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Intracortical Inhibition Increases during Postural Task Execution in Response to Balance Training

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Abstract—Intracortical inhibitory modulation seems crucial for an intact motor control and motor learning. However, the influence of long(er) term training on short-interval intracortical inhibition (SICI) is scarcely investigated. With respect to balance, it was previously shown that with increasing postural task difficulty, SICI decreased but the effect of balance training (BT) is unknown. The present study tested whether improvements in postural control due to BT are accompanied by changes in SICI. SICI was measured in the tibialis anterior by applying paired-pulse magnetic stimuli to the motor cortex in a BT group ($n = 13$) training 2 weeks on an unstable platform and a control (CON) group ($n = 13$) while performing three progressively demanding postural tasks: stable stance ('Stable'), standing on a movable platform partly secured with elastic straps ('Straps') or freely moving ('Free'). The BT group improved postural control significantly more than the CON-group ('Free' condition: $+80\%$ vs. $+21\%$; $p < 0.001$). For SICI, there was a main effect of POSTURAL TASK ($F_{2, 48} = 24.6$; $p < 0.001$) with decreasing SICI when task difficulty increased and a TIME × GROUP interaction ($F_{1, 24} = 5.9$; $p = 0.02$) caused by significantly enhanced SICI in the BT group in all three postural tasks after the training. The increases in SICI were significantly correlated with improvements in balance performance ($r = 0.56$; $p = 0.047$). The present study confirms previous findings of task-specific modulation of SICI when balancing. More importantly, training was shown to increase SICI and this increase was correlated with changes in balance performance. Thus, changes in SICI seem to be involved not only for the control but also when adapting upright posture with training.

Key words: balance control, balance practice, neural processing, SICI, TMS.

INTRODUCTION

Increasing evidence points to the importance of cortical structures for the control of upright human posture (for reviews see Jacobs and Horak, 2007; Taube et al., 2008). In line with this, several studies have detected functional and structural changes after balance training (BT) in cortical areas (for reviews see Taube et al., 2008; Taubert et al., 2012). Furthermore, correlations between the adaptations at the cortical level and changes in balance control were reported (Taube et al., 2007; Taubert et al., 2010; Taubert et al., 2011). However, to date it is not known whether, and if yes, how, intracortical inhibitory control changes with BT despite increasing evidence that intracortical inhibition plays a crucial role for motor control in general and postural control in particular. Indeed, it seems that populations with less pronounced levels of short-interval intracortical inhibition (SICI) such as seniors (Papegaaij et al., 2014a,b), children with attention-deficit/hyperactivity disorders (ADHD) (Gilbert et al., 2011) or children born very preterm (Flamand et al., 2012) show impaired motor coordination. Similarly, compared to young adults, elderly adults demonstrate less stable postures and a more rapid decline in SICI with increases in postural task difficulty (Papegaaij et al., 2014a,b). Based on these observations one may assume that high levels of SICI are beneficial. However, to date there are no longitudinal intervention studies that indicate how intracortical inhibitory control changes with BT.

Short-term learning (pre- and post-test within one day) of various tasks has consistently resulted in reduced levels of SICI (e.g. Camus et al., 2009; Cirillo et al., 2011; Leung et al., 2015; Perez et al., 2004). Furthermore, a recent meta-analysis revealed that subjects who displayed more pronounced reductions in SICI showed faster learning rates of visuomotor skills (Berghuis et al., 2017). Unfortunately, all of the above-mentioned studies measured SICI at rest rather than during performance of the actual learning task despite good evidence of task- and phase-specific modulation of inhibitory processes (Opie and Semmler, 2016; Papegaaij et al., 2014a,b; Sidhu et al., 2013; Soto et al., 2006). In addition, there are not many studies investigating long(er) term or retention effects of learning on intracortical inhibition. The few available studies suggest that the

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pattern of adaptation depends on the task at hand: strength training seems to result in reduced levels of SICI (Goodwill et al., 2012; Weier et al., 2012) whereas learning of more coordinative skills such as badminton may actually enhance the level of SICI (Dai et al., 2016). Furthermore, it was shown that professional musicians demonstrated larger intracortical inhibition and bigger recruitment of intracortical inhibitory connection, when high conditioning stimulus intensity is applied, compared to untrained control subjects. This might suggest that musicians present greater synaptic density in the cortex in response to long-term musical training (Rosenkranz et al., 2007). These findings seem reasonable as the inhibitory network of the motor cortex is considered to fulfill mainly two purposes: first, suppression of unwanted movements (Levin et al., 2014) and second, sharpening of the contrast between activity and rest or, differently phrased, between active muscles and muscles at rest (Beck and Hallett, 2011). It might therefore be assumed that during demanding coordinative skills, the inhibitory network is highly challenged to avoid unnecessary co-activations or co-movements.

When considering balance tasks, there is a consistent picture of increased corticospinal excitability and reduced intracortical inhibition when switching from simple to more challenging postural tasks (Papegaaij et al., 2016a,b; Papegaaij et al., 2014a,b). In addition, the learning of postural skills seems to alter the balance between inhibition and excitation as several studies have demonstrated reduced corticospinal and cortical excitability after several weeks of balance training (Beck et al., 2007; Penzer et al., 2015; Schubert et al., 2008; Soto et al., 2006; Taube et al., 2007). So far, it is not known whether the cortical inhibitory network contributes to this change. If so, one would expect increased levels of intracortical inhibition after balance training. The current study tested this hypothesis by means of applying a paired-pulse transcranial magnetic stimulation (TMS) paradigm during the performance of an easy, intermediate and highly demanding balance task before and after 2 weeks of BT. During BT, participants were training the highly demanding balance task. Therefore, we further hypothesized that neural adaptations should be most pronounced for this highly demanding balance task.

EXPERIMENTAL PROCEDURES

Participants

Twenty-six young adults (mean ± SD = 24 years ± 3) were integrated into the final analysis of this study. All participants gave their written consent to the experiment, which was approved by the local ethics committee. Participants were allocated to one of two groups: a balance training group (BT, n = 13, 4 females) or a control group (CON, n = 14, 5 females; one drop out). All participants performed the entire testing procedure before and after the training period.

Balance training

The BT group followed a specific training program over two weeks with a total of 6 training sessions. Training sessions constituted of a 10-min warm-up followed by 45 min of balancing on a movable platform (Model 16030, Lafayette Instrument Company®, USA). The participants received the instruction to stand with both feet on the freely moving platform while keeping it in a horizontal position as long as possible during 30 s. During each training session participants had to perform fifteen trials of 30 s on the platform with an inter-trial interval of 2 min to avoid fatigue. After each trial, participants received oral feedback about their time in balance. Participants of the CON group were asked to keep their normal routine of physical activity and were not allowed to start new forms of physical activity or training interventions during the process of the study.

Experimental protocol

Balance performance. During pre- and post-measurements, three trials were recorded for each participant in order to assess the time in balance while the platform was freely moving. The balance performance measure was the time (in seconds) in which participants kept the platform in a horizontal position within a deviation range of 5° to each side out of the total trial length of 30 s (in line with previous research; e.g. Taubert et al., 2010, 2011, 2012). Before the balance test, participants were familiarized with the platform. They performed two trials and were entitled to use a supporting hand rail.

Experimental procedure. Motor-evoked potentials (MEPs) as well as electromyographic recordings (EMG) of the tibialis anterior (TA) and the soleus (SOL) muscle were assessed during three different balance tasks that were performed in random order: 1) upright stable standing (Stable, Fig. 1A), 2) standing on the movable platform restrained with elastic straps (Straps, Fig. 1B) and 3) standing on the platform that was freely moving (Free, Fig. 1C). However, the order of conditions that was defined for the pre-measurement was adopted for the post measurement, too.

Neurophysiological recordings. Tms. TMS was applied using a 95-mm focal ''butterfly-shaped'' coil (D-

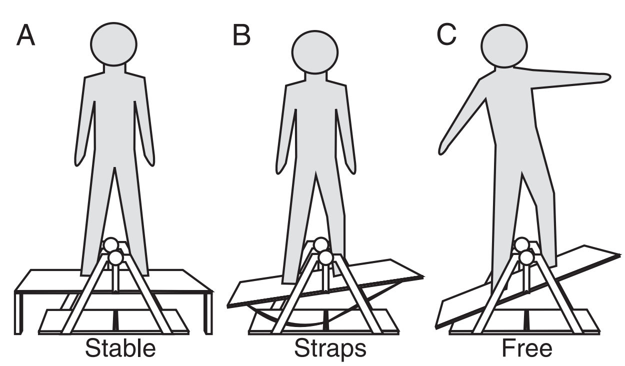

Fig. 1. Postural tasks performed during the experiment. Participants had to stand (A) on the unmoving platform ('Stable'), (B) on the movable platform that was secured with elastic straps ('Straps'), and (C) on the platform that was freely moving ('Free').

B80) and a MagPro X100 with MagOption magnetic stimulator (both MagVenture A/S, Farum, Denmark). MEPs were elicited by stimulating over the left motor cortex. At the beginning of the measurement, the motor hot spot of the tibialis anterior was detected by shifting the coil until we found the optimal position for eliciting MEPs with minimal stimulation intensity. Afterward, the coil was mechanically fixed with a custom-built helmet that minimized movements of the coil relative to the head (Ruffieux et al., 2017). The location was marked on the skull in order to check whether the coil moved during the experiment. For each participant, the active motor threshold (aMT) was determined as the lowest stimulation intensity that elicited an MEP higher than 50 μV in TA in three out of five trials in the 'Stable' and the 'Straps' condition (Kujirai et al., 1993). The aMT obtained in the 'Straps' condition was used for the 'Free' condition, too. Stimulation intensity for single pulses was set to 1.2 aMT for each condition throughout the experiment. Double-pulse stimulations with an interval of 2.5 ms were applied in order to assess short-interval intracortical inhibition (SICI). Stimulation intensity of the suprathreshold test pulse was set to 1.2 aMT while the preceding conditioning stimulus was set to 0.8 aMT. The interstimulus interval of 2.5 ms was based on previous experiments assessing SICI during execution of postural tasks (Papegaaij et al., 2016a,b; Papegaaij et al., 2014a,b; Soto et al., 2006). For each postural task, 20 single and 20 paired pulses were elicited by TMS, which resulted in measurement times of around 3 min for each task. To reduce variability in MEP size induced by the postural task and to minimize the influence of an altered bEMG, TMS was triggered only when participants kept the platform in a horizontal position within a deviation range of 5° to each side. The minimal interval between stimulations was set to 4 s.

To determine SICI during rest (lying), the resting MT was determined (MEPs higher than 50 μV in TA in three out of five trials) and the paired-pulse paradigm was applied with 0.8 MT for the preceding conditioning stimulus and 1.2 MT for the test pulse. The rest condition (lying) was recorded at the end of pre- and post-measurement, respectively, with 48 single and 48 paired pulses.

EMG recording. Bipolar surface electrodes (Blue sensor P, Ambu®, Bad Nauheim, Germany) were used to record surface EMG of the TA and SOL muscle. The reference electrode was attached on the tibia plateau. The EMG signals were amplified (1000 x), sampled at 4 kHz, and band-pass filtered (10–1000 Hz). Data were recorded using custom-made software (LabView® based, National Instruments®, Austin, Texas).

Data analyses

The average of the 'time in balance' of the three recorded trials while participants were standing on the freely moving platform (i.e. 'Free' condition) was used to quantify changes in balance behavior. Peak-to-peak amplitudes of elicited MEPs (for the single and paired pulse stimulation) were computed. The mean amplitudes of SICI were expressed as percentage of inhibition using the following formula: 100 - (conditioned MEP/test MEP × 100), according to previous research (Kuhn et al., 2017; Papegaaij et al., 2014a,b).

For the background EMG activity (bEMG), the root mean square of the bEMG signal was calculated for a time interval of 100 ms before the stimulation and absolute values are reported.

Statistical analyses

Data were checked for normal distribution prior to analysis. SICI data and bEMG were logarithmically transformed due to a skewed distribution.

Behavioral data (i.e. the 'time in balance') for the 'Free' condition were logarithmical transformed due to non-normal distribution and consequently analyzed in two-way repeated measures analyses of variance (ANOVAs) with the factors GROUP (BT vs. CON) and TIME (Pre vs. Post).

To investigate the training effect on the bEMG, and the amount of SICI, three-way repeated measures analyses of variance (ANOVAs) with the factors GROUP (BT vs. CON), TIME (Pre vs. Post) and BALANCE TASK ('Stable' vs. 'Straps' vs. 'Free') were performed. In the case of the SICI analysis, bEMG and MEP amplitudes were added as covariates and correlations between those variables were performed to test their potential effects on the SICI results.

For the analysis of SICI during rest (lying), a two-way ANOVA with the factors TIME (Pre vs. Post) and GROUP (BT vs. CON) was applied.

Change in the aMT was explored with three-way repeated measures analyses of variance (ANOVAs) with the factors GROUP (BT vs. CON), TIME (Pre vs. Post) and BALANCE TASK ('Stable' vs. 'Straps').

In case of significant main effects and/or interactions, post hoc Student's *t*-tests with Bonferroni's correction were applied. A Greenhouse–Geisser correction was performed when the assumption of sphericity was violated. Data are displayed as mean ± standard deviation (SD). The significance level was determined at $p < 0.05$. All statistical analyses were calculated with the software R (R Team RC, 2013).

RESULTS

Behavioral data

The ANOVA for the balance performance (time in balance) revealed a significant GROUP effect ($F_{1,\ 22} = 8.8$; $p < 0.001$), TIME effect ($F_{1,\ 22} = 44.2$; $p < 0.001$), and an interaction of GROUP × TIME ($F_{1,\ 22} = 12.9$; $p < 0.001$). The results are presented in the Fig. 2.

Neurophysiological data

Sici. There was a significant main effect of BALANCE TASK ($F_{2,\ 48} = 25.1$; $p < 0.001$). Post-hoc tests revealed that the amount of SICI decreased from 'Stable' standing (52.1% ± 6.7) to 'Free' standing (18.9% ± 5.3; $p < 0.001$) and from 'Straps' (45.6% ± 6.1) to the 'Free' condition (18.9% ± 5.3; $p < 0.001$). No significant

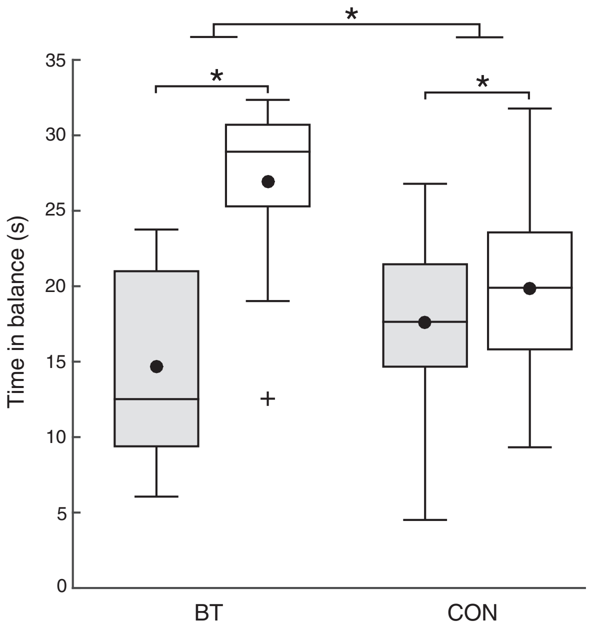

Fig. 2. Time in balance performance before and after the balance training for the training (BT) and control group (CON). Participants were measured while performing the 'Free' condition on the balance device. Gray and white bars represent pre- and post-measurements, respectively. The black dots represent the mean values while the horizontal lines within the boxes indicate the median values. The box covers the 25th–75th percentiles, the whiskers represent the range, and the black crosses indicate outliers (* = p < 0.05).

difference was observed between the 'Stable' standing and the 'Straps' condition (p = 0.4).

Noteworthy, there was a significant GROUP × TIME interaction for SICI in the TA ($F_{1,\ 24}$ = 8.1; p = 0.008; see Fig. 3). Post-hoc tests revealed that after 2 weeks of balance training, SICI was significantly increased in the BT group (p = 0.001; +18%), whereas the CON group presented a non-significant decrease in SICI (p = 0.11; −6%). In contrast, when measuring SICI at rest (lying), no significant main effect of TIME ($F_{\mathbf{1,\ 24}}$ = 0.04; p = 0.83) or interaction effect of GROUP × TIME ($F_{\mathbf{1,\ 24}}$ = 0.05; p = 0.81) was detected (BT: pre 63.8% ± 26.1; post 63.5% ± 19.9; CON: pre 59.18% ± 32.0; post 64.6% ± 17.5). To determine if our main results were affected by potential confounders, we added the bEMG activity and test MEP amplitude as covariates in the analysis of SICI modulation during balance execution. The BALANCE TASK ($F_{1,\ 48}$ = 25; p < 0.001) effect remained significant, as well as the interaction GROUP × TIME ($F_{1,\ 24}$ = 8.9; p < 0.001). Moreover, no significant correlation was found between changes in intracortical inhibition and changes in the bEMG for the TA muscle in any condition ('Stance', 'Straps' and 'Free'; all p < 0.6). Similarly, the test MEP sizes did not correlate with SICI values in any condition ('Stance', 'Straps' and 'Free'; all p < 0.3).

Background EMG activity. For the TA data are displayed in the Fig. 4. There was a significant main effect of BALANCE TASK ($F_{2,\ 48}$ = 230; p < 0.001) and TIME ($F_{1,\ 24}$ = 33.1; p < 0.001), the latter resulting from a decrease in bEMG activity between the pre- and post-test. Post-hoc tests revealed that bEMG activity increased from the 'Stable' (0.009 mV ± 0.003) to the 'Straps' condition (0.018 mV ± 0.012; p < 0.001), from the 'Straps' condition (0.018 mV ± 0.012) to the 'Free' condition (0.115 mV ± 0.06; p < 0.001). There were no GROUP ($F_{1,\ 24}$ = 1.2; p = 0.2) or TIME × GROUP ($F1_{,\ 24}$ = 0.9; p = 0.3) effects.

For the SOL, there was a significant main effect of TIME ($F_{1,\ 24}$ = 6.5; p = 0.02) indicating that bEMG activity was significantly reduced after training. In addition, there was a significant main effect of BALANCE TASK ($F_{2,\ 48}$ = 13.6; p < 0.001). However, there were no differences between groups over time (TIME × GROUP $F_{1,\ 23}$ = 0.03; p = 0.96).

Changes in motor threshold. For the 'Stable' and 'Straps' condition, the aMT, a measure of neuronal excitability (Mavroudakis et al., 1994), was determined in the pre- and post-measurement (see Fig. 5). When comparing the aMTs, a significant main effect of TIME ($F_{1,\ 23}$ = 8.9; p = 0.006), a significant main effect of BALANCE TASK ($F_{1,\ 23}$ = 12.9; p = 0.002) with higher aMT in the stable condition, and a significant interaction of TIME × GROUP ($F_{1,\ 23}$ = 5.1; p = 0.03) were apparent. Post-hoc tests indicated that these effects were due to increases in aMT in the intervention group ('Stable' +10%, p = 0.046; 'Straps' +14%, p = 0.004) whereas aMTs in the control group remained unchanged ('Stable' +0.1%; 'Straps' +4%; all p < 0.27).

Correlation analyses. No significant correlation was found between changes in intracortical inhibition and changes in the bEMG for the TA muscle in any condition ('Stance', 'Straps' and 'Free'; all p < 0.6). Similarly, the test MEP sizes did not correlate with SICI values in any condition ('Stance', 'Straps' and 'Free'; all p < 0.3). However, the increase in SICI during 'Stable' stance was significantly correlated with improvements in balance performance (r = 0.56; p = 0.47*;* see Fig. 6). Furthermore, there was a trend of significance for the correlation between increases in SICI during the 'Straps' condition and changes in balance performance (r = 0.53; p = 0.08).

DISCUSSION

This study investigated changes in intracortical inhibition in response to balance training. In short, our results demonstrate that balance training leads to an increase in the amount of intracortical inhibition during the execution of balance tasks. This increase was correlated with improvements of balance performance. Moreover, the level of SICI was modulated with respect to the amount of postural challenge and this modulation was still present after the training but at a higher threshold indicating a decrease in the perceived balance difficulty. In addition, the active motor threshold during the execution of the different balance tasks increased after training. Noteworthy, this is the first study demonstrating that balance training does not only alter

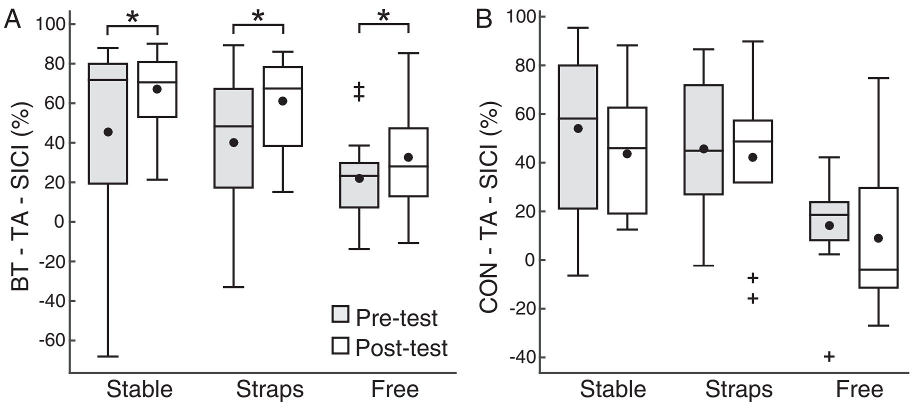

Fig. 3. Results in the tibialis anterior (TA) before and after training. (A) displays the SICI results for the balance training (BT) group and (B) shows the SICI values for the control group (CON). Lower values for SICI represent less inhibition. Gray and white bars represent pre- and post-measurements, respectively. The black dots represent the mean values while the horizontal lines within the boxes indicate the median values. The box covers the 25th–75th percentiles, the whiskers represent the range, and the black crosses indicate outliers ($^{*}=p<0.05$).

cortical/corticospinal excitability but also intracortical inhibition.

Training-related adaptations in intracortical inhibition

The current results indicate increased levels of SICI in the TA after 2 weeks of specific balance training on an unstable device. Noteworthy, the increase in SICI was apparent in all 3 test conditions: during stable stance, standing with straps and in the freely moving stance condition. This is an important fact in order to better interpret the current data. As expected, participants not only significantly increased their 'time in balance' after the training but also considerably altered their muscular activity, leading to drastically reduced EMG activities in the unstable test condition 'Free'. In contrast, muscular activity of both SOL and TA remained unchanged in the more stable 'Straps' condition. Although we could neither detect any significant correlations between the change in bEMG activity and the change in SICI nor any correlations between (non-apparent) changes in the test MEP and the amount of SICI, it might have been argued that the altered level of bEMG influenced the outcome of the paired pulse paradigm. Taking into account the 'Straps' stance condition, this potential limitation can be ruled out as this condition nicely showed that despite comparable bEMG and test-MEP values in pre- and post-measurement, SICI nevertheless was significantly reduced. This points to a cortical phenomenon of the present findings and indicates that indeed intracortical interneurons changed their susceptibility toward TMS in response to balance training. The previously reported reductions in cortical and/or corticospinal excitability after balance training (Beck et al., 2007; Taube et al., 2007; Schubert et al., 2008; Penzer et al., 2015) may therefore be explained – at least in part – by increased levels of intracortical inhibition. Furthermore, the significant correlation between increases in SICI and improvements in postural task execution support the earlier assumption (cf. Taube et al., 2007) that cortical adaptations are essential in order to improve balance control. The present finding of significantly increased active motor thresholds after BT fits very well into this picture, too. It seems that after BT, the motor cortical contribution is generally reduced indicated by a) decreased cortical/-corticospinal excitability (for review see Taube et al., 2008), b) increased levels of intracortical inhibition (present study) and c) increased active motor thresholds during postural task execution (present study). In this context, it was previously argued that BT may lead to a 'shift in movement control' from cortical to more subcorti-

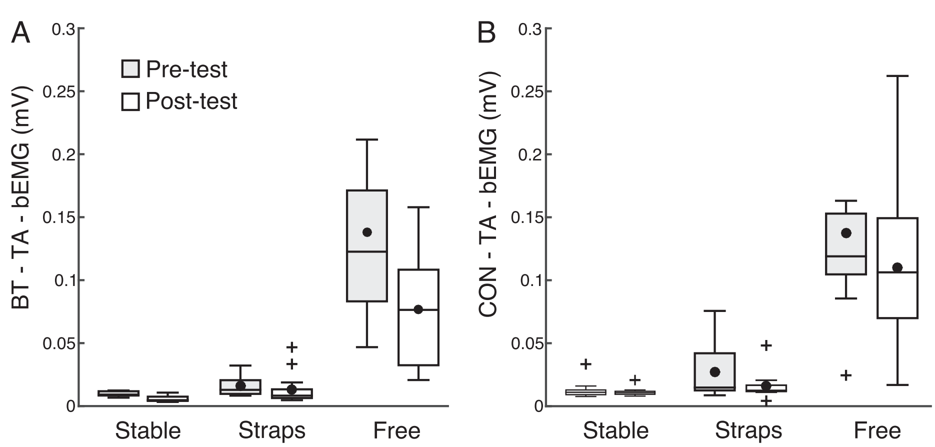

Fig. 4. bEMG of the three balance tasks in the tibialis anterior (TA) before and after training. (A) displays the bEMG activity for the balance training (BT) group and (B) shows the values for the control group (CON). Gray and white bars represent pre- and post-measurements, respectively. The black dots represent the mean values while the horizontal lines within the boxes indicate the median values. The box covers the 25th–75th percentiles, the whiskers represent the range, and the black crosses indicate outliers ($^{*}=p<0.05$).

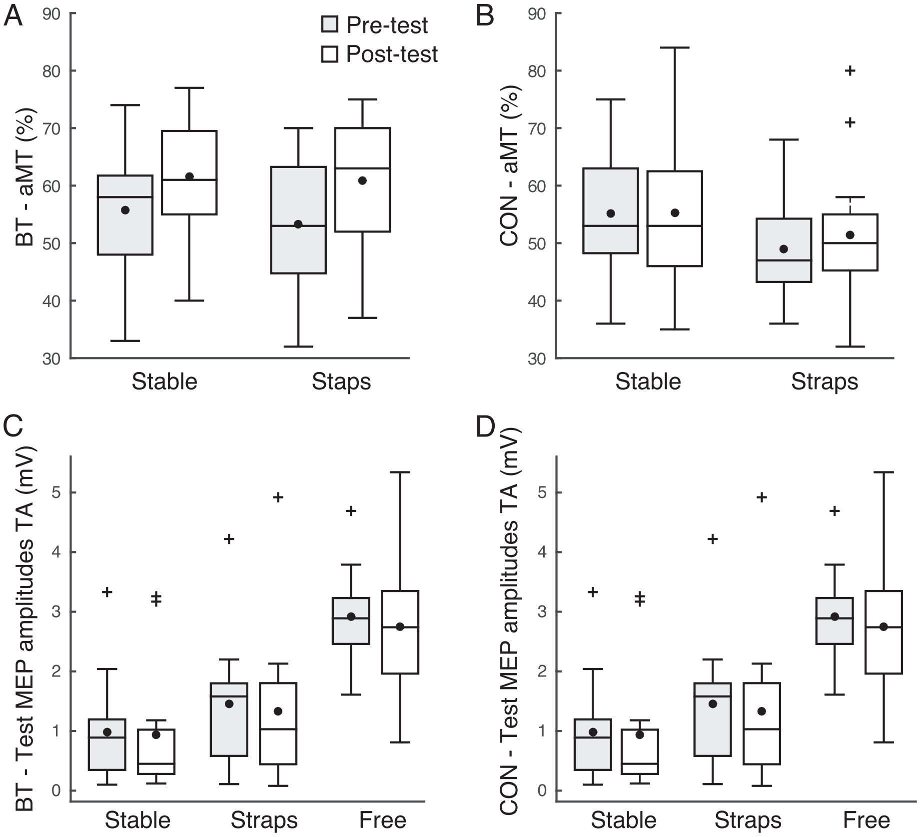

Fig. 5. Results of the active motor threshold (aMT) and motor-evoked potential (MEP) before and after training. (A) and (C) display the aMT and MEP results for the balance training (BT) group. (B) and (D) show the aMT and MEP values for the control group (CON). Gray and white bars represent pre- and post-measurements, respectively. The black dots represent the mean values while the horizontal lines within the boxes indicate the median values. The box covers the 25th–75th percentiles, the whiskers represent the range, and the black crosses indicate outliers (* = p < 0.05).

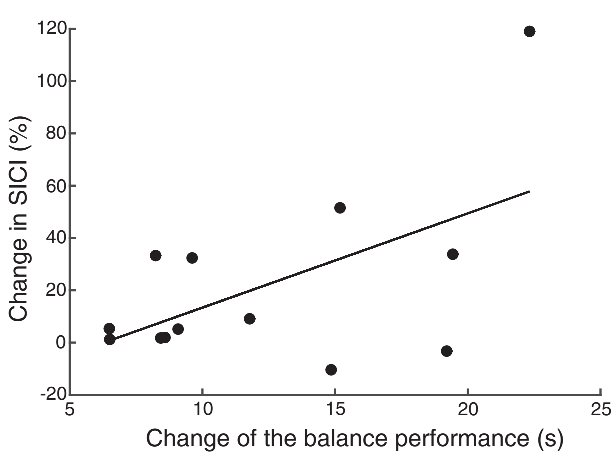

Fig. 6. Training-related percentage differences of pre- and post-measurement of the balance performance ('time in balance') were illustrated on the abscissa while percentage changes in the amount of SICI were displayed on the ordinate. The regression line clearly demonstrates that greater improvements in stance stability (longer 'time in balance') were accompanied by greater increases in SICI (r = 0.56; p = 0.047).

cal and cerebellar structures (Taube et al., 2008) as it was shown for other motor learning tasks (e.g. Puttemans et al., 2005).

Task-related adaptations in intracortical inhibition

Before and after training, there was a decrease in inhibition with increases in postural task difficulty in both groups, the BT and the CON. This confirms previous studies that reported reduced intracortical inhibition with increases in postural task difficulty (Papegaaij et al., 2016a, b; Papegaaij et al., 2014a,b; Soto et al., 2006). It seems reasonable to assume that reducing intracortical inhibition when experiencing a more challenging postural task may facilitate the excitability of motor cortical areas so that they are more easily activated when a loss of balance is actually experienced (Papegaaij et al., 2016a, b). However, the threshold to reduce SICI seems to be altered after BT as higher levels of SICI can be seen after training for each level of postural task difficulty. Thus, the central nervous system might perceive the postural challenge that is associated with each postural task to a lesser extent after training so that the cortical system can be 'discharged'. Alternatively, the increase in intracortical inhibition after BT might be considered as a direct consequence of the reduced muscular activity as voluntary muscle contractions are known to decrease SICI (Ridding et al., 1995; Zoghi et al., 2003). However, as in the condition with 'Straps' the bEMG was comparable in pre- and post-measurement and there was no correlation between bEMG and SICI (for details see section '*Training-related adaptations in intracortical inhibition*'), the modulation of SICI seems to be rather independent from changes in bEMG. When considering both the task- and training-dependent changes of SICI it seems therefore reasonable to assume that SICI is modulated depending on the individual postural challenge (and/or threat) that is associated with each specific postural task.

Task-specific long(er) term effects of training on SICI

The majority of previous studies investigated the influence of short-term interventions on the modulation of SICI (Berghuis et al., 2017). These short-term interventions consistently led to reduced levels of SICI (for review see Berghuis et al., 2017). However, it seems extremely unlikely that learning and especially overlearning should further and further reduce intracortical inhibition despite the fact that populations with less pronounced SICI reveal less well-developed motor performance (Flamand et al., 2012; Gilbert et al., 2011; Papegaaij et al., 2014a,b). Therefore, it is not surprising that the few long(er) term studies that are available reported conflicting results concerning the change in SICI. After strength training, reduced SICI was reported (Goodwill et al., 2012; Weier et al., 2012) while a cross-sectional study comparing badminton athletes with control subjects revealed enhanced levels of SICI in the athletes (Dai et al., 2016). The authors assumed that the extensive practice of highly coordinative skills led to this increase in SICI. The present study confirms and extends this knowledge as we have shown for the first time in a longitudinal setup that the level of SICI can be increased with long(er)-term training when measured during the execution of the acquired task. It might therefore be assumed that during demanding coordinative skills such as balancing, the inhibitory network is highly challenged to avoid unnecessary co-activations and/or co-movements. In contrast, strength tasks may rather rely on the ability to release inhibitory constraints in order to fully activate the muscle(s). Thus, we assume that long-term training adapts intracortical inhibition in a task-specific manner. This assumption is further supported by the fact that we detected no adaptations of SICI when measured at rest (lying). This is an important finding as most previous (short-term) studies investigating adaptations of SICI in response to motor learning measured SICI at rest (see *Introduction* for details). Based on the current results but also on previous research assessing other neurophysiological parameters (e.g. Schubert et al., 2008), it is therefore recommended to measure SICI not only at rest but more importantly during the execution of the task that was actually learned (exercised).

CONCLUSION AND PERSPECTIVE

The reduced motor thresholds during balancing as well as the correlation of improved postural control and increased levels of SICI during the execution of balance tasks after participating in a balance training program demonstrate the occurrence of cortical plasticity in general and adaptation of inhibitory circuits in particular for the acquisition of balance skills in humans. The change in intracortical inhibition seems to be task-specific as it was not detected when measuring at rest.

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CONFLICT OF INTEREST

There are no conflicts of interest.

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