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Error compensation during finger force production after one and four-finger voluntarily fatiguing exercise

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Abstract

The effect of muscle fatigue on error compensation strategies during multi-finger ramp force production tasks was investigated. Thirteen young, healthy subjects were instructed to produce a total force with four fingers of the right hand to accurately match a visually displayed template. The template consisted of a 3-s waiting period, a 3-s ramp force production (from 0 to 30% maximal voluntary contraction, MVC), and a 3-s constant force production. A series of twelve ramp trials was performed before and after fatigue. Fatigue was induced by a 60-s maximal isometric force production with either the index finger only or with all four fingers during two separate testing sessions. The average percent of drop was 38.2% in the MVC of the index finger after index-finger fatiguing exercise and 38.3% in the MVC of all fingers after four-finger fatiguing exercise. The ability of individual fingers to compensate for each other's errors in order for the total force to match the preset template was quantified as the error compensation index (ECI), i.e. the ratio of the sum of variances of individual finger forces and the variance of the total force. By comparing pre- and post-fatigue performance during four-finger ramp force production, we observed that the variance of the total force was not significantly changed after one- or four-finger fatiguing exercise. The ECI significantly decreased after four-finger fatiguing exercise, especially during the last second of the ramp; while the ECI remained unchanged after index finger single-finger fatiguing exercise. These results suggest that the central nervous system is able to utilize the abundant degrees of freedom to compensate for partial impairment of the motor apparatus induced by muscle fatigue to maintain the desired performance. However, this ability is significantly decreased when all elements of the motor apparatus are impaired.

Introduction

The human motor system possesses numerous possible combinations of, for example, joint postures to achieve a desired functional goal (pistol shooting, (Scholz et al. 2000)). For any given movement, the reduction of these multiple possibilities (degrees of freedom) to select a single one to be utilized was first identified as a problem of motor redundancy by Bernstein (1935;1967). Many researchers have attempted to solve this problem by investigating rules that the central nervous system (CNS) utilizes when selecting a motor program (cf. Seif-Naraghi and Winters 1990; Latash 1996). More recently, the problem of motor redundancy has been reevaluated and viewed from a more positive perspective, subsequently re-labeled as the principle of abundance (Gelfand and Latash 1998; Latash 2000). Simply stated, the CNS does not develop unique solutions to motor control problems. Instead it develops families of solutions based on a number of task specific functionally important variables that are stabilized for the given task (Schoner 1995; Scholz and Schoner 1999; Scholz et al. 2000; 2002). According to this principle, within the motor system, if an element introduces error into a

movement other elements may compensate for that error in order to maintain overall performance near the targeted goal. This phenomenon is termed error compensation.

To exemplify this concept, imagine an individual is asked to produce isometric finger flexion forces simultaneously with four fingers in order to generate a total force that matches a preset ramp template (e.g. 30% maximal voluntary contraction [MVC] over 3 seconds). If one finger increases its force contribution then it introduces an error into the total force. If other fingers reduce their relative contributions to the total force in response to this error, then it can be said that they are compensating for that error, resulting in matching the total force to the preset template. In this example, error compensations among finger forces occur in such a way that allows the desired time-varying total force following the template despite individual finger force contribution variations during the 3 sec interval. The ratio of the sum of the variances of individual finger forces to the variance of total force is used as an index to quantify the degree of error compensation, i.e. error compensation index (ECI). The ECI reflects the finger's ability to compensate for each other's errors over the time course of multi-finger force production: the larger the ECI, the greater the ability to compensate for errors. Similar quantification has been used to examine compensatory strategies in coordinated multi-finger tasks of time-force profiles (Latash et al. 2001; 2002; Scholz et al. 2002).

Fatigue is a condition that has been defined as an acute impairment of performance that results in a decreased ability to produce a desired force (Enoka and Stuart 1992). Fatigue is often not localized to one muscle group or an individual physiological process within muscle. Rather, it often involves several processes acting in parallel including the muscle and structures continuing up the entire neural axis (cf. Enoka and Stuart 1992; Gandevia 2001). It has been demonstrated that a fatigued motor system exhibits a decreased accuracy of performance (Sparto et al. 1997b; Forestier and Nougier 1998; Forestier et al. 2002; Evans et al. 2003; Walsh et al. 2004; 2006; Allen and Proske 2006). However, there are only a few studies that analyzed compensatory strategies in response to decreased performance accuracy after fatigue (Bonnard et al. 1994; Sparto et al. 1997a; Cote et al. 2002; Hufnuss et al. 2006). Bonnard et al. (1994) and Sparto et al. (1997a) both described compensatory strategies after fatigue, but neither evaluated the accuracy of post-fatigue outcome performance. Cote et al. (2002) examined the effects of elbow extensor fatigue on sawing and observed increases in movement amplitude at the wrist, shoulder and trunk and decreases in sawing force and elbow movement amplitude. These changes can be labeled as compensatory because they resulted in a preservation of the characteristics of the sawing trajectory after fatigue. Furthermore, Hufnuss et al. (2006) reported that, in response to muscle fatigue induced distal (extensor digitorum communis) or proximal (triceps brachii) to the elbow, different compensatory strategies were observed to preserve motor performance of throwing movement in the horizontal plane. These studies support the idea that the CNS is able to utilize the abundance of the motor apparatus to compensate for partial impairment of the system, such as muscle fatigue.

Individual finger forces are precisely perceived during single- and multi-finger tasks (Li 2006; Li and Leonard 2006). As such, individual fingers are possibly integrated into a meaningful synergy that allows error compensation during functional activities such as multi-finger pressing and grasping (Latash et al. 1998b; Li et al. 1998b; Santello and Soechting 2000). Additionally, a central reorganization of finger synergies after fatigue has been observed during multi-finger MVC tasks (Danion et al. 2000; 2001). Danion et al. (2000; 2001) observed that fingers were more independent, i.e., impaired interactions, after four finger fatigue and that there was progressively less recruitment of the index finger during four-finger MVC tasks after index finger fatigue. These findings suggest that the central organization of commands to the fingers is altered after fatigue and, more importantly, is different after one- vs. four-finger fatigue.

The objective of the present study was to investigate the difference in fatigue effects on error compensation strategies after index- and four-finger fatigue, by quantifying the ECI during four-finger ramp force production pre- and post-fatigue. Index-finger fatigue could lead to central reorganization (Danion et al. 2001) such that potential errors induced the fatigued index finger could be compensated for by other fingers during four-finger ramp force production, i.e., preservation of motor performance (cf. Cote et al. 2002). Therefore, we hypothesized that the ability of fingers to compensate for errors after index finger fatigue would remain unchanged. In contrast, due to impaired interactions among fingers after four-finger fatigue (cf. Danion et al. 2000), we hypothesized this ability (error compensation) would be decreased after four-finger fatigue during four-finger ramp force production.

Materials and Methods

Thirteen young and healthy subjects participated in this study (6 male and 7 female; ranging from 22 to 37 years old). Subjects were screened for any significant orthopedic or neurologic injury to the dominant upper extremity impeding their ability to complete finger force production tasks. All subjects were right handed when observed during the signing of consent forms and by subjective reports. All subjects gave informed consent according to the procedures approved by The Institutional Review Board of the University of Montana and all procedures were consistent with The Declaration of Helsinki.

Apparatus

Four unidirectional piezoelectric force sensors (model 208CO2; Piezotronic Inc.) were used to measure individual finger forces. The sensors were mounted on aluminum posts, covered with cotton pads and placed within a 90mm×140mm aluminum frame. The frame was placed into a groove in a wooden board. The frame was adjustable horizontally within the groove. The sensors were adjustable vertically within the frame to accommodate individual hand anatomy. Analog output signals from the sensors were connected to separate signal conditioners (model 484B11, PCB Piezotronics Inc., USA). Force signals were sampled at 1,000 Hz using a 16-bit analog-to-digital converter (PCI-6229, National Instruments, Austin, TX, USA). The system involved approximately 1% error over the typical epoch of recording of a constant signal. A PC desktop equipped with customized LabVIEW software (National Instruments) was used for data acquisition and processing.

During testing, the participant sat in a height-adjustable chair, with the upper arm (dominant side) at approximately 45° of abduction in the frontal plane and 45° of flexion in the sagittal plane, and the elbow at approximately 135° of flexion. The right forearm resting on the wooden board was stabilized using two medial-laterally adjustable locking aluminum pillars to maintain forearm orientation throughout the duration of the experiment. The proximal and distal interphalangeal joints were positioned into slight flexion to the degree of subject comfort and optimal force production. The wrist was maintained in slight extension (about 20°) due to the height of the force sensors position on top of the wooden board. Both the wrist and the forearm maintained contact with the wooden board during the experiment. The non-dominant upper extremity was placed on top of the testing table. This apparatus (Fig 1) was similar to the apparatus used previously (Latash et al. 2002).

Procedures

Subjects completed two separate testing sessions. One session consisted of a 60-s maximum voluntary contraction (MVC) fatiguing exercise for the index finger only. The other session consisted of a 60-s MVC fatiguing exercise for all four fingers. Sessions were spaced at least two days, but no more than three days, apart in order to ensure that neither delayed onset muscle

soreness nor fatigue had any influence on the results of the trials. The order of the fatiguing exercise was randomized among subjects.

The procedure of each session was organized according to the flow chart in Figure 2 adopted from previous studies (Danion et al. 2000;2001). Subjects first performed MVC tasks for each individual finger [index (I); middle (M); ring (R); and little (L) finger] and for all four fingers (IMRL). Subjects were given three trials for each MVC task and the trial with the largest force was recorded. Trials were interspersed with 20-s rest periods to avoid fatigue during the MVC trials.

After collecting MVC data, subjects were asked to complete a series of ramp force task trials (Fig 3). A ramp template was displayed as a thick red line on the computer screen. Each ramp force trial lasted 9 seconds long with 3 distinct segments: zero force in the 1st 3 seconds, a ramp from zero to 30% MVC of the IMRL task, and a 3-s plateau at 30% of MVC. Subjects were asked to replicate this red ramp template to the best of their ability by pressing down with all four fingers simultaneously. The total force of four fingers was displayed on the screen. A full scale of the visual display was fixed at 60% MVC. Twelve practice trials were completed during the first session in order to familiarize the subject with the task and negate any motor learning issues that might have confounded the data. Twenty seconds of rest were allotted to the subject between each practice trial to avoid fatigue. A series of 12 ramp trials was saved.

A fatiguing exercise consisting of a 60-s MVC of the index finger or all four fingers followed. Another series of I or IMRL MVC tests was completed immediately following the fatiguing exercise. This was then followed by another series of 12 ramp tasks. The ramp template was adjusted to 30% of the newly-measured post-fatigue I or IMRL MVC. Post-fatigue MVC and ramp trials were interspersed with a 20-s MVC of the index or four fingers to maintain fatigue. In order to further verify the effectiveness of the fatiguing exercise in generating a physiologic fatigue, surface EMG data from the flexor digitorum superficialis (FDS) muscle was collected before and after four-finger fatiguing exercise from a single volunteer who did not participate in the experiment. The mean power frequency of FDS surface EMG, as expected (Bigland-Ritchie et al. 1981), decreased from 168 Hz to 112 Hz immediately following four-finger fatiguing exercise.

Two researchers were present throughout all experiments. One researcher provided consistent instruction and orientation to each subject. The second researcher monitored all time parameters throughout each session. Both researchers assisted in correctly positioning each subject and monitoring his/her pushing strategy for possible errors. Each researcher retained his specific duty throughout all data testing in order to remain as consistent as possible.

Data Analysis

Data analysis was performed off-line using customized MatLab programs. Peak force (MVC) was measured for pre- and post-fatigue conditions. The force signals from individual sensors were used to analyze force variance profiles. The method was well established (Latash et al. 2002; Scholz et al. 2002; Shinohara et al. 2003; 2004).

For each series of ramp force production, 12 trials were aligned by the beginning of the trial (Fig 3A). Average profiles of individual finger forces [$F_i(t)$] and of the total force [$F_{tot}(t)$] were computed. Time profiles of the variances of the individual finger forces and of the total force were computed over these trials [$VarF_i(t)$ and $VarF_{tot}(t)$, respectively]. The time profile of the sum of variances of individual finger forces [$\Sigma VarF_i(t)$] was also computed (Fig 3B). Variance values were further averaged across the subjects over the 1st, 2nd, 3rd 1-s segments of the ramp.

We were particularly interested in the relationship between $\text{VarF}_{tot}(t)$ and $\Sigma\text{VarF}_i(t)$. According to the equality theorem (Loeve 1977), one could expect $\Sigma\text{VarF}_i(t) = \text{VarF}_{tot}(t)$, if the finger forces deviate from their preferred profiles independently of each other. It has been reported this relationship was influenced by the actual force produced by four fingers, independent of age and MVC (Shinohara et al. 2003). Therefore, a ratio of $\Sigma\text{VarF}_i(t)$ (Fig 3B, dotted line) to $\text{VarF}_{tot}(t)$ (Fig 3B, solid line) was computed to assess trends in finger error compensation strategies despite differences in the magnitude of actual forces produced between pre- and post-fatigue conditions. This ratio was termed as the error compensation index (ECI). Increasing ECI corresponds with a better ability of the fingers to covariate their forces to compensate for each other's errors. If the $\text{ECI} = 1$, finger forces vary over the ramp independently of one other. If the $\text{ECI} < 1$, there is error amplification.

Statistics

Descriptive statistics were used to analyze the respective results. Paired Student t-tests were used to compare the effect of fatigue on the dependent variables (ECI, VarF_{tot} , ΣVarF_i) for two fatiguing exercises, respectively. Repeated measures ANOVAs were used with factors TIME (three levels, 1st, 2nd, 3rd sec) and FATIGUE (two levels, pre vs. post) to analyze the segmental and overall differences in the ECI values during either the four- or one-finger fatiguing protocols. Post hoc Tukey's honest significant tests were utilized when necessary. The level of significance was set at $p \leq 0.05$.

Results

After fatiguing exercise, the average percent of drop in the MVC of the index finger after one-finger fatiguing exercise was 38.2% and 38.3% in the MVC of IMRL after four-finger fatiguing exercise.

Different fatiguing exercises resulted in different effects on finger interaction during the ramp force production, as illustrated by data from a representative subject in Figure 4. One-finger fatiguing exercise did not result in visible changes in the variance of the total force [$\text{VarF}_{tot}(t)$] or the sum of the variance [$\Sigma\text{VarF}_i(t)$] (Fig 4A&B). Although $\text{VarF}_{tot}(t)$ was similar, $\Sigma\text{VarF}_i(t)$ was remarkably decreased after four-finger fatiguing exercise (Fig 4C&D). Averaged across all subjects, the post-fatigue ΣVarF_i for the entire force ramp was significantly smaller than the pre-fatigue ΣVarF_i after four-finger fatiguing exercise ($t_{[12]}=2.86$, $p=0.01$), but not after one-finger fatiguing exercise. The averaged VarF_{tot} was not significantly changed after one- or four-finger fatiguing exercises (Fig 5A).

The error compensation index (ECI), the ratio of $\Sigma\text{VarF}_i(t)$ to $\text{VarF}_{tot}(t)$, was used to quantify the ability of individual fingers to compensate for each other's errors during the ramp task. No significant difference in the ECI of pre-fatigue tests was found between the two fatiguing exercises. Averaged across all subjects, the ECI was not significantly changed during the entire ramp force production after one-finger fatiguing exercise. The averaged ECI was significantly decreased after four-finger fatiguing exercise ($t_{[12]}=2.58$, $p=0.02$).

The ECI was further averaged for the 1st, 2nd, 3rd 1-s segments (i.e., ECI1, ECI2, ECI3, respectively) during the 3-s ramp force production (Fig 6). After the four-finger fatiguing exercise (Fig 6A), a 2×3 ANOVA revealed significant effects of FATIGUE ($F_{[1,12]}=4.75$, $p=0.05$), TIME ($F_{[2,24]}=14.91$, $p<0.001$), and a significant interaction of FATIGUE × TIME ($F_{[2,24]}=23.44$, $p=0.04$). Post hoc analyses demonstrated that the ECI was significantly smaller during the 3rd second, but not during the 1st or 2nd second of the ramp production after fatigue ($p=0.01$). A 2×3 ANOVA showed a significant effect of TIME ($F_{[2,24]}=18.62$, $p<0.001$) after one-finger fatiguing exercise (Fig 6B). No significant effect of FATIGUE or a significant effect of interaction was found.

Discussion

In the present study, we examined the effects of muscle fatigue on error compensation strategies during multi-finger ramp force production. Fatigue was induced by a 60-s maximal isometric force production with the index finger only or with all four fingers. This fatiguing protocol lead to significant decreases in MVC after both one- and four-finger fatiguing exercise, comparable to results described in previous studies (Danion et al. 2000; 2001). By comparing pre- and post-fatigue performance of four-finger ramp force production, we observed that the variance of the total force was not significantly different after one- or four-finger fatiguing exercise. The ability of the fingers to compensate for each other's errors (ECI) significantly decreased after four-finger fatiguing exercise, especially during the last second of the ramp. This ability remained unchanged after one-finger fatiguing exercise.

Our observations of different fatigue effects on error compensation were consistent with and supported by previous findings (Danion et al. 2000;2001). Danion et al. (2000) reported impaired finger interactions after fatigue of all fingers as a result of a central reorganization. In contrast, after fatigue, the index finger was progressively less recruited during multi-finger MVC force production tasks (Danion et al. 2001). Despite progressively less recruitment of the index finger, we observed error compensation preservation among fingers. This suggests that decreased contributions from one finger do not significantly impair the other fingers' ability to compensate for errors. However, impaired interactions among all four fingers resulted in a significantly decreased ability to compensate for errors after four-finger fatiguing exercise. Taken together, these results indicated task-dependent central reorganizations after fatigue.

Our observation of error compensation preservation after index finger fatigue is consistent with previous studies of the effects of fatigue on multi-joint coordination (Forestier and Nougier 1998; Cote et al. 2002; Hufnuss et al. 2006). Forestier and Nougier (1998) examined the effects of wrist flexor fatigue on the kinematics and accuracy of throwing a handball. They found that movement of the arm (elbow, wrist and hand) was centrally reorganized to maintain an accurate motor performance after fatigue. Similarly, by analyzing sawing motion after fatiguing the elbow extensor group (the assumed primary contributor to this motion), Cote et al. (2002) observed a decrease in elbow movement that was compensated for by increasing the movement amplitude at the wrist, shoulder and trunk, resulting in an unchanged sawing trajectory.

Collectively, these observations demonstrate that the motor system is able to utilize the abundant degrees of freedom to compensate for partial impairment of the motor apparatus after fatigue, thus supporting the notion of the principle of motor abundance. Conversely, four-finger fatigue could be viewed as fatigue of all effectors during four-finger ramp force production. We observed that fatigue of all four fingers resulted in a significantly decreased ability of fingers to compensate for each other's errors. This finding could be interpreted as evidence that the ability of the system to compensate for impairment has certain limits, particularly when all effectors are impaired, for example, by fatigue.

Detailed analysis revealed that a significant reduction in the error compensation ability occurred during the third segment of ramp force production after four-finger fatiguing exercise. The third segment can be viewed as a transition between the ramp force phase and the plateau force phase of the time-force profile. During the ramp phase the CNS has to continuously invoke a timing strategy of increasing finger force production, in addition to stabilization of the total finger force, in order to match the ramp force template. The plateau phase allows for the total force stabilization synergy to dominate. Latash et al. (2004) found that the timing synergy was separate from the force stabilization synergy and did not display error compensation like that of the force synergies. During this transition, the CNS is switching from a balance of a timing synergy and a force stabilization synergy of the fingers to a dominant

force stabilization strategy. It has been observed that the changing of finger force synergies occurs in anticipation of changing tasks by the CNS (Shim et al. 2005). In conjunction with this concept, impaired interactions of the fingers are observed after fatigue (Danion et al. 2001). Therefore we postulate that changes observed during the 3rd segment of the ramp phase were due to errors in anticipation and transition of finger synergies.

Compensatory strategy after impairment is a developing topic in motor control with potential broad impacts on rehabilitation (Latash and Anson 2006). In the present study, we used the hand as a model to examine compensatory strategies after fatigue-induced impairments simulating two conditions: partial impairment and system impairment. The partial impairment is induced by one-finger fatiguing exercise, while the entire system impairment is produced after four-finger fatiguing exercise. Our results suggest that the central nervous system utilizes the abundant degrees of freedom to compensate for partial impairment of the motor apparatus to maintain the desired performance. This ability, however, is significantly decreased when impairment of all elements of the motor apparatus occurs.

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Figure 1.
Illustration of experimental settings.

Figure 2.
Illustration of experimental protocol.

Figure 3.

A) An overlay of 12 trials from a representative subject before fatigue. **B)** The relationship between the sum of the variances of individual finger forces ($\Sigma VarFi$) and the variance of the total force ($VarFtot$). The error compensation index (ECI) is quantified as the ratio of $\Sigma VarFi$ to $VarFtot$.

Figure 4.

Representative data from one subject across all four conditions. Note that the relationship between VarF_{tot} and ΣVarF_i is preserved after one-finger fatiguing exercise (A: PreOne vs. B: PostOne), while ΣVarF_i is dramatically decreased without notable changes in VarF_{tot} after four-finger fatiguing exercise (C: PreAll vs. D: PostAll). One: one-finger fatigue; All: four-finger fatigue.

Figure 5.

Variances (A) and the error compensation index (ECI) (B) averaged over the entire force ramp and across all subjects. Standard error bars are shown. Note that $\Sigma VarFi$ significantly decreased after four-finger fatiguing exercise, resulting in a significant reduction in the ECI. Asterisk: $p < 0.05$; One: one-finger fatigue; All: four-finger fatigue.

Figure 6.

The error compensation index (ECI) averaged over the 1st, 2nd, and 3rd one-second segment before and after four- (A) and one-finger (B) fatiguing exercise. Note that a significant reduction in the ECI was observed only in the 3rd segment of the force ramp after four-finger fatiguing exercise. Asterisk: $p < 0.05$; One: one-finger fatigue; All: four-finger fatigue.