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Modulation of cortical activity as a result of task-specific practice

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Abstract

This report aims to examine the role of task-specific practice in the modification of finger *force enslaving* and to provide empirical evidence for specific EEG frequency bands accompanying such practice may be an *end-effectors* dependent phenomenon. Nine handed naïve subjects without any training in music participated in a pre- and post-practice sessions separated by 12 practice sessions. Subjects performed a series of isometric force production tasks at 10% and 50% maximum voluntary contraction (MVC) with two rates of force development separately by index and ring fingers. Task-specific practice aimed at suppressing the contribution of neighboring fingers was achieved via visual feedback of force traces. Behavioral data (accuracy of force production and amount of *force enslaving*) and EEG data in frequency domain obtained via *Morlet* Wavelet transforms were analyzed. The major behavioral finding is that task-specific practice significantly enhanced the accuracy of force production and individuated control of the “most enslaved” ring finger ($P < 0.01$), but not the index finger. The major novel EEG findings are: (a) modulation of EEG activity within alpha band (8–12 Hz) in the central area of the brain as a function of practice was similar for both fingers and (b) after practice, modulation of EEG activity within gamma (30–50 Hz) band was *end-effectors* specific. Both behavioral and EEG patterns suggest an effect of task-specific practice on the reduction of force enslaving and that modulation of practice-related plasticity in the human cortex is *end-effectors* dependent phenomena.

Keywords: *Force enslaving*; End-effectors; EEG; Wavelet transforms

The identification of the neural basis underlying the ability to selectively control human fingers is an important scientific question. One practical aspect of multi-finger activity is related to movement deficits in patients (e.g., deficits in stroke patients most evident in limbs contralateral to the stroke site [2,27] and deficits of finger coordination in aged subjects [36–38]). Another aspect of multi-finger movements as required in such skills as playing musical instruments is that when one finger is moved, the other fingers involuntarily move and contribute to the total force production. This process is referred to as the *force enslaving* phenomenon [18,26,48]. Historically, *force enslaving* phenomenon has been widely investigated from anatomical [11], neurophysiological [35,7,13,39], biomechanical [12,25,48] and motor control [22–24,26,48] perspectives. A current notion of *force enslaving* phenomenon is that the characteristics of finger interaction potentially reflect both the peripheral design of the hand musculature and its central neural coordination [27]. However, a number of recent motor control [8,27] and EEG studies [42,39,43] have provided evidence suggesting that this phenomenon may be defined by neural factors.

In our recent study, neural underpinning of *force enslaving* phenomenon as evidenced by modulation of cortical activity following extensive practice has been investigated in piano players by means of EEG [39]. Behaviorally, *force enslaving* has been shown to be significantly less in experienced piano players versus age matches controls. Reduced inter-finger dependency in piano players was highly correlated with enlargement of movement-related cortical potentials (see reference [16] for review of MRCP). In our work, the higher amplitude of MRCP was associated with advanced control of both index and ring fingers.

Naïve subjects (without any musical instruments experience) usually have increased *force enslaving* after 4 weeks of extensive practice focused on increased accuracy of force production by individual fingers. However, it is possible to enhance control of individual fingers if practice specifically focuses on reduction

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of fingers *force enslaving* [4]. In the present study, we (a) further addressed specific question of whether it is possible to reduce fingers *force enslaving* and achieve independent control of individuated fingers via *task-specific practice* [28], aimed at suppressing the activation of neighboring fingers and (b) examined specific features of modulation of brain electrical activity as a function of *end-effectors* selectively involved in a task production. We were specifically interested in modulation of EEG activity in the EEG gamma band range (30–50 Hz) as a function of practice specifically aimed at reducing fingers *force enslaving*. However, since *alpha* activity (8–12 Hz) has historically been an important measure, we also report these data.

Subjects in our study were all right handed, college students ($n = 9$, aged 19–25 years old) with no history of pathologies to either hand or wrist. The degree of hand dominance was assessed according to Edinburgh Handedness Inventory [30]. Subjects signed an informed consent form approved by the IRB of The Pennsylvania State University.

Subjects were seated comfortably in an electrically shielded room. 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 four load cells. The position of the load cells was determined for each subject and adjusted individually as necessary. The subjects' task involved performing isometric force production with a single specified finger of the right hand (index or ring) while maintaining contact with all load cells, that is, the other three fingers. It was important that subjects should not lift or use the uninvolved fingers in task produced by specified finger.

All subjects were given an initial practice session to become familiar with the behavioral task. This practice session and the first experimental (pre-training) 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 it twice and the overall MVC was calculated as the average of two trials. This was done for each finger and each session. Both, the first (pre-practice) and the second (post-practice) experimental sessions consisted of eight tasks in which subjects were asked to produce two different force levels, 10% and 50% of their MVC with their index or ring finger at slow and fast rates of force development. For the actual task, the subjects were presented with horizontal target line on the computer screen representing 10% and/or 50% MVC. The subjects were instructed to reach the target line at its intersection with vertical line corresponding to either 400 or 800 ms (fast and slow, for 10% MVC), and 1000 or 4000 ms (fast and slow, for 50% MVC), at the constant rate of force development [29]. 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 within 10% and 50% MVC tasks. After reaching the required force level, subjects were asked to match their force trace with the target line for the remainder of the trial. 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 60 trials for each task. The detailed experimental procedure was published elsewhere [44,45,40,42,39,43,41].

During extensive practice (12 sessions, 3 days a week for 4 weeks) performing the tasks, subjects received visual feedback when uninvolved fingers contributed to force produced by specified finger. Specifically, four light emitting diodes (LEDs), corresponding to each of the four fingers were displayed at the bottom of the computer monitor. If an uninvolved finger contributed more than 5% MVC, the LEDs were activated (turning to RED) signaling that the uninvolved finger(s) contributed to task production. The LEDs were GREEN when the forced produced by the uninvolved finger(s) was below the 5% threshold.

The EEG was recorded with Ag/AgCl electrodes using a *Quik-Cap* Electrode Helmet at 19 electrode sites: FP1, FP2, Fz, F3, F4, FCz, FC3, FC4, Cz, C3, C4, CPz, CP3, CP4, Pz, P3, P4, O1 and O2 according to the international 10–20 system [17]. 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.

All EEG data sets were linear detrended and baseline corrected, and epoched by a NeuroScan 4.1 software package. Any trials containing prominent eye artifact were removed from further analysis. A time epoch was calculated from 2000 ms prior to force initiation to 5000 ms after force termination, thus creating an epoch 7000 ms in duration. The wavelet used for EEG analysis in this study was the Morlet wavelet [46,40] and implemented via the Matlab wavelet toolbox. The TF energy of EEG trials was averaged and the mean time-varying energy of movement-induced EEG waveforms in 8–13 and 30–50 Hz frequency bands across trials was computed. The absolute values of the wavelet coefficients (C) were plotted, and the clusters of dominant energy distributions within these frequency bands were noted. The scale space of the wavelet transform was windowed separately to cover various frequency bands, to increase the resolution and to stress between-condition differences. The dependent variables for behavioral (*force enslaving*) data were first analyzed using a 2 (session: pre, post-training) × 2 (criterion force: 10%, 50%) × 2 (rate of force: fast, slow) × 2 (*end-effectors*: index, ring) within subjects repeated measures ANOVA.

We found that the absolute mean error was reduced for the ring finger after the 4-week practice period. For the ramp phase, the ANOVA indicated a significant effect of session only for the ring finger, $F(1, 8) = 40.53$, $P < 0.005$) which reflects that the accuracy of force output produced by the ring finger increased as a function of practice. Overall, there was less absolute mean trajectory errors generated in the static phase than in the ramp phase, $F(1, 8) = 38.345$, $P < 0.01$. For the static phase, the ANOVA indicated a significant effect of criterion force, $F(1, 8) = 68.316$, $P < 0.0001$, and end-effectors, $F(1, 8) = 9.3215$, $P < 0.001$. The interaction between *end-effectors* × *force* × *rate of force* was also significant, $F(1, 8) = 27.72$, $P < 0.005$. The

Newman-Keuls post hoc test showed that the smallest error occurred in the index finger 10% fast condition, 0.56*N* (S.D. 0.15), while the largest error was observed in the ring finger 50% fast condition, 4.09*N* (S.D. 0.69). Most importantly, the ANOVA indicated a significant effect of session only for the ring finger, $F(1, 8) = 35.69$, $P < 0.01$. The greater accuracy and lack of benefit of practice for the index finger most likely reflects greater experience of our subjects in using their index as compared to their ring finger for specific tasks.

In terms of *force enslaving*, the ANOVA revealed a significant difference between end-effectors, $F(1, 8) = 19.791$, $P < 0.01$, with the index finger being more independent than ring finger regardless of force level and effect of practice. It was also found that the percent of *force enslaving* (i.e., finger dependency) increased as a function nominal force, $F(1, 5) = 113.68$, $P < 0.005$. In specific, total force enslaving was reduced following practice for ring finger only (pre 50% fast, $X = 22.54$, S.D. = 9.72; post 50% fast, $X = 16.18$, S.D. = 4.89; pre 50% slow, $X = 19.34$; S.D. = 12.94; post 50% slow, $X = 12.99$, S.D. = 6.87). There was also a significant interaction between *end-effector*s × *criterion force*, $F(1, 8) = 12.04$, $P < 0.05$. Newman-Keuls post hoc tests revealed that the great-

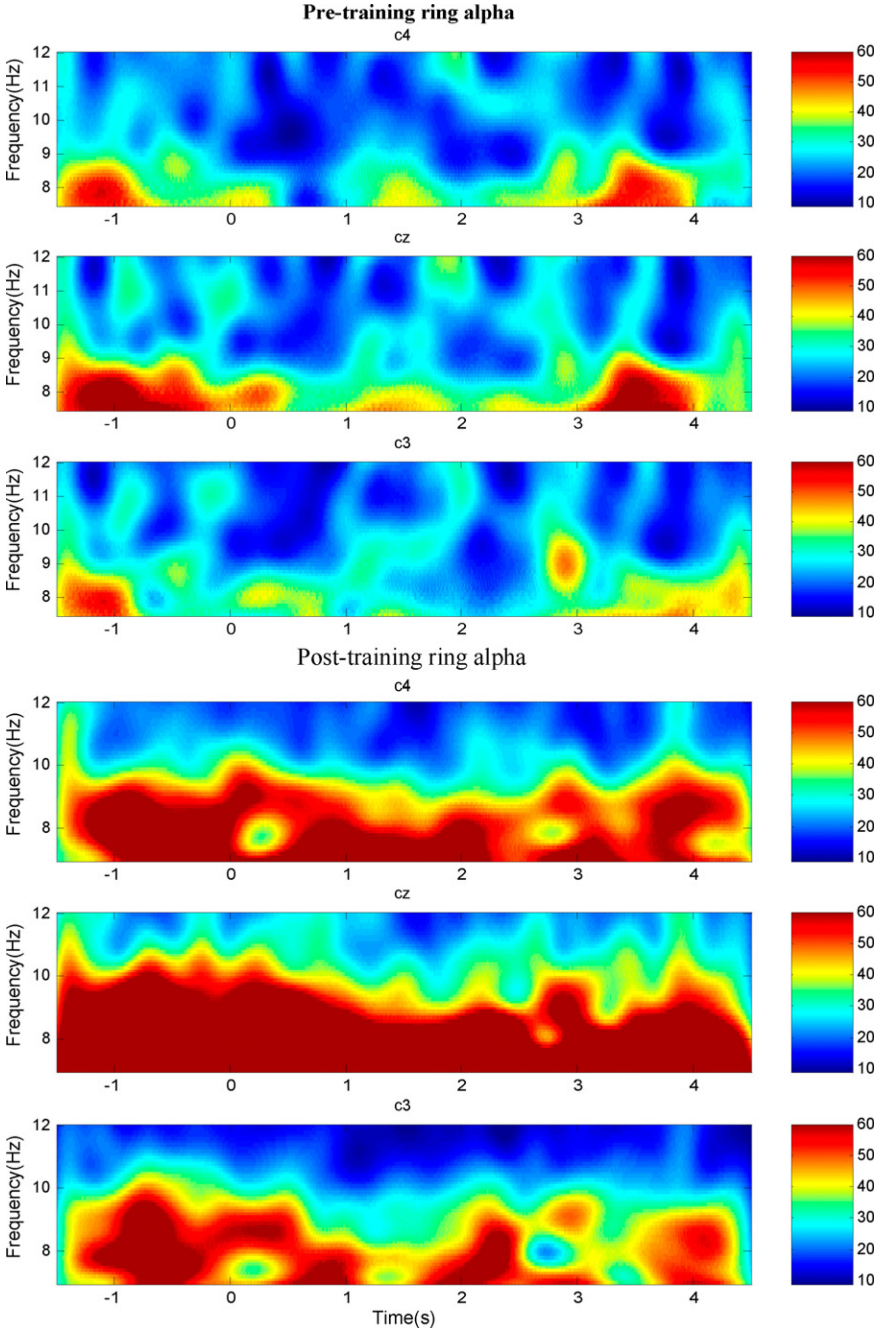


Fig. 1. (Top) Wavelet map of EEG alpha at Cz, C3, C4 of ring finger prior to practice; (bottom) wavelet map of EEG alpha Cz, C3, C4 of ring finger post-practice. Note, 0 on *X*-axis corresponds to force onset.

est percent of force enslaving was observed when ring finger produced 50% MVC tasks. The least percent of *force enslaving* were observed when index finger produced 10% MVC tasks. Again, practice only influenced the ring finger, $F(1, 8) = 10.047$, $P < 0.05$, indicating that extensive practice did not influenced percent of index finger *force enslaving*.

The most prominent modulations of EEG activity in frequency domain as a function of practice were observed for 50% MVC tasks. In the following analysis, we will emphasize EEG data for 50% MVC tasks pre and post-training. Visually, pre-practice EEG records revealed considerable drop in alpha power (e.g., alpha desynchronization) approximately at the onset of force initiation. This was true for both fingers. Interestingly, the *alpha* power was localized centrally approximately 200 ms prior to its significant drop at the force onset. It should be noted *alpha* power (e.g., alpha synchronization) increased approximately 700 ms after the force onset, regardless of finger observed. This drop in *alpha* power was not present at the force onset post-practice. In contrast to pre-practice, *alpha* activity increased during both ramp and static phases (at least 1000 ms after peak force). This was true for both fingers.

To further accentuate and define more precise timing of *alpha* power modulation as a function of practice and end-effectors, the time–frequency (TF) maps of EEG *alpha* at central-electrode sites (Cz, C3, C4) were elaborated. Specifically, the TF wavelet coefficients across all trials within each condition were computed for all subjects at 19 electrode sites with frequency window of 8–12 Hz and plotted as 2D color maps. Different temporal patterns of time-lock to force onset *alpha* desynchronization were present pre and post-practice regardless of end-effectors. Specifically, the presence of high power *alpha* was evident post-practice up to 4 s after the force onset. In addition, the averaged absolute values of TF coefficients indicating the power of the *alpha* energy were computed. There was significantly less *alpha* power produced by the ring finger both before, $F(1, 8) = 20.77$, $P < 0.01$ and after practice, $F(1, 8) = 14.34$, $P < 0.05$ (Fig. 1).

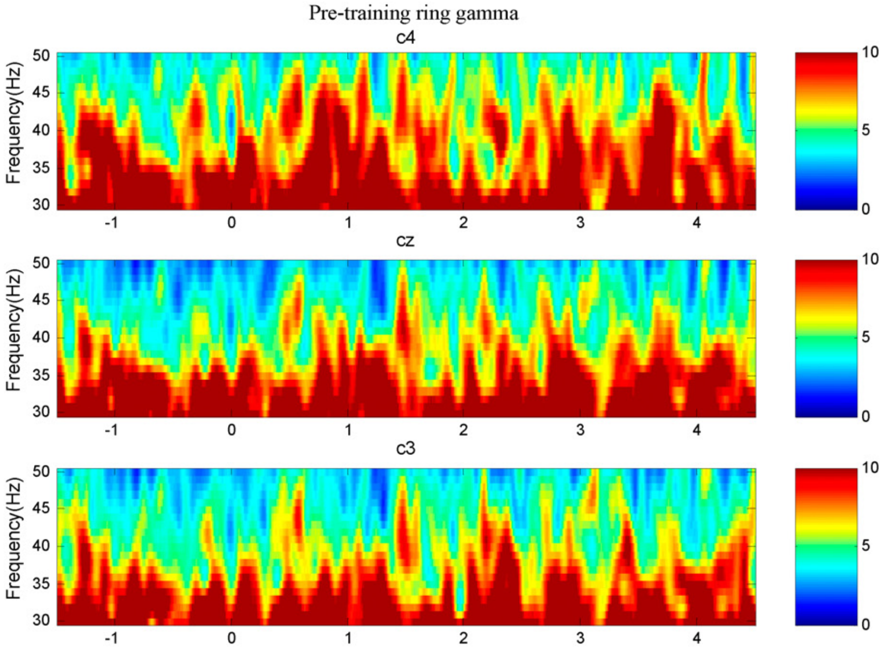
For *gamma*, the TF wavelet coefficients across all trials within each condition were computed with frequency window of 30–50 Hz. The most prominent changes in *gamma* (30–50 Hz) power as a function of finger and practice were present at central-electrode sites (Cz, C3 and C4). Visually and statistically, power of the *gamma* band prior to practice was significantly higher for both fingers, $F(1, 8) = 15.52$, $P < 0.001$. However, there was a temporal difference in *gamma* activation between index and ring fingers as a function of practice. Specifically, burst of *gamma* activity was present for the index finger prior to practice (approximately 800 ms after force onset) and was scattered throughout the whole trial duration after practice. In contrast, *gamma* activity was scattered throughout the trial duration for the ring finger prior to practice and time-locked to peak force (approximately 800 ms after force onset) after practice. These patterns of gamma activity were bilateral and present similarly at C3, C4 and Cz electrode sites (Fig. 2).

In this study, we extended our previous work with experienced piano players by using participants who were less experienced with such multiple finger tasks. The primary behavioral findings from this study confirmed our previous work and showed that the accuracy increased with the extensive practice sessions of three times a week over 4 weeks but only for the ring finger. This suggests that it was only the less practiced ring finger that benefited from practice and that their index finger performance had reached a plateau, at least for our type of tasks. That is to say, the index finger in our participants was more independent initially and thus was limited in the amount of change it could show. It is possible that further extensive training would result in changes that could be mapped onto our physiological measures. For the ring finger, error rate was less in the lower force (10% MVC) as compared to the higher force condition (50% MVC) as well as the lower rate of force condition. This is consistent with other existing empirical research which shows that percent of *force enslaving* increases as a function of nominal force [12,31,42,39]. Further, both accuracy and independent control of individual fingers may be enhanced via deliberate practice and *task-specific training* [28].

Overall, behavioral results from our study support the hypothesis that the structural constraints imposed on individuated finger control is not a hard-wired phenomenon and can at least partially be overcome by *task-specific training*. An important implication is that *task-specific training* may enhance both the accuracy and independent control of the “most *enslaved*, ring finger” [48,43]. Therefore, it is feasible to suggest that “task-specific treatment visual feedback” may be a critical component of effective applied approaches to rehabilitation in focal hand dystonia [3] and stroke patients [47] suffering from impaired control of localized movements.

The theoretical understanding of this work is supported by numerous studies suggesting the possibility of plastic changes in the brain associated with learning [6,5,32–34,49]. In support of this notion, early EEG studies demonstrated alteration of brain electrical activity as a function of extensive practice [19,21]. However, this is the first EEG study demonstrating that plastic changes in the brain as a result of task-specific practice are *end-effectors* dependent within the EEG gamma band range. The amount of anatomical constraints (i.e., mechanical constraints that exist between the tendons and the muscles in the fingers [11]) may be a factor contributing the features of brain plasticity as a result of task-specific practice.

In terms of EEG activity accompanying enhanced individuated control of the fingers we found the following. First, *alpha* desynchronization with onset of force production was observed prior to practice regardless of finger involved. Second, following practice, the *alpha* desynchronization with force onset was not present. It should be also noted that as reported previously a significant increase of MRCP was seen prior to and after force onset (i.e., motor potential, MP [10,20], and movement-monitoring potential, MMP [14], produced by ring finger after practice [4]). Third, high power burst of *gamma* activity around the peak force was seen during the static phase with the index finger and throughout the task with the ring finger prior to practice. After practice, *gamma* activity with the ring finger was similar to that of the index finger prior to practice. This suggests that *gamma* band activity may index the successful acquisition of motor responses [40]. Considering the fact that the *gamma* band rhythm is an important sign of focused arousal [9] allowing



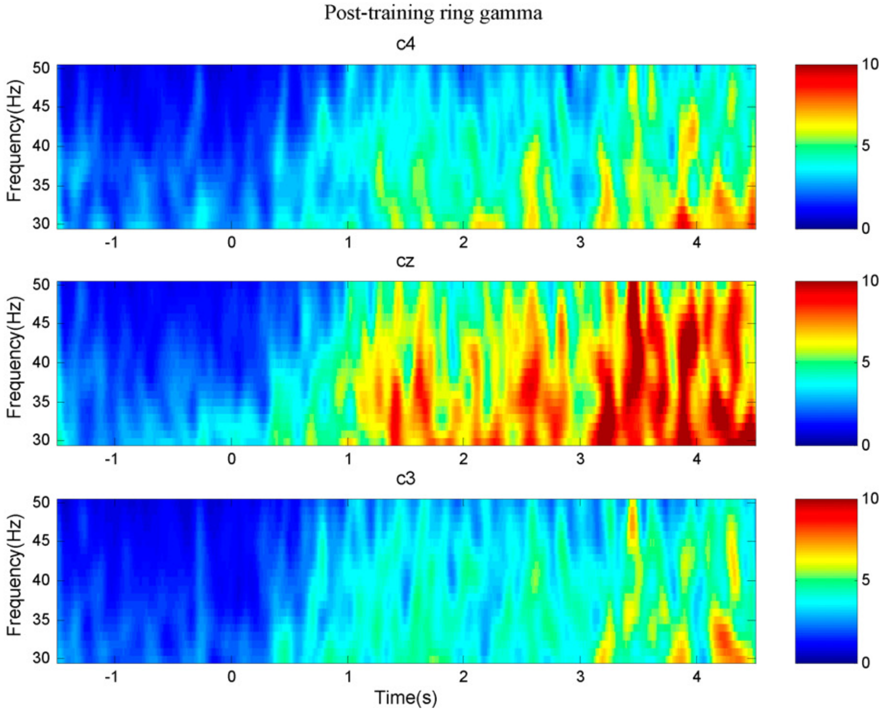


Fig. 2. (Top) Wavelet map of EEG gamma at Cz, C3, C4 of ring finger prior to practice; (bottom) wavelet map of EEG gamma Cz, C3, C4 of ring finger post-practice. Note, 0 on *X*-axis corresponds to force onset.

sufficient execution of motor responses and an important, universal operator in the brain function [1] it is feasible to suggest the observed EEG patterns may serve as neural underpinning of enhanced individuated control of the ring finger.

To conclude, contrasting features of EEG patterns accompanying deliberate practice with special emphasis on independent control of index versus ring fingers suggests that modulation of practice-related plasticity in the human cortex [49,15] is an end-effectors dependent phenomenon. Further, utilization of both EEG *alpha* and *gamma* band activity allows for additional information regarding changes following practice not found in either EEG frequency band alone.

References

[1] E. Basar, C. Basar-Eroglu, T. Demiralp, M. Schurmann, Time and frequency analysis of the brain's distributed gamma band system, IEEE Eng. Med. Biol. 14 (1995) 400–410.

[2] D. Bourbonnais, S. Vanden NOven, Weekness in patients with hemiparesis, Am. J. Occup. Ther. 43 (1989) 313–319.

[3] V. Candia, C. Wienbruch, T. Elbert, B. Rockstroh, W. Ray, Effective behavioral treatment of focal hand dystonia in musicians alters somatosensory cortical organization, Proc. Natl. Acad. Sci. U.S.A. 100 (2003) 7942–7946.

[4] H. Chiang, S. Slobounov, W. Ray, Practice-related modulations of force enslaving and cortical activity as revealed by EEG, Clin. Neurophys. 115 (5) (2004) 2013–2024.

[5] J. Classen, J. Liepert, S.P. Wise, M. Hallett, L. Cohen, Rapid plasticity of human cortical movement representation induced by practice, J. Neurophysiol. 79 (1998) 1117–1123.

[6] L.G. Cohen, Functional relevance of cortical plasticity demonstrated with transcranial magnetic stimulation (TMS), Electroencephal. Clin. Neurophysiol. 103 (1) (1997) 21.

[7] J.G. Colebatch, M.P. Deiber, R.E. Passingham, K.J. Friston, R.S.J. Frackowiak, Regional cerebral blood flow during voluntary arm and hand movements in human subjects, J. Neurophysiol. 65 (1991) 1392–1401.

[8] F. Danion, M.L. Latash, Z.M. Li, V.M. Zatsiorsky, The effect of fatigue on multifinger co-ordination in force production tasks in humans, J. Physiol. 523 (2) (2000) 523–532.

[9] J. De France, D.E. Sheer, Focussed arousal, 40 Hz EEG and motor programming, in: D. Giannitrapini, L. Murii (Eds.), The EEG of Mental Activities, Karger, Basel, 1998, pp. 153–168.

[10] L. Deecke, H. Kornhuber, Human freedom, reasoned will, and the brain: the Bereitschaftpotential story, in: M. Jahanshahi, M. Hallett (Eds.), The Bereitschaftpotential: Movement-Related Cortical Potentials, Kluwer Academic/Plenum Publishers, New York, 2003, pp. 283–321.

[11] M. Fahrer, Interdependent and independent actions of the fingers, in: R. Tubiana (Ed.), The Hand, Saunders, Philadelphia, PA, 1981.

[12] M. Flanders, J.F. Soechting, Kinematics of typing: parallel control of the two hands, J. Neurophysiol. 67 (5) (1992) 1264–1274.

[13] S.T. Grafton, Functional mapping of sequence learning in normal humans, J. Cognit. Neurosci. 7 (4) (1995) 497–510.

[14] E. Grünewald-Zuberbier, G. Grünewald, Goal-directed movement potentials of human cerebral cortex, Exp. Brain Res. 33 (1978) 135–138.

[15] M. Hallett, Plasticity of the motor cortex and recovery from stroke, Brain Res. Rev. 36 (2001) 169–174.

[16] M. Jahanshahi, M. Hallett (Eds.), The Bereitschaftpotential: Movement-Related Cortical Potentials, Kluwer Academic/Plenum Publishers, New York, 2003.

[17] H.H. Jasper, The ten-twenty electrode system of the International Federation, Electroenceph. Clin. Neurophysiol. 1 (1958) 371–375.

[18] S.L. Kilbreath, D.C. Gandevia, Limited independent flexion of the thumb and fingers in human subjects, J. Physiol. 479 (1994) 487–497.

[19] R. Kristeva, Bereitschaftspontential of pianists, Ann. N.Y. Acad. Sci. U.S.A. 425 (1984) 477–482.

[20] R. Kristeva, D. Cheyne, W. Lang, G. Lindengen, L. Deecke, Movement-related potentials accompanying unilateral and bilateral finger movements with different inertial loads, Electroenceph. Clin. Neurophysiol. 75 (1990) 410–418.

[21] W. Lang, O. Zilch, C. Koska, G. Lindinger, L. Deecke, Negative cortical DC shifts preceding and accompanying simple and complex sequential movements, Exp. Brain Res. 74 (1989) 99–104.

[22] M.L. Latash, S. Li, F. Danion, V.M. Zatsiorsky, Central mechanisms of finger interaction during one- and two-hand force production at distal and proximal phalanges, Brain Res. 924 (2) (2002) 198–208.

[23] M.L. Latash, J.F. Scholz, F. Danion, G. Schoner, Finger coordination during discrete and oscillatory force production tasks, Exp. Brain Res. 146 (2002) 1419–1432.

[24] M.L. Latash, K. Yarror, J.C. Rothwell, Changes in finger coordination and responses to single pulse TMS of motor cortex during practice of a multifinger force production task, Exp. Brain Res. 151 (2003) 60–71.

[25] J.N.A.L. Leijnse, C.J. Snijders, J.E. Bonte, J.M.F. Landsmeer, J.J. Kalker, J.C.V.D. Meulen, G.J. Sonneveld, S.E.R. Hovius, The hand of the musician: the kinematics of the bidigital finger system with anatomical restrictions, J. Biomech. 26 (10) (1993) 1169–1179.

[26] Z.M. Li, M.L. Latash, K.M. Newell, V.M. Zatsiorsky, Motor redundancy during maximal voluntary contraction in four-finger tasks, Exp. Brain Res. 122 (1998) 71–78.

[27] S. Li, M. Latash, G. Yue, V. Siemionov, V. Sahgal, The effects of stroke and age on finger interaction in multi-finger force production tasks, Clin. Neurophys. 114 (2003) 1646–1655.

[28] K.M. Newell, Motor skill acquisition, Annu. Rev. Psychol. 42 (1991) 213–237.

[29] K.M. Newell, L.G. Carlton, On the relationship between peak force and peak force variability in isometric tasks, J. Motor Beh. 17 (1985) 230–241.

[30] R.C. Oldfield, The assessment and analysis of handedness: the Edinburgh inventory, Neuropsychologia 9 (1971) 97–113.

[31] D. Parlitz, T. Peschel, E. Altenmuller, Assessment of dynamic finger forces in pianists: effects of training and expertise, J. Biomech. 31 (11) (1998) 1063–1067.

[32] A. Pascual-Leone, N. Dang, L.G. Cohen, J.P. Brasil-Neto, A. Cammarota, M. Hallett, Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills, J. Neurophysiol. 74 (3) (1995) 1037–1045.

[33] A. Pascual-Leone, F. Tarazona, M.D. Catala, Applications of transcranial magnetic stimulation in studies on motor learning, TMS EEG (Suppl. 51) (1999) 157–161.

[34] J.N. Sanes, J.P. Donoghue, Plasticity and primary motor cortex, Ann. Rev. Neurosci. 23 (2000) 393–415.

[35] M.H. Schieber, Individuated movement of rhesus monkeys: means of quantifying the independence of digits, J. Neurophysiol. 65 (1991) 1381–1391.

[36] K. Shim, B. Lay, V. Zatsiorsky, M. Latash, Age related changes in finger coordination in static prehension tasks, J. Appl. Physiol. 213 (2004) 213–224.

[37] M. Shinohara, C. Li, N. Kang, V. Zatsiorsky, M. Latash, Effects of age and gender on finger coordination in MVC and submaximal force-matching tasks, J. Appl. Physiol. 94 (2003) 259–270.

[38] M. Shinohara, M. Latash, V. Zatsiorsky, Age effects on force produced by intrinsic and extrinsic hand muscles and finger interaction during MVC tasks, J. Appl. Physiol. 95 (2003) 1361–1369.

[39] S. Slobounov, H. Chiang, J. Johnston, W. Ray, Modulated cortical control of individual fingers in experienced musicians: an EEG study, Clin. Neurophysiol. 113 (2002) 2013–2024.

[40] S.M. Slobounov, K. Fukada, R. Simon, M.P. Rearick, W. Ray, Neurophysiological and behavioral indices of time pressure effects on visuomotor task performance, Brain Res. Cognit. Brain Res. 9 (3) (2000) 287–298.

[41] S. Slobounov, M. Hallett, S. Stanhope, H. Shibasaki, Role of cerebral cortex in human postural control, Clin. Neurophysiol. 116 (2005) 315–323.

[42] S. Slobounov, J. Johnston, H. Chiang, W. Ray, Cortical potentials accompanying enslaving effect in single versus combination of fingers force production tasks, Cognit. Brain Res. 113 (2002) 1444–1453.

[43] S. Slobounov, J. Johnston, H. Chiang, W. Ray, Movement-related potentials are force or end-effector dependent: evidence from a multifinger experiment, Clin. Neurophysiol. 113 (2002) 1125–1135.

[44] S.M. Slobounov, W. Ray, Movement-related potentials with reference to isometric force output in discrete and repetitive tasks, Exp. Brain Res. 123 (1998) 461–473.

[45] S. Slobounov, W. Ray, R. Simon, Movement-related potentials accompanying unilateral finger movement with special reference to rate of force development, Psychophysiology 35 (1998) 1–12.

[46] C. Tallon-Baudry, O. Bertrand, C. Delpuech, J. Jernier, Stimulus specificity of phase-locked and non-phase-locked 40 Hz visual responses in human, J. Neurosci. 16 (3) (1997) 4240–4249.

[47] N.M. Weinberger, Dynamic regulation of receptive fields and maps in the adult sensory cortex, Annu. Rev. Neurosci. 18 (1995) 129–158.

[48] V.M. Zatsiorsky, Z.M. Li, M.L. Latash, Enslaving effect in multi-finger force production, Exp. Brain Res. 131 (2000) 187–195.

[49] U. Ziemann, W. Muellbacher, M. Hallett, L. Cohen, Modulation of practice-dependent plasticity in human motor cortex, Brain 124 (2001) 1171–1181.