigue could be due to a higher reliance on tactile feedback to maintain a stable grasp during fatigue

In the previous section, we showed that the controller could minimize the variances of the normal forces during fatigue to minimize the undesirable effects of increased physiological tremor. In addition, our results showed that the variance of the vertical tangential forces (F_{TH}^X and F_{VF}^X) and horizontal tangential forces (F_{TH}^Y and F_{VF}^Y) increased during fatigue.

This was also accompanied by a decrease in the average grip force and an increase in the average magnitude of the load force and horizontal tangential force of the fatigued digit (Singh et al., 2013). The decrease in the average grip force and increase in load force would reduce the safety margin. Safety margin is defined as the difference between the minimal grip force to prevent slipping and the employed grip force (Westling & Johansson, 1984). One possibility is that the decreased safety margin and increased trial-by-trial variance of tangential forces during fatigue could be a strategy employed by the controller to increase the feedback from tactile afferents. The tactile afferents encode information on slip (Haugland & Hoffer, 1994; Westling & Johansson, 1987); direction of fingertip force vector (Edin, Westling, & Johansson, 1992; Johansson, 1996) and even friction (Farfán, Albarracín, & Felice, 2013). An increase in tactile feedback would be crucial for decreasing $\|F^Z\|$ in a controlled fashion to minimize energy expenditure during fatigue and at the same time maintain a sufficient, albeit reduced, safety margin to prevent the handle from slipping.

Adaptive changes in the structure of variance at the two levels of the hierarchy

We expected the adaptations to fatigue to be consistent with our previous studies where both V_{UCM} and V_{ORT} increased in accurate force production tasks during fatigue with V_{UCM} showing a larger increase (Park et al., 2012; Singh, SKM, Zatsiorsky, & Latash, 2010a; Singh et al., 2010b; Singh et al., 2012). Therefore, our second hypothesis was that indices of force stabilizing synergies would increase at both levels of the hierarchy. This hypothesis was partially confirmed only for *group-index*.

The increase in V_{UCM} and V_{ORT} (as shown in our previous studies) during fatigue could be partially due to changes in the gains of feedback loops (Windhorst & Kokkoroyiannis, 1991). Feedback gains have been associated with the accuracy of performance in redundant tasks (Todorov & Jordan, 2002; Yang, Scholz, & Latash, 2007). However, an increase in

feedback gains during fatigue would be expected to result in changes in both V_{UCM} and V_{ORT} as has been shown in the accurate force production studies. So the null results for V_{UCM} at the TH-VF level in prehension tasks cannot be explained in terms of possible changes in feedback gains.

It is possible that the absence of changes in V_{UCM} is due to a trade-off between force-stabilizing synergies at two levels of the assumed hierarchy. It has been shown in the past that there is an inherent trade-off between synergies at two hierarchical levels (for details cf. Gorniak, Zatsiorsky, & Latash, 2007; Gorniak et al., 2009; Latash, Gorniak, & Zatsiorsky, 2008). In particular, an increase in V_{UCM} at the upper level of the hierarchy leads to higher V , but also to an increase in variance of the VF force. This latter effect contributes to higher V_{ORT} at the lower level of the hierarchy potentially resulting in lower V . As a result, a large increase in V at the upper level of the hierarchy could have a strong negative effect on the synergy stabilizing the VF force at the lower level of the hierarchy. The current results show that the controller in response to fatigue of either the thumb or index finger did not adopt the strategy of increasing the synergy index at the highest level (as could be expected from earlier studies, (Singh & Latash, 2011; Singh et al., 2010b; Singh et al., 2012).

Conclusions and future work

In summary, the results from the previous paper (Singh et al., 2013) and the current study show that fatigue of a single digit leads to some complex adaptations in the average and trial-by-trial variance of the digits' applied forces and moments in a prehension task. Adaptations of the average grip force, load force, and moments of force violate the principle of superposition during fatigue whereas the trial-by-trial variances of these variables continue to obey the principle of superposition. During fatigue, the average value and variance of the load resisting forces applied by the fatigued digit increased. On the contrary, the average value of the grip force for the fatigued digit decreased but the variance of the grip force showed no significant change. Furthermore, when we decomposed the changes in variance into components that do not affect the performance variable (V_{UCM}) and the ones that do (V_{ORT}), the adaptations in these two components during fatigue were largely limited by a trade-off between force-stabilizing synergies at the TH-VF and IF level. We have explained the adaptations (during fatigue) in the trial-by-trial variance of forces and moments of force within the framework of the referent configuration hypothesis, through the roles of the tactile afferents in maintaining stable precision grasps, and through the hierarchical organization of synergies.

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Appendix

Table A

Statistical parameters for the three-way RM ANOVA (*Fat* (Fatigue), *G* (Group) and *T* (Torque) as factors) for V_{UCM} , V_{ORT} and V of F^X , F^Y , F^Z and M^Y at the TH-VF and IF levels. Only the significant effects are shown. The main effect of *T* was significant for all the dependent variables.

Statistical Parameters			
TH-VF Level	<i>F</i>	<i>df</i>	<i>p</i>
$\text{Var}(F_{TH}^X)$			
<i>Fat</i>	4.53	1,70.3	<0.05

Statistical Parameters			
TH-VF Level	F	df	p
$Fat \times T$	3.92	2,70.3	<0.05
$Var(F_{TH}^Y)$			
Fat	4.5	1,69.5	<0.05
$Fat \times G$	9.8	1,69.5	<0.01
$Fat \times G \times T$	3.2	2,69.5	<0.05
$Var(M_{VF}^Y)$			
Fat	8.2	1, 23.5	<0.01
$Var(M_{VF, F^Z}^Y)$			
Fat	4.6	1,70.4	<0.05
$V_{ORT}(F^X)$			
Fat	7.88	1,62.9	<0.05
$Fat \times G$	20.43	1,62.9	<0.001
$Fat \times G \times T$	3.27	2,62.8	<0.05
$V_{ORT}(F^Z)$			
Fat	7.57	1,18.9	<0.05
$Fat \times G$	7.23	1,18.9	<0.05
$V_{ORT}(M^Y)$			
Fat	11.8	1,22.1	<0.01
$Fat \times G$	5.4	1,22.1	<0.05
$V(F^X)$			
$Fat \times G$	8.6	1,63.9	<0.01
$Fat \times T$	4.6	2,63.9	<0.05
$Fat \times G \times T$	5.0	2,63.9	<0.05
$V(F^Z)$			
$Fat \times G$	4.8	1,70.1	<0.05
IF Level			
$V_{ORT}(F^X)$			
Fat	7.81	1,103.9	<0.01
$Fat \times G$	6.6	1,103.9	<0.05
$V_{UCM}(F^Y)$			
Fat	9.26	1,70.1	<0.01
$V(F^X)$			
Fat	2.98	1,69.1	=0.08
$Fat \times G$	6.9	1,69.1	<0.05
$V(F^Y)$			
Fat	5.3	1,27.22	<0.05
$Fat \times G$	4.7	1,27.22	<0.05

Figure 1 A-C

Figure 1D

Figure 1.

A) The three different torque conditions (pronation, 0 and supination torque). The coordinate axes for the experiment are shown on the right. B) The fatiguing exercise setup for *group-thumb*. C) The fatiguing exercise setup for *group-index*. D) An illustration of the control problem at the TH-VF level of the hypothetical control hierarchy. Note that 'd' is the moment-arm for the tangential forces applied by the digits about the geometrical center of the handle. Inset: Schematic illustration of the experimental setup.

Figure 2.

Average variance of forces: F^X (panel A); F^Z (panel B); F^Y (panel C); and M^Y_{VF} (panel D) at the TH-VF level. Before ($\square$) and during-fatigue ($\blacksquare$) for *group-thumb* (left side) and before ($\square$) and during-fatigue ($\blacksquare$) for *group-index* (right side). PR- pronation torque; 0 – zero-torque; SU- supination torque. * indicates main effect of *Fatigue* for that particular group.

Figure 3.

Average V_{UCM} (panel A) and V_{ORT} (panel B) for F^X , and for F^Z (panels C and D) respectively at the TH-VF level. Before ($\square$) and during-fatigue ($\blacksquare$) for *group-thumb* (left side) and before ($\square$) and during-fatigue ($\blacksquare$) for *group-index* (right side). PR- pronation torque; 0 – zero-torque; SU- supination torque. * indicates main effect of *Fatigue* for that particular group.

Figure 4. Average V_{UCM} (panel A), V_{ORT} (panel B) and ΔV (panel C) at the TH-VF level for M^Y . Before ($\square$) and during-fatigue ($\blacksquare$) for *group-thumb* (left half of each panel) and before ($\square$) and during-fatigue ($\blacksquare$) for *group-index* (right half of each panel). PR- pronation torque; 0 – zero-torque; SU- supination torque. * indicates main effect of *Fatigue* for that particular group.

Figure 5.

Average ΔV for F^X (panel A) and F^Z (panel B) at the TH-VF level. Average ΔV for F^X (panel C) and F^Y (panel D) at the IF level. Before ($\square$) and during-fatigue ($\blacksquare$) for *group-thumb* (left side) and before ($\square$) and during-fatigue ($\blacksquare$) for *group-index* (right side). PR- pronation torque; 0 – zero-torque; SU- supination torque. * indicates main effect of *Fatigue* for that particular group. $\odot$ indicates main effect of *Fatigue* approached significance.

Figure 6. 95% confidence ellipse plotted around the points of wrench application for the 20 *sub-trials* of the TH and VF for each torque condition, PR- pronation torque (black); 0 – zero-torque (white); SU- supination torque (dark grey) for a representative participant.

Figure 7.

A) A hypothetical control scheme with two types of neural variables. NV_1 specifies the desired value (average, μ) of a performance variable. Fatigue triggers a chain reaction in the elements of the vector μ such that the grasped object is still in translational and rotational equilibrium. NV_2 specifies synergies (co-variation matrix σ) that may or may not stabilize that performance variable. The elements of matrix σ are also matrices. For example, σ_{11} is a co-variation matrix that specifies the co-variation of the elemental variables of $\mu_F(F^X)$. These elemental variables also have to interact to stabilize other performance variables like $\mu_M(M^Y)$. Fatigue does not induce correlated changes amongst the elements of NV_2 . B) Setting a value of referent aperture (AP_{REF}) leads to active force production against the walls of the hand-held object because of the difference between the actual aperture (AP_{ACT}) and AP_{REF} (upper panel). AP_{CTR} is the coordinate of the center of AP_{REF} . AP_{CTR} is prone to fluctuations due to an increase in physiological tremor during fatigue. The controller responds to the fluctuations in AP_{CTR} by minimizing the variance of AP_{REF} .

Table 1

Changes in variance components and indices of synergy for *group-thumb* and *group-index* during fatigue. ‘↑’ implies increase, ‘↓’ implies decrease and ‘≈’ implies no statistically significant change.

Variable	<i>Group-Thumb</i>		<i>Group-Index</i>	
	TH-VF	IF	TH-VF	IF
$V_{UCM}(F^X)$	≈	≈	≈	≈
$V_{ORT}(F^X)$	↑	↑	↓	↑
$V(F^X)$	↓	↓	↑	≈
$V_{UCM}(F^Y)$	≈	↑	≈	↑
$V_{ORT}(F^Y)$	≈	≈	≈	≈
$V(F^Y)$	≈	≈	≈	↑
$V_{UCM}(F^Z)$	≈	↑	≈	↑
$V_{ORT}(F^Z)$	↑	≈	≈	≈
$V(F^Z)$	↓	≈	≈	≈
$V_{UCM}(M^Y)$	≈	≈	≈	≈
$V_{ORT}(M^Y)$	↑	≈	≈	≈
$V(M^Y)$	≈	≈	≈	≈