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Clinical Neurophysiology 113 (2002) 2013–2024

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Modulated cortical control of individual fingers in experienced musicians: an EEG study

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Accepted 4 September 2002

Abstract

Objective: The present research was designed to address the nature of interdependency between fingers during force production tasks in subjects with varying experience in performing independent finger manipulation. Specifically, behavioral and electroencephalographic (EEG) measures associated with controllability of the most enslaved (ring) and the least enslaved (index) fingers was examined in musicians and non-musicians.

Methods: Six piano players and 6 age-matched control subjects performed a series of isometric force production tasks with the index and ring fingers. Subjects produced 3 different force levels with either their index or ring fingers. We measured the isometric force output produced by all 4 fingers (index, ring, middle and little), including both ramp and static phases of force production. We applied time-domain averaging of EEG single trials in order to extract 4 components of the movement-related cortical potentials (MRCP) preceding and accompanying force responses.

Results: Three behavioral findings were observed. First, musicians were more accurate than non-musicians at reaching the desired force level. Second, musicians showed less enslaving as compared to non-musicians. And third, the amount of enslaving increased with the increment of nominal force levels regardless of whether the index or ring finger was used as the master finger. In terms of EEG measures, we found differences between tasks performed with the index and ring fingers in non-musicians. For musicians, we found larger MRCP amplitudes at most electrode sites for the ring finger.

Conclusions: Our data extends previous enslaving research and suggest an important role for previous experience in terms of the independent use of the fingers. Given that a variety of previous work has shown finger independence to be reflected in cortical representation in the brain and our findings of MRCP amplitude associated with greater independence of fingers in musicians, this suggests that what has been considered to be stable constraints in terms of finger movements can be modulated by experience.

Significance: This work supports the idea that experience is associated with changes in behavioral and EEG correlates of task performance and may have clinical implications in disorders such as stroke or focal hand dystonia. Practice-related procedures offer useful approaches to rehabilitation strategies. © 2002 Elsevier Science Ireland Ltd. All rights reserved.

Keywords: Force; Enslaving; Movement-related cortical potentials; Musicians

1. Introduction

When individuals produce either maximal (Zatsiorsky et al., 1998, 2000) or sub-maximal force levels (Slobounov et al., 2000, 2002a,b,c) with one finger, the other fingers involuntarily contribute to the total force production. This phenomenon has been termed the force enslaving, or interdependency of fingers (Kilbreath and Gandeiva, 1994; Li et al., 1998; Zatsiorsky et al., 2000). The force enslaving phenomenon has been widely investigated from anatomical (Fahrer, 1981; Nordin and Frankel, 1989), neurophysiological (Schieber, 1991, 1999; Colebatch et al., 1991; Grafton et al., 1991; Slobounov et al., 2000), biomechanical (Flanders and Soechting, 1992; Soechting and Flanders, 1992; Leijnse et al., 1993; Zatsiorsky et al., 1998) and motor control (Latash et al., 1998, 2002; Li et al., 1998; Zatsiorsky et al., 2000) perspectives. In this literature, 3 main mechanisms have been related to the enslaving phenomenon: (i) mechanical constraints that exist between the tendons and the muscles in all fingers (Fahrer, 1981; Nordin and Frankel, 1989); (ii) motor units in the flexor and extensor muscles being co-activated (Bernardi et al., 1996), and (iii) the repre-

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PII: S1388-2457(02)00298-5

CLINPH 2002089

sentation of various fingers in the cerebral cortex (Alexander and Crutcher, 1990; Hepp-Reymond and Maier, 1991; Schieber and Hibbard, 1993).

Using multi-finger force production tasks, the enslaving effect is reported to be nearly symmetrical, non-additive and larger for neighboring fingers (Li et al., 1998; Zatsiorsky et al., 2000). These initial studies used maximal isometric force production tasks. More recently, we have varied the force level and observed both ramp and static phases of these isometric force tasks in relation to enslaving (Slobounov et al., 2002a,b,c). We found that (1) the amount of enslaving increased with increments of nominal force levels whether the index, middle, ring or little fingers were used as the master finger; (2) enslaving is the strongest in the fingers directly adjacent to the master finger; and (3) in terms of enslaving, the index finger was more 'independent' than the other 3 fingers, regardless of nominal force produced, followed by the little, middle, and ring fingers. Research has shown that the activation of one digit can lead to activation of other digits and is proportional to the loci of other digits and to the rate of force development (Amis, 1987; Kinoshita et al., 1995; Li et al., 1998). Recent research from our laboratory and others has sought to move beyond a purely anatomical explanation of enslaving to examine the role of cortical processes.

In the present paper, we extend this work by examining individuals who have had extensive experience with digit manipulation (piano players) with those who have not. Years of experience enable expert musicians to perform precise and reproducible motion patterns with an independent coordination of playing and non-playing fingers (Flanders and Soechting, 1992; Parlitz et al., 1998). Specifically, professional piano players are able to relax their playing fingers immediately after each touch, whereas control subjects remain in a state of tension much longer after the touch (Parlitz et al., 1998). Moreover, acquisition of muscle strength in musicians is related to the enhancement of mobility of the fourth (ring) finger (Lee, 1990), despite its higher dependency on other fingers due to a strong biomechanical linkage (Fahrer, 1981; Kilbreath and Gandevia, 1994) and substantial overlap of the cortical territories associated with adjacent digits (Schieber and Hibbard, 1993).

In terms of cortical processes, research has shown that parameters of use are related to cortical representation. For example, Elbert and his colleagues reported that in well-practiced right-handed string players (e.g. violin players), there was an increase in cortical representation of the fingers of the left hand but not in the right (Elbert et al., 1995). Likewise, loss of use through accident or disease has also resulted in cortical reorganization, which can form the basis of new treatment approaches (e.g. Taub et al., 2002). In this paper, we further explore the nature of interdependency between fingers during force production tasks in different subject populations and argue that individuated finger control in musicians can be modulated by experience which may induce specific effects on behavioral and EEG correlates of task performance.

2. Materials and method

2.1. Subjects

Six piano players (two males, 4 females, mean age 29.2 years, range 21–40 years) with at least 10 years of experience were included in the 'musician' group. The subjects were recruited from the Music Department of Penn State University and practiced at least 2 h a day (mean 5.2 h). Six age-matched control subjects (one male, 5 females, mean age 29.2 years) were included in the 'non-musician' group. All subjects were right-handed (Oldfield, 1971) with no history of neurological conditions or pathologies to either the hand or wrist. Subjects signed an informed consent form approved by the Institutional Review Board of The Pennsylvania State University prior to experimental sessions.

2.2. 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. The 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. When the subjects felt the uninvolved finger(s) were involuntarily producing forces, they were instructed to let them do so.

All subjects were given a practice session to become familiar with the behavioral task. The practice session and the 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, subjects were asked to press the load cell with the specified finger and produce as much force as possible for 5000 ms. The subjects 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 6 tasks in which the subject was asked to produce 3 different force levels, 10, 25, and 50% of their MVC with either index or ring fingers. For the actual task, the subjects were presented with a horizontal target line on the computer screen representing either 10, 25, or 50% of their MVC (the experimental procedure was published elsewhere, Slobounov et al., 1998, 2000b, 2002a,b,c). On-line feedback regarding the subjects' current force level (force trace) produced only by the specified finger was also given. The subjects were instructed to reach the target line at its intersection with a vertical line corresponding to 200 ms (for 10% MVC), 500 ms (for 25% MVC), and 1000 ms (for 50% MVC), at a constant slope (rate of force development, Newell and Carlton, 1985). Changing the time in which the subjects were required to reach the target force level and asking subjects to maintain a constant slope was done so that the rate of force development remained constant regardless of the force level. After reaching the required force level, subjects were asked to match their force trace with the target line for the remainder of the trial (see Fig. 1). The entire trial length was 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.

2.3. Behavioral data acquisition

Force pressure was measured with 4 Entran Devices, Inc. *EL* 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 TM 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.

2.4. 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 the force trajectory formation of both the ramp and static phases was computed (see also Slobounov et al., 2000). The values of 40 repetitions for each condition were averaged within subject and then again averaged between subjects.

The amount of enslaving for each non-instructed (enslaved) finger was calculated by a procedure similar to that of Danion et al. (2000) 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.

2.5. 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,

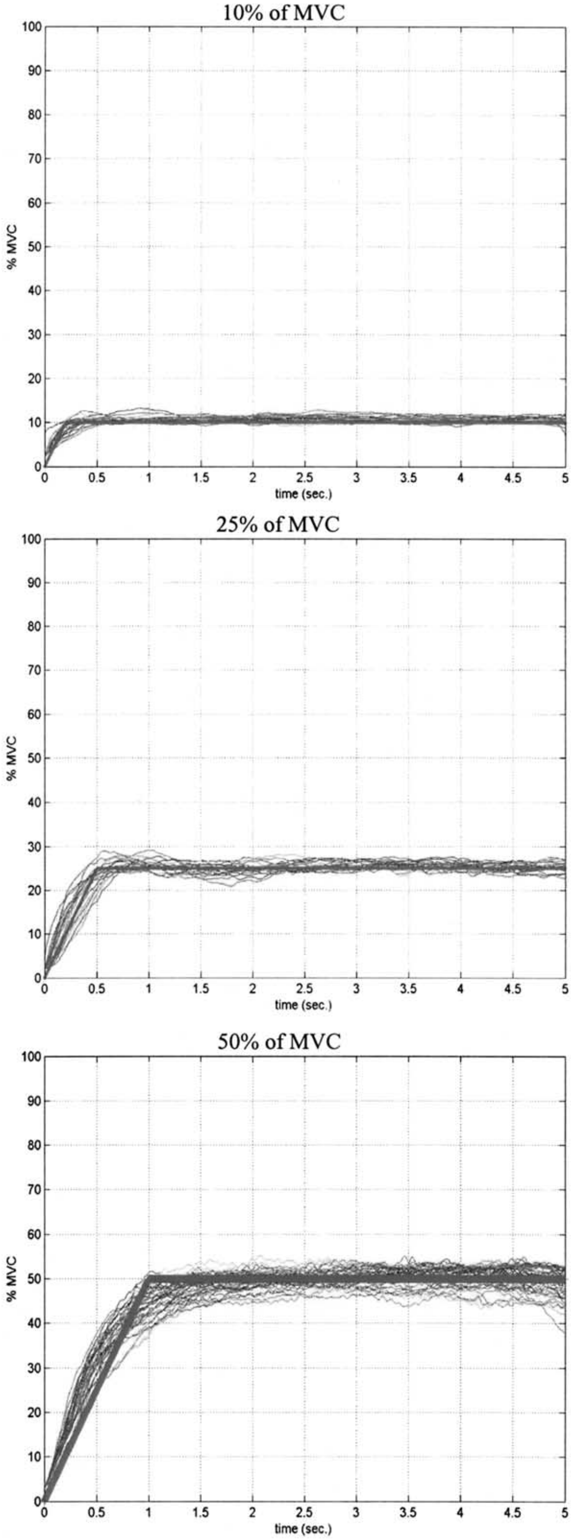


Fig. 1. Representative examples of force–time trajectory formation for the index finger when musicians performed 10, 25 and 50% of maximum voluntary contraction (MVC) tasks. Forty superimposed trials are shown with respect to the target force. Note the rate of force development is required to remain constant, so that the ramp phase was accomplished within 200 ms (10%), 500 ms (25%) and 1000 ms (50%) time frames.

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 band-pass 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.

2.6. 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 fourth 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 Bereitshaftspotential ($\mathrm{BP}_{-600\ \mathrm{to}\ -500}$) 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 ($\mathrm{MP}_{-100\ \mathrm{to}\ 0}$) 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; Foit et al., 1982). The MMP was further divided into the ramp and static phases (see also Slobounov et al., 2002a,b,c). The MMPramp was measured as the mean negativity matched with the ramp phase of the force production. The MMPstatic 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 (see Fig. 2). 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.

2.7. Statistical analysis

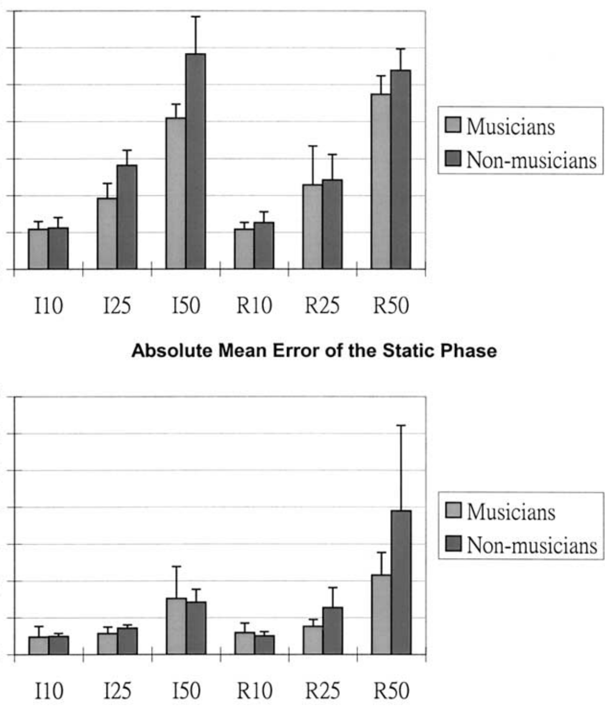
Both the accuracy and enslaving data were estimated using the Statistica software package. A 3-way repeated measures analysis of variance (ANOVA) was used to analyze the accuracy data for 3 independent variables; group (musicians vs. non-musicians), finger (index vs. ring finger), and force level (10, 25, and 50% of MVC). The dependent variables for the accuracy were the mean absolute errors for both the ramp and static phases. The dependent variables for estimating the amount of enslaving were the percentage of force contributed from non-involved fingers during the static phase (2000–4000 ms).

A 3-way repeated measures ANOVA was used for analysis of EEG data. The dependent variables were the amplitude of the 4 MRCP components at each electrode site under study. A significance level of $P < 0.05$ was employed.

3. Results

3.1. Behavioral data

Representative examples of force traces obtained from musicians performing 10, 25 and 50% MVC tasks by index finger is shown in Fig. 1. Two 2×3 repeated measures ANOVAs were carried out on the behavioral data for group, end-effector, and criterion force as factors. The mean absolute error of both the ramp and static phases is shown in Fig. 2. For the ramp phase, the main effect of



Absolute Mean Error of the Static Phase

Fig. 2. Mean absolute error of the ramp phase and the static phase during 3 levels (10, 25 and 50% MVC) of force produced by index and ring fingers. Note the accuracy of force production reduced as a function of nominal force level in both subjects (musician and non-musicians) groups. The data are averaged over all subjects. Error bars show S.E.

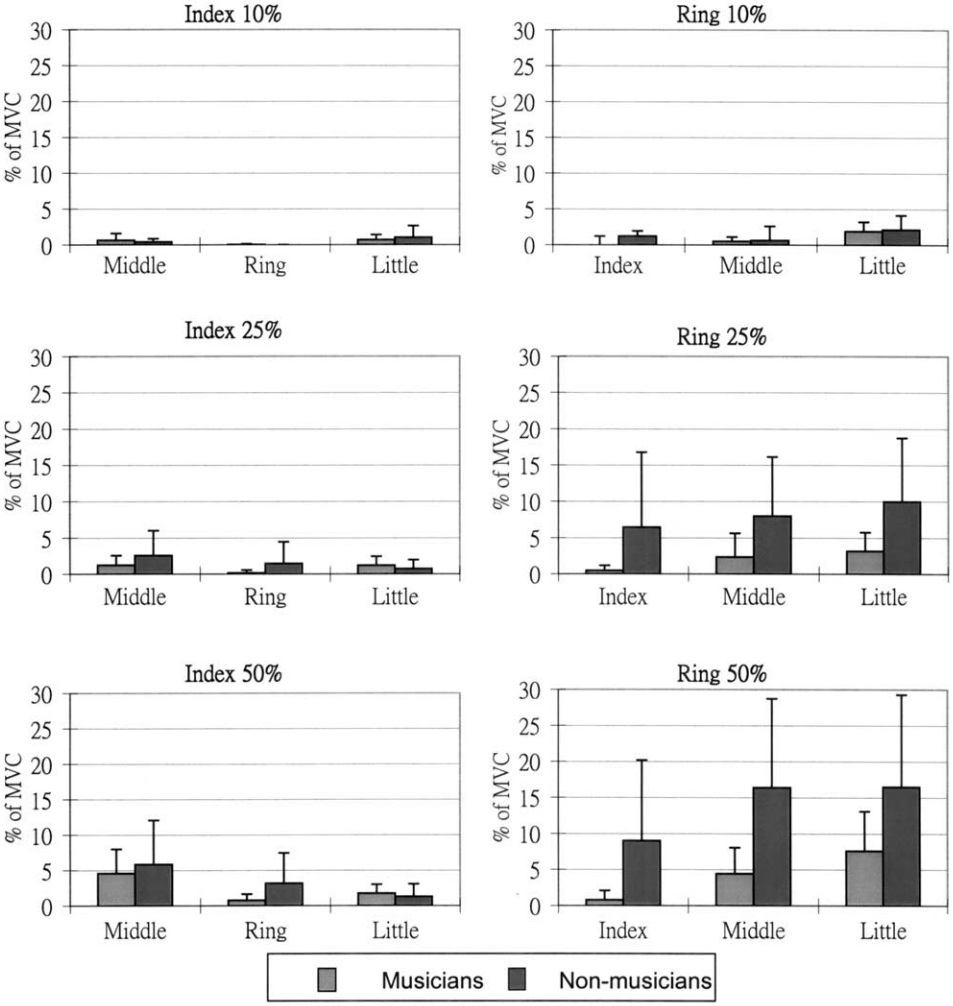


Fig. 3. Averaged values across musicians and non-musicians representing the percent of enslaving: the contribution of all 3 of the uninvolved fingers in terms of percentage of their MVC when the index and/or ring finger(s) was master finger performing 10, 25 and 50% of MVC tasks. Note, enslaving was highest when non-musicians performed 50% task by the ring finger.

group was significant, $F(1,5) = 13.623$, $P < 0.05$, showing that musicians were better able to reach the required force level than non-musicians. As can be seen from Fig. 2, the main effect of force is highly significant $F(1,10) = 384.45$, $P < 0.001$ with the greatest error at 50% MVC. In contrast, the main effect of group for the static phase was not significant.

The main effect of finger was not significant for the ramp and static phases suggesting that musicians and non-musicians were equally accurate when using either index or ring fingers. In addition, consistent with previous studies (Slobounov et al., 2000; Sliffkin and Newell, 2000), Newman–Keuls post hoc tests revealed that the absolute mean errors of both the ramp and static phases proportionally increased as a function of nominal force, $P < 0.001$.

A differential amount of enslaving between the groups and fingers was observed in this study (see Fig. 3). First, the amount of enslaving was significantly larger for the ring finger than for the index finger in non-musicians,

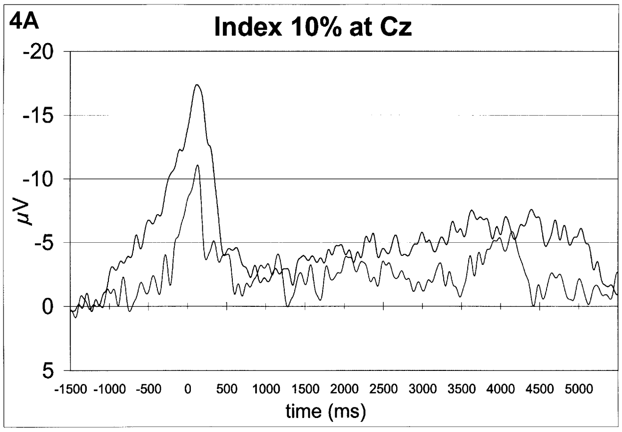


Fig. 4. Grand averaged waveforms of MRCP for musicians and non-musicians at frontal–central electrode sites preceding and accompanying (A) 10% (B) 25% and (C) 50% fingers isometric force production tasks. The black vertical line indicates the movement initiation triggered by a signal from the load cell.

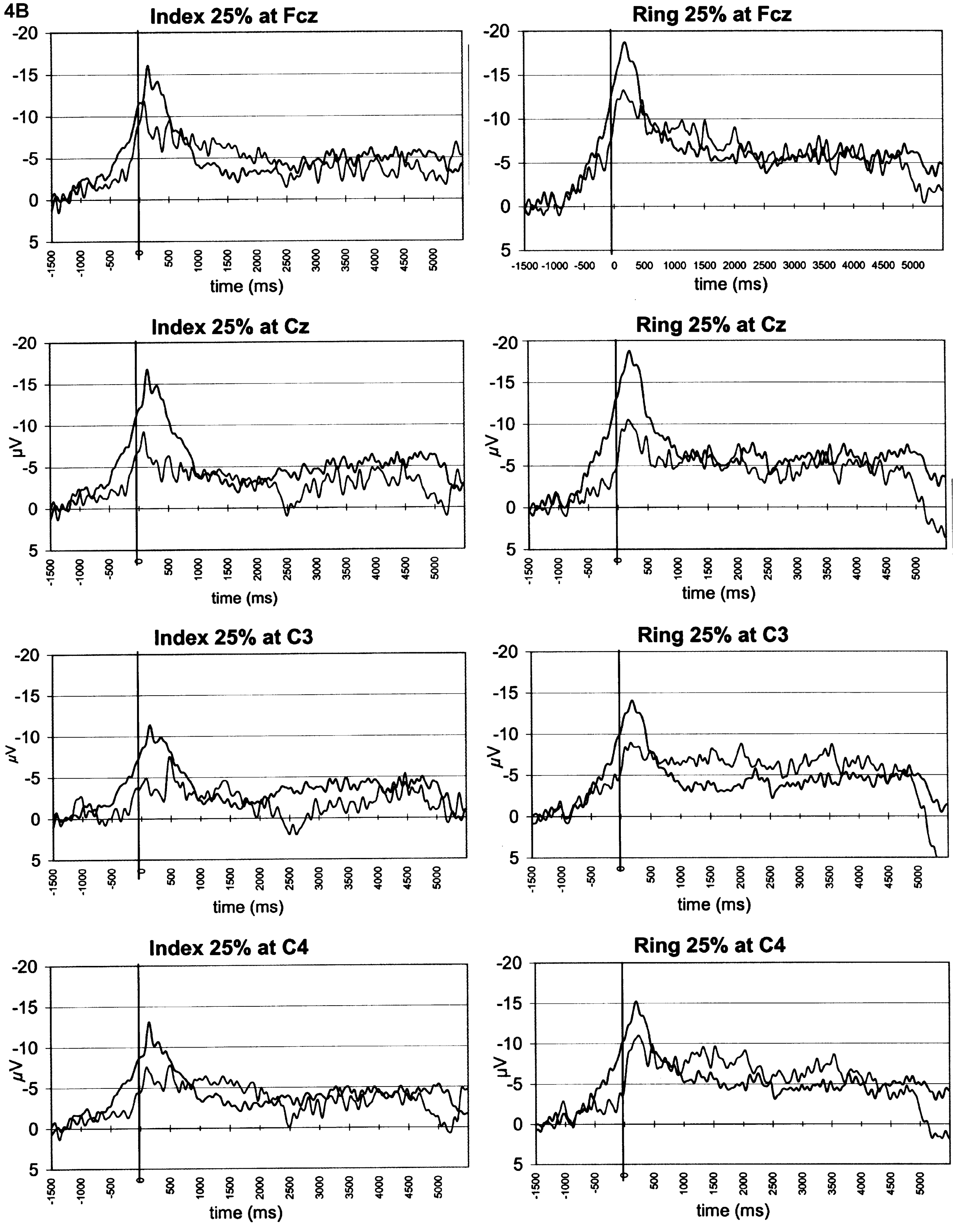
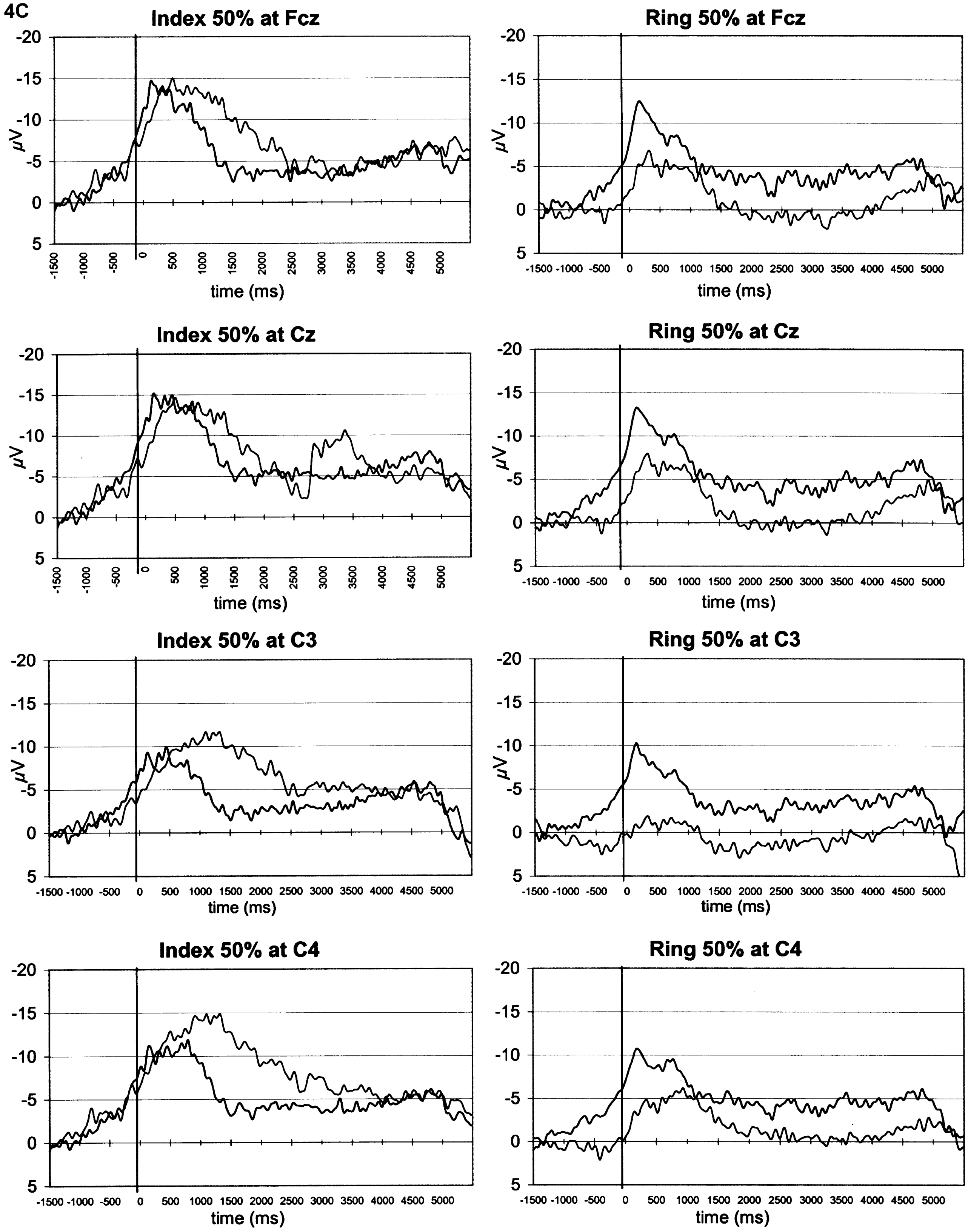


Fig. 4. (*continued*).



Index 50% at Fcz

Ring 50% at Fcz

Index 50% at Cz

Ring 50% at Cz

Index 50% at C3

Ring 50% at C3

Index 50% at C4

Ring 50% at C4

Fig. 4. (*continued*).

$F(1,5) = 12.74$, $P < 0.05$. Interestingly, less interdependency of fingers as reflected in the lack of significant enslaving differences between fingers was observed in musicians. Second, the main effect of force level was significant, $F(2,10) = 9.65$, $P < 0.005$, showing that the amount of enslaving increased with the increment of nominal force level regardless of whether the index or ring finger performed the task. There was also a significant interaction between fingers and groups, $F(1, 5) = 6.95$, $P < 0.05$, which resulted in the ring finger in non-musicians being associated with higher levels of enslaving.

3.2. Motor-related cortical potentials (MRCP)

The grand average waveforms of MRCP at the central (C3, Cz, FCz, C4) electrode sites associated with force production tasks performed by index and ring fingers in both group of subjects are shown in Fig. 4. As can be seen in this figure, the largest MRCP amplitudes were observed when musicians performed the 10% MVC task with the index finger. Interestingly, a similar amount of negativity prior and during initiation of force was observed at both contra-lateral and ipsilateral electrode sites with the maximum at the vertex (Fcz and Cz). A $2 \times 2 \times 3$ repeated measures ANOVA was performed to test the effects of group (musicians versus non-musicians), finger (index versus ring finger), and nominal force (10, 25 and 50% MVC) separately on the amplitude of the 4 MRCP components at each electrode site under study.

3.2.1. $BP_{-600\ to\ -500}$

For $\mathrm{BP}_{-600\ \mathrm{to}\ -500}$, there was a significant main effect of finger, $F(1,5) = 8.49$, $P < 0.05$ at Fz, Fcz, Cz, C3 and C4 electrode sites, indicating the differential involvement of associated cortical areas in preparation for the index and ring fingers. Post-hoc Newman–Keuls' tests revealed that the smallest amplitude of $\mathrm{BP}_{-600\ \mathrm{to}\ -500}$ was observed when non-musicians performed the task using the ring finger, which was significantly different from that associated with the index finger ($P < 0.01$). The largest amplitude of $\mathrm{BP}_{-600\ \mathrm{to}\ -500}$ was observed when musicians performed the task using the index finger. No significant differences in amplitude of $\mathrm{BP}_{-600\ \mathrm{to}\ -500}$ were observed between index and ring fingers in musicians ($P > 0.05$). The amplitude of $\mathrm{BP}_{-600\ \mathrm{to}\ -500}$ did not change as a function of nominal force level in both musicians and non-musicians ($P > 0.05$).

3.2.2. $MP_{-100\ to\ 0}$

For $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$, the main effect of group was significant, $F(1,5) = 36.85$, $P < 0.05$ at Fz, Fcz, Cz, C3 and C4 electrode sites with musicians showing larger amplitude $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$. The main effect of finger was significant only when non-musicians performed the task $F(1,5) = 28.29$, $P < 0.05$ with larger amplitude $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$ being associated with the index finger performing the task. The differences in amplitude of $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$ for index and ring fingers were not significant for musicians. Further, the amplitude of $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$ was proportionally reduced as a function of nominal force level in musicians regardless of the finger performing the task ($P < 0.05$). This trend was also observed in non-musicians only when the ring finger (not index) was performing the task.

3.2.3. MMPramp

In this period, the main effect of group was not significant. There was a significant interaction between group, finger and nominal force level, $F(2, 10) = 6.04$ ($P < 0.05$) at Fz, Fcz, Cz, C3 and C4 electrode sites. In addition, the main effect of finger was significant only when non-musicians performed the task, $F(1,5) = 14.39$ ($P < 0.05$). Similar to $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$, the larger amplitude of MMPramp was associated with the index finger performing the task ($P < 0.05$). The amplitude of MMPramp was proportionally reduced as a function of nominal force level in musicians regardless of the finger performing the task ($P < 0.05$). This was observed in non-musicians only when the ring finger (not index) was performing the task.

3.2.4. MMPstatic

In this period, the main effect of group was not significant ($P > 0.05$). There was a significant interaction between group, finger and the nominal force level ($F(2, 10) = 16.03, P < 0.05$) at Fz, Fcz, Cz, C3 and C4 electrode sites. There was also a significant interaction between finger and force level ($F(2, 10) = 8.36$, $P < 0.01$). Additional ANOVAs revealed that the main effect of finger was significant when non-musicians performed the task ($F(1, 5) = 8.34$, $P < 0.05$). In contrast, the differences in amplitude of $\mathrm{MP}_{-100\ \mathrm{to}\ 0}$ for index and ring fingers were not significant for musicians. The amplitude distribution of MRCP components for both groups of subjects at the Cz electrode site is shown in Fig. 5.

4. Discussion

This study extended our previous work on enslaving by examining behavioral and EEG responses in terms of producing varied force levels at a constant rate of force development with the index and ring fingers. As with our previous research, participants were studied both during the achievement of the desired force (ramp phase) and its attainment (static phase) at sub-maximal force levels. Both our previous work (Slobounov et al., 2002a,b,c) and that of others (Zatsiorsky et al., 2000, Latash et al., 2002) have ruled out exclusively peripheral explanations of enslaving suggesting the importance of central mechanisms. Given this, we sought to better understand the enslaving process by using individuals who had considerable experience with controlled finger responses (i.e. piano players). Overall, our findings are complementary to existing knowledge about

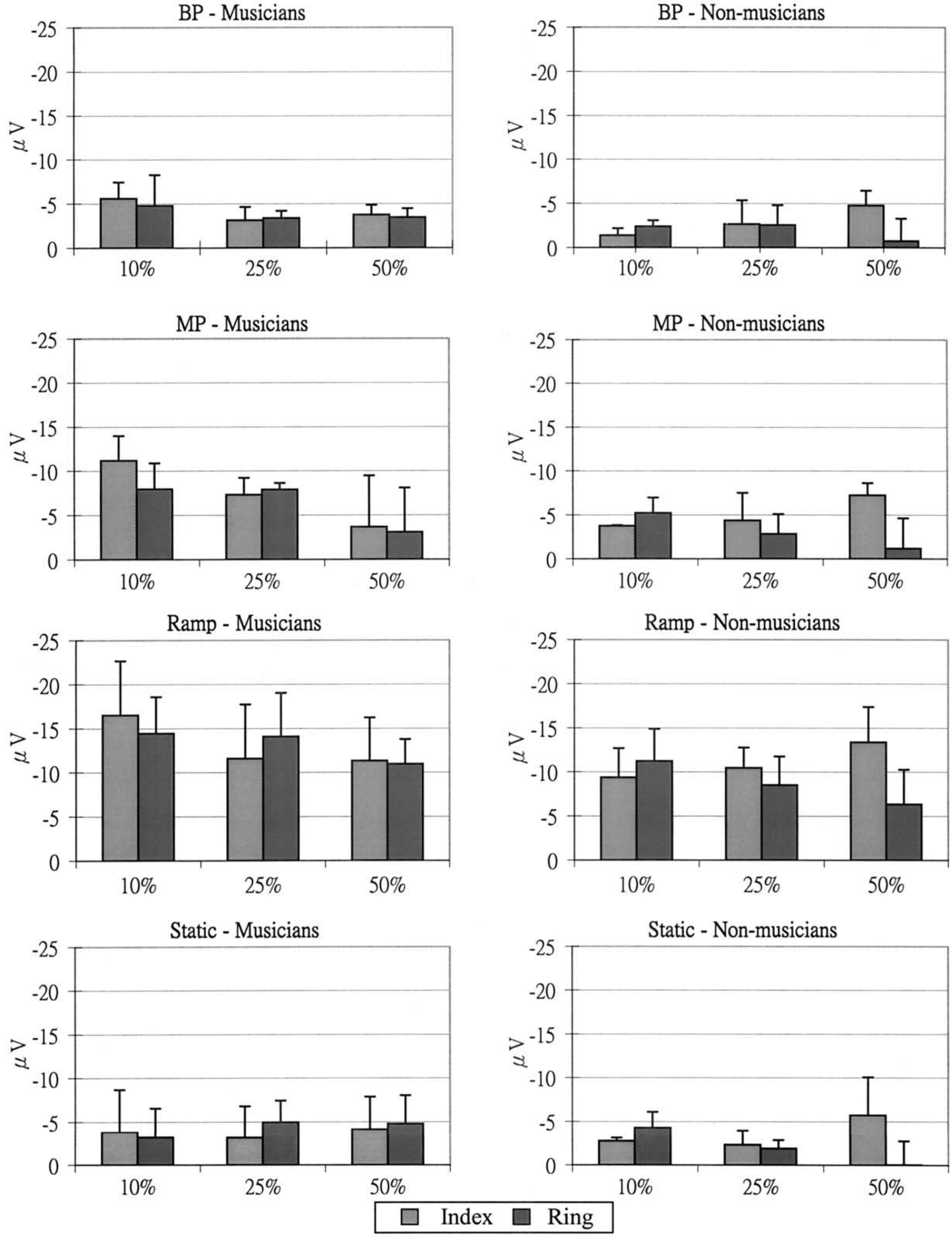


Fig. 5. The amplitude distribution of MRCP components for musicians and non-musicians; Bereitschaftpotential (BP), motor potential (MP) MMPramp and MMPstatic at Cz electrode site are shown during 10, 25 and 50% MVC associated with tasks produced by the index and ring fingers. The data are averaged over all subjects. Error bars show S.E.

enslaving, suggesting, however, that experience modulates important aspects of the enslaving phenomenon.

At least 3 major observations considering both the maintenance and ramp phases of force production can be made from our current results. First, in terms of error, musicians were more accurate than non-musicians at reaching the desired force level. Both groups, however, were equally accurate in terms of maintaining the force level. Second, non-musicians showed greater enslaving in the ring as compared to the index finger, which is consistent with our previous work. Musicians, on the other hand, showed less enslaving between fingers which suggests better control of their individual fingers. And third, the amount of enslaving increased with the increment of nominal force levels regardless of whether the index or ring finger was used as the master finger. This effect was modulated by group suggesting that (a) musicians (i.e. piano players) had better control over their fingers across all force levels, and (b) although the enslaving in musicians increased with the increment of nominal force, this effect was not as strong as in non-musicians.

Our data suggest an important role for previous experience in terms of the independent use of the fingers, which has been shown to be reflected in cortical representation in the brain (see Buonomano and Merzenich, 1998, for an overview of cortical plasticity). For example, Elbert and his colleagues reported that in well-practiced right-handed string players (e.g. violin players), there was an increase in cortical representation of the fingers of the left hand which would be used for fine manipulation of the strings but not the right hand which would be used only for gross motor movements of the bow (Elbert et al., 1995). Our results with non-musicians are also consistent with the ‘spill-over’ hypothesis of Kilbreath and Gandevia (1994) which suggests that cortical organization is such that commands to one flexor muscle ‘spill-over’ to progressively more remote finger flexors.

EEG correlates associated with finger force production in non-musicians in the present study were similar to that reported in our previous work. That is to say, we found differences in a variety of movement monitoring EEG potentials between tasks performed with the index finger and those performed with the ring finger. In our previous work, we suggested that the index finger, having comparatively independent origin and action (Kaplan, 1959) was controlled quite differently than the other fingers even under similar isometric force production tasks. Further, we suggested that despite multiple overlapping representations of different fingers in the primary motor cortex, shown recently in both single neuron studies in monkeys (Schieber and Hibbard, 1993) and blood flow measurements in humans (Sanes et al., 1995; Colebatch et al., 1991; Grafton et al., 1991), cortical activation associated with preparation for movement and its execution is end-effector specific.

Our current work with musicians suggests a rationale for understanding this specificity. On a global level, musicians did not show the differences between fingers found in our previous and current work with non-musicians. In particular, in the current study musicians showed no significant differentiation between the ring and index fingers for the $BP_{-600\ \mathrm{to}\ -500}$ and $MP_{-100\ \mathrm{to}\ 0}$ components. It is assumed that through practice, central control of the movement of these fingers has differentially developed in comparison with non-musicians who have less opportunity to practice individualized manipulation. This is also consistent with recent findings in the monkey showing practice-dependent changes in the functional topography of the primary motor cortex (Nudo et al., 1996). Specifically, motor practice induces the recruitment of additional units in a local network specifically representing the trained motor functions rather than body parts (Karni et al., 1998). Hence, since the index finger is more frequently used by non-musicians and both the ring and index fingers are used by musicians (e.g. string and piano players) in their activities, this would result in both a functionally extended sensory-motor representation and a larger electro-cortical activation.

Current research shows that cortical organization as related to use in musicians is not restricted to a single modality. That is to say, not only were the hand areas in the brains of string players shown to be expanded, as compared to non-musicians (Elbert et al., 1995), but it has also been shown that there are increased cortical representations related to relevant auditory properties of musical tones (Pantev et al., 1998; Pantev et al., 2001; see Zatorre and Peretz, 2001 for an overview). Thus, a general principle of cortical organization can also be applied to our current enslaving data further suggesting a rationale for understanding central involvement in the phenomenon. This opens some intriguing questions for future research in the area. For example, although frequent use and experience appear to be critical variables in the role of cortical organization, at this point it is difficult to clearly articulate the role of experience from the role played by such developmental factors as the age that an individual first begins to play an instrument or extensively practice motor movements, a question not often considered within the motor control literature. Clearly, such variables as time practicing, attention, skill level, nature of the task (e.g. keyboarding vs. piano playing), and developmental sequence are critical variables for future research.

Whereas enslaving appears to be related to lack of practice and thus, under-use, there also appears to be an overuse phenomenon. For example, Braille readers who use 3 fingers on both hands to read also show a different cortical organization which appears to be less well-organized topographically than non-Braille readers. Further, these individuals misperceive which of their fingers is being touched (Sterr et al., 1998). Thus, the other side of the story concerning frequent use and cortical organization is that overuse, whether in terms of musicians or others who perform constant digital manipulation (e.g. keyboarders), may lead to motor disorders such as focal hand dystonia (Bara-Jimenez et al., 1998; Elbert et al., 1998). 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 focal hand dystonia in particular (e.g. Candia et al., 1999). In this manner, older perspectives in rehabilitation of motor responses which suggest little in the way of central nervous system plasticity will give way to a utilization of basic research findings related to central processes.

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