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Acquisition and reacquisition of motor coordination in musicians

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Precise control of movement timing plays a key role in musical performance. This motor skill requires coordination across multiple joints and muscles, which is acquired through extensive musical training from childhood. However, extensive training has a potential risk of causing neurological disorders that impair fine motor control, such as task-specific tremor and focal dystonia. Recent technological advances in measurement and analysis of biological data, as well as noninvasive manipulation of neuronal activities, have promoted the understanding of computational and neurophysiological mechanisms underlying acquisition, loss, and reacquisition of dexterous movements through musical practice and rehabilitation. This paper aims to provide an overview of the behavioral and neurophysiological basis of motor virtuosity and disorder in musicians, representative extremes of human motor skill. We also report novel evidence of effects of noninvasive neurorehabilitation that combined transcranial direct-current stimulation and motor rehabilitation over multiple days on musician's dystonia, which offers a promising therapeutic means.

Keywords: motor control; movement disorders; motor learning; neuroplasticity; music

Introduction

Plastic adaptations of the nervous system when people practice performance skills induce changes in sensory, motor, and cognitive functions, as well as in their underlying neural architecture.[1,2] Extensive practice allows for mastery and maintenance of exceptional sensorimotor skills (i.e., virtuosity) seen in athletes[3,4] and musicians.[5,6] However, repetitive use of a specific body portion for a prolonged period occasionally causes maladaptive plastic changes in the sensorimotor system by interacting with several triggering factors, such as psychological[7] and biomechanical stresses,[8] personality traits,[9] and genetic predispositions.[10,11] Consequently, fine motor control can be severely impaired due to loss of voluntary control of fine motor movements and muscular cramping.[12] This highly disabling movement disorder, termed *task-specific focal dystonia*, is prevalent among trained individuals, such as musicians, writers, surgeons, and athletes (e.g., yips in golfers and darts players).[13,14] Task-specific focal dystonia in musicians (i.e., "musician's dystonia") occurs significantly more frequently than the corresponding problems related to other occupations, such as hand writing, computer typing, or performing surgery.[15] Yet, there is still a lack of knowledge concerning its phenomenology, pathophysiology, and effective treatment, the last being the most crucial because musician's dystonia frequently terminates professional careers. This article first summarizes recent advances in research into acquisition, loss, and reacquisition of musicians' motor skills and then introduces outcomes of our novel intervention using noninvasive transcranial stimulation for musician's dystonia.

Acquisition of fine motor control through musical practice

Dexterous use of musical instruments requires fine motor control. For example, individuated finger movements play a key role in precise control of movement timing and force during musical

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performance. This is because variations of the spatiotemporal features of music often require multiple fingers to move with differing timing, speed, and direction and to compensate for innate neuromuscular constraints. Expert pianists display equal independence of movements across fingers[16] over various tempi,[17] which differs greatly from the movements observed in musically untrained individuals.[18,19] These motor skills are likely to be acquired through extensive musical practice,[20] although the possible contribution of genetic factors to the ability in practicing should be noted.[21] Furthermore, practice-dependent improvements of individuated finger movements can be further facilitated through provision of visual feedback regarding movement accuracy.[20,22] A study using transcranial magnetic stimulation (TMS) demonstrated the representation of skilled finger movements in the primary motor cortex, depending on the biographic history of musical training.[23] For example, coordination of the finger movements elicited by TMS differed substantially among pianists, violinists, and nonmusicians.[23] Interestingly, several TMS studies reported reduced surround inhibition between digits at the motor cortex in musicians compared to nonmusicians.[24,25] This predicts movement covariation across fingers (i.e., synergistic coordination) not only in the same direction but also in the opposite direction. A combination of several patterns of movement coordination across fingers then enables production of multifinger movements with a variety of timing and speed even without independent control. It is therefore still unclear whether the highly individuated finger movements in trained musicians reflect either patterned movement coordination across fingers[26] or independent control of movements across fingers.[27,28]

Transcranial direct-current stimulation (tDCS) allows for probing neuroplasticity of the motor system underlying skilled finger movements in musicians. This noninvasive electrical stimulation with weak current modulates cortical excitability depending on the polarity of electrodes.[29] Following motor practice together with tDCS over the primary motor cortices of both hemispheres (bihemispheric tDCS), fine motor control was facilitated only in pianists who had commenced musical training after age 7 years.[30] It is therefore likely that the motor system is optimized particularly in trained musicians who commenced musical training at an early age. Such an early optimization may lead to increased stability of a precisely tuned neuronal network associated with production of dexterous motor actions. These characteristics of neuroplasticity can be related to the fact that musicians who started musical training at a later age have a higher risk of developing focal dystonia.[11] In addition, the excitability-facilitating tDCS during rest enhanced and degraded fine control of the contralateral finger movements in nonmusicians and expert pianists, respectively.[31] This suggests that musical training shapes motor outputs through selectively activating and deactivating neurons in the motor cortex so as to accomplish dexterous coordination of multiple fingers. It is also possible that the facilitating stimulation disrupted the optimized resting-state neural network in pianists,[32] which can result in lowering fine motor control.

Fast performance of finger movements is also a key element of motor virtuosity. In general, there is a speed–accuracy tradeoff in motor action.[33] However, daily piano practice enables the production of faster finger movements while it maintains an astonishingly high amount of rhythmic accuracy of movements.[34] Expert pianists are therefore capable of speeding up skilled finger movements without lowering movement accuracy.[17,35] Recording of finger muscular activities demonstrated shorter duration of the muscular contraction in pianists who play faster.[36] A smaller amount of muscular force exertion is associated with smaller signal-dependent noise in the motor commands,[37] which may underlie the achievement of high precision of movement during fast piano performance. Indeed, several studies demonstrated smaller neuronal activities at the motor cortex in trained musicians than in nonmusicians.[1]

The human hand consists of 27 bones and 36 muscles. Control of a large number of degrees of freedom therefore costs computationally. However, a smaller number of movement patterns[16] and muscular activations[36] can serve as building blocks of various movement repertoires in musical performance. These building blocks, called synergies, are likely to be represented in the primary motor cortex[23] and presumably serve to simplify hand motor control.

Loss of fine motor control in musician's dystonia

Musicians who strive for virtuosic musical performance tend to engage in extensive practice over hours every day for years.[5,38] This inevitably heightens potential risks of developing overuse syndromes at the neuromuscular system, which include task-specific tremor,[39–41] acute and chronic pain,[13] and focal dystonia.[15] Focal dystonia is a most disabling disorder, which is characterized by loss of fine motor control of the hand, arm, embouchure, larynx, tongue, and foot.[13,42–45] For example, embouchure dystonia destabilizing the adequate tone production is prevalent among 8% of brass players.[46,47] Focal hand dystonia also threatens musicians who play keyboard, string, and brass instruments.[15] Typical symptoms are involuntary hyperflexion of the finger joints and/or excessive cramping of finger muscles, which deteriorates the spatiotemporal accuracy of sequential finger movements and impairs hand dexterity.[48–50] Nevertheless, it still remains unclear whether musician's dystonia influences sensory functions.[51–54]

A challenge in diagnosing musician's dystonia is that the symptom is often subtle, and the unaffected body portion also behaves abnormally so as to compensate for the symptom.[55] Clinicians have to effectively integrate visual and auditory information while diagnosing dystonia in order to accurately identify the affected body portion, finger movements, and so forth. However, such an accurate diagnosis can be a nontrivial issue, firstly because clinicians have not necessarily experienced intensive instrumental training, and secondly because the symptom often appears when a musician is playing fast.[48] It is therefore of crucial importance to develop a quantitative measure of diagnosing musician's dystonia precisely.[56] A combination of simple data measurements, such as MIDI information,[49,50] acoustic signals,[47] and movement kinematics,[48] with state-of-the-art data analysis techniques, such as machine learning and multivariate analyses, is a promising approach.

Task-specific focal dystonia yields maladaptive changes in the sensorimotor system. Neurophysiological studies using TMS have demonstrated loss of intracortical inhibition[57,58] and surround inhibition[59] at the primary motor cortex contralateral to the hand affected by focal dystonia. Studies using functional magnetic resonance imaging (fMRI) also found functional abnormalities at both the contralateral and ipsilateral primary motor cortices[60–64] in musicians with focal hand dystonia. Abnormal functional connectivity between motor and sensory cortices was also observed in pianists with focal hand dystonia, in which afferent sensory input from a single finger facilitates motor neurons that are connected with both adjacent and remote fingers.[65,66] This is likely to elicit task-irrelevant involuntary finger movements and loss of independent control of movements across fingers. Functional abnormalities associated with musician's dystonia were also observed at the premotor area and cerebellum.[60,64,67] Furthermore, the volume of the middle putamen was enlarged in pianists with focal hand dystonia, which was also positively correlated with rhythmic variability of sequential finger movements.[68]

Reacquisition of hand dexterity

To normalize functional abnormalities caused by musician's dystonia, several therapeutic approaches have been attempted. One of the most effective noninvasive interventions is constraint-induced (CI) therapy.[69–72] CI therapy has been found to improve fine motor control of the hand in pianists and guitarists with focal dystonia,[71] and normalize abnormal representation of the fingers at the somatosensory cortex.[72] Musicians with focal dystonia may also benefit from pedagogical motor retraining as a therapeutic means.[73] Another effective treatment option is an injection of botulinum toxin into the affected muscle, which ensures a long-term benefit in performance ability.[74,75] Effects of brain surgery (i.e., ventro-oral thalamotomy) on musician's dystonia still remain controversial[76,77] and in need of further empirical evidence. Several studies also reported that sensory retraining using muscle vibration[78] and tactile electric stimulation[79] is beneficial in terms of improvement of fine motor control in focal hand dystonia.

Noninvasive transcranial stimulation techniques also provide ways of normalizing the abnormal neuronal activities at the sensorimotor cortices in musician's dystonia. For example, a case report using repetitive transcranial magnetic stimulation (rTMS) at 1 Hz over the primary motor cortex contralateral to the affected hand in a violinist with focal dystonia demonstrated effective improvement of fine motor control.[80] However, a potential risk of causing side effects, such as epileptic seizure, limits the clinical use of rTMS. Transcranial DCS is also capable of modulating the cortical excitability depending on the polarity of the electrode.[29] Several studies attempted to inhibit abnormal overactivity of the affected motor cortex using excitation–inhibition tDCS over the affected motor cortex; however, all failed.[81,82] In contrast, a recent study that combined bihemispheric tDCS over the bilateral motor cortices in combination with bimanual mirrored finger movements successfully ameliorated the symptom of pianists with focal hand dystonia.[83] In this study, the cathodal electrode was placed over the affected motor cortex for inhibiting the excitability, whereas the anodal electrode was placed over the unaffected motor cortex for facilitating the excitability. Using this bihemispheric tDCS, we attempted to transfer motor commands from the unaffected to the affected motor cortex via the corpus callosum. Following tDCS with motor training over 24 min, rhythmic variability of finger movements by the affected hand during piano performance was decreased. In addition, the amount of the decrease was positively correlated with severity of the symptoms prior to the intervention. It is therefore likely that the bihemispheric tDCS with the bimanual motor retraining offers a novel therapeutic option for musician's dystonia.

To investigate whether a long-term intervention using this technique enhances therapeutic effectiveness, we conducted a case study with a 32-year-old male pianist who had focal dystonia at the right index finger. This patient had suffered from focal hand dystonia for 3 years and had no treatment history of using botulinum toxin. He underwent the aforementioned bihemispheric tDCS with the bimanual motor training over two successive days (24 min of intervention each day), and movement accuracy was evaluated by asking him to play a simple melody synchronized with a metronome (interkeystroke interval 200 ms) with the affected right hand before and after the intervention on each of the days. The details of the experiment were the same as in our previous work.[83] We observed decreases in the variability of both the interkeystroke intervals (Fig. 1A) and keystroke velocity (Fig. 1B) during the 2 days of intervention, which confirmed

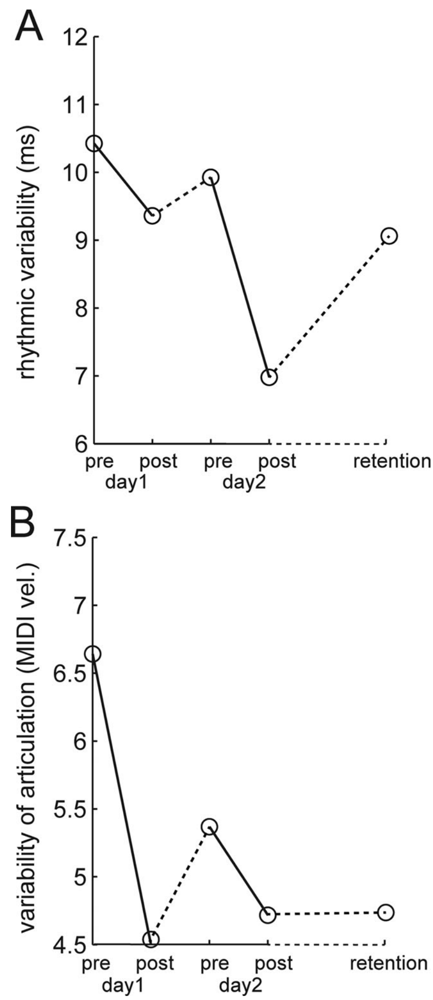

Figure 1. Changes in variability of the interkeystroke interval (A) and keystroke velocity (B) of a pianist with focal hand dystonia at the right index finger who was playing a simple melody with the affected right hand. The patient performed the intervention using bihemispheric tDCS and bimanual retraining over two successive days, and the motor test was performed before and after each intervention and 1 week after the final intervention (retention test).

progressive improvement of fine motor control. A retention test that was performed 1 week after the final intervention further demonstrated residual effects of the intervention (Fig. 1A and B). These findings therefore suggested accumulated and long-lasting effects of the intervention over multiple days on both rhythmic accuracy of movements and accuracy of force production in the pianist with focal hand dystonia.

Conclusion

Extensive musical practice is a two-edged blade that can facilitate or degrade fine motor control. An increasing number of cross-sectional studies have addressed differences in movement kinematics, muscular activation, and force between trained musicians and untrained individuals.[84] However, a lack of longitudinal studies that pursue changes in movement organization through musical practice limits the understanding of the optimal practice regime and pedagogical guidance to maximize motor skill acquisition and minimize risks of developing movement disorders. Although transcranial stimulation intervention has proven to be a promising tool for musician's dystonia, future studies should address its underlying neurophysiological mechanism by probing neuronal adaptation of the sensorimotor system using neuroimaging and transcranial stimulation techniques. It is also important to compare clinical effects of different intervention techniques, such as sensory and motor retraining, transcranial stimulation, injection of botulinum toxin, and prescription of medications, on musician's dystonia.

Conflicts of interest

The authors declare no conflicts of interest.

References

1. Jäncke, L. 2009. The plastic human brain. *Restor. Neurol. Neurosci.* **27:** 521–538.
2. Münte, T.F., E. Altenmüller & L. Jäncke. 2002. The musician's brain as a model of neuroplasticity. *Nat. Rev. Neurosci.* **3:** 473–478.
3. Nielsen, J.B. & L.G. Cohen. 2008. The Olympic brain. Does corticospinal plasticity play a role in acquisition of skills required for high-performance sports? *J. Physiol.* **586:** 65–70.
4. Yarrow, K., P. Brown & J.W. Krakauer. 2009. Inside the brain of an elite athlete: the neural processes that support high achievement in sports. *Nat. Rev. Neurosci.* **10:** 585–596.
5. Jabusch, H.C. *et al.* 2009. The influence of practice on the development of motor skills in pianists: a longitudinal study in a selected motor task. *Hum. Mov. Sci.* **28:** 74–84.
6. Krampe, R.T. & K.A. Ericsson. 1996. Maintaining excellence: deliberate practice and elite performance in young and older pianists. *J. Exp. Psychol. Gen.* **125:** 331–359.
7. Ioannou, C.I. & E. Altenmuller. 2014. Psychological characteristics in musicians dystonia: a new diagnostic classification. *Neuropsychologia* **61:** 80–88.
8. Leijnse, J.N. & M. Hallett. 2007. Etiological musculo-skeletal factor in focal dystonia in a musician's hand: a case study of the right hand of a guitarist. *Mov. Disord.* **22:** 1803–1808.
9. Enders, L. *et al.* 2011. Musician's dystonia and comorbid anxiety: two sides of one coin? *Mov. Disord.* **26:** 539–542.
10. Schmidt, A. *et al.* 2009. Etiology of musician's dystonia: familial or environmental? *Neurology* **72:** 1248–1254.
11. Schmidt, A. *et al.* 2013. Challenges of making music: what causes musician's dystonia? *JAMA Neurol.* **70:** 1456–1459.
12. Cohen, L.G. & M. Hallett. 1988. Hand cramps: clinical features and electromyographic patterns in a focal dystonia. *Neurology* **38:** 1005–1012.
13. Altenmüller, E. & H.C. Jabusch. 2009. Focal hand dystonia in musicians: phenomenology, etiology, and psychological trigger factors. *J. Hand Ther.* **22:** 144–154; quiz 155.
14. Chang, F.C. & S.J. Frucht. 2013. Motor and sensory dysfunction in musician's dystonia. *Curr. Neuropharmacol.* **11:** 41–47.
15. Altenmüller, E. *et al.* 2012. Musician's cramp as manifestation of maladaptive brain plasticity: arguments from instrumental differences. *Ann. N.Y. Acad. Sci.* **1252:** 259–265.
16. Furuya, S., M. Flanders & J.F. Soechting. 2011. Hand kinematics of piano playing. *J. Neurophysiol.* **106:** 2849–2864.
17. Furuya, S. & J.F. Soechting. 2012. Speed invariance of independent control of finger movements in pianists. *J. Neurophysiol.* **108:** 2060–2068.
18. Häger-Ross, C. & M.H. Schieber. 2000. Quantifying the independence of human finger movements: comparisons of digits, hands, and movement frequencies. *J. Neurosci.* **20:** 8542–8550.
19. Zatsiorsky, V.M., Z.M. Li & M.L. Latash. 2000. Enslaving effects in multi-finger force production. *Exp. Brain Res.* **131:** 187–195.
20. Furuya, S., A. Nakamura & N. Nagata. 2014. Acquisition of individuated finger movements through musical practice. *Neuroscience* **275:** 444–454.
21. Mosing, M.A. *et al.* 2014. Practice does not make perfect: no causal effect of music practice on music ability. *Psychol. Sci.* **25:** 1795–1803.
22. Chiang, H., S.M. Slobounov & W. Ray. 2004. Practice-related modulations of force enslaving and cortical activity as revealed by EEG. *Clin. Neurophysiol.* **115:** 1033–1043.
23. Gentner, R. *et al.* 2010. Encoding of motor skill in the corticomuscular system of musicians. *Curr. Biol.* **20:** 1869–1874.
24. Kang, S.Y., M. Hallett & Y.H. Sohn. 2012. Synchronized finger exercise reduces surround inhibition. *Clin. Neurophysiol.* **124:** 1622–1627.
25. Kang, S.Y., M. Hallett & Y.H. Sohn. 2013. Exercise-induced strengthening of inter-digital connections in musicians. *Clin. Neurophysiol.* **124:** 1622–1627.
26. Santello, M., M. Flanders & J.F. Soechting. 2002. Patterns of hand motion during grasping and the influence of sensory guidance. *J. Neurosci.* **22:** 1426–1435.
27. Parlitz, D., T. Peschel & E. Altenmüller. 1998. Assessment of dynamic finger forces in pianists: effects of training and expertise. *J. Biomech.* **31:** 1063–1067.
28. Slobounov, S. *et al.* 2002. Modulated cortical control of individual fingers in experienced musicians: an EEG study. *Clin. Neurophysiol.* **113:** 2013–2024.
29. Nitsche, M.A. & W. Paulus. 2000. Excitability changes induced in the human motor cortex by weak transcranial direct current stimulation. *J. Physiol.* **527** Pt 3**:** 633–639.

30. Furuya, S. *et al.* 2013. Early optimization in finger dexterity of skilled pianists: implication of transcranial stimulation. *BMC Neurosci.* **14:** 35.
31. Furuya, S. *et al.* 2014. Ceiling effects prevent further improvement of transcranial stimulation in skilled musicians. *J. Neurosci.* **34:** 13834–13839.
32. Lin, C.S. *et al.* 2013. Sculpting the intrinsic modular organization of spontaneous brain activity by art. *PLoS One* **8:** e66761.
33. Fitts, P.M. 1954. The information capacity of the human motor system in controlling the amplitude of movement. *J. Exp. Psychol.* **47:** 381–391.
34. Furuya, S., A. Nakamura & N. Nagata. 2013. Transfer of piano practice in fast performance of skilled finger movements. *BMC Neurosci.* **14:** 133.
35. Goebl, W. & C. Palmer. 2013. Temporal control and hand movement efficiency in skilled music performance. *PLoS One* **8:** e50901.
36. Winges, S.A. *et al.* 2013. Patterns of muscle activity for digital coarticulation. *J. Neurophysiol.* **110:** 230–242.
37. Harris, C.M. & D.M. Wolpert. 1998. Signal-dependent noise determines motor planning. *Nature* **394:** 780–784.
38. Platz, F. *et al.* 2014. The influence of deliberate practice on musical achievement: a meta-analysis. *Front. Psychol.* **5:** 646.
39. Lee, A. *et al.* 2013. Task-specific tremor in violinists: evidence of coactivation in the 3 to 8 Hz frequency range. *Mov. Disord.* **28:** 1890–1892.
40. Lee, A. *et al.* 2014. Electrophysiological characteristics of task-specific tremor in 22 instrumentalists. *J. Neural Transm.* DOI: 10.1007/s00702-014-1275-2.
41. Lee, A. *et al.* 2014. Coherence of coactivation and acceleration in task-specific primary bowing tremor. *J. Neural Transm.* **121:** 739–742.
42. Altenmüller, E. & H.C. Jabusch. 2010. Focal dystonia in musicians: phenomenology, pathophysiology and triggering factors. *Eur. J. Neurol.* **17**(Suppl 1): 31–36.
43. Frucht, S.J. 2009. Embouchure dystonia—portrait of a task-specific cranial dystonia. *Mov. Disord.* **24:** 1752–1762.
44. Frucht, S.J. & G. Estrin. 2010. "Losing one's chops": clues to the mystery of embouchure dystonia. *Neurology* **74:** 1758–1759.
45. Halstead, L.A., D.M. McBroom & H.S. Bonilha. 2014. Task-specific singing dystonia: vocal instability that technique cannot fix. *J. Voice.* **1997:** 92–97.
46. Steinmetz, A. *et al.* 2013. From embouchure problems to embouchure dystonia? A survey of self-reported embouchure disorders in 585 professional orchestra brass players. *Int. Arch. Occup. Environ. Health* **87:** 783–792.
47. Lee, A. *et al.* 2014. Quantification of instability of tone production in embouchure dystonia. *Parkinsonism Rel. Dis.* **20:** 1161–1164.
48. Borich, M., S. Arora & T.J. Kimberley. 2009. Lasting effects of repeated rTMS application in focal hand dystonia. *Restor. Neurol. Neurosci.* **27:** 55–65.
49. Furuya, S. & E. Altenmüller. 2013. Finger-specific loss of independent control of movements in musicians with focal dystonia. *Neuroscience* **247C:** 152–163.
50. Jabusch, H.C., H. Vauth & E. Altenmüller. 2004. Quantification of focal dystonia in pianists using scale analysis. *Mov. Disord.* **19:** 171–180.
51. Cheng, F.P., M. Grossbach & E.O. Altenmuller. 2013. Altered sensory feedbacks in pianist's dystonia: the altered auditory feedback paradigm and the glove effect. *Front. Human Neurosci.* **7:** 868.
52. Lee, A. *et al.* 2013. Alteration in forward model prediction of sensory outcome of motor action in focal hand dystonia. *Front. Human Neurosci.* **7:** 172.
53. Lim, V.K. *et al.* 2003. Perceptual differences in sequential stimuli across patients with musician's and writer's cramp. *Mov. Disord.* **18:** 1286–1293.
54. van der Steen, M.C. *et al.* 2014. Basic timing abilities stay intact in patients with musician's dystonia. *PLoS One* **9:** e92906.
55. Rosset-Llobet, J. *et al.* 2009. The challenge of diagnosing focal hand dystonia in musicians. *Eur. J. Neurol.* **16:** 864–869.
56. Peterson, D.A. *et al.* 2013. Rating scales for musician's dystonia: the state of the art. *Neurology* **81:** 589–598.
57. Ridding, M.C. *et al.* 1995. Changes in the balance between motor cortical excitation and inhibition in focal, task specific dystonia. *J. Neurol. Neurosurg. Psychiatry* **59:** 493–498.
58. Stinear, C.M. & W.D. Byblow. 2004. Impaired modulation of intracortical inhibition in focal hand dystonia. *Cereb. Cortex* **14:** 555–561.
59. Sohn, Y.H. & M. Hallett. 2004. Disturbed surround inhibition in focal hand dystonia. *Ann. Neurol.* **56:** 595–599.
60. Kadota, H. *et al.* 2010. An fMRI study of musicians with focal dystonia during tapping tasks. *J. Neurol.* **257:** 1092–1098.
61. Kimberley, T.J. & K.A. Pickett. 2012. Differential activation in the primary motor cortex during individual digit movement in focal hand dystonia vs. healthy. *Restor. Neurol. Neurosci.* **30:** 247–254.
62. Lerner, A. *et al.* 2004. Regional cerebral blood flow correlates of the severity of writer's cramp symptoms. *Neuroimage* **21:** 904–913.
63. Oga, T. *et al.* 2002. Abnormal cortical mechanisms of voluntary muscle relaxation in patients with writer's cramp: an fMRI study. *Brain* **125:** 895–903.
64. Pujol, J. *et al.* 2000. Brain cortical activation during guitar-induced hand dystonia studied by functional MRI. *Neuroimage* **12:** 257–267.
65. Rosenkranz, K. *et al.* 2008. Sensorimotor reorganization by proprioceptive training in musician's dystonia and writer's cramp. *Neurology* **70:** 304–315.
66. Rosenkranz, K. *et al.* 2005. Pathophysiological differences between musician's dystonia and writer's cramp. *Brain* **128:** 918–931.
67. Haslinger, B. *et al.* 2010. Sensorimotor overactivity as a pathophysiologic trait of embouchure dystonia. *Neurology* **74:** 1790–1797.
68. Granert, O. *et al.* 2011. Sensorimotor skills and focal dystonia are linked to putaminal grey-matter volume in pianists. *J. Neurol. Neurosurg. Psychiatry* **82:** 1225–1231.
69. Berque, P., H. Gray & A. McFadyen. 2013. A combination of constraint-induced therapy and motor control retraining in the treatment of focal hand dystonia in musicians: a long-term follow-up study. *Med. Probl. Perform. Art.* **28:** 33–46.
70. Candia, V. *et al.* 1999. Constraint-induced movement therapy for focal hand dystonia in musicians. *Lancet* **353:** 42.

71. Candia, V. *et al.* 2002. Sensory motor retuning: a behavioral treatment for focal hand dystonia of pianists and guitarists. *Arch. Phys. Med. Rehabil.* **83:** 1342–1348.
72. Candia, V. *et al.* 2003. Effective behavioral treatment of focal hand dystonia in musicians alters somatosensory cortical organization. *Proc. Natl. Acad. Sci. USA* **100:** 7942–7946.
73. van Vugt, F.T. *et al.* 2014. Musician's dystonia in pianists: long-term evaluation of retraining and other therapies. *Parkinsonism Rel. Disord.* **20:** 8–12.
74. Jabusch, H.C. *et al.* 2005. Focal dystonia in musicians: treatment strategies and long-term outcome in 144 patients. *Mov. Disord.* **20:** 1623–1626.
75. Schuele, S. *et al.* 2005. Botulinum toxin injections in the treatment of musician's dystonia. *Neurology* **64:** 341–343.
76. Charness, M.E. 2013. Brain surgery for musician's dystonia. *Ann. Neurol.* **74:** 627–629.
77. Horisawa, S. *et al.* 2013. Long-term improvement of musician's dystonia after stereotactic ventro-oral thalamotomy. *Ann. Neurol.* **74:** 648–654.
78. Rosenkranz, K. *et al.* 2009. Regaining motor control in musician's dystonia by restoring sensorimotor organization. *J. Neurosci.* **29:** 14627–14636.
79. Schabrun, S.M. *et al.* 2009. Normalizing motor cortex representations in focal hand dystonia. *Cereb. Cortex* **19:** 1968–1977.
80. Kieslinger, K. *et al.* 2013. Successful treatment of musician's dystonia using repetitive transcranial magnetic stimulation. *Clin. Neurol. Neurosurg.* **115:** 1871–1872.
81. Buttkus, F. *et al.* 2011. Single-session tDCS-supported retraining does not improve fine motor control in musician's dystonia. *Restor. Neurol. Neurosci.* **29:** 85–90.
82. Buttkus, F. *et al.* 2010. Failure of cathodal direct current stimulation to improve fine motor control in musician's dystonia. *Mov. Disord.* **25:** 389–394.
83. Furuya, S. *et al.* 2014. Surmounting retraining limits in musicians' dystonia by transcranial stimulation. *Ann. Neurol.* **75:** 700–707.
84. Furuya, S. & E. Altenmüller. 2013. Flexibility of movement organization in piano performance. *Front. Human Neurosci.* **7:** 173.