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Perception of finger forces within the hand after index finger fatiguing exercise

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Abstract

The effect of fatigue on finger force perception within a hand during ipsilateral finger force matching was examined. Thirteen subjects were instructed to match a reference force of an instructed finger using the same or different finger within the hand before and after index finger fatigue. Absolute reference force targets for the index or little finger were identical during pre- and post-fatigue sessions. Fatigue was induced by a 60-s sustained maximal voluntary contraction (MVC) of the index finger. Index finger MVC decreased approximately 29%, while there was a non-significant (about 5%) decrease in the little finger MVC. The results showed that: 1) The absolute reference and matching forces of the instructed fingers were not significantly changed after fatigue, while the total forces (sum of instructed and uninstructed finger forces) were increased after fatigue. 2) The relative forces (with respect to corresponding pre- and post-fatigue MVCs) of the index finger increased significantly in both reference and matching tasks, while the relative forces of the little finger remained unchanged after fatigue. 3) Matching errors remained unchanged after fatigue when the fatigued index finger produced the reference force, while the errors increased significantly when the fatigued index finger produced the matching force. 4) Enslaving (difference between total and instructed finger forces) increased significantly after fatigue, especially during force production by the fatigued index finger and when the little finger produced matching forces at higher force levels. 5) Enslaving significantly increased matching errors particularly after fatigue. Taken together, our results suggest that absolute finger forces within the hand are perceived within the CNS during ipsilateral finger force matching. Perception of absolute forces of the fatigued index finger is not altered after fatigue. The ability of the fatigued index finger to reproduce little finger forces is impaired to a certain degree, however. The impairment is likely to be attributable to altered afferent/efferent relationships of the fatigued index finger.

Keywords

force matching; fatigue; finger; enslaving

Introduction

Force perception has typically been studied using a contralateral force matching paradigm (Gandevia and McCloskey 1977a,b; Cafarelli and Bigland-Ritchie 1979; Kilbreath et al. 1997; Jones 2003; Jones and Piateski 2006). In this paradigm, a reference force produced by one muscle group is matched by a force produced by the same (homologous) or different (non-homologous) muscle group of the contralateral limb. In a non-homologous muscle matching task, reference forces produced by a smaller muscle group, such as the index finger flexors, are overestimated in magnitude when matched by a larger muscle group, such as the elbow flexors, while the elbow flexors' reference force is underestimated by the finger flexor matching

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force. When expressed with respect to corresponding maximal voluntary contractions (MVC), the relative reference and matching forces are closely approximated (Jones 2003). The absolute magnitude of the reference force is usually only matched accurately during homologous matching tasks (Jones 1989). When the maximum force-generating capacity is decreased by alterations in the state of the matching muscles (e.g. length change (Cafarelli and Bigland-Ritchie 1979); or partial curarization (Gandevia and McCloskey 1977a), the subject perceives, as a result of the alteration, that the intensity of the reference force of the contralateral homologous muscles has increased. The relative matching force (percent of the maximal forces that are obtained by the matching muscle in the altered state), is similar to the relative reference force. These results suggest that forces are perceived relative to maximal force-generating capabilities of the muscles during contralateral force matching. These results suggest that force perception is based on a sense of effort (Gandevia and McCloskey 1977a,b; Gandevia 1987).

In contrast to the results obtained during contralateral force matching paradigms, absolute, rather than relative, magnitude of finger forces appear to be perceived and reproduced during ipsilateral finger force matching paradigms, even though the maximal force-generating capacities are significantly different between fingers (Li and Leonard 2006). For example, when an index finger reference force is matched by a weaker little finger, the little finger force underestimates the index finger force. However, the matching errors (difference between the absolute index and little finger forces) are significantly minimized when the total force of all (instructed and uninstructed) fingers are compared between the reference and matching periods. This phenomenon of uninstructed finger force production is called `enslaving' (Li et al. 1998; Kilbreath et al. 2002; Li et al. 2003). A series of studies showed that enslaving is largely mediated by the central nervous system (CNS) (Danion et al. 2000, 2003; Li et al. 2000; Latash et al. 2002; Li et al. 2004). In another study (Li 2006), the absolute reference force of the index finger during multi-finger force production was accurately reproduced by the index finger during the matching period. These results demonstrate that absolute forces of both instructed and uninstructed fingers within a hand are perceived within the CNS during ipsilateral force matching.

During both ipsilateral and contralateral experimental paradigms, matching involves three phases: perception (of reference force), memory, and production (of matching force). During the matching process, information pertaining to the perceived reference force is retrieved from memory and compared with the matching force estimation. The CNS might try to match effort (sense of effort matching), or match afferent signals that relate to force magnitudes, or match direct commands (efferent signals that produce the intended force). Alternatively, we propose that the CNS uses a combination of afferent and efferent signals to estimate the reference force and that it later uses such information to generate appropriates matching forces. A few previous studies supported this alternative view. Results were similar in two studies in which reference forces were: a) produced by fatigued muscle(s) and matched by unfatigued contralateral muscle (s) (Gandevia and McCloskey 1978; Jones and Hunter 1983), and b) produced by unfatigued muscle(s) and matched by fatigued contralateral muscle(s) (Carson et al. 2002). Each study showed increased matching errors after fatigue. Altered afferent inputs from the fatigued muscle might have influenced the relationship between the sense of effort and descending commands (Carson et al. 2002), such that estimation of either reference or matching forces based on the altered relationship led to a mismatch during the matching task and thus larger matching errors.

In the present study, the primary purpose was to examine the effect of fatigue on ipsilateral finger force matching. The maximal force-generating capability of the index (I) finger was expected to decrease after an index finger fatiguing exercise, while the little (L) finger maximal force was expected to remain unchanged. As such, the same absolute force represented a higher relative force for the index finger after fatigue, while absolute and relative forces of the little finger would be the same. Thus, the effect of index finger fatigue on matching performance, particularly in hetero-finger tasks (I/L and L/I), would provide further insights regarding relative vs. absolute finger force matching within a hand, It was also of interest to compare these results with those of contralateral matching results (Gandevia and McCloskey 1978; Jones and Hunter 1983; Carson et al. 2002) to assess whether or not similar mechanisms might be involved in ipsilateral and contralateral matching.

Materials and methods

Methods

Thirteen subjects (26.3±6.0 years of age; 11 men and 2 women) participated in the experiment. All subjects were right-handed according to their preferential use of the right hand during writing and eating. All subjects gave informed consent and all procedures were approved by the Institutional Review Board of The University of Montana and conformed to the Declaration of Helsinki.

Apparatus

During testing, the subject was seated facing a testing table. The two upper limbs were symmetrical with respect to the body midline with the upper arms at approximately 15° of abduction in the frontal plane and elbow joints at approximately 90° of flexion. The right hand and fingers were positioned on a measurement device. Four unidirectional piezoelectric force sensors (208C02, PCB Piezotronics, Inc., Depew, NY) were used to measure individual finger forces. Analogue output signals from the sensors were connected to separate signal conditioners (model 484B11, PCB Piezotronics). Force signals were sampled at 1000 Hz using a 16-bit analog-to-digital converter (PCI-6229, National Instruments, Austin, TX). The resolution of the system was 2.715 mN/bit. A PC desktop equipped with customized LabVIEW software (National Instruments) was used for data acquisition and processing. A Matlab program was written for data analysis.

Procedure

The experiment consisted of two sessions: pre-fatigue and post-fatigue. The index finger fatigue was produced by a 60-s isometric MVC force production by the index finger. Index finger fatigue was maintained by a 20-s MVC force production between two consecutive trials in the post-fatigue session. This protocol is adopted from previous studies (Kruger et al., in press; Danion et al. 2000, 2001).

At the beginning of the experiment, subjects were asked to produce MVCs using the index finger and the little finger. The highest peak value from three trials was considered as the MVC force. Similarly, MVCs of the index and little fingers were recorded after the fatigue inducing exercise. Based on individual pre-fatigue MVCs, two levels of target force were created: 15% and 35% MVCs of the index and little fingers, respectively, for both pre- and post-fatigue matching sessions, i.e., the target forces were the same pre- and post-fatigue.

Force matching tasks

As illustrated in Figure 1, subjects were instructed to generate a reference force to a pre-determined visual target using an instructed finger. Force data were displayed visually on a computer monitor positioned in front of the subject. This force was held for 5 seconds (vertical dashed line in Fig. 1 A). This was immediately followed by a 3-second relaxation period, and then subjects were instructed to reproduce the same force as in the first period, but without visual feedback, using the same or another instructed finger and maintain this force to the end of the trial (4 s). During force relaxation (5 to 8 sec time period), traces of all finger forces were displayed to ensure force relaxation.

During each trial, subjects were explicitly instructed to match the magnitude of the reference force, i.e. match the force rather than the level of effort, and to maintain a produced force level during the matching period. The interval between two consecutive trials was approximately 20 seconds. Subjects had a rest to avoid any possible finger fatigue during the interval during the pre-fatigue session. During post-fatigue trials, subjects performed a 20-s index finger MVC between trials to maintain fatigue. Subjects received no feedback regarding force matching accuracy during the experiment. Eight force-matching conditions were used:

(1) I/L task: reference force (F_{REFER}) generated by the index finger (I) and matching force (F_{MATCH}) generated by the little finger (L) at two target force levels, i.e., I/L 15 (15% MVC) and I/L 35 (35% MVC), respectively.

(2) L/I task: F_{REFER} by L, and F_{MATCH} by I, i.e., L/I 15 and L/I 35.

(3) I/I task: F_{REFER} by I, and F_{MATCH} by I, i.e., I/I 15 and I/I 35.

(4) L/L task: F_{REFER} by L, and F_{MATCH} by L, i.e., L/L 15 and L/L 35.

The order of force-matching tasks was randomized in each session, thus a different order of the task was presented during the pre- and post-fatigue sessions. Each force-matching condition was conducted in a block of four trials. Approximately 8 to 10 practice trials were allowed for each subject before performing the main experiment.

Data Analysis

To standardize data analysis, we selected a 1-s period of force production for both reference and matching forces when forces were most stable. The mean force from 3.5 – 4.5 sec was calculated for the reference force, and the mean force from 10.5 – 11.5 sec was calculated for the matching force, i.e., 0.5 s prior to the end of reference and matching periods. Based on the 1-s force data, the following dependent variables were computed.

Absolute forces generated by both the instructed fingers (i.e., instructed finger forces) and all fingers (i.e., total finger forces) were calculated. Absolute forces were recorded finger forces in Newton (N). Relative forces were also calculated as percent of corresponding pre- and post-fatigue MVCs.

To evaluate enslaving effect, the differences between total finger force and instructed finger force (i.e., total finger force – instructed finger force) were calculated at each trial. To evaluate the force-matching performance in terms of accuracy, constant errors (CEs) were calculated from the instructed finger forces (iCE) and from the total finger force (tCE). iCE was defined as the difference between matching and reference forces of the instructed fingers. Similarly, tCE was calculated to account for contributions of the uninstructed finger forces (i.e., enslaving) to the force-matching performance. Positive CE values indicate that the matching force overestimated the reference force and negative values indicate underestimation.

Statistics

Repeated-measures ANOVAs were used to evaluate the effect of fatigue on force production for both the instructed and all fingers during reference and matching force periods. Factors included FATIGUE (2 levels: pre- and post), PERIOD (2 levels: reference and matching), Force-Level (2 levels: 15% and 35% MVC), and TASK (4 levels: I/I, I/L, L/I and L/L). To assess the effect of fatigue on matching performance, ANOVAs was performed for the CE in each task, with factors FATIGUE, Force-Level, and ENSL (2 levels: with and without enslaving). Whenever necessary, Tukey HSD post-hoc tests were used to detect loci of the significance. Descriptive statistics were also used. The level of significance was set at $p \leq 0.05$.

Results

After a 60-s MVC fatiguing exercise of the index finger, the index finger MVC, on average, decreased from 50.2 N to 35.6 N, about a 29.1% drop. There was a non-significant decrease of 5.4% in the little finger MVC after the index finger fatigue (26.1 N vs. 24.7 N).

Effect of fatigue on absolute finger forces

The following results refer to experiments in which subjects were instructed to produce a reference force with one finger (I or L) following a pre-determined visual target and to reproduce the same amount of force with the same or another finger within the hand (I or L) after a 3-s rest interval. The pre-determined target was created based on pre-fatigue MVCs and was kept the same for both pre- and post-fatigue sessions. On average, both reference and matching forces of the instructed fingers were not significantly changed after fatigue. Table 1 summarizes instructed finger and total finger forces. A four-way ANOVA showed main effects of Force-Level ($F_{[1,12]}=159.78$, $p<0.001$) and TASK ($F_{[3,36]}=76.44$, $p<0.001$). There were significant interactions of TASK × Force-Level ($F_{[3,36]}=45.35$, $p<0.001$), TASK × PERIOD ($F_{[3,36]}=32.27$, $p<0.001$), Force-Level × PERIOD ($F_{[1,12]}=27.21$, $p<0.001$), and TASK × Force-Level × PERIOD ($F_{[3,36]}=30.66$, $p<0.001$). Post-hoc tests showed that the reference and matching forces were different in the hetero-finger matching tasks (i.e., I/L and L/I). There were no changes in the homo-finger matching tasks (i.e., I/I and L/L) both pre and post fatigue. Specifically, in I/L task, the index finger reference force was significantly greater than the little finger matching force during both pre- and post-fatigue sessions ($p<0.001$). This difference, however, was found only at 35% MVC. In L/I tasks, the little finger reference forces were approximated by the index finger matching forces during the pre-fatigue session, while during the post-fatigue session, the index finger matching force was greater than the little finger reference force at both the 15% and 35% MVC conditions ($p<0.002$).

In contrast to the instructed finger force, the total force (the sum of forces from the instructed and un-instructed fingers) increased significantly after fatigue ($F_{[1,12]}=32.81$, $p<0.001$). A four-way ANOVA also showed main effects of Force-Level ($F_{[1,12]}=103.35$, $p<0.001$) and TASK ($F_{[3,36]}=53.02$, $p<0.001$), and a significant interaction of FATIGUE × PERIOD × Force-Level × TASK ($F_{[3,36]}=4.04$, $p=0.014$). Post-hoc tests showed that in I/L tasks, the total matching force was greater than the total reference force at 15%MVC after fatigue ($p=0.003$), but smaller at 35% MVC after fatigue ($p=0.006$); and in L/L tasks, the total matching force was greater than the total reference force during post-fatigue session at 35% MVC ($p=0.004$).

Comparisons of absolute and relative forces

When all instructed finger forces were expressed with respect to corresponding pre- and post-fatigue MVCs, i.e., relative forces (%MVC) (Fig 2B), a pattern of results different to those expressed in absolute forces (N) was observed. For homo-finger (I/I and L/L) tasks, the relative reference force and the relative matching force in the pre-fatigue session were not significantly different (Fig 2B, I/I and L/L tasks, filled circles). After fatigue, both relative reference force and relative matching force in I/I tasks increased significantly ($F_{[1,12]}=36.39$, $p<0.001$), but were not different from each other, resulting in a parallel shift (Fig 2B, I/I task, filled squares); while no significant changes in relative forces were observed after fatigue during L/L tasks (Fig 2B, L/L task, filled squares).

During I/L tasks, the relative reference forces of the index finger were significantly smaller than the relative matching forces of the little finger before fatigue ($p<0.001$). After index finger fatigue, the relative reference forces of the fatigued index finger increased significantly ($p<0.001$). The relative matching forces of the non-fatigued little finger, however, did not show significant increases. Index finger fatigue resulted in a horizontal shift (Fig 2B, I/L task)

During L/I tasks, the relative reference force of the little finger was significantly greater than the relative matching force of the index finger at the higher force level ($p<0.001$), but not at the lower force level before fatigue. After index finger fatigue, the relative reference forces of the little finger were not significantly changed; the relative matching force of the fatigued index finger increased significantly ($p<0.001$) at the higher force level, but not the lower force level, i.e., a vertical shift (Fig 2B, L/I).

Effect of fatigue on enslaving

Enslaving was calculated as the difference between the total finger force and the instructed finger force. Enslaving increased significantly after fatigue ($F_{[1,12]}=21.07$, $p<0.001$) (Fig 3). A four-way ANOVA also showed main effects of PERIOD ($F_{[1,12]}=9.24$, $p=0.010$), Force-Level ($F_{[1,12]}=29.30$, $p<0.001$), and TASK ($F_{[3,36]}=9.21$, $p<0.001$), and a significant interaction of FATIGUE × PERIOD × Force-Level × TASK ($F_{[3,36]}=9.83$, $p<0.001$). As depicted in Figure 3, post-hoc tests showed that the fatigue effect on enslaving was primarily associated with force production by the fatigued index finger, i.e., during both the reference period ($p<0.001$) and the matching period ($p<0.001$) of the I/I tasks; the reference period of the I/L tasks ($p<0.001$); and during the matching period of the L/I tasks ($p<0.001$). It was also found that enslaving increased after fatigue when the little finger produced the matching forces such as the matching periods in I/L tasks ($P<0.001$) and in L/L tasks at 35% MVC ($p<0.001$). There was no change in enslaving when the little finger produced the reference forces.

Effect of fatigue and enslaving on matching errors

Force matching errors were expressed as constant error (CE), i.e., the difference between the absolute reference and matching forces. CE was calculated for the instructed finger forces (iCE) and for the total (instructed and non-instructed) finger forces (tCE), respectively, before and after fatigue. Since uninstructed finger forces (ENSL) were included in tCE, the difference between iCE and tCE reflected the effect of ENSL on matching errors.

As illustrated in Fig 4, both ENSL and fatigue influenced matching errors. In general, ENSL increased matching errors in almost all conditions, except for minimizing matching errors during I/L tasks at the high force level. Matching errors remained unchanged after fatigue when the reference force was produced by the fatigued index finger (i.e., I/I and I/L), while the errors increased significantly when the matching force was produced by the fatigued index finger (i.e., L/I). A notable exception was that errors increased significantly in L/L tasks after fatigue at 35% MVC. Detailed results for each condition are as follows.

For I/I tasks, there were main effects of ENSL ($F_{[1,12]}=17.47$, $p=0.001$) and Force-Level ($F_{[1,12]}=13.37$, $p=0.003$), and a significant interaction of ENSL × FATIGUE × Force-Level ($F_{[1,12]}=6.05$, $p=0.030$). No main effect of FATIGUE was found. Post-hoc tests showed that tCE was significantly different from iCE at 35% MVC during the post-fatigue session ($p<0.001$), changing from underestimation to overestimation.

Similarly, there was no main effect of FATIGUE in I/L tasks. There were main effects of ENSL ($F_{[1,12]}=12.04$, $p=0.005$) and Force-Level ($F_{[1,12]}=28.84$, $p<0.001$), and a significant interaction of ENSL × FATIGUE × Force-Level ($F_{[1,12]}=10.59$, $p=0.007$). Post-hoc tests showed that tCE was greater than iCE at 15% MVC before and after fatigue ($p<0.017$); while tCE became smaller than iCE at 35% MVC before and after fatigue ($p<0.007$).

Both ENSL ($F_{[1,12]}$=8.81, p=0.012) and FATIGUE ($F_{[1,12]}$=5.89, p=0.032) significantly influenced matching errors in L/I tasks. There were also significant interactions of ENSL × FATIGUE ($F_{[1,12]}$=7.17, p=0.020) and ENSL × Force-Level ($F_{[1,12]}$=13.94, p=0.002). According to post-hoc tests, tCE was increased after fatigue at 15% (p=0.002) and 35% MVC, both iCE and tCE increased after fatigue (p<0.001), and tCE was greater than iCE pre and post fatigue (p<0.001).

ENSL significantly increased matching errors in L/L tasks, especially after fatigue. The ANOVA showed main effects of ENSL ($F_{[1,12]}$=6.73, p=0.023) and FATIGUE ($F_{[1,12]}$=8.59, p=0.013), and a significant interaction of ENSL × FATIGUE ($F_{[1,12]}$=6.06, p=0.030). Post-hoc tests showed that iCE and tCE increased after fatigue (p<0.002), and that tCE was significantly larger than iCE during post-fatigue (p=0.003), but not during the pre-fatigue session.

Discussion

Subjects were instructed to match a reference force of an instructed finger using the same or different finger within the hand before and after index finger fatigue. The results showed that: 1) The absolute reference and matching forces of the instructed fingers were not significantly changed after fatigue (Fig 2A), while the total forces (sum of instructed and uninstructed finger forces) were increased after fatigue, resulting in significant increases in enslaving (Fig 3). 2) The relative forces (with respect to corresponding pre- and post-fatigue MVC) of the index finger increased significantly post fatigue during both reference and matching periods, while the relative forces of the little finger remained unchanged (Fig 2). 3) Matching errors remained unchanged after fatigue when the reference force was produced by the fatigued index finger, while the errors increased significantly when the matching force was produced by the fatigued index finger. A notable exception was that errors increased significantly in L/L tasks after fatigue at 35%MVC. 4) Enslaving (ENSL, difference between total and instructed finger force) increased significantly after fatigue, especially during force production (reference or matching) by the fatigued index finger, and when the little finger produced the matching forces at 35% MVC (Fig. 3). 5) ENSL significantly increased force matching errors particularly after fatigue, except for minimization of matching errors at a high level in I/L tasks (Fig 4).

Matching of absolute finger forces within the hand after fatigue

In the present study, index finger MVC decreased about 29% after an index finger fatiguing exercise, while there was a non-significant decrease in the little finger MVC (about 5%). Therefore, after index finger fatigue, the same absolute index finger force represented a higher (increased) relative force, while there was no such change in little finger forces. We observed that, to match increased relative forces (but same absolute forces) generated by the fatigued index finger, relative matching forces generated by the little finger remained unchanged in I/L tasks. In contrast, to match the same relative, but also the same absolute reference forces generated by the little finger, the relative matching forces generated by the fatigued index finger significantly increased in L/I tasks (Fig 2B). Results showing no significant changes in absolute reference and matching forces after fatigue but significant changes in relative forces after fatigue with unchanged matching errors of instructed fingers (iCE) further support our previous studies (Li 2006;Li and Leonard 2006) that absolute finger forces are matched within a hand. These results, obtained during an ipsilateral matching paradigm, however, are considerably different from previous reports that used a contralateral matching paradigm (e.g., Carson et al. 2002;Proske et al. 2004). In these studies, relative forces are matched closely, despite significant differences in absolute forces after muscle fatigue. The contrasting results between ipsilateral and contralateral force matching paradigms may be related to different underlying mechanisms (discussed later).

Effects of fatigue on enslaving forces and matching errors

Results of fatigue effects on enslaving forces and matching errors warrant attention. In contrast to the unchanged forces produced by instructed finger after fatigue (Fig 2A), uninstructed finger forces (ENSL) increased significantly after index finger fatigue, evident in I/I, I/L, and L/I tasks when the fatigued index finger produced the same absolute force but at a higher relative level. Slobounov et al. (2002) reported previously that ENSL increased with the level of force production in unfatigued muscles. Our results, demonstrating increased ENSL after fatigue, confirm and extend this result. ENSL increases with the level of relative, rather than absolute force. Our results were also consistent with another study (Danion et al. 2000) showing that during MVC attempts after fatigue, ENSL was not changed when the test was performed at the same site that had produced force during the fatiguing exercise. The unchanged ENSL was likely due to the fact that the level of relative force was the same during pre- and post-fatigue MVC attempts (100%MVC).

ENSL has been reported to significantly minimize matching errors of total forces (tCE) when compared to matching errors of instructed finger forces (iCE), particularly during I/L tasks at high force levels in non-fatigued conditions (Li and Leonard 2006). After index finger fatigue, we observed a similar phenomenon of minimization of matching errors during I/L tasks at a high force level. This result indicated that increased ENSL associated with increased level of relative force of the fatigued index finger was accurately perceived within the CNS and was subsequently compensated for by increased matching ENSL, resulting in matching error minimization and no change in matching errors after fatigue. In other words, the fatigued index finger force was matched accurately. The ability of the fatigued index finger to match little finger forces appeared to be impaired, however. For example, matching errors (both iCE and tCE) were significantly increased after fatigue during L/I tasks. The increased errors could be attributed to two factors: significantly increased matching force after fatigue and its associated increased ENSL.

Mismatch of finger force estimation after fatigue

As outlined in the Introduction, force matching involves perception, memory, and production. During the matching period, production of a matching force is adjusted by comparing the perception of the reference force retrieved from memory. Motor memory is related to the rest interval (Miall et al. 1995). Rest intervals were kept constant in the present study. It is not likely that motor memory plays an important role in force matching after fatigue. Force is perceived according to a combination of peripheral inputs and descending motor commands. Descending motor commands are modified by concurrent peripheral inputs (Gandevia and McCloskey 1977b; Kilbreath et al. 1997), resulting in an altered relationship between the sense of effort and descending commands after fatigue (cf. Carson et al. 2002). As a result, force production of the fatigued index finger could be altered.

A mismatch between perception of reference force and perception of matching force could lead to increased matching errors. In contralateral matching paradigms, increased errors were observed due to a mismatch that resulted from fatigue-induced alterations in perception of either reference (Gandevia and McCloskey 1978; Jones and Hunter 1983) or matching (Carson et al. 2002) forces. A mismatch could also be induced by digital anesthesia in a contralateral weight estimation paradigm, and result in larger errors (Kilbreath et al. 1997). In the present study using an ipsilateral matching paradigm, matching errors increased significantly due to altered afferent/efferent relationships of the fatigued index finger (L/I task), but remained unchanged during non-fatigued finger force matching (I/L task).

These contrasting results, especially increased errors in contralateral force matching with the reference force produced by the fatigued muscle (Gandevia and McCloskey 1978; Jones and

Hunter 1983) and unchanged errors in ipsilateral force matching (I/L tasks), suggest that the underlying mechanisms mediating ipsilateral and contralateral force matching are potentially very different. It appears that the absolute magnitude of reference force is perceived during ipsilateral matching, while the reference force is perceived relatively during contralateral matching. During contralateral matching paradigms, perception of relative reference force is altered in the fatigued muscle, and is used subsequently as a reference for matching force estimation by contralateral, unfatigued homologous muscles (Gandevia and McCloskey 1978; Jones and Hunter 1983), resulting in larger matching errors. Because the absolute magnitude of reference force is perceived in the ipsilateral matching, even though the index finger MVC decreased after fatigue, an unchanged little finger matching force could be produced in I/L tasks. Taking into consideration increased ENSL in I/L tasks and unchanged matching errors (iCE and tCE), one can conclude that the fatigued index finger force is accurately perceived. The observation of unchanged matching errors in I/I tasks after fatigue is not trivial. It suggests that the absolute reference force is perceived and that there is no mismatch between perception of reference force and perception of matching force. The differences in results between contralateral and ipsilateral tasks might also be related to methodology. Subjects in contralateral matching studies (e.g., Carson et al. 2002) kept reference forces maintained during the matching period. This might have biased subjects to match the relative force (effort). In contrast, reference and matching forces were produced sequentially after a rest period in the present experiment.

A notable exception to the present results was the significant increases in matching errors in L/L tasks at 35% MVC after index finger fatigue. The results showed that ENSL increased in the matching force period while it remained unchanged during the reference period in L/L tasks, resulting in increased matching errors. Although not statistically significant, it is possible that the difference in the little finger relative matching force (41.4% MVC) and the relative reference force (36.4% MVC) (see Table 1) was physiologically different enough to result in higher ENSL in the matching period and thus cause an increase in matching errors similar to the results of fatigue in the index finger.

Concluding remarks

The results provide further evidence that absolute magnitudes of finger forces are perceived within the hand and perception of absolute forces of the fatigued index finger is not altered after fatigue. Preservation of perception of absolute finger forces after fatigue signifies the importance of absolute finger force perception within the hand. This ability allows multiple fingers to be integrated into a meaningful synergy for desired functions, particularly in circumstances when precise control of individual finger forces and moments of force are required, e.g., to provide pen stabilization during hand-writing (Latash et al. 2003) and grasp stability during grasping tasks (Johansson et al. 1999; Pataky et al. 2004). The ability of the fatigued index finger to reproduce little finger forces is impaired to a certain degree, however. The impairment is likely to be attributable to altered afferent/efferent relationships of the fatigued index finger.

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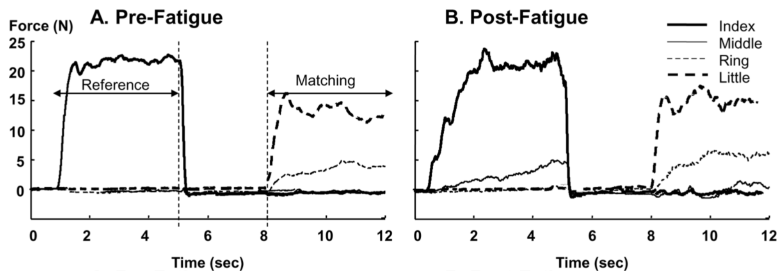

Figure 1.

Representative I/L finger matching tasks at 35% MVC before (A) and after (B) fatigue. Note that the instructed finger (I and L) forces produced similar amount of forces pre and post fatigue sessions, whereas uninstructed finger forces (enslaving) increased during both reference and matching periods after fatigue.

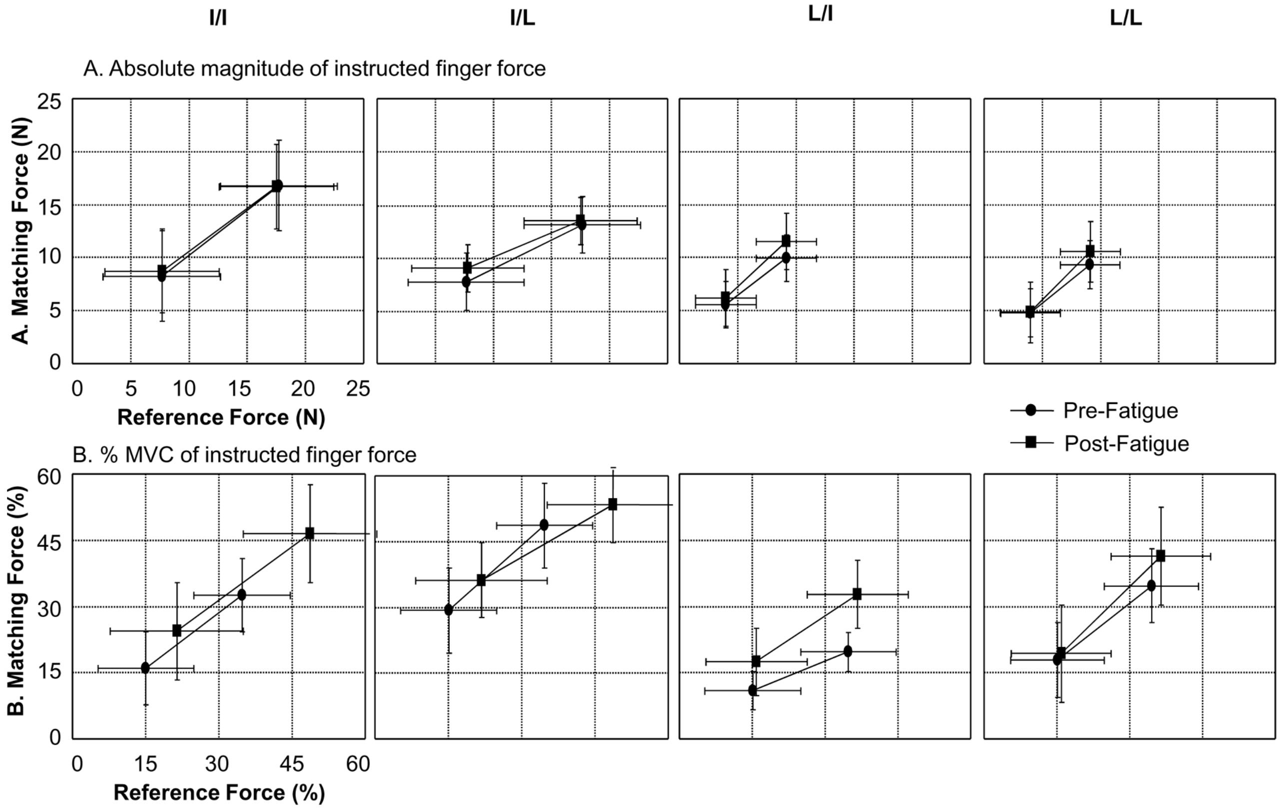

Figure 2.
The absolute (A) and relative (B) forces of the instructed fingers for each matching condition. The relative force was defined as percent of corresponding MVC before and after index finger fatiguing exercise. Note that there were no significant changes in the absolute forces before and after fatigue. The relative force of the index finger increased dramatically while there were minimal changes in the little finger relative forces in I/L and L/I tasks (B). Standard errors of data points are presented in Table 1.

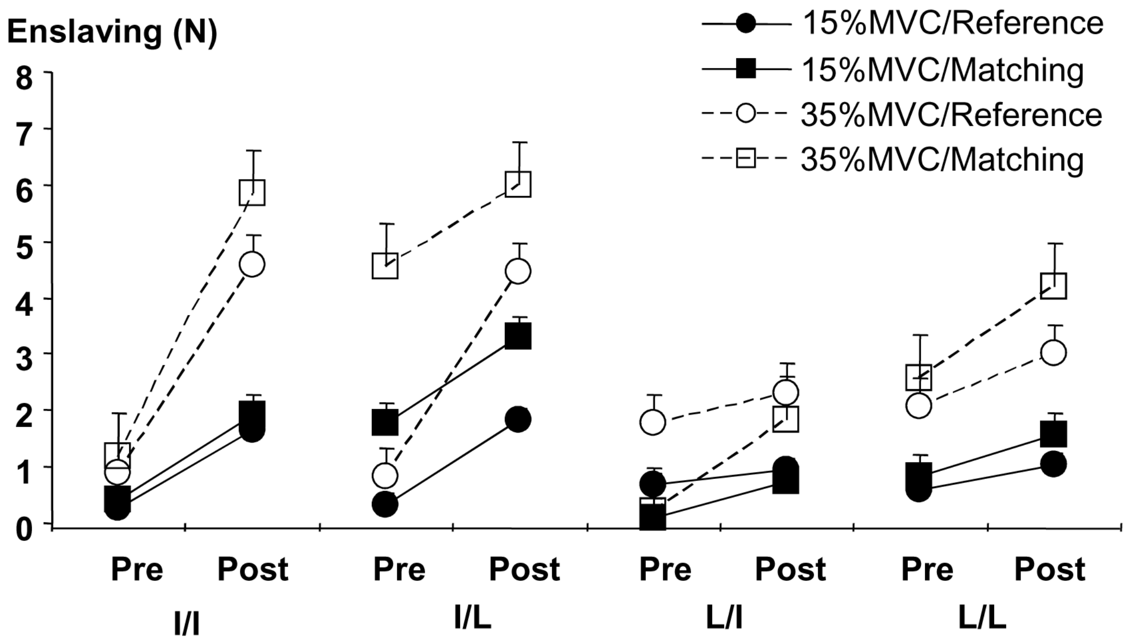

Figure 3.
The effect of fatigue on enslaving. Reference and Matching represent the reference and matching periods, respectively. Note that enslaving increased during the reference and matching force production periods by the index finger and the matching force production periods by the little finger.

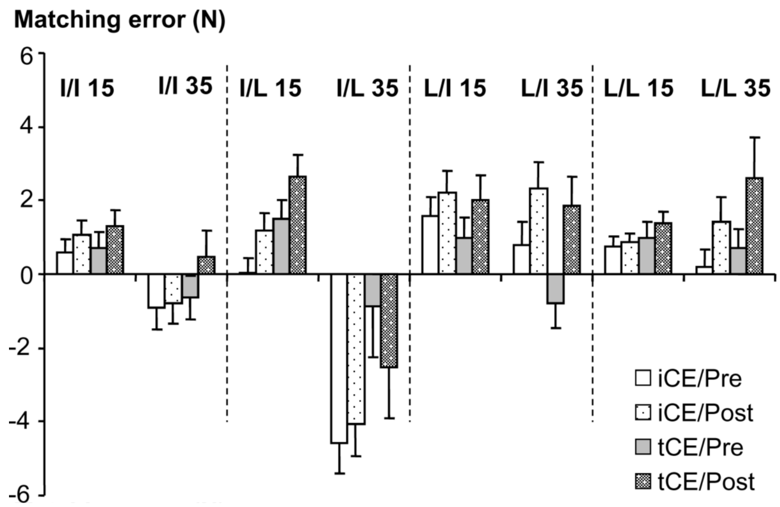

Figure 4.
The effect of fatigue on matching errors. iCE and tCE represented matching errors for the instructed finger forces and the total forces, respectively. Pre and Post represent the pre- and post-fatigue sessions, respectively. The difference between iCE and tCE represents matching errors caused by enslaving.

Table 1

Mean and standard error (SE) of the reference and matching forces for all conditions. I/L represents the task in which the index (I) finger produces the reference force and the little (L) finger produces the matching force. Similar coding for I/I, L/L and L/I. There are two reference force levels, 15% and 35% MVC (e.g. I/L 15: reference force of the index finger (I) at 15% MVC, matching force by the little finger (L)). Reference and Matching represent reference and matching force production periods, respectively. Instructed and Total are forces produced by the instructed finger (I or L) and by all fingers (sum of the instructed and uninstructed finger forces), respectively. Relative represents the percentage with respect to MVC of the finger. Values in ( ) represent standard errors. Units are Newtons in Instruct and Total, and Percentage in Relative.

			Pre-Fatigue			**Post-Fatigue**		
			Instruct	**Total**	**Relative**	**Instruct**	**Total**	**Relative**
I/I	15	Reference	7.7 (0.5)	7.9 (0.5)	15.0 (0.5)	7.7 (0.5)	9.3 (0.8)	21.4 (4.0)
		Matching	8.2 (0.8)	8.7 (0.9)	15.9 (2.7)	8.7 (0.6)	10.7 (0.9)	24.4 (5.3)
I/I	35	Reference	17.7 (1.2)	18.6 (1.3)	34.8 (0.4)	16.8 (1.6)	18.0 (1.7)	48.7 (9.0)
		Matching	17.5 (1.1)	22.1 (2.1)	32.5 (4.2)	16.7 (1.3)	22.6 (2.5)	46.5 (10.8)
I/L	15	Reference	7.7 (0.5)	8.0 (0.5)	15.1 (0.2)	7.8 (0.5)	9.6 (0.7)	21.8 (4.3)
		Matching	7.7 (0.8)	9.5 (1.0)	29.3 (6.5)	9.0 (0.8)	12.3 (1.2)	36.2 (9.3)
I/L	35	Reference	17.7 (1.2)	18.5 (1.3)	34.7 (0.3)	17.5 (1.1)	22.0 (2.1)	48.7 (9.5)
		Matching	13.1 (1.5)	17.6 (2.2)	48.6 (11.3)	13.5 (1.5)	19.5 (2.4)	53.4 (12.7)
L/I	15	Reference	4.0 (0.3)	4.7 (0.4)	15.1 (0.3)	4.0 (0.3)	4.9 (0.4)	15.9 (1.2)
		Matching	5.6 (0.6)	5.7 (0.7)	10.9 (3.9)	6.2 (0.7)	6.9 (0.7)	17.4 (6.7)
L/I	35	Reference	9.2 (0.7)	10.9 (0.9)	34.8 (0.4)	9.2 (1.0)	10.2 (1.1)	36.7 (2.3)
		Matching	10.0 (0.7)	11.5 (0.8)	19.7 (6.1)	11.5 (0.7)	13.4 (1.0)	32.7 (8.5)
L/L	15	Reference	4.0 (0.3)	4.6 (0.3)	15.1 (0.3)	4.0 (0.3)	5.0 (0.4)	15.9 (1.2)
		Matching	4.7 (0.5)	5.6 (0.7)	17.8 (3.4)	4.8 (0.5)	6.4 (0.5)	19.3 (4.4)
L/L	35	Reference	9.1 (0.7)	11.2 (0.8)	34.5 (0.9)	9.3 (1.0)	11.9 (1.2)	36.4 (2.6)
		Matching	9.1 (0.7)	12.1 (0.9)	34.7 (6.8)	10.5 (1.2)	14.7 (1.9)	41.4 (10.0)