Taube W

Neurophysiological Adaptations in Response to Balance Training

Neurophysiologische Anpassungen an Gleichgewichtstraining

Department of Medicine, Movement and Sport Science, University of Fribourg, Schweiz

ZUSAMMENFASSUNG

Gleichgewichtstraining verbessert nicht nur die posturale Kontrolle sondern steigert darüber hinaus die Explosivkraft, verbessert das Sprungverhalten und fördert die Regeneration nach Verletzungen. Des Weiteren reduziert Gleichgewichtstraining die Inzidenz von Knie- und Sprunggelenksverletzungen. Es stellt sich die Frage, wie das zentrale Nervensystem (ZNS) sich an Gleichgewichtstraining anpasst, um all diese (unterschiedlichen) Funktionen zu gewährleisten. Der vorliegende Übersichtsartikel beleuchtet neuronale Anpassungsreaktionen des ZNS, die der verbesserten Gleichgewichtsfähigkeit, der erhöhten Explosivkraft und der Reduktion von Verletzungen der unteren Extremität zugrunde liegen. Es wird die Plastizität des ZNS unterstrichen und ein besonderes Augenmerk auf Anpassungsvorgänge spinaler und kortikaler Strukturen gelegt. Dabei werden Erkenntnisse von elektrophysiologischen Messungen wie auch Ergebnisse von bildgebenden Verfahren vorgestellt. Studien, in denen die spinale Reflexaktivität mittels peripherer Nervenreizung während der Ausführung von Gleichgewichtsaufgaben erfasst wurde, legen den Schluss nahe, dass sich die Erregbarkeit spinaler Reflexe durch Gleichgewichtstraining reduziert. Der Einsatz von transkranieller Magnetstimulation zur Abschätzung der kortikalen Aktivität während der Durchführung von postural anspruchsvollen Aufgaben hat aufgezeigt, dass die Aktivität des motorischen Kortex zu Anfang der Gleichgewichtsintervention hoch ist und mit zunehmender Bewegungsautomatisierung abnimmt. Dahingegen wird vermutet, dass die Aktivität in einigen subkortikalen Strukturen eine gegenläufige Entwicklung aufzeigt. Neueste Erkenntnisse mit bildgebenden Verfahren unterstützen diese Vorstellung und zeigen darüber hinaus auf, dass sich graue und weiße Hirnsubstanz sehr schnell an ein Gleichgewichtstraining anpassen, so dass schon nach zwei Trainingstagen strukturelle Veränderungen im Gehirn nachweisbar sind. Aufgrund der vorliegenden Studien kann gefolgert werden, dass vor allem supraspinalen Anpassungen des ZNS eine zentrale Bedeutung für die Steigerung der funktionellen Parameter (Gleichgewicht, Explosivkraft, allgemeine Bewegungskontrolle, etc.) zukommt.

Schlüsselwörter: Sensomotorisches Training, Posturale Kontrolle, Neuronale Plastizität, Spinale Reflexe, Kortikale Mitwirkung.

SUMMARY

Balance training is effective not only to improve postural control but also the rate of force development, the jumping behaviour, and the regeneration after injury. Furthermore, balance training reduces the incidence of ankle and knee injuries. The question is how the central nervous system (CNS) adapts in response to balance training in order to fulfil all these (different) actions. The present review article discusses neural adaptations within the CNS, which may be responsible for improving postural control, increasing explosive force and reducing the incidence of lower limb injuries after balance training. It emphasizes the plasticity of the sensorimotor system in general and spinal and cortical adaptations in particular. Current findings are displayed that were obtained with electrophysiological methods and imaging techniques. Studies investigating the spinal reflex circuitries during postural tasks by means of peripheral nerve stimulation suggest that balance training reduces the excitability of spinal reflexes. Experiments involving transcranial magnetic stimulation in order to infer changes in cortical excitability propose high cortical excitability at the beginning of balance training interventions, which decreases with improved task automatization. Changes in subcortical structures are less well understood but may partly undergo contrary development than adaptations of the primary motor cortex. Recent findings obtained by various imaging techniques support this idea and further highlight that grey and white brain matter adapt rapidly in response to balance training so that structural changes are already detectable after two training sessions. Based on the current knowledge it can be concluded that most likely supraspinal adaptations within the CNS are mainly responsible for improving functional parameters like balance skills, explosive strength or coordinative movement control.

Key Words: Sensorimotor training, postural control, neural plasticity, spinal reflexes, cortical contribution.

INTRODUCTION

It is well established that balance training improves postural skills and is highly effective in reducing the incidence of lower limb injuries in many team sports. Apart from its prophylactic character, balance training improves the regeneration of neuromuscular structures following injury and efficiently prevents injury re-occurrence (for references see 23). From a performance related point of view, balance training is known to enhance not only balance skills but also the rate of force development (e.g. 5) and the performance in jumping movements (24). Thus, balance training has a great impact on motor performance. The present review article elaborates how the central nervous system (CNS) adapts in response to balance training in order to fulfil all these ac-

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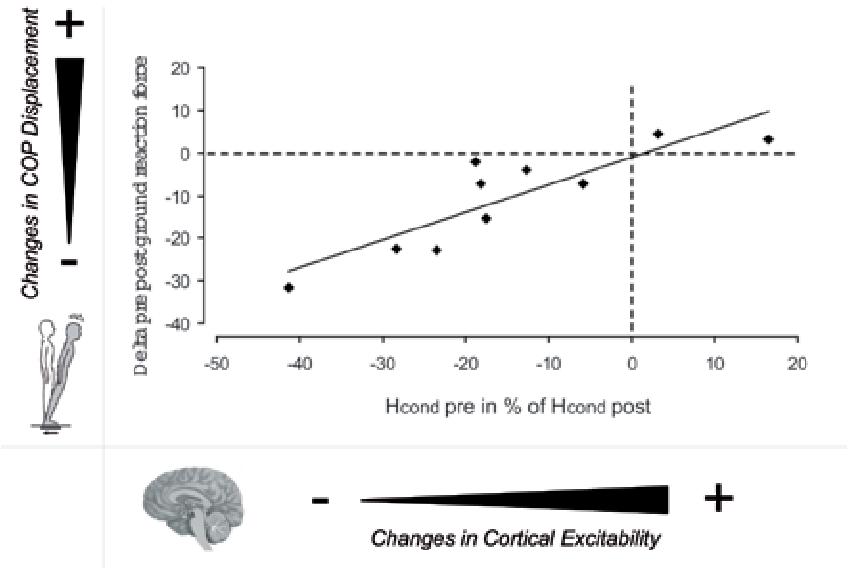

Figure 1: Interrelation of cortical plasticity and changes in stance stability. Balance training related differences of pre and post measurement of the cortical excitability (expressed as H_{cond} (conditioned H-reflex) pre as % of H_{cond} post) are illustrated on the abscissa while changes in the vertical peak ground reaction force (center of pressure displacement) are displayed on the ordinate. The regression line demonstrates that greater improvements in stance stability were accompanied by greater reductions in the cortical excitability, which was expressed in a significant correlation of these two parameters. ($r=0.87$; $P<0.01$). Modified from Taube et al. (22).

tions. Most of the studies cited in this article refer to “classical balance training” (described in detail in 23) although it is well known that balance skills can be improved by other interventions such as slacklining (12), dancing (8) alpine skiing (15) or inline skating (21), too. Based on word limitations, this qualitative review article has no right to completeness and gives no detailed description of the electrophysiological approaches used to identify adaptations going along with balance training. For a more thorough presentation please see the following review articles (23,29,33).

HOW CAN BALANCE TRAINING IMPROVE POSTURAL SKILLS?

Instant reflex adaptations in response to changes of the postural setting

Llewellyn and co-workers (16) demonstrated in humans that changes in the support surface influences spinal reflex processing. In their experiment, they asked subjects to either walk over ground or over a small beam. As soon as subjects had to perform the more challenging task of walking over the beam, they demonstrated reduced H-reflex responses. Subsequent experiments confirmed reduced H-reflexes when postural demands were increased (2,7). The H-reflex was measured in those studies, as this reflex shares some similarities with the stretch reflex. Thus, excitation of the Ia-afferents is mediated to the spinal cord and is transmitted there onto the α-motoneuron, which in turn activates the muscle. Changes of the H-reflex size without concurrent changes of the background muscular activity are therefore thought to point towards modified spinal processing of afferent information. Presynaptic inhibition is the most likely mechanism responsible for the reflex inhibition observed in more challenging postural tasks (10). Presynaptic inhibition allows that the excitation of the Ia afferents is not fully transmitted to the postsynaptic neuron (the α-motoneuron). This means that the presynaptic transmitter release is reduced without affecting the postsynaptic side, which is still susceptible to other inputs. During balance control, presynaptic inhibition therefore allows the reduction of spinal reflexes without affecting the input of supraspinal sites to the α-motoneuron pool. As a consequence, it may be speculated that movements are controlled to a lesser extent by reflexes but rather by supraspinal centres (20,22).

The functional significance of reducing spinal reflex responses in more challenging postural settings was interpreted as a way of reducing unwanted joint oscillations (13,16). Keller et al. (12) described this scenario in the following way: “The unwanted and uncontrollable joint oscillations are assumed to origin from muscle stretch reflexes that occur when a fast deflection of the slackline or a fast tilt of a classical balance training device takes place and the counteracting stretch reflex results in an overshooting joint repositioning. This overcorrection may trigger subsequent stretch reflexes that are probably responsible for the build-up of the described joint oscillations.”

Interestingly, reflex responses are not only inhibited as postural complexity increases, but they are also facilitated once postural demands become less challenging, for instance by additional mechanical support (10,30) or augmented visual feedback (25). It is therefore argued that presynaptic inhibition is intensified or weakened in order to allow a flexible and adequate reflex adaptation to meet the requirements of the task.

Spinal adaptations after longer periods of balance training

Based on the above-mentioned studies showing reduced reflex excitability when increasing postural demands, it may be speculated that balance training may also target these spinal reflex responses in order to improve postural control. This seems indeed to be the case as quite many studies demonstrated that improved balance skills went along with reduced H-reflexes after several weeks of balance training (6,22,24,31). Similarly, four weeks of slackline training proofed to be efficient to ameliorate performance on the rope and at the same time reduce the H-reflex (12). Thus, it seems likely that the CNS learns during balance training to adequately adjust spinal reflex responses so that reflex mediated joint oscillations can be avoided.

However, it has to be mentioned that these reflex adaptations are not a phenomenon, which can be generalized to all movements but are strictly related to the task, in which they are elicited. In this respect, 6 weeks of balance training reduced H-reflexes exclusively during a postural task on the treadmill (fast backward translation)

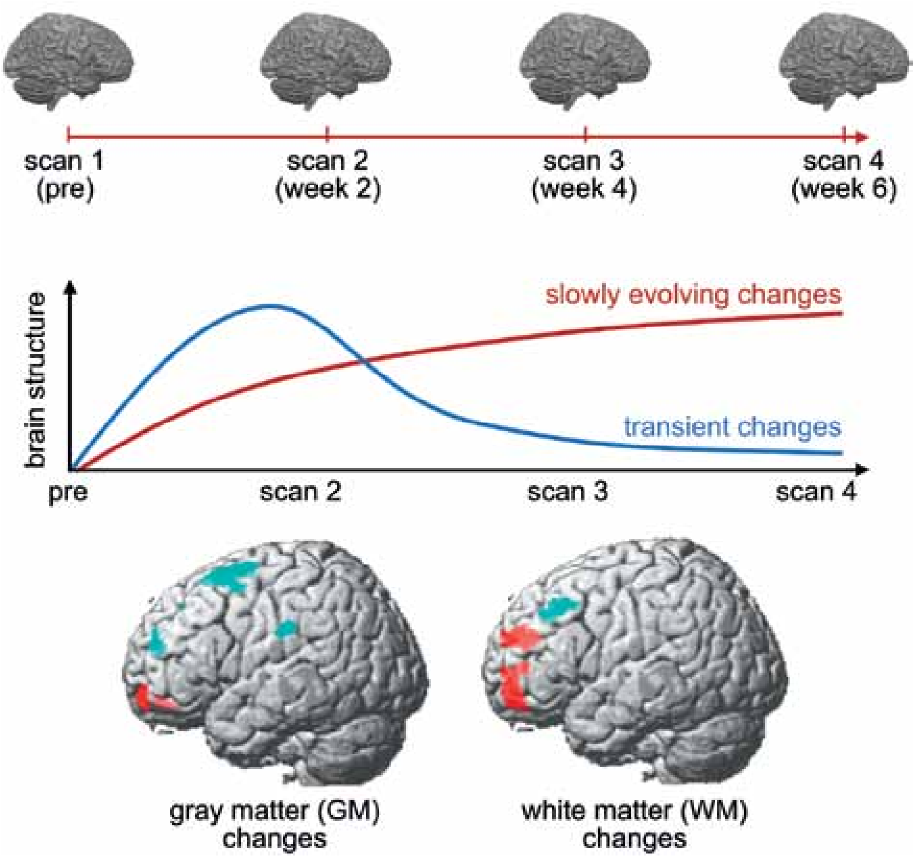

Figure 2: Changes in gray matter and white matter in response to 6 weeks of balance training. To assess structural changes during the training period, magnetic resonance imaging and diffusion-weighted imaging scans were performed at baseline (scan 1) and every second week during balance training (scan 2-4) (27). Trained subjects displayed transient as well as slowly evolving structural changes in frontal and parietal brain areas (for details see text). Modified from Taubert et al. (29).

but not during unperturbed stance (24). In another study, evidence was provided that not only the task itself may be crucial for the training related H-reflex modulation but also the phase of the movement, i.e. when the H-reflex was elicited after the onset of perturbation (22): After 4 weeks of balance training, subjects were tested while compensating for rapid posterior displacements of the support surface. During the early compensation phase (around 50 ms after the onset of perturbation) the H-reflex remained unchanged whereas the H-reflex was significantly inhibited after training when measured in the late compensation phase (around 120 ms after the onset of perturbation). Furthermore, spinal reflexes may even be facilitated when they are relevant to counteract the perturbation (3). Thus, balance training does not change the spinal reflex behaviour per se but rather seems to improve the ability to find the right "reflex setting" for certain postural conditions. In other words, balance training improves the task-specific reflex modulation.

Adaptations within the brain in response to balance training

The compensatory reaction in response to sudden perturbations is composed of activity, which is resulting from activation of spinal reflex circuits followed by activity processed by a transcortical loop. The spinal contributions are generally termed short- (SLR) and medium-latency responses (MLR) and occur after approximately 50 ms and 70 ms, respectively. The subsequent muscular activity around 90 to 120 ms is already influenced by motor cortical centres and is called long-latency response (LLR) (26). Apart from the motor cortex (for review: 9,23), multiple supraspinal structures such as the basal ganglia, the cerebellum, and the brainstem have important functions in the organization of posture (14, for review 32). However, due to the better methodological accessibility of cortical compared to subcortical structures during the execution of whole-body movements, adaptations following balance training are best investigated for the motor cortex. In this respect, motor cortical activity was shown to decrease after 4 weeks of balance training (1,19,22). Most interestingly, subjects who showed the greatest adaptation of their motor cortical activity displayed also the most profound improvements in postural control (Figure 1). As there was no such correlation between spinal adaptations (changes in the H-reflex) and changes in stance stability, the improvement in balance performance was argued to rely mostly on supraspinal plasticity (22).

The reduction in cortical activity after several weeks of balance training displays some parallels with skill acquisition studies. These studies have shown for hand and finger movements (for example by means of fMRI) that motor cortical activity was large during the initial training phase (i.e. during skill acquisition) but decreased with progressive training (i.e. automatization). Conversely, activity in subcortical regions like the basal ganglia and the cerebellum increased with increasing task automatization (e.g. 18). Recent imaging studies investigating balance training support this view. Taubert and colleagues (27) assessed structural short (two sessions of practise) and long-term changes (after 6 training sessions and in a retention test 3 months afterwards) of gray and white matter. Interestingly, they could differentiate slowly evolving increases in parts of the orbitofrontal cortex and rapid transient gray matter changes in sensorimotor areas (27,29). Furthermore, in the same subjects increased fronto-parietal network connectivity was observed by means of fMRI (28). Altogether, these results propose that the structural changes in response to balance training were closely linked to behavioural alterations (improved balance performance) and thus, are of functional relevance. Furthermore, these studies

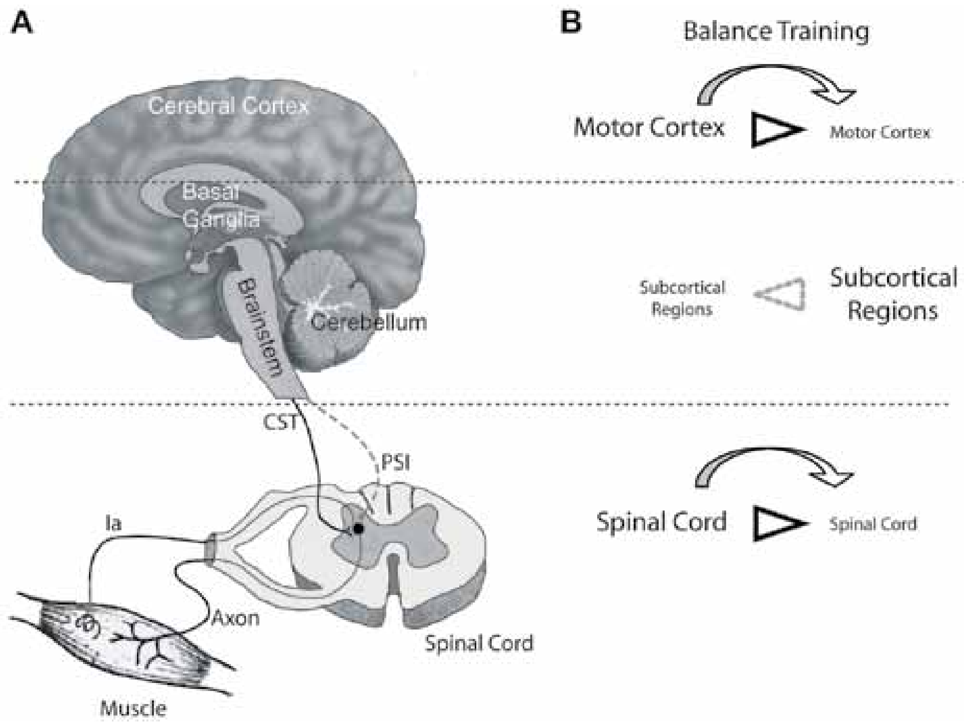

Figure 3: Balance training induced adaptations assessed during postural tasks. A: Structures of the nervous system, which are considered to play an important role in the maintenance and recovery of balance (more details in Taube et al. (23)). B: Balance training is thought to reduce spinal reflex excitability by increasing the supraspinally induced presynaptic inhibition (PSI). This reduction ( ) is schematically illustrated in the bottom section. Another well documented adaptation after balance training is the reduction in cortical involvement (first section). It is therefore assumed that training of balance skills and the subsequent improvements in postural control strongly rely on adaptations of subcortical structures (indicated as a grey dotted triangle in the middle line). Modified from Taube et al. (23).

support the notion that learning of balance skills undergoes dynamic patterns of neural activity with respect to early and late(er) stages of learning (Figure 2).

The abovementioned studies (27,28,29) did not specifically focus on changes within subcortical networks after balance training although these networks may take a prominent role in the process of learning postural skills. Nashner (17) compared short-term learning of balance strategies in cerebellar patients with the acquisition of healthy control subjects. Subjects were first tested while applying posterior directed translational platform displacements. After some trials, the perturbation was changed and the translation was replaced by a backward rotation of the feet. Thus, in both conditions, the triceps surae was stretched in a very similar way. However, during translational displacement, a compensatory contraction of the calf muscle (in this case a LLR) is appropriate to regain balance whereas during rotational displacement it is not. Thus, subjects had to adapt to the new postural perturbation by reducing the activity of the triceps surae. Healthy subjects adapted their LLR within 3 to 5 trials and drastically reduced the postural sway whereas the cerebellar patients were either significantly slower or unable to do so. Consequently, it can be argued that the cerebellum plays an important role in modulating task specific muscular activity. Furthermore, the importance of cerebellar structures for the acquisition of balance skills makes it reasonable to assume that balance training induces a similar "shift in movement control" from cortical to more subcortical and cerebellar structures (Figure 3) as described in the skill acquisition studies mentioned above (e.g. 18).

Structural gray matter changes in association with balance training have been reported as early as after two training sessions (27). Therefore, it is reasonable to assume that balance training accomplished over a long period of time (several years) leads to fundamental structural plasticity within the CNS. In a recent study, it was highlighted that the hippocampus formation of professional female dancers and slackliners is differently structured compared to the one of recreational sportswomen (8). However, it has to be mentioned that these data were obtained in a cross-sectional study design so that it cannot be entirely ensured that the differences are really linked to the training or whether they are based on some genetic predispositions of the professional athletes or based on coincidental interindividual differences. However, the relatively great number of participants (21 athletes versus 20 controls) makes these drawbacks rather unlikely.

HOW CAN BALANCE TRAINING ENHANCE THE RATE OF FORCE DEVELOPMENT?

Schubert et al. (19) assessed alterations in the excitability of direct corticospinal pathways following balance training. After training, cortical excitability was reduced during the execution of a postural task. However, when balance trained subjects were measured in a voluntary explosive strength task where the same muscles were activated, enhanced cortical excitability was evident. In the voluntary strength task, a dynamic dorsiflexing torque was applied at the ankle joints of both feet by an ankle ergometer and subjects were instructed to counteract this torque as accurately and as soon as they were able to detect it. The improved explosive force production may therefore be caused by an enhanced cortical drive to the agonistic muscles. It can be speculated that (synaptic) efficiency of direct corticospinal projections to the muscles encompassing the ankle joint had been increased by balance training and could be utilized in the voluntary contraction. A stronger neural drive (increased mean EMG activity (4); enhanced median frequency (5)) to the trained muscles after balance training could be quantified by means of surface EMG. Interestingly, the increase of the rate of force development (RFD) could be observed for the ankle and knee joint but was dependent on the training regime: When the ankle joint was restrained by a ski-boot and the training targeted primarily the muscles encompassing the knee joint, RFD of the knee extensor muscles was increased (4). However, if the ankle could freely move during training, adaptations in the ankle extensor muscles could be observed (5) whereas no improvements could be seen for the knee extensor muscles (24). The enhanced RFD after balance training seems also to influence the jumping behaviour as several studies reported improved jumping performance after balance training (11,24).

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Korrespondenzadresse:
Wolfgang Taube
University of Fribourg
Department of Medicine
Movement and Sport Science
Boulevard de Pérolles 90
1700 Fribourg
Schweiz
E-Mail: wolfgang.taube@unifr.ch