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# TASK-DEPENDENT CHANGES OF CORTICOSPINAL EXCITABILITY DURING OBSERVATION AND MOTOR IMAGERY OF BALANCE TASKS

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**Abstract—Non-physical balance training has demonstrated to be efficient to improve postural control in young people. However, little is known about the potential to increase corticospinal excitability by mental simulation in lower leg muscles. Mental simulation of isolated, voluntary contractions of limb muscles increase corticospinal excitability but more automated tasks like walking seem to have no or only minor effects on motor-evoked potentials (MEPs) evoked by transcranial magnetic stimulation (TMS). This may be related to the way of performing the mental simulation or the task itself. Therefore, the present study aimed to clarify how corticospinal excitability is modulated during AO + MI, MI and action observation (AO) of balance tasks. For this purpose, MEPs and H-reflexes were elicited during three different mental simulations (a) AO + MI, (b) MI and (c) passive AO. For each condition, two balance tasks were evaluated: (1) quiet upright stance (static) and (2) compensating a medio-lateral perturbation while standing on a free-swinging platform (dynamic). AO + MI resulted in the largest facilitation of MEPs followed by MI and passive AO. MEP facilitation was significantly larger in the dynamic perturbation than in the static standing task. Interestingly, passive observation resulted in hardly any facilitation independent of the task. H-reflex amplitudes were not modulated. The current results demonstrate that corticospinal excitability during mental simulation of balance tasks is influenced by both the type of mental simulation and the task difficulty. As H-reflexes and background EMG were not modulated, it may be argued that changes in excitability of the primary motor cortex were responsible for the MEP modulation. From a functional point of view, our findings suggest best training/rehabilitation effects when combining MI with AO during challenging postural tasks.** 

**Key words: motor imagery, action observation, postural control, transcranial magnetic stimulation, balance tasks.**

## INTRODUCTION

Postural control plays an important role in daily life and undergoes fundamental development during the lifespan (Granacher et al., 2011a). For healthy young and elderly subjects but also for many different patient groups, physical balance training was shown to be an effective means to improve postural control (Granacher et al., 2011b) and to reduce the risk of falling (Sherrington et al., 2008). However, physical balance training is not possible for temporarily immobilized subjects. Therefore, alternative, non-physical forms of training should be considered, such as motor imagery (MI) or action observation (AO). MI, on the one hand, is defined as perception and/or imagination of body movement without sensory stimulation (Jeannerod, 1995). It can be experienced in the third-person (visual information) and the first-person perspective (visual and kinaesthetic perspective; Annett, 1995). The kinaesthetic perspective was shown to promote learning more effectively (Callow et al., 2013) and to induce greater changes in corticospinal excitability (Stinear et al., 2006) than the visual perspective. AO, on the other hand, can be categorized into two subcategories: passive and active AO. For the former, the participant passively observes a movement and for the latter, one observes the movement in order to successfully imitate it afterward. Another possibility to train non-physically is to combine AO with MI (AO + MI), meaning that subjects observe the movement while imagining doing the movement themselves. In general, the efficiency of mental simulation (e.g. MI, AO or AO + MI) is most likely explained by an overlap of active brain regions between motor execution and mental simulation (Caspers et al., 2010; Macuga and Frey, 2012; Hetu et al., 2013; Vogt et al., 2013).

With respect to postural control, MI of static postural tasks was demonstrated to improve performance in these tasks in elderly people (Hamel and Lajoie, 2005). Likewise, AO improved accomplishment of a ‘‘sit-to-stand/back-to-sit’’ and walking performance (Tia et al., 2010). Recently, 4 weeks of both AO + MI and MI of balance tasks were shown to effectively improve performance of highly variable and unpredictable balance actions in the young (Taube et al., 2014a).

However, despite the knowledge about these behavioral adaptations in static and dynamic postural tasks, the underlying neural processes for non-physical balance training are scarcely investigated. Although numerous Transcranial magnetic stimulation (TMS) studies have explored modulation of corticospinal

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*Abbreviations:* ANOVA, analysis of variance; AO, action observation; MEPs, motor-evoked potentials; MI, motor imagery; PNS, peripheral nerve stimulation; RMS, root mean square; RMT, resting motor threshold; TA, tibialis anterior; TMS, transcranial magnetic stimulation.

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excitability during mental simulation of voluntary movements of the upper extremity (for a review see Fadiga et al., 2005; Loporto et al., 2011), there are only few studies targeting the lower extremity and none addressing modulation of corticospinal excitability during balance tasks. Regarding voluntary movements of the lower extremity, two studies found an increase of corticospinal excitability during MI of foot dorsiflexion and knee movement, respectively (Tremblay et al., 2001; Liepert and Neveling, 2009). In addition, Liepert and coworkers observed that MI of foot dorsiflexion resulted in greater MEP amplitudes than AO of the same task. Finally, Bakker et al. (2008) compared MEP modulation between mental simulation of foot dorsiflexion and gait (Bakker et al., 2008). In line with other studies, they found MEP facilitation during MI of foot dorsiflexion (Tremblay et al., 2001; Liepert and Neveling, 2009) but no significant effect when imaging normal walking. Thus, there might be a distinct difference between voluntary foot movements and more automatic actions such as gait. This raises the question whether it is possible to activate the corticospinal system during mental simulation of dynamic balance tasks? For rehabilitation, this is important to know as the primary motor cortex is well known to be involved in static (Tokuno et al., 2009) and dynamic postural control (Taube et al., 2006) and displays profound adaptations in response to physical balance training (Beck et al., 2007; Taube et al., 2007a; Schubert et al., 2008). Thus, it might be assumed that mental simulation of balance tasks should modulate corticospinal excitability in order to be most effective for non-physical balance training during immobilization. Thus, the aim of this study was to evaluate corticospinal excitability during AO + MI, MI and passive AO of differently demanding balance tasks. Furthermore, to get a better idea where the change in excitability takes place, H-reflexes were elicited by means of peripheral nerve stimulation (PNS). So far, the implication of spinal structures during mental simulation remains controversial. For both, MI and AO, some studies found increased (Bonnet et al., 1997; Gandevia et al., 1997; Hale et al., 2003; Cheng et al., 2005) others reduced (Baldissera et al., 2001; Montagna et al., 2005) and again others unchanged H-reflex amplitudes (Abbruzzese et al., 1996; Yahagi et al., 1996; Aoyama and Kaneko, 2011). So far, no study explored changes of the H-reflex when combining AO with MI (AO + MI). Furthermore, there is no study assessing spinal excitability during mental simulation of balance tasks.

The aim of this study was to evaluate corticospinal and spinal excitability during AO + MI, MI and passive AO of differently demanding balance tasks. The study design (balance tasks and mental simulation conditions) resembled the one we used in a recent fMRI study (Taube et al., 2015) in order to allow direct comparisons. We hypothesized that corticospinal facilitation would be most pronounced during AO + MI and less prominent during passive AO. Furthermore, a difficult balance task (i.e. dynamic perturbation) was assumed to increase corticospinal excitability more than a simple balance task (i.e. standing). Based on the very controversial findings in the literature about H-reflex modulation during mental simulation, we further hypothesized that mental simulation primarily involves supraspinal centers and therefore did not expect relevant task-dependent changes of the H-reflex.

## EXPERIMENTAL PROCEDURES

### Participants

Fifteen healthy adults (age 27 ± 4.6, five females) volunteered for this study. All subjects declared written consent before participating in this study that was approved by the local Ethics Committee.

### Methods

Throughout the experiment, subjects were lying at rest in a supine position and looked at a monitor that was placed approximately 1 m above their head. The subjects were instructed to perform three different mental simulations of two different balance tasks. The mental simulations consisted of (1) AO + MI, (2) MI, and (3) passive AO. For AO + MI, subjects were asked to watch a video of a person performing a balance task and at the same time imagine performing the task themselves. Subjects were instructed to imagine themselves as the person in the video shown in a mirror. This was done because it has previously been proposed that mirror images facilitate imitation (Koski et al., 2003) and observational learning (Higuchi et al., 2012). In the MI, subjects had to close their eyes and imagine performing the respective task. During AO + MI and MI was performed in a first-person kinesthetic perspective. In contrast, the instruction for the passive AO was to watch the video without any additional mental effort. Two balance tasks were shown in the videos: (1) standing still on stable ground (STATIC; Fig. 1A) and (2) compensating a medio-lateral perturbation while standing on a free-swinging platform (DYNAMIC; Fig. 1B). Subjects were carefully introduced to the tasks and familiarized with the videos by the experimenter before the experiment started.

In each of the six conditions (three mental simulations * two balance tasks) the video was repeated 20 times. During ten trials, motor-evoked potentials (MEPs) elicited by TMS were evoked from the target muscle soleus (SOL). Concurrently, MEPs were also recorded from the tibialis anterior (TA) muscle. Similarly, 10 soleus H-reflexes were elicited in each condition by means of PNS (see section below). In order to precisely time the mental simulation, the start of each trial was signaled by a tone that occurred every 2 s. In every second trial, TMS or PNS was applied 1.4 after this tone. At this time, the person in the video had shifted his weight on the right leg, meaning that the soleus should be activated in order to counteract the perturbation. The constant rhythm and the tone were particularly important for the MI where subjects had their eyes closed. Before and after each condition, a short rest period was given, during which subjects were instructed to fixate a cross on the screen. During each rest period, five stimulations of each TMS and PNS were applied to elicit control MEPs and control

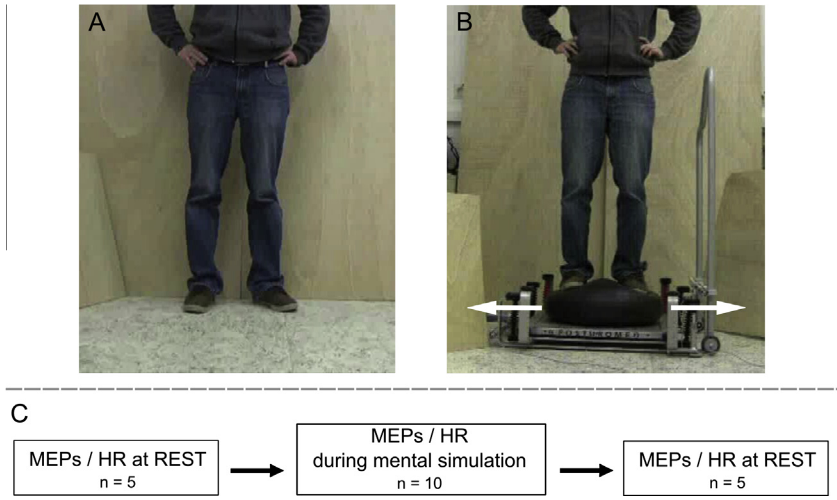


**Fig. 1.** Illustration of the experimental design. (A) and (B) display the static and the dynamic balance task, respectively. (C) MEPs and H-reflexes (HR) recorded during the experimental conditions were normalized to the corresponding resting MEPs/HR recorded before and after the respective condition.

H-reflexes (CONTROL), respectively. The interstimulus interval was set to 4 s. The experimental setup is illustrated in Fig. 1.

The six conditions were run in random order. This procedure was repeated two times in order to control for effects of fatigue or changes in attention.

## EMG recording

MEPs were recorded using bipolar surface electrodes (Blue sensor P, Ambu®, Bad Nauheim, Germany). Electrodes were attached on the right SOL and TA muscles after skin preparation. The reference electrode was placed on the tibia plateau. EMG signals were amplified (1000 times), sampled at 4 kHz, and band-pass filtered (10–1000 Hz). Data were recorded using custom-made software (LabView® based, National Instruments®, Austin, TX, USA) and stored on a computer.

## TMS protocol

The left motor cortex was stimulated using a 95-mm focal ‘‘butterfly-shaped’’ coil (D-B80) and a MagPro X100 with MagOption magnetic stimulator (both MagVenture A/S, Farum, Denmark) to evoke MEPs in the right SOL. As the threshold at rest is lower for the TA than for the SOL, the current setup allowed the recording of MEPs in TA, too. Single pulses with a biphasic waveform were applied. The coil was initially positioned approximately 0.5 cm anterior to the vertex and over the midline. It was then moved anterior and to the left while MEP sizes of the SOL were monitored to determine the optimal position for eliciting MEPs with minimal intensity. In this position the coil was mechanically fixed. To ensure a constant coil position throughout the experiment, the coil position relative to the head was controlled by an image-based navigation system (LOCALITE TMS Navigator, LOCALITE GmbH, Sankt Augustin, Germany). The resting motor threshold (RMT) was determined for each subject to be the lowest stimulation intensity that elicited an MEP larger than 50 μV in SOL in three out of five trials (Kujirai et al., 1993). The RMT was 56 ± 14% of maximal stimulator output. During the experiment, stimulation intensity was set to 1.2 RMT.

## PNS

Tiabial nerve was stimulated by an electrical stimulator (Digitimer DS7A, Hertfordshire, UK). The anode (10 × 5 cm dispersal pad) was fixated below the patella on the anterior aspect of the knee. The cathode (2 cm in diameter) was placed in the popliteal fossa and moved until the optimal location for eliciting a muscular response in the SOL was found. In a first step, a H-reflex recruitment curve was recorded by progressively increasing the stimulation intensity. When the M-wave reached a plateau, two to three further stimulations with markedly increased intensity were applied in order to obtain the maximal value ($M_{max}$). On the basis of the H-reflex recruitment curve, the H-reflex was adjusted to correspond to 20% of $M_{max}$ and this stimulation intensity was used throughout the experiment (for trials with mental simulation and control trials). Eleven out of the 15 subjects that were measured with TMS participated in the H-reflex measurements.

## Data analysis and statistics

In order to avoid biased MEP/H-reflex amplitudes due to voluntary or involuntary contractions, trials with enhanced EMG activity before the MEP and the H-reflex, respectively, were removed. Thus, if the peak amplitude in a time interval of 100 ms before stimulation reached 4× the standard deviation of the individual mean, the trial was discarded. Moreover, root mean square (RMS) values of the EMG signal (background activity) were calculated for the same time window for the remaining condition and control trials. In order to ensure that background activity was not enhanced in trials with mental simulation, a three-way repeated measures analysis of variance (ANOVA) with the factors LEVEL of ACTIVITY (condition vs. rest), mental SIMULATION (AO + MI vs. MI vs. passive AO), and balance TASK (dynamic vs. static) was performed on the RMS values.

Peak-to-peak amplitudes of the MEPs/H-reflexes were determined. For each of the six conditions, the mean amplitudes were normalized to the mean MEP/H-reflex recorded during the corresponding rest periods (i.e. the rest periods directly before and after each condition). This normalization allowed comparisons across subjects and over time (beginning and end of the experiment; see Fig. 1).

To see which conditions differed from rest, one-sample t-tests were calculated for each condition comparing the normalized MEP/H-reflex amplitudes to a reference value of 1 (corresponding to 100% of the resting amplitude).

In order to evaluate the effects of simulation type and balance task on MEP/H-reflex amplitudes, the normalized values were analyzed by separate a two-way repeated measures ANOVAs for each dependent variable (MEP amplitudes in SOL and TA and H-reflex amplitudes in SOL) with the factors mental SIMULATION (AO + MI vs. MI vs. passive AO) and balance TASK (dynamic vs. static). Significant main effects were followed by post-hoc Student's *t*-tests with Bonferroni correction.

Data are presented as mean ± standard error of the mean (SEM). The significance level was defined at $p < 0.05$. Statistics were calculated using SPSS 21.0 for Windows (IBM® SPSS® Statistics 2, Chicago, IL, USA).

## RESULTS

### TMS

MEPs in the soleus: On average, 5% of MEPs were excluded from statistical analysis due to an enhanced background EMG activity prior to stimulation. The ANOVA revealed no differences between the background EMG in trials with mental simulation and in resting control trials: LEVEL of ACTIVITY ($F_{1,\ 14} = 0.06$; $p = 0.82$), MENTAL SIMULATION ($F_{2,\ 28} = 0.254$; $p = 0.78$), and BALANCE TASK ($F_{1,\ 14} = 0$; $p = 0.99$).

The effect of mental simulation on soleus MEP amplitudes from a representative subject is illustrated in Fig. 2. The analysis of the soleus MEPs (Fig. 3) showed significant main effects of MENTAL SIMULATION ($F_{2,\ 28} = 5.75$; $p = 0.008$, Fig. 3A) and BALANCE TASK ($F_{1,\ 14} = 9.91$ $p = 0.007$, Fig. 3B) and a significant interaction effect of MENTAL SIMULATION × TASK ($F_{2,\ 28} = 4.66$; $p = 0.02$). Post hoc comparison for the dynamic task revealed that AO + MI and MI induced significantly greater MEPs than passive AO ($p = 0.002$; $p = 0.016$). No statistical difference was found between AO + MI and MI ($p = 0.68$) for the dynamic task. For the static task, post hoc comparisons between mental simulation conditions did not show significant differences.

One-sample *t*-tests revealed that MEPs during AO + MI ($p = 0.001$) and MI ($p = 0.001$) of the dynamic balance task and MI of the static task ($p = 0.015$) were significantly facilitated compared to the control MEPs recorded at rest (Fig. 3C).

For the TA muscle there was also no significant difference in background EMG between the rest condition and the background EMG during mental simulation: LEVEL of ACTIVITY ($F_{1,\ 14} = 1.80$; $p = 0.20$), MENTAL SIMULATION ($F_{2,\ 28} = 1.30$; $p = 0.29$), and BALANCE TASK ($F_{1,\ 14} = 1.91$; $p = 0.19$). For the MEPs, it can be seen that there was a main effect of MENTAL SIMULATION ($F_{2,\ 28} = 3.6$, $p = 0.041$) but no effect of BALANCE TASK ($F_{1,\ 14} = 1.85$, $p = 0.20$) and no interaction of MENTAL SIMULATION × BALANCE TASK ($F_{2,\ 28} = 0.17$, $p = 0.84$). Post-hoc tests revealed no significant differences between the three mental simulation conditions.

MEPs during AO + MI ($p = 0.004$) and MI ($p = 0.016$) of the dynamic task and MI of the static task ($p = 0.017$) were significantly increased compared to the control MEPs (Fig. 4).

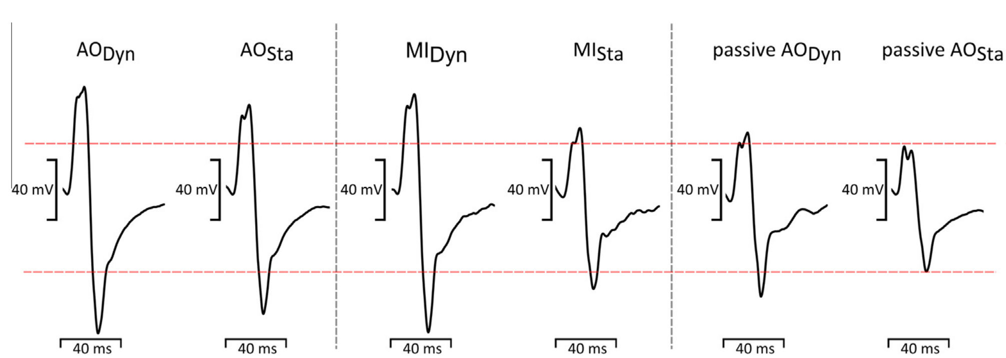


**Fig. 2.** Soleus MEP amplitudes of one exemplary subject showing the modulation across conditions. Each waveform represents the average of 10 MEPs. Action observation combined with motor imagery (AO + MI) as well as motor imagery (MI) alone produced larger MEPs than passive action observation (passive AO). Mental simulation of the dynamic balance task (Dyn) facilitated MEPs more than simulation of the static balance task (Sta).

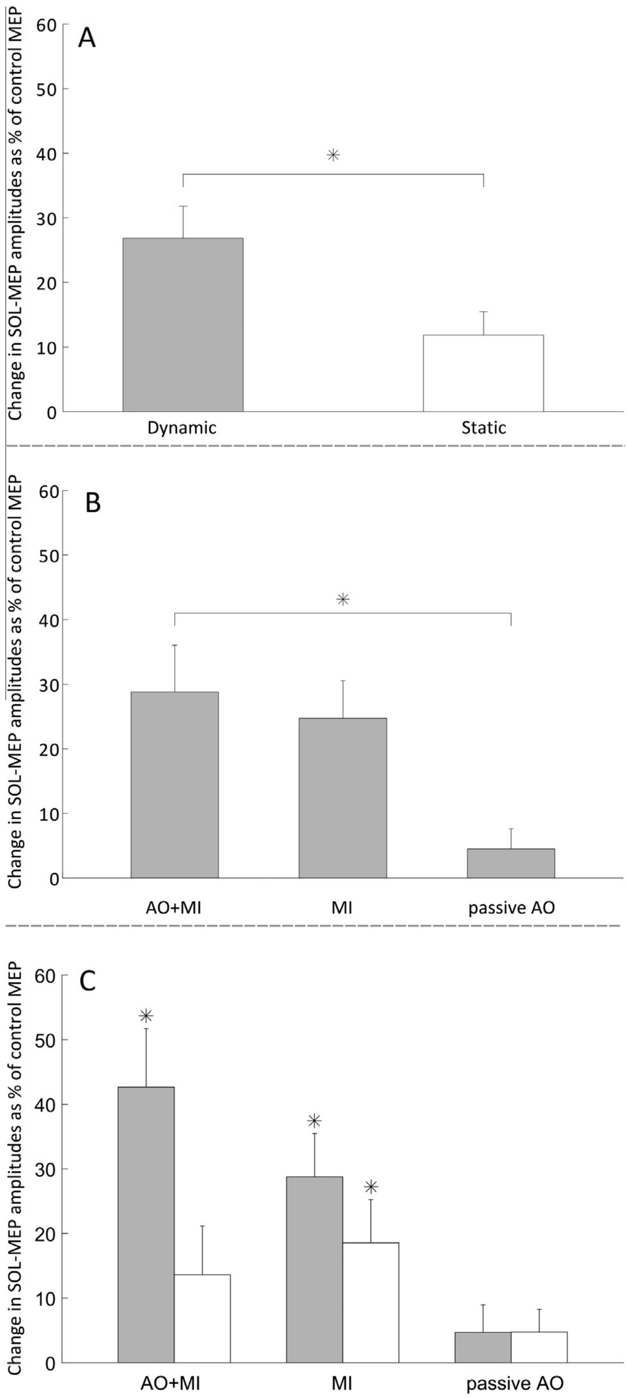


**Fig. 3.** Modulation of corticospinal excitability during mental simulation for the soleus muscle. Values represent percentage changes of MEP amplitude compared to control MEPs during rest. (A) Simulation of the dynamic task facilitated MEPs significantly more than the static task. (B) The type of mental simulation influenced the modulation of the corticospinal excitability with the largest facilitation during the combination of action observation and motor imagery (AO + MI) followed by motor imagery alone (MI) and passive AO. (C) The interaction between task complexity and mental simulation is displayed. Asterisks indicate conditions where MEPs were significantly facilitated compared to MEPs at rest. All data are presented as group mean; error bars represent standard error of the mean. Gray and white bars represent the dynamic and the static task, respectively. $^{*}p < 0.05$, $^{**}p < 0.01$.

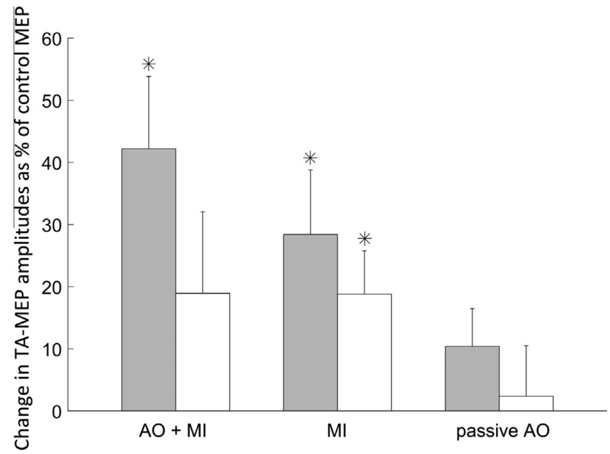


**Fig. 4.** Normalized tibialis anterior MEP amplitudes (mean ± SE) for the six experimental conditions. Although the modulation across conditions was similar to that of the soleus muscle (Fig. 3C), there was only a significant main effect for MENTAL SIMULATION ($F_{2,\,28} = 4.55$, $p < 0.19$). Gray and white bars represent the dynamic and the static task, respectively. $^{*}p < 0.05$, $^{**}p < 0.01$.

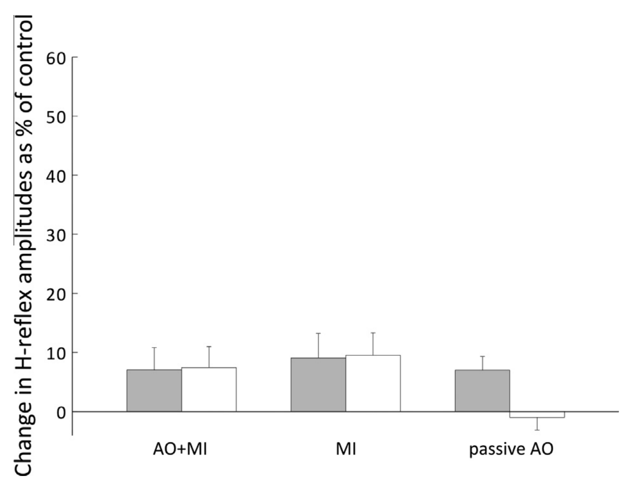


**Fig. 5.** Modulation of the soleus H-reflex during action observation combined with motor imagery (AO + MI), motor imagery (MI) and passive action observation (passive AO) of balance tasks. Values represent percentage changes of H-reflex amplitudes compared to control H-reflexes during rest. There was no modulation of the H-reflex, independent of the condition. All data are presented as group mean; error bars represent standard error of the mean. Gray and white bars represent the dynamic and the static task, respectively.

## H-reflex

On average 1% of the H-reflexes were removed from statistical analysis due to increased background EMG activity prior to stimulation. There was no difference in the background EMG in trials with and without mental simulation: LEVEL of ACTIVITY ($F_{1,10} = 0.65$; $p = 0.43$), MENTAL SIMULATION ($F_{2,20} = 2.04$; $p = 0.16$), and BALANCE TASK ($F_{1,10} = 0.49$; $p = 0.50$). A two-way repeated measures ANOVA of the H-reflex amplitudes did not reveal any main effect or interaction; neither MENTAL SIMULATION ($F_{2,20} = 0.5$; $p = 0.62$, Fig. 5A), nor the BALANCE TASK ($F_{1,10} = 1.4$; $p = 0.27$), nor the interaction of MENTAL SIMULATION ×

BALANCE TASK ($F_{2,20} = 0.3$; $p = 0.72$) turned out to be significant, indicating comparable H-reflexes across all conditions and tasks. H-reflex amplitudes during conditions presented no significant difference to control H-reflexes (Fig. 5).

## DISCUSSION

The results of this study show that both task complexity and the type of mental simulation influence corticospinal excitability. In general, MEP facilitation in the SOL was always more pronounced for the dynamic than static task. Furthermore, AO + MI of the dynamic task resulted in the largest increase in corticospinal excitability followed by MI and AO. In contrast, neither H-reflexes nor the background EMG were modulated. This may indicate changes of excitability within the primary motor cortex during mental simulation of balance tasks.

### Comparison of balance tasks (task difficulty)

Previous studies investigating the upper extremity have shown that task complexity influences MEP facilitation, meaning that in the more complex task larger MEPs occurred than in the simpler task (Kuhtz-Buschbeck et al., 2003; Roosink and Zijdewind, 2010). Our results in the soleus muscle are in line with this observation and show that a challenging, dynamic balance task increased corticospinal excitability more than a relatively easy, static balance task. In contrast, the H-reflex and the background EMG were not influenced by task complexity. In this way, mental simulation of balance tasks may share some similarities but also present some differences with actual execution of balance tasks. Tokuno et al. (2009) demonstrated that cortical excitability increased when subjects switched from supported to unsupported standing while the H-reflex was suppressed. Our results indicate that activation at the supraspinal level is comparable in simulated and actually executed balance tasks but not the activity at the spinal level. This observation is also supported by one of our most recent studies (Taube et al., 2014a): In subjects who mentally trained (simulated) balance tasks, behavioral adaptations were similar to those after physical balance training. However, there was no reduction of the H-reflex as reported in many previous studies investigating physical balance training (Taube et al., 2007a,b). Thus, it seems that mental simulation of balance tasks neither in the short-(current study) nor in the long-term (Taube et al., 2014a) affects spinal reflex circuits.

### Comparison of mental simulations

For the upper extremity, several studies have shown MEP facilitation during MI and AO of arm, hand, and finger movements (Clark et al., 2004; Sakamoto et al., 2009; Roosink and Zijdewind, 2010). Clark et al. (2004) found similar increases in corticospinal excitability independent whether participants (a) passively observed the action, (b) observed the action with the intention to imitate it later on (called active observation), or (c) imagined the task. In contrast, most other studies found greatest activity during active observation (observation to imitate) followed by MI and passive AO (Sakamoto et al., 2009; Roosink and Zijdewind, 2010). Similarly, for the lower extremity, Liepert and Neveling (2009) reported greater MEP facilitation in the TA muscle when participants imagined a dorsiflexion compared to passively observing the movement. Thus, there is good evidence that the way a motor action is mentally simulated influences corticospinal excitability. In support of this notion, fMRI data demonstrated that the combination of AO + MI resulted in greater brain activity than AO or MI alone (Macuga and Frey, 2012; Nedelko et al., 2012; Berends et al., 2013; Villiger et al., 2013; Vogt et al., 2013). The current results extend these previous findings, as they show for the first time differences in corticospinal excitability of the soleus muscle during AO + MI, MI, and passive AO of balance tasks. Furthermore, this is one of the few studies investigating the effects of mental simulation by combining TMS with PNS in order to account for changes at the spinal level. This is an important ascertainment as previous studies using H-reflex measures during mental simulation reported contradictory findings: some studies showed no changes at all (e.g. Abbruzzese et al., 1996) while others demonstrated H-reflex facilitation (e.g. Bonnet et al., 1997) or even H-reflex suppression (e.g. Oishi et al., 1994). In the present study, neither the H-reflex nor the background EMG activity was modulated across conditions. Consequently, the larger MEP facilitation during AO + MI and MI compared to AO is unlikely to result from changes at the spinal level. More likely, supraspinal centers accounted for the MEP modulation. As TMS activates the corticomotoneurons mostly in an indirect way (trans-synaptically or at the axon hillock) and the corticospinal fibers are thought to be free from presynaptic inhibition (Nielsen and Petersen, 1994; Jackson et al., 2006), the current MEP modulation is probably caused by changes in the excitability of cortical interneurons and/or of the corticomotoneurons themselves. Nevertheless, it has to be noted that the authors of this study are well aware that the comparison of MEPs and H-reflexes (background EMG) is not the best method to make conclusions about the involvement of the primary motor cortex (for more detail see Petersen et al., 2003). Cervicomedullary stimulation in isolation or in combination with the H-reflex (CMS-conditioning of the H-reflex; see for example (Taube et al., 2014b) would have provided more valid results. However, due to the unpleasant sensation arising from cervicomedullary stimulation it was not possible to apply this method as even well-accustomed subjects were not able to focus on the mental simulation any more.

### Difference between soleus and tibialis results

Although the pattern of MEP modulation in the tibialis muscle resembled the one of the soleus muscle, the effects were less prominent and there was only an overall effect of mental simulation but no difference between the static and the dynamic task. The reason for the weaker MEP modulation in the tibialis might be related to the nature of the perturbation task. When physically performing this task, primarily the extensor muscles have to be activated in order to compensate the perturbation. It might therefore be assumed that the tibialis muscle is only slightly (co-) activated in order to stabilize the ankle joint. Thus, the difference in the activity level of the TA in the static standing task and the dynamic perturbation task might not be so pronounced than in the soleus. In this way, our results would be well in line with previous studies showing that mental simulation primarily affected corticospinal excitability of muscles involved in the imagined or observed movement (Fadiga et al., 1999; Gangitano et al., 2001; Maeda et al., 2002). Furthermore, the entire experimental setup was geared to measure changes in activity in the target muscle SOL. For instance, motor threshold was determined with respect to the soleus. Thus, we cannot exclude that the stimulation intensity of the TMS might have been already too high for the TA, leading to potential ceiling effects. In addition, the H-reflex was only measured for the soleus muscle so that we cannot make any assumptions about potential changes in Ia afferent transmission for the TA.

### Comparison of TMS and fMRI data

The present results show that corticospinal excitability depends on the complexity of the balance task and the kind of mental simulation (AO + MI, MI, AO). The pattern of MEP modulation with the highest activity during AO + MI of the dynamic task and hardly any activity during passive AO is therefore very similar to the general pattern of brain activity derived from our recent fMRI measures (Taube et al., 2015). In this previous study, we used exactly the same experimental design as in the current study to make direct comparisons possible. It was observed that AO + MI and MI activated an overlapping motor network involving SMA, cerebellum and putamen. AO + MI additionally recruited the PMv and PMd. No activity was found in any of those areas for the passive AO condition. Comparison of dynamic and static balance tasks revealed differential activity in SMA and cerebellum during AO + MI while no differences could be seen during passive AO or MI. Furthermore, although the same experimental design (the same balance tasks and the same mental simulations) was used in the fMRI study no activity in the primary motor cortex was observed except for AO + MI of the dynamic task after a region of interest (ROI) analysis.

The reason for this discrepancy is in all likelihood not related to a differential brain activation pattern of the respective participants (five participants were the same in the two experiments) but is more likely derived from the fact that few studies at all have seen activity during MI and AO + MI with fMRI (Macuga and Frey, 2012; Nedelko et al., 2012; Hetu et al., 2013). The cause for this remains speculative. Functional MRI is known to have a considerably lower temporal resolution than TMS. Thus, the temporal sensitivity of the fMRI might not be high enough to detect subtle, short-lasting changes of activity in the primary motor cortex even if these activities are repeated several times. Additionally, the lack of activity in the primary motor cortex when recorded with fMRI (see Hetu et al., 2013) may also be explained by the method of analysis. In fact, most fMRI studies used an analysis of the whole brain which seems not sensitive enough to detect subtle, short-lasting motor cortical activities. Using another analysis such as small volume correction on a ROI improves the sensitivity and induces a better detection of M1 activity, especially in complex designs with multiple conditions. Using this kind of analysis, Sharma et al. (2008) and Taube et al. (2015) detected activity in the primary motor cortex during mental simulation. However, although significant activation was detected during AO + MI of balance tasks, no graded activity that depended on the task difficulty or the mental simulation technique (AO + MI, MI, passive AO) could be observed (Taube et al., 2015). Thus, TMS seems much more sensitive to detected subtle changes in the excitability of motor cortical neurons.

## FUNCTIONAL CONSIDERATION AND CONCLUSION

It is known that non-physical training by mentally simulating postural tasks can improve balance performance (Hamel and Lajoie, 2005; Tia et al., 2010; Taube et al., 2014a). However, the underlying neural mechanisms are scarcely investigated. Although this seems important to further improve non-physical training interventions. Recently, brain activation patterns during AO + MI, MI, and passive AO of different balance tasks were assessed by means of fMRI (Taube et al., 2015). The results indicated that AO + MI of challenging balance tasks was most effective to activate motor regions such as the SMA, pre-motor areas, cerebellum, and basal ganglia that are all involved in postural control. The current study confirms and extends these findings by showing that excitability of the motor cortex is also modulated depending on the task and the kind of mental simulation. Thus, non-physical balance training should concentrate on demanding balance exercises. Furthermore, the combination of MI and AO seems very promising.

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## REFERENCES

Abbruzzese G, Trompetto C, Schieppati M (1996) The excitability of the human motor cortex increases during execution and mental imagination of sequential but not repetitive finger movements. Exp Brain Res 111:465–472.

Annett J (1995) Motor imagery – perception or action. Neuropsychologia 33:1395–1417.

Aoyama T, Kaneko F (2011) The effect of motor imagery on gain modulation of the spinal reflex. Brain Res 1372:41–48.

Bakker M, Overeem S, Snijders AH, Borm G, van Elswijk G, Toni I, Bloem BR (2008) Motor imagery of foot dorsiflexion and gait: effects on corticospinal excitability. Clin Neurophysiol 119:2519–2527.

Baldissera F, Cavallari P, Craighero L, Fadiga L (2001) Modulation of spinal excitability during observation of hand actions in humans. Eur J Neurosci 13:190–194.

Beck S, Taube W, Gruber M, Amtage F, Gollhofer A, Schubert M (2007) Task-specific changes in motor evoked potentials of lower limb muscles after different training interventions. Brain Res 1179:51–60.

Berends HI, Wolkorte R, Ijzerman MJ, van Putten MJ (2013) Differential cortical activation during observation and observation-and-imagination. Exp Brain Res 229:337–345.

Bonnet M, Decety J, Jeannerod M, Requin J (1997) Mental simulation of an action modulates the excitability of spinal reflex pathways in man. Cogn Brain Res 5:221–228.

Callow N, Roberts R, Hardy L, Jiang D, Edwards MG (2013) Performance improvements from imagery: evidence that internal visual imagery is superior to external visual imagery for slalom performance. Front Hum Neurosci 7:697.

Caspers S, Zilles K, Laird AR, Eickhoff SB (2010) ALE meta-analysis of action observation and imitation in the human brain. Neuroimage 50:1148–1167.

Cheng YW, Tzeng OJ, Hung D, Decety J, Hsieh JC (2005) Modulation of spinal excitability during observation of bipedal locomotion. NeuroReport 16:1711–1714.

Clark S, Tremblay F, Ste-Marie D (2004) Differential modulation of corticospinal excitability during observation, mental imagery and imitation of hand actions. Neuropsychologia 42:105–112.

Fadiga L, Buccino G, Craighero L, Fogassi L, Gallese V, Pavesi G (1999) Corticospinal excitability is specifically modulated by motor imagery: a magnetic stimulation study. Neuropsychologia 37:147–158.

Fadiga L, Craighero L, Olivier E (2005) Human motor cortex excitability during the perception of others' action. Curr Opin Neurobiol 15:213–218.

Gandevia SC, Wilson LR, Inglis JT, Burke D (1997) Mental rehearsal of motor tasks recruits alpha-motoneurones but fails to recruit human fusimotor neurones selectively. J Physiol 505(Pt 1):259–266.

Gangitano M, Mottaghy FM, Pascual-Leone A (2001) Phase-specific modulation of cortical motor output during movement observation. NeuroReport 12:1489–1492.

Granacher U, Bridenbaugh SA, Muehlbauer T, Wehrle A, Kressig RW (2011a) Age-related effects on postural control under multi-task conditions. Gerontology 57:247–255.

Granacher U, Muehlbauer T, Gollhofer A, Kressig RW, Zahner L (2011b) An intergenerational approach in the promotion of balance and strength for fall prevention – a mini-review. Gerontology 57:304–315.

Hale BS, Raglin JS, Koceja DM (2003) Effect of mental imagery of a motor task on the Hoffmann reflex. Behav Brain Res 142: 81–87.

Hamel MF, Lajoie Y (2005) Mental imagery. Effects on static balance and attentional demands of the elderly. Aging Clin Exp Res 17:223–228.

Hetu S, Gregoire M, Saimpont A, Coll MP, Eugene F, Michon PE, Jackson PL (2013) The neural network of motor imagery: an ALE meta-analysis. Neurosci Biobehav Rev 37:930–949.

Higuchi S, Holle H, Roberts N, Eickhoff SB, Vogt S (2012) Imitation and observational learning of hand actions: prefrontal involvement and connectivity. Neuroimage 59:1668–1683.

Jackson A, Baker SN, Fetz EE (2006) Tests for presynaptic modulation of corticospinal terminals from peripheral afferents and pyramidal tract in the macaque. J Physiol 573:107–120.

Jeannerod M (1995) Mental-imagery in the motor context. Neuropsychologia 33:1419–1432.

Koski L, Iacoboni M, Dubeau MC, Woods RP, Mazziotta JC (2003) Modulation of cortical activity during different imitative behaviors. J Neurophysiol 89:460–471.

Kuhtz-Buschbeck JP, Mahnkopf C, Holzknecht C, Siebner H, Ulmer S, Jansen O (2003) Effector-independent representations of simple and complex imagined finger movements: a combined fMRI and TMS study. Eur J Neurosci 18:3375–3387.

Kujirai T, Caramia MD, Rothwell JC, Day BL, Thompson PD, Ferbert A, Wroe S, Asselman P, Marsden CD (1993) Corticocortical inhibition in human motor cortex. J Physiol 471:501–519.

Liepert J, Neveling N (2009) Motor excitability during imagination and observation of foot dorsiflexions. J Neural Transm 116: 1613–1619.

Loporto M, McAllister C, Williams J, Hardwick R, Holmes P (2011) Investigating central mechanisms underlying the effects of action observation and imagery through transcranial magnetic stimulation. J Mot Behav 43:361–373.

Macuga KL, Frey SH (2012) Neural representations involved in observed, imagined, and imitated actions are dissociable and hierarchically organized. Neuroimage 59:2798–2807.

Maeda F, Kleiner-Fisman G, Pascual-Leone A (2002) Motor facilitation while observing hand actions: specificity of the effect and role of observer's orientation. J Neurophysiol 87:1329–1335.

Montagna M, Cerri G, Borroni P, Baldissera F (2005) Excitability changes in human corticospinal projections to muscles moving hand and fingers while viewing a reaching and grasping action. Eur J Neurosci 22:1513–1520.

Nedelko V, Hassa T, Hamzei F, Schoenfeld MA, Dettmers C (2012) Action imagery combined with action observation activates more corticomotor regions than action observation alone. J Neurol Phys Ther 36:182–188.

Nielsen J, Petersen N (1994) Is presynaptic inhibition distributed to corticospinal fibers in man. J Physiol 477:47–58.

Oishi K, Kimura M, Yasukawa M, Yoneda T, Maeshima T (1994) Amplitude reduction of H-reflex during mental movement simulation in elite athletes. Behav Brain Res 62:55–61.

Petersen NT, Pyndt HS, Nielsen JB (2003) Investigating human motor control by transcranial magnetic stimulation. Exp Brain Res 152:1–16.

Roosink M, Zijdewind I (2010) Corticospinal excitability during observation and imagery of simple and complex hand tasks: implications for motor rehabilitation. Behav Brain Res 213:35–41.

Sakamoto M, Muraoka T, Mizuguchi N, Kanosue K (2009) Combining observation and imagery of an action enhances human corticospinal excitability. Neurosci Res 65:23–27.

Schubert M, Beck S, Taube W, Amtage F, Faist M, Gruber M (2008) Balance training and ballistic strength training are associated with task-specific corticospinal adaptations. Eur J Neurosci 27:2007–2018.

Sharma N, Jones PS, Carpenter TA, Baron JC (2008) Mapping the involvement of BA 4a and 4p during motor imagery. Neuroimage 41:92–99.

Sherrington C, Whitney JC, Lord SR, Herbert RD, Cumming RG, Close JC (2008) Effective exercise for the prevention of falls: a systematic review and meta-analysis. J Am Geriatr Soc 56:2234–2243.

Stinear CM, Byblow WD, Steyvers M, Levin O, Swinnen SP (2006) Kinesthetic, but not visual, motor imagery modulates corticomotor excitability. Exp Brain Res 168:157–164.

Taube W, Schubert M, Gruber M, Beck S, Faist M, Gollhofer A (2006) Direct corticospinal pathways contribute to neuromuscular control of perturbed stance. J Appl Physiol 101:420–429.

Taube W, Gruber M, Beck S, Faist M, Gollhofer A, Schubert M (2007a) Cortical and spinal adaptations induced by balance training: correlation between stance stability and corticospinal activation. Acta Physiol 189:347–358.

Taube W, Kullmann N, Leukel C, Kurz O, Amtage F, Gollhofer A (2007b) Differential reflex adaptations following sensorimotor and strength training in young elite athletes. Int J Sports Med 28:999–1005.

Taube W, Lorch M, Zeiter S, Keller M (2014a) Non-physical practice improves task performance in an unstable, perturbed environment: motor imagery and observational balance training. Front Hum Neurosci 8:972.

Taube W, Leukel C, Nielsen JB, Lundbye-Jensen J (2014b) Repetitive activation of the corticospinal pathway by means of rTMS may reduce the efficiency of corticomotoneuronal synapses. Cereb Cortex.

Taube W, Mouthon M, Leukel C, Hoogewoud HM, Annoni J-M, Keller M (2015) Brain activity during observation and motor imagery of different balance tasks: an fMRI study. Cortex 64:102–114.

Tia B, Mourey F, Ballay Y, Sirandre C, Pozzo T, Paizis C (2010) Improvement of motor performance by observational training in elderly people. Neurosci Lett 480:138–142.

Tokuno CD, Taube W, Cresswell AG (2009) An enhanced level of motor cortical excitability during the control of human standing. Acta Physiol 195:385–395.

Tremblay F, Tremblay LE, Colcer DE (2001) Modulation of corticospinal excitability during imagined knee movements. J Rehabil Med 33:230–234.

Villiger M, Estevez N, Hepp-Reymond MC, Kiper D, Kollias SS, Eng K, Hotz-Boendermaker S (2013) Enhanced activation of motor execution networks using action observation combined with imagination of lower limb movements. PLoS One 8:e72403.

Vogt S, Di Rienzo F, Collet C, Collins A, Guillot A (2013) Multiple roles of motor imagery during action observation. Front Hum Neurosci 7.

Yahagi S, Shimura K, Kasai T (1996) An increase in cortical excitability with no change in spinal excitability during motor imagery. Percept Mot Skills 83:288–290.

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