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Practice-related modulations of force enslaving and cortical activity as revealed by EEG

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Abstract

Objective: To examine the role of practice in the modification of force enslaving and motor-related cortical potentials using finger force production tasks. This study follows-up previous studies in our laboratory using experienced piano players.

Methods: Two experiments were performed. In Expt. 1, 6 subjects participated in a pre and post EEG session separated by 12 practice sessions which were conducted 3 days a week for 4 weeks. With visual feedback regarding the accuracy of force output, subjects produced one of two force levels with either their ring or index finger. Experiment 2 followed a similar procedure to that of Expt. 1 with additional visual feedback to the degree of finger independency. Both behavioral (isometric force output) and EEG data preceding and accompanying force responses were measured.

Results: In Expt. 1 we found that forced enslaving increased along with improved accuracy following 4 weeks of practice. We found a reduction of motor potential (MP) amplitude for the index but not the ring finger following practice. Experiment 2 showed an increase in accuracy and reduction in force enslaving after practice with adequate feedback. The amplitude of MP for the index finger also decreased after practice as in Expt. 1. In contrast, the amplitude of MP for the ring finger increased after practice.

Conclusions: The present study extends our earlier work with piano players and shows the role of practice in modifying behavioral and cortical measures. The concluding theme emergent from our studies is that individuated finger control is not hard-wired, but rather plastic and greatly influenced by deliberate practice.

Significance: This research supports the idea that experience and practice are associated with changes in behavioral and EEG correlates of task performance and have clinical implications in disorders such as stroke or dystonia. Practice-related procedures offer useful approaches to rehabilitation strategies.

Keywords: Finger independent control; Practice; EEG

1. Introduction

The identification of neural basis underlying the ability to control human fingers has received considerable scientific interest (Fetz and Cheney, 1980; Schieber, 1991; Grafton et al., 1992). This research has examined both *overt* performance parameters as well as *covert* brain mechanisms involved in a variety of motor skills produced by fingers including grasping, writing, keyboarding, and playing musical instruments (Kilbreath and Gandevia, 1994; Elbert et al., 1995; Schlaug, 2001). In a previous research paper examining the role of experience as related to finger independence, we studied experienced piano players and matched controls and reported differential behavioral and EEG results for the two groups (Slobounov et al., 2002b). Overall, musicians showed enhanced ability to control individuated finger movement. We hypothesized that this was related to the differential practice of finger movements between the piano players and the non-piano players. In the present paper, we further examine this hypothesis in two experiments that focus on the role of extensive practice in determining finger independence and the corresponding cortical modulations.

Numerous studies have shown that practice may cause the changes in human cortical activation (Haier et al., 1992; Cohen, 1997; Classen et al., 1998; Toni et al., 1998; Lotze et al., 2003). Early EEG studies revealed alteration of brain

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electrical activity to be a function of extensive practice (Kristeva, 1984; Lang et al., 1989). In particular, the amplitude of movement-related cortical potentials (MRCP) was shown to be changed from the early phase of learning to the later stage of skilled performance (Lang, 2003). Consistent changes in cortical activation patterns (TMS studies) as a function of practice of motor skills have been recently reported by Cohen (1997) and Pascual-Leone et al. (1995, 1999). Moreover, recent behavioral and brain imaging studies have clearly demonstrated the task-specific changes in cortical activity that accompany the acquisition of various motor skills (Hikosaka et al., 2002; Sanes and Donoghue, 2000; Ungerleider et al., 2002). However, no consistent studies examining the electro-cortical alterations associated with acquisition of individuated control of individual fingers have been reported.

There is a fundamental limitation to the capacity of the human motor system to control individuated fingers in that when a person intends to move only one finger, he or she will involuntarily move other fingers as well (Kilbreath and Gandevia, 1994). This phenomenon has been recently discussed in the motor control literature under the rubric of force *enslaving effect*, or interdependency of fingers (Zatsiorsky et al., 2000). Interdependent action of fingers has been the object of anatomical (Fahrer, 1981), neurophysiological (Schieber, 1991; Colebatch et al., 1991; Grafton et al., 1995), biomechanical (Leijnse et al., 1993; Zatsiorsky et al., 2000) and motor control (Li et al., 1998; Latash et al., 2003) research. It has been hypothesized that a central rule exists that regulates the contribution of individuated fingers during the force production tasks via a central neural drive (Li et al., 1998). Considering the scalp-recorded EEG potentials as a reflection of the central neural drive from the cortex to the involved muscle groups (see Jahanshahi and Hallett, 2003 for review), the alterations of MRCP as a function of interdependency of fingers may directly indicate the contribution of central mechanisms to the enslaving phenomenon (Slobounov et al., 2002a).

It has been suggested previously that the structural constraints imposed on individuated finger control is a hard-wired phenomenon preserved at both peripheral (Fahrer, 1981; Leijnse et al., 1993; Li et al., 1998; Zatsiorsky et al., 2000), and central (Schieber, 1991; Colebatch et al., 1991; Grafton et al., 1995) structures. However, there are several empirical findings suggesting that these structural constraints could be partially overcome by practice (Flanders and Soechting, 1992; Parlitz et al., 1998). For example, individuals such as piano players who have performed the task faster and developed independent finger responses, appear to have enlarged cortical representations of fingers (Elbert et al., 1995; Karni et al., 1995, 1998). In addition, individuated control of the ring finger can be improved in individuals such as violin and piano players, despite its higher dependency on other fingers due to a strong biomechanical linkage (Fahrer, 1981), which appears to be related to enlargement of MRCP amplitude at pre-central electrode sites (Slobounov et al., 2002b). These recent findings suggest that what has been considered to be stable structural constraints imposed on individuated finger control in piano players can be modulated by experience.

In the present study, the practice induced alteration in individuated fingers force production patterns and associated changes in scalp recorded MRCP were further examined. Two experiments were designed to test the hypotheses that: (a) novice subjects will display concomitant behavioral and electro-cortical outcome patterns for individual fingers after extensive practice using visual feedback depicting accuracy of force production, and (b) both accuracy of force production, and most importantly, independent finger control can be enhanced by means of deliberate practice (with special emphasis on both the reduction of force enslaving and the reduction of error of force production) using adequate feedback. It is also expected that enhanced accuracy and independent fingers control in force production tasks will accompany specific alteration in MRCP patterns which may indicate the formation of task-relevant neuro-cognitive strategy (Smith et al., 1999; Slobounov et al., 2000).

2. Experiment 1

In this experiment we examined the effect of extensive practice in production of isometric force by individual fingers on behavioral and MRCP outcome patterns. The visual feedback regarding the accuracy of the force produced by the most enslaved (ring) and the least enslaved (index) fingers during both ramp and static phases was provided and its effect on behavioral and EEG patterns was assessed prior to and after practice.

2.1. Methods

2.1.1. Subjects

Six subjects (2 males, 4 females, mean age 24.5, range 19–32 years old) college students with no history of pathologies to either the hand or wrist and without any formal training in music participated in this experiment. All subjects were right handed, according to Edinburgh Handedness Inventory (Oldfield, 1971). Subjects signed an informed consent form approved by the Institutional Review Board of The Pennsylvania State University prior to experimental sessions.

2.1.2. Experimental procedure

Subjects were seated comfortably in an electrically shielded room with the lights dimmed. Their right forearms rested on a table while their hands were placed so that their index, middle, ring, and little fingers were positioned comfortably atop 4 load cells. The position of the load cells was determined for each subject and adjusted individually. Subjects' task involved performing isometric force production with a single specified finger of the right hand while maintaining contact with all the load cells, that is, with the other 3 fingers. It was important that subjects should not lift or use the uninvolved fingers in force production. In the cases that the subjects felt the uninvolved finger(s) were involuntarily producing forces, they were instructed to let them do so.

Each subject participated in two EEG session (pre and post) separated by 12 practice sessions for 3 h, 3 days a week for 4 weeks. The practice session and experimental session were all conducted on separate days. Maximum voluntary contraction (MVC) of each finger was determined before any task was performed. To assess the MVC, the subject was asked to press the load cell with the specified finger and produce as much force as possible for 5000 ms. The subject did this twice and the overall MVC was calculated as the average of two trials. This was done for each finger and before each session. The experimental session consisted of 8 tasks in which the subject was asked to produce two different force levels, 10% and 50% of their MVC and two rates of force development (50% MVC/s, fast and 12.5% MVC/s, slow) with either index or ring fingers.

For the actual task, the subject was presented with a horizontal target line on the computer screen, the procedure having been published elsewhere (Slobounov and Ray, 1998; Slobounov et al., 1998, 2000, 2002a). On-line feedback regarding the subjects' current force level (force trace) produced only by specified finger was given. After reaching the required force level as accurately as possible, subjects were instructed to match their force trace with the target line for the remainder of the trial. The trial durations were always 5000 ms. The contractions were self-paced and the subjects were instructed to maintain a consistent time interval in between trials, which was approximately 8–10 s in length. Subjects performed 40 trials for each task. The order in which the 8 conditions were carried out was randomized for each subject.

2.1.3. Behavioral data acquisition

Force pressure was measured with 4 EL (Entran Devices Inc.) load cells which register the displacement via a strain gauge bridge incorporated in the cell, and each output was transduced via a separate Coulbourn Instrument Transducer Coupler Type A (strain gauge bridge) amplifier. The excitation voltage was set at 7.5 V and the gain was set to (500) with DC coupling. The amplified signal was directed to a National Instruments AT-MIO-16E-10 12-bit A/D board, sampled at a rate of 100 Hz and written to the hard drive of a PC 486 computer. Calibration was achieved by using regression analysis to determine the function relating the force applied, by use of weights of various magnitudes, to that of the voltage output from each load cell. The behavioral data were collected and visual feedback of the subject's force trace was provided by a specially developed program using VisualBasic software.

2.1.4. Behavioral data analysis

For each task, the ramp phase of force production was defined as the time period from the initiation of force production to the point at which the subject reached the required force. The static phase was measured from 2000 to 4000 ms after onset of the force production. To assess the accuracy of force production, the mean absolute error of both the force trajectory formation of the ramp and static phases was computed (see also Slobounov et al., 2002a). The values of 40 repetitions for each condition were averaged within subject and then again averaged between subjects.

The amount of enslaving was calculated similar to Danion et al. (2000) for each non-instructed (enslaved) finger as the mean force produced by that finger normalized to its individual MVC averaged across the time period of the static phase (2000–4000 ms) for each of the 40 trials. The force enslaving was from 2000 to 4000 ms after onset of the force production (Slobounov et al., 2002c).

2.1.5. EEG data acquisition

The continuous EEG was recorded with Ag/AgCl electrodes using a Quik-Cap Electrode Helmet measuring the electrical activity at 17 electrode sites: FP1, FP2, Fz, F3, F4, FCz, FC3, FC4, Cz, C3, C4, CPz, CP3, CP4, Pz, P3, P4, according to the International 10–20 system (Jasper, 1958). Linked earlobes served as reference and electrode impedances were kept below 5 kΩ. The signals were measured using a programmable DC coupled broadband SynAmps amplifier (NeuroScan Inc., El Paso, TX). The EEG signals were amplified (gain 1000, recording range set for ± 55 mV) and bandpass filtered in the DC to 100 Hz frequency range. The EEG data were sampled at 500 Hz, using a separate 16-bit analog-to-digital converter for each channel. Data were collected using NeuroScan's Scan 4.1 software package and written to and stored on a Pentium 166 MHz IBM computer.

2.1.6. EEG data analysis

The EEG signals were first corrected for eye movements (ocular artifact reduction option of NeuroScan's Scan 4.1 software). The load cell trace of the specified finger was used as the trigger, and epochs were established 1500 ms before and 5500 ms after its onset. Electrode DC shift was compensated for off-line by a 4th-order trend correction of each channel over the entire recording epoch in order to remove a drift in the data that extends beyond the sample epoch (linear detrend option of NeuroScan's Scan 4.1 software). The baseline was derived from the average of the segment from 1500 to 1200 ms before the trigger point for each channel. Each epoch was visually inspected and those with artifacts were removed.

The 4 components of MRCP were extracted as: (i) the mean negativity measured between 600 and 500 ms prior to force initiation referred to as *Bereitschaftspotential* (BP) reflecting the cortical activation associated with the early stages for preparation of motor responses (Kornhuber and Deecke, 1965); (ii) the mean negativity measured between 100 ms prior to motor onset and motor onset referred to as *motor potentials* (MP) reflecting the cortical activation associated with later stages for preparation of motor responses (Kristeva et al., 1990); (iii) the mean negativity measured from motor onset to termination of motor onset referred to as *movement monitoring potential* (MMP) (Grünewald-Zuberbier and Grünewald, 1978). The MMP was further divided into the ramp and static phases (see also Slobounov et al., 2002a). The MMP_{ramp} was measured as the mean negativity matched with the ramp phase of the force production. The $\text{MMP}_{\text{static}}$ phase was measured as the mean negativity from 2000 to 4000 ms after the motor onset and represents the portion of the task in which the subjects have maintained the required target force. The MRCP components were calculated for electrode sites representing the frontal, central, and parietal cortical areas. Consistent with current literature, we emphasize results from the frontal-central electrode sites.

2.1.7. Statistical analysis

Behavioral data were estimated using the Statistica software package. A repeated measures analysis of variance (ANOVA) was used to analyze the accuracy data for 4 independent variables, End-effector (index versus ring finger), Force level (10% and 50% of MVC), Rate of force development (slow versus fast) and Session (pre versus post). The dependent variables for the accuracy were the mean absolute errors for both ramp and static phases. The dependent variables for estimating the amount of enslaving were the percentage of force contributed from non-involved fingers during static phase (2000–4000 ms).

A repeated measures ANOVA was used for analysis of EEG data, with the end-effector, nominal force level, rate of force development and session as factors. The dependent variables were the amplitude of the 4 MRCP components at each electrode site under study. A $P < 0.05$ level significance level was employed.

2.2. Results

2.2.1. Behavioral data

2.2.1.1. Accuracy. The representative isometric force traces for one participant performing all task conditions with the index finger prior to and after practice are illustrated in Fig. 1. In addition, the absolute mean error of force production during both ramp and static phases after the 4 weeks of practice is presented in Fig. 2. In this paper, the behavioral data will be presented for the static phase only. The ANOVA indicated a significant effect of force ($F(1,5) = 68.316$, $P < 0.0005$), with 50% condition greater error than that of 10% condition. There were significant main effects of finger ($F(1,5) = 9.3215$, $P < 0.05$) and session ($F(1,5) = 110.28$, $P < 0.0005$), indicating the larger error for the ring finger, which was

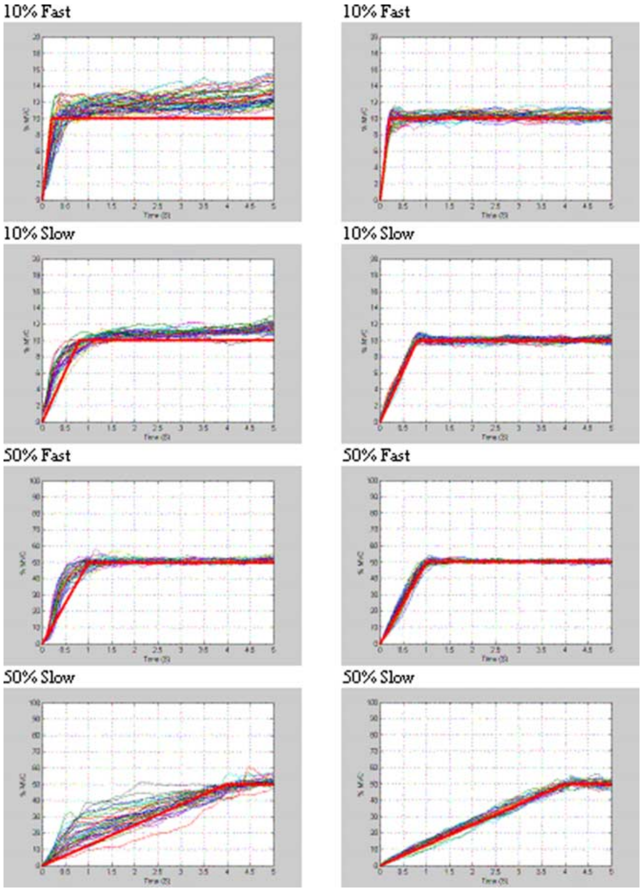

Fig. 1. The representative examples of force-time trajectory formation for one subject performing isometric force production accuracy tasks by the index finger during pre (left column) and post (right column) practice sessions. Forty superimposed trials are shown with respect to the target force.

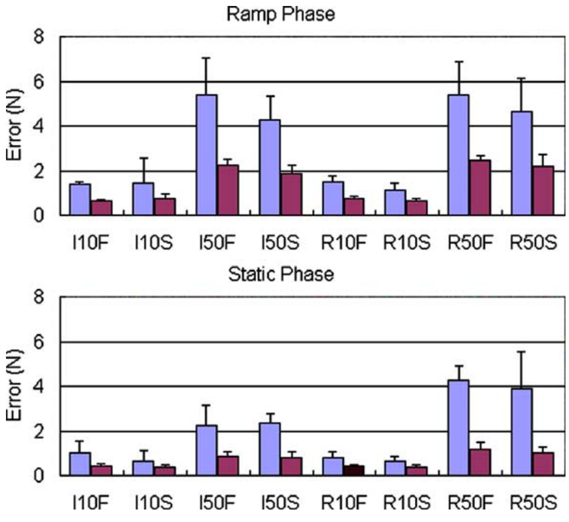

Fig. 2. Mean absolute error of the ramp phase and the static phase for all conditions of force produced by index and ring fingers. Note that the accuracy of force production increased as a function of practice. The data are averaged over all subjects. Error bars show standard errors.

significantly reduced as a function of practice. A 3-way interaction between Session × End-effector × Force was significant ($F(1,5) = 10.56$, $P < 0.05$). The Newman-Keuls post hoc test showed that the smallest error was observed in the ring finger 10% condition, 0.39 N (SD 0.08), and the largest error occurred during the ring finger 50% condition, 3.65 N (SD 1.14). Overall, the absolute mean error for the static phase reduced as a function of practice regardless of finger and/or nominal force level.

2.2.1.2. Force enslaving. The ANOVA indicated that the main effect of session was significant ($F(1,5) = 12.42$, $P < 0.05$), indicating that the total amount of force enslaving increased for both index and ring fingers as a function of practice (see Fig. 3). It should be noted that the amount of MVC across all subjects for both index and ring fingers also increased as a function of practice ($F(1,5) = 14.275$, $P < 0.05$). In addition, there was a significant effect of the criterion Force ($F(1,5) = 62.02$, $P < 0.0001$), with a high force having greater force enslaving than that of the low force condition. There was a significant difference between end-effectors ($F(1,5) = 36.48$, $P < 0.005$) with the index finger having less force enslaving than that of the ring finger. Interestingly, Newman-Keuls post hoc tests revealed that the ring finger became most enslaved in the 50% condition after practice.

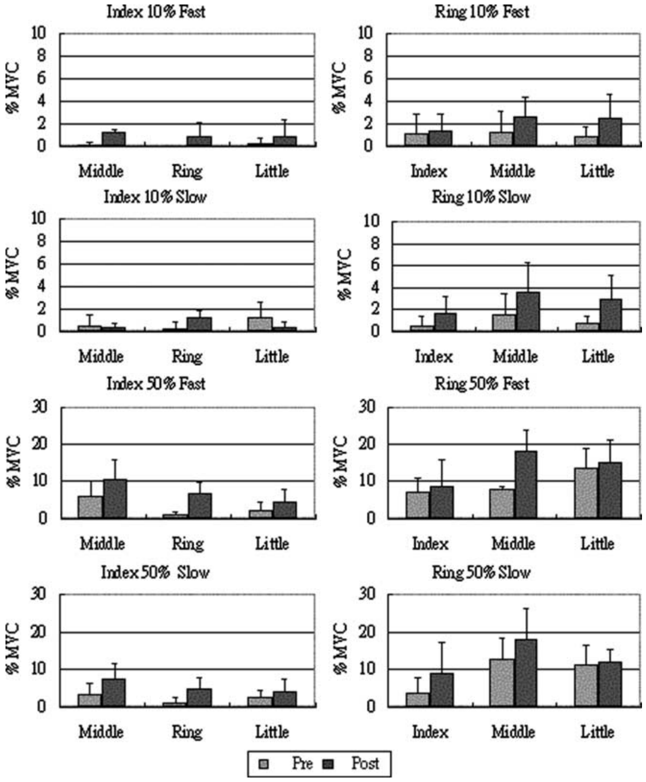

Fig. 3. Averaged values representing percent of enslaving: the contribution of all three uninvolved (slaved) fingers with respect to their MVC is shown when the index and/or ring finger(s) was a master finger performing the task. Note, the percent of enslaving was highest for the ring finger in the 50% MVC task after practice emphasizing the accuracy of force production.

2.2.2. EEG data

2.2.2.1. Motor-related cortical potentials (MRCP). Overall, there was a gradual increase of cortical negativity started about 2 s prior to force onset for both end-effectors and task conditions. The largest amplitude for all MRCP components was observed for the index finger at frontal-central electrode sites (Fz, F3, FCz, FC3, Cz and C3) with the maximum at vertex (Cz) prior to practice. This effect was most obvious in the 50% of MVC task for the index finger performing the fast condition (− 11.67 μV, SD 3.77). The lowest amplitude was observed for the ring finger performing the slow condition, − 4.54 μV (SD 3.72), prior to practice. The grand averaged waveforms of motor-related cortical potentials (MRCP) at Cz electrode site are shown in Fig. 4.

2.2.2.1.1. BP. No significant main effects were observed within the BP at all electrode sites under study. This finding supports previous research in that the BP generally reflects the intention to initiate motor action (see Jahanshahi

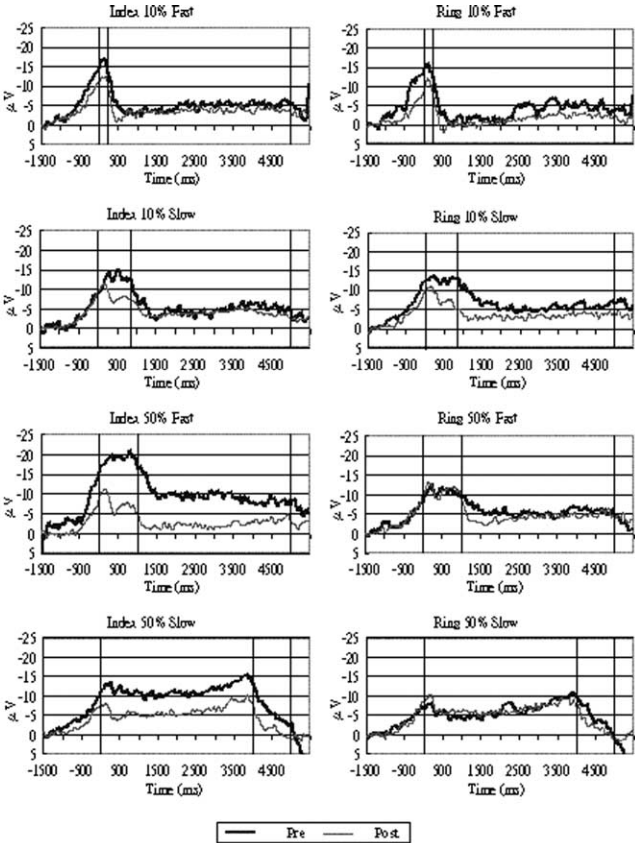

Fig. 4. Grand averaged waveforms of MRCP for the index and ring fingers at Cz electrode site prior to (thick lines) and after (thin lines) practice emphasizing the accuracy of force production. The vertical lines from left to right represent force onset (triggered by a signal from the load cell), time-to-target force, and force termination, respectively.

and Hallett, 2003 for review) and does not fluctuate relative to force production task or anatomical constraints (Slobounov et al., 2002a). However, there was a significant interaction between Session × Rate of force ($P = 0.042$). Newman-Keuls post hoc tests revealed that the fast condition prior to practice demonstrated the highest BP amplitude regardless of end-effector at Cz and Fz electrode sites. No other main effects or interactions were significant in this period.

2.2.2.1.2. MP. A significant main effect of session was observed only for the index finger at Fz, F3, Fcz, Cz and C3 electrode sites ($P < 0.001$), indicating the reduction of MP amplitude as a function of practice. For the ring finger, the MP amplitude was not changed as a function of practice. The ANOVA also indicated a significant main effect of rate of force, $F(1,5) = 24.84$, $P < 0.01$, with the fast condition showing greater amplitude of MP than that of the slow condition at Cz electrode site. The interactions between Force × End-effector as well as Rate of force × End-effector were significant, $F(1,5) = 8.032$, $P < 0.05$ and $F(1,5) = 8.885$, $P < 0.05$, respectively.

2.2.2.1.3. MMP_{ramp}. Similar to MP, a significant main effect of session was observed only for the index finger at frontal-central electrode sites ($P < 0.001$), indicating the reduction of MMP_{ramp} amplitude as a function of practice. For the Cz electrode site, a significant main effect of the criterion Force was observed ($F(1,5) = 17.48$, $P < 0.01$), with the 50% condition greater than that of the 10% condition. There were significant differences on the Rate of force ($F(1,5) = 30.28$, $P < 0.05$) and Session ($F(1,5) = 34.13$, $P < 0.005$) factors. The interaction between Session × End-effector and Session × Force × End-effector were also significant ($F(1,5) = 6.99$, $P < 0.05$; $F(1,5) = 56.96$, $P < 0.001$, respectively).

2.2.2.1.4. MMP_{static}. There was a main effect of session only for the index finger at Cz electrode site ($F(1,5) = 9.61$, $P < 0.05$), indicating the reduction of $\text{MMP}_{\text{static}}$ as a function of practice. The interaction between Session × Force × Finger was also significant ($F(1,5) = 18.949$, $P < 0.01$) at Cz. Newman-Keuls post hoc tests revealed that the greatest and least $\text{MMP}_{\text{static}}$ amplitude were both observed for the index finger prior to practice, -6.7 μV (SD 3.96), and after practice, -1.82 μV (SD 2.29).

2.3. Discussion

This study extended our previous work examining the cortical correlates of individual fingers control (Slobounov et al., 2002a,b,c). The effect of extensive practice with special emphasis on accuracy of isometric force produced separately by the index and ring finger in this experiment was examined in terms of behavioral and EEG data. The major behavioral finding from this experiment is that force enslaving increased along with improved accuracy of force production after 4 weeks of extensive practice. It should be noted that in this experiment subjects were instructed to solely produce the task as accurate as possible. The reduced absolute error of force production after practice is generally attributed to neural adaptation (Semmler and Enoka, 1998) and/or motor learning (Schmidt, 1998; Newell and Carlton, 1985). On the other hand, unexpected increased force enslaving could be explained by the fact that the maximal voluntary contraction (MVC) also increased after practice. It has been shown recently that the percent of enslaving for both the index and ring fingers proportionally increased as a function of nominal force (Slobounov et al., 2002a,c). Accordingly, since the nominal force increased with practice, the percent of enslaving should increase as well. An alternative explanation is that subjects *intentionally* activated non-involved fingers in order to accommodate the task demands to produce the required force as accurate as possible.

At the cortical level, reduced amplitude of MRCP for the index finger as a function of practice is consistent with numerous EEG (Kristeva, 1984; Smith et al. (1999) and other neuroimaging (Haier et al., 1992; Karni et al., 1995) studies. Surprisingly though, the amplitude of MRCP for the ring finger remained unchanged despite the increased accuracy of force production. Thus, the accuracy of force produced by the index (less enslaved) and ring (most enslaved) fingers consistently increased with practice, although MRCP did not. Therefore we argue that MRCP are more indicative of amount of force enslaving (Slobounov et al., 2002a) and subjects' effort (Deecke, 1990; Deecke and Kornhuber, 2003) rather than increased accuracy of task production.

3. Experiment 2

In this experiment we examined the effect of deliberate practice with special emphasis on reduction of finger force enslaving on behavioral and MRCP outcome patterns. Accordingly, the online visual feedback regarding both the activation of neighboring fingers (force *enslaving feedback*) and accuracy of the force produced by the *master* (index and/or ring finger) was provided and its effect on behavioral and EEG patterns was assessed prior to and after practice.

3.1. Methods

3.1.1. Subjects

Six subjects (2 males, 4 females, mean age 25.3, range 21–29 years old) were all right-handed with no history of pathologies to either the hand or wrist and without any formal training in music. The degree of hand dominance was assessed by a 12-point questionnaire (Edinburgh Handedness Inventory, Oldfield, 1971). Subjects signed an informed consent form approved by the Institutional Review Board of The Pennsylvania State University.

3.1.2. Experimental procedure

The experimental procedure was generally similar to Expt. 1 with a modification of the practice sessions (9 h per week for 4 weeks) and the addition of force enslaving feedback being provided. For the enslaving feedback, 4 light emitting diodes (LEDs), corresponding to each of the 4 fingers (index, middle, ring and little), were displayed at the bottom of the computer monitor for each trial. Two different LED thresholds were set for the master finger as well as for the enslaved fingers. These were determined by the experimental setting and by the thresholds for the three enslaved fingers, which were calculated as 5% of the middle finger's MVC. The middle finger was chosen as the reference since it lies between the ring and index fingers. Five percent of MVC was chosen to create a buffer zone, thus allowing the subject to place the enslaved finger on its load cell without setting off the trigger. Before each block of trials, the subjects were informed which of the two possible master fingers (index versus ring) would be used for the upcoming trial. In addition, the LED corresponding to the master finger became yellow. It returned to white once the force produced by the master finger reached the threshold. The LEDs for the enslaved fingers turned to green when the forced produced was beyond the set threshold.

3.1.3. Behavioral data acquisition and behavioral data analysis

This procedure was carried out as for Expt. 1.

3.1.4. EEG data acquisition and analysis

This procedure was carried out as for Expt. 1.

3.2. Results

3.2.1. Behavioral data

3.2.1.1. Force enslaving. Averaged values representing the percent of enslaving across all subjects for the static phases are reported in Fig. 5. The ANOVA indicated that there was a main effect of end-effectors ($F(1,5) = 19.791$, $P < 0.01$), with the index finger having less enslaving than that of the ring finger. It was also found that force enslaving increased as a function of the criterion Force ($F(1,5) = 113.68$, $P < 0.005$). The factor Session was significant ($F(1,5) = 10.047$, $P < 0.05$) indicating that force enslaving decreased with practice.

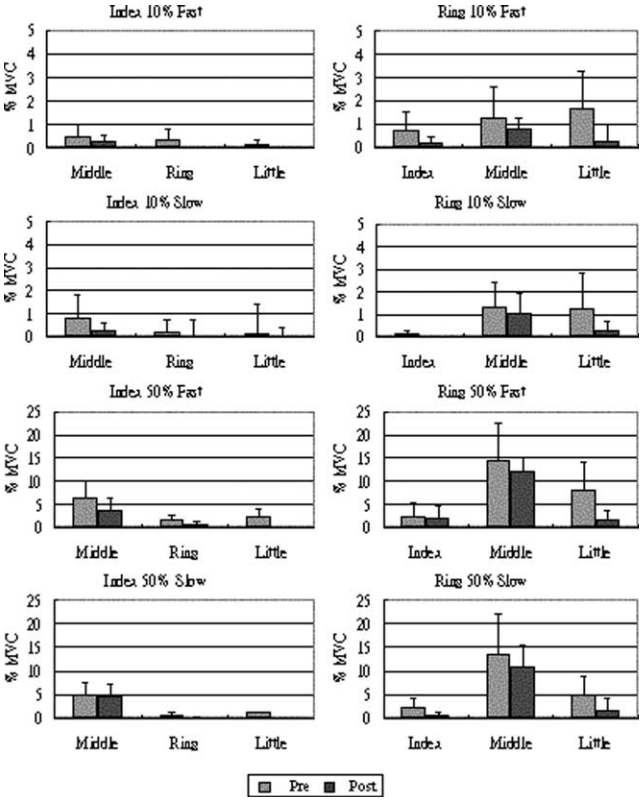

Fig. 5. Averaged values representing percent of enslaving: the contribution of all three uninvolved (slaved) fingers with respect to their MVC is shown when the index and/or ring finger(s) was a master finger performing the task. Note, overall, the percent of enslaving considerably reduced after practice but was still highest for the ring finger in the 50% MVC task.

3.2.1.2. Accuracy. The absolute mean error of force production during both ramp and static phases was reduced after the 4-week practice period (see Fig. 6). For the static phase, the ANOVA indicated a significant effect of Session ($F(1,5) = 34.234$, $P < 0.001$), and highly significant criteria Force ($F(1,5) = 68.316$, $P < 0.0001$) and End-effectors ($F(1,5) = 9.3215$, $P < 0.001$). The interaction between End-effector × Force × Rate of force was also significant ($F(1,5) = 27.72$, $P < 0.005$). The Newman-Keuls post hoc test showed that the smallest error observed in the index finger performing 10% fast condition, 0.56 N (SD 0.15), while the largest error was observed in the ring finger performing 50% fast condition, 4.09 N (SD 0.69).

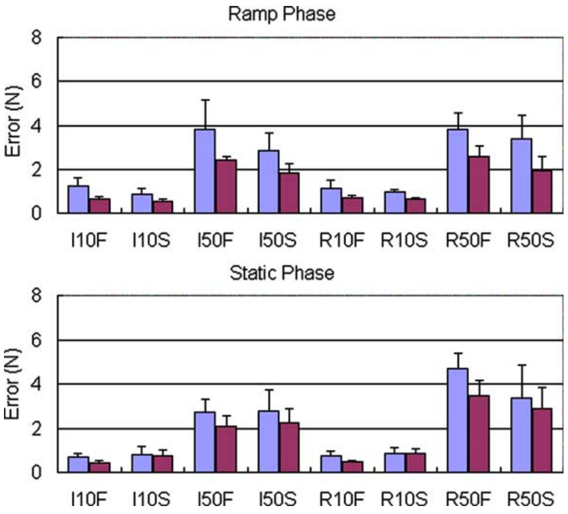

Fig. 6. Mean absolute error of the ramp phase and the static phase for all conditions of force produced by index and ring fingers. Note that the accuracy of force production increased as a function of practice. The data are averaged over all subjects. Error bars show standard errors.

3.2.2. EEG data

3.2.2.1. MRCP. Overall, the amplitude of the MRCP was end-effector specific and changed as a function of practice. It increased for the ring finger following deliberate practice with special emphasis on force enslaving reduction. Similar to Expt. 1, the amplitude of MRCP decreased for the index finger as a result of deliberate practice (see Fig. 7).

3.2.2.1.1. BP. The ANOVA indicated significant main effects of Session ($F(1,5) = 6.66$, $P < 0.05$) and Force ($F(1,5) = 8.16$, $P < 0.05$) at Cz electrode site similar to other frontal-central areas under study. Significant interactions between Session × Force × End-effector ($F(1,5) = 14.94$, $P < 0.05$) and between Session × Rate of force × End-effector ($F(1,5) = 7.66$, $P < 0.05$) were also revealed. The highest amplitude of the BP was observed for the index finger prior to practice performing 10% MVC condition, -5.08 μV (SD 3.27), and the lowest amplitude of the BP was observed for the ring finger performing the 50% MVC condition, -1.20 μV (SD 2.53).

3.2.2.1.2. MP. For the motor potential (MP), the ANOVA indicated a significant main effect of Session ($F(1,5) = 21.87$, $P < 0.01$). This was most evident at Cz, Fcz and C3 electrode sites. Similar to BP, the interaction between Session × Force × End-effector ($F(1,5) = 18.16$, $P < 0.05$) was significant. The highest amplitude of the MP was observed for the index finger prior to practice when performing the 10% MVC condition, -15.51 μV (SD 7.43), and the lowest amplitude of MP was observed for the ring finger when performing the 50% MVC condition, -5.45 μV (SD 4.14).

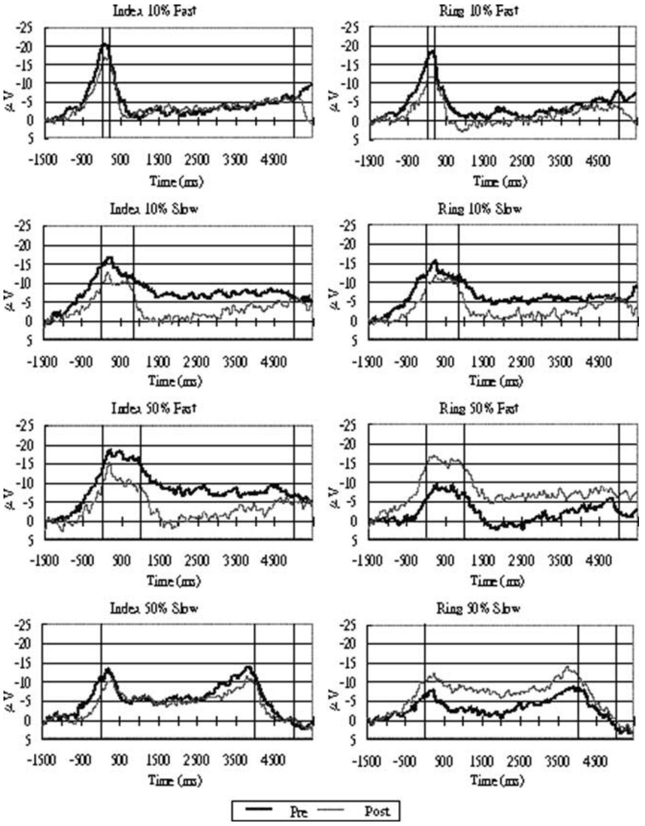

Fig. 7. Grand averaged waveforms of MRCP for index and ring fingers at Cz electrode site prior to (thick lines) and after (thin lines) practice with the emphasis on individual finger control. The vertical lines from left to right represent force onset (triggered by a signal from the load cell), time-to-target force, and force termination, respectively.

3.2.2.1.3. MMP_{ramp}. The main effect of Session was not significant for all electrode sites under study, $P > 0.05$. There was a significant main effect of the criterion Force ($F(1,5) = 13.35$, $P < 0.05$). Rate of force was also significant ($F(1,5) = 10.69$, $P < 0.05$), with the fast condition having greater amplitude than that of the slow condition. A 3-way significant interaction between Session × Force × End-effector ($F(1,5) = 18.16$, $P < 0.05$) was observed. The highest amplitude of the MMP_{ramp} was observed for the ring finger in the 50% MVC condition, -16.96 μV (SD 9.25), and lowest amplitude of MMP_{ramp} was observed for the index finger in the 10% MVC condition, -6.05 μV (SD 5.41).

3.2.2.1.4. MMP_{static}. No significant main effects were observed for this MRCP component at any electrode site. However, there was a 2-way significant interaction between Force × Rate of force ($F(1,5) = 15.95$, $P < 0.05$). In addition, the interaction between Session × Force × End-effector ($F(1,5) = 18.16$, $P < 0.05$) was also significant. The lowest amplitude of $\text{MMP}_{\text{static}}$ was observed for the ring finger prior to practice, -1.95 μV (SD 3.93), and which was significantly increased after practice, -5.49 μV (SD 4.51).

3.3. Discussion

The major behavioral finding from this experiment is that individual finger control may be considerably improved by means of deliberate practice with special emphasis on the reduction of both force enslaving and the accuracy enhancement of force production. This was most evident in the behavioral data when analyzing the ring finger after practice. This evidence supports our previous hypothesis based on existing empirical findings (Slobounov et al., 2002b; Flanders and Soechting, 1992; Parlitz et al., 1998) that the structural constraints imposed on individuated finger control is not a hard-wired phenomenon and could be partially overcome by deliberate practice. In terms of EEG measures, a reduction in the amplitude of the MRCP was observed after practice for the index finger across all conditions which were similar to Expt. 1. This was not the case for the ring finger. In particular, as the ring finger became more independent (i.e. less enslaving), the amplitude of the MRCP significantly increased. In fact, the amplitude of the MRCP for the ring finger after practice was as high as that of the index finger prior to practice. This finding is consistent with previous MRCP research indicating the enhancement of negative cortical potential in the early phase of the visuomotor learning task over the prefrontal cortex and other frontomedial areas (Lang, 2003; Deecke and Kornhuber, 2003).

4. General discussion

Based on previous work from our laboratory, we examined the role of practice as related to force enslaving and the concomitant EEG changes. Since our initial work with piano players suggested an important role for experience in finger independence (Slobounov et al., 2002b), the present experiments allowed us to address this question directly. Although Expt. 1 found an improvement in accuracy which would be expected from practice, it also found an increase in force enslaving which might not initially be expected. This suggests an initial tradeoff between accuracy and force enslaving. It also suggests that our subjects after 4 weeks of practice were still early in their achievement of an independence of individual finger control. Given that the piano players in our previous study had at least 10 years of experience, the question arises as to the point in the learning trajectory that once accuracy is achieved, force enslaving is decreased. If, however, force enslaving was sought to be reduced directly as in our second experiment, then it is possible to achieve both a reduction in force enslaving and an increase in accuracy in a fairly short period. As consistent with both our previous work (Slobounov et al., 2002a,b,c) and that of others (Zatsiorsky et al., 2000; Latash et al., 2002a,b) these results are in agreement with a view that rules out exclusively peripheral explanations of force enslaving and emphasizes the importance of central mechanisms.

In terms of cortical measures, we found EEG changes consistent with our previous work showing EEG to be more sensitive to rate of force development rather than force itself (Slobounov et al., 1998). Concerning the role of experience, we found the greatest motor potential changes in both experiments to be for the index finger as compared to the ring finger. One way to understand this finding is to suggest that our subjects prior to the experiments had more experience in making skilled movements with their index finger than their ring finger. Thus, the 4 weeks of practice had more effect on the index finger in terms of motor potentials. This finding is consistent with our previous musician study in that non-piano players showed a differential finger response whereas musicians did not. It is an open question as to the time duration naïve subjects would begin to show ring finger EEG changes consistent with less force enslaving as seen in our previous study with musicians. It is also possible given that the ring finger is more tightly connected to the neighboring fingers by ligaments than the index finger that there is more structural limitations on the ring than index finger.

It is suggested that the amount of muscle mass activated in the task is inversely related to the cortical activation (Kitamura et al., 1993). Previously we have found that the amplitude of the MRCP varied among fingers (Slobounov et al., 2002a). Due to the fact that the force produced by enslaved fingers increased after 4 weeks of practice, both index and ring fingers showed larger force enslaving. As a result, the MRCP of the index finger decreased after practice with the involvement of other fingers. However, the amplitude of MRCP in the ring finger in the 10% tasks was reduced since less force enslaving was observed during low level of force. Therefore, the reduction of MRCP after practice needs to be further investigated. There are a variety of factors which may influence this relationship. One could be structural in that ring and index fingers are differentially coupled with those nearby. While this was taking place on a peripheral level, the central process required inhibitory processes to both reduce enslaving and increase accuracy. This interaction of peripheral and central factors could explain the differential cortical results between the ring and index finger in our second experiment as well as be an important area for future research.

The concluding theme emergent from these experiments is that individuated finger control is not hard-wired, but rather plastic and greatly modulated by deliberate practice. This modulation can be seen through the formation of task-relevant neuro-cognitive strategies (Smith et al., 1999; Slobounov et al., 2000) which enable individuals to accomplish an accurate control of individuated fingers. The manner in which individual fingers may be peripherally constrained through differential ligament structure must also be considered and should be included in the final equation concerning the role of structural processes, central processes and that of practice. One implication of this current work is that practice-related procedures may be a critical component of new effective approaches to rehabilitation in general (e.g. Taub et al., 2002) and such disorders as focal hand dystonia in particular (e.g. Candia et al., 1999, 2002, 2003). For example, treatment directed toward the reduction of force enslaving as well as treatment related feedback may improve individuated control of individual fingers. An interesting question would be the manner in which pre-morbid motor learning would influence post-morbid recovery. By answering such questions, older perspectives in rehabilitation of motor responses which suggest little in the way of central nervous system plasticity should give way to an exploitation of basic research findings related to central processes and the types of skills to be practiced.

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