Brain Reorganization and Neural Plasticity in Elite Athletes With Physical Impairments

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NAKAZAWA, K. Brain reorganization and neural plasticity in elite athletes with physical impairments. Exerc. Sport Sci. Rev., Vol. 50, No. 3, pp. 118–127, 2022. Use-dependent and impairment-specific brain plasticity are hypothesized to interact and enhance neural reorganization in the central nervous system (CNS) of athletes with physical impairments. Paralympic brain studies are helpful in achieving a fundamental understanding of the underlying neural mechanism related to CNS reorganization after physical therapy or athletic training. Information learned from these individuals also provides new insights into sports- and rehabilitation-related neuroscience. Key Words: Paralympic athlete, brain, reorganization, neural plasticity, rehabilitation

INTRODUCTION
Paralympic athletes impress us with their incredible performances in competitions. Despite the physical impairments that these individuals have, they engage in daily physical training to improve their performance and increase their chances of winning. It is well known that the intense motor practices that elite athletes, musicians, or ballet dancers engage in induce both functional and structural plastic changes in their brains (1–3). The underlying property of these plastic changes is called experience- or use-dependent neural plasticity, which refers to fundamental neural properties leading to sustained functional and anatomical remodeling of different areas in the central nervous system. In the brains of Paralympic athletes, therefore, use-dependent plastic change is considered to occur because of the motor practices in which they are regularly involved. There is, however, another factor that cannot be ignored when considering the plastic changes in Paralympians’ brains: injury-dependent plasticity. After a damage to the brain, such as a stroke, a widespread regenerative reaction is known to take place, which eventually induces a reorganization of the synaptic connectivity patterns of surviving neurons (4). As those injury-dependent plastic changes in the CNS are highly specific to the type of physical impairments, they are defined, as a whole, as impairment-specific plasticity in the present article. In Paralympic athletes, both impairment-specific and use-dependent plastic processes are considered to be involved in the plastic changes that take place in their brains.

What we found in a series of studies on Paralympians’ brains is that they are uniquely reorganized depending on the types of physical impairments and motor practices in which the athletes have been engaged. The extent of plastic brain change apparently is more notable in Paralympic athletes than in elite unimpaired athletes, such as Olympic athletes, which is assumed to be related to the interaction of impairment-specific plasticity with use-dependent plasticity. In animal studies, it is well known that use-dependent plastic processes interact with regenerative neural reactions to brain damage, such as stroke (5–7). In humans, based on an elegant series of studies, Paul Zehr and his colleagues proposed a hypothesis that training-induced neural plasticity is amplified after individuals experience brain lesions (8). The authors demonstrated that the cross-education effect in strength training was more enhanced in hemiplegic individuals than in unimpaired individuals (9,10). There is a possibility, therefore, that the enhanced plasticity that occurs after individuals experience lesions in the CNS induces more remarkable plastic changes in...
elite Paralympic athletes than in those individuals who do not participate in athletic training.

In the present review article, plastic changes in various Paralympians’ brains will be introduced and discussed with relevant previous studies. Most studies on Paralympic athletes are case studies. Therefore, the number of cases is inevitably small. However, by gathering and carefully examining each Paralympic athlete case, a hypothetically common characteristic was elucidated, and the following hypotheses could be derived: (I) the brain function and structure of athletes with physical impairments would be reorganized differently than those of unimpaired athletes in a manner that underlies their impairments as well as athletic-specific training, and that (II) the factors playing a major role in brain reorganization are related to impairment-specific and use-dependent plasticity (Fig. 1). Notably, these hypotheses cannot be tested within the current knowledge and the limited amount of data available. Rather, they provide a perspective for future studies relevant to the unknown neuroplastic capacity of the human brain. In this review article, examples of unique reorganization in the motor systems of athletes with physical impairments are introduced along with recent advances in related research fields, and perspectives for future research will be provided.

Athletes With an Amputation: Bilateral Motor Cortices Are Involved in Controlling a Prosthesis

Paralympic athletes with amputations have exhibited amazing performance over the last decade. Mizuguchi et al. (11) studied functional magnetic resonance images (fMRIs) of the brain of a long jump Paralympic athlete with a unilateral below-knee amputation. Mizuguchi N, Nakagawa K, Tazawa Y, Kanosue K, Nakazawa K. Functional plasticity of the ipsilateral primary sensorimotor cortex in an elite long jumper with below-knee amputation. NeuroImage Clin. 2019; 23:101847. (CC BY 4.0).
amputation (Para-long jumper), who won gold medals at the Summer Paralympics in 2012 and 2016 and held the long jump world record in his category (T44, 8.40 m). Figure 2 demonstrates activated brain regions when the Para-long jumper voluntarily activated muscles around the left and right lower limb joints. Mizuguchi et al. (11) found that there was significant activation on both sides of the motor cortex (M1) only when the Para-long jumper was exerting voluntary contraction of his knee muscles on his amputated side. There was no such bilateral M1 activation when he exerted muscle contractions around the other lower limb joints, including the amputated ankle joint. The authors statistically confirmed that the observed bilateral M1 activation in the Para-long jumper was unique, as it was not observed in individuals with a below-knee amputation or unamputated long jumpers.

To test whether specific bilateral M1 activation would be observed in other athletes with a prosthesis, they subsequently performed the same fMRI experiment on a Paralympic high-jumper with a below-knee amputation. The results showed bilateral M1 activation only when the high jumper exerted knee muscle contraction. They further performed transcranial magnetic stimulation (TMS) to test whether ipsilateral corticospinal excitability in the knee extensor rectus femoris muscle on the amputated side would be enhanced in this high jumper. The results revealed that motor evoked potentials were elicited in the rectus femoris muscle on the amputated side when the ipsilateral M1 was stimulated with TMS. Figure 3 depicts the input-output relations of the corticospinal tracts in both rectus femoris muscles, demonstrating the higher ipsilateral corticospinal excitability in the rectus femoris muscle on the amputated side (Nakazawa K, Nakanisih T, Sasaki A., unpublished data, 2020). These results, together with those of Mizuguchi et al. (11), suggest that the observed bilateral M1 activation in elite Paralympic athletes is related to long-term athletic training, in other words, motor practice with an athletic prosthesis in sports activity, although the number of samples was too small to lead to a firm conclusion.

To further examine the relation between bilateral M1 activation and prosthesis use, Nakanish et al. (12) recruited 30 individuals with unilateral lower limb amputations (14 transtibial and 16 transfemoral amputations) who regularly participated in sports activities and performed the same fMRI experiments as with Paralympic athletes. The authors found that 12 out of 30 participants demonstrated significant ipsilateral M1 activation, and there was a significant correlation (P < 0.05) between years of participation in sports and the ipsilateral M1 activation level. These findings supported the idea that ipsilateral M1 activation would be related to the use of prostheses with higher activity levels than daily activity use levels.

Regarding ipsilateral M1 activation in unilateral lower limb amputees, a series of TMS studies from Hordacre’s group demonstrated higher relative ipsilateral M1 excitability to the contralateral M1 (13) and modulation of intracortical inhibition during the rehabilitation period (14). Specifically, in Hordacre et al. (13), the relative excitability of ipsilateral and contralateral corticmotor projections to alpha-motoneurons innervating the quadriceps muscle of the amputated limb was assessed, and it was demonstrated that amputees had greater excitability of ipsilateral corticmotor projections than the control group. The higher ipsilateral corticmotor projection to the motoneurons whose activity controls the quadriceps of the amputated limb is in line with the observed higher activation of the ipsilateral M1 of the Para-long jumper in Mizuguchi et al. (11). However, in the nonathletes who had unilateral lower limb amputations in Mizuguchi et al. (11), no higher activation of the ipsilateral.

Figure 3. A. Relations between the intensity of transcranial magnetic stimulation (TMS) to the left and right sides of the primary motor cortex and the amplitude of motor evoked potentials (MEPs). B. Electromyographic (EMG) waveforms elicited by TMS with various stimulus intensities. Blue lines show responses to ipsilateral stimulation, and black lines show responses to contralateral stimulation. (Nakazawa K, Nakanish T, Sasaki A., unpublished data, 2020.)
M1 on the amputated side was observed. This may have been due to technical differences in detecting neural excitability in the motor cortex, that is, fMRI and TMS. There is a possibility that in the nonathlete amputees in Mizuguchi et al. (11), the excitability of the ipsilateral M1 was not high enough to be detected by fMRI, although the relative excitability might have been higher in the ipsilateral M1 of these individuals than in nonamputees.

Another noteworthy result reported by Hordacre et al. (13) was that the higher relative excitability of the ipsilateral M1 was associated with increased step-time variability for amputated and nonamputated limbs, suggesting that corticomotor projections from the ipsilateral M1 to alpha-motoneurons innervating the amputated limb quadriceps muscle would interfere with gait. It is uncertain whether the ipsilateral M1 activation on the amputated side observed in both Paralympic long jumpers and high jumpers is associated with higher prosthetic motor skills, although the result of Nakanishi et al. (12) suggests that this activation is related to longer use due to sports activity. Future longitudinal studies are required to clarify the functional relevance of higher ipsilateral M1 excitability.

**Para-Power Lifters: Superior Upper Limb Function in Individuals With Complete Spinal Cord Injury**

Para powerlifting is a Paralympic sport in which athletes compete in tests of upper body strength; this event is part of the bench press discipline. Many Para-power lifters have lower limb impairments, which makes it difficult for them to stabilize their trunks and lower limbs on the bench. Therefore, they usually fix their trunk and lower limbs to the bench using straps. It seems that Para-power lifters have a major disadvantage from a biomechanical point of view compared with unimpaired lifters because they cannot use their lower limbs. Despite this apparent disadvantage, many world records in matched weight divisions and with similar conditions are higher in Para-power lifters than in unimpaired athletes. The initial motivation to study Para-power lifters by Nakanishi et al. (15) was to answer the simple question of why Para-power lifters are stronger than unimpaired lifters, although they serendipitously discovered motor functional superiority not only in athletes but also in individuals with complete spinal cord injuries in general.

Nakanishi et al. (15) tested force fluctuations during a gripping task at four different force levels: 2%, 10%, 30%, and 65% of maximum voluntary force effort. Fourteen individuals with complete spinal cord injury (cSCI), 15 wheelchair users with other lower limb impairments, and 12 unimpaired controls participated in the study.

Figure 4A demonstrates a representative example of grip force fluctuations in the three groups. The cSCI group had significantly (P < 0.05) higher force steadiness levels, that is, lower coefficient of variance (CV) values than the physically unimpaired group (Fig. 4B) at all force levels, and at 10% maximum voluntary contraction (MVC) and 65% MVC levels than the lower limb impairment group. Of note was that the force steadiness level at 65% MVC was almost two times higher in the cSCI group than in the other two groups.

Resistance training, misuse, fatigue, and aging are known to influence the level of force fluctuations (16). Motor unit firing characteristics, such as the firing rate (17), firing rate variability (16,18), and synchronization between motor units (19), are known to be associated with force fluctuations. Therefore, the observed force steadiness in individuals in the cSCI group suggests that there are specific features in motor unit firing activities in individuals with complete spinal cord injuries. To the author’s knowledge, motor unit activities, that is, recruitment and firing rate coding during highly stable force exertion, have

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**Figure 4.** A. Representative force traces during isometric contraction at 30% maximum voluntary contraction (MVC) force. B. Force steadiness levels of all groups. Mean ± SE of the coefficient of variance (CV) during the grip tasks at four target force levels (2%, 10%, 30%, and 65% MVC). †P < 0.10 compared between lower limb disability (LLD) and healthy groups. *P < 0.05, **P < 0.01 compared between the complete spinal cord injury (cSCI), and LLD and healthy groups. [Adapted from Nakanishi T, Kobayashi H, Obata H, Nakagawa K, Nakazawa K. Remarkable hand grip steadiness in individuals with complete spinal cord injury. Exp. Brain Res. 2019; 237(12):3175–3183. Copyright © 2019 Springer Nature. Used with permission.]
not yet been investigated; therefore, this issue is an open question for future studies.

Regarding power lifting, 4 out of 14 complete cSCI participants were Para-power lifters. They showed high steadiness of their grip forces, although no statistically significant differences were found compared with the other cSCI participants. From this result, we cannot conclude that power lifting training further enhances the higher gripping force stability of cSCI individuals. Rather, force steadiness, that is, an aspect of upper limb motor function, might be developed in large part because of impairment-related neural processes. It also should be noted, however, that there were significant correlations between the force steadiness level and years of sports participation (duration of sports activity participation) in the cSCI group ($r = -0.626$, $P < 0.05$) and the lower limb impairment group ($r = -0.607$, $P < 0.05$). This result suggests that use-dependent plastic changes also play a role in developing superior upper limb motor functions in individuals with complete paraplegia.

The possible cause of the observed higher force steadiness in individuals in the cSCI group may be an unexpected training effect that resulted from compensatory upper-limb use after lower limb impairments resulting in greater force control ability. However, the fact that the force steadiness (CVs) of individuals in the other lower limb impairment group was not comparable to that of individuals in the cSCI group led Nakanishi et al. (15) to reject the hypothesis that compensatory upper limb use is the major factor causing higher grip force steadiness. What is the major cause of the markedly higher upper-limb force steadiness observed in individuals in the cSCI group? The complete loss of afferent inputs from lower limbs might be a possible explanation, because all individuals with cSCI in the study had complete afferent signal blocks, whereas no participants with complete sensory loss were in the other lower limb impairment group in the study by Nakanishi et al. (15). It has been reported that cortical reorganization in individuals with spinal cord injury (SCI) increases with decreased afferent sensory signals (20,21). In animal studies, somatotopy in the cortical somatosensory area has been demonstrated to be altered to a large extent after complete deafferentation at the cervical spinal cord level (22). Taken together, these findings suggest that the specific reorganization processes that occur in individuals with cSCI, specifically after complete deafferentation, contribute to the higher force steadiness observed.

To further explore the plastic changes in the brains of cSCI individuals, Nakanishi et al. (23) compared the functional and structural brain images with those individuals without physical impairments.

**Figure 5.** A. Activated brain regions of each group during the force control task. Only clusters that surpassed a cluster-level threshold corrected at a familywise error (FWE) of $P < 0.05$ were plotted. B. Cluster size and brain signal intensity in the left primary motor cortex (M1) of members of each group. Box-and-whisker plot of the number of activated voxels and brain signal intensity during the force control task at three target forces [10%, 20%, and 30% maximum voluntary contraction (MVC)] compared between the two groups [spinal cord injury (SCI), blue bar; able-bodied (AB), green bar]. Boxes represent the 25th and 75th percentiles of the cluster size and brain signal intensity. The median and mean values are indicated by a horizontal bar and cross mark, respectively. The black dashed line shows the range of total data used in the analysis (SCI, blue bar; AB, green bar). [Adapted from Nakanishi T, Nakagawa K, Kobayashi H, Kudo K, Nakazawa K. Specific brain reorganization underlying superior upper limb motor function after spinal cord injury: a multimodal MRI study. Neurorehabil. Neural Repair 2021; 35(3):220–232. Copyright © 2021 SAGE Publications. Used with permission.]
Figure 5A shows activated brain areas when cSCI and physically unimpaired individuals attempted to produce three different grip forces, that is, 10%, 20%, and 30% of maximal voluntary force effort. Figure 5B compares the sizes of the activated areas in the left M1 with the cluster size and brain signal intensity quantified from magnetic resonance imaging (MRI) signals. The activated area in M1 was significantly smaller in individuals in the cSCI group than in individuals in the physically unimpaired group during the exertion of the same grip force levels. A similar phenomenon has been observed in professional musicians and elite athletes (24,25). This phenomenon typically is described as “neural efficiency.” For example, Krings et al. (26) reported that M1 activation during finger movement was smaller in skilled musicians than in individuals who were not musicians. Consistently, Naito and Hirose (27) also reported that M1 activation during ankle movements was extremely small in a top-level soccer player. It seems that the reduced M1 activation reported in Nakanishi et al. (23) could be regarded as “neural efficiency.” However, further longitudinal studies are needed to explore whether this phenomenon truly takes place in the brains of individuals with complete paraplegia along with the development of upper limb motor functions.

Nakanishi et al. (23), using multimodal MRI measurements, including task fMRI, resting-state fMRI, and T1-weighted structural images, found unique structural and functional features in the brains of individuals with cSCI. Figure 6A shows differences in functional connectivity between individuals in the SCI and physically unimpaired groups. In this figure, the increased functional connectivity areas in SCI subjects relative to individuals in the physically unimpaired groups are plotted ($P < 0.001$, uncorrected). Functional connectivity analysis revealed that SCI subjects had stronger functional connectivity between the superior parietal lobule (SPL) and the left primary motor cortex ($P < 0.001$, uncorrected). Structural analysis further demonstrated a significantly larger ($P < 0.001$, uncorrected) gray matter volume in the bilateral SPL in the SCI group (Fig. 6B).

The SPL is known to be important for maintaining an internal representation of the body’s state (28). Specifically, the SPL receives strong anatomical projections from the primary somatosensory area and projects to the frontal lobe (29). The SPL is the neural basis by which information about joint positions and limb segment positions is integrated to determine where a person’s arm is or where a segment of the person’s arm is (30). Wolpert et al. (28) reported the results of a force control test in a patient with an SPL lesion. The patient could not maintain his grip force despite having normal somatosensory function. Thus, the SPL likely plays a key role in force control through its sensorimotor integration function. Furthermore, the internal representation and model function of the SPL and cerebellum may directly influence force control performance because it is necessary for a person to keep his or her upper limbs in a certain position. Increased gray matter volume and functional connectivity to the M1 might enhance the body schema of the upper limbs and contribute to greater force control performance in individuals with cSCI. However, further studies are needed regarding this matter, as there was no direct evidence for the relation between the observed functional and structural reorganization and the greater performance reported in Nakanishi et al. (23).

In summary, Nakanishi et al. (15) discovered superior upper limb motor function in individuals with cSCI. This is not specific to Para-power lifters but generally applies to individuals with complete paraplegia. Nakanishi et al. (23) subsequently revealed fundamental aspects of both structural and functional reorganization of the brains of individuals after SCI. Markedly higher upper limb motor function in individuals with cSCI is assumed to develop largely because of injury-dependent plastic changes after cSCI, although use-dependent plastic changes also take part in developmental processes as the second factor. The revealed superior upper limb function in individuals with complete spinal cord injuries and relevant structural and functional reorganization of their brains may relate to and underpin the amazing performance of Para-power lifters.
A Swimmer With Cerebral Palsy and an Amputee Archer: Reorganization in the Brain After a Substantial Injury in the Early Developmental Stage and the Cortical Leg Motor Area Expanded Widely to the Lateral Side

Thus far, we have discussed CNS reorganization in athletes with amputations and SCI, which can be regarded as examples of noncongenital impairments. In the final part of this article, we discuss athletes with congenital impairments, that is, cerebral palsy (CP) and congenital upper-limb loss. These are single cases but are examples that demonstrate remarkable plastic changes in the brains of these individuals, most likely through developmental stages after congenital impairments.

A swimmer with CP

Figure 7 shows brain MRI images of a Paralympic swimmer with CP (31). A large somatosensory lesion area and M1 in the right hemisphere caused motor and sensory paralysis on the left side of her body. She was ambulant with a foot drop on the affected side, whereas her left elbow joint was flexed at approximately 90° because of hypertonia in her elbow flexors, demonstrating the typical posture and gait style in persons with hemiplegic CP. First dorsal interosseus (FDI) motor cortical areas of both hemispheres identified with TMS demonstrated that her FDI cortical representation had shifted to the area innervating the trunk or lower limb muscles controlled by the impaired side of the brain.

It is well known that perinatal brain lesions are associated with variable functional outcomes, whereas those in adulthood typically lead to severe functional impairments with little potential for recovery (32). Overall, her motor functions on land seemed to be within the known range of functional motor outcomes of persons with perinatal unilateral brain lesions, whereas her dynamic swimming motion in water was strikingly different from her motor actions on land and surpassed the expected range given the size of the brain lesion. Electromyographic (EMG) activity during swimming demonstrated well-coordinated patterns compared with spastic activities on the paretic side while walking on land. This corresponded with the fact that she showed a typical hemiplegic-type gait pattern and posture on land, whereas in water, she could move her body more dynamically, in a manner that is difficult to distinguish visually from the movements of unimpaired individuals.

The neural mechanisms underlying higher motor function in water are likely due to cortical reorganization resulting from use-dependent plasticity and reinforcement mechanisms induced by long-term repetitive swimming practice.

As mentioned, the outcomes of perinatal brain lesions are known to vary widely. The observed swimming motor actions in this Paralympic swimmer with a large unilateral brain lesion provide a window through which we can explore fundamental research questions regarding neurorehabilitation for persons with brain lesions that occur in early life, that is, the modulators of developmental plasticity that might be targeted to achieve better functional outcomes (33).

An amputee archer

Nakagawa et al. (34) studied reorganization in the M1 area of a 35-year-old archer born without both upper limbs who holds the world record for the farthest accurate shot in archery. The amputee archer engages in competitive archery using his feet and uses his feet for daily life activities, such as using a knife and fork and driving a car.

Figure 8 shows the brain activity of the amputee archer and 1 representative control subject during right toe movements. M1 activation was more widespread in the amputee archer than in individuals in the control group during all tasks and shifted toward the lateral side of M1 during contraction of the toe and knee muscles. A motor mapping experiment using navigated TMS also revealed that the M1 area receiving stimulation elicited motor-evoked potentials from the toe, lower leg, and thigh muscles; these potentials were markedly larger in the amputee archer than in 12 control subjects. Furthermore, the amputee archer’s motor maps were shifted toward the lateral side of M1.

Figure 7. Brain images and transcranial magnetic stimulation (TMS) targets are indicated in red and yellow dots. As shown in this brain image, the black-colored area reflects the large area most likely damaged due to a stroke that the individual had perinatally. Note that the yellow dot in the right hemisphere is located more temporally than the yellow dot in the left hemisphere. [Adapted from Nakazawa K, Obata H, Nozaki D, Uehara S, Celnik P. “Paralympic brain”. Compensation and reorganization of a damaged human brain with intensive physical training. Sports (Basel). 2020; 8(4):46. CC BY 4.0.]
It is well recognized that immobilization and disuse (e.g., paralysis and acquired amputation) shrink the motor representation innervating the affected body part (35,36). Cortical representations of intact body parts are expanded after limb amputation, probably due to compensation for missing body parts (37–39). In most cases, motor representation expands toward and subsequently replaces the presentation of amputated body parts. Similar compensation-induced M1 expansion in intact body parts has been confirmed in individuals with other disorders, such as SCI (40) and stroke (4). Furthermore, Yu et al. (41) suggested that amputees with and without special skills with an intact body part also exhibit an expansion of M1 representation of the body part, although the size of cortical representation seemed larger in those with special skills than in those without special skills. Thus, motor skills in individuals with physical impairments seem to be related to the size of M1 representations. For physically unimpaired individuals, motor training generally induces expansion of the M1 representation of the trained body parts (42,43). When motor training is continued more extensively in the long term, the pattern of change in M1 representations seems to be divided into two directions, either expansion or reduction (24). Some studies have suggested that a shrinking motor representation reflects efficient neural control, as mentioned in the previous section in this article, which has been reported, for example, in results from an elite soccer player (27) and a professional pianist (26). In contrast, expanded representations in frequently used body parts have been shown in racquetball players (44) and professional musicians (45). Despite extensive research on cortical reorganization over the last few decades, it remains unclear what factors determine the direction of cortical reorganization associated with the motor experience of physically unimpaired individuals. Longitudinal assessments along with sports training or rehabilitation time courses are needed to further understand the determining factors and underlying neural mechanisms of the changes in motor cortical representation. The possibility that the observed larger lower limb motor area in the amputee archer is congenital cannot be eliminated at present. This remains an open question.

LIMITATIONS
There are several limitations in the articles referenced in this review, which in turn cause the present review to interpret and discuss the presented data from those articles within a limited scope. Most studies on Paralympic athletes are case studies. As in many studies investigating elite athletes, musicians, or rare pathophysiological states, it is technically difficult to derive a common feature from statistically sufficient numbers of samples, that is, in our case, Paralympians' brains. However, by gathering and carefully examining each Paralympic athlete case, a hypothetically common characteristic could be derived. This is the proposed hypothesis schematically presented in Figure 1. Although the functional and structural brain reorganizations observed in each case study are considerably different, those outcomes would be induced by impairment-specific and use-dependent neural plasticity, which have common neural bases and are considered to be enhanced in Paralympic athletes. Therefore, each case provided essential information to build the hypothesis, although there are unavoidable limitations in case studies.

There is another limitation in those studies that assessed the reorganization of Paralympian brains. No studies at present have assessed functional and structural changes in athletes with physical impairments using longitudinal methods. It should, therefore, be kept in mind that we cannot logically eliminate...
the possibility that the states of brain reorganization observed are not different from the initial states, that is, their brains have not been reorganized substantially from the initial states.

SUMMARY

We hypothesized that (I) the brain function and structure of athletes with disabilities could be reorganized more than those of able-bodied athletes in a manner that underlies their impairments and athlete-specific training and that (II) the factors playing a major role in brain reorganization are use-dependent and impairment-specific plasticity. In this review article, a number of examples of CNS reorganization from individuals participating in different Paralympic sports were introduced and discussed in light of the current understanding of neuroplasticity in the human CNS.

Paralympic brain studies have just started, and in the initial stage, they have revealed that there are variable brain reorganizations in athletes with different impairments and in different sports that are the outcomes of long-term intervention of motor practices with physical impairments. Knowledge regarding fundamental neural mechanisms underlying the Paralympic brain can provide valuable information to improve the performance of athletes and to recover motor functions in persons with physical impairments.

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References

1. Nielsen JB, Cohen LG. The olympic brain. Does corticospinal plasticity play a role in acquisition of skills required for high-performance sports? J. Physiol. 2008; 586(1):65–70.
2. Elbert T, Pantev C, Wienbruch C, et al. Increased cortical representation of the fingers of the left hand in string players. Science. 1995; 270:305–7.
3. Nielsen J, Crone C, Hultborn H. H-reflexes are smaller in dancers from The Royal Danish Ballet than in well-trained athletes. Eur. J. Appl. Physiol. Occup. Physiol. 1993; 66:116–21.
4. Jones TA. Motor compensation and its effects on neural reorganization after stroke. Nat. Rev. Neurosci. 2017; 18(5):267–80.
5. Nudo RJ, Wise BM, Sijbers F, Miliken GW. Neural substrates for the effects of rehabilitative training on motor recovery after ischemic infant. Science. 1996; 272:1791–4.
6. Allred RP, Jones TA. Unilateral ischemic sensorimotor cortical damage in female rats: forelimb behavioral effects and dendritic structural plasticity in the contralateral homotopic cortex. Exp. Neurol. 2004; 190:433–45.
7. Allred RP, Kim SY, Jones TA. Use it and/or lose it-experience effects on brain remodelling across time after stroke. Front Hum Neurosci. 2014; 8:379.
8. Sun Y, Zehr EP. Training-induced neural plasticity and strength are amplified after stroke. Exerc. Sport Sci. Rev. 2019; 47:223–9.
9. Dragert K, Zehr EP. High-intensity unilateral dorsiflexor resistance training results in bilateral neuromuscular plasticity after stroke. Exp. Brain Res. 2013; 225:93–104.
10. Sun Y, Ledwell NMH, Boyd LA, Zehr EP. Unilateral wrist extension training after stroke improves strength and neural plasticity in both arms. Exp. Brain Res. 2018; 236(7):2209–21.
11. Mizuguchi N, Nakagawa K, Tazawa Y, Kanose K, Nakazawa K. Functional plasticity of the ipsilateral primary sensorimotor cortex in an elite long jumper with below-knee amputation. NeuroImage Clin. 2019; 23:101847.
38. Pascual-Leone A, Peris M, Tormos JM, Pascual AP, Catalá MD. Reorganization of human cortical motor output maps following traumatic forearm amputation. *Neuroreport*. 1996; 7:2068–70.

39. Raffin E, Pellegrino G, Di Lazzaro V, Thielscher A, Siebner HR. Bringing transcranial mapping into shape: sulcus-aligned mapping captures motor somatotopy in human primary motor hand area. *Neuroimage*. 2015; 120:164–75.

40. Nardone R, Holler Y, Brigo F, et al. Functional brain reorganization after spinal cord injury: systematic review of animal and human studies. *Brain Res*. 2013; 1504:58–73.

41. Yu XJ, He HJ, Zhang QW, et al. Somatotopic reorganization of hand representation in bilateral arm amputees with or without special foot movement skill. *Brain Res*. 2014; 1546:9–17.

42. Kami A, Meyer G, Jezzard P, Adams MM, Turner R, Ungerleider LG. Functional MRI evidence for adult motor cortex plasticity during motor skill learning. *Nature*. 1995; 377:153–8.

43. Pascual-Leone A, Nguyen D, Cohen LG, Brasil-Neto JP, Cammarota A, Hallett M. Modulation of muscle responses evoked by transcranial magnetic stimulation during the acquisition of new fine motor skills. *J. Neurophysiol*. 1995; 74:1037–45.

44. Pearce AJ, Thickbroom GW, Byrnes ML, Mastaglia FL. Functional reorganisation of the corticomotor projection to the hand in skilled racquet players. *Exp. Brain Res.* 2000; 130:238–43.

45. Bangert M, Schlaug G. Specialization of the specialized in features of external human brain morphology. *Eur. J. Neuresci.* 2006; 24:1832–4.