

Neural Processes Distinguishing Elite from Expert and Novice Athletes

Daniel E. Callan, PhD* † and Eiichi Naito, PhD*

Abstract: This commentary builds on a companion article in which Kim et al compare brain activation in elite, expert, and novice archers during a simulated target aiming task (Kim et al. 2014. *Cogn Behav Neurol*. 27:173-182). With the archery study as our starting point, we address 4 neural processes that may be responsible in general for elite athletes' superior performance over experts and novices: neural efficiency, cortical expansion, specialized processes, and internal models. In Kim et al's study, the elite archers' brains showed more activity in the supplementary motor area and the cerebellum than those of the novices and experts, and showed minimal widespread activity, especially in frontal areas involved with executive control. Kim et al's results are consistent with the idea of specialized neural processes that help coordinate motor planning and control. As athletes become more skilled, these processes may mediate the reduction in widespread activity in regions mapping executive control, and may produce a shift toward more automated processing. Kim et al's finding that activity in the cerebellum rose with increasing skill is consistent both with expansion of the finger representational area in the cerebellum and with internal models that simulate how archers manipulate the bow and arrow when aiming. Kim et al prepare the way for testing of neuromodulation techniques to improve athletic performance, refine highly technical job skills, and rehabilitate patients.

Key Words: functional magnetic resonance imaging, supplementary motor area, cerebellum, athlete, neural efficiency

(*Cogn Behav Neurol* 2014;27:183-188)

fMRI = functional magnetic resonance imaging. **GABA** = gamma-aminobutyric acid. **MI** = primary motor cortex. **SMA** = supplementary motor area.

Received for publication November 18, 2014; accepted November 18, 2014.

From the *Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology (NICT), Osaka University, Osaka, Japan; and †Multisensory Cognition and Computation Laboratory, Universal Communication Research Institute, National Institute of Information and Communications Technology (NICT), Kyoto, Japan.

Supported in part by JSPS KAKENHI, Grant-in-Aid for Scientific Research on Innovative Areas (No. 26120003) and Grant-in-Aid for Specially Promoted Research (No. 24000012).

The authors declare no conflicts of interest.

Reprints: Daniel E. Callan, PhD, Center for Information and Neural Networks (CiNet), National Institute of Information and Communications Technology (NICT), Osaka University, 2A6, 1-4 Yamadaoka, Suita, Osaka 565-0871, Japan (e-mail: dcallan@nict.go.jp).

Copyright © 2014 by Lippincott Williams & Wilkins

In a companion article in this issue, Kim et al (2014) report using a simulated aiming task to explore the neural processes underlying archery skill in elite, expert, and novice archers. The study is unique, first in having recruited as its elite group some of the world's best archers: 13 medalists from the Olympics, Asian Games, and/or World Championships. The expert group was college students from the Korean Archery Association. The novice group was college students with no archery experience. Previous studies have focused only on comparing experts with novices. The second unique feature of this study is that it sought differences in neural mechanisms between elite and expert athletes, all of whom had considerable archery experience.

Elite athletes possess greater speed, strength, endurance, coordination, accuracy, consistency, automaticity, and efficiency than less proficient athletes (Nakata et al, 2010). Depending on the requirements of the sport, these abilities account for the elites' superior performance. Together with muscle and cardiovascular fitness, differential and specialized neural processing contributes to their exceptional abilities.

Four neural processes may enhance performance in athletes:

- *Neural efficiency* can reflect 2 different processes. The first is a reduction in neural activity in certain brain regions as a particular skill becomes more automated and less controlled (Debarnot et al, 2014). The second is a reduction of activity in sensory and motor cortex, reflecting more efficient processing made possible by less energy expenditure (Naito and Hirose, 2014; Nakata et al, 2010).
- *Cortical expansion* refers to a progressively larger area of cortex being used for topographic representation as a result of training in motor skills (Nudo et al, 1996) and/or sensory discrimination (Recanzone et al, 1993).
- *Specialized processing* refers to a specific brain region (or network of regions) carrying out processes related to some aspect of a task through experience-dependent learning, thus allowing for better performance.
- *Internal models* simulate the input and output characteristics of the relevant control system (Kawato, 1999). With archery, an internal model would simulate the dynamics of the bow, including the tension, visual aiming angle, and distance to the target. Error-feedback learning based on the distance between where the arrow hits and the center of the target can be used to train the internal model.

For an extensive overview of neural processes involved with skill learning in athletics, see Chang (2014), Debarnot et al (2014), and Nakata et al (2010).

These 4 neural processes are relevant to discussing the differences and similarities in brain activity among the elite, expert, and novice archers in Kim et al's study. In their experimental task, participants inside a functional magnetic resonance imaging (fMRI) scanner were shown a projected image of a static archery target. The image was the same size as it would look from 70 meters away, the distance of a regulation archery range. Within 10 seconds of first seeing the target, participants went through the mental preparations of aiming an arrow at the target, and they pushed a button to signal the moment that they felt most ready and they mentally released the bowstring.

One advantage of using such a simple task is that the stimulus and motor response characteristics were the same for the elite, expert, and novice groups. The experimental design ensured that differences in brain activity among the groups did not arise from differences in task difficulty. The primary difference among the groups was their mental imagery concerning the timing of imagined shooting. Because no one actually shot an arrow, the authors could not measure the participants' accuracy at hitting the target in relation to the time that they released the bowstring. Thus, we cannot judge how closely the participants' own beliefs about their optimal timing of bowstring release would have matched their performance at hitting the target.

Constraints on body movement are an inherent problem in assessing brain activity during athletic tasks using fMRI and magnetoencephalography scanners. The tight space and recording requirements of scanners prevent participants from shooting real arrows, playing golf, and dancing. However, for tasks such as piloting an airplane using a flight simulator, the controls and visual stimuli used in fMRI and magnetoencephalography can be the same as in the real world (Callan et al, 2012, 2013).

When the fMRI scanner does not let participants perform an athletic skill, as in Kim et al's archery study, the researchers often use mental imagery tasks (Calvo-Merino et al, 2006; Chang et al, 2011; Kim et al, 2008; Milton et al, 2007; Ross et al, 2003). Because Kim et al's elite and expert archers had extensive experience using a real bow and arrow, they could probably imagine realistically, ie, mentally simulate, the process of releasing the bowstring at the time they considered optimal. The novice group, however, did not have any archery experience, and so they were unlikely to have been able to imagine realistically holding, aiming, and releasing the bowstring. Even though all participants reported at the end of the experiment that they had been aiming and not just looking at the targets, the novice group likely required more planning and cognitive processing to accomplish the task.

NEURAL EFFICIENCY

The brain imaging results of Kim et al's study agree with many other studies (Chang et al, 2011; Haier et al,

1992; Jancke et al, 2000; Milton et al, 2007) that showed more widespread brain activity, indicating less neural efficiency, in novices than experienced performers. This type of neural efficiency is a reduction in neural activity in certain brain regions as a particular skill becomes less controlled and more automated (Debarnot et al, 2014).

For example, in Kim et al's study, the novices had greater activity than the expert and elite archers in the superior frontal gyrus, inferior frontal gyrus, and ventral prefrontal cortex. This difference likely reflects the novices' greater need for controlled (executive) motor planning to carry out the simulated archery task. The skilled archers, by contrast, performed more automatically. Based on these results, we may conjecture that 1 characteristic of expert and elite athletes is greater use of automated neural processes attained through extensive experience. This means less use of executive control processes, which may reduce efficiency.

While moving from executively controlled to more automated processing can be considered a way to enhance neural efficiency (Debarnot et al, 2014), another way is to lessen energy expenditure. Energy can be saved by reducing activity in the sensory and motor cortex in response to familiar stimulus or movement parameters or demands. This form of neural efficiency has been reported in athletes (Bernardi et al, 2013; Naito and Hirose, 2014) and skilled musicians and ballet dancers (Hanggi et al, 2010; Haslinger et al, 2004; Jancke et al, 2000; Koeneke et al, 2004; Krings et al, 2000).

For example, Naito and Hirose (2014) used fMRI to compare brain activity during a foot rotation task in 7 athletes: the elite football (soccer) player Neymar da Silva Santos Júnior, 3 other professional and 1 amateur football players, and 2 professional swimmers. Of all the participants, Neymar had the least activity in the foot area of the primary motor cortex (M1). The authors proposed that his low activity and high neural efficiency resulted from many years of rich and dynamic use of the ankle joints (Naito and Hirose, 2014).

The authors' conclusion was supported by their finding that all 4 of the professional footballers had a smaller area of activity in the foot region of M1 than did the professional swimmers, who also use their feet extensively but in a more highly patterned manner (Naito and Hirose, 2014).

This energy-saving form of neural efficiency may allow higher reproducibility with less effort, in addition to expanding the control capacity needed to produce a wide variety of foot movements. Just as with professional keyboard musicians (Gärtner et al, 2013), professional football players may have an experience-enabled expansion of gray matter in M1. A professional footballer like Neymar may need to recruit only a limited portion of his expanded motor-cortical neuronal networks to control simple foot movements. This leaves considerable resources in his remaining neural networks that he can assign to controlling elaborate foot movements (Naito and Hirose, 2014).

Elite and expert archers might be expected to show this same energy-saving form of neural efficiency in

cortical sensory and motor areas representing the fingers, hand, and arm, all of which are required for bowstring release. This, however, is not what Kim et al found. Rather, only their elite group showed significant activity in the finger, hand, and arm representation area of M1. We determined this from the activity listed in Kim et al's Table 1 and Supplemental Digital Content 2 (<http://links.lww.com/CBN/A48>), in reference to the somatotopic representation center in M1 reported by Indovina and Sanes (2001). Kim et al found no activity in this region for the expert or novice archers. It is possible that the bilateral M1 representation that Kim found merely reflected the button press, but if this were so, Kim et al would have seen the activity in all 3 groups.

CORTICAL EXPANSION

Another possibility put forward by Kim et al is that the elite archers' activity in the finger, hand, and arm representation area of M1 reflects automated processes related to movement planning and execution that the elite archers attained through extensive experience and that improved their aiming capabilities. While increased M1 activity in the archers with extensive experience may seem at odds with the processes of neural efficiency, it is consistent with the processes of cortical expansion. As defined earlier, cortical expansion is a progressively larger area of cortex used for topographic representation as a result of training in motor skills (Nudo et al, 1996) and sensory discrimination (Recanzone et al, 1993).

Several studies have shown unusually strong cortical representation in M1 in athletes and musicians as a result of their skill learning (Bangert and Schlaug, 2006; Elbert et al, 1995; Gaser and Schlaug, 2003; Meister et al, 2005; Pearce et al, 2000). For example, elite racquetball players have a larger cortical representation of the hand than do novices (Pearce et al, 2000). The somatotopic representation of the left-hand fingers of stringed instrument players has been reported to be experience-dependent and larger than that of nonmusicians (Elbert et al, 1995). Furthermore, the location of cortical expansion corresponds to the hand or fingers required to play a particular instrument (Bangert and Schlaug, 2006).

In the Kim et al study, only the elite archers had activity in the finger, hand, and arm representation area of M1 (see Kim et al's Table 1 and Supplemental Digital Content 2 [<http://links.lww.com/CBN/A48>]). However, the activity difference between the elite archers and the expert and novice groups was not significant, as shown by the lack of differential activity for this region in Kim et al's Table 2 and Supplemental Digital Content 3 (<http://links.lww.com/CBN/A49>).

It is unclear under what conditions the brain uses cortical expansion or neural efficiency. While Hanggi et al (2010) have made some suggestions, further research is needed to explain how these 2 apparently contradictory processes relate to athletes' skill. Continuing research should consider factors such as type and complexity of the task, whether the movement is imagined or actually executed,

anatomic versus functional expansion and contraction, and the participants' experience with the skill.

According to a broad survey of the literature on motor skill learning, the brain begins to acquire a new motor skill—during the first week or so of learning—by expanding the motor representation in M1 (Floyer-Lea and Matthews, 2005; Karni et al, 1995; Pascual-Leone et al, 1995). This “functional field” may expand at least in part because a decrease in gamma-aminobutyric acid (GABA) inhibition unmasks pre-existing synaptic connections (Floyer-Lea et al, 2006). When a person has trained extensively in the motor skill over many years, the motor representations shrink as the brain becomes able to control the skill more and more efficiently (Krings et al, 2000). The greater efficiency could result from improved function of motor-cortical synapses (Picard et al, 2013). Thus, the brain's self-reorganization function, eg, expanding and shrinking central motor representations, is essential when people learn new motor skills and remains essential in promoting efficient control over those skills throughout people's lifespan.

This process—of cortical expansion followed by shrinking because of greater neural efficiency—can also be seen to apply to damaged brains. For example, after focal damage in the M1 hand section, the brain recruits contralesional M1 (ipsilateral to the hand) to control hand movements for the first month, but after 6 months the brain uses only the undamaged section of M1 that is contralateral to the hand (Jang et al, 2004). Likewise, within a year after the internal capsule has been injured, vicarious activity in the broader bilateral motor regions diminishes as motor functions recover (Ward et al, 2003). In people with brain damage, GABA seems to be a key transmitter allowing the short-term expansion of cortical representation (Glodzik-Sobańska et al, 2004). Finally, synaptic scaling (Turrigiano, 1999, 2011), a homeostatic mechanism that may stabilize plasticity in the nervous system, could be key in consolidating a motor skill and shrinking central motor representation by increasing synaptic efficiency. Learning more about how the brain repairs itself after injury could help explain the neural processes underlying elite athletic performance.

SPECIALIZED PROCESSING AND INTERNAL MODELS

Breaking new ground, Kim et al sought to answer the question of what brain processes differentiate elite from expert archers, even though both groups have considerable experience. The authors found that the elite archers had significantly greater activity in 2 brain regions: the supplementary motor area (SMA) and the cerebellum.

The SMA is thought to mediate planning and integration in executing complex motor tasks (Lotze et al, 1999). As Kim et al point out, the SMA may facilitate the movement planning and aiming that enhance elite archers' targeting abilities. The results support the idea that increasing activity in the SMA aids in the specialized processing, acquired through experience, that facilitates performance. In part, processing in the SMA may explain

why skilled athletes and performing artists do not require the same extensive use of the frontal regions as do novices.

Consistent with this hypothesis is the authors' earlier finding that during the mental imagery of aiming, elite archers had their predominant activity in the SMA, while novice archers had widespread activity in the SMA, premotor cortex, inferior frontal region, basal ganglia, and cerebellum (Chang et al, 2011). Similarly, professional musicians have been shown to have greater activation in the SMA than do novice musicians, whose activity is widespread (Lotze et al, 2003). However, contrary to the results of these studies as well as the Kim et al study, Ross et al (2003) reported an inverse relationship between SMA activity and skill in a mental imagery task of a golf swing.

This apparent discrepancy between findings about the influence of SMA activity and mental imagery may be explained by Kasess et al (2008). They found that SMA activation during motor imagery suppresses M1 activation. Their results show the importance of the SMA not only in preparing and executing intended movements, but also in suppressing movements that are represented in the motor system though not performed. Thus, how deeply the SMA is engaged in suppressing movements may depend largely on the type of motor task. Archery mainly requires small finger movements, while a golf swing requires full-body movements.

The cluster of activity that Kim et al found in the SMA may also have included portions of the rostral cingulate motor area. Greater activation in this area for elite than expert and novice archers is noteworthy in that this area has been linked to processes governing self-monitoring of internal status (Yamagishi and Anderson, 2013). In Yamagishi and Anderson's study, participants pressed a button to start the presentation of a visual stimulus when they felt that their attentional focus was optimal. This task was similar to that in the Kim et al study, in which participants pressed a button when they had mentally taken optimal aim at the target and were ready to release the bowstring. It is entirely possible that the neural activity that Kim et al found reflects specialized processes that govern the self-monitoring of internal status. That these processes are improved by extensive experience in elite athletes may in part explain their extraordinary abilities.

The cerebellum is the other brain region in which Kim et al found greater activity for elite than expert and novice archers. Many studies have shown that athletes and performing artists with extensive experience have significant expansion and activity in the cerebellum. These increases have been noted in musicians (Gaser and Schlaug, 2003; Lotze et al, 2003), rock climbers (Di Paola et al, 2013), basketball players (Park et al, 2009), badminton players (Di et al, 2012), and short-track speed skaters (Park et al, 2012). However, some studies report less activity in the cerebellum with greater expertise in golf (Ross et al, 2003) and archery (Chang et al, 2011). Kim et al also report less activity, though in a different region of the cerebellum.

The cerebellum is thought to sharpen sensory input, temporal coordination, processing of motor articulation and

perception, and representation of internal models (Callan et al, 2007). Kim et al report that right cerebellar dentate activity correlates with archery skill level (see Kim et al's Tables 1 and 2, Supplemental Digital Content 2 [<http://links.lww.com/CBN/A48>] and Supplemental Digital Content 3 [<http://links.lww.com/CBN/A49>]). Interestingly, the right cerebellar dentate represents the right hand and fingers (Grodd et al, 2001). This region is also known to have projections to the contralateral M1 (Dum and Strick, 2003).

The high cerebellar activity may follow processes like those of cortical expansion seen in the motor (Nudo et al, 1996) and sensory cortices (Recanzone et al, 1993). It is also possible that the cerebellar activity that Kim et al found to be greater for elite than expert and novice archers reflects an internal model that simulates how archers manipulate the bow and arrow when aiming. One way to test this hypothesis would be to use a task that gives error-feedback and see if the error correlates with activity in the cerebellar region that is thought to instantiate the internal model.

In any case, specialized processing in the cerebellum may allow elite athletes better performance and more efficient processing than in novices by making many of the planning and control processes automated rather than executively controlled. In Kim et al's study, this specialized processing may account in part for the elite archers' lower activity in brain regions involved with executive control, such as the superior frontal gyrus, inferior frontal gyrus, and ventral prefrontal cortex.

CONCLUSIONS

The strength of Kim et al's archery study is in elucidating neural processes that may be responsible for performance differences between elite and expert athletes in many sports. The authors' elite archers had strong activation in both the cerebellum and the SMA. In the cerebellum, the authors found a correlation between activation and archery skill level. Specialized processing in the SMA and cerebellum may account not only for elite athletes' high performance but also for their low reliance on executively controlled motor planning and execution. By contrast, Kim et al's novice archers had strong activity in frontal executive and motor planning areas.

Why do some athletes develop certain specialized neural processes? Likely from a genetic predisposition combined with extensive training. Given new discoveries in neuromodulation methods, we can imagine a future in which elite athletic performance could be facilitated by, eg, transcranial direct current stimulation of targeted brain regions to increase learning via enhanced long-term potentiation (Coffman et al, 2014; Floel, 2014; Prichard et al, 2014). We can already enhance performance through reinforcement learning based on feedback of one's own activity in a specific brain region (Shibata et al, 2011). Techniques like these can be extended to help rehabilitate ill or injured patients, as well as to advance the specialized skills of workers in hazardous operations such

as aviation, space, and deep sea environments in which a performance error can have drastic consequences.

REFERENCES

- Bangert M, Schlaug G. 2006. Specialization of the specialized in features of external human brain morphology. *Eur J Neurosci*. 24:1832–1834.
- Bernardi G, Ricciardi E, Lorenzo S, et al. 2013. How skill expertise shapes the brain functional architecture: an fMRI study of visuo-spatial and motor processing in professional racing-car and naïve drivers. *PLoS One*. 8:1–11.
- Callan D, Gamez M, Cassel D, et al. 2012. Dynamic visuomotor transformation involved with remote flying of a plane utilizes the ‘Mirror Neuron’ system. *PLoS One*. 7:1–14.
- Callan D, Kawato M, Parsons L, et al. 2007. Speech and song: the role of the cerebellum. *Cerebellum*. 6:321–327.
- Callan D, Terzibas C, Cassel D, et al. 2013. Differential activation of brain regions involved with error-feedback and imitation based motor simulation when observing self and an expert’s actions in pilots and non-pilots on a complex glider landing task. *NeuroImage*. 72:55–68.
- Calvo-Merino B, Grezes J, Glaser DE, et al. 2006. Seeing or doing? Influence of visual and motor familiarity in action observation. *Curr Biol*. 16:1905–1910.
- Chang Y. 2014. Reorganization and plastic changes of the human brain associated with skill learning and expertise. *Front Hum Neurosci*. 8:1–7.
- Chang Y, Lee JJ, Seo JH, et al. 2011. Neural correlates of motor imagery for elite archers. *NMR Biomed*. 24:366–372.
- Coffman BA, Clark VP, Parasuraman R. 2014. Battery powered thought: enhancement of attention, learning, and memory in healthy adults using transcranial direct current stimulation. *NeuroImage*. 85:895–908.
- Debarnot U, Sperduti M, Di Rienzo F, et al. 2014. Experts bodies, experts minds: how physical and mental training shape the brain. *Front Hum Neurosci*. 8:1–16.
- Di X, Zhu S, Jin H, et al. 2012. Altered resting brain function and structure in professional badminton players. *Brain Connect*. 2:225–233.
- Di Paola M, Caltagirone C, Petrosini L. 2013. Prolonged rock climbing activity induces structural changes in cerebellum and parietal lobe. *Hum Brain Mapp*. 34:2707–2714.
- Dum RP, Strick P. 2003. An unfolded map of the cerebellar dentate nucleus and its projections to the cerebral cortex. *J Neurophysiol*. 89:634–639.
- Elbert T, Pantev C, Wienbruch C, et al. 1995. Increased cortical representation of the fingers of the left hand in string players. *Science*. 270:305–307.
- Floel A. 2014. tDCS-enhanced motor and cognitive function in neurological diseases. *NeuroImage*. 85:934–947.
- Floyer-Lea A, Matthews P. 2005. Distinguishable brain activation networks for short- and long-term motor skill learning. *J Neurophysiol*. 94:512–518.
- Floyer-Lea A, Wylezinska M, Kincses T, et al. 2006. Rapid modulation of GABA concentration in human sensorimotor cortex during motor learning. *J Neurophysiol*. 95:1639–1644.
- Gärtner H, Mínerop M, Pieperhoff P, et al. 2013. Brain morphometry shows effects of long-term musical practice in middle-aged keyboard players. *Front Psychol*. 4:1–13.
- Gaser C, Schlaug G. 2003. Brain structures differ between musicians and non-musicians. *J Neurosci*. 23:9240–9245.
- Glodzik-Sobanska L, Slowik A, Kozub J, et al. 2004. GABA in ischemic stroke: proton magnetic resonance study. *Med Sci Monit*. 10:88–93.
- Grodd W, Hulsmann E, Lotze M, et al. 2001. Sensorimotor mapping of the human cerebellum: fMRI evidence of somatotopic organization. *Hum Brain Mapp*. 13:55–73.
- Haier RJ, Siegel BV, MacLachlan A, et al. 1992. Regional glucose metabolic changes after learning a complex visuospatial/motor task: a positron emission tomographic study. *Brain Res*. 570:134–143.
- Hanggi J, Koeneke S, Bezzola L, et al. 2010. Structural neuroplasticity in the sensorimotor network of professional female ballet dancers. *Hum Brain Mapp*. 31:1196–1206.
- Haslinger B, Erhard P, Altenmüller E, et al. 2004. Reduced recruitment of motor association areas during bimanual coordination in concert pianists. *Hum Brain Mapp*. 22:206–215.
- Indovina I, Sanes JN. 2001. On somatotopic representation centers for finger movements in human primary motor cortex and supplementary motor area. *NeuroImage*. 13:1027–1034.
- Jancke L, Shah NJ, Peters M. 2000. Cortical activations in primary and secondary motor areas for complex bimanual movements in professional pianists. *Cogn Brain Res*. 10:177–183.
- Jang SH, Cho SH, Kim YH, et al. 2004. Cortical activation changes associated with motor recovery in patients with precentral knob infarct. *NeuroReport*. 15:395–399.
- Karni A, Meyer G, Jezzard P, et al. 1995. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*. 377:155–158.
- Kassess CH, Windischberger C, Cunnington R, et al. 2008. The suppressive influence of SMA on M1 in motor imagery revealed by fMRI and dynamic causal modeling. *Neuroimage*. 40:828–837.
- Kawato M. 1999. Internal models for motor control and trajectory planning. *Curr Opin Neurobiol*. 9:718–727.
- Kim J, Lee HM, Kim WJ, et al. 2008. Neural correlates of pre-performance routines in expert and novice archers. *Neurosci Lett*. 445:236–241.
- Kim W, Chang Y, Kim J, et al. 2014. An fMRI study of differences in brain activity among elite, expert, and novice archers at the moment of optimal aiming. *Cogn Behav Neurol*. 27:173–182.
- Koeneke S, Lutz K, Wustenberg T, et al. 2004. Long-term training affects cerebellar processing in skilled keyboard players. *NeuroReport*. 15:1279–1282.
- Krings T, Topper R, Foltys H, et al. 2000. Cortical activation patterns during complex motor tasks in piano players and control subjects: a functional magnetic resonance imaging study. *Neurosci Lett*. 278:189–193.
- Lotze M, Monotoya P, Erb M, et al. 1999. Activation of cortical and cerebellar motor areas during executed and imagined hand movements: an fMRI study. *J Cogn Neurosci*. 11:491–501.
- Lotze M, Scheler G, Tan HR, et al. 2003. The musician’s brain: functional imaging of amateurs and professionals during performance and imagery. *NeuroImage*. 20:1817–1829.
- Meister I, Krings T, Foltys H, et al. 2005. Effects of long-term practice and task complexity in musicians and nonmusicians performing simple and complex motor tasks: implications for cortical motor organization. *Hum Brain Mapp*. 24:345–352.
- Milton J, Solodkin A, Hlustik P, et al. 2007. The mind of expert motor performance is cool and focused. *NeuroImage*. 35:804–813.
- Naito E, Hirose S. 2014. Efficient foot motor control by Neymar’s brain. *Front Hum Neurosci*. 8:594.
- Nakata H, Yoshie M, Miura A, et al. 2010. Characteristics of the athletes’ brain: evidence from neurophysiology and neuroimaging. *Brain Res Rev*. 62:197–211.
- Nudo RJ, Milliken GW, Jenkins WM, et al. 1996. Use-dependent alterations of movement representations in primary motor cortex of adult squirrel monkeys. *J Neurosci*. 16:785–807.
- Park IS, Lee KJ, Han JW, et al. 2009. Experience-dependent plasticity of cerebellar vermis in basketball players. *Cerebellum*. 8:334–339.
- Park IS, Lee NJ, Kim TY, et al. 2012. Volumetric analysis of cerebellum in short-track speed skating players. *Cerebellum*. 11:925–930.
- Pascual-Leone A, Nguyet D, Cohen LG, et al. 1995. Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *J Neurophysiol*. 74:1037–1045.
- Pearce AJ, Thickbroom GW, Byrnes ML, et al. 2000. Functional reorganisation of the corticomotor projection to the hand in skilled racket players. *Exp Brain Res*. 130:238–243.
- Picard N, Matsuzaka Y, Strick P. 2013. Extended practice of a motor skill is associated with reduced metabolic activity in M1. *Nat Neurosci*. 16:1340–1347.
- Prichard G, Weiller C, Fritsch B, et al. 2014. Effects of different electrical brain stimulation protocols on subcomponents of motor skill learning. *Brain Stimul*. 7:532–540.

- [Recanzone GH, Schreiner CE, Merzenich MM. 1993. Plasticity in the frequency representation of primary auditory cortex following discrimination training in adult owl monkeys. *J Neurosci.* 13: 87–103.](#)
- [Ross JS, Tkach J, Ruggieri PM, et al. 2003. The mind's eye: functional MR imaging evaluation of golf motor imagery. *AJNR Am J Neuroradiol.* 24:1036–1044.](#)
- [Shibata K, Watanabe T, Sasaki Y, et al. 2011. Perceptual learning incepted by decoded fMRI neurofeedback without stimulus presentation. *Science.* 334:1413–1415.](#)
- [Turrigiano G. 1999. Homeostatic plasticity in neuronal networks: the more things change, the more they stay the same. *Trends Neurosci.* 22:221–227.](#)
- [Turrigiano G. 2011. Too many cooks? intrinsic and synaptic homeostatic mechanisms in cortical circuit refinement. *Annu Rev Neurosci.* 34:89–103.](#)
- [Ward NS, Brown MM, Thompson AJ, et al. 2003. Neural correlates of outcome after stroke: a cross-sectional fMRI study. *Brain.* 126:1430–1448.](#)
- [Yamagishi N, Anderson S. 2013. The relationship between self-awareness of attentional status, behavioral performance and oscillatory brain rhythms. *PLoS One.* 8:1–12.](#)