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Task-dependent activation of distinct fast and slow(er) motor pathways during motor imagery

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ABSTRACT

Background: Motor imagery and actual movements share overlapping activation of brain areas but little is known about task-specific activation of distinct motor pathways during mental simulation of movements. For real contractions, it was demonstrated that the slow(er) motor pathways are activated differently in ballistic compared to tonic contractions but it is unknown if this also holds true for imagined contractions.
Objective: The aim of the present study was to assess the activity of fast and slow(er) motor pathways during mentally simulated movements of ballistic and tonic contractions.
Methods: H-reflexes were conditioned with transcranial magnetic stimulation at different interstimulus intervals to assess the excitability of fast and slow(er) motor pathways during a) the execution of tonic and ballistic contractions, b) motor imagery of these contraction types, and c) at rest.
Results: In contrast to the fast motor pathways, the slow(er) pathways displayed a task-specific activation: for imagined ballistic as well as real ballistic contractions, the activation was reduced compared to rest whereas enhanced activation was found for imagined tonic and real tonic contractions.
Conclusions: This study provides evidence that the excitability of fast and slow(er) motor pathways during motor imagery resembles the activation pattern observed during real contractions. The findings indicate that motor imagery results in task- and pathway-specific subliminal activation of distinct subsets of neurons in the primary motor cortex.

Introduction

It is commonly agreed that motor imagery and the physical execution of a motor task share overlapping neural activation [1]. Jeannerod [2] proposed in his 'neural simulation theory' that "the motor system is part of a simulation network that is activated under a variety of conditions" [p.103, 2] such as during motor imagery and action observation. In support of this, several studies have shown similar activation of brain areas during real task execution and mental simulation of motor tasks [3,4]. However, not only does motor imagery activate similar brain areas than actual movements but these areas are also activated differently depending on the task. For example, mental simulation using action observation and/or motor imagery of a complex task compared to a less complex task consistently leads to higher activity in motor centers such as the cerebellum, the pre-motor cortex, the supplementary motor area or the primary motor cortex [5,6]. Furthermore, during motor imagery corticospinal excitability and short-interval intracortical inhibition were shown to be modulated depending on the complexity of the task, the phase of the movement and the involved muscle(s) [7,8]. Thus, activity within the primary motor cortex shows muscle-, phase- and task-specific modulation during motor imagery. However, it is not known, whether these changes in corticospinal excitability are the result of an overall change in motor cortical excitability or by task-specific activation of distinct cortical neurons in the primary motor cortex (M1) that activate specific motor

Abbreviations: ANOVA, analysis of variance; EMG, electromyography; ISI, interstimulus interval; H_{max}, maximum H-reflex; M_{max}, maximum M-wave; MEP, motor evoked potential; TMS, transcranial magnetic stimulation; M1, primary motor cortex.

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pathways. Thus, the aim of this study was to evaluate the task-specific excitability of fast and slow(er) motor pathways during motor imagery and physical execution of tonic and ballistic contractions. As the excitability of different corticospinal projections is strongly influenced by cortical neurons, a distinct and task-specific modulation of motor pathways during motor imagery without overt movements and/or muscular activity most likely reflects subliminal activation of cortical neurons within M1.

When comparing the activity of distinct fast and slow(er) motor pathways of physically executed movements by conditioning the H-reflex with transcranial magnetic stimulation (TMS) at different interstimulus intervals (ISIs), it has been shown that ballistic and tonic contractions reveal comparable early facilitations. In contrast, a late inhibition was shown for ballistic contractions and a late facilitation for tonic contractions [9,10]. The early TMS-induced facilitation of the H-reflex is considered to be evoked by fast motor pathways, whereas the effects found for "later" ISIs (e.g. late facilitation or late inhibition) are thought to reflect excitation/inhibition of slow(er) motor pathways [11].

In another study involving TMS stimulation at the cervicomedullary junction [10], the authors showed that the late TMS-induced facilitation is of cortical origin. This observation supports the idea that the motor command for ballistic contractions is restricted to fast motor pathways whereas slow motor pathways are inhibited. From a functional point of view, this selective recruitment was interpreted to allow a direct and prompt muscle activity without long-lasting and inflexible parts of the motor command [10]. In contrast, during tonic contractions, both fast and slower motor pathways are activated simultaneously probably in order to ensure a long-lasting persistent muscular activation [10]. It is not known, so far, if this pathway-specific activation of distinct motor pathways is also evident when mentally simulating ballistic and tonic contractions. Therefore, the present study assessed for the first time the activity of fast and slow motor pathways during both real task execution and motor imagery of ballistic and tonic contractions using the H-reflex conditioning technique. It was expected to find similar activation patterns for imagined and real contractions. Similar activation patterns would illustrate for the first time that imagined contractions result in a task-specific subliminal modulation of distinct neurons within M1.

Materials and methods

Participants

Fourteen volunteers participated in this experiment. As three participants could not constantly perform mental contractions without activating the target muscle, only eleven participants (27.5 ± 4.5 years, 1.75 ± 0.08 m, 69.1 ± 11.7 kg; 3 female) were included in the final data analysis. All subjects were free of neurological and/or orthopaedic injuries and gave written informed consent after reading an information sheet explaining the applied methods and devices. The measurements were approved by the local ethics commission and followed the latest version of the Declaration of Helsinki.

Apparatus

Electromyography: Muscular activity was recorded from the right leg using surface electromyography (EMG). EMG was measured from soleus (SOL) and tibialis anterior (TA). After shaving and cleaning the skin with abrasive gel and disinfectant, self-adhesive electrodes (Blue Sensor P, Ambu A/S®, Bad Nauheim, Germany) were attached to the muscle bellies according to the SENIAM guidelines [12] with an interelectrode distance of 2 cm. A common reference electrode was placed medially above the tibial bone and EMG signals were tested for movement artefacts by actively and passively shaking the leg. Interelectrode impedance of the bipolar electrode configurations was under 5 kΩ. EMG recordings were sampled at 4 kHz (PCI-6229, National Instruments, Canyon Park, USA), amplified (x1000), filtered with a band-pass filter (10–1000 Hz) and stored on a PC (LabView-based software, Imago Record, Pfitec, Endingen, Germany) for offline-analysis.

Peripheral nerve stimulation: Electrical stimulation (Digitimer DS7A, Digitimer Ltd, Hertfordshire, UK) to the posterior tibial nerve evoked H-reflexes in SOL. The electrical stimuli consisted of square-pulses of 1 ms duration. A 5*5 cm rubber electrode was attached on the anterior aspect of the knee and served as the anode. The cathode (2 cm diameter) was attached to the back of the knee after moving the electrode stepwise to the best position for eliciting H-reflexes in the SOL. An H/M recruitment curve [13] was recorded at rest before the main experiment to assess the resting maximum H-reflex (H_{max}) and maximum M-wave (M_{max}). The stimulation intensity was then adjusted for each condition to evoke H-reflexes on the ascending part of the H-reflex recruitment curve with amplitudes corresponding to 20% of M_{max} of the resting state [14]. The stimulation intensity was re-adjusted prior to each condition in order to guarantee comparable test H-reflex amplitudes for inter-individual comparisons.

Transcranial Magnetic Stimulation: TMS was used to elicit motor evoked potentials (MEPs) in SOL and TA. TMS was performed using a double-cone coil (Magstim, Whitland, UK) connected to a magnetic stimulator (Magstim 200, Magstim, Whitland, UK). The coil was aligned tangentially to the sagittal plane with its center 1–2 cm to the left of the vertex and moved stepwise to the left hemisphere to find the optimal position for evoking MEPs in SOL of the contralateral (right) leg. The handle of the coil was pointing backwards so that a posterior-anterior current in the brain was induced. The hotspot was defined as the location with the largest and most consistent MEPs in the soleus muscle. The position of the coil was marked on the subject's scalp using a felt pen and the position of the coil relative to the head was constantly checked throughout the experiment. The motor threshold was defined as the lowest stimulator output at which MEPs with amplitudes of more than 100 μV were evoked in at least 3 of 5 consecutive trials. As the level of background EMG and mental effort varied between conditions, the motor threshold was defined for each condition separately. During the conditions, the inter-stimulus interval randomly varied between 4 and 5.5 s. The stimulation intensity was adjusted to 120% motor threshold of the respective condition.

SOL H-reflex conditioning: H-reflex conditioning allows the differentiation of the excitability of fast and slow(er) motor pathways at rest and during activity. For this purpose, the effect of a conditioning TMS pulse on a test H-reflex is assessed by varying the ISI between the test stimulus (H-reflex) and the conditioning TMS pulse [11]. The variation of the ISI therefore allows the assessment of the excitability of the different fast and slow(er) motor pathways. Thus, this stimulation method provides a more detailed view on the excitability of the corticospinal tract than the analysis of an unconditioned single pulse MEP as this compound potential subsumes the excitability of fast and slow(er) motor pathways. When differentiating the corticospinal projections, the term "fastest motor pathway" refers to the direct cortico-motoneuron pathway i.e. the corticospinal fibers emerging from M1 and projecting directly to spinal motoneurons via monosynaptic connections. These monosynaptic pathways shape the initial part of the early facilitation (within the first 0.5 to 1 ms) whereas later parts of the early facilitation are influenced by more indirect corticospinal projections that also emerge from M1 but project to spinal interneurons. In contrast to the early facilitation, where the

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anatomical origin is well understood, the physiological basis of the motor pathways responsible for late TMS-induced effects is less clear. So far, it is established that the effects mediated via slow(er) motor pathways are of cortical origin [10], although the exact anatomical pathways are unknown. Nevertheless, it might be speculated that these slow(er) motor pathways are the same pathways that are activated by paired-pulse TMS when assessing the long latency cortical facilitation. Independent of the anatomical and/or physiological basis, the use of different ISIs allows to assess the excitability of distinct motor pathways what in turn allows to conclude about the excitability of different fast and slow motor pathways.

In the rest condition (see details in next paragraph), a conditioning protocol with the following ISIs was applied: −6, −5, −4, −3, −2, −1, 0, +4, +8, +12, and +16 ms. Negative ISIs indicate that the H-reflexes were evoked prior to TMS whereas positive ISIs indicate that the electrical nerve stimulation occurred after the TMS. The latency of the peripheral H-reflex volley to arrive at the motoneuron pool is 2–5 milliseconds longer than the descending volley of the TMS. Consequently, the earliest conditioning effect of the corticospinal pulse on the test H-reflex can be found when the peripheral pulse is evoked 2 to 5 ms before the TMS (ISIs −2 to −5 ms). The early facilitation was identified from the ISI-curve measured at rest by detecting the ISI that resulted in the first facilitation followed by an inhibition of the test H-reflex 1 to 2 ms later. The early facilitation was used to test alterations in the activation of fast pathways when physically executing or mentally simulating contractions (details below). Additionally, another four positive ISIs (+4, +8, +12 and +16 ms) were included to test excitability of slower motor pathways (late facilitation or inhibition). If, for example, the early facilitation was identified at ISI -3 ms in the rest condition, the following ISIs were used for the subsequent conditions: −3, +4, +8, +12, +16 ms. In addition, a test H-reflex, which was not conditioned by TMS, was included. Twelve conditioned H-reflexes for each ISI as well as twelve test H-reflexes were recorded in each condition. Thus, 144 stimulations were applied during the rest condition (12 ISIs * 12 stimulation per ISI) and 72 stimulations (6 ISIs * 12 stimulations per ISI) for each of the other four conditions. The order of the ISIs and the order of the conditions were randomized.

Experimental protocol

Setup: During the entire experiment, the participants were seated in a custom-made chair that restricted movements of the thighs and trunk. The head of the subject was fixed in a toby collar that was attached to the chair avoiding head movements. The TMS coil was mechanically fixed using an articulated arm (Manfrotto, Cassola, Italien) which was also attached to the chair. The participant's right foot was placed on a wooden foot plate with a built-in force transducer (Kistler 9311B, Sindelfingen, Germany) for the visualization of exerted force. Participants were asked to perform plantarflexions by contracting the triceps surae muscle of the right leg.

Conditions and timing of stimulation: ISI-curves were recorded under five conditions. In all participants, a first ISI-curve was measured at rest (i). This “rest” condition served as a reference for the other four conditions: physically executed “real ballistic” (ii) and “real tonic” contractions (iii), motor imagery of “mental ballistic” (iv), and “mental tonic” contractions (v). Measurements started always with the “rest” condition. The order of the other conditions was randomized. In all conditions, the start of each trial (see Fig. 1) was indicated by a first tone (duration: 200 ms; frequency: 300 Hz) that was followed by a second tone after one second (duration: 100 ms; frequency: 500 Hz) and a third tone that was given 1.4 s after the start of the trial (duration: 100 ms; frequency: 700 Hz). The exerted force of the right foot was continuously visually displayed and participants were asked to match the exerted force with a red target line. During the “rest” condition (i), participants were instructed to relax their muscles to avoid any movements. The test H-reflex was always stimulated after 1.4 s (ii) During the “real ballistic” contractions, subjects were asked to perform dynamic contractions with the third tone. The peak of the target line was individually adjusted to the equivalent of 30% of the individual maximum force. After familiarization with the task, the onset of muscle activity was visually evaluated from the raw data of 30 practice trials without stimulation. Thereafter, the timing of stimulation was programmed so that for each subject the test H-reflex occurred approximately 50 ms after the onset of the voluntary ballistic contraction to match the level of muscular activity between the ”real ballistic” and “real tonic” contractions. (iii) In the “real tonic” condition, participants were instructed to meet the red target line. In this condition, a slow increase of the target force level was followed by a plateau representing 30% of the individual maximum force. The test H-reflex was always stimulated after 1.4 s (iv) Participants were instructed to imagine “mental ballistic” contractions without moving the black running line. The timing of stimulation was identical to the “real ballistic” condition. (v) In the “mental tonic” condition, participants were asked to imagine a tonic contraction without any muscular activation. The test H-reflex was always stimulated after 1.4 s.

Data analysis

The data were analyzed offline (Imago Record, Pfitec, Endingen, Germany). Peak-to-peak amplitudes were assessed from the unrectified EMG for conditioned H-reflexes as well as for the unconditioned test H-reflex. The test H-reflex served as a reference for the conditioned H-reflexes. The size of the intra-individual mean of the conditioned H-reflexes for each ISI was expressed as a percentage of the intra-individual mean of the test H-reflex amplitude of the corresponding condition. Based on these analyses, one ISI-curve per condition and participant was calculated (see Figs. 2 and 3).

The size of the early facilitation was compared between conditions in order to test for condition-specific effects on fast motor pathways. Differences in the excitability of slow(er) motor pathways were evaluated by calculating the mean of the positive ISIs (+4, +8, +12 and + 16 ms) for every condition. Thus, a single value for each participant and condition was calculated based on the four different ISIs. It is noted here that an ANOVA with the factors ISI (+4 vs. +8 vs. +12 vs. +16 ms) and condition (rest vs. tonic vs. ballistic) revealed the same results but was considered inappropriate as we were not interested in the interaction effects. To further test whether mental and physical execution of the same contraction type result in a different modulation, the percentage differences compared to rest were calculated for each condition (see Fig. 4).

Background EMG was evaluated by calculating root mean square EMG values (RMS analysis) in the 100 ms prior to stimulation. In conditions with motor imagery, trials in which the peak amplitude of the background EMG exceeded 30 μV in the 100 ms time window prior to stimulation were excluded. Trials were also excluded when the level of background EMG exceeded 150% of background EMG prior to the stimulation. During the real contractions, background EMG was analysed in the 15 ms before the stimulation. Such a short time interval was chosen in order to take into account the fast changing signal during ballistic contractions.

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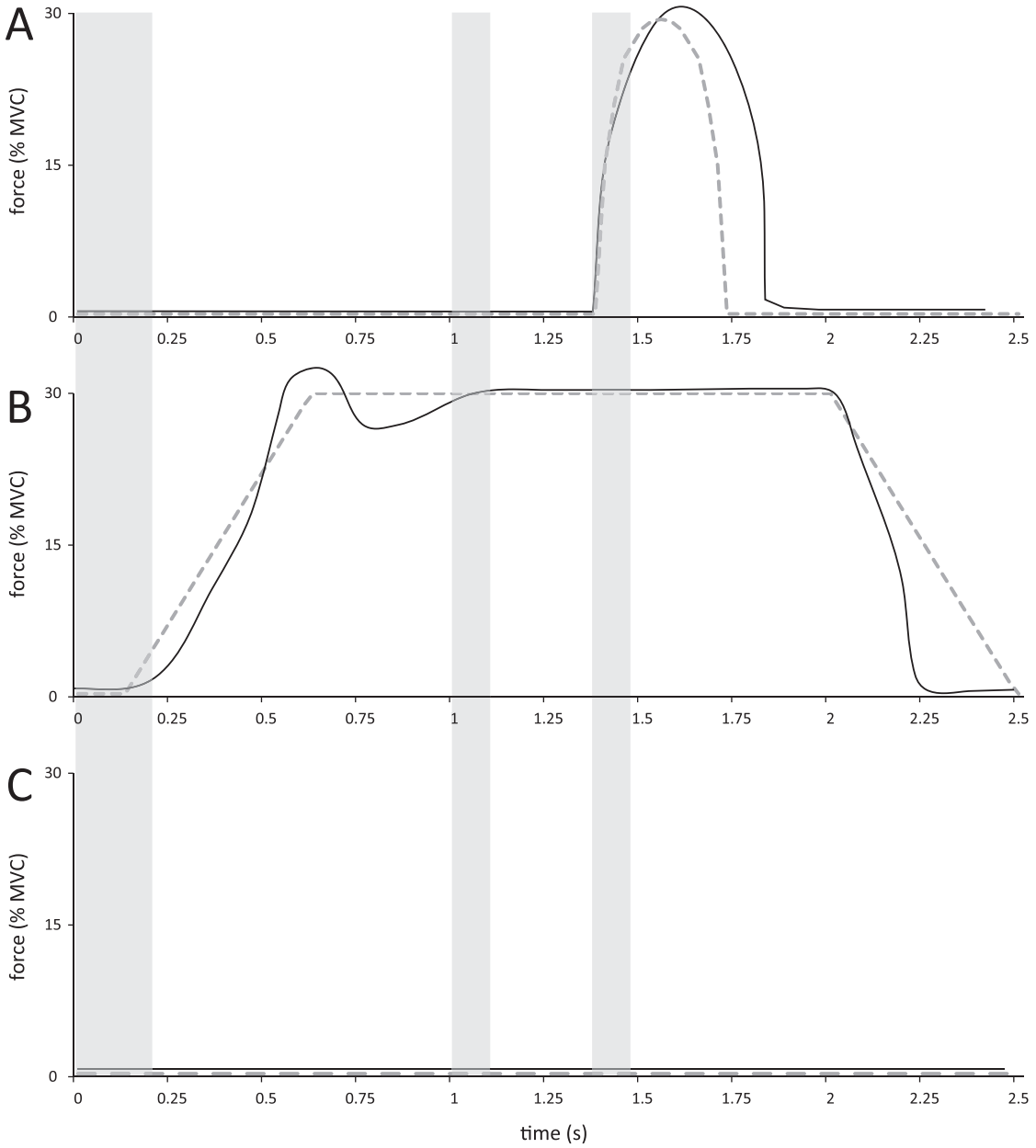

Fig. 1. Schematic of the tasks of the different conditions. The tones were identical between conditions and are indicated by the vertical grey areas. A first tone indicated the start of a trial and was followed by a second tone after one second. The third tone was given after 1.4 s. In all conditions, the test H-reflex was stimulated after around 1.4 s. Participants were asked to perform a ballistic contraction (A) with a peak force of around 30% of MVC. All participants were asked to match the black running line with the grey target line (dotted) as precisely as possible. Similar to the ballistic contractions, participants were asked to match the target line in the tonic task (B). (C) Shows the task in the rest condition where participants were asked to relax throughout all trials.

Statistical analysis

All results were tested for normal distribution using the Shapiro-Wilk test. In cases where raw data were not normally distributed, a log transformation was applied prior to further statistical testing (log-transformations are mentioned in the results section). Analyses of variance (ANOVA) were performed to evaluate differences between conditions. The assumption of sphericity was tested using the Mauchly's test and if the assumption was violated, the Greenhouse-Geisser correction was applied. One-way repeated measures ANOVA was calculated to test for differences in the size of the early facilitation between the real ballistic contractions, the real tonic contractions and rest. A second one-way repeated measures ANOVA was used to evaluate the differences between conditions for the positive ISIs, representing the late effects of the ISI-curve (conditions: ballistic real, tonic real, rest). Analogous to the real contractions, differences between mental ballistic contractions, mental tonic contractions and rest were evaluated using separate one-way repeated measures ANOVAs for both the size of the early facilitation and the late effects (positive ISIs).

To test if the mental and physical execution of a contraction (ballistic vs. tonic) results in a different modulation of the fast and slow(er) motor pathways, the percentage modulation of each condition compared to rest were compared using two separate two-way repeated measures ANOVAs with factors contraction

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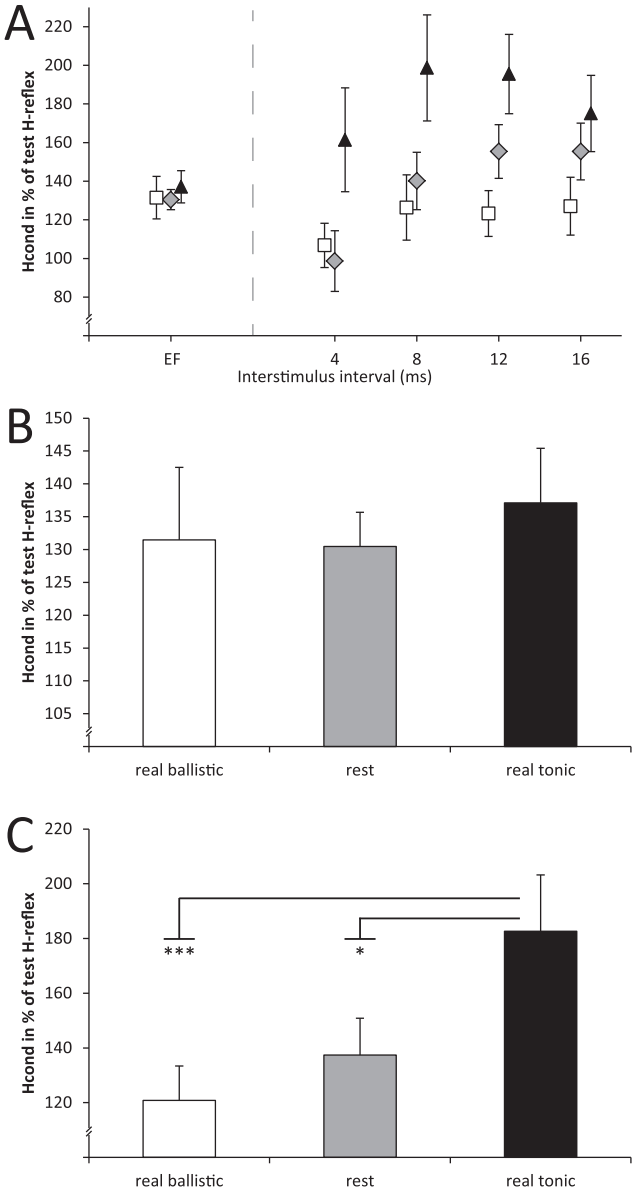

Fig. 2. Data of the H-reflex conditioning technique for the "rest" (grey), "real ballistic" (white), and "real tonic" (black) conditions are shown. The illustrated data represent the group mean results. (A) shows the recorded interstimulus interval curves of the three different conditions. The size of the early facilitation (EF) for each condition is shown on the left side of the vertical grey dotted line. The data points on the right side of the axis represent the excitability of the indirect corticospinal pathways for each condition. (B) The size of the early facilitation measured during rest, ballistic contractions, and tonic contractions are shown. No significant differences between conditions were found. (C) The four data points shown on the right side of the y-axis in (A) represent the indirect corticospinal pathways. The mean of these four data points was calculated for each condition and is displayed as the bar graph for "rest", "real ballistic" and "real tonic" conditions. Compared to the reference "rest" condition, excitability was (insignificantly) disfacilitated for "real ballistic" contractions. Furthermore, a significant facilitation was found for the "real tonic" compared to the "rest" condition and for the "real tonic" compared to the "real ballistic" condition. (Data are shown as mean values ± standard error of the mean. *** indicates $p < 0.001$; * indicates $p \leq 0.05$).

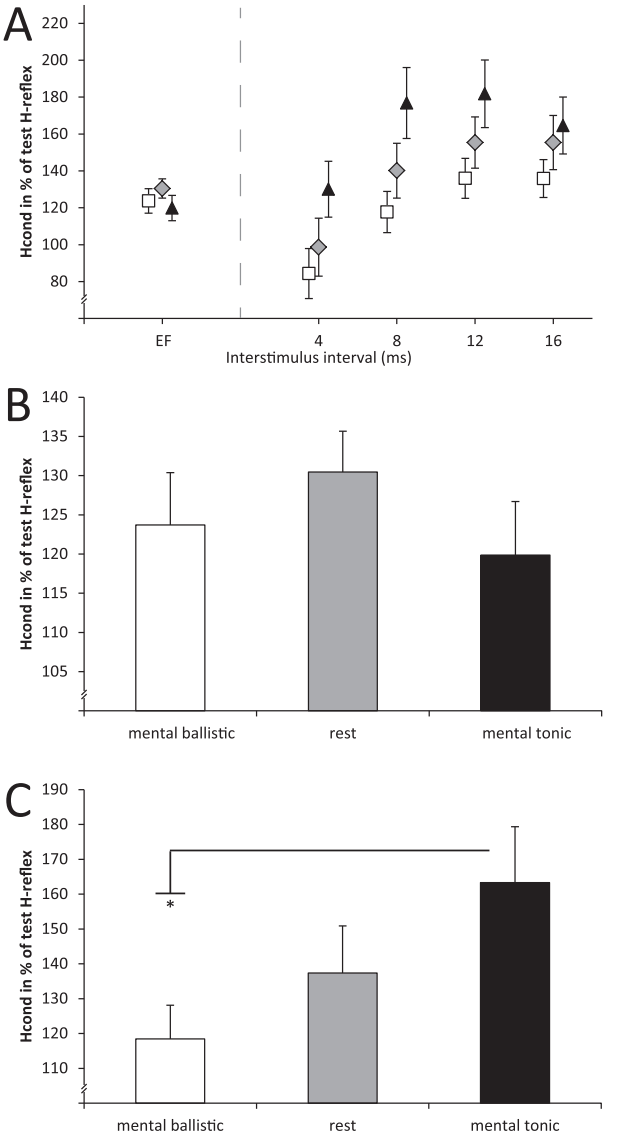

Fig. 3. Data of the H-reflex conditioning technique for the "mental ballistic" (white), "rest" (light grey), and "mental tonic" (black) conditions are shown. The illustrated data represent group mean results. Section (A) displays the interstimulus interval (ISI) curves for the three conditions. The size of the early facilitation (EF) is shown on the left side of the dotted grey line for each condition. On the right side of this line, the data points representing indirect corticospinal pathways are shown. Section (B) displays the size of the early facilitation for each condition. The size was not different between "mental ballistic", "rest" and "mental tonic". (C) shows the average excitability of the indirect corticospinal projections (mean of the ISIs +4; +8; +12; +16 ms). The "mental tonic" condition differed significantly from the "mental ballistic" condition. Compared to the reference "rest" condition, the excitability was either (insignificantly) up- or down-regulated. (Data are shown as mean values ± standard error of the mean. * indicates $p \leq 0.05$).

(tonic vs. ballistic) and execution (real vs. mental). The first ANOVA was used to compare the modulation of the fast motor pathways and the second ANOVA was used to compare the effects on the slow(er) pathways.

The level of background EMG prior to stimulation was compared with two separate one-way repeated measures of ANOVA between the conditions "rest", "mental ballistic", and "mental tonic" for both the early facilitation and the late effects. Furthermore, potential differences between "real ballistic" and "real tonic" were evaluated using a paired Student's t-test.

In the case of significant F-values ($p \leq 0.05$), Bonferroni-corrected Student's t-tests were calculated to assess differences between conditions. Effect sizes are presented as partial eta square values (small effect: 0.01, medium effect: 0.06, large effect: 0.14). SPSS 23.0 software was used for all statistical analyses. Data are presented as group mean values ± standard deviation, if not indicated otherwise.

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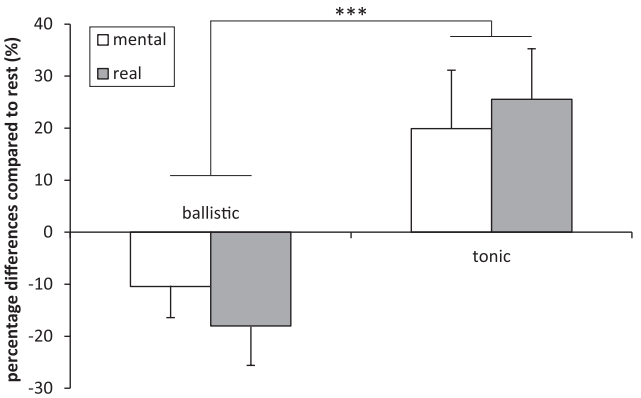

Fig. 4. Percentage differences between ballistic and tonic contractions compared to rest for the indirect (slow) corticospinal pathways during mental and real contractions. Data are shown as the group mean results. In both "mental ballistic" and "real ballistic" contractions, the excitability was inhibited compared to rest. In contrast, "mental tonic" and "real tonic" contractions showed a facilitation. A statistically significant difference was found for the type of contraction (ballistic vs. tonic) but not for the way of task execution (mental vs. real) and the interaction of contraction type with task execution. (Data are shown as mean values ± standard error of the mean. *** indicates $p = 0.001$).

Results

Real contractions: The size of the early facilitation did not differ between "rest", "real ballistic", and "real tonic" conditions (Fig. 2A and B; $F_{2,\ 20} = 0.24$; $\eta_p^2 = 0.023$; $p = 0.79$). When analyzing the effects of real contractions on the size of the conditioned H-reflexes for the slow(er) pathways, raw data deviated from normality and were therefore log-transformed before calculating the ANOVA. For the slow(er) pathways, a significant effect of "condition" was found when comparing the "rest", the "real ballistic", and "real tonic" conditions (Fig. 2A and C; $F_{2,\ 20} = 8.27$; $\eta_p^2 = 0.45$; $p = 0.002$). Pairwise comparisons showed a significant difference between "real ballistic" and "real tonic" conditions ($p = 0.004$) as well as a significant difference between "real tonic" and "rest" ($p = 0.05$). No significant differences were found for the comparison of rest versus ballistic real contractions ($p = 0.72$).

Mental contractions: Similar to the real contractions, no significant difference in the size of the early facilitation was found between "mental ballistic", "mental tonic", and "rest" conditions (Fig. 3A and B; main effect of condition: $F_{2,20} = 1.34$; $\eta_p^2 = 0.12$; $p = 0.29$). However, the data show that compared to rest, mental simulation of a contraction resulted in a dis-facilitation for ballistic and a facilitation for tonic contractions in the excitability of the slow(er) motor pathways (Fig. 3A and C). A significant main effect of "condition" was found (data were log-transformed; $F_{2,20} = 6.82$; $\eta_p^2 = 0.41$; $p = 0.006$). Pairwise comparisons showed a significant difference between "mental tonic" and "mental ballistic" conditions ($p = 0.017$). Pairwise comparisons did not show significant differences between "rest" and "mental ballistic" conditions ($p = 0.183$) nor between the "rest" and "mental tonic" conditions ($p = 0.315$).

Mental versus real contractions: To test whether the mental and physical execution of a contraction resulted in a different modulation of the activity in the fast and slow(er) motor pathways, separate two-way repeated ANOVAs were calculated for the size of the early facilitation and for the late facilitation/inhibition. For the early facilitation, no significant main effect for contraction (tonic vs. dynamic; $F_{1,10} = 0.15$; $\eta_p^2 = 0.02$; $p = 0.71$) and the way of execution (mental vs. real; $F_{1,10} = 3.07$; $\eta_p^2 = 0.24$; $p = 0.11$) was found. Similarly, no execution * contraction interaction effect was found ($F_{1,10} = 0.15$; $\eta_p^2 = 0.02$; $p = 0.71$). Concerning the slow(er) pathways, a statistically significant main effect for contraction ($F_{1,10} = 23.27$; $\eta_p^2 = 0.70$; $p = 0.001$) was found (see Fig. 4). However, there was neither a significant main effect for execution ($F_{1,10} = 0.56$; $\eta_p^2 = 0.05$; $p = 0.47$) nor a significant interaction effect of execution * contraction ($F_{1,10} = 0.38$; $\eta_p^2 = 0.04$; $p = 0.55$). Thus, real and imagined contractions resulted in comparable neural activity in cortical neurons responsible for the activity of the slow(er) pathways.

Background EMG levels: The background EMG prior to stimulation did not differ between "rest", "mental ballistic", and "mental tonic" conditions ($F_{2,20} = 1.40$; $\eta_p^2 = 0.12$; $p = 0.27$). Furthermore, no significant difference in muscular activity was found when comparing "real ballistic" (0.025 ± 0.026 mV) and "real tonic" (0.025 ± 0.023 mV) contractions ($p = 0.87$).

Discussion

This study assessed the excitability of distinct fast and slow(er) motor pathways under different conditions. The study proves that motor imagery of ballistic and tonic contractions has similar effects on the excitability of fast and slow(er) motor pathways as the physical execution of the same tasks. Importantly, the excitability of these pathways strongly depends on activity of cortical neurons within the primary motor cortex. It can therefore be argued that the task-specific facilitatory or inhibitory effects represent a task-specific modulation of neurons in M1.

Real contractions: Since the introduction of the H-reflex conditioning technique by Nielsen et al. [11], several studies assessed the excitability of distinct pathways in different tasks and contraction types [9,10,15,16]. It has been consistently shown that different contraction types influence the excitability of the slow(er) pathways in a task-specific manner. Furthermore, Taube et al. [10] provided evidence that cortical activation during ballistic tasks is restricted to fast motor pathways whereas slow(er) pathways are dis-facilitated or inhibited. The finding of the descending cortical command being restricted to fast corticospinal pathways was interpreted as a way to temporally focus the motor command during ballistic contractions. Our data of "real ballistic" and "real tonic" conditions resemble these findings. As mentioned above, the data of the real contractions showed no contraction-specific modulation in the size of the early facilitation but a contraction-specific modulation in the excitability of the slow(er) pathways. A potential bias caused by differential background EMG levels during tonic and ballistic contractions could also be excluded as the background EMG at the time of stimulation did not differ between conditions. It has to be mentioned that a previous study [17] found different sizes of the short-latency facilitation at different times during a ramp-and-hold task with the largest facilitation at the very onset of the contraction and a smaller facilitation during tonic contractions. In the present study, however, the test H-reflex occurred approximately 50 ms after the onset of contraction. This short delay might explain why the early facilitation was found to be similar for the tonic and ballistic contractions as the facilitatory effect decreases abruptly already very shortly after the onset of contraction [17]. The stimulation intensity used in this study might be a second possible explanation why no contraction-specific modulation in the size of the early facilitation was found. Assuming that the early facilitation results from the convergence of descending and peripheral inputs at the motoneuron level, it is possible that the high stimulation intensity of TMS (120% of the respective motor threshold) resulted in a strong activation of spinal motoneurons being too large to be sensitive to small fluctuations caused by the different motor tasks (ceiling effect). Thus, it cannot be entirely ruled out whether the

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fast pathways did not also show a contraction-specific activation or whether the supra-threshold TMS stimulation prevented any further facilitation of the H-reflex.

Motor imagery of tonic and ballistic contractions: Jeannerod [2] states in his simulation theory that imagined and physically executed movements show overlapping brain activation, which has been repeatedly confirmed by fMRI [5,6] and TMS experiments [7,8,18]. Furthermore, task-specific brain activation was also found during motor imagery [5,6] and there is increasing evidence that not only motor planning centers such as supplementary-motor area, pre-motor cortex, basal ganglia, or cerebellum, but also that the primary motor cortex is active during mental simulation of a motor tasks [6,19,20]. It is, however, not known whether corticomotoneurons or other neurons within M1 show an increased activity during motor imagery. One might argue that a layer-specific activation of cortical neurons during motor imagery [21] may preferentially increase activity in the superficial layers of M1, but this activity might also result in a subliminal activation of corticomotoneurons. Therefore, the present study assessed the excitability of distinct fast and slow(er) projections that depend on the activity of distinct cortical neurons [10] during motor imagery of tonic and ballistic contractions and compared this activity with the activity at rest. As all trials with an enhanced level of background EMG were excluded from the analysis, changes between conditions can most likely be explained by a task-specific activation of cortical neurons. A facilitation was assumed for the slow(er) pathways during “mental tonic” contractions compared to “rest” whereas a disfacilitation for slow(er) pathways was hypothesized for “mental ballistic” compared to “rest”. Thus, we expected that late ISIs would be affected by motor imagery and that this modulation would result in a contraction-specific disfacilitation for ballistic or facilitation for tonic contractions. In fact, the excitability of the slow(er) pathways during “rest”, “mental ballistic” and “mental tonic” conditions differed significantly (Fig. 3). Furthermore, the pairwise comparisons showed a significant difference between “mental ballistic” and “mental tonic” conditions. The comparison with “rest” showed a statistically insignificant facilitation for “mental tonic” and a non-significant disfacilitation for “mental ballistic”, which resembles the activation patterns during the physically executed contractions. Thus, the imagination of different contraction types resulted in a contraction-specific up- or down-modulation of the excibability of specific motor pathways compared to “rest”. This confirms but also extends the simulation theory of Jeannerod [2]. Jeannerod described a network of brain areas that are similarly activated during motor execution and mental simulation. The present observations indicate that not only the brain areas ‘overlap’ but also that different types of imagined and real contractions result in a task-specific subliminal modulation of distinct neurons within M1.

The results of the current study show that neurons within M1 show a contraction-specific subliminal facilitation or inhibition compared to the resting state. This contraction-specific modulation of cortical neurons may also influence the outcomes of interventions with motor imagery training. Cortical reorganization induced by mental practice is well accepted [22] and findings suggest that motor imagery training and physical training result in comparable plastic changes in the motor system [23]. Furthermore, motor imagery training was shown to elicit limb- and/or muscle-specific adaptations [23]. Based on the present study, one could expect not only limb- and/or muscle-specific but also a contraction-specific plasticity after motor imagery training. Thus, future studies should assess the influence of different mental contraction types on neural plasticity in healthy and clinical populations.

Notes

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